Social Contagion in Common Marmosets (*Callithrix jacchus*): Implications for Cognition, Culture and Welfare

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I declare that this thesis is a presentation of my original work that has not been submitted for any other degree or award. All additional sources of contribution have been acknowledged accordingly.

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Abstract

The social transmission of social behaviours in nonhuman primates has been understudied, experimentally, relative to instrumental, food-related behaviours. This is disproportional in relation to the comparatively high percentage of potential social traditions reported in wild primates. I report a systematic survey of the social learning literature and provide quantitative evidence of the discrepancy (Watson and Caldwell, 2009). Addressing the identified deficit in experimental work on social behaviours, I also report three empirical studies investigating the contagious nature of affective states in captive, socially housed marmosets.

I carried out an observational study, to determine whether marmosets are influenced by spontaneously produced neighbour calls to perform a range of behaviours associated with similar affect. My results supported a neighbour effect for anxiety in marmosets. Consistent with previous findings for chimpanzees (Baker and Aureli, 1996; Videan et al., 2005), I also found evidence for neighbour effects for aggression and affiliation (Watson and Caldwell, 2010). Through experimental playback, I investigated contingent social contagion in the auditory and visual modalities. The playback of pre-recorded affiliative (chirp) calls was found to be associated with marmosets spending increased time in a range of affiliative behaviours. Playback of video showing conspecifics engaged in a positive affiliative behaviour (allogrooming) also appeared to cause marmosets to spend longer performing various affiliative behaviours. My results indicate that social contagion of affiliation is a multi-modal phenomenon in marmosets and also represent the first evidence that allogrooming is visually contagious in primates.

Sapolsky (2006) conceptualised culture as the performance of species-typical behaviours to an unusual extent, termed ‘social culture’. Researchers have yet to directly investigate a transmission mechanism. I investigated whether a social culture of increased affiliation could be initiated in marmosets through the long-term playback, of positive calls, or of video of positive behaviour. The results were consistent with a relatively long-lasting influence of the playback of affiliative calls across several affiliative behaviours. The effect appeared to last substantially beyond the specific hours of playback, between playbacks, and after playback had ceased, potentially indicating a temporary shift in social culture. These results are preliminary but provide some support for the proposal that auditory social contagion may be a transmission mechanism for social culture. The long-term video playback of allogrooming appeared to result in a transitory shift in performance of the identical behaviour (increased allogrooming) after playbacks had ceased.

In addition to theoretical implications for social cognition and social culture, my findings have potential practical application for the enhancement of welfare in captive marmosets through sensory, and non-contact social, enrichment.

Publications and Conference Presentations

Publications

Watson, C. F. I. and Caldwell, C. A. (2009). Understanding behavioral traditions in primates: are current experimental approaches too focused on food? *International Journal of Primatology*, *30*, 143-167.

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International Presentations

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National Presentations

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Watson, C. F. I., Caldwell, C. A., and Buchanan-Smith, H. M. (2010). Does the audio playback of conspecific chirp calls improve the welfare of captive marmosets (*Callithrix jacchus*)? Poster presented at the Universities Federation for Animal Welfare, Animal Welfare Conference, recent advances in animal welfare science, York, UK, 30th June.

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Table of Contents

Chapter 3: General Methods………………………………………………………. 84

Chapter 4: The Effect of Spontaneous Neighbour Vocalisations on Marmoset Social Behaviour………………………………………. 132

Chapter 1

Thesis Introduction and Overview

1.1 Introduction

Do monkeys behave more amicably if conspecifics nearby behave amicably? The answer to this question has profound implications, both theoretically and practically. Furthermore, this and similar questions have to date been noticeably understudied relative to those regarding the social transmission of instrumental actions in nonhuman primates.

For this thesis, I carried out experimental research on social behaviour in monkeys. I explored the spread, or contagion, of affect between individuals (I use the term affect as a more objective alternative to emotion). More specifically, I investigated whether the behaviour of monkeys is influenced by the kind of social behaviour performed by individuals in nearby groups.

If it is demonstrated that nearby groups exert such an influence, a further goal is then to discover whether the effect can be manipulated. Can more amicable behaviour be initiated in groups of monkeys, through the simulation of nearby groups engaged in friendly (affiliative) behaviour? Such simulation could be achieved through video and audio playback. I examine the short and long-term effect of such playback, and consider the implications for our understanding of nonhuman primate culture, and for captive animal welfare.

In this chapter I give a brief introduction to the overall themes of the thesis: social cognitive processes, culture in nonhuman primates, social and communicative behaviours, communication and animal welfare. Within this background context I present the main thesis strands, and explain why they are interesting and important.

Terminology will be discussed, with most detail provided for concepts of central relevance to the thesis. The definitions used for the purposes of the thesis will be stated clearly to avoid any ambiguity (refer to Tables 1.1 and 1.2 for a summary). I also provide an outline of the thesis chapters. Some of the material presented in this chapter has been published previously (Watson and Caldwell, 2009; 2010).

1.2 Social Cognitive Processes

1.2.1 Classification Schemes

Opinion is divided on how best to categorise and define social processes and mechanisms. Accordingly, there have been various contrasting attempts to create a classification scheme (e.g. Galef, 1988; Whiten and Ham, 1992; Heyes, 1994; Whiten et al. 2004; Hoppitt and Laland, 2008). Whiten and Ham (1992) subdivided social processes into social influence (contagion, exposure, social support and matched-dependent learning), and social learning (stimulus enhancement, observational conditioning, imitation and goal emulation). In their taxonomy, social learning involves one individual learning “some aspect of behavioural similarity” (p. 248) from another, whereas social influence does not. In social influence the individual is exposed to some sort of social influence from another individual that with asocial learning leads to a convergence in behaviour (Whiten and Ham, 1992). Heyes (1994) applied the principles of animal learning theory (developed in relation to asocial learning) to the categorisation of social learning mechanisms. Heyes’ classification excludes those social processes that she does not classify as forms of social learning; i.e. matched-dependent learning, social facilitation and contagion. Thus, she includes some but not all of the social processes corresponding to those Whiten and Ham (1992) referred to as social influence. In contrast, Hoppitt and Laland (2008) classified certain social processes as forms as social learning that others (e.g. Whiten and Ham, 1992; Heyes, 1994) excluded from this category, such as social facilitation (referred to here as mere presence facilitation, see below) and response facilitation (here termed as social facilitation). However, Hoppitt and Laland (2008) subclassified each social learning process according to whether it leads directly, or "influences the observer in a way that might lead indirectly", to social learning (denoted by a symbol in superscript, Table I, p. 109-110). Whiten et al. (2004) revised the taxonomy of Whiten and Ham (1992) in relation to nonhuman apes, but excluded forms of social influence.

In this thesis I subdivided social processes into social learning and social influence. Here, I define social learning as: "any situation in which the behaviour, or presence, or the products of the behaviour, of one individual influence the *learning* of another" (Caldwell and Whiten, 2002, p.193, italics added). In general, learning involves some degree of lasting change on an individual's behaviour (e.g. Coussi-Korbel and Fragaszy, 1995). Here, I classify cognitively simpler forms of social processes, those that may indirectly lead to social learning, as forms of social influence.

Terminology

In the absence of consensus, the terminology of social processes can be extremely confusing. Similar or identical terms have been paired with different definitions.
In the sub-sections below, the discussion regarding social learning and transmission biases relates chiefly to my literature survey and review (Chapter two), while the introduction to social influence relates largely to the empirical chapters (Chapters four, five and six).

1.2.2 Social Learning

There is a substantive amount of literature relating to the definition of social learning mechanisms, especially relating to imitation, but there is not space here to provide a comprehensive review. Table 1.1 details the definitions used here for social learning mechanisms discussed in this thesis: local enhancement, stimulus enhancement, emulation and imitation. It is important to note that some researchers have divided the latter two terms into a variety of sub-terms (e.g. Whiten et al., 2004).

1.2.3 Social Transmission Biases

Biases in social transmission occur when individuals adopt certain cultural variants rather than others (Boyd and Richerson, 1985). It is important to recognise that when an individual is said to adopt or choose one cultural variant over another, this is convenient shorthand only, and does not imply intention or conscious choice. Two main types of social transmission biases are referred to here, conformist bias and model-based biases. Conformity was originally defined as a frequency-dependent transmission bias; a disproportionate tendency to copy the majority (Boyd and Richerson, 1985; 2005; Henrich and Boyd, 1998). Some researchers have adopted an alternative, slightly broader, definition as the tendency to adopt and retain the group ‘normative’ variant despite the discovery of an alternate behaviour (e.g. Whiten et al., 2005). I refer to the latter definition in this thesis. Model-based transmission bias relates to the selection of a particular cultural variant instead of another based on an attribute of the demonstrator. For example, individuals may selectively copy ‘models’ perceived to be successful, termed prestige bias (e.g. Henrich and Gil-White, 2001), or those most similar to themselves. Model-based biases will be discussed further in relation to possible future work in Chapter seven.

1.2.4 Social Influence

There is even less consensus regarding the use of social influence terminology than for types of social learning, which has resulted in an often contradictory and inconsistent use of terms. I will describe the types of social process referred to in this thesis, before discussing them in relation to terminology used by other researchers. Here I draw distinctions between three types of social influence. In classification these processes have sometimes been represented collectively by a single term (e.g. contagion), or represented by only one variant. A nearby conspecific can influence an individual in a number of distinct ways through contagion. First, they may influence their neighbour through mere passive social presence (termed here ‘mere presence facilitation’), e.g. through stimulating an increase in general activity level or arousal. Second, through performing a particular behaviour the conspecific may influence another to perform the *identical* behaviour, already in its behavioural repertoire (referred to as ‘social facilitation’ here). Third, the display of a particular behaviour by a nearby conspecific may stimulate the individual to perform a *range* of behaviours within the same affective class as the behaviour performed by the conspecific (labelled here as ‘social contagion’), these behaviours all being in its repertoire. Precise definitions for these terms are listed in Table 1.1.

Zajonc (1965) originally used the term ‘social facilitation’ to describe the effect of the mere social presence of a conspecific. Clayton (1978) applied the same term to refer instead to the influence on an individual to perform the identical behaviour as a conspecific, more or less as I do (but see below). Thorpe (1963), and Whiten and Ham (1992) labelled this effect as ‘contagion’. All these definitions share the idea that the behaviour shown by the individual(s) under social influence matches exactly the behaviour of the conspecific(s) effecting the influence (excepting Zajonc, 1965). In contrast, Hoppitt and Laland (2008) applied the term ‘response facilitation’ after Byrne (1994), to refer to the effect termed here as social facilitation. In their classification scheme (Hoppitt and Laland, 2008), social facilitation refers to the influence of the mere presence of a conspecific, and they do not include a term for the effect labelled as social contagion here. I decided to apply the term social facilitation in consensus with the majority of the literature, after Clayton (1978) (e.g. Addessi and Visalberghi, 2001; Ferrari et al., 2005).

Given that the focus of my empirical studies was social influence, I wished to distinguish clearly between variants. Social influence on the identical matching behaviour (social facilitation) is therefore distinguished from influence on a matching class of behaviours, a somewhat broader effect (social contagion). In relation to the ‘neighbour effect’ (see definition, Table 1.1) I defined social contagion previously (Watson and Caldwell, 2010) as ‘‘the spread of affect or behaviour from one individual (A) to another individual or other individuals (B)’’ (adapted from Levy and Nail, 1993, but with nonhuman primates explicitly in mind). Within this thesis, I used a definition of social contagion that allowed a clearer distinction from social facilitation, as it is defined here (see Table 1.1).

Although the definition used here for social facilitation was adapted from that of Clayton (1978), there is an important difference between them. Clayton stipulated explicitly that the influence last *only* while the conspecific remains present and carries out the behaviour, excluding any longer-lasting effect. He defined social facilitation as “an increase in the frequency or intensity of responses or the initiation of particular responses already in an animal’s repertoire, when *shown in the presence* of others engaged in the same behavior *at the same time”* (1978. p. 374, italics added). In contrast, my definitions of social facilitation and social contagion are intentionally not time-limited. For the investigation of non-contingent, relatively long-term effects of social influence investigated in Chapters five and six, I looked for effects of social contagion (or social facilitation) that corresponded to a lasting effect on experience, at least to the extent that the effect lasted beyond the specific hours of playback of conspecific behaviour (auditory or visual). Even when investigating contingent, short-term influence of playback in these chapters I allowed for a delay in influence (in Chapter five the immediate effect is 15 sec; in Chapter six the short-term effect assessed is over the entire 5-min observation period with video playback confined to the first 95 sec). Coussi-Korbel and Fragaszy (1995) stated that behavioural coordination was not simultaneous, but sequential.

1.2.5 The Importance of Cognitively Simple Social Processes

Much scrutiny has been levelled at determining exactly which mechanisms underlie the more complex forms of social learning, (e.g. imitation: Tomasello, 1990; Heyes, 1993; Byrne, 2003; Horner and Whiten, 2005; etc.). In contrast, cognitively simpler forms of social influence have received far less attention. However, more basic social processes, such as social contagion, are of interest in their own right, as well as potentially underpinning more cognitively complex social processes. I investigate what I believe to be simple social influence in Chapters four, five and six.

Table 1.1 Definitions for terms of social processes discussed in the thesis: classed as social influence, social learning and transmission biases giving citation of the reference source.

Class of terms	Term	Definition	Reference
social influence	social influence	Cognitively simpler forms of social processes, relative to social learning, that may lead indirectly to social learning.	Adapted from Hoppitt and Laland (2008).
	social presence facilitation	The influence on behaviour of the mere presence of conspecifics.	Adapted from Zajonc (1965) but using a different term.
	social facilitation	The presence of a conspecific, or conspecifics, engaged in a particular behaviour results in an increase in the frequency or duration or the probability of the initiation of the same behaviour in another individual or individuals, the behaviour being already in their repertoire.	Adapted from Clayton's definition of social facilitation (1978).
	social contagion	The presence of a conspecific, or conspecifics, engaged in a particular behaviour results in an increase in the frequency or duration or in the probability of the initiation of behaviours within the same affect class in another individual or individuals, these behaviours being already in their repertoire.	Adapted from Clayton's (1978) definition of social facilitation but applied to a broader effect.
	neighbour effect	Social contagion resulting from the influence of the vocalisations emitted by conspecifics on the behaviour of nearby individuals.	Adapted from Baker and Aureli (1996).
social learning	social learning	Any situation in which the behaviour, or presence, or the products of the behaviour, of one individual influence the learning of another.	Caldwell and Whiten (2002).
	local enhancement	After, or during a demonstrator's presence, or interaction with objects, at a particular location, an observer is more likely to visit or interact with objects in that location.	Hoppitt and Laland (2008).
	stimulus enhancement	The presence of an individual draws an observer's attention to a particular object or part of an object, thus enhancing the observer's opportunity to learn about the object.	Caldwell and Whiten (2002).
	emulation	The observer gains information from observing a demonstrator, but may use a different method to achieve the same outcome of an action sequence, or goal.	Adapted from Tomasello (e.g. 1990); Caldwell and Whiten (2002); Whiten et al. (2004).
	imitation	The observer learns something about the form of an act by seeing it done.	Thorndike (1898); Whiten et al. (2004).
social transmission biases	social transmission biases	When the process of cultural transmission favours some cultural variants over others.	Boyd and Richerson (1985).
	frequency dependent social conformity	A disproportionate tendency to copy the majority.	Adapted from Boyd and Richerson (1985).

Class of terms	Term	Definition	Reference
social transmission biases	social conformity	The adoption of the group normative variant despite the discovery of an alternate behaviour.	For example, Whiten et al. (2005).
	model-based biases	The tendency to adopt the behaviour of a particular demonstrator/model based on a particular characteristic of the model.	Adapted from Boyd and Richerson (1985).

1.3 Culture in Nonhuman Primates

1.3.1 Group-specific Behavioural Traditions

Defining Culture

Culture has been viewed historically as a defining feature of the human species. The question of whether or not any nonhuman animals possess traditions and/or culture is highly contentious. The answer to this question is to a large extent dependent on how culture is defined. At one end of the spectrum definitions exclude species of nonhuman animal *a priori*, for example by including within the definition a cultural component displayed only by humans, such as complex symbolic language, religion or law, for example Hill (2009) who has expressed doubt as to whether earlier Hominins such as Neanderthals had culture. At the other extreme, some definitions are so broad and inclusive that they admit the possibility of cultural behaviour in an extremely wide range of taxa (e.g. Bonner, 1980).

Perry (e.g. 2009) drew a distinction between the terms culture and tradition. While she is comfortable using the term ‘tradition’ in relation to nonhuman animals, defined as “a behavior pattern shared by its practitioners due to some form of social learning” (Perry, 2009, p. 247), she has avoided applying the term ‘culture’. She states that researchers investigating animal traditions have focused on social learning, but that the term culture has other implications that may not pertain to animal traditions.

Most definitions at least share the idea that social learning is central to culture. Some definitions of culture do not specify the particular underlying social learning mechanisms (e.g. Caldwell and Whiten, 2006). However, other definitions stipulate certain mechanisms as a necessary component of culture (e.g. Galef, 1992; Tomasello, 1990). It has been suggested that animal traditions and human culture are fundamentally dissimilar because the underlying mechanisms of transmission on which they rely are different (Galef, 1992; Hill, 2009). Galef (1992) considers imitation and teaching to be central to human culture whereas he views animal culture as resting only on relatively simple mechanisms, such as stimulus enhancement. Critics of this perspective have questioned whether the majority of human cultural traditions are transmitted exclusively through teaching and imitation (e.g. Laland and Hoppitt, 2003). The importance placed on these particular social learning mechanisms is partly based the assumption that they allow a higher fidelity of transmission, especially in terms of supporting cumulative cultural change (Tomasello, 1990; Galef, 1992). However, Heyes (1993) maintained that reliable cultural transmission depends on associative processes, rather than specific learning mechanisms.

Overall, while most researchers would not claim that nonhuman animals have traditions or culture to any extent as complex as humans, and whilst admitting some qualities of human culture as probably distinct, the study of the evolution of culture, whether homologous or analogous, is facilitated by at least a moderately inclusive definition (Laland and Hoppitt, 2003). Here, I have adapted (see Table 1.1) the following definition: “cultural behaviours are those which are (*1*) specific to members of a group … and (*2*) transmitted via some form of social learning” (Caldwell and Whiten, 2006, p. 653). Here this definition is distinct from the term ‘social culture’ (see section 1.3.2). For the purposes of the thesis (Chapter two especially), I use the terms behavioural traditions and cultural variants interchangeably.

The Ethnographic Method

According to the definition of culture adopted here, in order to identify a behaviour as cultural, researchers need to provide evidence of both group specificity, and social transmission. In order to fulfil the criterion of group specificity, one popular approach, formulated by Whiten et al. (1999) involves looking for behaviours which are present in some populations whilst remaining completely absent from others. This approach has been referred to as the ’method of exclusion’ (Whiten et al., 1999), and also as the ‘ethnographic method’ (e.g. Laland and Janik, 2006), the ‘geographic method’ (van Schaik et al., 2003) and as the ‘group contrasts approach’ (e.g. Perry, 2009). Here I refer to it as the ethnographic method. By this method, behaviours that are present in some groups of individuals and not in others are first identified. Any variation in behaviour that can be explained by ecological variation (and therefore asocial learning as opposed to social transmission) is then excluded. The remaining behaviours have then been considered as likely traditions, assuming that genetic explanations for the variation in behaviour can be excluded.

Critics of the ethnographic method object that the exclusion of ecological and genetic differences explanations is a ‘plausibility judgement’, and point to the risk of a type I error, the classification of behavioural variants as cultural when they are they are instead the result of asocial learning (e.g. Galef, 1992). Conversely, others underline the likelihood, inherent in the methodology itself, of making a type II error, of mislabelling true traditions as having been asocially learned because of behavioural convergence between groups (e.g. Perry, 2009). The method focuses on variation in behaviour as a *heuristic*, however the fact that behaviours are similar between groups does not preclude social transmission. Cultural selection may have led to similar solutions in different groups.

Criticisms notwithstanding, the ethnographic method has become the standard method used in the field (e.g. Laland and Janik, 2006; Laland and Galef, 2009). It has the advantage of utility, and systematic surveys applying the method have identified potential behavioural traditions in wild populations of various species of nonhuman primate species (e.g. van Schaik et al., 2003; Perry et al., 2003). For this reason, this is the methodology on which I focus for identifying potential traditions in wild populations in Chapter two.

Mathematical and statistical approaches to inferring cultural behaviour in populations have since increased the range of methodological tools available in this field (e.g. Laland et al., 2009). For example, Researchers have recently developed a suite of novel methods for assessing the likelihood that a potentially cultural behaviour has been socially learned, with greater accuracy, termed the option-bias method (e.g. Kendal et al., 2009).

The Importance of Social and Communicative Traditions

Social and communicative traditions are cultural variants of behaviours used in social and communicative contexts. I exclude from this category any social behaviours related to food in any way (see Chapter two). Included in this category are behaviours used during courtship, aggression, play and communicative behaviours, including vocalisations. Social traditions represent a particularly interesting class of cultural behaviours for a variety of reasons. Social traditions appear to be numerous among wild nonhuman primates. Social behaviours are also relatively easier to identify as having been socially learned, than are food related behaviours (although see Sterelny, 2009, for an opposing view). Social and communicative traditions are described and their importance discussed in greater depth in Chapter two, along with the need for more experimental work investigating this class of cultural variants.

1.3.2 Social Culture: Sapolsky

So far I have discussed various definitions and methodological approaches that have conceptualised culture as a set of discrete, group-specific behaviours. However, this is not the only perspective from which to study or to think about primate culture. Certainly, behaviours outwith the typical species repertoire represent the behaviours for which social influence is most easy to demonstrate. However, social influence can also act on those behaviours already present in the species repertoire (see above).

Sapolsky (2006) has proposed an alternative, wider conception of culture or social style which he termed ‘social culture’ in which “a particular style of sociality permeates an array of behaviors” (p. 643). Table 1.2 outlines the main differences between the two alternative conceptions of culture. Sapolsky was prompted to formulate this concept following observations of an apparent shift in social culture in a wild population of baboons (Sapolsky and Share, 2004). After the death of the most aggressive males in the group, through an illness contracted from foraging in a dump, the group was left with a much higher number of females than males. The remaining males were significantly less aggressive and more affiliative. However, the change to a more pacific social atmosphere did not revert to the more aggressive style even after the death of all the original (progenitor) males in the troop and the influx of adolescent males from other locales (Sapolsky and Share 2004).

Table 1.2 Definitions and key attributes of the two main conceptions of culture in nonhuman primates discussed in this thesis.

Group-specific Behavioural Traditions (Whiten et al., 1999)	**Social Culture (Sapolsky, 2006)**
"cultural behaviours, or behavioural traditions, should in some way be particular to a group or population, and, importantly, they should be socially transmitted"	"the performance, to an unusual degree, of an array of species typical behaviours within a particular group"
Presence of particular behaviours in some groups and absence in others	Performance of particular behaviours to an atypical degree in some groups and not others
Discrete behaviours	Continuous behaviours
Behaviours absent from species-typical repertoire	Behaviours present in species-typical repertoire

For the purposes of this thesis I use the following definition of Sapolsky's 'social culture 'as involving 'the performance, to an unusual degree, of an array of species typical behaviours within a particular group'. For example, a social group may engage in amicable behaviours much more often than might be expected from the species average. If we are searching for evidence of this type of social culture, the performance of species specific behaviours to an unusual extent, then social behaviours represent an obvious starting point. What is more, this notion of social culture provides a useful method of operationalising culture if taking an experimental approach to studying social behaviours, as I am here.

Experimental Research on Social/Communicative Behaviours

Experimental research is complementary to observational field work and of great importance in uncovering the cognitive processes, or the mechanisms, involved in the initiation, transmission and maintenance or eventual dissipation of social traditions in wild populations. However, it is relatively difficult to study the social transmission of social behaviours experimentally, especially in comparison with the experimental study of food related behaviours (this issue is considered in further depth in Chapter two). When studying food-related behaviours, researchers can design foraging tasks in order to motivate subjects to perform a specific novel behaviour (which functions to access the food reward). In contrast, in experimental research on social behaviour I do not have the same opportunity to motivate an innovation, and I cannot rely on opportunistic observations of spontaneous innovations in social behaviour of the type often identified only with thousands of hours of field observation. Instead, here I take the approach of experimentally investigating species-typical behaviours; social behaviours that I can be sure to observe, albeit at varying levels (allowing me to investigate both social transmission and potential consequent group variation in behaviour).

1.4 Animal Communication: Behaviours and Vocalisations

Communication is an important strand in this thesis; communicative behavioural variants that represent potential traditions are described (Chapter two), marmoset vocalisations are outlined (Chapter three) and investigated systematically (Chapters four and five), and the transmission of visual and auditory signals is effected through playback manipulation (Chapters five and six). It is therefore necessary to introduce some basic concepts and terminology relating to communication systems in general, and to vocal communication in particular.

Communication is essentially a social phenomenon (e.g. Seyfarth and Cheney, 2003). Through the process of communication in animals, one individual (the sender) influences the behaviour of another individual (the receiver) via the transmission of a signal (e.g. Shettleworth, 1998). The channel for signal transmission can be auditory (vocalisations, buttress-drumming in chimpanzees), visual (e.g. gestures, postures and facial expressions), olfactory (scent marking a territory), or related to other senses. Different sensory channels are referred to as modalities. The transmission of a particular signal can either be restricted to a particular modality or multi-modal (see Partan and Marler, 2005). In the experimental studies in this thesis (Chapters five and six), I manipulate one modality at a time. Whether the receiver receives a signal depends on their degree of attentional focus, and their ability to detect the signal and to discriminate it from other similar signals (e.g. Hauser, 1996). Even if the signal is directed from sender to receiver, the signalling cues are rarely confined to these individuals (e.g. Hauser, 1996), thus the signal can influence individuals other than the ‘intended’ receiver either of the same species (of special relevance to the neighbour effect, see section 1.2.2) or of a different species to the sender (e.g. Fallow and Magrath, 2010). It is important to note here that the use of the word ‘intended’ does not imply intentionality. The meaning of a call from the perspective of a ‘receiver’ may also differ from that of the ‘sender’ (Marler, 1961, cited in Seyfarth and Cheney, 2003).

Vocal Communication

Vocalisation, other than food calls represents an example of a non-food related communicative behaviour and is therefore of particular interest to social cognition research in general, and of particular relevance this thesis. The classification of auditory/vocal communication, can be approached in two main ways, either through the structural properties of the call (frequency, duration), or in terms of apparent function (as inferred from the behavioural context of call usage). One practical approach is first to categorise calls into discrete types through structural analyses, and second to infer function from observed behavioural context. In many animals, vocal communication structure has evolved ‘acoustic nonlinearity’, variation of call frequency and intensity to increase the number of call types that can be received reliable by receivers (e.g. Partan and Marler, 2005). Communication signals can be dichotomised broadly as either graded or discrete. Graded signals are continuous, whereas discrete signals are largely mutually exclusive. The second step, assigning function to call type, would be straightforward if call type were reliably associated with a particular discrete context, but in practise interpretation is often difficult (e.g. Hauser, 1996). In consequence, some researchers have encouraged naming vocal calls in terms of their sound instead of their function, to avoid determinism, for example ‘peep’ rather than ‘alarm call’. In recognition of this advice, here I have selected in preference those terms applied to marmoset calls relating to call sound, (see Table 3.5, Chapter three). Both structural and behavioural analysis is required in order to understand the function of auditory vocalisation in a species (e.g. McLanahan and Green, 1978).

Some researchers have attempted to classify vocal calls (and animal signals in general) as either being exclusively intrinsic or referential, that is either motivated by internal affective states of the sender or indicative of external referents (events or objects). However, critics have objected that vocalisations can be both at once (e.g. Seyfarth and Cheney, 2003; Sugiura, 2007).

Researchers classifying calls according to function have assigned broad labels to groups of call types with apparently the same general function. Alarm calls are specific vocalisations made in response to being threatened or having detected predators (Zuberbühler, 2009). Zuberbühler (2009) conceptualised mobbing calls as “a sub-type of alarm calls, one that is linked with relatively specific antipredator behavior” (p. 277), i.e. mobbing behaviour. I discuss both alarm calls and mobbing calls further in Chapter four. In a general sense, calls can be either context-general (used in a wide range of contexts) or context-specific. I refer to context “in the sense of the external events preceding and surrounding the signal” (Partan and Marler, 2005). In the thesis I draw a more particular distinction. Within a class of calls related to a certain category of affect (e.g. anxiety), calls may be relatively context –generalised, while still being related to that particular affective class (e.g. the ‘ek’ call of the common marmoset), or they may be relatively context-specific in the sense that they tend to be associated with a specific response in the receiver (e.g. the ‘seep’ call, related to the startle response), see Chapter four.

1.5 Marmosets

Marmosets represent an ideal subject of study for the investigation of social/communicative behaviours, and of social culture, for a variety of reasons. Marmosets are small, sociable, New World monkeys. They normally give birth to twins and rear their young cooperatively, within extended family groups. Indeed, marmosets belong to the group of primates, other than humans, which relies most on cooperative rearing; providing a unique comparative perspective (Burkart et al., 2009a). As cooperative rearers, marmosets are relatively highly socially tolerant, and prosocial with strong intersocial bonds (Burkart and van Schaik, 2010). They show a strong tendency to attend to the behaviour of conspecifics, and are thus relatively likely to be susceptible to social influence and contagion. The suitability of the marmoset as a study species is discussed further in Chapter three.

Vocal Communication in Marmosets

Marmosets vocalise frequently and produce a diverse range of calls. *Callithrix jacchus* "appears to utilize an overtly discrete call system but with gradations within recognizable call types" (Jones, 1993, p. 21), i.e. appears to use relatively distinct, easily distinguishable, vocal signals. Vocalisation plays an especially important communicative role for marmosets, since they live arboreally in densely vegetated habitats in which the opportunity for visual communication is limited. Thus, vocalisation offers a valuable window to the study of social culture in this species.

Plate 1.1 Young marmoset vocalising in the wild

Photo: Hannah Buchanan-Smith

Vocalisations have long been noted as a particularly striking aspect of marmoset behaviour. In 1957 Sanderson observed that marmosets produce:

" an astonishing number of different kinds of noises, from high-pitched keening sounds that carry extraordinary distances, have ventriloquial properties, and seem to penetrate a listener's head, to all manner of twitterings, chirrupings, squeaking, mumblings, chattering and other sound combinations both regular and of an irregular kind that cannot be described in words." (Sanderson, 1957, p.52)

Of historical interest, Sanderson also notes that pet marmosets became extremely popular with aristocrats in the sixteenth century when they were brought back from South America by Spaniards (Sanderson, 1957). An important factor in the particular value placed on marmosets by aristocrats, was what Sanderson refers to as their "endless *'conversation'"* ; their vocalisation (Sanderson, 1957, p. 50: italics, and inverted commas, in original publication). Plate 1.2 shows a marmoset depicted in a family portrait painting of 1567. The name marmoset derives from *marmouset*, the name given to them by the French aristocracy, who especially valued marmosets (*marmouset* derives from the old word meaning boy or man of very short height). The second part of the Latin name of the particular species studied in this thesis, the common marmoset, is *jacchus*, which means 'leaper' (Sanderson, 1957).

Plate 1.2 Portrait painting 'The Cobham Family' (William Brooke 10th Baron Cobham) painted by 'The Master to the Countess of Warwick', dated 1567, and detail showing one of his children restraining a pet marmoset, on display at Longleat House (© Longleat Enterprises).

1.6 Captive Animal Welfare: Environmental Enrichment

Animal Welfare

Historically, discussion about animal welfare was prompted by moral and ethical concerns (e.g. Young, 2003) and the emergence of evidence for sentience in animals (Dawkins, 2006). Animal welfare has been defined in many ways, from a variety of perspectives, but approaches to animal welfare can be broadly divided into three categories: biological functioning, subjective experience, and natural living (e.g. Held and Spinka, 2011). According to the biological functioning perspective, the welfare of an animal is determined by its physical health, while adherents to the subjective experience highlight the importance of psychological well-being and affective state. Proponents of the natural living approach view welfare as dependent on the degree to which an animal is able to live and behave in a similar way to its wild conspecifics.

How you choose to measure animal welfare depends to a large extent on the way in which you define or conceptualise it. Biological functioning can be measured directly either through short-term physiological measures such as heart rate, blood pressure and levels of stress hormones or through long-term physical values including longevity, reproductive success, growth rate and coat condition (e.g. Broom, 1991). Measuring some of these indices involve invasive procedures that are likely to cause stress to the animal (e.g. Dawkins, 2006). Another objection of this approach to assessing welfare is that some of these indicators can be problematic to interpret. For example, stress hormones such as cortisol are also elevated during periods of high activity (e.g. Rushen, 1991). When an animal is in a state of poor health it is also likely to be experiencing decreased welfare, in which case this method is a good index. However an animal may be in good health but still experience reduced welfare so that additional complementary measures are required.

Almost by definition, subjective well-being must be evaluated indirectly. One way to assess psychological well-being is through careful observation of behaviour, posture and vocalisations (e.g. Buchanan-Smith, 2010). Observation of normal behaviour allows behavioural changes to be identified that may indicate a reduction in welfare, e.g. a decrease in social interaction. Certain behaviours are especially valuable indicators of welfare state (see Chapter three). The presence of abnormal behaviour, especially stereotypies is usually indicative of poor welfare. The presence of abnormal behaviour (e.g. inappropriate social interactions with others in their group) can indicate poor welfare (Buchanan-Smith, 2011). Other indicators of diminished welfare include reduced time for behaviour to return to normal after stressful events. Two techniques aimed at appraising the animal’s perspective on which factors may improve subjective well-being deserve mention, and will be discussed in relation to enrichment below. The subjective well-being approach to welfare is inconsistent with the view that animals are non-sentient beings. Even those who view animals as sentient beings tend to agree that gauging the subjective experience of another species by indirect means is problematic since assessing it within our own species is challenging (e.g. Dawkins, 2006).

The most common way to evaluate the extent to which an animal is able to live naturally is to compare the daily activity budgets in captivity with those observed in wild conspecifics, and to observe whether the animal is motivated to expresses the natural behaviours in its species repertoire (i.e. are natural behaviours performed at an appropriate level) (e.g. Badihi, 2006). The captive environment itself should ideally allow and encourage the expression of natural behaviour (e.g. Buchanan-Smith, 2010). However, because captive settings differ so much from wild habitats it is probably neither appropriate nor necessary to match wild activity budgets (Sheperdson, 1998). Time budgets are not available for all species, and budgets coded by researchers in wild contexts may display bias towards or against certain behaviours due to the impact of the observer’s presence (e.g. Veasey et al., 1996).

The welfare of captive animals is important from a number of different standpoints. Poor welfare can have economic consequences either through increased financial costs (e.g. veterinarian bills) or through reduced productivity (e.g. livestock quality on farms) (Young, 2003). Research facilities require consistency across individuals to ensure valid empirical results (e.g. biomedical studies may produce unreliable results with varying individual welfare) (Badihi, 2006). Views of the general public regarding animal welfare are also influential to organisations (e.g. attitudes towards intensive and organic farming). Captive animals are housed in a variety of different environments including zoos, farms and research facilities. In relation to animal welfare, this thesis focuses on the latter.

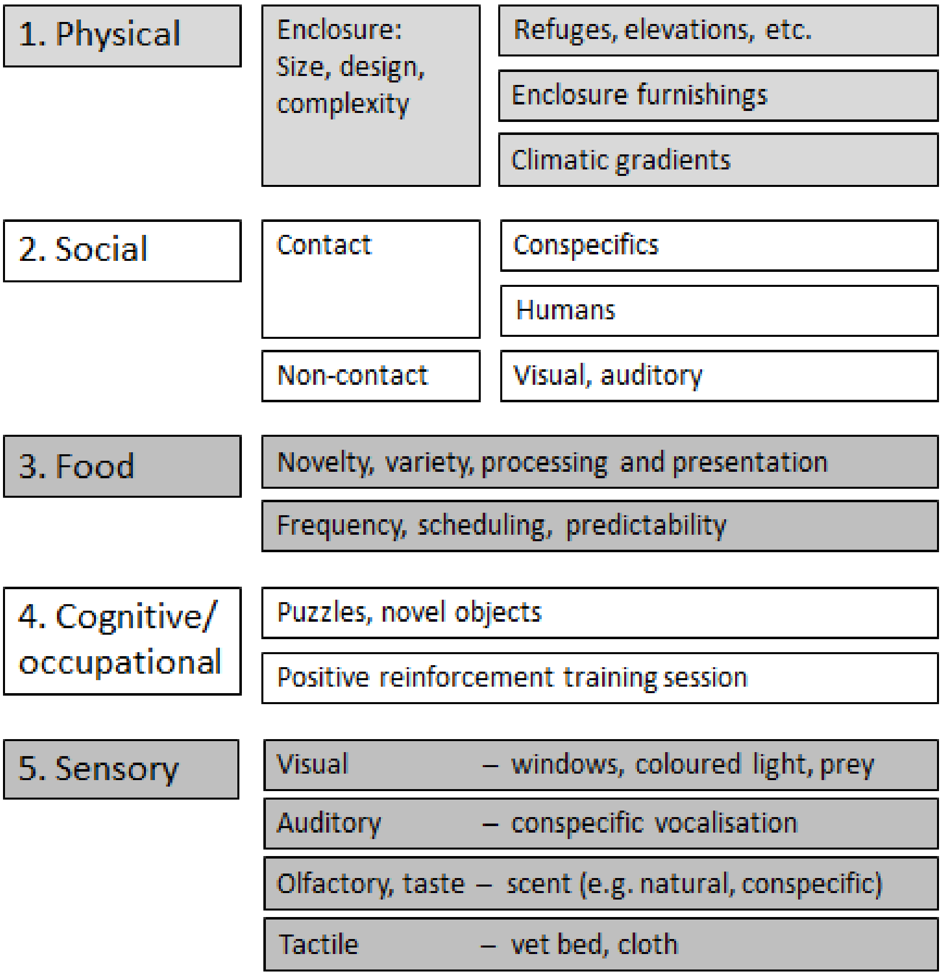
Environmental Enrichment

Russell and Burch (1959, reprinted 1992) proposed the 3Rs, Replacement, Reduction and Refinement as the three central tenets fundamental to the humane use of animals in laboratory research. Now generally recognised, these guiding principles form the basis of certain legislature, for example the UK Home office (Buchanan-Smith, 2011). Of the 3Rs, the investigations in this thesis apply specifically to refinement, defined more recently as “any approach which avoids or minimises the actual or potential pain, distress and other adverse effects experienced at any time during the life of the animals involved and which enhances their well-being” (Buchanan-Smith et al., 2005, p. 379-380). Fundamental to refinement is ‘environmental enrichment’. Although it has been defined in many different ways, in essence environmental enrichment has the aim of improving the well-being, the welfare, of captive animals (Buchanan-Smith, 2011). Sheperdson (1998) termed it as “an animal behavior principle that seeks to enhance the quality of captive animal care by identifying and providing the environmental stimuli necessary for optimal psychological well-being” (p. 1).

Recent conceptions of welfare underline that good welfare entails not only the absence of negative welfare (pain, suffering etc.), but importantly the presence of improved welfare, positive affect and experience (e.g. Boissy et al., 2007). Enrichment is focused on the addition of positive aspects to the environment, rather than on the reduction of negative features (Buchanan-Smith, 2011). Environmental Enrichment aims to enhance the welfare of captive animals through changes to husbandry and to housing. It can be subdivided into five main overlapping categories: physical, social, food, occupational/cognitive and sensory (see Fig 1.1 adapted from Buchanan-Smith, 2011, p. 43). Several key concepts underlie enrichment: novelty and complexity, choice and control (Buchanan-Smith, 2011). More complex environments lead to enhanced welfare (e.g. Jensvold, 2001), and the addition of enrichment usually increases complexity. Novelty is an important element of complexity, but is time-limited; e.g. once explored, novel objects lose their novelty. However, sudden increases in complexity and high levels of novelty may be undesirable since excessive unpredictability can cause stress (e.g. Chamove and Anderson, 1989). The execution of enrichment should be carefully planned and monitored. Increases in complexity to the five overlapping elements of enrichment (Fig. 1.1) lead to increased choice, and therefore to some degree control. Increased control is linked to predictability which may in turn lead to a reduction in stress. Badihi (2006) found that marmosets with control over lighting conditions in their cage displayed increased welfare relative to a yoked control group, i.e. exposed to the same illumination but with no control. Buchanan-Smith (2011) encourages the investigation of control over positive events, such as the delivery of auditory and visual stimulation, rather than control over minimising negative events. This will be discussed further in Chapter seven.

With multiple enrichment possibilities, how can we determine which ones are best to give? There are at least two methods that can be applied to assess an animal’s view of enrichment options. First, the animal can be given a preference test to determine which conditions they like best of out of a series of choices. One criticism of the forced-choice preference test is that selection of one option over the other may simply reflect the least

Fig 1.1 The five overlapping categories of environmental enrichment (adapted from Buchanan-Smith, 2011).



aversive stimuli rather than one that the animal finds preferential or rewarding (e.g. Young, 2003). Preference tests do not provide any index of the strength of motivation (Bateson, 2004). Dawkins (1983) applied ‘consumer-demand theory’ (a branch of behavioural economics) to pioneer a motivation-based approach to animal welfare enabling the indirect quantification of motivation. The motivation of an animal to use a particular enrichment option is assessed through the cost they are willing to pay to access it relative to other selections. For example, Mason et al. (2001) placed mink into an enclosure, subdivided into sections, with different enrichment options in each chamber, such as a toy, a swimming pool and the opportunity to view another mink. Access to different chambers was provided through weighted one-way doors. Motivation of mink for different enrichment choices were measured through their relative willingness to pay the cost of pushing through the weighted door to access particular options (Mason et al., 2001). One criticism of this approach is that it may encourage focus on things essential to animal well-being as opposed to ‘luxuries’ that may lead to enhanced welfare (e.g. Young, 2003).

In general, behavioural researchers of captive non-human primates are in an advantageous position to be able to inform on aspects of welfare, being familiar at first hand both with the behaviour and needs of the primate species themselves, and with the practical demands and limitations of the captive environment (zoo, laboratory etc.). Attempts at improving the welfare of captive primates are often focused on changes to husbandry, to the structural environment, or to food-related enrichment. However, the social environment has a huge influence on the welfare of individuals. Vocalisations are an often neglected aspect of welfare. Here, since we investigate the influence of nearby social groups on individual social behaviour our research is likely to be highly relevant to captive welfare. Further, because we aim to manipulate social behaviour through audio and video playback, the findings of our thesis have potential welfare applications for visual and auditory sensory and social non-contact environmental enrichment (see Fig. 1.1).

1.7 Overview of Thesis Chapters

In Chapter two I review the literature on social learning and cultural behaviours. Researchers have noted the discrepancy between the relative numbers of nonfood-related behavioural traditions reported in the wild and food-related ones, and the almost exclusive investigation of food-related behaviours in an experimental context. I report the results of a systematic literature survey in which I assess the perceived discrepancy quantitatively. I highlight the need for experimental studies of social and communicative traditions in primates.

With the aim of addressing this need I carry out behavioural research in the laboratory on, cognitively simple, social influence. In Chapter three I consider, briefly, the advantages and limitations of this approach. I provide details of our study population, socially housed marmosets, along with information concerning housing and husbandry. I also describe the general methods used for the empirical studies that I report: observation of the animals, coding their behaviour, and the statistical analysis of the resulting data.

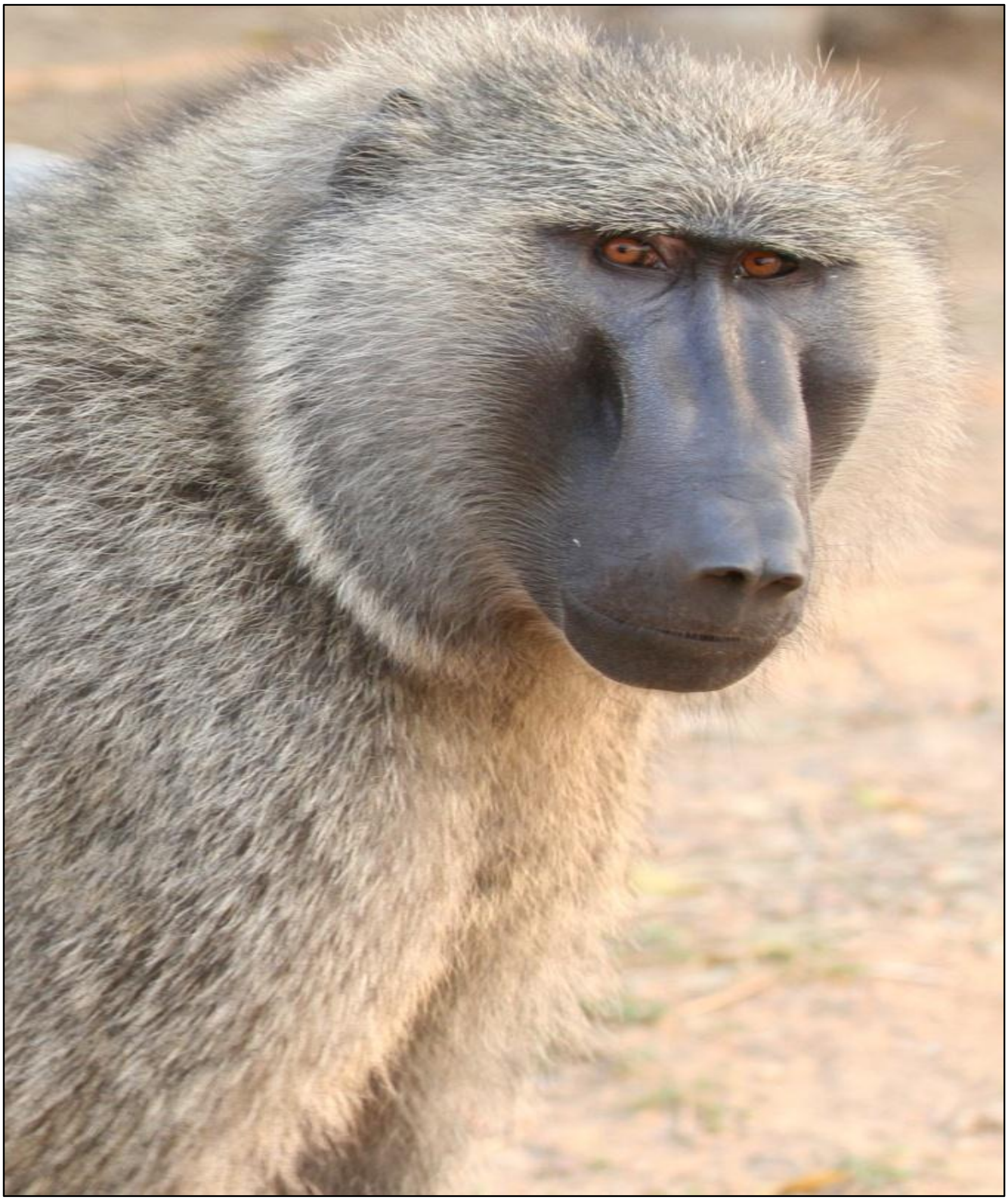
The empirical work in this thesis starts in Chapter four, with an observational study of the effect of spontaneously produced neighbour vocalisations on the behaviour and vocalisations of receivers. The aim here is to determine whether affective states are contagious in marmosets through the auditory modality (as has previously been found in chimpanzees).

In Chapter five I report a follow-up experimental (playback) study, investigating the causal influence of relatively positive vocalisations on the behaviour and vocalisations of receivers. I aim, firstly, to reinforce my initial findings regarding the contagious nature of affective states in marmosets. Secondly, I investigate whether playback of positive calls can lead to a longer-term change in behaviour beyond the manipulation phase (hence potentially indicative of at least a temporary change in social culture). Throughout the thesis, I use ‘long-term’ to refer to changes that correspond to a non-contingent delayed effect (i.e. outwith specific playback periods) of between several hours and several days. Specifically, such changes can be considered to be long-term only relative to any short-term contingent effects, I do not claim here that they are long-term in a wider, more general sense.

The experimental research in Chapter six is logically similar to that in Chapter five, but this time exploring the visual modality. I investigate the influence of the video playback of positive social behaviours (mutual grooming) on the behaviour of observers, once again looking for immediate, and relatively long-lasting, effects. In Chapter seven, I end the thesis by providing a summary my findings, and discussion of the implications of my research outcomes, from both theoretical and practical perspectives, and make suggestions for future research.

Chapter 2

Understanding Behavioural Traditions in Primates: Are Current Experimental Approaches Too Focused on Food?



The overall aim of this thesis, as outlined in Chapter one, is to investigate the social transmission of social/communicative behaviours in nonhuman primates through experimental study. In the current chapter I highlight the neglect of social behaviours relative to food-related behaviours in experimental research on social learning in primates, despite the significant number of apparent social traditions reported in the field. A systematic literature survey is carried out to assess the perceived discrepancy quantitatively. I discuss aspects of social and communicative customs that make them especially interesting, and then consider reasons why experimental approaches are crucial to developing a full understanding of behavioural traditions. The material contained in this chapter is published in Watson and Caldwell (2009).

2.1 Introduction

Recently, field primatologists have started to uncover evidence for behavioural traditions involving communication and other social behaviours, as well as those related to feeding (Whiten et al., 2001). Arguably, the evidence for these social behaviours being culturally transmitted is even stronger than for the relatively better known foraging behaviours (Caldwell and Whiten, 2006), although some researchers take the opposite view (e.g. Sterelny, 2009). However, experimental research on social learning in nonhuman primates, although often geared toward helping us understand the mechanisms involved in the transmission of behaviours in the wild, typically has focused more on instrumental tasks involving feeding and foraging. Consequently, although we know a great deal about the mechanisms involved in learning about food and foraging skills in primates, there is a gap in current knowledge regarding how social behaviours and other nonfood-related behaviours, are learned. Here I attempt to quantify this discrepancy. I also make a case for the importance of experimental study of nonfood-related behavioural traditions, particularly social conventions, and suggest directions that such research might take.

I have taken a broad and inclusive perspective on cultural traditions in primates. As discussed in the previous chapter, there has been much debate about the scope of the term culture, and the appropriateness or otherwise of its usage within the literature on nonhuman animals (Galef, 1992; Whiten et al., 2003). However, as stated in Chapter one, I use the terms culture and tradition interchangeably to refer to behaviours that are specific to members of a group, e.g., they are observed to occur within certain populations but not others, or to occur in different forms in different populations, and are believed to be transmitted via some form of social learning (Caldwell and Whiten, 2006). Behaviours that show cultural variation of this kind are extremely interesting for a number of reasons, including their potential to provide important insights into understanding the evolutionary roots of human culture (Heyes and Galef, 1996).

It is also partly on this basis that I justify the restriction of the current discussion specifically to nonhuman primates. The other reason for focusing on primates is simply due to the sheer abundance of reports of cultural behaviours within this group. Although evidence for traditions in non-primate taxa, particularly in cetaceans (Rendell and Whitehead, 2001) but also in mammals other than primates (e.g. meerkats, Thornton et al., 2010; Thornton and Clutton-Brock, 2011), birds (Slagsvold and Wiebe, 2011) and fish (Laland et al., 2011), continues to accumulate, researchers have reported the majority in primates. Field studies of apes and monkeys have provided prolific evidence for the existence of group-specific behaviours that one cannot easily explain in terms of genetic or ecological variables. Recent systematic surveys of field sites applying the ethnographic method have revealed the diversity of such apparent cultural variants (Panger et al., 2002; Perry et al., 2003; van Schaik et al., 2003; Whiten et al., 1999, 2001). Primates are therefore a particularly interesting phyletic group for researchers interested in culture in nonhumans.

2.1.1 The Importance of Social Traditions

Compared to food-related traditions researchers have neglected the topic of social traditions; however, it is an interesting subject of study for a number of reasons. First, it is becoming increasingly apparent that social traditions are particularly prevalent among cultural behaviours in primates. Social behaviours have been identified as potentially cultural variants by primatologists not only in chimpanzees (Whiten et al., 1999), but also in orangutans (van Schaik et al., 2003) and capuchins (Perry et al., 2003). Social traditions may be even more prevalent than the current literature suggests, given that they are inherently somewhat harder to study than food-related traditions. McGrew (2004) noted that subsistence activities are by their nature more conspicuous, especially ones that involve tools. Some of the first published observations of chimpanzee behaviour were of material culture (McGrew, 1992, 2004). Further, where subsistence activities involve tool use, the presence or absence of this tool can indicate which behaviours may be employed by particular communities (van Schaik and Knott, 2001). One can therefore investigate behaviours indirectly by examining artefacts that researchers have already observed being used in other groups. This approach circumvents to some degree the necessity for habituation and extensive observation, and also permits relatively straightforward comparisons across multiple sites.

In contrast, one can determine social behaviours only once the community is habituated to close range observation (McGrew, 2004). Nakamura and Nishida (2006) have highlighted that even after such observation, cross-site comparison is not as simple for social behaviours, which may be relatively subtle. Researchers may need to observe in field sites other than their own, with the express aim of drawing comparisons, before they recognise such behaviours as group-specific.

Social behaviours concerning subtle local variations in vocal communication may not become apparent without specific acoustic analysis (Whiten et al., 2001). Researchers would also have to be confident in excluding ecological explanations for the variation in call structure (vocalisation structure is adapted to carry the signal within the environment in which it evolved and would have been exposed to different selective pressures in a dense forest environment as compared to very sparse vegetation).

Traditions involving social behaviours are also particularly interesting from the aspect of the mechanisms involved in learning and maintaining them. First is the simple reason that there is less ambiguity about whether or not they really are cultural. Although I here assume that a large number of primate behaviours, both food-related and nonfood-related, are indeed cultural, it is important to note that critics maintain that it is almost impossible to rule out completely the possibility that group-specific behaviours are a result of subtle ecological differences influencing individual learning or environmental shaping (Galef, 1992, 2004; Laland and Hoppitt, 2003). However, it can be argued that intergroup variation in social communicative behaviours is substantially harder to explain by recourse to ecological factors than are subsistence behaviours (Whiten and van Schaik, 2007). Although, some critics disagree, cautioning that the content of social behaviours can be conflated with the transmission channel (e.g. Sterelny, 2009).

Further, researchers have observed particular social and communicative group-specific behaviours either change in prevalence or cease altogether over the years, or alter slightly in form (Perry et al., 2003). Thus it is also harder to attribute contrasts in behaviour to genetic variation between populations (Whiten and van Schaik, 2007) than for the relatively long-standing subsistence-related behavioural traditions. A further reason for considering social behavioural traditions to be particularly interesting is that the relatively arbitrary pairings of form and function are likely to ensure interesting variation between populations as a consequence of social learning. The form of food-related traditions, because of their inherent goal, is more obviously tied to their function. Therefore even socially learned forms are likely to resemble one another at different sites. But this is not the case for social behaviours, excepting in some vocal behaviours, whose form is not necessarily as constrained by function. Several researchers have highlighted the significance of the relatively arbitrary nature of the form of social traditions (Boesch, 2003; de Waal, 2001; Whiten et al., 2003).

Because the form appears to be independent from the function of the behaviour, a particular behaviour can convey various communicative functions according to which social group the individual belongs and, alternately, a particular meaning can be expressed by different behaviours in different populations (Boesch, 2003). For example, leaf-clipping appears to have different meanings to different populations of chimpanzees. Chimpanzees in Mahale and Budongo can use it to initiate courtship and before copulation, but Taï chimpanzees use it mainly before buttress drumming or to signal frustration, and chimpanzees in Bossou use it in a play context (Boesch, 1996, 2003; Whiten et al., 2001).

Further, although Mahale chimpanzees can signal courtship by leaf-clipping, Taï chimpanzees can use a knuckle-knock to perform this function. Another implication of the dissociation between form and function is that individuals learning such arbitrary conventions must learn not only the correct form, but also the correct context in which to use the behaviour if they are to communicate effectively within their groups (Ferrari, et al. 2006). In addition, social and communicative conventions, given their huge importance within human culture relative to subsistence traditions (Perry et al., 2003; Whiten et al., 2003), are liable to prove particularly interesting in providing anthropological insights.

Social traditions are also interesting in that we still understand little about their ultimate function. Food-related behavioural traditions appear to be more obviously, and directly, connected to fitness gains than are social traditions. It must be assumed that social behaviours also have some positive adaptive consequences, but because it is less obvious what these are, they are still an active area of debate within the scientific community.

There are often existing alternative species-universal behaviours available in the repertoire to achieve apparently the same function as some of the cultural traditions. In a case such as this, what is the adaptive value of having learned a new and alternative behaviour by social learning? Researchers have suggested two alternatives. First, cultural alternatives may offer subtle further benefits. In their literature survey, Reader and Laland (2001) found that the most frequent innovators were low-ranking primates that may benefit from performing novel behaviours because existing behaviours are unlikely to prove successful to them in gaining access to limited resources. Boesch and Tomasello (1998) suggested that the chimpanzee social traditions leaf-clipping in Mahale and knuckle knock in Taï present a less overt means to attract the attention of oestrous females for lower-ranking males, compared with the available species-general behaviours, e.g., branch shake (Whiten et al., 2001). Evidence that low-ranking males use these behaviour patterns more frequently than comparatively high-ranking males would lend support to this hypothesis. Another testable prediction would then follow, that low-ranking males may use the more conspicuous behaviours to a greater extent if they rise sufficiently in status. If the relatively inconspicuous behaviours do present a more adaptive alternative to other low status males then they might be expected to spread.

Second, social learning may help individuals to follow the latest fashions in cultural behaviours (Whiten et al., 2001). Certain social traditions appear to be transient relative to food-related traditions; e.g., hand-sniffing in one group of wild capuchin monkeys lasted only 7 years (Perry et al., 2003). Whiten et al. (2001) suggested that the ability to follow such fads, or less stable behaviours, may actually represent an adaptive advantage. For example, male chimpanzees might demonstrate their fitness by picking up on the latest attention-drawing courtship signal (Whiten et al., 2001).

Another possibility is that social traditions may help to advertise the identity of an individual as a member of a group, as do some social conventions in humans. If so, we might expect them to be conspicuous and displayed in the presence of individuals of another social group, for example when an immigrant first joins the group or during confrontations between groups (Perry, 2009). Perry originally thought that the unusual social traditions observed in capuchin monkeys (Perry et al., 2003, e.g. hand sniffing) might function to advertise group membership. She eventually dismissed this explanation as unlikely, because these behaviours are performed away from the rest of the group in silence, and have never been observed in the presence of individuals from different social groups (Perry, 2009). However, the possibility remains that social traditions in some nonhuman primates may function to signify group membership.

In summary, the adaptive function of social and communicative behavioural traditions is still open to question. Nakamura and Nishida (2006) noted that the difficulty in identifying their function and their arbitrary nature seems to have limited the research on social traditions. However, it is these very aspects of such behaviours that make them most fascinating.

2.1.2 The Role of Experimental Work in Understanding Traditions

Why, then, is it so essential to develop experimental research on the topic of social traditions in primates? Primatologists are conducting much observational research on such behaviours in natural populations, and we can learn a great deal from such approaches. However, I argue that to understand behavioural traditions fully, one must support field observations with experimental work. Experimental research allows us to test hypotheses that would simply be unfeasible within the context of observational field research.

There remains some doubt as to whether apparently cultural behaviours are socially learned at all (Galef, 2004), and the issue is difficult to resolve on the basis of field observations alone. Without strong confirmation that particular species are capable of learning certain behaviours via social transmission, observational data comparing populations will always be open to the criticism that the variation is attributable to either environmental or genetic differences. However, if experimental research can show that, under controlled conditions, a particular behaviour can be learned by social transmission then conclusions about its transmission within natural populations are considerably strengthened.

Experimental studies provide the possibility of uncovering the cognitive capacities for social learning inherent in particular species of nonhuman primate and so strengthening the inference that such social transmission occurs in the wild. However, a limitation of this approach is that demonstrating certain social learning in captivity can only show that such social transmission is *possible,* not that it *does* occur in natural contexts. One alternative approach is to infer social learning of behaviours in wild populations from diffusion patterns. For example, mathematical models based on data of the observed social diffusion of novel behaviours through a captive population (e.g. Kendal et al., 2007), can be applied to wild diffusion data to identify social learning. A limitation is that to apply this technique detailed information on diffusion patterns in the wild population is necessary.

Given that it is difficult to establish, on the basis of field observations, that social transmission is occurring at all, it is perhaps unsurprising that it is even more difficult to determine the precise mechanism(s) that might be involved (Whiten, 2000).

Experimental research represents a particularly strong approach by which we can attempt to address questions about the possible roles of social learning mechanisms, such as imitation, emulation, and stimulus enhancement (see Chapter one, Table 1.1), in the learning of a particular behaviour (Caldwell and Whiten, 2006).

Early reports of geographical variation in chimpanzee foraging behaviour (Goodall, 1973; McGrew, 1992) encouraged experimental work investigating whether observation of others' techniques would influence chimpanzees' manipulation of artificial foraging devices. Whiten et al. (1996) designed an artificial fruit for this purpose. The artificial fruit was in fact a box containing a food reward, which was protected by several locks, each of which the subject could manipulate in more than a single way. Whiten et al. (1996) found that observer chimpanzees were more likely to use the method that they had seen demonstrated than the alternative solution. Their experiment provided strong support for the notion that group-specific foraging behaviours in chimpanzees might be socially transmitted and therefore cultural. More recently Horner et al. (2006) and Whiten et al. (2005, 2007) have shown that alternative foraging techniques introduced into different captive chimpanzee groups are faithfully transmitted and can be maintained for long periods of time. Again, their research gives strong support for the idea that social learning may account for the variation in foraging techniques between natural populations.

Similarly, the possibility that primates might learn about what to eat from their conspecifics also gave rise to experimental literature investigating the social learning of food preferences. For example, Visalberghi et al. (Visalberghi and Addessi, 2000, 2001) showed that, although capuchins are reliably influenced to eat more of a novel food when those around them are also eating, it does not seem to matter whether the appearance of the conspecifics' food matches that of the observer, indicating social facilitation only. Research such as this has been extremely influential in understanding the likely proximate mechanisms, which may be extremely simple, that might be involved in the social transmission of food preferences in primates. There is now extensive experimental research investigating the social transmission of food-related behaviours in primates, and the success of such research only serves to emphasize how valuable experimental research on social traditions could be.

2.2 Literature Survey

2.2.1 Introduction

In reviewing the recent literature on social learning in primates, I aimed to quantify the perceived discrepancy between the relative proportion of food-related to nonfood-related behavioural traditions reported in wild primates, compared with the proportion of experimental studies investigating social learning of food-related and nonfood-related behavioural traditions. Thus I aimed to reveal the extent of the gap in our current knowledge of social learning in primates.

In attempting to draw conclusions about the relative proportions of research on certain kinds of behaviours vs. others, it is important to acknowledge that any such inferences will be influenced by exactly how the different behaviours are classified. The division of behavioural traditions into broad functional categories is not a straightforward matter. Although some researchers have used roughly analogous categories to classify behavioural traditions, others have used very different taxonomies. For example, van

Schaik et al. (2006) classified potentially cultural innovations in orangutans and chimpanzees as subsistence skills, comfort skills, or communicative variants (signal and social behaviours). In contrast, Sapolsky (2006) has actively encouraged conceptualizing categories as overlapping, rather than distinct. However, McGrew (1998, 2004) drew a simple distinction between subsistence and non-subsistence behaviours.

Here, motivated primarily by my interest in contrasting amounts of research concerning food and nonfood-related behavioural traditions, I chose, like McGrew (1998, 2004) to divide behavioural traditions broadly into subsistence (food-related) and non-subsistence (nonfood-related) behaviours. I also further divided food-related traditions into three subcategories: food choice (behaviours simply involving food choice); foraging and food processing behaviour (foraging and food processing behaviours not involving tool use); and tool use (foraging and food processing behaviours involving tool use); the latter two categories are mutually exclusive. I also divided nonfood-related traditions into three subcategories: comfort and hygiene, social and communicative, and other behaviours because these are the most salient divisions. Regarding the other category, there are still behaviours that defy easy classification within my chosen taxonomy because mine, like the aforementioned ones, divides behaviours according to their apparent function. Seemingly non-functional behaviours, such as the curious tradition of stone handling among particular groups of Japanese macaques (Huffman, 1984), therefore remain difficult to categorise.

2.2.2 Method

Journal screening

I aimed to search a representative sample of the contemporary articles published on social learning rather than to conduct an exhaustive search of all material published on this subject. Accordingly, I conducted a systematic search spanning the 10 most recent years literature published in the 25 most relevant journals: Advances in the Study of Behavior, American Journal of Primatology, American Journal of Physical Anthropology, Animal Behaviour, Animal Cognition, Annual Review of Anthropology, Behaviour, Behavioural Processes, Biological Reviews, Cognitive Science, Current Anthropology, Evolutionary Anthropology, Folia Primatologica, International Journal of Primatology, Journal of Comparative Psychology, Journal of Human Evolution, Learning and Behavior, Nature, Philosophical Transactions of the Royal Society London Series B: Biological Sciences, PLoS Biology, Primates, Proceedings of the National Academy of Sciences of the United States of America, Proceedings of the Royal Society B, Science, and Scientific American.

I searched for articles on Web of Science (http://wok.mimas.ac.uk), covering a 10-yr period from 01-05-1997 to 30-04-2007, and using the following search terms: social-learning OR imitation OR cultur* OR observational-learning OR socialtransmission OR social-diffusion OR behavio$ral-tradition OR stimulus-enhancement OR local enhancement OR traditions. The search covered all document types in English, disregarding book reviews, meeting abstracts, letters that were not articles, and editorial material. Some of the journals on my list were not established until after 1997 and so the search did not cover the full 10-yr period in all cases.

The articles produced by the initial search were screened to exclude those that did not relate to social learning in nonhuman primates in some way, by examination of the abstract and key words. In cases of ambiguity, I read the full article. I included review articles with only a relevant subsection. I could not search some papers by keywords because they were not available on Web of Science, and so systematically scanned relevant journal issues for articles meeting our criteria. Hence there was an element of judgment involved in the articles included. I read the full text of all of the remaining articles: 159 in total (the complete bibliography in given in appendix A).

Descriptions of Wild Behavioural Traditions

In reading the full text of the complete list of articles (N = 159), I noted all citations of field observations of potentially cultural behaviours. The citations were not necessarily primary reports of these field observations. I counted behaviours as potential cultural variants according to the judgment of the author of the article in which they were cited. The only criteria I imposed beyond this were that I counted only the behaviours that were known to show some degree of group specificity, e.g., known to be absent from another group or groups of the same species, and only behaviours that were different in type rather than simply by degree, i.e., higher levels of a particular behaviour in one group than in another. These criteria were chosen to facilitate the identification of reported group-specific behavioural traditions, to the exclusion of cultural behaviours fitting the broader definition of culture, ‘social culture’ (introduced in Chapter one). Also, I counted only observations of wild populations, i.e., groups with no barrier of human construction enclosing them. I then checked the resulting list of potentially cultural variants for redundancy (the same behaviour in the same species mentioned more than once). Following this process, I compiled a list of 209 behaviours. To my knowledge, this is the first attempt to quantify the number of wild cultural traits cited within the primate social learning literature (Table 2.1 shows a complete list of the behaviours). I then classified the behaviours as either food- or nonfood-related. Food-related behaviours included those involving the procurement of water for drinking, because this is a subsistence activity even though it involves a substance with no calorific content. Any behaviour that involved food in any way was placed into the food category so as not to inflate falsely the nonfood behaviours category. For example, I counted grooming behaviours or leaf manipulation involving the inspection or handling of parasites as food-related behaviours because field researchers have observed individuals to consume parasites whilst performing these behaviours on at least some occasions. Similarly, nest destruction, in Pongo, was classified as a food-related behaviour because insects are uncovered and eaten during the demolition process (van Schaik et al., 2003).

Food-related behaviours were subdivided into food choice behaviours, foraging and food processing behaviours, and tool use. I classified tool use behaviour according to the definition given by Beck (1980, p. 10): “the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool.” Nonfood-related behaviours were subclassified into categories of social/communicative and comfort/hygiene (Fig. 2.1).

Table 2.1 The 209 primate cultural variants cited in the literature surveyed.

No.	Taxon	Behaviour	Main citation	Classification
1	*Pan*	pestle pound	Whiten et al. (2001)	food: tool use
2	*Pan*	ant-dip-single	Whiten et al. (2001)	food: tool use
3	*Pan*	ant-dip-wipe	Whiten et al. (2001)	food: tool use
4	*Pan*	ant-fish (arboreal)	Whiten et al. (2001)	food: tool use
5	*Pan*	ant-club	Hicks et al. (2005)	food: tool use
6	*Pan*	nut-crack: stone hammer on stone anvil	Whiten et al. (2001)	food: tool use
7	*Pan*	nut-crack: stone hammer on wood anvil	Whiten et al. (2001)	food: tool use
8	*Pan*	nut-crack: wood hammer on wood anvil	Whiten et al. (2001)	food: tool use
9	*Pan*	nut-crack: wood hammer on stone anvil	Whiten et al. (2001)	food: tool use
10	*Pan*	nut-crack: *Elaeis guineenis*	Humle and Matsuzawa (2001)	food: tool use
11	*Pan*	nut-crack: *Panda oleosa*	Humle and Matsuzawa (2001)	food: tool use
12	*Pan*	nut-crack: *Carapa procera*	Humle and Matsuzawa (2001)	food: tool use
13	*Pan*	nut-crack: *Coula edulis*	Humle and Matsuzawa (2001)	food: tool use
14	*Pan*	nut-crack: other (e.g. ground)	Whiten et al. (2001)	food: tool use
15	*Pan*	nut-crack: use of anvil prop.	Humle and Matsuzawa (2001)	food: tool use
16	*Pan*	termite-fish: leaf midrib	Whiten et al. (2001)	food: tool use
17	*Pan*	termite-fish: non-leaf materials	Whiten et al. (2001)	food: tool use
18	*Pan*	termite-dig	Humle and Matsuzawa (2004)	food: tool use
19	*Pan*	termite-puncture	Heaton and Pickering (2006)	food: tool use
20	*Pan*	brush-sticks	Nishimura et al. (2003)	food: tool use
21	*Pan*	tool-set for termite harvest	Whiten (2005)	food: tool use

22	*Pan*	expel/stir: insects	Whiten et al. (2001)	food: tool use
23	*Pan*	bee-probe	Whiten et al. (2001)	food: tool use
24	*Pan*	honey-hammer/club	Hicks et al. (2005)	food: tool use
25	*Pan*	honey-dip	Boesch and Tomasello (1998)	food: tool use
26	*Pan*	drink water: stick/twig probe	Matsuzaka et al. (2006)	food: tool use
27	*Pan*	drink water: stem sponge	Matsuzaka et al. (2006)	food: tool use
28	*Pan*	drink water: moss sponge	Matsuzaka et al. (2006)	food: tool use
29	*Pan*	drink water: leaf-folding	Tonooka (2001)	food: tool use
30	*Pan*	drink water: leaf sponge	Matsuzaka et al. (2006)	food: tool use
31	*Pan*	drink water: leaf spoon	Tonooka (2001)	food: tool use
32	*Pan*	drink water: timing of leaf modification: leaf sponge	Matsuzaka et al. (2006)	food: tool use
33	*Pan*	drink water: leaf selectivity	Tonooka et al. (2001)	food: tool use
34	*Pan*	drink water: ‘wadges’ of fruit	Tonooka et al. (2001)	food: tool use
35	*Pan*	algae-fish/scoop	Boesch and Tomasello (1998)	food: tool use
36	*Pan*	lever open: termite mound entrance	Whiten et al. (2001)	food: tool use
37	*Pan*	hook stick	Boesch and Tomasello (1998)	food: tool use
38	*Pan*	gum gouge	Boesch and Tomasello (1998)	food: tool use
39	*Pan*	marrow-pick	Whiten et al. (2001)	food: tool use
40	*Pan*	stick dig: decayed tree trunk	Nishimura et al. (2003)	food: tool use
41	*Pan*	ectoparasite: leaf-fold	Boesch (2003)	food: tool use
42	*Pongo*	leaf gloves	van Schaik et al. (2003)	food: tool use
43	*Pongo*	tree-hole: tool use	van Schaik et al. (2003)	food: tool use
44	*Pongo*	seed extraction: tool use	van Schaik et al. (2003)	food: tool use
45	*Pongo*	branch scoop	van Schaik et al. (2003)	food: tool use

46	*Cebus*	leaf wrap: *Autmersis* caterpillar	Panger et al. (2002)	food: tool use
47	*Cebus*	nut-crack: stone hammer (on stone or wood anvil): *Cebus libidinosus*	Fragaszy et al. (2004)	food: tool use
48	*Cebus*	nut-crack: stone hammer and anvil: *Cebus apella*	Ottoni et al (2005)	food: tool use
49	*Cebus*	digging with stones	Moura (2007)	food: tool use
50	*Macaca*	oyster-crack: stone hammer on rock anvil	Malaivijitnond et al. (2007)	food: tool use
51	*Ceropithecus*	*Acacia* pod dip: in tree exudate	Hosey et al. (1997)	food: tool use
52	*Pan*	food-pound: on wood	Whiten et al. (2001)	food: foraging/food processing
53	*Pan*	food-pound: on other (e.g. stone)	Whiten et al. (2001)	food: foraging/food processing
54	*Pan*	food-pound: *Strychnos*	Humle and Matsuzawa (2001)	food: foraging/food processing
55	*Pan*	ant-fishing perches	Hicks et al. (2005)	food: foraging/food processing
56	*Pan*	surface-dig (driver ant grubs)	Boesch (2003)	food: foraging/food processing
57	*Pan*	deep-dig (driver ant grubs)	Boesch (2003)	food: foraging/food processing
58	*Pan*	ectoparasite(?): leaf-groom	Whiten et al. (2001)	food: foraging/food processing
59	*Pan*	ectoparasite: leaf-inspect	Whiten et al. (2001)	food: foraging/food processing
60	*Pan*	ectoparasite: leaf-squash	Whiten et al. (2001)	food: foraging/food processing
61	*Pan*	ectoparasite: index-hit (squash on arm)	Whiten et al. (2001)	food: foraging/food processing
62	*Pan*	ectoparasite: index to palm	Nakamura and Nishida (2006)	food: foraging/food processing
63	*Pongo*	bouquet feeding	van Schaik et al. (2003)	food: foraging/food processing
64	*Pongo*	nest destruction	van Schaik et al. (2003)	food: foraging/food processing
65	*Pongo*	dead twig sucking	van Schaik et al. (2003)	food: foraging/food processing
66	*Gorilla*	pattern of ant consumption/ seasonal ant eating	Ganas and Robbins (2004)	food: foraging/food processing
67	*Gorilla*	folding nettle leaf blades	Ganas et al. (2004)	food: foraging/food processing

68	*Cebus*	army ant following	Panger et al. (2002)	food: foraging/food processing
69	*Cebus*	fulcrum: *Pithecellobium saman*	Panger et al. (2002)	food: foraging/food processing
70	*Cebus*	rub: husk: *Sterculia apetala*	Panger et al. (2002)	food: foraging/food processing
71	*Cebus*	pound: *Randia spp.*	Panger et al. (2002)	food: foraging/food processing
72	*Cebus*	pound: *Cecropia peltata*	Panger et al. (2002)	food: foraging/food processing
73	*Cebus*	rub: *Cecropia peltata*	Panger et al. (2002)	food: foraging/food processing
74	*Cebus*	pound: *Tabebuia ochracea*	Panger et al. (2002)	food: foraging/food processing
75	*Cebus*	rub: *Tabebuia ochracea*	Panger et al. (2002)	food: foraging/food processing
76	*Cebus*	rub: *Pithecellobium saman*	Panger et al. (2002)	food: foraging/food processing
77	*Cebus*	rub: *Acacia spp.* fruit and thorns	Panger et al. (2002)	food: foraging/food processing
78	*Cebus*	rub: annona reticulata	Panger et al. (2002)	food: foraging/food processing
79	*Cebus*	pound: *annona reticulata*	Panger et al. (2002)	food: foraging/food processing
80	*Cebus*	pound: *Apeiba tibouru*	Panger et al. (2002)	food: foraging/food processing
81	*Cebus*	pound: *Bactris minor*	Panger et al. (2002)	food: foraging/food processing
82	*Cebus*	pound: *Genipa amaericana*	Panger et al. (2002)	food: foraging/food processing
83	*Cebus*	rub: *Genipa amaericana*	Panger et al. (2002)	food: foraging/food processing
84	*Cebus*	pound: *Mangifera indica*	Panger et al. (2002)	food: foraging/food processing
85	*Cebus*	pound: *Quercus spp.*	Panger et al. (2002)	food: foraging/food processing
86	*Cebus*	pound: insects in branches	Panger et al. (2002)	food: foraging/food processing
87	*Cebus*	rub: *Stemmandenia donnell-smithii*	Panger et al. (2002)	food: foraging/food processing
88	*Cebus*	tap: *Stemmandenia donnell-smithii*	Panger et al. (2002)	food: foraging/food processing
89	*Cebus*	pound: vertebrate prey	Panger et al. (2002)	food: foraging/food processing
90	*Cebus*	rub: vertebrate prey	Panger et al. (2002)	food: foraging/food processing
91	*Cebus*	skilled pound	O’Malley and Fedigan (2005)	food: foraging/food processing

92	*Cebus*	squirrel-killing technique: neck-bite	Rose et al. (2003)	food: foraging/food processing
93	*Cebus*	squirrel hunting technique: active search	Rose et al. (2003)	food: foraging/food processing
94	*Cebus*	squirrel hunting technique: rearguard intercept	Rose et al. (2003)	food: foraging/food processing
95	*Cebus*	squirrel hunting technique: grab and flail	Rose et al. (2003)	food: foraging/food processing
96	*Cebus*	squirrel hunting technique: launch and pin	Rose et al. (2003)	food: foraging/food processing
97	*Cebus*	coati nest raiding technique: division of effort	Rose et al. (2003)	food: foraging/food processing
98	*Cebus*	coati nest raiding technique: cause female to move pups	Rose et al. (2003)	food: foraging/food processing
99	*Cebus*	coati nest raiding technique: force pups from nest and take on ground	Rose et al. (2003)	food: foraging/food processing
100	*Cebus*	coati nest raiding technique: exhaust larger pups by attempted drowning	Rose et al. (2003)	food: foraging/food processing
101	*Macaca*	potato washing	Matsuzawa (2003)	food: foraging/food processing
102	*Macaca*	wheat placer mining	Matsuzawa (2003)	food: foraging/food processing
103	*Macaca*	“give-me-some” gesture	Perry and Manson (2003)	food: foraging/food processing
104	*Macaca*	root washing in rivers	McGrew (1998)	food: foraging/food processing
105	*Macaca*	apple washing	Reader (2004)	food: foraging/food processing
106	*Macaca*	louse egg-handling techniques	Tanaka (1998)	food: foraging/food processing
107	*Macaca*	enter water to catch octopus and eat	McGrew (1998)	food: foraging/food processing
108	*Macaca*	food-washing	Perry and Manson (2003)	food: foraging/food processing
109	*Pan*	fresh *Strychnos* eating	Boesch (2003)	food: food choice
110	*Pan*	mature pith chew	Boesch (2003)	food: food choice
111	*Pan*	winged *Thoracotermes* sp. eating	Boesch (2003)	food: food choice
112	*Pan*	lemon eating	Reader (2004)	food: food choice
113	*Pan*	mango eating	Reader (2004)	food: food choice
114	*Pan*	leaf swallowing: medicinal plant use (e.g. *Aspilia*)	Huffman (1997)	food: food choice

115	*Pan*	leaf swallowing: *Polycephalium capitatum*	Humle and Matsuzawa (2001)	food: food choice
116	*Pan*	leaf swallowing: *Ficus mucosa*	Humle and Matsuzawa (2001)	food: food choice
117	*Pan*	eating: oil palm fruit	Humle and Matsuzawa (2004)	food: food choice
118	*Pan*	eating: oil palm petiole/pith	Humle and Matsuzawa (2004)	food: food choice
119	*Pan*	eating: oil palm flower	Humle and Matsuzawa (2004)	food: food choice
120	*Pan*	eating: oil palm resin	Humle and Matsuzawa (2004)	food: food choice
121	*Pan*	eating: oil palm heart	Humle and Matsuzawa (2004)	food: food choice
122	*Pan*	eating: oil palm fibres of dead wood	Humle and Matsuzawa (2004)	food: food choice
123	*Pongo*	slow loris eating	van Schaik et al. (2003)	food: food choice
124	*Gorilla*	weaver ant eating (*Oecophylla longinoda*)	Deblauwe et al. (2003)	food: food choice
125	*Gorilla*	fungus farming termite (*Cubitermes sp.*) eating: ignored	Deblauwe et al. (2003)	food: food choice
126	*Gorilla*	eating: *Crematogaster sp.*	Deblauwe et al. (2003)	food: food choice
127	*Gorilla*	eating: *Macrtermes muelleri*	Deblauwe et al. (2003)	food: food choice
128	*Gorilla*	eating: *Camponotus vividus*	Deblauwe et al. (2003)	food: food choice
129	*Gorilla*	eating: *Camponotus brutus*	Deblauwe et al. (2003)	food: food choice
130	*Gorilla*	eating: *Pachycondyla tarsata*	Deblauwe et al. (2003)	food: food choice
131	*Macaca*	eating: dead fish on shore	McGrew (1998)	food: food choice
132	*Macaca*	frog and lizard catching and eating	McGrew (1998)	food: food choice
133	*Pan*	club	Whiten et al. (2001)	non-food: social/communicative
134	*Pan*	aimed-throw	Whiten et al. (2001)	non-food: social/communicative
135	*Pan*	rain dance	Whiten et al. (2001)	non-food: social/communicative
136	*Pan*	grooming hand-clasp: palm-to-palm	McGrew et al. (2001)	non-food: social/communicative
137	*Pan*	grooming hand-clasp: non-palm-to-palm	McGrew et al. (2001)	non-food: social/communicative
138	*Pan*	knuckle-knock	Whiten et al. (2001)	non-food: social/communicative

139	*Pan*	branch-slap	Whiten et al. (2001)	non-food: social/communicative
140	*Pan*	leaf-strip	Whiten et al. (2001)	non-food: social/communicative
141	*Pan*	leaf-clip: fingers	Whiten et al. (2001)	non-food: social/communicative
142	*Pan*	leaf-clip: mouth: before buttress drumming/to signal frustration	Boesch (2003)	non-food: social/communicative
143	*Pan*	leaf-clip: mouth: play context	Boesch (2003)	non-food: social/communicative
144	*Pan*	leaf-clip: mouth: courtship	Boesch (2003)	non-food: social/communicative
145	*Pan*	shrub-bend	Whiten et al. (2001)	non-food: social/communicative
146	*Pan*	stem pull-through	Whiten et al. (2001)	non-food: social/communicative
147	*Pan*	branch din	Whiten et al. (2001)	non-food: social/communicative
148	*Pan*	social scratch	Nakamura et al. (2000)	non-food: social/communicative
149	*Pan*	leaf-pile pulling	Nishida et al. (2003)	non-food: social/communicative
150	*Pan*	missile throw	Boesch and Tomasello (1998)	non-food: social/communicative
151	*Pan*	branch haul	Boesch and Tomasello (1998)	non-food: social/communicative
152	*Pan*	play start	Boesch and Tomasello (1998)	non-food: social/communicative
153	*Pan*	build ground-nest: play initiation	Boesch (2003)	non-food: social/communicative
154	*Pan*	build coarse ground-nest: attraction of sexually active females	Boesch (2003)	non-food: social/communicative
155	*Pan*	dialectical variation: phrase structure in ‘long’ calls	McGrew (1998)	non-food: social/communicative
156	*Pan*	mutual genital touch	Nakamura and Nishida (2006)	non-food: social/communicative
157	*Pan*	heel tap	Nakamura and Nishida (2006)	non-food: social/communicative
158	*Pan*	sputter	Nakamura and Nishida (2006)	non-food: social/communicative
159	*Pan*	throw splash	Nakamura and Nishida (2006)	non-food: social/communicative
160	*Pan*	catch and toy with hyraxes (*Dendrohyrax dorsalis*)	Matsuzawa (2003)	non-food: social/communicative
161	*Pongo*	snag riding	van Schaik et al. (2003)	non-food: social/communicative

162	*Pongo*	kiss-squeak: leaves	van Schaik et al. (2003)	non-food: social/communicative
163	*Pongo*	kiss-squeak: hands	van Schaik et al. (2003)	non-food: social/communicative
164	*Pongo*	leaf-wipe: kiss-squeak context	van Schaik et al. (2003)	non-food: social/communicative
165	*Pongo*	play nests	van Schaik et al. (2003)	non-food: social/communicative
166	*Pongo*	raspberry	van Schaik et al. (2003)	non-food: social/communicative
167	*Pongo*	symmetric scratch	van Schaik et al. (2003)	non-food: social/communicative
168	*Pongo*	throat scrape	van Schaik et al. (2006)	non-food: social/communicative
169	*Pongo*	snag crashing	van Schaik et al. (2003)	non-food: social/communicative
170	*Pongo*	nest smack	van Schaik et al. (2006)	non-food: social/communicative
171	*Pongo*	twig biting	van Schaik et al. (2003)	non-food: social/communicative
172	*Cebus*	hand sniffing	Perry et al. (2003)	non-food: social/communicative
173	*Cebus*	sucking on body parts	Perry et al. (2003)	non-food: social/communicative
174	*Cebus*	finger-in-mouth game	Perry et al. (2003)	non-food: social/communicative
175	*Cebus*	hair-passing game	Perry et al. (2003)	non-food: social/communicative
176	*Cebus*	toy game	Perry et al. (2003)	non-food: social/communicative
177	*Cebus*	spider monkey grooming	Rose et al. (2003)	non-food: social/communicative
178	*Cebus*	tolerance of indigo snake (*Drymarchon corais*)	Rose et al. (2003)	non-food: social/communicative
179	*Cebus*	mobbing of large spectacled owl	Rose et al. (2003)	non-food: social/communicative
180	*Cebus*	tolerance of boa constrictors <1m long (no mob/alarm call)	Rose et al. (2003)	non-food: social/communicative
181	*Cebus*	juveniles drop branches, bark, bounce and display at caiman (partly a game?)	Rose et al. (2003)	non-food: social/communicative
182	*Cebus*	affiliative interaction with howler monkeys	Rose et al. (2003)	non-food: social/communicative
183	*Cebus*	stone-banging	Moura (2007)	non-food: social/communicative
184	*Cebus*	club	Van Schaik and Pradhan (2003)	non-food: social/communicative
185	*Macaca*	bathing behaviour	McGrew (1998)	non-food: social/communicative

186	*Macaca*	grooming contact calls	McGrew (1998)	non-food: social/communicative
187	*Macaca*	courtship posture: female mounts male	McGrew (1998)	non-food: social/communicative
188	*Alouatta*	hand-holding behaviour	Brockett et al. (2005)	non-food: social/communicative
189	*Pan*	self-tickle	Whiten et al. (2001)	non-food: comfort/hygiene
190	*Pan*	leaf-napkin	Whiten et al. (2001)	non-food: comfort/hygiene
191	*Pan*	fly-whisk	Whiten et al. (2001)	non-food: comfort/hygiene
192	*Pan*	leaf-dab	Whiten et al. (2001)	non-food: comfort/hygiene
193	*Pan*	seat-vegetation	Whiten et al. (2001)	non-food: comfort/hygiene
194	*Pan*	leafy-twigs as sandals	McGrew (1998)	non-food: comfort/hygiene
195	*Pan*	ground nest	Boesch and Tomasello (1998)	non-food: comfort/hygiene
196	*Pan*	postcoital penis cleaning	O’Hara and Lee (2006)	non-food: comfort/hygiene
197	*Pongo*	leaf napkin	van Schaik et al. (2003)	non-food: comfort/hygiene
198	*Pongo*	branch as swatter	van Schaik et al. (2003)	non-food: comfort/hygiene
199	*Pongo*	bunk nest/rain hat	van Schaik et al. (2003)	non-food: comfort/hygiene
200	*Pongo*	sun cover	van Schaik et al. (2003)	non-food: comfort/hygiene
201	*Pongo*	hide under nest	van Schaik et al. (2003)	non-food: comfort/hygiene
202	*Pongo*	scratch stick	van Schaik et al. (2003)	non-food: comfort/hygiene
203	*Pongo*	autoerotic tool	van Schaik et al. (2003)	non-food: comfort/hygiene
204	*Pongo*	carry *Campnosperma* leaves: for nest	van Schaik et al. (2006)	non-food: comfort/hygiene
205	*Pongo*	branch cushion	van Schaik et al. (2006)	non-food: comfort/hygiene
206	*Gorilla*	use of stick: to test water depth	Breuer et al. (2005)	non-food: comfort/hygiene
207	*Gorilla*	use of branch as bridge	Breuer et al. (2005)	non-food: comfort/hygiene
208	*Macaca*	masturbation	McGrew (1998)	non-food: comfort/hygiene
209	*Macaca*	stone handling	Nahallage and Huffman (2007)	non-food: other

Table 2.2 The thirty-nine experimental studies investigating social learning in primates in the literature survey

Study	Species	Classification
Visalberghi et al. (1998)	*Cebus apella*	food reinforcer - food choice
Prescott et al. (2005)	*Saguinus fuscicollis and Saguinus labiatus*	food reinforcer - food choice
Queyras et al. (2000)	*Callithrix jacchus*	food reinforcer - food choice
Drapier et al. (2003)	*Cebus apella*	food reinforcer - food choice
Visalberghi and Addessi (2000)	*Cebus apella*	food reinforcer - food choice
Visalberghi and Addessi (2001)	*Cebus apella*	food reinforcer - food choice
Huffman and Hirata (2004)	*Pan troglodytes*	food reinforcer - food choice: leaf swallowing
Brown et al. (2005)	*Callithrix jacchus*	food reinforcer - food choice: infant begging
Bugnyar and Huber (1997)	*Callithrix jacchus*	food reinforcer - foraging/food processing: artificial novel foraging task
Voelkl and Huber (2000)	*Callithrix jacchus*	food reinforcer - foraging/food processing: artificial novel foraging task
Caldwell and Whiten (2003)	*Callithrix jacchus*	food reinforcer - foraging/food processing: artificial novel foraging task
Caldwell and Whiten (2004)	*Callithrix jacchus*	food reinforcer - foraging/food processing: artificial novel foraging task
Price and Caldwell (2007)	*Colobus guereza*	food reinforcer - foraging/food processing: artificial novel foraging task
Whiten (1998)	*Pan troglodytes*	food reinforcer - foraging/food processing: artificial novel foraging task
Custance et al. (1999)	*Cebus apella*	food reinforcer - foraging/food processing: artificial novel foraging task
Stoinski et al. (2001)	*Gorilla gorilla*	food reinforcer - foraging/food processing: artificial novel foraging task

Study	Species	Classification
Stoinski and Whiten (2003)	*Pongo pygmaeus and Pongo abelii*	food reinforcer - foraging/food processing: artificial novel foraging task
Custance et al. (2006)	*Macaca nemestrina (and Homo sapiens)*	food reinforcer - foraging/food processing: artificial novel foraging task
Moscovice and Snowdon (2006)	*Saguinus oedipus*	food reinforcer - foraging/food processing: artificial novel foraging task
Horner et al. (2006)	*Pan troglodytes (and Homo sapiens)*	food reinforcer - foraging/food processing: artificial novel foraging task
Custance et al. (2001)	*Pongo pygmaeus*	food reinforcer - foraging/food processing: artificial novel foraging task
Call et al. (2005)	*Pan troglodytes*	food reinforcer - foraging/food processing: artificial novel foraging task
Rigamonti et al. (2005)	*Macaca nemestrina (and Homo sapiens)*	food reinforcer - foraging/food processing: artificial novel foraging task
Drapier and Thierry (2002)	*Macaca tonkeana*	food reinforcer - foraging/food processing: food processing technique on novel food
Horner and Whiten (2005)	*Pan troglodytes (and Homo sapiens)*	food reinforcer - tool use: artificial novel foraging task
Horner and Whiten (2007)	*Pan troglodytes (and Homo sapiens)*	food reinforcer - tool use: artificial novel foraging task
Whiten et al. (2005)	*Pan troglodytes*	food reinforcer - tool use: artificial novel foraging task
Hayashi et al. (2005)	*Pan troglodytes*	food reinforcer - tool use: wild observed foraging task (introduced to captive group)
Celli et al. (2004)	*Pan troglodytes*	food reinforcer - tool use: wild observed foraging task (introduced to captive group)
Bonnie et al. (2007)	*Pan troglodytes*	food reinforcer - other - arbitrary actions: tokens: spread of arbitrary conventions
Brosnan and De Waal (2004)	*Cebus apella*	food reinforcer - other - arbitrary actions: tokens: exchange
Myowa-Yamakoshi and Matsuzawa (1999)	*Pan troglodytes*	food reinforcer (some) - other - arbitrary actions - do-as-I-do: object-related actions
Ducoing and Thierry (2005)	*Macaca tonkeana*	food reinforcer - other - leaning pole on wall

Study	Species	Classification
Subiaul et al. (2004)	*Macaca mulatta*	food reinforcer - other - cognitive imitation
Ferrari et al. (2006)	*Macaca mulatta*	no food reinforcer - social/communicative: neonatal imitation of facial and hand gestures
Yunger and Bjorklund (2004)	*Pongo pygmaeus*	no food reinforcer - other - do-as-I-do: object-related actions
Bjorklund et al. (2002)	*Pan troglodytes*	no food reinforcer - other- do-as-I-do: object-related actions
Myowa-Yamakoshi and Matsuzawa (2000)	*Pan troglodytes*	no food reinforcer (food used but not as direct reward) - other -do-as-I-do: object-related actions
Hardie and Buchanan-Smith (2000)	*Saguinus fuscicollis and Saguinus labiatus*	no food reinforcer - other - interspecies facilitation: responses to novel objects

Experimental Studies of Social Learning

From the search results, I assessed experimental papers that reported research explicitly, and directly, investigating social learning. Studies in which the subjects did not have the opportunity to display social learning were excluded. I included only studies involving some form of experimental manipulation, and therefore disregarded purely observational studies of captive primates. Thirty-nine studies fulfilled these criteria (Table 2.2). The 39 experimental studies were classified, first according to whether or not food was used as a reinforcer, analogous to the division of wild traditions into those that are motivated by food rewards and those that are not. Second, I considered whether or not the studies involved experimental tasks that resembled a wild tradition identified by the survey, and if so I further classified them into subcategories similar to those of the wild traditions.

Inter-rater Reliabilities

In order to index inter-rater reliabilities approximately 10% (16) of the total number of articles reviewed for the current survey (159), and previously coded by myself, were coded by an independent rater, my principal supervisor Dr Christine Caldwell. I calculated inter-rater reliabilities an as index of agreement between myself and Christine. We agreed completely on the classification of the articles into experimental and non-experimental; and into those mentioning potential cultural behaviours or not. Our index of agreement on the total number of cultural variants mentioned in the articles was 96%. The variants where there were discrepancies between myself and the independent rater involved splitting and lumping issues but since the behaviours in question were mentioned in several articles within the survey we are confident that these differences of opinion would not have altered the total number of identified cultural variants.

We agreed on the classification of experimental articles and potential cultural behaviours into food and non-food behaviours; on the genus in each case; and on the classification of the experimental studies into sub-types of behaviour investigated (e.g. nonfood, food reinforcer used). Our index of agreement on the classification of cultural variants into sub-divisions of food and non-food behaviours was 99%. In summary, the calculated inter-rater reliabilities were extremely high: all greater than 95%.

2.2.3 Results

Descriptions of Wild Behavioural Traditions

Close reading of the articles uncovered 209 potential cultural variants representing seven genera of apes and monkeys (Table 2.3). Of the wild observations collected from citations in the articles, overall 132 (63%) were food-related and 77 (37%) were nonfood-related behaviours. When considering the overall figures it is important to note that some species and genera are overrepresented in the sample. For example, observations of chimpanzee behaviours account for almost half of the total number of behaviours reported in the literature survey, whereas ape behaviours overall represent approximately two-thirds of the behaviours (Table 2.3). However, when the percentage of food- and nonfood-related behaviours for each genus are averaged out, i.e., weighting each genus equally, the average percentage figures produced for food- and nonfood-related cultural variants are in fact similar to the actual percentage figures (Table 2.3). It seems therefore that the data are not misleadingly skewed by the large number of chimpanzee behaviours in the sample. Examining the figures for each genus, the general trend is a somewhat higher percentage of food-related than of nonfood-related behaviours, with *Pongo* perhaps a noteworthy exception.

Table 2.3 The number and proportion of food and non-food cultural variants for each of the seven genera represented in the literature survey.

Genera	**Potential cultural variants cited**				
	Total	**of which food-related**		**of which nonfood-related**	
Pan	102	66	(65%)	36	(35%)
Pongo	28	8	(29%)	20	(71%)
Gorilla	11	9	(82%)	2	(18%)
Cebus	51	37	(73%)	14	(27%)
Macaca	15	11	(73%)	4	(27%)
Ceropithecus	1	1	(100%)	0	(0%)
Alouatta	1	0	(0%)	1	(100%)
Totals	**209**	**132 (63% of total)**	**average percentage = 60%**	**77 (37% of total)**	**average percentage = 40%**

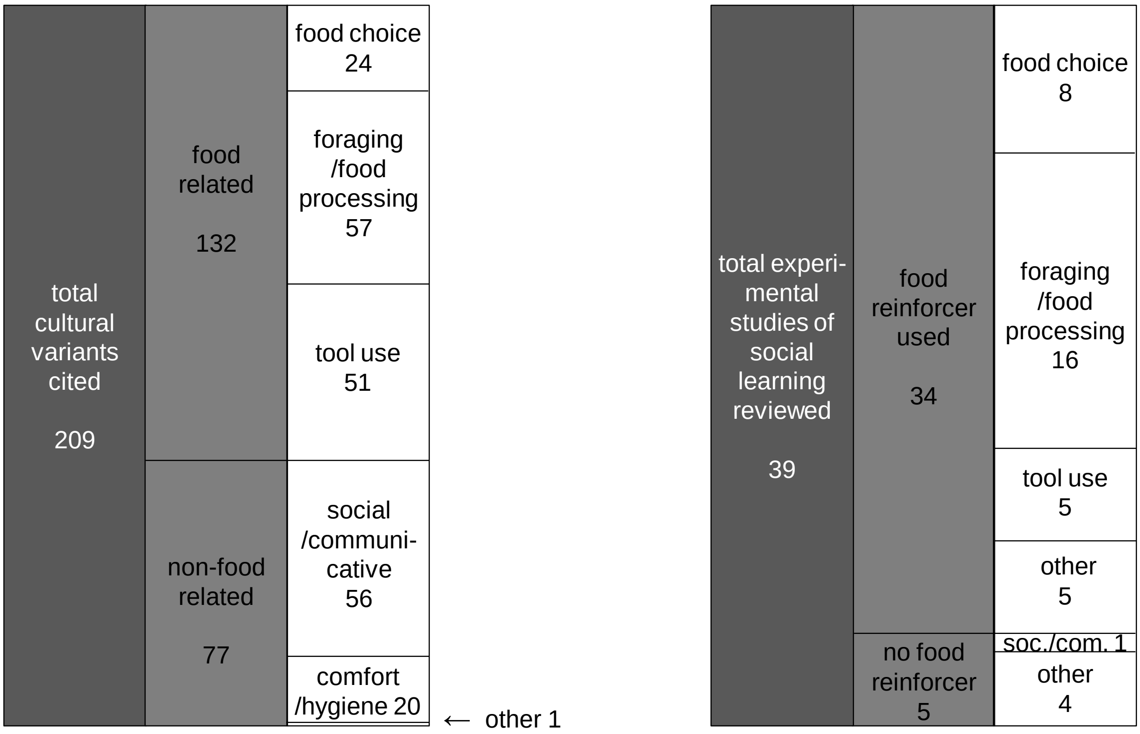
Of the 132 food-related behaviours: 24 were classified as food choice; 57 as foraging/food processing; and 51 as tool use behaviours. Food choice behaviours included traditions of food preference such that a particular group chose to make use of a food resource that other groups ignore, e.g., slow loris eating by *Pongo* (van Schaik et al., 2003). Foraging behaviours included extractive foraging behaviours with no tool use such as deep dig for driver ant grubs in *Pan* (Boesch, 2003); food processing behaviours that did not involve tool use, such as apple washing in *Macaca* (Reader, 2004); hunting-related behaviours such as the squirrel-killing technique in *Cebus* (Rose et al., 2003); and ectoparasite-related behaviours such as louse egg handling techniques in *Macaca* (Tanaka, 1998). Tool use behaviours included use of tools in extractive foraging for food and water such as seed extraction tool use in *Pongo* (van Schaik et al., 2003); food processing such as pestle-pounding *Pan* (Whiten et al., 2001); and use of a tool for protection when handling irritant food such as leaf gloves in *Pongo* (van Schaik et al., 2003).

I subdivided the 77 nonfood-related behaviours into social/communicative and comfort/hygiene behaviours. Social and communicative behaviours included behaviours observed in the context of courtship; mostly attention-getters such as branch slap in *Pan* (Whiten et al., 2001). They also included behaviours used in agonistic contexts, such as threatening displays like aimed throw in *Pan* (Whiten et al., 2001). I also placed affiliative behaviours in this category, such as the grooming hand-clasp in *Pan* (McGrew et al., 2001) or sucking on body parts in *Cebus* (Perry et al., 2003). In addition, behaviours used in the context of play were included, with many attention-getters to initiate play, such as leaf pile pulling in *Pan* (Nishida and Wallauer, 2003). I categorised the relatively rare interspecific communicative traditions, such as putative antipredator behaviours, e.g., stone-banging in *Cebus* (Moura, 2007), and interspecific interactions, such as *Cebus* grooming *Ateles* (Rose et al., 2003), within the social and communicative behaviour category. Some behaviours represented local trends in vocal communication, such as the throat scrape used by mother orangutans in some groups toward their offspring (van Schaik et al., 2006).

Comfort and hygiene behaviours included body cleaning behaviours, such as leaf-napkin in *Pan* (Whiten et al., 2001) and *Pongo* (van Schaik et al., 2003). I also included swatting of insects in this category, e.g., fly-whisk in *Pan* (Whiten et al., 2001) and building forms of shelter or protection, such as seat vegetation use in some chimpanzees

(Whiten et al., 2001). Self-touching or stimulation also fell into this category, such as the use of a scratch stick by some groups of orangutans (van Schaik et al., 2003). Many of the behaviours that I classified as comfort/hygiene involved tool use, e.g., the apparent use of a stick by a gorilla to test water depth (Breuer et al., 2005). I classed 56 (73%) of the nonfood-related behaviours as social/communicative and 20 (26%) as comfort/hygiene. Stone handling in *Macaca* (Nahallage and Huffman, 2007) was the only behaviour that we could not readily classify as one of these two subcategories, so we labelled it as other (1%). Thus, social and communicative behaviours represented the majority of the nonfood-related behaviours. They accounted for 27% of the total number of behaviours reported as possible cultural variants in the literature surveyed. Plate 2.1 illustrates examples of a nonfood-related (stone handling) and a food-related potential behavioural tradition (apple washing).

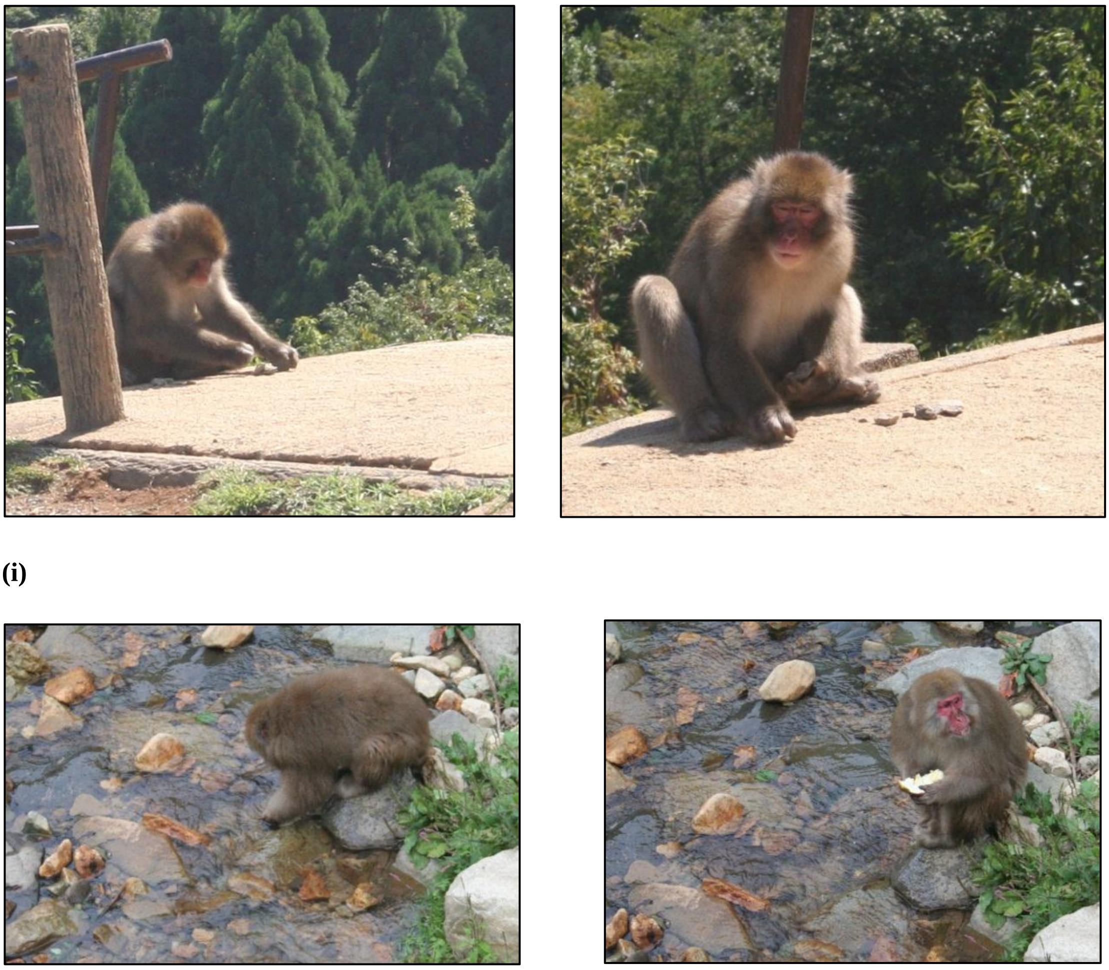
Fig. 2.1 Comparison of the proportion of food to nonfood-related (i) field observations of cultural variants cited and (ii) experimental studies investigating social learning, in the literature surveyed.



(i)

(ii)

Plate 2.1 Free-ranging *Macaca* engaged in: (i) in non-food-related behavioural tradition stone handling (cultural variant 209, Table 2.2) at Arashiyama Monkey Park, Kyoto, Japan; and (ii) in the food related behaviour: apple washing (cultural variant 105, Table 2.2) at Jigokudani Monkey Park, Yudanaka, Japan.



(i)

(ii)

Experimental Studies of Social Learning

Of the 39 articles that were experimental studies investigating social learning in primates, 34 (87%) involved the use of food as a reinforcer and 5 (13%) did not (Fig. 2.1). Of all the experimental studies, 29 (74%) investigated behaviours resembling wild food-related traditions, 1 (3%) study investigated behaviours resembling wild nonfood traditions, and 9 (23%) studies investigated behaviours that did not resemble any wild traditions, which we designated as other (Fig 2.1) Studies in which food was used as a reinforcer investigated the social learning of food selection and food processing and foraging behaviours, with and without tool use. Many investigated the social learning of novel extractive foraging tasks. The 5 studies that used food as a reinforcer but did not investigate behaviours resembling a wild tradition involved the social learning of a computer-based cognitive task (Subiaul et al., 2004); leaning a pole against a wall on which to climb (Ducoing and Thierry, 2005); token use (Bonnie et al., 2007; Brosnan and de Waal, 2004); and object-related actions (do-as-I-do; Myowa-Yamakoshi and Matsuzawa, 1999). This subset contained a study specifically designed to investigate the transmission of social/communicative traditions (Bonnie et al., 2007), yet the behaviours elicited were directly motivated by food rewards.

Of the experimental papers in which researchers did not use food as a reinforcer, only one study involved behaviours directly resembling wild nonfood traditions, investigating spontaneous neonatal imitation of hand and mouth gestures in macaques (Ferrari et al., 2006). However, the study did not contribute directly to the understanding of behavioural traditions because the tendency to imitate such behaviours is confined to a period of a few days after birth. Of the other four studies not using food as a reinforcer, one investigated the interspecific social facilitation of responses to novel objects in tamarins (Hardie and Buchanan-Smith, 2000) and 3 involved the social learning of object-related actions (do-as-I-do; Bjorklund et al. 2002; Myowa-Yamakoshi and Matsuzawa, 2000; Yunger and Bjorklund, 2004). One of the latter three studies (Myowa-Yamakoshi and Matsuzawa, 2000) involved an experimental task that was similar in some respects to the simulated foraging tasks classified as foraging/food processing; however, it is difficult to categorize the task as extractive foraging with no food reward involved. Although the classification of this task may be considered equivocal, had I decided to label it as a food task this would have inflated the already apparent discrepancy with the wild tradition data rather than reducing it.

2.3 Discussion

2.3.1 Literature Survey Findings

The current literature survey has provided quantitative confirmation of the perceived discrepancy between the proportions of food-related to nonfood-related behaviours observed in the field, compared with the proportion of studies investigating food and nonfood-related behaviours resembling wild traditions in an experimental context (Fig. 2.1). This is evidenced in terms of the use of food as a reinforcer and even more overwhelmingly in terms of the specific form of task investigated.

It is particularly striking that, although social/communicative behaviours accounted for 27% of the cultural variants reported in the field, only one of the 39 experimental studies aimed specifically to contribute to our understanding of the wild transmission mechanism of such behaviours (Bonnie et al., 2007). I nonetheless classified the study as involving food-motivated behaviours due to the use of food reinforcers. Also, although one nonfood study investigated behaviours resembling wild social communicative traditions (Ferrari et al., 2006), it was designed to investigate imitative ability in neonates rather than such traditions themselves. Given that social and communicative behavioural traditions make up an important proportion of the putative cultural behaviours observed in the wild, it is surprising that researchers have neglected the behaviours as a focus for experimental study (Bonnie et al., 2007; Day et al., commentary in Perry et al., 2003).

The figures I report are determined, to some extent, by the process of splitting or lumping behaviours into categories (Whiten et al., 2001). The figures are influenced first by the divisions made by the authors of the original papers I surveyed citing wild traditions and second by the divisions that we have drawn for the purposes of this analysis. There is no definite consensus on how to split and lump categories of behaviour, and some authors counted relatively fine variations of particular behaviour as separate cultural variants, whereas others lumped the more subtle variants of different behaviours into a single category. In making my own divisions, I endeavoured to keep consistent with those most commonly drawn in this field of literature.

Overall, I identified more citations of potentially cultural behaviours for chimpanzees in particular, and for apes in general, relative to the number for monkeys. The result could represent a real difference or, alternatively, the difference could be due to the higher total number of observation hours or number of different field sites for apes relative to monkeys. Irrespective of this imbalance, it is clear that behavioural traditions seem to be widespread in primate species, even acknowledging the caveat that my quantification of putative cultural behaviours relied on the judgement of the individual authors of each article surveyed. Ten years before this literature was carried out, Tomasello and Call (1997) noted that group-specific behaviours had been reliably recorded only for chimpanzees and Japanese macaques. In the intervening decade, the number of primate species for which this can be said appears to have grown considerably.

2.3.2 Previous Research Studying Social Learning in Nonhuman Primates without Food

Although scarce, some studies have explicitly attempted to investigate experimentally the social transmission of social and communicative behaviours in primates. A few key experimental papers were published >10 years ago, and hence are outside our survey period, which investigated the imitation of arbitrary gestural actions by chimpanzees (Custance et al., 1995; Hayes and Hayes 1952). Further, I did not include a similar study, conducted with an orangutan subject (Call 2001), because it was not published in one of the 25 journals that we searched. However, in any case, I would have classified these studies, like Bonnie et al. (2007), as involving food motivated behaviours due to the use of food reinforcers. In each of the studies, subjects were trained to respond to a human command, e.g., “Do this!”, typically over a relatively lengthy training period, using food as a reinforcer, and in some cases also verbal encouragement. The studies show that the apes were able to generalise the training to novel arbitrary actions and gestures that were not included in the training set.

Such experiments provided evidence that chimpanzees and orangutans possess the capacity to imitate arbitrary gestural actions. However, although arbitrary actions may show important similarities with gestural signals used in the wild, gestures made by primates in the field are unlikely to be reinforced in the same way as the imitated actions were in these experiments, usually with food, and this may have important implications for the mechanisms involved in learning.

All of the aforementioned studies used human demonstrators, but a further study that investigated the imitation of arbitrary gestures used conspecifics as models (Tomasello et al., 1997). Further, the study of Tomasello et al. (1997) aimed to elicit spontaneous imitation, rather than relying on extensive training. In these respects, this particular study might be expected to be especially illuminating in terms of determining whether and how arbitrary gestures might be socially learned in natural environments.

Tomasello et al. (1997) trained two chimpanzee demonstrators to perform arbitrary gestures at the sight of a human approaching with food. The chimpanzees that shared an enclosure with the trained demonstrators were therefore the real focus of the study. The gestures that were trained were raising the arms above the head; running the hands along the caging, both demonstrated by the same individual; and also bending over to touch the caging with the head, with a different demonstrator. On satisfactory production of the gestures, the demonstrators received food or the means to access food (a tool for dipping in otherwise inaccessible honey) within sight of the focal subjects, from the experimenter. Tomasello et al. (1997) reported that the target gestures were not performed by any of the observing chimpanzees in the group. However, they acknowledge limitations of the study. First, the experiment involved chimpanzees gesturing to humans, rather than to conspecifics, and second, the chimpanzees already had typical gestures that were used to beg from humans so perhaps they were not in need of a novel means of doing so. There is also the issue again of food reinforcement. The researchers responded to the gestures produced by the demonstrators with food. However, receiving food in response to an arbitrary gesture may not be a connection that is readily learned by observation. Nonetheless, the experiment is extremely interesting and provides valuable groundwork for the study of the social transmission of communicative behaviours.

Whiten et al. (2003) highlighted the lack of strong experimental evidence that chimpanzees are capable of learning the meaning of communicative behaviours through observation of conspecifics, and stated that the experiment of Tomasello et al. (1997) “begs for replication and elaboration” (p. 100).

One study designed to address this need (Bonnie et al., 2007) was the only one within the literature survey that directly investigated the transmission of social/communicative behaviours. The study was an innovative attempt to induce arbitrary social conventions in two groups of chimpanzees. Bonnie et al. (2007) noted that there is a need to investigate experimentally the transmission of arbitrary conventions, in which the meaning of the behaviour is obvious only to group members who share the convention. Thus Bonnie et al. (2007) have led the way in a new and promising direction for future experimental research.

In their experiment, two demonstrator chimpanzees, each from a different group, were trained, via food reinforcement, to retrieve tokens and place them in either a bucket or a pipe. A human experimenter, located on a tower above the enclosure, provided the reward by throwing the food down for the chimpanzee to catch. In the transmission phase, the demonstrators performed the behaviour in the presence of the other members of their group. Both options —pipe and bucket— were possible, and the experimenter would have rewarded either one. However, the demonstrators adhered to their trained behaviour. Further, all but one individual of the observing group members also faithfully adhered to the original method introduced by their demonstrator. Bonnie et al. (2007) therefore successfully generated two contrasting arbitrary traditions in the two groups.

However, despite the promise of the study, it did involve what was essentially a functional task with no actual gestures and food was once again used as a reward. It will be a challenge for future investigations on social transmission to build on the study, and use tasks even further removed from functional material traditions. Bonnie et al. (2007) define tool use traditions as “characterized by a functional, goal-oriented task with foreseeable outcomes” (p. 367), a much broader definition than that of Beck (1980; see above). The target actions in their study quickly, and reliably, resulted in a food reward. The task may appear superficially to be causally arbitrary, but it is certainly both functional and goal-directed, and in this sense it is a tool task. The task also fits Becks’ definition of tool use (Beck, 1980, p. 10). Sousa and Matsuzawa (2001) demonstrated that the use of tokens to exchange for a food reward is almost exactly equivalent to direct food rewards when used to reward and maintain intellectually demanding trained behaviours in chimpanzees. Arbitrary conventions in the wild such as leaf-clipping and the grooming hand-clasp are not rewarded with food when performed in the wild. In summary, the study represents a move in the right direction but there is much scope for improved studies in the future, including moving away from the use of food as a reinforcer.

2.3.3 Shifting Focus Away from Food

Food, it seems, has been used in some way in the vast majority of experimental studies of social learning, even where the behaviour under investigation is nonfood-related and very unlikely to be rewarded with food in the wild. Why has food been used almost universally as a reinforcer, even when the focus of the study has been social behaviours? Food appears to work reliably as a reinforcer, and there has been little impetus to use alternative motivators.

In a review of the literature on primate learning and cognition, not specific to social learning, Anderson (1998) highlighted the heavy reliance on food and water as reinforcers, even though social stimuli, such as the sight of conspecifics, either live or in videos or still photographs, have been highly effective in many contexts. Perhaps researchers are cautious about deviating from established paradigms. But there are good reasons to encourage just such a shift of focus, particularly within the field of social learning.

First, social and communicative behaviours are unlikely to be rewarded, or motivated, by food in natural environments. Therefore experiments which rely on food reinforcers to motivate arbitrary actions and communicative gestures could be criticized in terms of their ecological validity. To draw an analogy, Hare (2001) has criticised experimental methods that test for chimpanzees' understanding of others' visual perspective, in which chimpanzees can gain food reward through cooperation with a human experimenter. He has pointed out that this setup lacks external validity because it contrasts starkly to the fierce competition over limited resources typically observed between chimpanzees in natural environments. The implication is that we may get misleading results by using experimental paradigms that bear little relation to the natural contexts.

Further, it is already well known that food rewards are not a completely neutral reinforcer. Food rewards do not promote any and every behaviour with which they come to be associated, in equal measure. When using food as a reward, it is far easier to train behaviours that are already connected with feeding and foraging in the animal's natural repertoire, as Breland and Breland (1961) showed in their classic article. Indeed, such behaviours may spontaneously intrude into sequences of nonfood-related behaviours, which a human trainer attempts to establish through the use of food reinforcement. Breland and Breland (1961) also found training vocalisation with food reinforcement to be particularly problematic.

There is also good reason to believe that food- versus nonfood-related traditions may show very different diffusion patterns. Perry et al. (2003) highlighted the fact that most models of social transmission have been concerned with behaviours performed by single individuals that have a clear adaptive function, such as food choice, tool use, and food processing. In contrast, social conventions are typically performed dyadically, and have less obvious direct benefits to the individual performing them. Consequently, we should expect them to show somewhat different diffusion patterns (Perry et al. 2003).

Interestingly, Matsusaka et al. (2006) have made a similar point with regard to an apparently functionless behaviour. They noted that the non-essential leaf sponge use by chimpanzees to obtain water appeared to be transmitted horizontally, among juveniles. This contrasted with foraging techniques, such as nut-cracking, which were more likely to be transmitted vertically, from parent to offspring.

For these reasons, we might be well advised to steer away from the habitual reliance on food within experimental designs, if we aim to get the most revealing insights into the mechanisms and diffusion patterns that may be involved in the transmission of nonfood behaviours. Perhaps it is time to take up the challenge of developing new paradigms for the investigation of nonfood traditions such as social conventions.

However, such a conclusion begs the obvious question: what exactly are the reinforcers involved in nonfood-related traditions? Reinforcement is usually defined as a consequence that follows a response, which increases the probability of that response occurring under similar conditions in the future (Pryor 2002). Thus, reinforcers can take a wide variety of forms, many of which are far removed from food and drink. For comfort and hygiene behaviours, the answer seems fairly straightforward. The behaviours, by their very definition, appear to increase comfort or remove unpleasant bodily sensations, which no doubt operate as powerful reinforcers. However, for many social and communicative traditions the rewards are considerably less obvious. Many communicative traditions appear to act as attention getters, or to initiate courtship, play, or grooming. Therefore it would seem likely that social attention, at least from the individual(s) to whom the behaviour was targeted, may in itself be rewarding. For the behaviours that seem to be aimed at initiating affiliative social interaction, the pleasurable feedback from the interactions may well act as a direct reward. For other behaviours, such as threat displays, the departure of an unwelcome social partner may be similarly reinforcing. However, it should be noted that, in trying to determine which reinforcers are likely to reward behaviours in the wild we are making the tacit assumption that both the imitation and the continued performance of all behavioural traditions are indeed motivated by extrinsic reward. However, there is some evidence to suggest that this may not always be the case.

Concerning the initial spread of behavioural traditions, there is some evidence to suggest that reward is not always necessary. Primates have been observed to imitate without extrinsic reward. Russon and Galdikas (1993) have reported spontaneous attempts by rehabilitant orangutans to imitate humans with no apparent encouragement and in many cases, no contingent reward either. For example, one orangutan repeatedly attempted to hammer a nail into wood. However, it could always be argued that human contact had influenced these orangutans, and that subtle social reinforcement may have somehow contributed. But wild juvenile chimpanzees learning to crack nuts present a further example of imitation without reward.

Although it takes many years to become competent at cracking nuts, and so receive a reward, juveniles persist in their attempts to imitate the adults (de Waal, 2003; Inoue-Nakamura and Matsuzawa, 1997). However, it is conceivable that the object manipulation and exploration may in itself be intrinsically rewarding even with no food reward (Poole, 1992). It is also possible that scrounging from others is a mediating factor in juvenile nut-cracking attempts.

Researchers have proposed several theoretical models to explain the apparent lack of extrinsic reward in such instances. De Waal (2001) proposed the BIOL model (Bonding-and Identification-based Observational Learning) asserting that the motivation to imitate others, particularly significant others, lies in the urge to conform while extrinsic reward, such as food, merely acts as a secondary reinforcer. Similarly, Matsuzawa et al. (2001) proposed the master-apprenticeship model, e.g., in which infants learning to crack nuts are motivated not by food but by their motivation to imitate their mother.

Experimental work can also provide intriguing insights into the role of rewards in social learning. Bonnie and de Waal (2007) investigated the influence of reward on social learning in capuchin monkeys using an artificial foraging task. The task involved picking a target box out of the three boxes presented in each trial. In rewarded conditions, the target box contained a favoured food. Demonstrators were trained to open the target box, and the observer watched the demonstrator do this before their own trial. They found that reward for both the observer and the demonstrator was significantly more likely to result in the observer matching the choice of the demonstrator, versus a condition in which only the demonstrator was rewarded, and a condition in which neither the observer nor the demonstrator were rewarded.

However, the performance of the monkeys was significantly above chance even in these other two conditions, suggesting that direct reward is not the only factor mediating social learning (Bonnie and de Waal, 2007), and that the animals may be motivated to match behaviour even in the absence of rewards.

However, given that extrinsic reinforcers seem to be present in the majority of behavioural traditions, and given that rewards certainly seem to aid social learning in experimental contexts, it seems reasonable to seek alternative, more ecologically valid, nonfood reinforcers, that could potentially be used in social learning experiments investigating nonfood behaviours. In looking for reinforcers that might be valuably exploited within experiments on social learning in primates, it is worth examining the literature from other fields to see which nonfood reinforcers investigators have used to good effect.

Researchers have investigated and utilised nonfood reinforcers in asocial learning experiments. Reviewing the literature, Anderson (1998) has discussed the effectiveness of social stimuli and rewards in experiments on learning and cognition in primates, and concluded that “there is little doubt that social stimuli can be used as potent reinforcers for primates” (Anderson 1998, p. 160). Anderson (1998) showed that many studies had demonstrated the efficacy of visual access to live conspecifics, slides of conspecifics, and video of conspecifics.

The opportunity to be groomed by a human experimenter (Taira and Rolls, 1996) and also to groom the experimenter (Falk, 1958) have both been shown to operate as effective rewards for a rhesus monkey and a chimpanzee, respectively. Randolph and Brooks (1967) demonstrated that play, with a human experimenter, can also act as an effective reinforcer in a chimpanzee, for the conditioned response of a particular vocal call. Only if the chimpanzee gave a specific target call —a low guttural bark— would the experimenter turn toward the cage and engage in play with the chimpanzee. We consider this example to be particularly relevant here, as Randolph and Brooks (1967) were investigating the socialisation of vocal behaviour, and therefore they opted to use a social reinforcer to approximate the natural context of vocal responses in the wild.

Although the use of human experimenters to perform the reward is not ideal in terms of ecological validity, and presents significant practical issues, the aforementioned experiments still demonstrate the potential for using interaction, grooming, and play, as reinforcers in experiments. As well as in other fields of research, nonfood reinforcers are also routinely used in practical settings to motivate animals. It speaks volumes for the efficacy of nonfood reinforcers that professional animal trainers rely on them heavily. Animal trainers use nonfood reinforcers either as an alternative to food if an animal lacks the motivation to work for food (for some species, or certain individuals, social interactions and attention can be more rewarding than food), or simply to vary the rewards and maintain novelty (Pryor, 2002). Such nonfood reinforcers can include tactile reinforcement, e.g., a rub-down for marine mammals, or stroking for domesticated animals; social interaction; play or games or a desirable play object, e.g., a ball; and attention and/or vocal praise (Pryor, 2002). In the context of captive enrichment, Poole (1992) has proposed that exploration, curiosity-motivated behaviour, e.g., object manipulation, and play can be intrinsically rewarding activities.

Given the wide range of effective reinforcers other than food it is perhaps surprising that few, if any, researchers have used social reinforcers in experiments investigating social learning. Although replacing food reinforcers in social learning experiments presents practical issues, we believe that this approach offers significant potential benefits to those who are prepared to take up the challenge. Careful experimental design could counter many of the difficulties presented, e.g., individual variation in the level of motivation induced by a given reinforcer could be noted and taken into account at analysis. Social reinforcers may be particularly useful when investigating social behaviours that are likely to be reinforced socially in natural contexts.

2.3.4 Possibilities for Future Research

Several researchers have highlighted the possibility of experimentally investigating arbitrary social conventions and communicative behaviours. This new research direction presents new challenges. How can one study social and communicative behavioural traditions experimentally? I see a number of interesting possibilities for future research that will help to inform our understanding of natural social customs in primates.

First, and most basically, we need to know about what primates find reinforcing, other than food. Experimental research could readily test a wide range of possible stimuli to determine which function as effective reinforcers, and also their relative effectiveness in comparison with food rewards. This could help us to understand precisely what reinforces certain nonfood behavioural traditions observed in the field. Researchers could apply effective nonfood reinforcers in studies specifically targeted toward investigating the social transmission of social and communicative behaviours. For example, it might be possible to use social access as a reinforcer for a vocal response, similar to Randolph and Brooks' (1967) experiment, but perhaps involving conspecifics rather than humans. Communicative behavioural traditions are more likely to be rewarded with social access in the wild than they are with food, and therefore this might prove to be a more ecologically valid experimental design.

Also, as Whiten et al. (2003) suggested, it would be extremely interesting to replicate or expand on the experiment of Tomasello et al. (1997) attempting to investigate the social transmission of communicative behaviours. It is still an open question whether primates are capable of learning the meaning of a communicative behaviour through observation of conspecifics. Bonnie et al. (2007) have made important advances in this field, with their study of the transmission of arbitrary token exchange conventions. However, it would be interesting to investigate experimentally whether a two-action non-tool-use task, resembling an arbitrary gesture, could be socially transmitted within alternate groups using nonfood rewards (Whiten et al. 2005).

Whiten et al. (2005) and de Waal (2001) have suggested that the social reward of conformity may provide the impetus for copying others rather than the food reward. The type of conformity bias to which they refer is social conformity rather than frequency dependent conformity (see Table 1.1). One could directly compare the relative strengths of the different motivations by introducing a two-action tool use task to a group of primates via a demonstrator and then offering a greater food reward for the alternate, nonconformist action. Social reinforcers may be especially informative in investigating conformity. Communicative conventions are examples of coordination problems in game theoretical terms, i.e., it pays to be doing what others are doing (other examples typically given are the choice of the side of the road to drive on, or technological standards for product compatibility). Conformity bias, the tendency to adopt the group norm despite the discovery of alternative behaviours, might then be expected to be especially strong for social behaviours. This could be experimentally investigated by comparing conformity bias in food and nonfood behaviours and reinforcers, respectively.

Finally, one particular article identified in my literature survey is worthy of mention here even though it neither directly reported particular group-specific traditions nor involved experimental manipulation to investigate social learning in captivity because it offers particularly fascinating possibilities for future research. I have been concerned, in the current chapter, with the concept of culture as a set of discrete, group-specific behaviours, but it is important to note that there is an alternative, wider, conception of culture, introduced in Chapter one, termed social culture by Sapolsky (2006).

The change in cultural milieu that Sapolsky and Share (2004) observed seems to have been relatively permanent. Their study affords a window onto another intriguing experimental research opportunity, already outlined in Chapter one. De Waal and Johanowicz (1993) experimentally demonstrated a change in social culture. They grouped juvenile rhesus macaques, a species with high rates of aggression and low reconciliation rates, with stump-tailed macaques, a species with a more relaxed social style and high reconciliation rates (de Waal and Johanowicz 1993). The rhesus macaques in their study picked up on the social style of the stump-tailed macaques and reconciled at higher rates than would be expected for the species. However, they appeared to pick up on the general social atmosphere rather than directly imitating the stump-tailed macaques given that they used the form of reconciliation typical of their species rather than the stump-tailed form. Further, the juvenile rhesus macaques maintained this level of reconciliation even after being returned to a group of adult rhesus macaques (de Waal and Johanowicz 1993).

The experimental question is therefore whether a social culture, such as increased affiliative behaviour, can be facilitated in a captive population of primates through observation of other conspecifics performing affiliative behaviours. I aim to answer this question in Chapters five and six using the playback of auditory recordings of affiliative conspecific vocalisations; or of videos of conspecifics performing affiliative behaviour.

Several researchers have demonstrated that the vocalisations of groups of captive chimpanzees affect the behaviour of neighbouring groups via the neighbour effect or social contagion (Baker and Aureli 1996; Videan et al. 2005). Is it therefore possible that an affiliative social culture could be facilitated by showing videos of conspecifics performing affiliative behaviour or by playing auditory recordings of affiliative conspecific vocalisations? Such research could determine whether it is possible to influence behaviour in the long term, truly illustrating an effect of social culture.

2.4 Conclusion

I consider that social and communicative behavioural traditions in primates are extremely interesting for a number of reasons, and I have endeavoured to highlight the need for experimental research investigating them. My literature survey provided quantitative support for the observation that nonfood related behavioural traditions are relatively understudied compared with food related behavioural traditions and that food reinforcers overused, in experimental research on social learning in primates. I have suggested possible directions for future research on the topic, some of which are addressed in subsequent chapters.

Chapter 3

General Methods

In the current Chapter I outline, and provide justification for, the methods used in the subsequent empirical chapters of the thesis. I provide details of our study subjects, and the related housing and husbandry. Some of the material contained in this chapter has been published in a similar form in a published article (Watson and Caldwell, 2010) and in the related supplementary appendices available online.

3.1 Behavioural Research in the Laboratory

3.1.1 Advantages and Limitations

The over-riding advantage of carrying out behavioural research on animals housed in captivity is the precise control that the experimenter is able to exert over the experimental conditions, relative to a field context. The researcher is able both to manipulate the variables under investigation and, to some extent at least, to keep potentially confounding factors constant. Further, some experimental manipulations may simply be unethical or infeasible within a wild context.

For marmosets, the species investigated by the current thesis, there are severe limitations to field experiments not involving food because marmosets live arboreally, ranging widely and are therefore difficult to keep in sight for observation or in range for playback. Some innovative field experiments have been carried out on free-ranging marmosets (e.g. Pesendorfer et al., 2009). However, the study investigated a food-related behaviour and the marmosets were attracted to the experimental task apparatus by food.

A major limitation of laboratory studies is the extent to which they are ecologically valid: the extent to which the research relates to wild behaviour. Can the results of research on captive animals be extrapolated to wild populations? With respect to implications of the experimental work to the welfare of captive animals the conditions are valid since they are similar or identical to conditions in other laboratories and also to a large extent similar to other captive environments such as zoos etc.

Many behavioural studies in captivity involve isolating individuals from their social groups. For example, many studies have involved placing the marmoset in an unfamiliar cage and recording their behaviour (for example, their reaction to the introduction of an unfamiliar individual into a neighbouring cage: e.g. Cilia and Piper, 1997). The majority of vocalisation studies have involved the removal of marmosets from their home cage and transport to and relocation in a recording booth, either singly or in pairs (e.g. Pook, 1976; Goldmann, 2000; Yamaguchi, 2009). Because I was mainly interested in social behaviours and in order to maximise the ecological validity and relevance to captive welfare, I carried out all the experiments on marmosets housed in their usual social groups. I did not remove any individuals from their home cage or colony room. All focal marmosets in the studies were breeding adults housed socially either in breeding pairs or in family groups.

Although the observation of marmosets in their usual social milieu imposed some limitations, these were outweighed by the benefit of the increase in validity for the investigation of social influence and behaviours which was the main focus of this thesis. An example of a limitation (in Chapter four) is that audio recordings had a lot of background noise and could not be automatically processed (e.g. by discriminant function analysis). However, I was able to overcome this limitation by coding the audio recordings manually, according to mutually exclusive differences between call types in sound and visual spectrogram appearance (see section 3.4.4).

3.1.2 Ethical Implications

All three studies in the thesis (related in Chapters four, five and six) were approved by the University of Stirling Psychology Department Ethical Committee and complied with UK legal requirements, the guidelines (for the treatment of animals in behavioural research and teaching) of the Association for the Study of Animal Behaviour (ASAB) and the code of ethics of the Animal Behaviour Society (ABS).

3.2 The Marmosets: The Study Animals

3.2.1 The Common Marmoset (*Callithrix jacchus)*

Callithrix jacchus, the tuft-eared or common marmoset, is a species of New World monkey belonging to one of seven genera of the sub-family Callitrichinae of the family Callitrichidae. Marmosets are of very small size and weight (an adult in captivity weighs about 300g): the smallest of the anthropoid primates (Ford et al., 2009).

Callithix jacchus inhabits the Atlantic forest of north-eastern Brazil and is arboreal. The species is classified as Least Concern by the International Union for the Conservation of Nature and Natural Resources (IUCN, 2010). A contributory factor to the relative success of the species may be the wide range of habitat which it inhabits (including secondary forest, tree plantations and swamps) and the ability to rely on gum when fruit or other food sources are scarce. Plate 3.01 shows a marmoset in the wild.

Plate 3.01 Marmoset in the wild in Brazil.

Photo: Elspeth Reid

Common marmosets have a striking and attractive appearance. They have prominent large white tufts on the ears, alternating wide dark and narrow pale bands on their tail and a brindled black, brown and dark yellow pelage on their back (e.g. Buchanan-Smith, 2010). Plate 3.02 shows an adult marmoset.

Marmosets give birth predominantly to twin infants and rear their young cooperatively. Family groups consist of a single breeding pair and the adult and immature progeny. Breeding females inhibit the reproductive ability of co-habiting, socially subordinate females, through pheromones and social suppression (e.g. Saltzman et al., 1997).

Marmoset young are reared cooperatively within these extended family groups (e.g. Stevenson and Rylands, 1988).

Here I have provided a brief overview of the biology of the common marmoset. There is much existing literature providing thorough coverage of the biology of the common marmoset (see for example: Stevenson and Poole, 1976; Stevenson and Rylands, 1988; Rylands, 1993; and most recently: Ford et al., 2009).

3.2.2 Justification of Choice of Study Species

The common marmoset is well suited for the investigation of social influence, social behaviours and social culture for a number of reasons. As cooperative rearers common marmosets are socially tolerant and prosocial with a strong tendency to attend to other individuals in their group (e.g. Burkart and van Schaik, 2010). For these reasons they may expected to be particularly susceptible among non-human primates to social contagion.

With regard to potentially providing insight into human evolution, the study of marmosets presents a unique comparative perspective within living primates (Burkart et al. 2009a). Burkart (2009a) proposed that cooperative breeding may directly improve social cognition through increased spontaneous prosociality and drew parallels between humans and Callitrichids.

If one of the evolutionary/ultimate functions of social contagion is to increase or coordinate cooperation (e.g. Clayton, 1978) then it would be best to study this phenomenon in a highly cooperative species. The common marmoset is cooperative relative to other nonhuman primates (Burkart and van Schaik, 2010) cooperating in parental care, antipredator behaviour and in territorial defence (e.g. Stevenson and Rylands, 1988; Digby et al., 2007).

The results of theoretical modelling suggest that a particular trait is more likely to be maintained within a population, through social learning, if learners have numerous "cultural parents", for example through alloparenting or cooperative rearing (Enquist et al., 2010). This may have parallels for the maintenance of social culture. Since young marmosets have more than two cultural parents through alloparenting this may mean that changes in social culture are more likely to be maintained in marmosets than in species with a lower number of cultural parents. Marmosets are carried by group members other than their mother almost as soon as they are born (e.g. Yamamoto, 1993), providing a strong opportunity for social influence from alloparents.

The common marmoset is an ideal species for the investigation of social contagion through neighbour vocalisations (an effect which is investigated by observation in Chapter four and by experimental manipulation in Chapter five). Vocalisations play a very important role in both intergroup and intragroup communication in wild marmosets, especially as the dense vegetation in which they live makes visual communication difficult (e.g. Epple, 1968). Marmosets are known to retain a large proportion of their natural vocal repertoire in captivity and call frequently (Pook, 1976). Marmosets are also particularly suited as subjects for the investigation of the contagion of alarm because, being small and vulnerable to predation, they spend much of the day engaged in alarm-related and vigilance behaviors (e.g. Hankerson and Caine, 2004).

In addition, marmosets present several practical advantages as a study species. First, due to their relatively rapid rate of breeding (e.g. Tardif et al., 1984), and to the fact that their small body weight makes them economical to house and comparatively easy to handle (e.g. Buchanan-Smith, 2010), they are kept in large numbers in research laboratories. I had access to a large sample size at a nearby research facility, which allowed relatively high statistical power. Second, the conditions in which laboratory marmosets are housed allows a high degree of control over experimental conditions (see section 3.1 above). Lastly, in relation to the welfare issues that we investigated in the current thesis, the results are likely be applicable to a range of captive settings (as stated above) and because common marmosets are used frequently and widely for research in laboratories, any enrichment methods developed here have the potential to benefit a large number of individuals.

3.2.3 Study Subjects

All the marmosets used for the research carried out for the thesis were housed at the Medical Research Council Human Reproductive Sciences Unit, in Edinburgh. This facility maintains a captive population of around 300 individuals. All study animals were bred in captivity (over multiple generations): most individuals were born within the MRC but a few individuals were born at Harlan Laboratories (Shardlow, England). Further housing and husbandry details are given in section 3.3.

In order to help staff identify each marmoset an identity tag, a chain from which hangs a coloured metal disk with the identity code engraved, is placed around the neck of each marmoset (Plate 3.02). The colour of the tag relates the sex and birthplace of the individual (MRC-born individuals: older males, black (Bk); younger males, green (g);

females, yellow (y); Harlan-born individuals: males, blue (BB); females, white (no symbol). The identity code relates to their order of birth relative to others of the same sex wearing the same colour tag within the facility. The identity code and colour were used to identify each study animal used in the experimental studies (e.g. 145y: with y indicating yellow). The identity of each study animal used is listed in tables within the relevant chapters (Chapters four, five and six respectively).

Plate 3.02 Identity tag hanging from a chain round the neck of marmosets: (i) older male 805bk; and (ii) female 409y.

(i) **(ii)**

For the purposes of this thesis I defined the developmental stages of the marmoset as follows: infants aged 56 days (8 weeks) or less; juveniles aged 304 days (10 months) or less, but more than 56 days; and adults aged over 304 days (following: Ingram, 1977). Other researchers have divided the developmental stages differently. Yamamoto (1993) classifies marmosets of up to 5 months as infants, of 5-10 months as juveniles, and she divides marmosets of over 10 months into sub-adults (under 15 months) and young adults (of over 15 months). However, Badihi (2006) states that marmosets raised in captivity appear to pass the stage of constant dependency on the adults (the stage during which they are carried everywhere on an adult’s back) earlier than their wild counterparts. Plate 3.03 shows example images of each of the three age groups. All focal individuals observed in the studies were breeding adult marmosets. The age of focal marmosets at the start of each study ranged from 1 year 137 days to 17 years 211 days. Behavioural research was carried out on the study animals between March 2008 and September 2010.

3.3 Housing and Husbandry

3.3.1 Housing

All the study animals were housed within five caged colony rooms. Marmosets filmed for the stimulus video (Chapter six) were housed in two large uncaged rooms. The housing is subject to an artificial light cycle of 12 hours (07.00 - 19.00 with 10 min light dimming at the transition between light and dark). Natural light also enters the large rooms through windows to the exterior of the building and marmosets in the caged rooms have access to natural light when access to roof-top runs is provided, through plastic tubes, March-October (see plate 3.06). All housing is maintained at a temperature of between 21 and 25 degrees Celsius and at a humidity level of 53-55%.

Plate 3.03 The three developmental stages of *Callithrix jacchus* used in the current thesis: (i) two juvenile marmosets; (ii) an infant marmoset is carried on the back of an adult marmoset.

(i) **(ii)**

Housing in Home Cages Within Colony Rooms

Each colony room (4.5m wide by 6.5m long) contained two rows of four cages along the two longest facing walls. Each full size cage measured approximately: 1.1m deep by 1.5m wide by 2.3m high (Plate 3.04). Half sized cages were created for smaller groups of marmosets by dividing the full size cages in two, by inserting a removable opaque plastic divider, creating two half-size cages with similar dimensions overall but half as wide. Each home cage contained a stainless steel nesting box. Home cages were furnished with log to facilitate gouging and locomotion (Plate 3.05 (i)). At least one rubber matting platform (a section of rubber safety matting attached to the wire mesh of the cage using trimmed cable ties) was provided per cage to facilitate allogrooming (see plate 3.05 (ii)). Each home cage had a stainless steel metal dish containing dry pellet diet and a plastic bottle to dispense water, mounted on the internal side of the wire mesh. The cage floors consisted of two parallel metal trays, easily removed to facilitate cleaning, which were covered with a thick layer of sawdust to encourage foraging (see section 3.3.2).

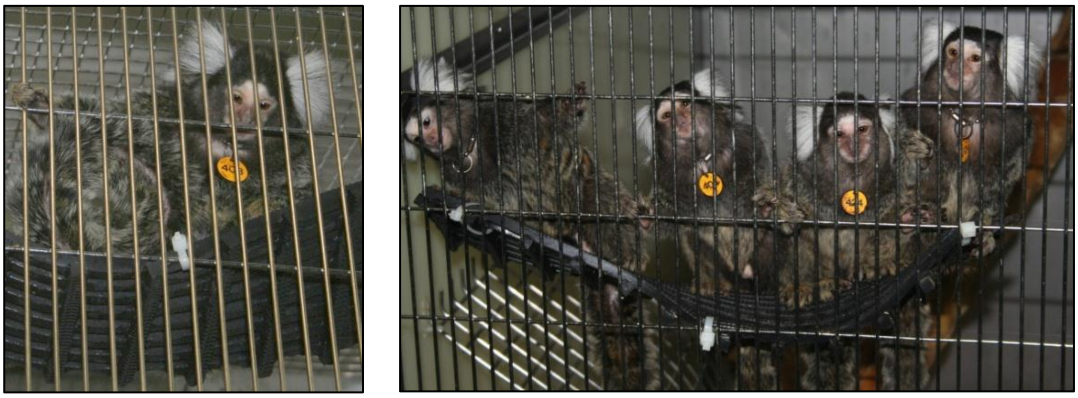
Marmosets were housed in pairs, family groups or same sex groups. The marmosets were in auditory (and olfactory) contact with the other groups in the same colony room and in visual contact with those individuals housed in the cages directly opposite to them. Marmosets were sometimes able to hear marmosets in other rooms. Members of staff could be heard and occasionally seen by marmosets in the colony rooms as they carried out their work.

Within three of the colony rooms, two groups at a time had access to separate enclosures in the roof-top run, through plastic tubing connecting the runs to the cages. Pregnant females and infant marmosets were not given access to roof-top runs because constant access was required for monitoring their health.

Plate 3.04 Home cage with plastic divider in place to create two half-size cages for small groups.

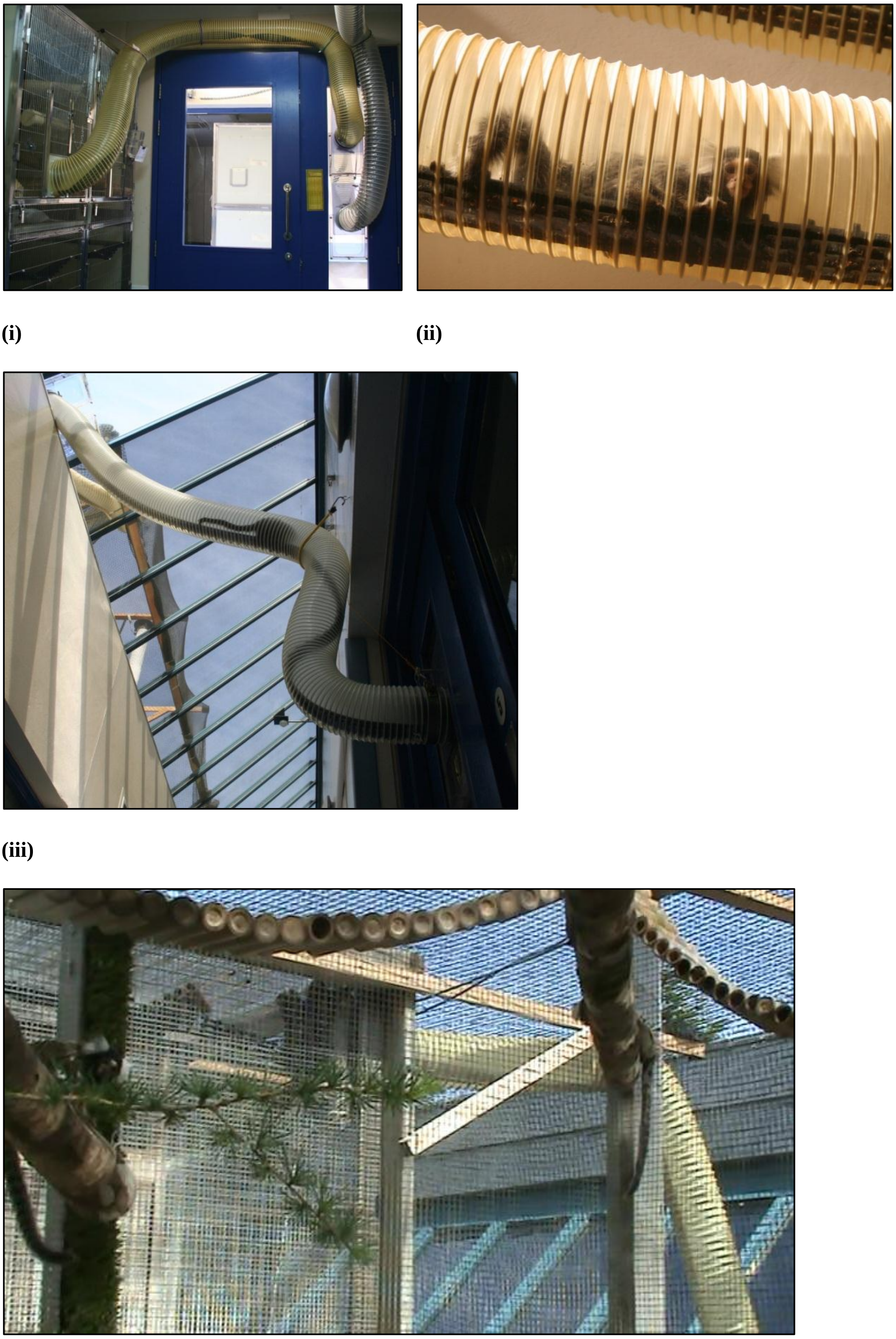
Plate 3.05 Home cage environmental enrichment: (i) logs for locomotion and gouging; (ii) rubber safety matting perch to encourage allogrooming and rest.

(i)



(ii)

Plate 3.06 Outdoor roof-top runs: (i) connections from home cages in colony rooms to the tube leading out of the colony room door; (ii) close-up of marmoset on rubber ladder inside tube; (iii) tube from colony room door, through the roof, to an individual roof-top run; and (iv) roof-top run itself with entrance tube from roof of building visible.



(i)

(ii)

(iii)

(iv)

Housing in Large Rooms

Four groups of about 10 marmosets were housed in large rooms. I filmed two of these groups to provide video footage as stimuli for the video playback study in Chapter six. These large rooms each have a window to the exterior of the building, an internal window looking onto the corridor and a door. Plate 3.07 shows the view from the laboratory through the internal window looking into a large room: the external window can be seen at the rear of the room. These large rooms were equipped with various environmental enrichment structures (Plate 3.07) and the large size of the room relative to the home cages facilitated natural leaping behaviour (Plate 3.08). In the rooms marmosets engaged in interaction with staff and with the experimenter, who wore surgical scrubs, rubber boots and sterile gloves to prevent disease transmission (Plate 3.09).

Plate 3.07 Large rooms, in which marmosets were filmed allogrooming (Chapter 6), showing wooden nest box and environmental enrichment of the physical room structure.

Plate 3.08 Housing in the large rooms provides space for natural leaping behaviour.

Plate 3.09 Marmoset/human interaction: on human lap (i) playing and (ii) resting.

(i)

(ii)

Positive human interaction provides enrichment (e.g. Waitt et al., 2002; Rennie et al., 2006) and also allows marmosets to cope better with laboratory husbandry and other procedures (Basset et al., 2003).

3.3.2 Husbandry

Cleaning

The floor of each caged colony room was cleaned daily, on week days, between 08.30 and 10.30. Floors were cleaned with water and disinfectant three times weekly: on Monday, Wednesday and Friday; and swept of dry debris twice weekly: on Tuesday and Thursday. The covering of sawdust on the floor of each home cage was replaced weekly on Monday. Home cages were washed once a month in a cage washing machine. Within three of the colony rooms two groups at a time had access to roof-top runs (see Plate 3.06). The access was rotated around the groups within the rooms with access during monthly cage cleaning when the tubes were also washed and disinfected. The large housing rooms were thoroughly cleaned once every 6-8 weeks. Food dishes and uneaten food were removed daily from the cages and large rooms.

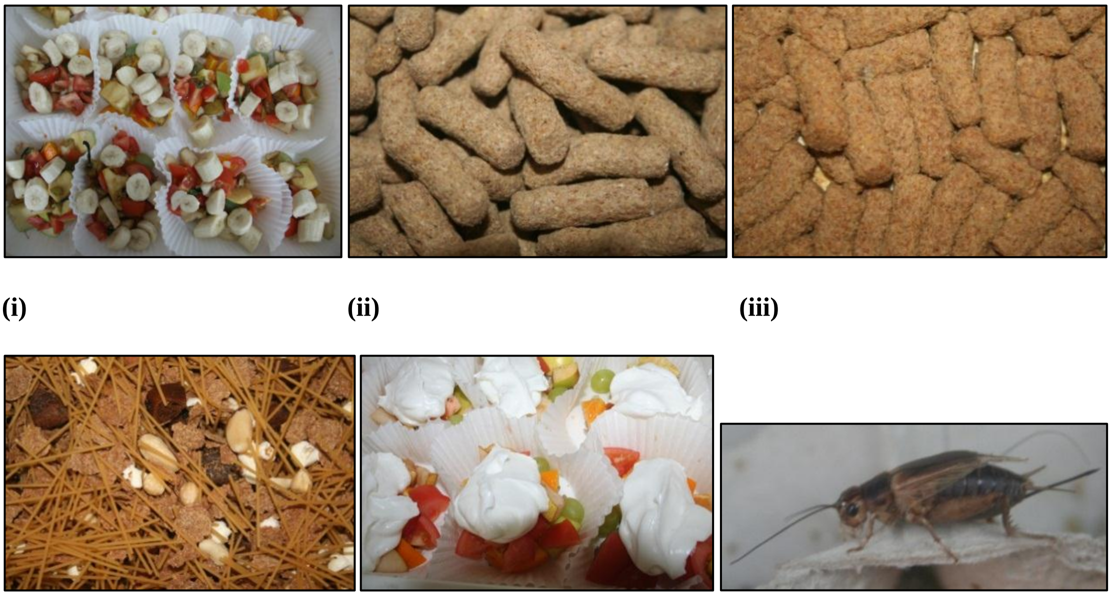
Feeding

The marmosets were fed daily on a diet consisting of a mixture of fresh fruit and vegetables. This was supplemented every other day with: commercially available pellet diet soaked in sugar-free Ribena™; dried fruit and whole peanuts in their shells; or with ‘porridge’ (a mixture of plain yoghurt and baby rice with supplements: Casilan 90 protein powder, vitamin D and Complan™). The diet was varied on different days of the week to prevent boredom with the diet; Table 3.1 shows the varied feeding schedule and Plate 3.10 displays the different dietary items. A scatter feed (Plate 3.10) consisting of a mixture of bran flakes, dry spaghetti, mixed whole nuts, chopped malt loaf and plain popcorn was added to the sawdust used to cover the cage floor and which is replaced weekly on Monday. Water and commercially available pellet diet were available ad libitum (dishes containing dry pellets and water bottles had their contents replaced weekly on Monday and topped up weekly on Friday).

Table 3.1 Daily variation in the marmoset weekly diet.

	Day						
Food item	Monday	Tuesday	Wednesday	Thursday	Friday	Saturday	Sunday
chopped apple	✓	✓	✓	✓	✓	✓	✓
chopped pear	✓	✓	✓	✓	✓	✓	x
chopped banana	✓	✓	✓	✓	✓	x	✓
chopped tomato	✓	✓	✓	✓	✓	x	x
grapes	✓	✓	✓	✓	✓	✓	✓
chopped orange	x	x	✓	x	x	✓	✓
chopped cucumber	✓	x	x	✓	x	x	x
chopped carrot	x	✓	x	x	✓	x	x
raisins	x	✓	x	✓	x	✓	✓
dates	x	✓	x	✓	x	✓	✓
peanuts in shells	x	✓	x	✓	x	✓	✓
pellet diet soaked in jelly with Ribena™	x	✓	x	✓	x	x	x
‘porridge’	✓	x	✓	x	✓	x	x

Plate 3.10 Marmoset Diet: (i) freshly chopped fruit; (ii) dry pellet diet; (iii) soaked pellet diet; (iv) forage/scatter feed (v) fruit with ‘porridge’; and (vi) a live cricket.



(i) **(ii)** **(iii)**

(iv) **(v)** **(vi)**

Live insects such as crickets and mealworms are provided for the marmosets to catch and eat once every several months; this provided enrichment through promoting natural pouncing behaviour (Plate 3.11) as well as dietary protein (e.g. Vignes et al., 2001).

Plate 3.11 Live insects provide enrichment as well as nourishment: (i) marmosets watching live crickets (ii) marmoset eating mealworm that he has caught.

(i) **(ii)**

Monitoring

Each marmoset was checked visually three times daily, on week days, for physical injury, births and deaths at 08.30; at 12.30; and at 16.45 (15.15 on Fridays). On weekend days and public holidays each marmoset was checked visually once daily. Marmosets were also examined physically whenever they were manually caught. They were caught for a variety of reasons. First, monthly to enable cage washing. Second, their identity tags were checked and cleaned approximately every two months. Third, females are caught and manually palpated to determine whether or not they are pregnant. Fourth, pregnant females were often required to be removed from their home cage to allow staff to loosen or remove their identity tag during the later stages of pregnancy, due to their increase in body size. Fifth, marmosets in early developmental stages are caught and weighed at regular intervals to assess growth rate and general health: infants are caught and weighed at 20 days old and at 40 days old and as juveniles: at 60 days old; and at 80; 100; 120; 140; 160; 180 and at 200 days old. Sixth, marmosets are caught for physical inspection if they are injured or physically unwell. Lastly, any individuals that are experimental subjects for MRC studies may be caught for blood sampling, dosing or ultra-sound scanning. Procedures are generally done in the morning before 13.00.

3.4 Behavioural Observation and Coding

All the studies carried out in this thesis involved observation of marmosets housed in home cages. In the current chapter I describe methodological details that apply to all the studies (reported below in Chapters four, five and six). Methodological details that apply to particular studies only are reported within the methods section of the relevant chapter.

3.4.1 Observational Procedure

A minimum of 5 days of habituation (to me as an observer) was carried out before each study. As the observer, I did not interact before or during the studies either positively or negatively with the study marmosets in these rooms in order to maintain a neutral relationship and therefore minimise the observer influence on the experimental results (e.g. Rennie and Buchanan-Smith, 2006). I also dressed in a uniform of a different colour to that of laboratory staff since non-human primates are known to distinguish visually between different humans, and by extension their attendant associations (e.g. Waitt et al., 2002). Rennie and Buchanan-Smith (2006) have recommended that a very visible method of visual recognition be employed by individual humans to facilitate identification of the individual by the primates and I employed this method here to identify myself as a neutral observer.

During each observation period I sat about 1.4 m from the cage housing the focal individual. To minimise disturbance to the subjects, the observer sat quietly for 5 min after entering the room (and following the initial setup of any moving equipment in each room) and for 2 min after movement of the observer (and of the equipment where relevant) between cages. Data were collected using a Psion Workabout (a handheld computer) running real-time event recording software (Observer 5; Noldus Information Technology, Wageningen, The Netherlands). I counterbalanced the order in which the focal individuals within each room were observed and also the time of day that observations were carried out in each room. Observations were made in four sessions (Chapter four) and in eight sessions (Chapters five and six), between 08.30 and 16.30, with each room being observed on an equal number of occasions in each of the sessions. Counterbalancing was considered to be especially important as the frequency of particular behaviours is known to be subject to diurnal variation (e.g. vocalisations: Jones, 1993). No observations were carried out in the 30min following daily feeding at 12.30.

Observation Session Duration

The observation length was set at 5 min in all studies. I decided on this length of time in order to balance the benefits of increased sample size with the necessity to sample behaviour over a sufficient time period.

Sampling Method

A continuous focal sampling method (Altmann, 1974; Martin and Bateson, 2007) was used to record the behavioural states and vocalisations of focal individuals in all the studies. Thus each focal individual was observed for 5 min at a time.

Multiple Focal Individuals in Same Group

I was unfortunately unable to draw all focal individuals from distinct social groups due to constraints of the laboratory setting, although there were no more than two focal individuals in any one focal group. My only practical alternative would have been to reduce the overall sample size. I did not consider that the issue of multiple focal individuals within the same social group would affect the results of the analyses substantially. For the two studies with a between subjects design (see Table 3.6) the number of focal individuals that were either one or two to a group were equalised, as far as was practically possible, between the experimental and control condition. For the long-term auditory playback study (Chapter five), the division was almost equal (control condition: two focals/group, n = 12, one focal/group, n = 4; experimental condition: two focals/group, n = 14, one focal/group, n = 2). All the focal individuals observed for the long-term playback study (Chapter six) were two to a focal group.

For the within subjects study investigating the contingent effect of visual playback of allogrooming (Chapter six) I used only focal individuals housed in separate focal groups. The two other studies of within subjects design (see Table 3.6) used at least some focal individuals housed in the same focal group. There was no risk of bias between conditions but focal individuals housed within the same focal group are not as clearly statistically independent as those housed in separate groups. However, take this to its logical extension and individuals housed in separate groups but within the same colony rooms are not completely independent of one another statistically, especially given that some are directly related. Data independence can be viewed as being on a continuum from completely independent to extremely dependent (Wehnelt et al., 2005). It is often not possible to sample totally independent data points in behavioural research. While two focal individuals in the same group cannot be considered as absolutely independent statistically neither are they very dependent. For the within subjects design neighbour effect study (Chapter four) less than half the focal individuals were housed with another focal individual. The within subjects design study investigating the immediate effect of chirp playback (Chapter five) had 14 focal individuals housed two to a focal group and two focals housed one per focal group. The results of this analysis may have been compromised and so the results of this analysis should be treated with caution. A reanalysis taking the mean for each pair of focals housed in identical focal groups as one data point could be carried out, but is likely to have unacceptably low statistical power given the low effect size to be detected and the reduced sample size considering that it would have to be carried out on only 9 data points.

Intra-rater Reliability

To evaluate intra-rater reliability for the live coding, a number of additional 5- minute sessions were videotaped (1%) during the neighbour effect study (Chapter four). These sessions were coded, as live observations, twice over two consecutive days by the observer. Intra-rater consistency assessed using the k correlation coefficient (Cohen's kappa) fell into the range considered by Fleiss (1981) as 'excellent' (duration/sequence based: k coefficient = 0.98; frequency/sequence based: k coefficient = 0.88).

3.4.2 Selection of Behaviours and Vocalisations

The definitions and behavioural categories (categories of affect: intergroup and intragroup agonism, affiliation, and anxiety; see below) of non-vocal behaviours mentioned in this section and coded in this thesis are tabulated in Table 3.3, section 3.4.3, and of the coded vocalisations are listed in Table 3.4, section 3.4.4. I selected behaviours and vocalisations for study based on two criteria. They were selected first as indicators of the four behavioural categories (henceforth referred to as affect categories) investigated in the current thesis: intra and inter-group aggression, affiliation and anxiety (all four affect categories in Chapter four, and in Chapters five and six affiliation only with aggressive and anxious behaviours investigated only as 'non-matching' behaviours, see below). Behaviours were chosen according to proposed functions and observed contexts given in the relevant literature. In some cases behaviours may be indicative of two types of affect (e.g. agitated locomotion may be indicative of anxiety and/or aggression) and in such an instance the behaviour was selected according to the predominant affect with which they are associated in the literature.

Second, they were selected for reasons of practicality involving the level of accuracy of recording that was possible. During the live coding (in Chapters four and five), as the observer, I had to be able to localise vocalisations easily to a particular individual by sight, so we chose only those calls made with the mouth open or partially open. Additionally, in Chapter four, during the video coding, all open mouth calls had to be distinguished easily, reliably and consistently from similar calls, not exclusively made with an open mouth, on the basis of examining the spectrogram visually and listening to the call (e.g. chatter is distinct from the spectrographically related calls: cough and ek).

For example, ‘ek’ (Pook, 1976) appears to indicate mild alarm, is a call made with the mouth half open, and it is easily distinguishable from spectrographically related calls: cough (the ek has much less noise character); and angry chatter (the ek has longer duration elements). Phee calls that were over 1.3 sec in length were coded and labelled as loud shrill calls to ensure that only open-mouthed phee calls were coded (Phees of that length are consistently made with the mouth open: for a more detailed explanation see Appendix B). Table 3.4, in section 3.4.4, lists the visual and spectrographic coding definitions of the eight calls coded in the studies in Chapters four and five.

Pilot studies indicated that it was possible to localise all selected call types to a particular focal individual. Localising calls to particular individuals can be difficult. Some of the calls are made with the mouth wide open and are very loud which makes it much easier to tell who is vocalising. However, other calls are made with the mouth closed and these calls are also quiet. In these cases looking for abdominal contractions can help to identify which individual is calling.

Localisation of calls to a particular individual was facilitated by the fact that calls are predominantly made during low activity or when the individual is stationary (Pook, 1976). Experienced listeners in previous studies have successfully isolated particular call types to specific individuals e.g. open mouth phee calls (roughly equivalent to loud shrill in the current study and presumably completely equivalent to Pooks’ loud shrill) (Norcross and Newman, 1993).

The localisation of the whirr call to a particular individual may not have always been reliably achieved, because the call is made with the mouth closed. Abdominal contractions indicate when this call is made but some of the calls made by the focal individual may not have been picked up. However, this call is an important affiliative call and as such it was considered important to code the call in order to assess the approximate call rate.

Affect Categories

The categories of affect of behaviours coded in the thesis were intergroup and intragroup agonism, affiliation, and anxiety. The affect category of each non-vocal behaviour is listed in Table are tabulated in Table 3.3, section 3.4.3, and of the coded vocalisations are listed in Table 3.4, section 3.4.4.

Intergroup Agonism

Behaviours found to be associated with agonistic threat in wild intergroup encounters include scent marking, anogenital displays and piloerection (e.g. Hubrecht 1985; Lazaro-Perea, 2001). These behaviours have also been observed in agonistic contexts in captivity (Stevenson and Poole, 1976). Epple (1970) highlights anogenital presenting as the best aggressive threat signal for the purposes of quantitative behavioural observation. Anogenital presenting is only rarely observed between individuals in the same group (e.g. Epple, 1970). Individuals in the current study were unable to make physical contact with other groups so no aggressive behaviours involving direct intergroup contact were possible. Intergroup aggressive behaviours coded in this study were therefore: anogential presenting; scent marking and ‘bristle’.

Many studies have shown piloerection to be associated with aggressive contexts (e.g. Stevenson and Poole, 1976) but it can reflect the anxiety associated with the situation as well as the aggression (Cilia and Piper, 1997). ‘Bristle’ has been defined, more specifically, as the full erection of body pelage (with or without the erection of tail pelage) and appears to be particularly linked to aggressive behaviours (Stevenson and Poole, 1976; Stevenson and Rylands, 1988). Bristle was chosen instead of the more general piloerection for this reason and because it was determined from the pilot study that it would be the most reliable form of piloerection to record since the observer was focusing mainly on the abdominal and mouth area of the focal individual in order to reliably record all vocalisations made by them. It was considered that tail pelage erection alone or semi-piloerection would have been less reliably and consistently recorded.

Both loud shrill calls and twitter calls have been noted during aggressive intergroup interactions both in the wild (e.g. Hubrecht, 1985: along with tsik calls) and in captivity (e.g. Gerber and Schnell, 2004). Loud shrill is the loudest call in the *Callithrix jacchus* repertoire (Epple, 1968) and is therefore the call best suited to long range communication. Norcross and Newman (1993) established that there are two different types of open mouth phee calls (loud shrill) according to the context in which they are produced: home-phee calls made by non-isolated marmosets in territorial contexts; and isolation phee calls made only by marmosets isolated from members of their social group or pair. Since none of the individuals in this study were isolated it could be assumed that all the loud shrill calls produced were territorial intergroup calls. Epple (1968) notes that loud shrill calls were heard in dialogues between groups of marmosets in association with twitter calls and behaviours indicative of aggression (such as anogenital presenting). Pook (1976) noted that loud shrill was predominantly used in communication between groups in different rooms but within auditory contact. Epple

(1968) has conjectured that the loud shrill may function to communicate the occupation of a territory to nearby groups.

Pook (1976) noted that twitter calls were made during loud shrill exchanges between groups, sometimes accompanied by scent marking and piloerection displays. Jones (1993) concludes that the twitter call is mainly an intergroup confrontational call, used when neighbouring groups are within visual contact. Jones also notes that twitter occurs in the context of social play between juveniles and suggests that this use may give these individuals experience of behaviours that they will use as adults in intergroup confrontations. Increased rates of twitter calls have also been recorded when food is anticipated (e.g. Jones, 1993; Goldman, 2000) and this may function to gather marmosets at feeding sites. The main function of the twitter call appears to be as an intergroup agonistic call.

Intragroup Agonism

Behaviours chosen as indicative of intragroup aggression were ‘chase’, ‘attack’ and ‘steal food’ (see Table 3.3 for behavioural definitions). ‘Angry chatter’ has been heard during wild intergroup encounters but in a captive environment appears to be mainly used during intragroup aggressive encounters involving food and emitted by the animal holding the food as an aggressive threat to an approaching animal (Pook, 1976; Epple 1968). Epple (1968) noted that it was also observed in females attempting to avoid unwanted copulation attempts.

Affiliation

Behaviours chosen to index affiliation were ‘allogrooming’, ‘grooming invite’ (when an individual ‘flops’; stretches out on their back or side it frequently elicits allogrooming (Stevenson and Rylands, 1976), ‘active affiliative contact’, ‘social play’ and ‘share food’. Of the chosen behaviours, social play is the most controversial because its adaptive function remains unclear, and due to the difficulty defining it owing to variability of the behaviour within and between species (e.g. Burghardt, 2005; Held and Spinka, 2011). However, in marmosets it is clearly delineated in the species ethogram, is identified visually by high activity non-aggressive contact with other individuals, and easily distinguished from aggressive contact by a lack of anxious, submissive or aggressive calls by either individual and the observation of pouncing, playful wrestling and inhibited bites (e.g. Stevenson and Poole, 1979, Stevenson and Rylands, 1988). During studies, I often observed social play in the form of relatively long bouts between juvenile individuals (personal observation).

The whirr call was referred to by Epple (1968) as a close contact call. Jones (1993) describes it as the most predominant call type in the vocal repertoire. Jones (1993) found that the whirr call rate increased with increased intragroup spacing (decreased physical and visual contact) and she concluded that the function of this call is most likely to keep track of where other group members are located. However, she also noted that the whirr might serve to form and maintain affiliative bonds since she found an increased call rate in newly formed pairs. Thus the function of the whirr call is not conclusive but it does appear to be made in affiliative contexts, thus its frequency of occurrence was recorded. The whirr calls appears to be used for intragroup communication since bouts are exchanged between group members (Jones, 1993).

The chirping call has mainly been referred to in the literature as a call used in affiliative and pleasurable contexts. Stevenson and Rylands (1988) classify chirping as amicable and given only to group members in close contact e.g. when resting in close contact but also in sight of food. Epple (1968) describes the calls as being given in close visual and bodily contact or when almost satiated with a lot of desired food. Goldman (2000) reported that chirping was uttered mainly in non-threatening, affiliative, social contexts. Pook (1976) describes chirping as being predominantly made in the excitement of food presentation but also in some aggressive contexts. In the current study, chirping was classified as an affiliative call because the majority of existing literature, and all published reports, classify it in this way.

Anxiety

Cilia and Piper (1997) identify a number of marmoset behaviours as indicators of anxiety in individuals, including self-scratching and self-grooming, thought to be displacement activities reflecting the individual’s anxiety, and also scent marking. Agitated locomotion indicates stress in marmosets (e.g. Badihi, 2006) and as such can be considered as indicative of anxiety in stressful situations, whether in submissive or aggressive contexts. Because of the association with aggressive circumstances, agitated locomotion may not be as reliable an indicator of anxiety as the other behaviours coded. In this thesis I used ‘self-scratch’, ‘self-groom’ and ‘scent mark’ as behavioural indicators of anxiety in addition to ‘agitated locomotion’ and ‘inactive alert’ (whether the marmoset is some distance from or in contact with another individual). Because the cage environment is restricted in terms of space and resting areas (e.g. as compared to the large rooms), marmosets being situated in close proximity to each other, but not engaged in any active affiliation, does not necessarily imply affiliation (Buchanan-Smith, personal communication). For this reason the distance from another marmoset is not taken into account for either ‘inactive alert’ or ‘inactive rest’ (see welfare indicators, Table 3.2 and 3.3).

The ‘ek’ call has been described as indicative of mild alarm (Epple, 1968; Stevenson and Rylands, 1988). Pook (1976) notes that ‘ek’ appears to indicate that an individual is unsure of the degree of potential danger that a particular situation presents. Here ‘ek’ is coded as an anxious call.

‘Tsik’ calls issued singly indicate alarm (e.g. Pook, 1976). They are heard in the context of predators and sometimes in intergroup conflict (Stevenson and Rylands, 1988). Tsik calls are made more frequently with increasing alarm/excitement (Epple, 1968). Tsik calls are also referred to as ‘mobbing calls’ (Epple, 1968) when issued in rapid succession. Tsik calls vocalised in this manner sound almost monosyllabic to human ears (Epple, 1968) and this has been classified as a different call in many studies (e.g. Pook, 1976; Stevenson and Rylands, 1988). Here I draw a similar distinction referring to the mobbing call, tsiks in close succession, as ‘rapid-fire tsik calls’ and to singly uttered tsik calls, simply as tsik calls. Tsik calls are indicative of anxiety but rapid-fire tsik calls indicate an increased degree of anxiety (e.g. Epple, 1968). Rapid-fire tsik calls were coded for the study in Chapter four, but were excluded from analysis because they were produced by marmosets in such a small number of observations.

Captive Welfare: Behavioural Indicators

Lastly, certain behaviours were also coded in all studies in the current thesis to allow assessment of the welfare of the focal individuals through behavioural indicators (with the exception of gouge which was not coded in Chapter four). Table 3.2 shows the behaviours used as indicators of positive and negative welfare. The behaviour self-groom is not considered a reliable indicator of negative welfare (e.g. Badihi, 2006). However, we coded self-groom in Chapter six to allow us to assess whether the video playback of conspecifics allogrooming influenced focal marmosets to increase allogroom only (as we predicted) or also self-groom (which as a self-directed behaviour may indicate negative welfare; e.g. Cilia and Piper, 1997).

Table 3.2 Positive and negative welfare indicators (desirable/positive (elevated levels indicate positive changes in welfare) and undesirable/negative (elevated levels indicate negative changes in welfare) behaviours for captive for *Callithrix jacchus* (adapted from Badihi, 2006). Asterisk (*) indicates behaviour not coded in Chapter four.

Positive	Negative
Allogroom	Scent Mark
Calm Locomotion	Self-scratch
Inactive Rest	Agitated Locomotion
	Inactive Alert
	Gouge*

3.4.3 Behavioural Definitions: Non-vocal Behaviours

Table 3.3 lists the definitions that were used for each behaviour coded in the thesis, under each behavioural category, and Plate 3.12 shows image stills of most of the behaviours.

Table 3.3 Definitions of behavioural terms used during live coding, with behavioural category.

Behavioural category	Term	Definition
Intergroup agonistic	Anogenital present	Individual presents genitals whilst raising the tail.
	Bristle	Individual displays full body piloerection (body pelage fully erect).
Intragroup agonistic	Steal food	Individual takes food directly and rapidly from another individual (often chased by the individual they have stolen from).
	Chase/Attack	Individual pursues another individual aggressively or Individual lunges at, or either attempts to or does: bite, cuff or scratch another individual (usually chastisement of infants and aggression towards adults).
Affiliative	Share food	Individual shares food (in their hand or mouth) or allows food to be taken when another reaches towards them with hand or mouth (tolerated scrounging). No aggressive or threatening behavior is seen.
	Grooming invite	Individual stretches out on back or side next to another individual: frequently elicits allogrooming.
	Allogroom	Individual cleaning the fur or skin of another individual using hand or mouth.
	Active affiliative contact	Individual performs affiliative contact (excluding allogrooming) towards another individual: nuzzling (rubbing muzzle) and licking (including the anogenital area) or body hug.
	Social play	Individual is engaged in high activity interaction with another individual involving non-aggressive playful contact (e.g. wrestling).
Anxious	Agitated locomotion	Individual is moving rapidly between locations (walking, running, climbing or jumping) with an exaggerated gait (excluding play). Their tail may tail either extended or rigid/arched.
	Inactive alert	Individual is stationary, awake and attentive to their surroundings. Individual may or may not be in close passive physical contact to another or other individuals.
	Self-scratch	Repeated movement of the individuals hand or foot with claws drawn rapidly across fur.
	Self-groom	Individual cleans their fur or skin with their hands or mouth.
	Scent mark	Individual rubs sternal or anogenital area over substrate.
	(Vertical flight)	Sudden startled and direct movement to upper section of cage followed by freezing: startle response.
Other	Feeding	Individual is chewing food.

	Active foraging	Individual is actively searching for food with hand(s) (in the bottom tray, pellet dish or food tray).
	Visual foraging	The direction of gaze of the individual appears to be focused on the pellet dish, food tray or on the sawdust on the cage floor and the individual appears to be visually scanning a small area.
Welfare indicators (additional)	Inactive rest	Individual is stationary with a relaxed facial expression and with eyes closed or open, usually with the tail curled around their body or through their legs. Individual may or may not be in close passive physical contact to another or other individuals.
	Calm locomotion	Individual is moving between locations (walking, running climbing or jumping) with a relaxed gait.
	Gouge	Individual is gnawing wooden logs with teeth.

Definitions modified from: Stevenson and Poole, 1976; Stevenson and Rylands, 1988; Badihi, 2006; Bassett, 2003 (vertical flight).

Plate 3.12 Thumbnail images of coded non-vocal behaviours.

Intergroup agonistic: (i) anogenital present; (ii) bristle

(i) **(ii)**

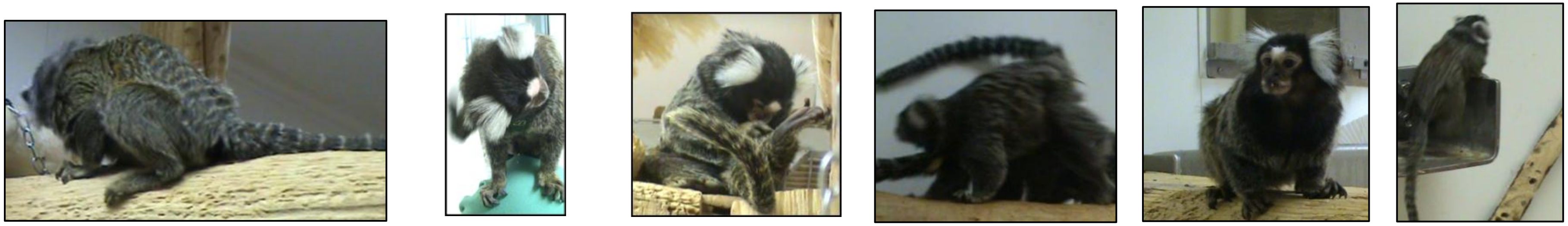
Intragroup agonistic: (i) attack

(i)

Affiliative: (i) share food; (ii) social play; (iii) grooming invite; (iv) allogrooming; (v) active affiliative contact

(i) **(ii)** **(iii)** **(iv)** **(v)**

Anxious: (i) scent mark; (ii) self-scratch; (iii) self-groom; (iv) agitated locomotion; (v) inactive alert; and (vi) vertical flight



(i) (ii) (iii) (iv) (v) (vi)

Welfare indicators (additional): (i) inactive rest; (ii) calm locomotion; and (iii) gouge

(i) (ii) (iii)

3.4.4 Vocalisation Coding Definitions

The identity of the different call types (loud shrill; twitter; chatter; chirp; whirr; ek; tsik; rapid-fire tsik; and seep) was established during a pilot study by visual and audio examination of spectrograms of pilot recordings in relation to the verbal descriptions (and in some cases spectrogram images) given by various researchers (Epple, 1968; Goldman, 2000; Jones, 1993; Pook, 1976; Stevenson and Rylands, 1988; Winter, 1978).

The nine different call types were considered to be sufficiently distinct to allow reliable and accurate identification by visual and auditory examination alone. Vocalisations made by marmosets can be divided into individual elements. Many calls, for example the twitter call, are made up of sequences of elements in series. Therefore an inter-bout interval had to be defined for each call type (see Table 3.4).

Fig. 3.1 shows spectrograms of each of the main call types coded along with the subsidiary calls: whirr and infant cry call. In Table 3.5 I relate the calls coded with the definitions and names used by researchers in previous studies. Appendix B lists the additional considerations for audio and spectrogram coding carried out in Chapter four. Appendix C, on the appended, DVD Appendices, contains a spectrogram video of the nine main call types.

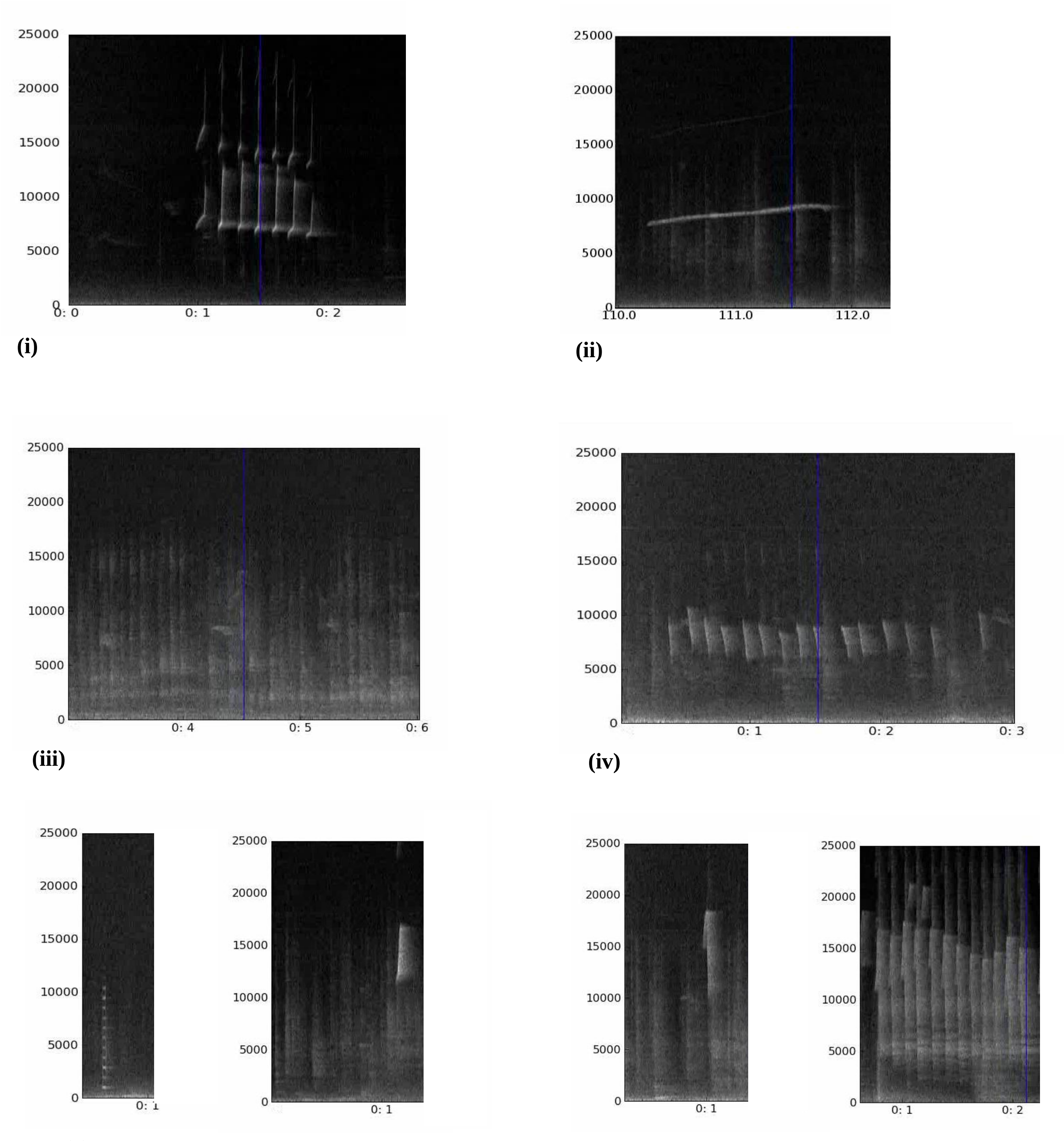
Table 3.4 Calls coded in the current thesis with their: behavioural category; description for visual identification in live coding; parameters for audio and spectrogram coding and the definition of a single call. Definitions of single call are given because vocalisations can be divided into individual elements and many call types are made up of sequences of these individual elements in series. The inter-bout interval is defined for each call type.

Behavioural category	**Vocalisation type**	**Live coding visual/ audio description**	**Spectrographic description**	**Definition of a single call**
Intergroup agonistic	Twitter	Mouth continuously open throughout, with lips slightly puckered and slight abdominal contractions visible.	A series of regularly spaced seep-like elements (but at lower frequency) characterized by a rapidly increasing fundamental frequency.	Sequence of elements: a phrase consists of several regularly spaced syllables. At least two elements present. Minimum inter-bout interval: 0.5 seconds (s). Overlapping calls coded separately.
	Loud shrill	Wide open mouth. Very loud, piercing whistle-like call (loudest element in vocal repertoire).	Fundamental frequency tends to increase smoothly across the call. Distinguish from whirr due to absence of cyclic frequency fluctuations. Distinguish from long phee calls by the high amplitude and longer duration of elements. Only calls with first/only syllable 1.3 s in length or over were counted as loud shrill (to exclude non-open mouth calls).	Single syllable or sequence of syllables. Classified as 1, 2 or 3 and more syllables. It was fairly easy to determine which elements belonged in the same call (since the syllables are made at the same frequency). Where overlap occurred best judgment was used.
Intragroup agonistic	Chatter	Body vibrates noticeably with abdominal contractions.	Series of low-pitched harsh elements similar to ek but distinguish since the elements are of shorter duration. Distinguish from cough due to the lack of 'noise' character.	Sequence of elements. Minimum inter-bout interval: 0.5 s (observed inter-element interval: about 0.05 s).
Affiliative	Chirp	Made with mouth closed or slightly open.	Series of elements uttered in rapid series characterized by constant descent in frequency over a range of 8-5 kHz.	Sequence of elements: at least two in series. Minimum inter-bout interval of 0.5 s (observed inter- element interval is around 0.15 s).
	(Whirr)	mouth closed	Element with cyclic frequency modulation (approximately 30 c/sec) Distinguish from loud shrill, phee and trill-phee by a lack of smoothly increasing frequency: whirr consists *solely* of cyclic frequency modulations. Whirr calls are of relatively short duration and mostly monosyllabic but do vary in length	Single element (does occur in more than one syllable sometimes and/or broken up but it is not possible to reliably distinguish whether two marmosets giving monosyllabic calls in close succession or one marmoset giving a multi-syllable call).

Anxious	Ek	Mouth slightly open (in contrast to 'cough' which is made with mouth closed).	Low-pitched harmonic stack, uttered singly or rapid series of two or more. Distinguish from cough by the lack of noise character.	Single element or sequence (one or two syllables in close succession). Minimum inter-bout interval: 0.5 s (interval between elements: about 0.1 s).
	Tsik	Mouth open (to about half full extent).	Consists of a rapidly decreasing fundamental frequency usually with a slight frequency peak at the start of the call.	Single element or two close together. Minimum interval: between elements: > 0.3 s
	(Rapid-fire tsik)	Mouth wide open and call repeated in rapid series. Very loud call.	As tsik but repeated in rapid series	Sequence of more than two elements (sounds virtually monosyllabic to human ear). Interval between tsiks must be 0.3 s or less. Inter-bout interval: greater than 0.3 s.
	Seep	Mouth open (in contrast to 'see' which is made with mouth closed)	A relatively short, continuously sharply increasing fundamental frequency (may have frequency trough at beginning). Minimum frequency of 8 kHz. Distinguish from see since is of a non-varying frequency whereas seep increases rapidly in frequency across the element.	Single element or a few together. Minimum inter-bout interval: 0.5 s.

(Call descriptions were taken mainly from Pook (1976) since he divided calls into open and non-open mouth variants but also from: (Epple, 1968; Stevenson and Rylands, 1988; Jones, 1993; Goldman, 2000)).

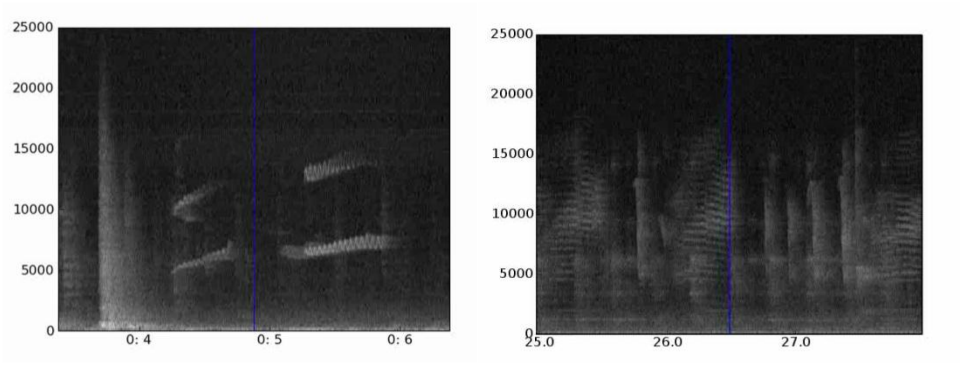
Figure 3.1 Spectrograms of the seven main types of *Callithrix jacchus* vocalisations coded and analysed in the current thesis: (i) twitter; (ii) loud shrill; (iii) chatter; (iv) chirp; (v) ek; (vi) seep; and (vii) tsik; and other relevant vocalisations: (viii) rapid-fire tsik; (ix) whirr call; and (x) the infant cry, call relevant to Appendix B, (here shown interspersed with infant tsik calls). On each spectrogram, the x-axis shows frequency in kHz and the y-axis shows time in sec.



(i) (ii)

(iii) (iv)

(v) (vi) (vii) (viii)



(ix) **(x)**

Table 3.5 Common marmoset (*Callithrix jacchus*) call names in previous studies of vocalisations equivalent (or roughly equivalent) to the vocalisation types coded, and/or mentioned in the present thesis.

Vocalisation name (used here)	Equivalent call names (given in other vocalisation studies)
twitter	‘twitter’ (Epple, 1968; Pook, 1976; Stevenson and Rylands, 1988; Jones 1993; Goldman, 2000)
loud shrill	roughly equivalent to ‘monosyllabic calls given in isolation’ (Epple, 1968) (but are non-isolation calls); equivalent to the wide open mouth calls/ top end of ‘loud shrill’ (Pook, 1976); equivalent to top end of ‘open-mouthed phee calls’ (Goldman, 2000); equivalent to top end of ‘home phee calls’ (Norcross and Newman, 1993)
chatter	‘chatters given when angry’ (Epple, 1968); ‘cackle’ (Pook, 1976); ‘cackle’ (‘erh erh’) (Stevenson and Rylands, 1988)
chirp	‘chirping’ (Goldman, 2000); ‘chirruping’ (Pook, 1976); ‘rhythmical contact calls given in close visual and bodily contact’ (Epple, 1968)
(whirr)	monosyllabic calls given in close visual contact (Epple, 1968); ‘short whirr’ and ‘whirr’ (Pook, 1976); whirr (Stevenson and Rylands, 1988); trill (Jones, 1993).
ek	‘egg’ (Epple, 1968); ‘ek’ (Pook, 1976; Stevenson and Rylands)
seep	‘warning call’ (Epple, 1968); seep class a (Pook, 1976); ‘whistle call’ (Winter, 1978)
tsik	tsik (Epple, 1968); tsak, seep class c and d (Pook, 1976);
(rapid-fire tsik)	‘tsik’ calls given in high excitement, mobbing call (Epple, 1968); ‘loud tsak’ (Pook, 1976)
infant cry call	‘infant squeal’ (Epple, 1968); ‘caw’ (Pook, 1976); ‘squeal call’ (Winter, 1978)

3.5 Statistical Analyses

Duration Measure

Percent time, spent in performance of the behaviour during the observation session, was used as a measure across all behaviours for consistency and was considered a suitable measure even for behaviours of relatively short duration, such as attack, as duration and frequency of such behaviours are strongly positively correlated (e.g. Badihi, 2006).

3.5.1 Study Design

Table 3.6 summarises the empirical studies in the thesis, listing for each the type of experimental design (within subjects or between subjects), the sample size, and duration of the stimulus effect investigated.

Table 3.6 Summary of all studies in the thesis: type of experimental design (within subjects or between subjects), sample size and the duration of the stimulus effect investigated.

Chap No.	Study Name	Duration of Stimulus Effect Analysed	Experimental Design	Intended N	Actual N
4	Neighbour Effect	immediate (within 15 sec after stimulus)	within-subjects	32	31
		overall (during observation of 5 min)	within-subjects	32 (16; 16)	31 (16;15)
5	Chirp Playback	immediate (within 15 sec after stimulus)	within-subjects	16	16
		longer-term (outwith specific playback period: mid-playback, minimum of 1 hr to maximum of 20 hr after most recent playback session; post-playback, minimum of 1 day to maximum of 6 days (5 days 21 hr) after all playback has ceased)	between-subjects	32 (16; 16)	31 (16;15)
6	Allogroom Playback	overall (during observation of 5 min)	within-subjects	16	16
		longer-term (outwith specific playback period: mid-playback, minimum of 1 hr to maximum of 20 hr after most recent playback session; post-playback, minimum of 1 day to maximum of 6 days (5 days 21 hr) after all playback has ceased)	between-subjects	32 (16; 16)	32 (16; 16)

3.5.2 Statistical Tests

Permutation Tests

Permutation tests were used to analyse the data. This was considered to be the most appropriate and statistically powerful method to use given that the behavioural data collected did not meet parametric assumptions and were drawn from a relatively small sample size (e.g. Adams and Anthony, 1996; Colegrave et al., 2005). In conventional parametric tests an intermediate test statistic is calculated based on the observed data and then compared to standard reference distributions obtained from theoretical probability distributions. Such tests rely on the assumption that the data is normally distributed. In contrast, permutation tests involve creating a distribution of possible outcomes (a probability distribution) directly from your own data, through re-shuffling it multiple times (resampling). For example, in a between-subjects design experiment with two conditions, the observations from both groups are first pooled (shuffled) and then reassigned to conditions at random (this represents one possible shuffled arrangement or permutation). The difference in sample means for this arrangement is then calculated. This procedure is repeated many times to create a distribution of possible outcomes. In permutation tests then, your observed result (i.e. in this thesis the mean difference across conditions or groups) is compared directly to this distribution (generated by the randomisation analysis and tailored specifically to the dataset); there is no *intermediate* (standardised) test statistic. Thus the permutation test assesses the probability that the pattern observed in the data could be obtained by chance. Permutation tests rely only on the assumption that every individual was equivalent before the observation began.

Here, for the studies of within-subjects design a program, the data was randomly shuffled across conditions (but not across individuals) in order to conserve the maximum amount of information in the analysis. In contrast, for those studies using a between-subjects design, the data was randomly shuffled across all individuals. The test statistic in all cases was the difference between means. Both analyses were performed using MATLAB and the custom-written code is given in Appendix F.

Each shuffled arrangement of the original data-set is referred to as a permutation. In instances where the number of possible different permutations (through shuffling the dataset) was small then the probability (p-value) could be calculated exactly an ‘exact permutation test’. However, in the majority of cases the number of possible permutations of a dataset was large so it was necessary to sample a subset. In such a cases, the permutation test used was a ‘randomisation test’ (i.e. an approximate exact test), and the probability was estimated based on a fixed number of permutations/iterations. For randomisation tests the data were shuffled 200,000 times, or ‘iterations’ (the recommended minimum number of iterations being 5000: Adams and Anthony, 1996). In all analyses, the data were shuffled without replacement, this refers to the fact that the data is being “shuffled” without duplicating any of it, and without removing or adding anything (an analogy would be shuffling a complete deck of cards 200,000 times).

All the statistical tests were one-tailed as clear directional predictions were made (except for the two-tailed post hoc tests) and the α-level was set at 0.05. For the directional (one-tailed) predictions, the *p*-value was not reported for means between which the difference was in the opposite to the predicted direction.

Throughout the thesis, I have used the mean as a measure of the central tendency of our data, in text tables and graphs, even though the data do not fit the normal distribution. This is to provide the most informative measure of central tendency since, given the large number of zeros in our data, the mode is often zero. There are a large number of zeros in the behavioural data since many of the behaviours investigated are performed infrequently in a captive setting.

It is important to emphasise, however, that the comparatively infrequent performance of particular behaviours need not imply a relatively low importance of the behaviour. For example, vertical flight may occur infrequently and the behaviour itself is of very short duration, but it is usually followed by a prolonged period of the marmosets remaining motionless and in an inactive alert state. Conversely, affiliative behaviours, even of brief duration or infrequent occurrence, are likely to have significance for the strengthening and maintenance of social relations (e.g. active affiliative contact: related to the pair bond between breeding pairs, Evans, 1983; allogrooming: related to the bond between breeding and nonbreeding females, Lazaro-Perea, 2004), and hence animal welfare.

Composite Behavioural Measures

An alternative approach to analysis would have been to combine the behaviours into one dependent variable (either through a principal components analysis or the combination of times) in order to increase the power of the analysis. However, relying solely on a composite measure for each affect category by combining behaviours would probably lose too much detail in terms of the specificity of the effects found. Therefore, results for individual behaviours were analysed. However, as an overall index of social contagion of affiliation I analysed a composite measure (combined times) of the 5 coded affiliative behaviours (Chapters five and six only). Composite measures of affect categories were also used for the ‘matching’ analysis (see below).

Family-wise Error Rate Correction

In the statistical analyses for all the studies, I carried out multiple tests within each behavioural category. All of the variables were selected carefully and were relevant to theory driven prediction. For example, in investigating an effect of social contagion of affiliation, a range of affiliative behaviours had to be assessed. Nonetheless, the risk of making Type I errors (rejecting the null hypothesis when there is no effect; false positives) increases with the number of tests carried out on a data set, or sub-set. To counter this tendency family-wise error rate correction can be applied (e.g. Caldwell et al., 2005). For example, the α-level is adjusted by dividing it according to the number of tests carried out (e.g. standard and sequentially-rejective Bonferroni method). However, applying this procedure incurs the converse risk of Type II errors (accepting the null hypothesis when the effect exists), especially when, as here, the size of any effects are likely to be low and therefore difficult to detect (Nakagawa, 2004). Critics of the Bonferroni method object that overly conservative correction may stifle research avenues (e.g. Moran, 2003). Moran recommends instead, reporting exact p-values and relying on careful interpretation of the results.

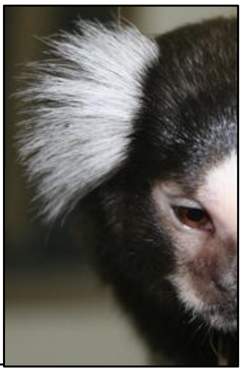
Because there are arguments both for and against family wise error correction, and in order to achieve an appropriate balance between the risk of making either Type I and II errors, I have retained the results without adjustment to provide more information for the reader in the Chapters reporting empirical data (four, five and six), as well as presenting and discussing the more conservative adjusted results (Bonferroni standard method). In each table of results I give an adjusted α-level beside those results that are significant before adjustment for family wise error rate. A separate section at the end of each results section summarises the results following correction for multiple testing. The results summary table in Chapter seven also shows the adjusted alongside the non-adjusted results.

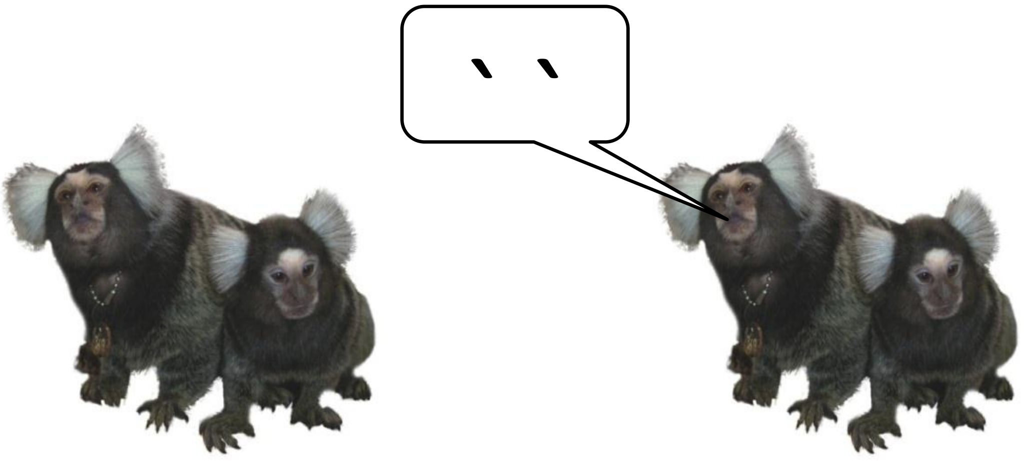
Matching Analysis

In Chapters five and six I used the classic social learning test of ‘matching’. I carried out an assessment of ‘matching’ to composite measures of same and different affect categories of the contagion stimulus. If I had assessed only whether a particular experimental manipulation (auditory playback of chirps or visual playback of allogrooming) elicited increases in behaviours associated with the same affect as the behaviour/call in the playback (as predicted), I would not know whether playback might also increase behaviours indicative of the other three affect categories (not predicted). If the playback manipulation was found to stimulate behaviours of the matching affect category as predicted, but to have no significant effect on any of the three non-matching affect categories, then this would strengthen the conclusions. Alternately, if the playback was found to be associated with increases in behaviours of affect category matching the contagion stimulus, but also led to increases across a number of non-matching affect categories, then such an effect may be explained more parsimoniously by a general increase in arousal or activity, rather than contagion specific to the matching affect.

Chapter 4

The Effect of Spontaneous Neighbour Vocalisations on Marmoset Social Behaviour





In Chapter two I highlighted the relative neglect of social/communicative behaviours in the experimental study of social transmission. In the current Chapter, I address this imbalance. Researchers have previously demonstrated an influence of neighbouring conspecific calls on the social behaviour of nearby chimpanzees, the neighbour effect, as stated in Chapter two. A neighbour effect for affiliation and for agonism has been found in chimpanzees (Baker and Aureli, 1996; Videan et al., 2005). Here, I extend the investigation of the neighbour effect to marmosets, and to the possible social contagion of anxious, as well as affiliative and agonistic behaviour, in an observational study. Most of the material presented in the following Chapter has been published previously (Watson and Caldwell, 2010).

4.1 Introduction

Researchers investigating social influences in nonhuman primates have recently tended to focus on the most cognitively complex social processes, such as imitation. However, despite being relatively simple cognitively, processes such as social contagion are likely to be functional in their own right, and may also support and influence cognitively complex social processes. For example, social facilitation, and social contagion, may enhance the advantages of group living by increasing behavioural synchrony (Clayton, 1978; Coussi-Korbel and Fragaszy, 1995) and may indirectly influence social learning (Hoppitt and Laland, 2008).

It has been suggested that social contagion in animals may be a precursor to the human capacity: empathy (e.g. de Waal, 2008; Palagi et al., 2009; Yoon and Tennie, 2010; O’Hara and Reeve, 2011). Researchers view emotional contagion in humans as a precursor to empathy (e.g. Hatfield et al., 1994). Although many argue that ‘theory of mind’ is necessary for empathy it may have simpler origins in prosociality and social contagion. Consequently, it is an important enterprise to establish how such simple processes operate in species of nonhuman primate.

Several studies have investigated whether social contagion could be demonstrated in chimpanzees through the influence of spontaneous neighbouring group vocalisations on individual social behaviour, termed the “neighbour effect” (Baker and Aureli, 1996; Videan et al., 2005). Baker and Aureli (1996) investigated the neighbour effect resulting from aggressive neighbour calls. They found that higher levels of chimpanzee agonistic vocalisations and noises in neighbouring groups were associated with an increase in intragroup agonistic behaviour and vocalisations in focal groups. Videan et al. (2005) replicated these findings with chimpanzees and also extended the evidence supporting the neighbour effect to affiliative behaviour. They found that the time spent by focal individuals in allogrooming behaviour and in giving grooming vocalisations increased significantly at higher levels of neighbour grooming vocalisations (Videan et al., 2005).

Here I use the term neighbour effect to refer to social contagion resulting from the influence of the vocalisations emitted by conspecifics on the behaviour of nearby individuals (see Chapter one). This observational study aims to explore the generality of the neighbour effect. Researchers directly investigating the neighbour effect in nonhuman primates have, to date, confined their focus to apes, specifically chimpanzees. I investigate the neighbour effect, for aggression, affiliation, and for anxiety in a species of New World monkey: common marmosets (*Callithrix jacchus*).

Anecdotal reports, and some quantitative studies, indicate that the behaviour of neighbouring groups influences the behaviour of captive marmosets. For example, Pook (1976) observed that twitter calls, an intergroup agonistic call, were also “infectious” (contagious), with calls in one social group being followed by calls from nearby groups.

Contagion is a semantically ambiguous term, referring both to calls in particular and also to the more general spread of affective states. Calls have been described as contagious if an initial call made by one individual then appears to spread to all members of the group who make a call or calls of the identical call type (e.g. tsiks in series or rapid-fire tsiks; the mobbing call). Here I discuss social contagion of affect in a more general sense, referring to the spread of affect and behaviour related to general agonism, affiliation, or anxiety. For example in the case of anxiety: we argue that if it can be demonstrated that neighbour anxiety-related calls appear to influence nearby marmosets to increase the time they spend in general anxiety-related behaviours, such as self-directed displacement behaviours, then this would be indicative of a social contagion or neighbour effect of anxiety through vocalisation.

The investigation of the contingent social contagion of anxiety is less straightforward, both conceptually and semantically, than that of agonism or of affiliation. Here I investigate two somewhat separate sub-divisions relating to the contagion of anxiety in this chapter. First, in the main study, I aimed to investigate the more diffuse concept of the social contagion of the affect of anxiety. Second, in the post hoc analysis, I sought to confirm, with quantitative and systematic data, that the alarm call, the seep call, when produced by neighbouring marmosets leads to the response of vertical flight in nearby individuals.

To avoid confusion I will deal with another semantically confusing term: alarm. *Alarm* refers both to alarm calls in the functional sense of the word, meaning that they apparently function to induce alarm in surrounding conspecifics (e.g. the seep or warning/alarm call), and also to calls apparently indicative of mild alarm or anxiety in the individual (e.g. the ek call).

Here my motivation was to include in the anxiety subcategory all calls that I considered indicative of anxiety but without a specific response in the receiver (see section 1.4, Chapter one).The ek call is not considered to be an alarm call other than it appears to express anxiety/alarm. The ek call has been described as indicating mild alarm with no definite response in the receiver (e.g. Stevenson and Rylands, 1988). Thus, I consider that the ek call is an anxiety-related call that may be expected to result in a neighbour effect of anxiety. Within my category of anxiety-related calls the ek call is the most context-generalised call. There are, to my knowledge, no previous studies investigating the neighbour effect of ek calls.

Tsik calls also appear to express alarm/anxiety (e.g. Stevenson and Rylands, 1988) and are produced in rapid series as mobbing calls in the presence of a potential predator. Tsik calls emitted singly are not necessarily given in response to a specific threat, although the production of tsik calls may lead to the production of rapid-fire tsik calls. Here I distinguish between tsik calls emitted close together that term the ‘rapid-fire tsik’ call (i.e. a true mobbing call) and those tsiks made singly: classified as a generalised anxious call. Although the tsik call has been observed to be a contagious call (e.g. Epple, 1968) it is not tied to a specific response in the receiver.

Hankerson et al. (2002) report directly investigating the effect of 'in situ' neighbouring group vocal alarm responses on focal groups in a different species of marmoset: *Callithrix geoffroyi*. However, their report is only available as a conference abstract and so few details are publicly available. According to information provided in the abstract, a model predator snake was shown to one group to elicit calls of alarm, and the neighbouring group had no visual contact, but was able to hear the alarm calls. The call types emitted are not specified in the abstract. The following morning and evening, the neighbouring group are reported to have spent less time in resting and grooming and more time than usual engaging in visual monitoring behaviours (Hankerson et al., 2002). Thus, this study examined the long-term effect of neighbour vocalisations rather than the contingent or immediate effect.

In summary, the neighbour effect for alarm-related calls has been described, and studied, in nonhuman primates, (e.g. Epple, 1968; Hankerson et al., 2002), although there remains scope for further quantitative investigation. However, I contend that a contingent neighbour effect for anxiety-related behaviour has yet to be demonstrated in nonhuman primates.

To date, investigations into the contingent effect of neighbour calls on nearby common marmosets have involved some degree of experimental manipulation involving isolation of individuals and/or playback of calls (e.g. published: Cross and Rogers, 2006; Chen et al., 2009; Yamaguchi et al., 2009; unpublished: Pook, 1976; Jones, 1993). Jones (1993) reported, in her thesis, that playback of twitter calls resulted in an increase in territorial behaviours in marmosets. However, her investigation was not carried out within the usual social context: subjects in this study were pairs separated from the colony room and transported to an acoustically isolated chamber to allow accurate audio recording of vocal responses.

Thus these studies have taken place under relatively artificial conditions, and social behaviours were not recorded. Several more naturalistic observational studies have been carried out, but these have not been systematic investigations of the type I now report. For example in one of his experimental studies Pook (1976) noted the responses of marmosets to surrounding calls, but recorded only those calls that elicited some sort of response; he did not record the total frequency of each call type investigated.

Several studies investigating a category of call combining tsik and rapid-fire tsik as one, found that the playback of familiar tsiks (Cross and Rogers, 2006) and hearing spontaneous tsiks produced by fellow group members in response to a specific alarming stimuli (Clara et al., 2008) appeared to reduce anxiety in marmosets. This finding is clearly inconsistent with the notion of contagion of anxiety/alarm. Clara et al. (2008) investigated mobbing calls in marmosets by exposing one particular individual within the group to a model predator and observing the reaction of the social group in terms of mobbing calls, anxiety-related behaviours, and later cortisol analysis. They were interested in the effects of experience on mobbing vocalisation within a group. However, in terms of the neighbour effect I investigate here, in their study it is difficult to distinguish between the neighbour effect (i.e. the effect of the first caller on the rest of the group), and the effect of the stimulus itself. Further, rapid fire tsik and tsik calls were not sub-classified, and therefore the number of tsik elements was recorded with no reference to call bouts. Rather than being quantitatively coded, anxiety behaviours were allocated a rank score corresponding to the general occurrence per minute during subjects exposure to each stimulus (one for a frequency of once or less, two for two to three times and three for three or more). Therefore there is still a lack of comprehensive, quantitative information on the effects of spontaneous neighbouring conspecific calls on marmosets, i.e. the neighbour effect.

Investigating the neighbour effect in marmosets is highly relevant to the captive welfare of marmosets. Welfare-focused studies have investigated the effect of a wide range of factors on marmoset social behaviour, for example human interaction (Manciocco and Vitale, 2008) and environmental influence (Gerber et al., 2002). However, no study, to my knowledge, has directly investigated the effect of neighbouring group behaviour on the behaviour of individual captive marmosets. Common marmosets (*Callithrix jacchus*), used extensively in medical research, are often housed in large colony rooms containing multiple cages containing groups of marmosets. Many studies have investigated the behavioural responses of captive marmosets to unfamiliar conspecifics (e.g. Cilia and Piper, 1997; Gerber and Schnell, 2004). Captive marmosets may be familiar with members of other groups housed within their colony room through auditory and possibly limited olfactory and visual contact. It is such limited intergroup interactions to which they are exposed daily. However, few, if any, observational studies have investigated the influence of such interactions on marmoset behaviour. Understanding the effects of such interactions is important for husbandry and welfare, as marmosets will be exposed to auditory and possibly limited olfactory and visual contact of neighbours on a daily basis.

In addition to the cognition and welfare implications, the current study may be expected to have some relevance to the behaviour of groups of marmosets in the wild. *Callithrix jacchus* inhabits overlapping home ranges (Stevenson and Rylands, 1988). It is to be expected, then, that marmosets in a particular group will be familiar to some extent with the overlapping neighbouring groups from periodic visual and/or auditory contact (and from relatedness in some cases) (French et al., 1995). Therefore observations of the effect of calls made by neighbouring groups (and rooms) in captivity, that are familiar with each other, is more ecologically valid than investigations in which completely unfamiliar conspecifics have been introduced to each other (see above).

Seep Call Function

The seep has been described as a warning call (Epple, 1968; Jones, 1993), and as an alarm call (e.g. Lazaro-Perea, 2001). Many researchers have observed that seep calls are frequently followed by behaviour in the surrounding marmosets that has been described as: the startle response (Epple, 1968); alarm-flight behaviour (Lazaro-Perea, 2001); and vertical flight (e.g. Bassett, 2003): marmosets flee upwards very quickly and then remain stationary and silent for several minutes. Bezerra and Souto (2008) reported that wild marmosets produced the seep call (they classify it as: ‘alarm call 2’) in response to the presence of the domestic dog, a ground predator. Although the seep call could be conceived as anxiety-related, it appears to be a very context-specific call, since it has been observed to lead consistently to the startle response in nearby marmosets. For this reason we excluded the seep call from the anxiety category containing more context-generalised anxious calls: ek and tsik. Nevertheless, in the current study I collected quantitative data relating the alarm-flight response to seep, allowing me to assess the function of this call.

The Neighbour Effect

I collected data on vocalisations and behaviours of 31 focal individuals and concurrent neighbour vocalisations within four behavioural categories: intragroup and intergroup aggression, intragroup affiliation and anxiety. I predicted that neighbour vocalisations of a particular behavioural category would influence nearby conspecifics (focals) to initiate or increase performance of behaviours within the same behavioural category.

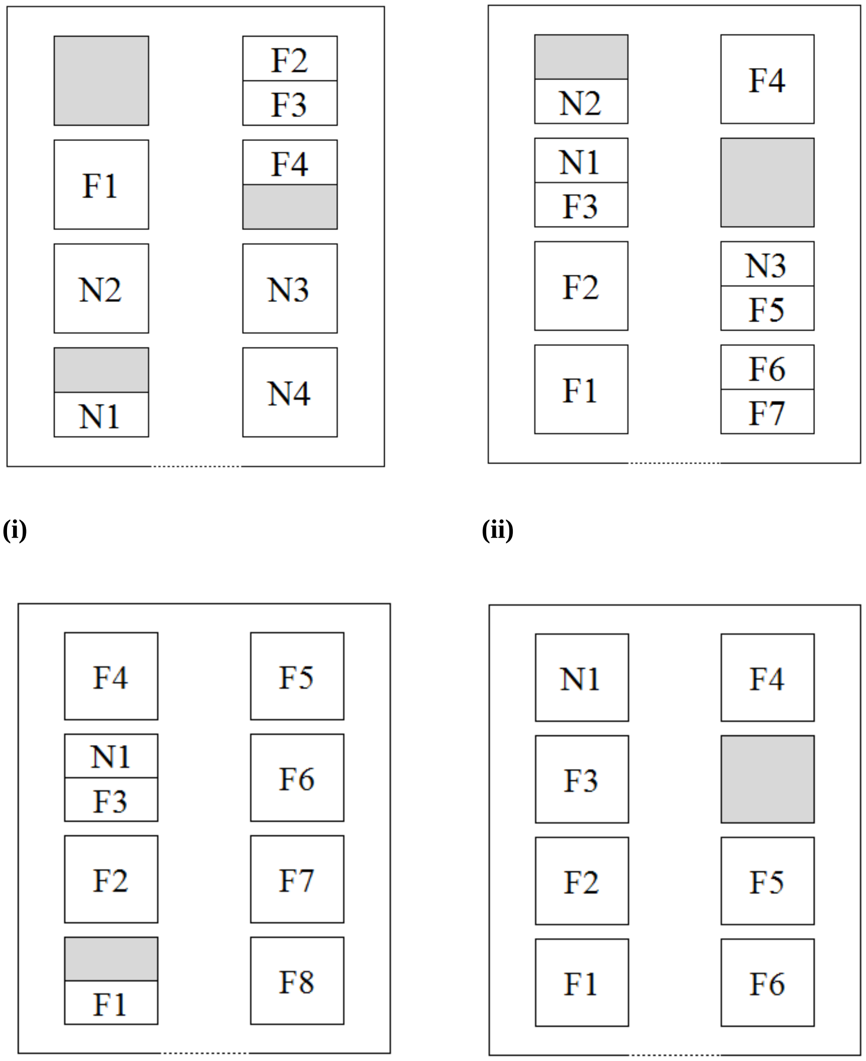
4.2 Method

4.2.1 Study subjects

The study animals were housed within four colony rooms at the Medical Research Council (MRC) Human Reproductive Sciences Unit, Edinburgh, Scotland (see Chapter three for further details). In total, the study population numbered 121 individuals: 61 breeding adults; 15 nonbreeding adults; 30 juveniles and 15 infants. The focal individuals in this study were 32 individuals, initially; eight in each of the four colony rooms (four breeding males and four breeding females, each housed in either a breeding pair or a family group). One male focal individual (988bk, room 3, focal 7) was later removed from the study because excessive aggression from his partner (174y) necessitated separation, leaving 31 focals. Over the study period there were also some changes to the non-focal group (‘‘neighbour’’) population in the study rooms: one adult and one infant died (adult 330y in group F1 room 2 was euthanised on the 26.03.08; infant of 279y in group F3 in room 1 died on 28.03.08), two infants were born (infants of 261y in group F1 in room 2 were born on 26.03.08), and three individuals were removed from the study rooms (the separated pair 988bk and 174y, pair F7, both removed from room 3 on 26.03.08; and NBA 338y removed from group F2 in room 4, also on 26.03.08).

At the outset of the study, the mean total number of individuals was 32 per room divided among a mean number of 9 social groups, with all 8 cages per room occupied except one cage in room numbers one, two and four. Fig. 4.1 shows a schematic diagram of the study room layout, and Table 4.1 gives details of focal individuals and of other members in their groups (focal group neighbours), and of individuals in non-focal groups (non-focal group neighbours). The marmosets had been habituated to the combined presence of the audio equipment and the observer over 11 days of practice data collection, before the study. Observational data collection was carried out from March 18th to April 7th 2008.

Fig. 4.1 Schematic diagram of the four colony rooms showing the label given to each group containing focal individual(s) and focal group neighbours F1 etc. and groups of non-focal group neighbours N1 etc. (i) room one (ii) room two (iii) room three (iv) room four. Shaded areas are empty half or whole cages.



(i) (ii) (iii) (iv)

Table 4.1 Subjects (focal marmosets and both focal and non-focal group neighbour population): individual identity, group identity, group type (pair or family), sex, developmental stage (key below), date of birth and age in years and days on the first day of study (18-03-08). Key: BA = breeding adult; NBA = nonbreeding adult; J = juvenile; I =infant; n = neighbour (non-focal population); Asterisk (*) indicates focal individuals housed together in the same focal group; focal information is given in bold font.

Room No.	Group id	Group type	Individual category	Individual id	Sex	Developmental stage	Date of birth	Age in years and days on first day of study
1	**F1**	**family**	**focal 1***	**198y**	**f**	**BA**	**02.06.03**	**4 yr 290**
			focal 2*	**148g**	**m**	**BA**	**12.01.06**	**2 yr 66**
			n	infant of 198y	m	J	03.01.08	0 yr 75
			n	infant of 198y	m	J	03.01.08	0 yr 75
	F2	**pair**	**focal 3***	**70Bl**	f	**BA**	**26.05.95**	**12 yr 297**
			focal 4*	**770Bk**	**m**	**BA**	**13.03.97**	**11 yr 5**
	F3	**family**	**focal 5***	**279y**	**f**	**BA**	**26.10.04**	**3 yr 144**
			focal 6*	**158g**	**m**	**BA**	**04.06.06**	**1 yr 288**
			n	infant of 279y	**f**	I	27.02.08	0 yr 20
	F4	**pair**	**focal 7***	**308y**	**f**	**BA**	**22.01.06**	**2 yr 56**
			focal 8*	**153g**	**m**	**BA**	**17.04.06**	**1 yr 336**
	N1	pair	n	332y	f	BA	13.03.07	1 yr 6
			n	154g	m	BA	01.05.06	1 yr 322
	N2	family	n	003BB	m	BA	22.09.99	8 yr 178
			n	336y	f	NBA	06.04.07	0 yr 347
			n	infant of 59y	f	J	22.11.07	0 yr 117
			n	infant of 59y	f	J	22.11.07	0 yr 117
	N3	pair	n	725Bk	m	NBA	17.07.95	12 yr 245
			n	166g	m	NBA	23.08.06	1 yr 208
	N4	family	n	327y	f	NBA	14.10.06	1 yr 156
			n	334y	f	NBA	18.03.07	1 yr 0
			n	333y	f	NBA	18.03.07	1 yr 0
2	**F1**	**family**	**focal 1**	**89g**	**m**	**BA**	**28.08.03**	**4 yr 103**
			n	261y	f	BA	14.06.04	3 yr 278
			n	330y	f	NBA	12.12.06	1 yr 97
			n	175g	m	NBA	12.12.06	1 yr 97
			n	178g	m	J	22.05.07	0 yr 301
			n	infant of 261y	m	I	02.03.08	0 yr 16
	F2	**family**	**focal 2**	**95y**	**f**	**BA**	**20.09.01**	**6 yr 180**
			n	4BB	m	BA	22.11.99	8 yr 117
			n	347y	f	J	20.08.07	0 yr 211
			n	181g	m	J	20.08.07	0 yr 211
			n	infant of 211y	m	I	01.02.08	0 yr 46
			n	infant of 95y	m	I	27.01.08	0 yr 51
	F3	**pair**	**focal 3**	**901Bk**	**m**	**BA**	**21.03.00**	**7 yr 363**
			n	227y	f	BA	07.10.03	4 yr 163
	F4	**family**	**focal 4***	**217y**	**f**	**BA**	**18.08.03**	**4 yr 223**
			focal 5*	**118g**	**m**	**BA**	**22.08.04**	**3 yr 209**
			n	infant of 222y	m	J	30.09.07	0 yr 170
			n	infant of 222y	m	J	30.09.07	0 yr 170
	F5	**pair**	**focal 6**	**328y**	**f**	**BA**	**02.11.06**	**1 yr 137**
			n	164g	m	BA	02.07.06	1 yr 260
	F6	**pair**	**focal 7**	**254y**	**f**	**BA**	**22.04.04**	**3 yr 331**
			n	810Bk	m	BA	29.04.98	9 yr 324
	F7	**family**	**focal 8**	**895Bk**	**m**	**BA**	**28.02.00**	**8 yr 19**
			n	287y	f	BA	07.03.05	3 yr 11
			n	infant of 287y	m	J	14.01.08	0 yr 64
			n	infant of 119y	f	I	02.03.08	0 yr 16
	N1	pair	n	138y	f	BA	29.05.02	5 yr 294
			n	91g	m	BA	03.11.03	4 yr 136
	N2	pair	n	326y	f	BA	06.10.06	1 yr 164
			n	173g	m	BA	04.12.06	1 yr 104
	N3	pair	n	292y	f	BA	20.07.05	2 yr 242

			n	805Bk	m	BA	05.04.98	9 yr 348
3	F1	**Pair**	**focal 1**	**899Bk**	**m**	**BA**	**28.02.00**	**8 yr 19**
			n	244y	f	BA	16.02.04	4 yr 19
	F2	**Family**	**focal 2**	**190y**	**m**	**BA**	**18.04.03**	**4 yr 335**
			n	004g	m	BA	09.03.02	6 yr 9
			n	179g	m	J	23.06.07	0 yr 269
			n	343y	f	J	23.06.07	0 yr 269
			n	infant of 190y	m	J	19.12.07	0 yr 90
			n	infant of 190y	m	J	19.12.07	0 yr 90
	F3	**Pair**	**focal 3**	**961Bk**	**m**	**BA**	**22.06.01**	**6 yr 270**
			n	319y	f	BA	28.06.06	1 yr 264
	F4	**Family**	**focal 4**	**55y**	**f**	**BA**	**02.01.01**	**7 yr 76**
			n	943Bk	m	BA	05.02.01	7 yr 42
			n	160g	m	NBA	24.04.06	1 yr 268
			n	346y	f	J	30.07.07	0 yr 232
			n	180g	m	J	30.07.07	0 yr 232
			n	infant of 55y	f	J	31.12.07	0 yr 78
			n	infant of 55y	m	J	31.12.07	0 yr 78
	F5	**Family**	**focal 5**	**816Bk**	**m**	**BA**	**08.06.98**	**9 yr 284**
			n	211y	f	BA	04.08.03	5 yr 320
			n	348y	f	J	01.09.07	0 yr 199
			n	349y	f	J	01.09.07	0 yr 199
			n	infant of 211y	f	I	01.02.08	0 yr 46
			n	infant of 211y	f	I	01.02.08	0 yr 46
	F6	**Family**	**focal 6**	**291y**	**f**	**BA**	**30.05.05**	**2 yr 293**
			n	120g	m	BA	28.09.04	3 yr 172
			n	321y	f	NBA	02.07.06	1 yr 260
	F7	**Pair**	**focal 7±**	**988Bk**	**m**	**BA**	**29.11.01**	**6 yr 110**
			n	174y	f	BA	25.02.03	5 yr 20
	F8	**pair**	**focal 8**	**286y**	**f**	**BA**	**04.03.05**	**3 yr 14**
			n	822Bk	m	BA	18.06.98	9 yr 274
	N1	pair	n	318y	f	NBA	23.03.06	1 yr 361
			n	151g	m	NBA	23.03.06	1 yr 361
4	F1	**family**	**focal 1***	**311y**	**f**	**BA**	**12.01.06**	**2 yr 66**
			focal 2*	**150g**	**m**	**BA**	**03.04.06**	**1 yr 350**
			n	infant of 311y	f	I	11.02.08	0 yr 36
			n	infant of 311y	m	I	11.02.08	0 yr 36
	F2	**family**	**focal 3**	**026y**	**f**	**BA**	**29.06.00**	**7 yr 263**
			n	846Bk	m	BA	09.11.98	9 yr 130
			n	338y	f	NBA	08.04.07	0 yr 345
			n	infant of 026y	f	J	11.09.07	0 yr 189
			n	infant of 026y	f	J	11.09.07	0 yr 189
			n	infant of 026y	f	I	14.02.08	0 yr 45
			n	infant of 026y	f	I	14.02.08	0 yr 45
	F3	**family**	**focal 4**	**155g**	**m**	**BA**	**01.05.06**	**1 yr 322**
			n	234y	f	BA	21.11.03	4 yr 118
			n	infant of 234y	f	J	17.07.07	0 yr 245
			n	infant of 234y	f	J	17.07.07	0 yr 245
			n	infant of 234y	f	I	04.03.08	0 yr 14
			n	infant of 234y	m	I	04.03.08	0 yr 14
	F4	**family**	**focal 5***	**276y**	**f**	**BA**	**03.10.04**	**3 yr 167**
			focal 6*	**749Bk**	**m**	**BA**	**20.08.90**	**17 yr 211**
			n	infant of 276y	f	J	10.09.07	0 yr 190
			n	infant of 276y	m	J	10.09.07	0 yr 190
			n	infant of 276y	f	I	10.02.08	0 yr 37
			n	infant of 276y	m	I	10.02.08	0 yr 37
	F5	**family**	**focal 7**	**074g**	**m**	**BA**	**25.06.03**	**4 yr 267**
			n	184y	f	BA	13.03.03	5 yr 5
			n	339y	f	NBA	17.04.07	0 yr 336
			n	340y	f	NBA	17.04.07	0 yr 336
			n	infant of 184y	m	J	16.01.08	0 yr 62
			n	infant of 184y	m	J	16.01.08	0 yr 62
	F6	**family**	**focal 8**	**281y**	**f**	**BA**	**27.10.04**	**3 yr 143**
			n	792Bk	m	BA	01.01.98	10 yr 77
			n	infant of 281y	m	J	16.11.07	0 yr 123
			n	infant of 281y	m	J	16.11.07	0 yr 123

N1	pair	n	324y	f	BA	03.07.06	1 yr 259
		n	147g	m	BA	07.10.05	2 yr 163

4.2.2 Live coding

A continuous focal sampling method was used to record the behavioural states and vocalisations of each of the 32 focal individuals, over a 5 min observation period, on each of 15 study days (see Chapter three for further details of the observation procedure). A total of 465, 5-min observations were recorded, although two were subsequently lost (leaving a total of 38.6 hr in all and 1.25 hr per focal individual). To allow the focal calls to be identified and differentiated from neighbour calls during subsequent audio coding, the precise event time of each focal individual vocalisation was recorded, along with the probable call type.

4.2.3 Audio recording

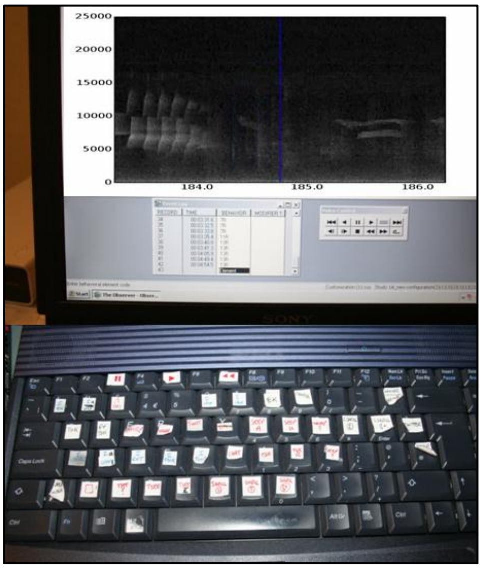
During each 5-min observation session I made a simultaneous 5-min audio recording to collect the vocalisations made by the focal individual and all other individuals within the colony room as well as the concurrent visual recording/observing of the focals behaviour. For the audio recording I used a tripod-mounted Zoom H4 digital recorder (sampling rate of 96 kHz and 24 bits with the gain level set to 127 dB) connected to an AKG-c 1000 directional microphone, mounted on a microphone stand. For each observation the sensitive end of the microphone was placed 20 cm from the centre of the front of the cage housing the focal individual. The use of one directional microphone was considered sufficient to collect the vocalisations of all individuals within the colony room following a pilot study comparing the recording output from a directional microphone with that from a centrally placed omnidirectional microphone. Plate 4.1 shows the apparatus used in experimental sessions.

Plate 4.1 Set-up for live coding and audio recording during each observation session. To the left of the frame is the seat for the observer with the handheld computer upon it, and the digital recorder nearby to allow simultaneous starting with the hand-held computer; to the right of the frame is the directional microphone in front of the focal home cage.

4.2.4 Audio and spectrogram coding

The 5-min audio track for each observation period was converted into a video consisting of a spectrogram (a plot of frequency against time) and the original audio track, using a custom-designed program. Each video was played and coded within the Observer 5 PC observation module, allowing us to identify and code focal and neighbour vocalisations (any individual audible within the room other than the focal individual) by a method of continuous recording (Martin and Bateson, 2007) and to superimpose these codes onto the corresponding observational data collected during live coding. Plate 4.2 shows the PC used for coding, displaying the screen appearance during Observer coding and the labelled keys. Each video was synchronised precisely with the time of the live observation using the beep emitted by the Psion Workabout at the end of each observation as a point of reference. When accurate measurements of frequency and time were required for call and call bout identification during the audio coding, we viewed the audio track as a spectrogram using the freely available software program ‘‘Sonic Visualiser 1.0’’ (http://www. sonicvisualiser.org/; licensed under the GNU general public license). Please refer to Chapter three for spectrograms of the different calls, coding definitions, and details of additional coding issues.

Plate 4.2 Audio and spectrogram coding procedure: lap-top PC showing coding session in the Observer on the screen and labelled keys for the call coding marked on the keyboard.



4.2.5 Statistical analysis

I investigated the effect of neighbour vocalisations on the behaviour of focal individuals, within the same affect category, in two ways (following Baker and Aureli, 1996). First, I investigated the immediate effect by comparing the proportion of behaviours carried out by individuals just before neighbour vocalisations with the proportion performed directly after. Second, I assessed the overall effect of neighbour vocalisations by comparing the behaviour of focal individuals between observation periods with high and low levels of neighbour calls. The former, sequential analysis allows firmer conclusions regarding causality and the latter has the benefit that any longer-lasting effect can be assessed.

Focal behaviour was summarised as the percentage of time spent in each behaviour by each individual in every 5-min observation period. Focal vocalisation was summarised as the total number of each call type emitted by the focal individual in each observation. Neighbour vocalisation was summarised as the total number of each call type produced by all individuals in the room except for the focal individual, including other members of the focal group.

First, to investigate the immediate effect of neighbour vocalisations in a particular behavioural category on focal individual behaviours within the same behavioural category, the mean proportion of focal behaviours occurring in the 15-sec interval before each type of neighbour vocalisation was compared with the proportion occurring in the 15-sec interval after, following the method of Baker and Aureli (1996) but using a shorter time interval. Mean proportions for each focal individual, for each combination of neighbour vocalisation and focal behaviour, were calculated using the ‘‘sequence lag analysis’’ function in the ‘‘Observer 5’’ program (Noldus Information Technology, Wageningen, The Netherlands). I considered an interval of 15 sec to be appropriate because marmosets change behavioural state relatively quickly. Mean proportions for the intervals preceding and following neighbour vocalisations were compared using approximate randomisation tests of paired sample t-tests (see Chapter three).

Second, to investigate the effect of the overall level of neighbour vocalisation upon the behaviour of focals the data sets were split in one of two ways. For the call types that occurred in greater than 75% of focal observations (twitter; ek) we split the data set into quartiles, according to the number of neighbour vocalisations occurring within each observation period, and compared the focal behaviour in the upper quartile observations with the lower. For other calls, the data set was split into those observations with zero neighbour vocalisations of a particular type (low neighbour vocalisation) and those with more than one such vocalisation (high neighbour vocalisation). I had intended to split the entire data set using the first method but the second method was necessary for call types (loud shrill; chatter; chirp; tsik; and for post hoc analysis only: seep) with more than 25% of observations containing zero neighbour vocalisations because there was no way of identifying a lower quartile. Hereafter the terms ‘‘high neighbour vocalisation’’ and ‘‘low neighbour vocalisation’’ (after Baker and Aureli, 1996; Videan et al., 2005) are used to refer to the conditions created by both methods of splitting the data set. The mean level of behaviour, or mean frequency of each call type per observation, for each focal individual was calculated from a variable number of observations depending on how many observations for each individual were in the high and in the low condition for each particular neighbour vocalisation type. Therefore, for the intended within-subjects analysis, some individuals were excluded by default from the analysis of certain neighbour vocalisations due to an absence of data from one or other of the conditions. I used permutation tests without replacement (i.e. the data was shuffled without duplication, see Chapter three for further detail of this method) to compare focal behaviour and vocalisation between observations with high and low neighbour vocalisation within the same affect category (see Chapter three).

4.3 Results

4.3.1 Neighbour Effect Results

4.3.1.1 Effect of the Overall Level of Neighbour Vocalisation

Table 4.2 displays the results of the statistical tests comparing the behaviour and vocalisations of the focal individual at high and low neighbour vocalisation within the same affect categories.

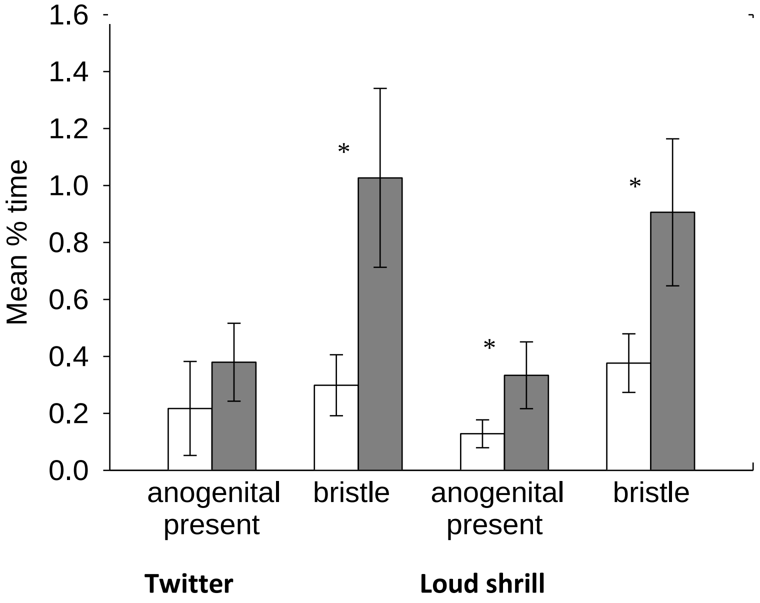
Agonistic Intergroup Neighbour Vocalisation

Neighbour twitter and loud shrill vocalisations occurred in 94.4 and 53.1% of observations, respectively. As predicted, the amount of time spent by focal individuals in intergroup agonistic behaviours was generally significantly higher in observations with a high level of neighbour twitter vocalisations (bristle: $N = 30$, $P = 0.004$) and with a high level of neighbour loud shrill vocalisations (anogenital present: $N = 31$, $P = 0.026$; bristle: $N = 31$, $P = 0.009$) than in observations with low levels of the respective neighbour vocalisations (Fig. 4.2). However, although marmosets spent longer in the intergroup agonistic behaviour, anogenital present, during high neighbour twitter than during low, the difference was nonsignificant ($N = 30$, $P = 0.062$). Intergroup agonistic vocalisations were all produced significantly more often by marmosets in observations with high levels of neighbour twitter vocalisations (twitter: $N = 30$, $P < 0.001$; loud shrill: $N = 30$, $P < 0.001$) and neighbour loud shrill vocalisations (twitter: $N = 31$, $P < 0.001$; loud shrill: $N = 31$, $P < 0.001$) than in observations with low levels of these neighbour calls (Fig. 4.2).

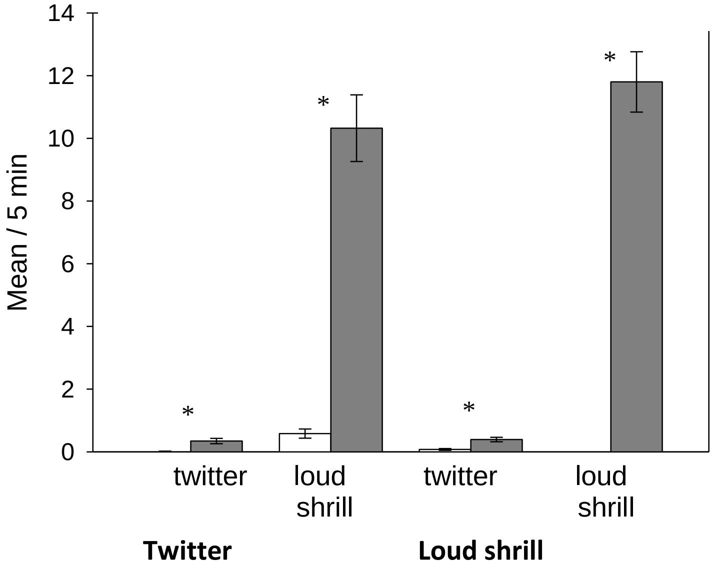
Table 4.2 Statistical test results for the analysis of the overall effect of neighbour vocalisation on focal marmoset behaviour; a comparison of the mean percent time (behaviours) and the mean frequency (calls) per observation session for observations with a high frequency of neighbour vocalisations (upper) and with a low frequency (lower). Asterisk (*) indicates *P* < 0.05. ns indicates a result in the predicted direction which was nonsignificant. Ŧ indicates means where the direction of difference is opposite to the predicted direction (one-tailed tests). ~ indicates two-tailed post hoc tests. Underlining indicates that p-values retain their significance at the adjusted α-level given in the far right-hand column.

Neighbour call	Focal call/behaviour	lower neighbour vocalisation mean	upper neighbour vocalisation mean	*N*	*P*	adjusted α-level
Twitter	anogenital present	0.217	0.380	30	0.062 ns	n = 4 α = 0.0125
	bristle	0.299	1.027	30	0.004 *	
	twitter	0.013	0.344	30	<0.001 *	
	loud shrill	0.583	10.323	30	<0.001 *	
Loud Shrill	anogenital present	0.128	0.334	31	0.026 *	n = 4 α = 0.0125
	bristle	0.376	0.906	31	0.009 *	
	twitter	0.076	0.393	31	<0.001 *	
	loud shrill	0.000	11.800	31	<0.001 *	
Chatter	composite of intragroup agonistic behaviour	0.015	0.082	27	0.043 *	n = 2 α = 0.025
	chatter	0.025	0.069	27	0.188 ns	
Chirp	share food	0.023	0.103	31	0.012 *	n = 5 α = 0.01
	grooming invite	0.019	0.182	31	0.024 *	
	allogroom	0.671	0.789	31	0.369 ns	
	active affiliative contact	0.154	0.332	31	0.149 ns	
	social play	0.119	0.015	31	Ŧ	
	chirp	0.000	0.226	31	0.031 *	
	feed ~	3.283	6.857	31	0.003 *	n = 2 α = 0.025
	forage ~	1.263	1.086	31	0.853 ns	
Ek	agitated locomotion	3.287	7.236	30	<0.001 *	n = 5 α = 0.01
	inactive alert	56.703	70.292	30	<0.001 *	
	scent mark	0.432	0.634	30	0.049 *	
	self-scratch	1.145	1.179	30	0.431 ns	
	self-groom	0.416	0.102	30	Ŧ	
	ek	0.063	0.595	30	0.094 ns	
	tsik	0.094	0.078	30	Ŧ	
Tsik	agitated locomotion	4.055	6.032	31	0.020 *	n = 5 α = 0.01
	inactive alert	57.626	68.078	31	<0.001 *	
	scent mark	0.595	0.539	31	Ŧ	
	self-scratch	0.774	1.490	31	<0.001 *	
	self-groom	0.229	0.322	31	0.318 ns	
	ek	0.597	0.049	31	Ŧ	
	tsik	0.008	0.081	31	0.125 ns	

Fig. 4.2 Effect of levels of neighbour intergroup agonistic vocalisation (twitter and loud shrill) on: (i) marmoset intergroup agonistic behaviours: anogenital present and bristle; (ii) marmoset intergroup agonistic vocalisations: twitter and loud shrill. Columns represent mean percentage time for behaviours and mean frequency per 5 min for vocalisations across focal individuals (± 1 SE) during observations with high (grey bars) and low (white bars) neighbour vocalisation. Asterisk (*) denotes significance.



(i)

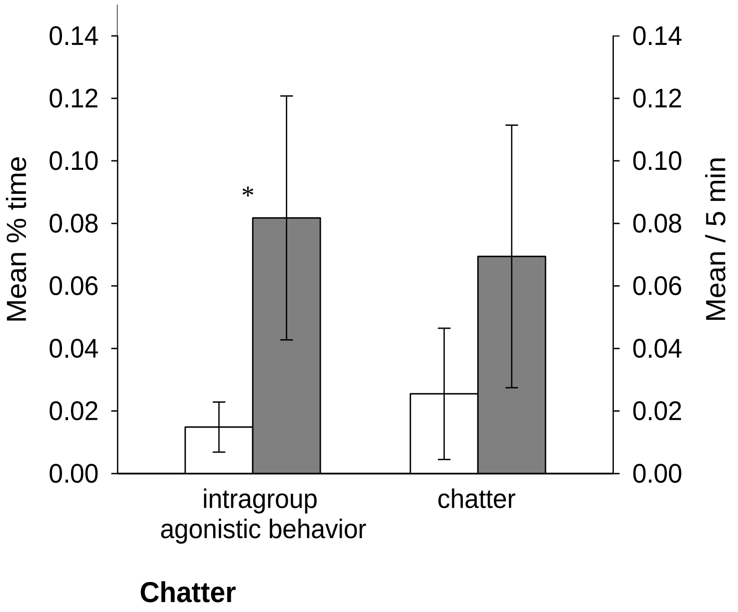


(ii)

Agonistic Intragroup Neighbour Vocalisation

Neighbour chatter vocalisations occurred in 39.7% of observations. The intragroup agonistic behaviours were collapsed into a single category as they occurred too infrequently to allow statistical analysis of the separate variables. Marmosets spent significantly more time in intragroup agonistic behaviours (composite of: steal food; chase; and attack) during observations with high neighbour chatter vocalisation than in observations with low neighbour chatter vocalisation (*N* = 27, *P* = 0.043; Fig. 4.3). However, although the mean rate of focal chatter was higher during high neighbour chatter vocalisation than during low the difference was not significant (*N* = 27, *P* = 0.188; Fig. 4.3).

Fig. 4.3. Effect of levels of neighbour intragroup agonistic vocalisation, chatter, on marmoset intragroup agonistic behaviour and vocalisation. Columns represent mean percentage time for behaviours and mean frequency per 5 min for vocalisations across focal individuals (± 1 SE) during observations with high (grey bars) and low (white bars) neighbour vocalisation. Asterisk (*) denotes significance.



Affiliative Neighbour Vocalisation

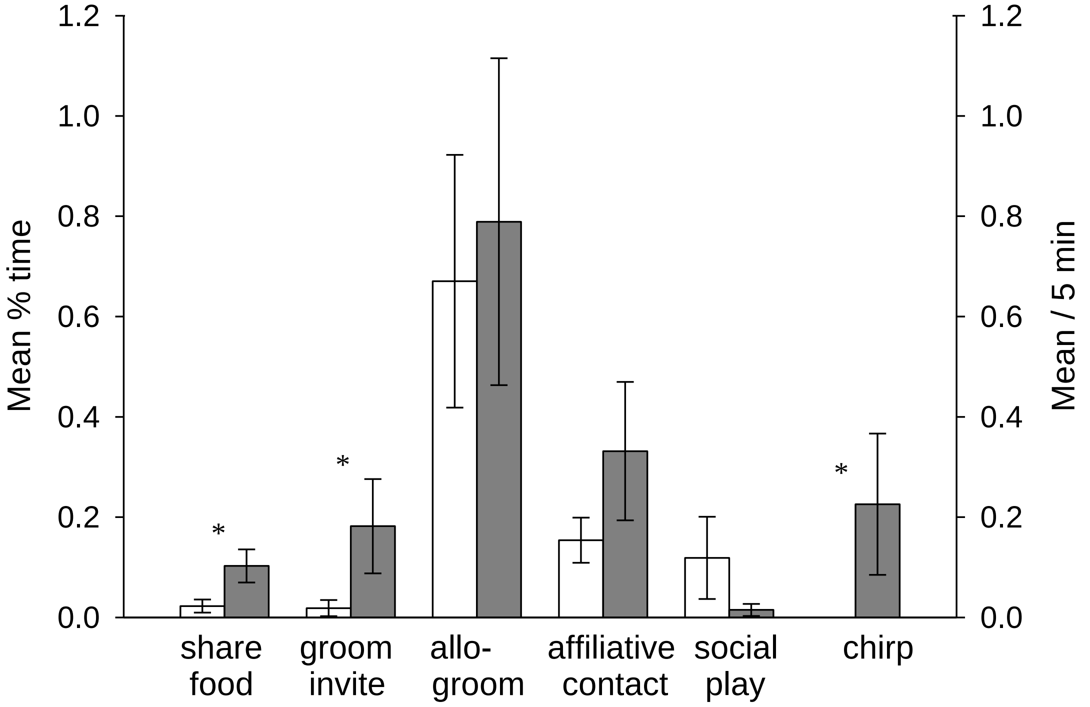
Neighbour chirp calls occurred in 64.6% of observations. During observations with high neighbour chirp vocalisation marmosets spent significantly more time sharing food ($N = 31$, $P = 0.012$) and in grooming invite behaviour ($N = 31$, $P = 0.024$) and emitted significantly more chirp calls ($N = 31$, $P = 0.031$) than in observations with low neighbour chirp vocalisation (Fig. 4.4). Marmosets spent more time allogrooming and in active affiliative contact during high neighbour chirp vocalisation observations than during low, but the differences did not reach significance (allogrooming: $N = 31$, $P = 0.369$; affiliative contact: $N = 31$, $P = 0.149$; Fig 4.4). Conversely, marmosets spent less time in social play during high neighbour chirp observations than during low.

The data were analysed, post hoc, to determine whether marmosets spent more time feeding and foraging during observations with high neighbour chirp vocalisation than with low. A significant difference was found for feeding ($N = 31$, two tailed, $P = 0.003$) but not for foraging behaviour ($N = 31$, two tailed, $P = 0.853$).

Anxious Neighbour Vocalisation

Neighbour ek vocalisations were present in 79.0% of the observations, and neighbour tsik vocalisations in 62.9% of the observations. Table 4.1 shows the statistical test results comparing the levels of focal alarm behaviours and vocalisations during observations with high and low ek, and tsik neighbour vocalisation; Fig. 4.5 illustrates the comparisons. As we predicted, the time spent by marmosets in both agitated locomotion and stationary alert was significantly higher in observations with high levels of neighbour ek (agitated locomotion: $N = 31$; $P < 0.001$; inactive alert: $N = 31$; $P < 0.001$) and for high levels of neighbour tsik than for low (agitated locomotion: $N = 31$;

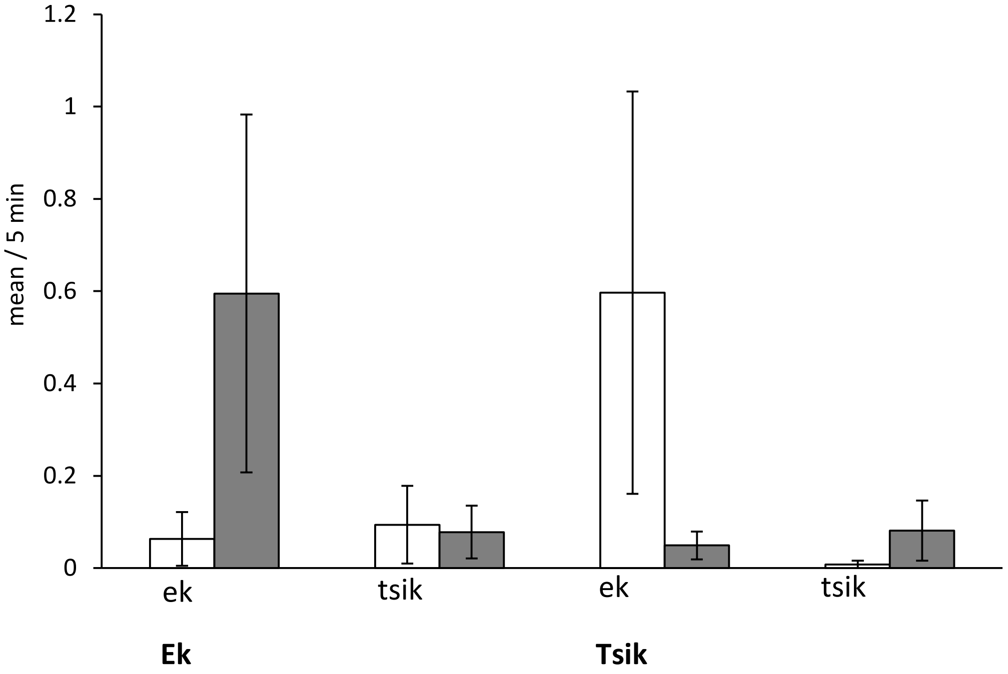
Fig 4.4 Effect of levels of neighbour affiliative vocalisation, chirp, on marmoset affiliative behaviours: share food; grooming invite; allogroom; active affiliative contact; social play and on marmoset affiliative vocalisation chirp. Columns represent mean percentage time for behaviours and mean frequency per 5 min for vocalisations across focal individuals (± 1 SE) during observations with high (grey bars) and low (white bars) neighbour vocalisation. Asterisk (*) denotes significance.



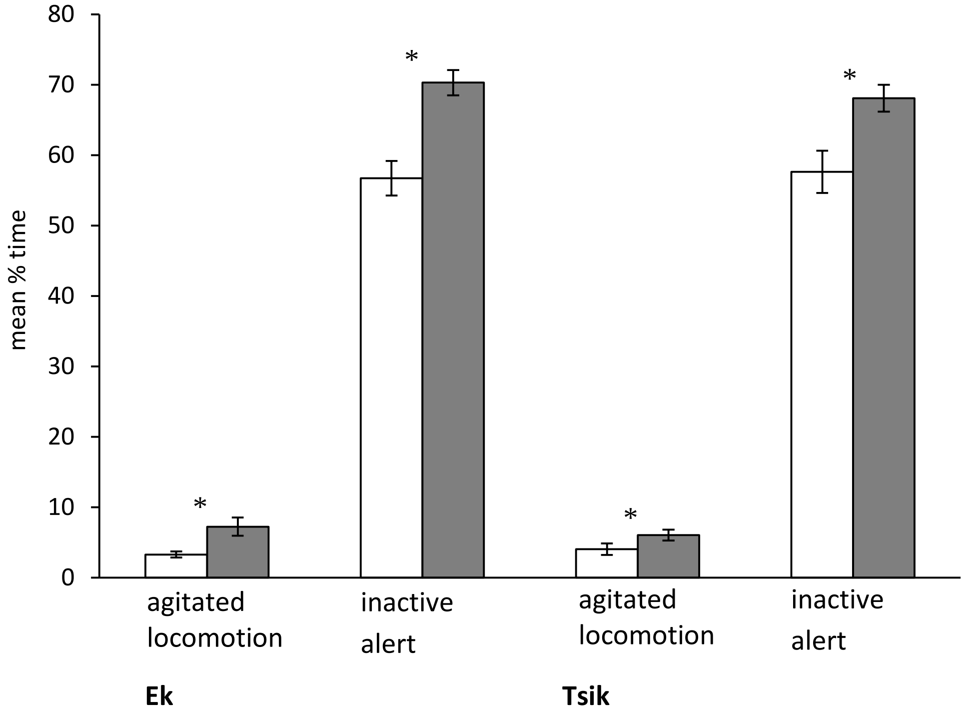
Chirp

P = 0.020; inactive alert: *N* =31; *P* < 0.001) (Fig. 4.5). Also as predicted, marmosets spent significantly longer scent marking at high levels of neighbour ek than at low (*N* = 31; *P* = 0.049) and scratching themselves at high levels of neighbour tsik than at low (*N* = 31; *P* < 0.001). As expected, marmosets spent longer scratching themselves and produced more ek and calls at high levels of neighbour ek calls than at low but the differences were not significant (self-scratch: *N* = 31; *P* = 0.431, ek: *N* = 31; *P* = 0.094). At high levels of neighbour tsik calls, marmosets spent more time autogrooming and

Fig 4.5 Effect of levels of neighbour anxious vocalisations, ek and tsik, on: (i) marmoset anxious vocalisations: ek and tsik; (ii) marmoset anxiety-related behaviours: agitated locomotion and inactive alert; and (iii) marmoset anxiety-related behaviours: scent mark; self-scratch; and self-groom. Columns represent mean percentage time for behaviours and mean frequency per 5 min for vocalisations across focal individuals (± 1 SE) during observations with high (grey bars) and low (white bars) neighbour vocalisation (* denotes significance).



(i)



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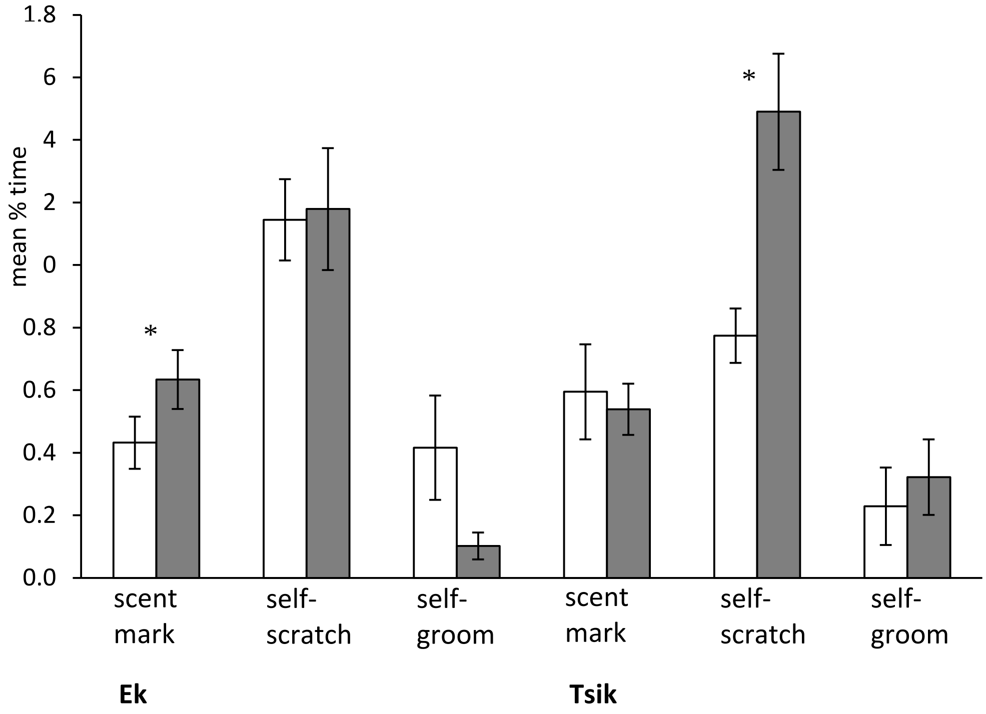


(iii)

emitted more tsiks than at low levels of neighbour tsik vocalisation, but the differences were nonsignificant (self-groom: *N* = 31; *P* = 0.318, tsik: *N* = 31; *P* = 0.125).

Contrary to our prediction, marmosets produced more tsiks in observations with low neighbour ek vocalisation than high; and produced more eks in low levels of neighbour tsiks than at high levels. Marmosets also spent more time scent marking at low levels of neighbour ek calls than at high.

4.3.1.2 Immediate Effect of Neighbour Vocalisation

Table 4.2 displays the results of the statistical tests comparing the proportion of 15-sec intervals before and after neighbour vocalisations during which focal behaviours and vocalisations in similar behavioural categories occurred. For the nine comparisons for which the difference did not lie in the predicted direction the *P* values are not reported. Within the first three behavioural categories, however, in all these four cases the two means were very similar to one another.

Agonistic Intergroup

As predicted, marmosets displayed a significantly higher mean probability of performing the agonistic intergroup behaviour, bristle, in the 15 sec following a neighbour agonistic intergroup call (twitter; loud shrill) than in the 15 sec before such a neighbour call ($N = 31$, $P = 0.019$; $N = 31$, $P = 0.010$; respectively). Also in the predicted direction, but not significant, were the following results: marmosets were more likely to perform anogenital present, or vocalise a twitter, following a neighbour twitter call; and were more likely to emit a twitter, or loud shrill, following a neighbour loud shrill (see Table 4.3). Two comparisons were not in the predicted direction: marmosets had a lower mean probability of performing anogenital present directly before a neighbour loud shrill call than after, and of producing a loud shrill call before a neighbour twitter call than after.

Agonistic Intragroup

The mean probability of marmosets engaging in intragroup agonistic behaviour (composite of chase; attack; steal food) was higher following neighbour intragroup chatter vocalisation than preceding, but this difference was not significant (N = 31; P =

Table 4.3 Statistical test results for the analysis of the immediate effect of neighbour vocalisation on focal marmoset behaviour; mean proportion of behaviours in the 15-sec pre-neighbour call with the mean 15-sec post-neighbour call. Asterisk (*) indicates *P* < 0.05. ns indicates a result in the predicted direction which was nonsigificant. Ŧ indicates means where the direction of difference is opposite to the predicted direction (one-tailed tests). ~ indicates two-tailed post hoc tests. Underlining indicates that p-values retain their significance at the adjusted α-level given in the far right-hand column.

neighbour call	focal call/behaviour	mean proportion pre-neighbour call	mean proportion post-neighbour call	*N*	*P*	adjusted α-level
Twitter	anogenital present	0.010	0.013	31	0.151 ns	n = 3 α = 0.017
	bristle	0.005	0.008	31	0.019 *	
	twitter	0.009	0.010	31	0.269 ns	
	loud shrill	0.007	0.005	31	Ŧ	
Loud Shrill	anogenital present	0.018	0.017	31	Ŧ	n = 3 α = 0.017
	bristle	0.004	0.010	31	0.010 *	
	twitter	0.011	0.013	31	0.336 ns	
	loud shrill	0.012	0.013	31	0.271 ns	
Chatter	composite of agonistic behaviour	0.005	0.012	31	0.343 ns	
	chatter	0.002	0.001	31	Ŧ	
Chirp	share food	0.001	0.006	31	0.008 *	n = 4 α = 0.0125
	grooming invite	0.000	0.001	31	0.500 ns	
	allogroom	0.005	0.006	31	0.262 ns	
	active affiliative contact	0.003	0.007	31	0.031 *	
	social play	0.000	0.000	31	-	
	chirp	0.004	0.003	31	Ŧ	
	feeding ~	0.036	0.037	31	0.836 ns	
	foraging ~	0.015	0.022	31	0.344 ns	
Ek	agitated locomotion	0.142	0.129	31	Ŧ	
	inactive alert	0.273	0.242	31	Ŧ	
	scent mark	0.014	0.016	31	0.200 ns	
	self-scratch	0.024	0.025	31	0.350 ns	
	self-groom	0.002	0.002	31	-	
	ek	0.003	0.004	31	0.313 ns	
	tsik	0.000	0.001	31	0.125 ns	
Tsik	agitated locomotion	0.120	0.112	31	Ŧ	
	inactive alert	0.218	0.191	31	Ŧ	
	scent mark	0.023	0.018	31	-	
	self-scratch	0.023	0.018	31	Ŧ	
	self-groom	0.002	0.002	31	-	
	ek	0.001	0.001	31	-	
	tsik	0.000	0.001	31	-	

0.343). The other comparison for this category was not in the predicted direction: there was a slightly lower mean probability of marmosets emitting intragroup agonistic calls (chatter) after neighbour chatter calls than before.

Affiliative

Consistent with my predictions, there was a significantly higher mean probability of marmosets engaging in the affiliative behaviours of food sharing (N = 31; P = 0.008), and active affiliative contact (N = 31; P = 0.031), after the neighbour affiliative call chirp than before. Also in the predicted direction, but not significant, marmosets were more likely to engage in allogrooming, and in grooming invite behaviour, after neighbour chirp calls than before (see Table 4.3). There was no difference between the mean probability of focal individuals engaging in social play before and after neighbour chirp vocalisation. For one of the comparisons the means were not in the predicted direction: marmosets produced more chirp calls before a neighbour chirp call than after. Regarding the post hoc tests: although marmosets had a higher mean probability of feeding and foraging directly following a neighbour chirp call than directly before the difference was not significant (feeding: N = 31, P = 0.836; foraging: N = 31, P = 0.344; both two-tailed).

Anxiety

As expected, there was a higher mean probability of marmosets performing scent mark and self-scratch, and of emitting an ek or tsik call directly after a neighbour ek call relative to before, but the difference was nonsignificant (scent mark: N = 31; P = 0.200; self-scratch; N = 31; P = 0.350; ek: N = 31; P = 0.313; tsik: N = 31; P = 0.125). Contrary to our predictions, marmosets were more likely to engage in agitated locomotion and to be in a state of inactive alert before neighbour ek and tsik calls rather than after. Marmosets were also more likely to scratch themselves before rather than after a neighbour tsik call.

4.3.2 Seep Call Function Results

Neighbour seep vocalisations occurred in 70.4% of our study observation sessions. I compared the mean proportion of vertical flight responses by focal marmosets 15 sec before a neighbour seep call to 15 sec after. In support of the anecdotal observations, we found a significant difference in the mean probability of marmosets performing vertical flight after a neighbour seep call (0.021) than before (0.004) ($N = 31$; $P < 0.001$).

4.3.3 Behavioural Welfare Indicators

In the main analysis I assessed the effect of high and low vocalisation on behaviours and calls within the same category of affect. Because I planned to play back chirp calls to marmosets in the next experiment (Chapter five) here I assessed the effect on behavioural welfare indicators of spontaneously produced neighbour chirp calls. Table 4.3 shows the results of statistical tests comparing the mean percent time that marmosets spent in behaviours indicative of positive and of negative welfare at high and low levels of neighbour chirp calls. Marmosets spent significantly longer in calm locomotion at high levels of neighbour chirp calls than low (calm locomotion: $N = 31$; $P < 0.000$), however they also spent significantly less time in inactive rest (inactive rest: $N = 31$; $P = 0.002$). It is possible that the decreased time resting may be partly explained by the increase in food sharing, feeding, and active affiliative contact (see Table 4.2) all positive or neutral welfare indicators, at high neighbour chirp levels.

Because the specific welfare effects of the neighbour chirp call seemed to be, at worst, neutral, and possibly positive, and because the influence on some social behaviours not considered as conventional welfare indicators was found to be positive (active affiliative contact and share food above) I considered it acceptable to play back pre-recorded chirp calls in the next chapter.

Table 4.4 Statistical test results for the analysis of the overall effect of neighbour vocalisation on behavioural indicators of positive and negative welfare in the focal individuals; mean percent time spent in behaviours indicative of positive and negative welfare per observation session for observations with a high frequency of neighbour vocalisations (upper) and with a low frequency (lower). Asterisk (*) indicates significance. Underlining indicates that p-values retain their significance at the adjusted α-level given in the far right-hand column.

Neighbour call	Focal behaviour	Valence of welfare indicator	lower neighbour vocalisation mean	upper neighbour vocalisation mean	*N*	*P*	adjusted α-level
Chirp	calm locomotion	+ve	1.316	2.287	31	<0.000 *	n = 2
	inactive rest		9.570	4.085	31	0.002 *	α = 0.025
	scent mark	-ve	0.457	0.654	31	0.061 ns	
	self-scratch		1.247	1.154	31	0.659 ns	
	agitated locomotion		5.493	5.014	31	0.490 ns	
	inactive alert		73.158	74.625	31	0.435 ns	

4.3.4 Family-wise Error Rate Correction

Following adjustment for multiple testing (see Chapter three), the results of the analyses of overall effects of intergroup agonistic and anxious neighbour vocalisations were mostly unaffected, however all the previously significant results for intragroup agonism and affiliation were rendered nonsignificant (see Table 4.2). For intergroup agonism, only one out of 7 originally significant results was lost (the overall influence of loud shrill on anogenital present). Two out of the 6 results significant at the non-adjusted α-level for a neighbour effect of anxiety disappeared (the influence of neighbour ek calls on scent marking behaviour and of neighbour tsik calls on agitated locomotion). Regarding the immediate effect of spontaneous neighbour calls, the only significant result retained was the increased probability of food sharing directly following a chirp (affiliative) call (see Table 4.3). The analyses on welfare indicators were not affected. Overall, following adjustment of the α-level, there was evidence for neighbour effects for intergroup agonism, anxiety and for affiliation, but not for intragroup agonism.

4.4 Discussion

4.4.1 Agonistic

As predicted, I found that the levels of intergroup agonistic behaviours (anogenital present, bristle, twitter and loud shrill) were all significantly higher at high levels of the neighbour intergroup vocalisations (twitter and loud shrill), than at low levels; the exception was focal anogenital present during neighbour twitter. This overall finding is consistent with a neighbour effect for intergroup aggression. The close temporal association found between the production of neighbour twitter and loud shrill calls and bristle behaviour in nearby marmosets provides support for a causal link. I speculate that the contagion of intergroup agonistic behaviour may improve co-ordination of group aggression toward conspecific groups encountered in the wild (e.g. Clayton, 1978).

Regarding intragroup aggression, we found, as expected, that the composite of marmoset intragroup aggressive behaviour was significantly higher at higher levels of the intragroup neighbour agonistic vocalisation (chatter) than at lower levels. This is consistent with the social contagion of intragroup aggression. Lack of evidence for a close temporal association between the neighbour call and focal behaviour indicates that we should infer a causal link only with some caution.

Previously, researchers have found evidence for an effect of agonistic intergroup neighbour calls and noises on aggressive intragroup behaviour in chimpanzees (Baker and Aureli, 1996; Videan et al., 2005). My results are broadly consistent with these findings in that they support the social contagion of aggression. Furthermore I have demonstrated a neighbour effect of agonistic behaviour for marmosets that is specific to each subclass: intergroup and intragroup, respectively.

4.4.2 Affiliative

Consistent with our prediction, we found that high overall levels of neighbour chirp calls were associated with significantly longer time spent by nearby marmosets in affiliative behaviours: grooming invite and share food and with more affiliative vocalising by focal marmosets (chirp call). Focal individuals were also significantly more likely to engage in food sharing and in active affiliative contact immediately after a neighbour chirp vocalisation than just before. The neighbour effect for active affiliative contact appears to be largely confined to the 15-sec interval post neighbour call. My results support the existence of an affiliative neighbour effect.

I suggest that the chirp call may function as an invitation for conspecifics to engage in affiliative contact. This would provide an explanation for the increase in grooming invite behaviour in focal individuals through the contagion of behaviour inviting affiliative contact and for the immediate increase in active affiliative contact following neighbour chirp. However, this explanation does not fully account for the greater time spent by marmosets in food sharing at relatively higher levels of neighbour chirp calls.

I categorised the chirp call as an affiliative call based on previous literature (Epple, 1968; Stevenson and Rylands, 1988). However, there appears to be no consensus on the exact function or context of this call. As well as being described as an affiliative vocalisation, the chirp call has also been frequently linked to feeding (Epple, 1968; Goldman, 2000), especially on highly favoured foods. Indeed, Vitale et al. (2003) referred to a particular *Callithrix jacchus* vocalisation as a solely food-associated call. They stated that they have heard marmosets making this call only while handling, eating or viewing favoured foods. However, given the low resolution of their spectrogram, it is difficult to know if the vocalisation they used is the same call I identify as chirp. A post hoc analysis of our data supports the association of chirping with feeding, although not with foraging. However, although an overall high rate of neighbour chirp calls was found to be associated with a significantly longer time spent in feeding by marmosets, there was no evidence for an immediate effect.

Kitzmann and Caine (2009) investigated the effect of chirp playback in *Callithrix geoffroyi*. Spectrograms provided in that report closely resemble those of *Callithrix jacchus* chirp calls in this study. Those authors noted an overall increase in the level of feeding behaviour following chirp playback, consistent with the overall neighbour effect found in this study and, contrary to our findings, in foraging behaviour. They did not investigate social behaviours or the immediate effect of chirp playback on feeding related behaviours. In the current study the link between spontaneous chirp calls and feeding may indirectly explain the apparent association of neighbour chirp with focal food sharing behaviour, but it does not explain the association with other affiliative behaviours unrelated to feeding. Pook (1976) stated, more specifically, that chirping was mainly associated with the excitement of feeding following the presentation of food. Another possible explanation, then, is that the chirp call is a more general expression of anticipatory excitement in expectation of a desirable and pleasurable event. The apparent contagion of chirp calls may indeed reflect the contagion of this positive arousal.

Regardless of the precise function of the chirp call, it does appear to be associated with nonthreatening events at least some of which are affiliative in nature. Thus, my findings provide supporting evidence for affiliative social contagion in accord with the findings of a previous study on chimpanzees (Videan et al., 2005). I have also presented new evidence bearing on the contextual use and function of the marmoset chirp vocalisation.

It is unclear exactly how affiliative social contagion through the chirp call relates to wild marmoset behaviour. Bezerra and Souto (2008) did not include an equivalent to the chirp call in their repertoire of wild *C. jacchus* vocalisations. It remains to be established whether the chirp call is confined to captive marmosets or whether it was not heard in the wild group due to the context in which calls were collected. Certainly, the chirp call seems to be important for the captive marmosets in this study because they use it frequently. The chirp call clearly merits further research attention.

4.4.3 Anxious

As I predicted, focal individuals spent significantly longer in agitated locomotion and in a state of inactive alert at overall high levels of the neighbour anxiety-related vocalisations ek and tsik than at low levels. My findings from the overall analysis support the proposition that hearing ek and tsik neighbour calls causes focal individuals to enter a state of increased alertness, consistent with the social contagion of mild anxiety. The social contagion of anxiety for the same type of call in the focal as the neighbour was in the predicted direction. However, for both anxiety-related calls investigated the other call type in the focal individuals was more likely at low levels of the other call type than at high. This suggests that neighbour ek vocalisations do not influence nearby individuals to produce tsik and vice versa, suggesting that the two anxiety calls are representative of separate anxious states.

Contrary to expectation, none of the anxiety-related neighbour calls appeared to have any immediate effect on individuals. Focal individuals were more likely to be in a state of inactive alert or agitated locomotion just before neighbour ek and tsik calls rather than just after. The sequential analysis indicates that the results for anxiety should be treated with some caution. The relationship between the neighbour anxious calls and focal behaviour may not be causal: individuals may, instead, have been influenced simultaneously by some external, anxiety provoking, event. Assessment of the neighbour effect from playback of pre-recorded anxiety-related calls in an explicitly non-anxiety provoking context would probably provide clearer evidence as to whether the relationship between anxious neighbour calls and focal anxiety-related behaviours is causal.

Taken together, my results provide some evidence to support a neighbour effect for anxiety, with stronger evidence for neighbour ek than for tsik. In wild marmosets the social contagion of anxiety is likely to have an adaptive function. Nakayama (2004) suggested that the contagion of anxiety (‘negative arousal’) in general may help individuals to avoid harm by increasing their level of alertness to potential threat. Indeed, vigilance is considered to be one of the main anti-predator strategies used by small primates along with concealment and flight (e.g. Cheney and Wrangham, 1987). Stojan-Dolar and Heymann (2010) concluded that the main function of vigilance in moustached tamarins appeared to be predator-related, but that it may also act to sustain group cohesion.

A fourth anti-predator behaviour observed in small primates is referred to as mobbing: many individuals within a social group vocalise and move towards or around a potential predator (e.g. Passamani, 1995). Wild marmosets have been observed to mob a variety of different predators, for example: a felid (a margay cat) (Passamani, 1995) a procyonid (the coati) and a mustelid (the tayra) (Bezerra and Souto, 2008).

In general, calls labelled as mobbing or alarm calls do not *a priori* function to influence the behaviour of conspecifics: there are other possible adaptive, ultimate, functions for mobbing calls. Mobbing of predators must confer some long-term benefit since it clearly carries an immediate cost to the caller (e.g. Curio, 1978; Bartecki and Heymann, 1987). Bartecki and Heymann (1987) observed snake-mobbing by wild tamarins and proposed that the adaptive function of mobbing is the cultural transmission of information about the identity of potential predators. Social contagion of anxiety, through hearing neighbour anxiety-related vocalisations, may contribute to the social learning of predator identity during mobbing (e.g. Passamani, 1995). However, experiments with tamarins suggest that for social learning to occur individuals may need to observe as well as to hear a conspecific demonstrator (Campbell and Snowdon, 2009).

A number of further possible functions for mobbing have been proposed (reviewed by Wheeler, 2008). Mobbing may function to alert the predator to the fact that it has been detected (e.g. perception advertisement: Zuberbühler, 2009), to alert other group members to the presence of the predator, or to force the predator to move away (e.g. Clara et al, 2008). Wheeler (2008) concluded that the hypothesis that best explained the evolution of mobbing in wild capuchin monkeys, across all contexts, was the recruitment of conspecifics to mob the predator ('mobbing recruitment': Curio, 1978). Wheeler (2008) did not discuss potential mechanisms for the recruitment of conspecifics to mobbing. The results of the current study suggest that the social contagion of anxiety, through hearing neighbour tsik calls, may facilitate mobbing recruitment. Neighbour tsik calls appear to increase agitated locomotion and tsik calls in nearby marmosets. I suggest that the social contagion of anxiety presents a likely mechanism for mobbing recruitment.

4.4.4 Seep Call Function

I found that marmosets were more likely to perform vertical flight after a neighbour seep call than before. My results provide quantitative evidence, consistent with previous anecdotal observations (e.g. Epple, 1968; Pook, 1976), that the seep call appears to induce vertical flight in nearby marmosets. It would be interesting to investigate the function of the alarm call further. It may be that the common marmoset has predator-specific variations of alarm calls such as the seep. Different predator models, or silhouettes, could be systematically applied to groups of marmosets and their behavioural and vocal responses towards different models recorded. The calls could then be acoustically analysed. However, there are some ethical and welfare implications of such research, for example, exposure to the models may lead to increases in stress and should therefore be very infrequent.

4.4.5 Captive welfare: Effect of Neighbour Calls

The demonstration of social contagion in marmosets has important implications for captive welfare. Although the apparent spread of mood and behaviour from neighbouring groups to nearby individuals is likely to occur also in the wild, it is likely to lead to more pronounced effects in the captive situation. Larger numbers of captive groups of marmosets are close together for much longer than might be expected in the wild, and captive marmosets do not have the same option of moving apart. Affiliative social contagion among captive groups may function to increase positive welfare behaviour, whereas the effect of the contagion of agonism and of alarm is more equivocal. Whilst increases in agonistic- and alarm-related behaviours are largely incompatible with the performance of affiliative behaviours within the same room it is possible that relatively infrequent bouts of alarm calling may have some (delayed) positive welfare effects (Chamove and Moodie; Moodie and Chamove, 1990). However, there have been criticisms of negative environmental enrichment of this type (e.g. Roush et al., 1992). An important factor highlighted by Chamove and Moodie (1990) is that the exposure to alarming or anxiety-inducing events should be infrequent and that the events themselves be temporary. In captive environments where anxious calls are unlikely to be heard from other groups, even infrequently, for example where there is only one social group, it is possible that the occasional playback of alarm or anxiety calls may provide environmental enrichment. However, in captive environments where marmosets are exposed daily to infrequent neighbour alarm-calling and anxiety calls it seems unlikely that additional negative enrichment would improve welfare. In some captive environments, especially where a large number of social groups are housed within close proximity, the welfare of marmosets may suffer from overly frequent exposure to neighbour alarm/anxious calls. Even in cases where contagion of anxiety related behaviours may be considered as enrichment, the element of choice and control is important in any practical application (see Chapter one). Marmosets should be given the opportunity to remove themselves from exposure to the negative enrichment.

Given the neighbour effect that has been demonstrated, the welfare of captive individual marmosets may be affected (either positively or negatively) depending on where they are placed. It is important, then, that the potential influence, both good and bad, of neighbouring groups on the welfare of nearby marmosets is taken into account in the captive management of marmosets.

4.4.6 Methodological issues

From a methodological perspective it would undoubtedly have been preferable to be able to discriminate between the calls made by ‘true’ neighbours (non-focal group neighbours) from those made by individuals within the same social group as the focal individual being observed (focal group neighbours). Given the nature of the calls investigated it was not feasible to determine focal individual group-mate calls from video footage or to code the calls of more than one individual during the ‘live’ coding. Although I was aware of this issue from the outset of my experimental design, I was also conscious that the only solution would have involved the isolation of marmosets from their social group. This would not only have been highly undesirable from a welfare perspective, but also with regard to ecological validity. I considered it very important (as stated in Chapter three) to investigate social contagion in a social context.

I had made the assumption that the calls made by the other members of the focal individuals’ groups (focal group neighbours/non-true neighbours) were likely to be to a large extent diluted by those made by the individuals of neighbouring groups (non-focal group neighbours/true neighbours), given the large number of social groups in each room. I can now attempt to theoretically assess the relative proportion of calls likely to have been produced by ‘true neighbour’ individuals relative to those likely to have issued from ‘non-true neighbour’, focal individual group mates. Assuming that the call rate is, on average, equally shared among adult and juvenile individuals I can examine the relative proportions likely to have been produced by each of these age categories that influenced the focal individual. Across all focal individuals in all rooms the maximum proportion of ‘non-true neighbour’ individuals was 18.5% whilst the minimum proportion of ‘true neighbours’ was 81.5%, with overall mean proportions of 8.7% and 91.3% respectively. Thus, I contend that the proportion of ‘non-true neighbour’ calls is likely to have been vastly outweighed by the proportion of ‘true neighbour’ calls.

Another methodological issue is that number of individuals visible to each focal individual varied. Focal individuals were able to see both focal group neighbours and non-focal group neighbours housed opposite. The numbers of each type of neighbour visible to each focal individual differed; according to the number of individuals in an individual's focal group and the composition of the colony room in which they were housed. This is likely to impact on the results to some degree but it was not practicable (or ethically acceptable) to equalise the number of each type of neighbour visible to each focal individual. However, since the design was within subjects, it was not considered to be a confounding factor.

4.5 Conclusion

The conclusions drawn from this study imply that the connection between neighbour calling and focal behaviour is causal. However, whether or not a causal connection exists cannot be established on the basis of the current data. Rather than displaying dependent responses to conspecific vocalisations, individuals may instead be reacting independently to similar external stimuli.

Another alternative explanation for the present results, instead of social contagion, is that focal behaviour may indeed be contingent on neighbour calls but may reflect either an entirely instinctive or entirely learned response, either selected for, or shaped by, direct interaction with conspecifics. This criticism probably applies more to the apparent contagion of intergroup aggression and anxiety, for the anxiety-related calls that appear to function as mobbing calls in greater frequency (the tsik call), than to intragroup aggression, affiliation or anxiety (for ek: the most context-generalised anxiety call). The chapter to follow will report a direct test of causality for the social contagion of affiliation, by monitoring behaviour of individuals when exposed to the playback of pre-recorded chirp calls. This will allow me to assess the effect on marmoset behaviour of chirp calls out of context and thus to address this limitation directly.

Although I cannot entirely exclude alternative explanations, it is likely that social contagion has an important influence given the strong and consistent associations between the overall level of neighbour calls and focal behaviour of the same affective category. Nonetheless, further research including experimental manipulation is needed to reveal the precise mechanisms underlying the neighbour effect.

Taken together, the results of this study provide the first systematic evidence to support the existence of a neighbour effect in marmosets. I have extended research into social affective contagion and provided further support for the generality of the neighbour effect.

Chapter 4a

Marmoset Call Rate Analysis

Marmoset Call Rates Analysis

4a.1 Introduction

Although many previous studies have investigated one or two types of calls in isolation, few have investigated the rates of many call types simultaneously, within an identical context, (with the exception of Pook, 1976). The data collected for this study provided me with the opportunity to assess the typical emission rate of many different call types from data collected in a typical captive social context, and coded from a comparatively large sample size.

The published information on call rates is somewhat limited. I surveyed the available data on mean call rates and carried out calculations where necessary to allow comparison with the rates calculated from our data. I display both sets of data, along with relevant comparative information, in the results section of this chapter.

4a.2 Methods

I calculated the mean call rates in the current study (Table 4.5) from data taken from the recordings of the individuals in four different colony rooms from a total of 106 adults and juveniles (see section 4.2 above): a total of 38.5 hr of audio recording taken over 15 days (over 9.5 hr per room). Both my audio recording and subject sample size were thus large relative to those of previous studies.

I measured the mean call rate per marmoset per hour by first calculating a mean number of calls per colony room per 5-min session (focal and neighbour calls). These values were then divided by the total number of individuals within that colony room (adults and juveniles) and a mean was calculated across rooms to give a mean number of calls per individual per 5-min session. This was then converted to an hourly rate per animal by multiplying by 12.

4a.3 Results and Discussion

Table 4.5 displays the mean call rates calculated from the current study data and rates for equivalent calls reported in previous studies. As stated in Chapter three, the call type referred to as phee encompasses the two sub-categories; loud shrill (long, open-mouthed phee calls) coded in the current study; and the shorter, closed or open-mouthed, phee calls. For studies in which the narrower category of loud shrill was coded the loud shrill rate only is given. To allow cross-comparison, for studies using only the broader category of phee call (inclusive of loud shrill calls) the mean phee call rate is given. The exception is Stevenson and Rylands (1988), who divided phee calls into mutually exclusive categories, phee and loud shrill, and assigned a nominal rate description to each.

Epple (1968) provided detailed descriptions of each call in captive marmosets' repertoire but did not report call rate; Winter (1978) gave call rates for one-day-old infants only; Stevenson and Rylands (1988) presented call rate as a nominal level category only (see Table 4.5); and Bezerra and Souto (2008) did not report the mean call rates of wild marmosets.

Table 4.5 Comparison of average call rates (per individual, per hr) in the current study with those reported in previous studies. * indicates information on call rates was classified as: very common; common; rare; or very rare; ^ indicates mean when loud shrill call defined as one syllable (allowing comparison with Goldman (2000); ~ indicates that the call type is quantified as the two separate call type totals of the composite call; - indicates rate of call type not investigated in the study.

Call type		**Previous studies of captive marmosets**				
	Current study	**Pook (1976)**	**Jones (1993)**	**Norcross and Newman (1993)**	**Goldman (2000)**	**Stevenson and Rylands (1988)***
Twitter	4.58	1.5	6.0	-	-	v. common
Loud Shrill	1.96 (2.38^)	6.2	-	-	(3.17)	common
(Phee)	-	5.4	3.6	9.6	-	common
Chatter	0.58	0.0	-	-	-	v. common
Chirp	1.36	0.6	-	-	-	common
(Whirr)	75.50	54.7	39.9	-	-	v. common
Ek	2.91	0.2	-	-	-	common
Tsik (audible to humans only)	2.62	0.1	-	-	-	common
Tsik (audible and inaudible to humans)	2.87	-	-	-	-	-
Rapid-fire tsik	0.24	0.0	-	-	-	common
Seep (audible to humans only)	1.07	0.0	4.0	-	-	common
Seep (audible and inaudible to humans)	1.33	-	-	-	-	-
(Seep-ek)	~	0.1	-	-	-	-

Jones (1997) reported phee call rates, but they are not representative of the mean rate under normal social circumstances. The main focus of her study was the effect of social isolation and new pair formation on phee call rate: thus, the reported rates were measured under various manipulated conditions. Similarly, Norcross and Newman studied the change in call rate of nonreproductive postpubertal marmosets on removal from the natal group (Norcross and Newman, 1997). Though, in an earlier study (Norcross and Newman, 1993), they gave a mean rate for breeding individuals in home cages in a territorial context (see Table 4.5).

Mean call rates for selected call types, are available in unpublished theses (Pook, 1976; Jones, 1993; and Goldman, 2000: see Table 4.4). Pook (1976, p. 105) reported mean call rates calculated from data collected in a preliminary investigation designed primarily to provide comparative data on the co-variance of vocalisation and activity rates in two species of marmoset. His call rates were based on a relatively long total sample duration of 24 hr, but from observation of two pairs of marmosets only. The pairs were housed within auditory but not visual contact with the pairs, and both males were wild caught 2 years prior to the study.

Jones (1993, p. 47) investigated diurnal variation in rates of the twitter, phee and whirr calls. Her rates were calculated from rates measured from the systematic audio coding of a relatively large audio sample: 10.5 hr over 5 days, with a subject sample size of 30 individuals. Her recordings were also made in the typical social context. However, there may have been an elevated rate of phee calls caused by a large number of separation phee calls due to a singly housed individual in the room. Further, both the twitter and phee rates might have been elevated due to the inclusion of daily 40-min sampling periods when one social group was moved to within visual contact of a neighbouring group which was otherwise only in auditory contact. Jones (1993) also provided a conservative estimate of seep call rate based on her experience as an observer.

Goldman (2000, p. 42) reported data from which we were able to calculate a mean rate for loud shrill calls. Goldman coded each separate syllable as a separate call (rather than each sequence of 1-3 calls as an individual call, as in the current study and Pook, 1976). To allow direct comparison, I therefore calculated an equivalent rate from my data by multiplying each call by its number of syllables (I coded the syllable number of each loud shrill call during coding) (see Table 4.4). Her audio recording was relatively long (over 12 hr) but her sample size was very small (one socially-housed group of 5 individuals).

Ultrasonic Calls

Whilst conducting the current study I saw marmosets opening their mouth wide as though to give an alarm call, but heard no sound emerge. However, other marmosets were observed to respond with a vertical flight response: providing strong evidence that they heard a functionally significant call. This observation suggests that such calls may have been in the ultrasonic frequency range. My recording equipment gave a frequency range of up to 28 kHz. I examined all the recorded audio both aurally and visually through spectrographic analysis (a visual representation of call frequency against time). During the spectrographic analysis of the recorded vocalisations it was possible to code calls in the ultrasonic range from their spectrographic trace alone. Although many calls have harmonic frequencies in the ultrasonic range, I also recorded calls with all or part of their fundamental frequencies in the ultrasonic range. Specifically, I recorded many seep calls with all or part of the call in the ultrasonic range, and some tsik calls with the start of the call in the ultrasonic range. The rates given in Table 4.5, above, were obtained in this way.

The comparison of the call rates found in different studies is somewhat limited by differences in social environment, group composition and identity and recording and/or observing methods. For example, Pook (1976) studied a mixture of marmosets bred in captivity and wild caught whereas all the other studies investigated captive-born marmosets only. Another difference is that Pook investigated the call rates of breeding individuals only whereas the other studies involved a mixture of reproductive and nonreproductive individuals. Norcross and Newman (1997; 1999) found that reproductive adults produce phee calls at a higher rate than noreproductive adults. However, the relative differences between the call type rates may not differ as much as the absolute differences.

In general, all my call rates are higher than those found by Pook (1976) with the exception of the loud shrill call, for which he found a much higher rate. One possible reason for this divergence is that Pook's rates were based on the first experiment in his thesis, when the two marmoset pairs had been newly formed from a larger lab colony. The loud shrills might then have been separation calls to the larger social group, rather than true 'home cage' territorial loud shrills. The phee call rates in all the previous studies indicate that our loud shrill call rate is not much higher, given that the phee constitutes the loud shrill and shorter phees (except for Pook, 1976 who classified phees as I did).

The affiliative whirr was the call type with the highest mean rate across all previous studies and our own consistently. The affiliative chirp call occurred at a similar but slightly higher rate relative to whirr calls in our study (0.018) compared to Pook's study (0.011).

The rate of whirr calls made by marmosets in the current study was just under twice as high as that found by Jones (1993). Conversely, however, the other call types investigated by Jones (the intergroup agonistic call: twitter; and the alarm call: seep) were produced at a much higher rate than in my study. The elevated rates for twitter (Jones, 1993) compared to my study may be due to the audio sample being collected during visual confrontation between two social groups in the middle of the day (see above).

Ultrasonic calls

A historical curiosity is that Sanderson (1957, p. 52) assumed that "it is certain that these tiny animals also carry on an apparently continuous flow of regulated sounds at supersonic levels". In contrast, Pook (1976) stated that he detected no calls of a purely ultrasonic nature (that is, calls with a fundamental frequency starting above the audible range for humans). Pook (1976) acknowledged it to be a generally accepted fact that many marmoset vocalisations contain ultrasonic frequencies, though he pointed out that these frequencies may not be functionally important.

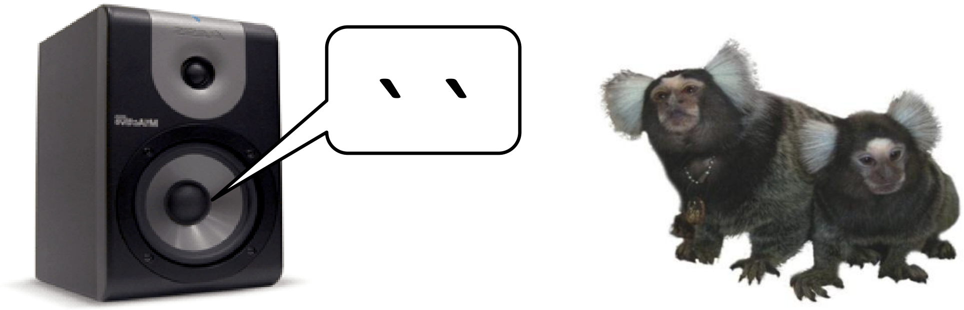
In the current study, the mean rate of ultrasonic seeps was found to be 0.26 calls/marmoset/hr and of part-ultrasonic tsiks, 0.25 calls/marmoset/hr. Since the division is an arbitrary one according to the capabilities of human hearing, I give the combined rate for both ultrasonic and audible tsik and seep calls in Table 4.5. I also give the rate for audible tsik and seep calls only, to allow direct comparison to previous studies that, presumably, did not quantify ultrasonic calls due to the technical limitations of their recording equipment.

4a.4 Future Research on Marmoset Call Rates

Typical call rates for marmosets in the wild are not available in the research literature. It would be very interesting to code audio footage recorded from marmoset social groups housed separately within large colony rooms, where there is limited opportunity for intergroup aggression, compared to the colony rooms containing many home cages.

Chapter 5

Chirp Playback Study: Effect of the Playback Pre-recorded Conspecific Affiliative Vocalisations on Marmoset Social Behaviour



In the previous chapter I found support, through an observational study, for a neighbour effect of affiliation in marmosets. In the current chapter I attempt to manipulate the neighbour effect, in an experimental study, through the playback of pre-recorded affiliative (chirp) calls. I thus test directly the inference of a causal link between spontaneously produced chirp calls and the behavioural changes in nearby marmosets. I also pursue suggestions, made in Chapter two and four, for the direct investigation of the transmission of Sapolsky's (2006) "social culture". I investigate whether a social culture of increased affiliation can be initiated in marmosets through the long-term playback of chirp calls.

5.1 Introduction

5.1.1 Short-term Chirp Playback and the Neighbour Effect

Results from the observational study in the previous chapter indicate that spontaneously produced neighbour affiliative chirp calls influence the behaviour of nearby marmosets. Marmosets were found to spend significantly longer in the affiliative behaviours of groom invite and food sharing at higher levels of neighbour chirp than at low levels. Marmosets were also found to be significantly more likely to engage in active affiliative contact, and in food sharing, immediately after a neighbour chirp call rather than before. However, because the evidence was correlational, it was not possible to determine with certainty that the neighbour chirp vocalisation was indeed the casual factor. The results were also consistent with a possible alternative explanation, namely that neighbour and focal individuals were responding similarly to an identical external event or circumstance. A playback study will provide a direct test of the direction of causality and negate the previous' studies issues of differentiating neighbour types. If we find that the playback of pre-recorded chirps, out of context, has a similar effect on marmosets as do spontaneously produced neighbour calls, then this would considerably strengthen the inference that the relationship between external calls and focal behaviour is causal.

The effect on the behaviour of marmosets of the playback of chirp calls, outwith the usual behavioural context, may also provide more precise evidence for the function and context of the common marmoset chirp call. As stated in the previous chapter, the function of the marmoset chirp call has yet to be absolutely determined. The chirp call has mostly been described as an affiliative call, but it may also be a food-related call.

Research on call playback in nonhuman primates has generally been largely confined to long-range calls (Biben and Symmes, 1991). In contrast, affiliative calls are a close range call and therefore relatively quiet. Previous research involving the playback of conspecific affiliative calls has been conducted to discover whether recorded primate vocalisations would elicit a species-typical response in call receivers. Biben and Symmes (1991) played pre-recorded affiliative ‘chuck’ calls to squirrel monkeys and successfully elicited chuck responses, with familiar calls prompting the longest dialogue. Other researchers have used alternatives to pre-recorded calls to provoke a response. Snowdon and Pola (1978) synthesised variants of the pygmy marmoset trill (whirr) call; and Snowdon and Teie (2009) specifically composed cello music, for playback, resembling cotton-top tamarin affiliative calls, to assess the behavioural response.

I am aware of only one published study involving the playback of marmoset chirp calls, or at least calls spectrographically similar to common marmoset chirp calls. The study, described in the previous chapter, involved a different species of marmoset, *Callithrix geoffroyi*, and investigated the influence of call playback on feeding and foraging, rather than on social behaviours (Kitzmann and Caine, 2009).

Here, I investigate the influence of the playback of affiliative conspecific chirp calls on the affiliative social behaviour of the common marmoset. I expected that pre-recorded conspecific chirp calls would have a similar effect on captive marmosets to that of spontaneously produced neighbour chirp calls.

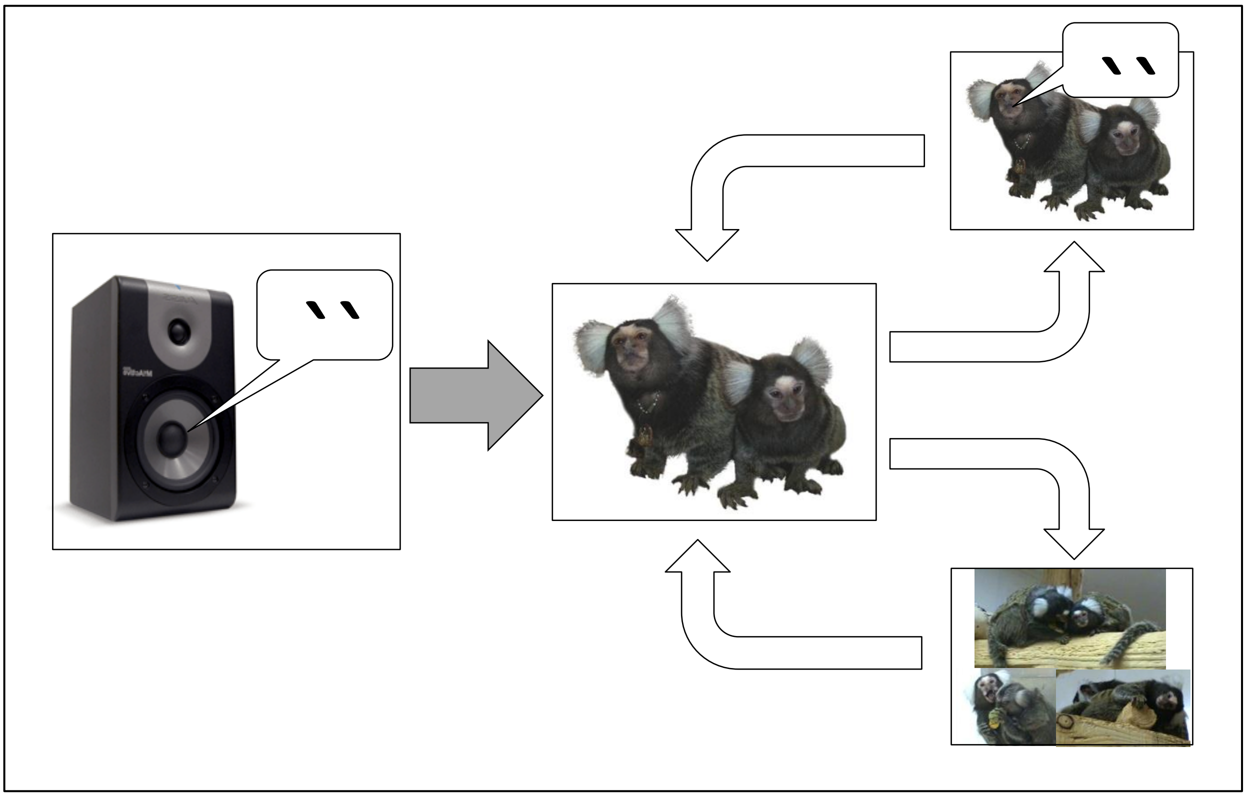
Based on the results of the previous chapter, I predicted that marmosets would be more likely to engage in active affiliative contact and share food directly following playback of chirp calls than before. I also expected marmosets to be more likely to engage in allogrooming and groom invite, after rather than before chirp playback, though the basis for this latter prediction is weaker; the greater probability of engaging in these behaviours, after spontaneous neighbour chirp calls, was not found to be significantly different in my previous study (Chapter four). This may, of course, have been due to our failure to detect an existing difference, or, alternatively, because no such difference exists.

5.1.2 Long-term Chirp Playback and Social Culture

The neighbour effect, demonstrated in Chapter four, has interesting implications for the within-group transmission of social culture, as defined by Sapolsky (2006), and outlined in Chapter two. I suggest that social contagion, or at least some form of social influence similar to social contagion, represents a possible transmission mechanism for social culture. Possible transmission mechanisms for social culture have been discussed, including observational learning (Sapolsky, 2006) and facilitation (de Waal and Johanowicz, 1993). However, researchers have, to the best of our knowledge, yet to directly investigate the transmission mechanism for social culture within species. My findings in Chapter four suggest that social contagion of affiliation occurs in marmosets and so provide the first step toward determining whether long-term changes can be facilitated through social contagion by experimental manipulation. I aimed to find out whether we could facilitate a social culture of increased affiliation, through social contagion, via the playback of pre-recorded affiliative conspecific vocalisations at an above average rate, for several hours, over many days.

How might a contingent effect of social influence, such as social contagion, lead to the transmission of social culture, a longer term change? Social contagion, initiated by playback, may set-up a self-perpetuating positive feedback cycle (i.e. sustained even in the absence of continued external playback). Fig. 5.1 illustrates a possible mechanism. Pre-recorded chirp calls are first played to a captive group of marmosets; the receiver marmosets may be influenced by this playback to produce more chirp calls themselves, and possibly also to perform affiliative behaviours (food sharing, active affiliative contact and inviting grooming). Nearby marmosets will be able to observe the affiliative behaviour, and to hear the affiliative calls of these nearby conspecifics, possibly stimulating these observers to vocalise chirps and to perform affiliative behaviours themselves. In this manner a self-sustaining positive feedback cycle may be initiated.

Fig. 5.1 Diagram showing a possible mechanism through which audio playback might initiate a long term change in social culture: through initial social contagion of affiliation leading receiver marmosets to increased chirp call production and performance of affiliative behaviour (active affiliative contact, groom invite, food sharing).



For the second, long-term playback part of the study, I made the decision to use recorded silence as a control instead of either of the alternative possibilities: a sound of the same pitch and length as the chirp; or a different call from the marmoset vocal repertoire. It may have been preferable to use a range of different controls, alongside the experimental and baseline conditions. However, it was not practical to implement more than one control condition, without a consequent reduction in statistical power.

In selecting a single control condition, therefore, a number of factors had to be taken into consideration. Firstly, the repeated playback of marmoset call types, in categories of affect other than affiliative, would have had ethical implications. Following the results of the previous chapter, the playback of agonistic or of anxious calls might be expected to influence marmosets towards behaviours considered to be indicative of negative welfare. I might expect the use of call types expressive of negative affect as controls to accentuate the difference between control and the experimental chirp playback (considered to be a call associated with positive affect). Consequently, having such a condition as our only control would not allow me to determine the influence of the chirp call per se, as any differences might simply be due to a reduction of the negative influence of the other call.

Regarding the other alternative, the use of sounds with similar pitch as the chirp call as a control might quite reasonably be expected to elicit a similar effect as the chirp call itself. Snowdon and Teie (2010) found that music, played on the cello, but composed to resemble tamarin affiliative calls elicited a similar species-typical response as the real call. The marmosets may be influenced by sounds of a similar structure due to conditioning as a result of the real call. For my purposes, distinguishing between the effects of a real call and an acoustically similar noise was relatively unimportant, since what we were interested in was the possibility of transmitting a social culture via social contagion, and also the potential welfare effects of call playback. As a result, a baseline control condition of recorded silence was selected as the most appropriate comparison for the experimental manipulation of chirp playback.

I predicted that the long-term playback of chirp calls to marmosets would lead to a greater positive increase in the time spent in affiliative behaviours, compared to marmosets exposed to the long-term playback of silence. Both playbacks were carried out through identical loudspeakers. The loudspeakers produce a slight hiss when switched on and for this reason both sets were switched on during the playback of either silence or silence interspersed with chirps.

5.1.3 Captive Marmoset Welfare Application

Efforts to improve the welfare of captive animals generally focus on structural changes to the physical housing environment, or improvements in husbandry, for example through changes to social groupings, or to feeding routines. Whilst some studies have investigated the effect of auditory stimulation effects on animal welfare, no studies, to my knowledge, have specifically investigated whether welfare can be improved through playback of positive conspecific vocalisations. There is good reason to believe that this may be effective. Studies with chimpanzees indicated that spontaneous affiliative vocalisations of neighbouring groups have a positive effect on the welfare of nearby conspecifics, an effect apparently mediated by social contagion. In Chapter four I replicated this finding in marmosets, the most frequently used New World primate in laboratory research and testing in the United Kingdom.

Research on the environmental enrichment for captive non-human primates through audio stimulation has focused largely on anthropocentric forms of stimuli, such as music. For example, researchers have, with mixed results, played: Mozart to bushbabies (Hanbury et al., 2009); harp music to African green monkeys (Hinds et al., 2007); live radio broadcast to baboons (Brent and Weaver, 1996); easy listening music to chimpanzees (Videan et al., 2007) and heavy metal music (Metallica) to cotton-top tamarins (Snowdon and Teie, 2010). Common marmosets, the subject of our current study, appear to prefer silence to music, of either fast or slow tempo (McDermott and

Hauser, 2007). Individuals were introduced into a v-shaped maze. Alternate audio stimuli were continuously played into the corresponding arm in which the individual was present. Preference for the stimuli was measured by the time spent in the arm associated with one stimulus relative to the other.

In a review of sensory stimulation as environmental enrichment for captive animals, Wells (2009) cautioned against the unempirically supported assumption that sounds found in the natural environment of the species are a priori more enriching than sounds unlikely to be encountered naturally by the animal, such as music. The empirical assessment of any form of potential auditory enrichment is necessary before it should be recommended or applied. However, encouraging the performance of behaviours that are natural and appropriate to the species is considered to be essential for enhanced welfare (e.g. Buchanan-Smith, 2010). It is therefore important to seek ecologically relevant stimuli that may be enriching.

Several researchers have attempted to enhance welfare through the playback of conspecific vocalisations, other than affiliative calls, to non-human primates. Shepherdson et al. (1989) played pre-recorded gibbon vocalisations twice daily over a loudspeaker, positioned 50 m away from an outdoor zoo enclosure housing a family group of gibbons, in an attempt to provide environmental enrichment through the simulation of a neighbouring social group. The vocalisations were recorded from a dueting song that, in gibbons, functions to delineate territory. The breeding pair vocalised and brachiated more frequently, and were more active during the half-hour after song playback than the same period before. Further, the auditory input required for such environmental enrichment appeared likely to be restricted to certain, ecologically relevant/valid stimuli. The pairs response appeared to be specific to the playback of gibbon songs of particular species only (unpublished data cited in Sheperdson et. al., 1989, p. 259), indicating that the same response may have been unachievable with more generic auditory stimuli.

For marmosets, the playback of calls produced by familiar conspecifics appears to have a somewhat calming effect. Cross and Rogers (2006) played back the anxiety-related mobbing vocalisation, while Rukstalis and French (2005) used the (contact and territorial) phee call. In both these studies, however, the calls were played to marmosets isolated from their usual social group, and the effect on stress was measured by physiological (cortisol analysis) rather than by behavioural means.

Researchers have yet to investigate the effect of the playback of affiliative calls on the welfare of marmosets. The current study investigated whether the playback of an above average rate of pre-recorded conspecific chirp calls to socially housed marmosets would lead to an increase in affiliative social behaviour. Depending on the outcome, the short-term and long-term effects of the playback of affiliative conspecific vocalisations may present potential practical applications in improving the welfare of captive marmosets.

Behavioural Welfare Indicators

Because I was interested in the possibility of applying playback as environmental enrichment, I wanted to assess any impacts on the welfare of captive marmosets of short- and long-term playback of a higher-than-average rate of pre-recorded chirp calls. I planned to carry out an analysis of behavioural welfare indicators not investigated in the main analysis (see Chapter three for an explanation of our choice of behavioural indicators).

5.2 Method

5.2.1 Study Subjects

Subjects were 32 focal individuals, initially; 16 in the control condition and 16 in the experimental condition, with eight in each of the four colony rooms (four breeding males and four breeding females, each housed in either a breeding pair or a family group). Because the speaker placement during the long-term playback was counterbalanced between the wall side and the door side of each colony room, equal numbers of focal marmosets were selected from each half of the rooms (wall side versus door side).

At the outset of the study the mean total number of individuals per room was 35 (36 in the control rooms and 34 in the experimental rooms) divided among a mean number of 9 social groups (10 in the control and 9 in the experimental rooms), with all 8 cages per room occupied except for a single cage in one room. Fig. 5.2 displays a schematic diagram of the layout of the study rooms, and Table 5.1 shows details about the focal subjects and the other members of their groups. Additional details regarding housing, husbandry and subjects were outlined in Chapter three.

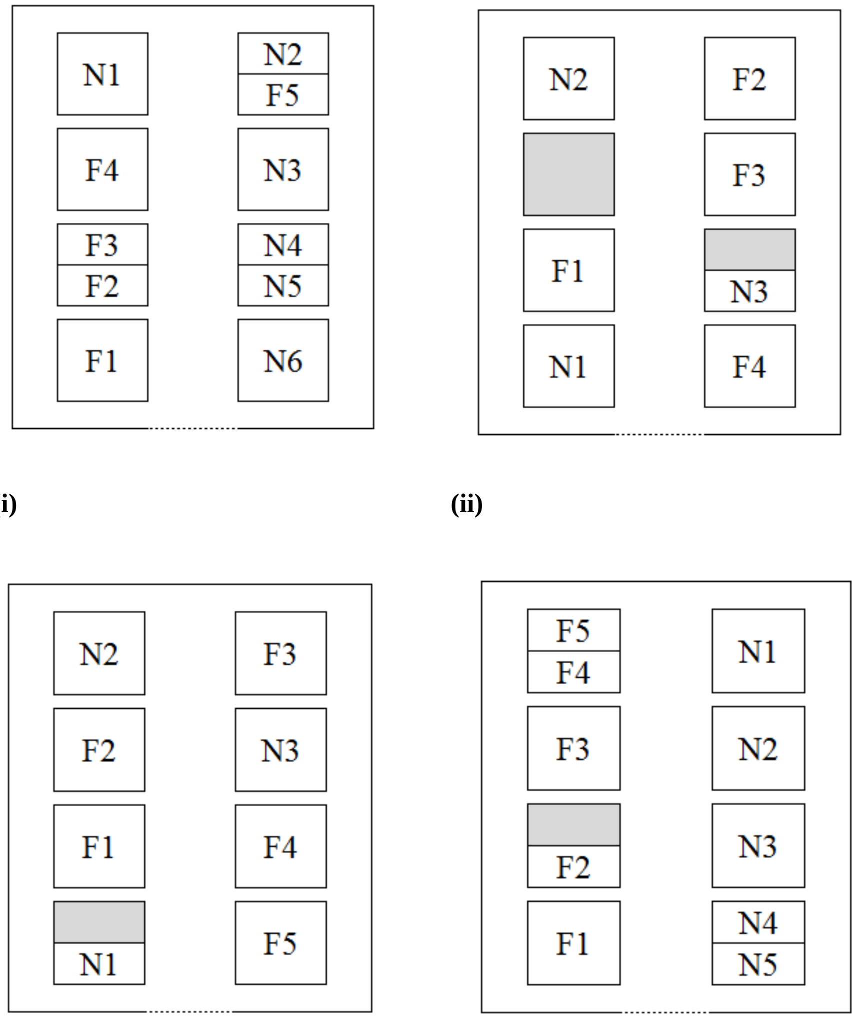
One focal female in the control condition (311y, focal 1 in room 4) was euthanised on 15.09.09 (for a biomedical study) after the short-term playback data collection, leaving 31 focals only for the subsequent long-term playback part of the experiment.

Some additional changes to the study population (members of focal groups, but not focal individuals) occurred during the course of the study. In the control condition rooms (two and four): one juvenile was removed and re-housed in another room due to fighting; and two infants were born (one died soon after and was replaced with a foster infant: from a non-focal group in room four). In the experimental condition rooms (three and five): 8 infants were born and survived their first few days (007v in room five gave birth to triplets and one of the infants was cross-fostered to 291y, room three, because she only had one surviving infant). Thus, during the study the number of infants in focal experimental groups increased more than the number of infants in control focal groups. I took these changes in group composition into account when analysing the data (see 5.2.4).

If I had been able to select non-pregnant breeding females only, then changes in the group compositions could have been avoided. However, there were practical and ethical constraints on our choice of focal individuals. In each room there were two non-focal groups with access to the roof-top runs (see Plate 3.06). It was impossible to observe individuals in groups with roof access because focal individuals had to be always present in the room for both playback and observation. Pregnant individuals and families with infants are not generally given access to the roof-top runs in case they need medical attention whilst within the roof-top run access tubes (the marmosets often sit within the tubes for long periods). It was important from a welfare perspective not to reduce the number of individuals allowed access to the roof-top runs as a result of our research. Because there were many individuals in each room who were either pregnant or with young infants in their group, and therefore unable to access the roof-top runs in any case, I was constrained to select these marmosets as focal individuals.. Throughout the study, access to the roof-top runs was alternated between the two non-focal groups per room monthly.

The marmosets had been habituated to the presence of the playback trolley over the course of two overnights; and to the long-term playback stand over four overnights. They were habituated to the combined presence of the playback trolley and the observer over 5 days of practice data collection. After the first 5 days of pre-playback data collection, the marmosets were habituated to the short-term playback from the speaker on the trolley for a further 3 days of practise data collection before the short-term playback data collection began. For the current study I wore a surgical mask throughout observations, whilst in the presence of the marmosets, to comply with the contemporary UK H1N1 virus regulations. The observational data was collected between the 22nd July and the 29th September 2009.

Figure 5.2 Schematic diagram of the four colony rooms and group arrangement on study day one (22.07.08) showing the label given to each group containing focal individual(s) F1 etc. and neighbour groups N1: (i) room two (ii) room three (iii) room four (iv) room five.



(i) (ii) (iii) (iv)

Table 5.1 Individual id, group id, group type (pair or family), sex, developmental stage (key below), date of birth and age in years and days on the first day of study baseline (22.07.09): of focal marmosets and nonfocals housed within the same group as the focal marmosets. * indicates focal individuals housed together in the same focal group; focal information is given in bold font; ± indicates the focal individual euthanised between the short-term and long-term playback.
Key: BA = breeding adult; NBA = nonbreeding adult; J = juvenile; I =infant; n = neighbour (nonfocal population).

Rm. No.	Group id	Group type	Individual category	Individual id	Sex	Developmental stage	Date of birth	Age in years and days at start of study
2	**F1**	**family**	**focal 1***	**279y**	**f**	**BA**	26.10.04	4 yr 269
			focal 2*	**158g**	**m**	**BA**	04.06.06	3 yr 48
			n	infant of 279y	f	J	28.12.08	0 yr 206
			n	infant of 279y	m	J	28.12.08	0 yr 206
			n	infant of 279y	f	I	02.06.09	0 yr 50
	F2	**pair**	**focal 3**	**198g**	**m**	**BA**	**10.02.08**	**1 yr 163**
			n	052v	f	BA	02.03.07	2 yr 142
	F3	**pair**	**focal 4**	**355y**	**f**	**BA**	**07.10.07**	**1 yr 288**
			n	118g	m	BA	22.08.04	4 yr 334
	F4	**family**	**focal 5***	**1116**	**f**	**BA**	**25.09.06**	**2 yr 300**
			focal 6*	**190g**	**m**	**BA**	**19.12.07**	**1 yr 215**
			n	infant of 1116	f	I	06.07.09	0 yr 16
			n	infant of 1116	m	I	06.07.09	0 yr 16
	F5	**pair**	**focal 7***	**357y**	**f**	**BA**	**19.11.07**	**1 yr 245**
			focal 8*	**189g**	**m**	**BA**	**19.12.07**	**1 yr 215**
3	**F1**	**family**	**focal 1***	**319y**	**f**	**BA**	**28.06.06**	**3 yr 24**
			focal 2*	**961Bk**	**m**	**BA**	**22.06.01**	**8 yr 30**
			n	376y	f	NBA	**05.05.08**	1 yr 78
			n	201g	m	NBA	**05.05.08**	1 yr 78
			n	389y	f	J	**05.10.08**	0 yr 290
			n	infant of 319y	f	J	**05.03.09**	0 yr 139
			n	infant of 319y	m	J	**05.03.09**	0 yr 139
	F2	**family**	**focal 3***	**055y**	**f**	**BA**	**02.01.01**	**8 yr 201**
			focal 4*	**862Bk**	**m**	**BA**	**09.04.99**	**10 yr 104**
			n	380y	f	NBA	03.06.08	1 yr 48
			n	206g	m	NBA	03.06.08	1 yr 48
			n	infant of 55y	f	J	01.05.09	0 yr 82
			n	infant of 55y	f	J	01.05.09	0 yr 82
	F3	**family**	**focal 5***	**291y**	**f**	**BA**	**30.05.05**	**4 yr 80**
			focal 6*	**120g**	**m**	**BA**	**28.09.04**	**4 yr 297**
			n	379y	f	NBA	26.05.08	1 yr 57
			n	205g	m	NBA	26.05.08	1 yr 57
			n	392y	f	J	28.10.08	0 yr 287
			n	infant of 291y	f	J	03.04.09	0 yr 111
			n	infant of 291y	m	J	03.04.09	0 yr 111
	F4	**family**	**focal 7***	**345y**	f	**BA**	**17.07.07**	**2 yr 5**
			focal 8*	**088g**	m	**BA**	**20.08.03**	**5 yr 336**
			n	infant of 345y	f	J	22.05.09	0 yr 61
			n	infant of 345y	m	J	22.05.09	0 yr 61
4	**F1**	**family**	**focal 1*±**	**311y**	f	**BA**	**12.02.06**	**3 yr 191**
			focal 2*	**157g**	m	**BA**	**04.06.06**	**3 yr 48**
			n	infant of 311y	f	I	14.06.09	0 yr 38
			n	infant of 311y	m	I	14.06.09	0 yr 38
	F2	**family**	**focal 3***	**234y**	f	**BA**	**18.03.07**	**2 yr 126**
			focal 4*	**155g**	m	**BA**	**01.05.06**	**3yr 82**
			n	371y	f	NBA	04.03.08	1 yr 140
			n	200g	m	NBA	04.03.08	1 yr 140
			n	385y	f	NBA	09.08.08	0 yr 347
			n	211g	m	NBA	09.08.08	0 yr 347
	F3	**family**	**focal 5***	**276y**	f	**BA**	**03.10.04**	**4 yr 292**
			focal 6*	**749Bk**	m	**BA**	**26.08.96**	**12 yr 331**
			n	384y	f	NBA	14.07.08	1 yr 8

			n	210g	m	NBA	14.07.08	1 yr 8
			n	395y	f	J	16.12.08	0 yr 218
			n	396y	f	J	16.12.08	0 yr 218
			n	infant of 276y	f	J	20.05.09	0 yr 63
			n	infant of 276y	m	J	20.05.09	0 yr 63
	F4	**family**	**focal 7**	**331y**	**f**	**BA**	**12.01.06**	**3 yr 191**
			n	146g	m	BA	**07.10.05**	**3 yr 288**
			n	infant of 331y	f	J	20.06.09	0 yr 68
			n	infant of 331y	m	J	20.06.09	0 yr 68
	F5	**family**	**focal 8**	**792Bk**	**m**	**BA**	**01.01.98**	**11 yr 202**
			n	309y	f	BA	28.01.06	3 yr 175
			n	204g	m	NBA	21.05.08	1 yr 62
5	**F1**	**family**	**focal 1***	**007v**	**f**	**BA**	**15.01.07**	**2 yr 188**
			focal 2*	**176g**	**m**	**BA**	**03.05.07**	**2 yr 80**
			n	infant of 007v	f	J	21.04.09	0 yr 92
	F2	**Pair**	**focal 3***	**335y**	**f**	**BA**	**02.04.07**	**2 yr 111**
			focal 4*	**177g**	**m**	**BA**	**03.05.07**	**2 yr 80**
	F3	**family**	**focal 5***	**145y**	**f**	**BA**	**17.07.02**	**7 yr 5**
			focal 6*	**173g**	**m**	**BA**	**04.12.06**	**2 yr 229**
			n	387y	f	NBA	11.09.08	0 yr 314
			n	214g	m	NBA	11.09.08	0 yr 314
			n	infant of 145y	m	J	18.05.09	0 yr 65
			n	infant of 276y	m	J	20.05.09	0 yr 63
	F4	**Pair**	**focal 7**	**036g**	**m**	**BA**	**30.09.02**	**6 yr 296**
			n	031v	f	BA	12.02.07	2 yr 160
	F5	**Pair**	**focal 8**	**347y**	**f**	**BA**	**20.08.07**	**1 yr 336**
			n	182g	m	BA	01.09.07	**1 yr 324**

5.2.2 Playback Stimuli

Experimental playback tracks were constructed by inserting chirp call exemplars into silence at particular intervals. Control playback tracks were of equal length to the experimental tracks but consisted of 'recorded silence' only.

Individual Chirp Call Exemplars

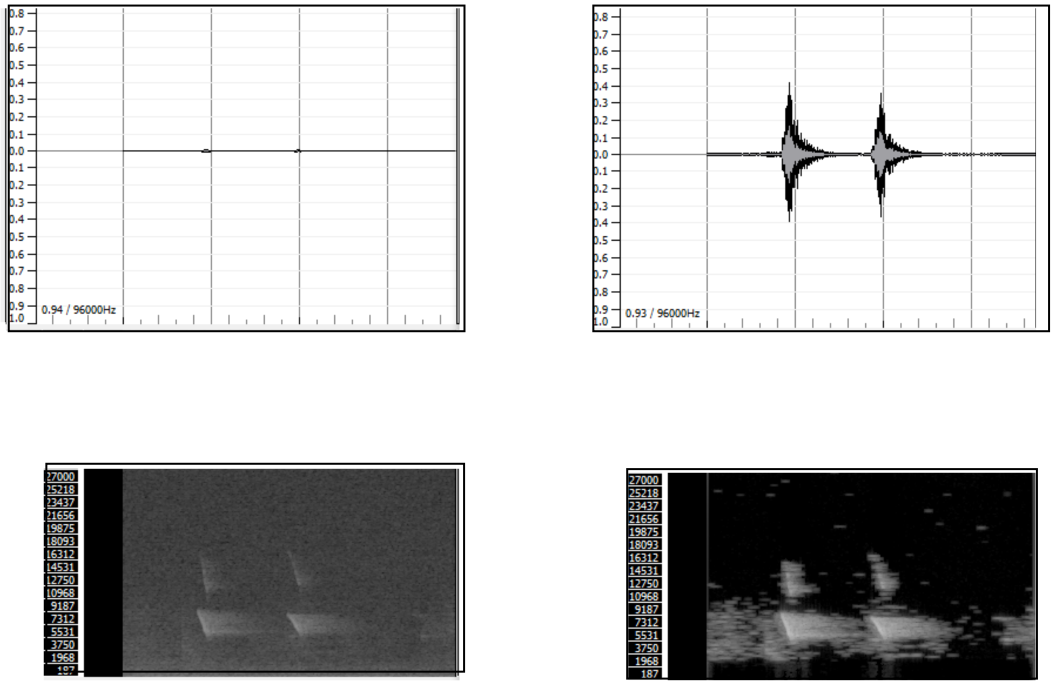
The 32 different chirp call exemplars, inserted into both the long and short-term playback tracks, were selected and cut from 38.6 hr of audio recording of calls vocalised spontaneously by socially housed marmosets during the neighbour effect study reported in chapter four (definition of a single chirp call as given in Table 3.4). It was important to use multiple call exemplars for a number of reasons: first, to minimise the chance of habituation by the marmosets to individual chirp exemplars; second, to ensure that the stimuli were truly representative of chirp calls as a class; third, to avoid ‘pseudo-replication’, a common methodological flaw in audio playback experiments, as highlighted by reviewers (e.g. Kroodsma et al., 2001); and fourth, to ensure a mix of calls from acoustically relatively familiar and unfamiliar individuals. For these reasons, as large a variety of different chirp call exemplars were selected from the audio footage as was possible, given the considerable practical constraint of the need for acoustic clarity. Chosen calls needed to be whole and clearly audible, without too much background room noise or any overlap with other marmoset calls. A total of 32 chirp calls were selected on this basis, consisting of between 2 and 11 syllables, between 0.5 and 2.5 sec in duration, and produced by a minimum of 6 different marmosets. Because the audio recording from which the calls were taken was made of the calls produced by entire colony rooms of marmosets, not by isolated individuals, it was not possible to know precisely how many individuals produced the 32 chirp exemplars. However, I can be certain that no less than 6 marmosets emitted the calls because the recording was made from 4 different colony rooms, and in two cases within the same room the observed focal individuals were known to have vocalised the chirp. Audio clips of two example calls of the 32 individual chirp call stimuli used are available in Appendix D on the appended DVD Appendices. The example chirp playback calls should be played at a relatively low volume.

All chirp call exemplars from the original recording, and edited using ‘Wave Pad Master’s Edition’ professional audio editing software for Windows (NCH® Software), available for purchase online (http://www.nch.com.au/software/audio.html). The quality of the recording from the neighbour effect study was not ideal for several reasons. Firstly, some of the recorded spontaneous calls were made by individuals at some distance from the microphone. Also, the acoustic quality of the room was very poor (many acoustically reflective surfaces) and there was much extraneous background noise (caused by swinging hanging enrichment devices and food pellets being moved in metal dishes etc.). Furthermore, the chirp call itself is a relatively quiet within group call. Acoustic editing was therefore carried out to isolate chirp exemplars from the background noise and to raise them to an audible level.

All 32 chirp exemplars were first normalised by 75%, to raise their volume, and then equalised (using a high pass filter with the slope set manually from 2536 up to 3075 Hz), to remove extraneous background noise below the frequency range of the calls whilst leaving them intact. The high pass filter range was set after having determined, through spectrographic examination, that the lowest point of any of the 32 selected chirp calls was 3187 Hz. All exemplars were treated identically in a batch conversion. To further reduce background noise, a spectral subtraction was also carried out. A portion of ambient noise (a clip of background noise only) was converted in an identical manner to the chirp exemplars (as above). A 6-sec sample of the ‘treated’ ambient noise was then used to carry out a spectral subtraction on each of the 32 chirp clips. This procedure resulted in background noise being cancelled out from the chirp clips because it had a spectral range similar to that of the identically treated ‘background noise only’ clips. Chirp calls were subsequently further normalised, on an individual basis, in order to maximise their signal to noise ratio, without acoustic distortion.

To ensure that the actual chirp calls had remained intact during the editing process, including the harmonic frequencies, both the original and edited chirp audio clips were spectrographically examined. The spectrogram generating program Sonic Visualiser 1.6 was used for this purpose (freely available software program, http://www.sonicvisualiser.org/, licensed under the GNU general public license). Fig. 5.3 shows an example: the edited version of chirp call number 8 (ii) has the same essential frequency trace (and harmonics) as the unedited version of the same call (i) but is much louder (see amplitude graph) and with the background noise removed (the shade of the spectrogram surrounding the chirp call traces is black, indicating ambient silence, rather than speckled white as in the original clip, indicating ambient background noise).

Fig 5.3 Chirp stimuli (number 8) before (i) and after (ii) acoustic editing as a spectrogram, lower diagrams (in frequency Hz, with brighter white indicating a higher amplitude, speckling indicates ambient noise), and as an amplitude graph, upper diagrams (in decibels), through the audio analysis software 'Sonic Visualiser 1.6'.



(i) **(ii)**

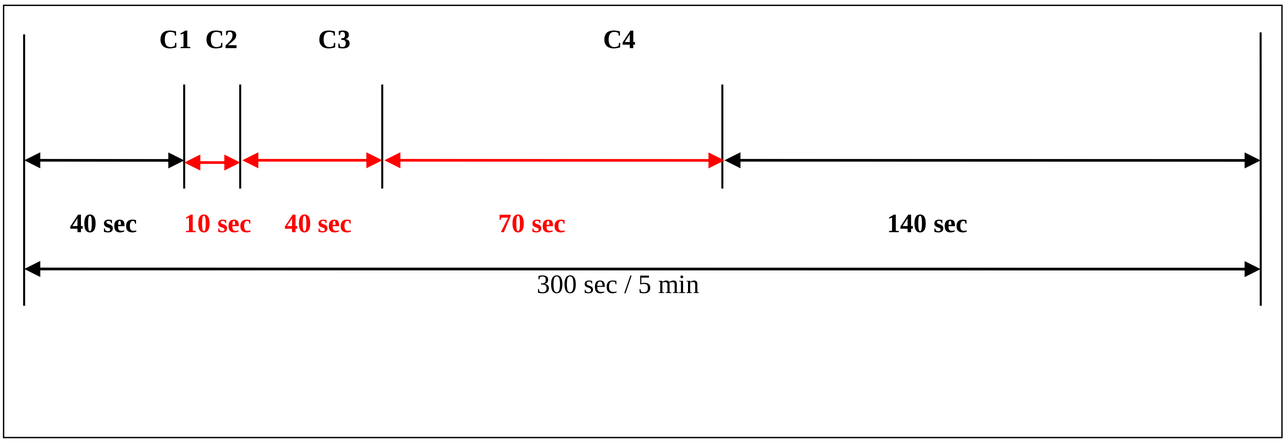
The individual chirp exemplars recorded most clearly, in the study in the previous chapter, were likely to be those made by the focal individuals and the other members of their group and it is therefore conceivable that such chirp calls may be overrepresented in the playback exemplars. Focal individuals in the current study that were focal individuals, or their group members, in the previous study may then be more familiar with the exemplars than the other focals. This may influence the results of the between-subjects long-term chirp playback experiment, but I consider it unlikely. The number of focal individuals in this study that were members of the focal group in the previous study was almost equalised between the control (8 focals) and experimental (6 focals) condition. Further, assuming that individuals are more likely to experience social contagion from familiar calls, the direction of difference represented by the slight discrepancy in numbers would have favoured the control rather than the experimental condition.

Short-term Playback Tracks

Each short-term playback experimental track consisted of 5 minutes of silence with four chirp calls inserted at precise points within the first half of the track (Fig. 5.4). The first chirp was inserted at 40 sec to allow time for pre-chirp playback focal behaviour to be recorded. The subsequent three chirps were inserted with inter-chirp intervals of 10, 40, and 70 sec. A total of 16 novel, 5-min, experimental, short-term tracks were constructed: two sets of 8 tracks containing 32 non-repeated, randomly ordered chirp exemplars. The order in which the chirp calls were inserted was pre-determined using an online non-duplicating random sequence generator, which generates randomness based on atmospheric noise (Mads Haahr, School of Computer Science and Statistics, Trinity College: http://www.random.org, as used by and cited in journal articles, e.g. Kellar and Abraham (2005). The order of inter-chirp interval lengths was counterbalanced (in four different patterns).

The short-term playback track for marmosets in the control rooms consisted of a 5-min track of silence. This was not a control track for the investigation of the short-term effect of chirp playback. A control track was unnecessary because the experiment was within subjects, comparing behaviour of the same individuals before and after playback. I carried out observation and playback with the 16 focal marmosets in the control rooms throughout the short-term study to equalise any effect of the observation procedure (minus the chirp playback) on the marmosets in the control and experimental condition for the long-term part of the study.

Fig. 5.4 Diagram representing the construction of an experimental short-term playback track (C1-4 represent the four chirp call exemplars; the inter-chirp intervals in red (grey in monochromatic print-outs) represent those whose order was counterbalanced over the 16 novel tracks).



The rate of playback of four chirps per 5 min was selected to be representative of the chirp rate in the observations in the ‘upper’ category for neighbour chirps (observations with more than one neighbour chirp) in the neighbour effect study, in Chapter four. The median number of chirps per upper observation, four, was taken as the most appropriate measure of central tendency, because the data from the neighbour effect study were not normally distributed. The rate of chirp playback in the ‘short-term’ playback tracks was required to represent the upper end of the range of chirp calls per observation because the current study was to investigate whether the effect of recorded neighbour chirp calls on behaviour was similar to that of spontaneously produced neighbour chirp calls. In addition to the playback of pre-recorded chirps, during the short-term playback observations, the other individuals in the colony room may emit chirp calls themselves. However, given that 34% of the total 5-min observation sessions recorded in the previous experiment had zero neighbour chirp calls this number is likely to be low relative to the number on the playback track.

The three inter-chirp intervals used in the experimental short-term playback track were chosen based on an examination of average inter-chirp intervals within the ‘upper’ range of observations for neighbour chirp calls in the neighbour effect study. To calculate the mean inter-chirp interval, I listed all observations, out of the total 463 5-min observation sessions, in the neighbour effect study that were in the ‘upper’ category, numbered them from 1-214 and picked 20 at random using a random number generator (http://www.random.org, as above). I calculated the mean inter-chirp interval by noting the time in seconds between the beginnings of each successive chirp bout, coded from the room calls. The result was a mean of 39.8 sec from the first 20 observations, and 40.1 sec upon adding a further 10 randomly selected observations with more than one chirp (room and focal), indicating good agreement. The inter-chirp interval is of extremely variable length, with a range from 5–152 sec. As mentioned, the mean inter-chirp interval per observation was 40 sec, and the median was 28 sec. The inter-chirp intervals for the current study were chosen to be representative of those in the ‘upper observations’ in the neighbour effect study whilst being long enough to allow sequential lag analysis of the 15 sec prior to and following the chirps.

Long-term Playback Tracks

The long-term control track consisted of a 90-min long track of ‘recorded silence’. A total of 22 novel 90-min long-term experimental tracks were constructed by joining 36 novel, separately created, 10-min chunks together in a randomised combination (using random.org, as above). Each 5 min of long-term experimental track contained 18 chirp exemplars with 18 different inter-chirp intervals (chirps and inter-chirp intervals were inserted in continuum and were therefore of equal number). The 18 different inter-chirp intervals were randomly ordered within each 5-min section (using random.org, as above). Details of the inter-chirp interval lengths used are given in Table 5.2.

Each novel 10-min section was created by the insertion of the chirp exemplars into silence. The chirp calls were randomly ordered such that the 32 exemplars were each used once before any repetition (i.e. given that there are 18 chirps per 5 min, exemplars were each used once within each 10 min with 4 exemplars used twice; each exemplar being repeated exactly 9 times every 80 min of playback). The 10 min tracks were themselves ordered randomly to create the 90-min tracks, with each used once before any repetition so that each 10-min track was repeated only once every 6 hr of playback.

A rate of chirp playback of 18 chirps per 5 min was selected to match the median number of chirps in the upper 5% of all 463 observations for chirp frequency in the neighbour effect study. This rate was almost twice that of the short-term playback. The long-term playback rate was intentionally well above average because the playback duration per day (a mean of 3 hr) of a simulated a higher chirp rate social culture was relatively short when compared to what it was intended to artificially simulate: the continuous presence of individuals producing chirps at a higher than average rate. Again, there will be chirps made by individuals in the room, in addition to the playback tracks, but this is likely have little impact relative to the high rate in the playback tracks.

The lengths of the 18 inter-chirp intervals, used in the long-term experimental tracks, were selected to represent each of the quartiles of the range of inter-chirp call intervals found in the top 5% of the 463 observations for chirp frequency in the neighbour effect study. I was to some extent constrained in our choice because the inter-chirp intervals were required to sum 300 sec, because the chirps and intervals were continuous (unlike in the short-term playback in which chirps were confined to a discrete 100-sec period). Table 5.2 details the specific inter-chirp intervals chosen and the number of chirps used for both long-term and for short-term playback tracks.

Table 5.2 Number of chirp calls, and number and length of inter-chirp intervals, per 5 min in the experimental condition playback tracks: short-term and long-term.

Period	Chirp calls (per 5 min)	inter-chirp intervals (per 5 min)	Inter-chirp interval lengths used (sec)
Short-term Playback	4	3 (chirps restricted to first half of 5 min)	10, 40, 70
Long-term Playback	18	18 (continuous)	2.5, 2.5, 2.5, 2.5, 3.0, 3.5, 4.0, 4.5, 5.5, 7.0, 9.0, 10.5, 12.0, 14.0, 19.0, 38.0, 70.0, 90.0

5.2.3 Experimental Procedure

Observational Coding Procedure

A continuous focal sampling method was used to record the behavioural states of each of the 32 focal individuals, over a 5-min observation period, on each of 30 observational study days. Since the affiliative behaviours of interest are performed relatively infrequently, the social behaviours were defined as those performed by the focal animal ‘to’ other individuals and also those behaviours performed ‘from’ other individuals to the focal marmoset. Behavioural definitions of the behaviours coded are provided in Table 3.1. In total; 950 observation sessions were coded. Please refer to Chapter three for further details of the observation procedure.

Observations were made during all four stages of the experimental procedure: (i) long-term pre-playback: 5 days of observation; (ii) short-term playback: 12 days of observation (with playback occurring whilst the observer was present); (iii) long-term mid-playback: 5 days of observation (with simultaneous playback occurring in different rooms plus 6 days of playback only: with the observer absent from rooms during playback); and (iv) long-term post-playback: 5 days of observation.

Playback Procedure

Both short-term and long-term playback tracks were played back to the colony room through an active monitor speaker (Alesis M1Active 520 USB) connected (via a ground loop isolator to cancel out electrical interference) to a lap-top PC (Sony Vaio VGN-NR21J or Dell PP18L). Active monitor speakers were chosen to ensure a flat frequency response, i.e. a high fidelity reproduction across the frequency spectrum with no particular sections of the range either distorted or removed. This ensured that the recorded marmoset calls were reproduced as similarly to spontaneously produced calls as possible. The speakers also have a separate tweeter to enable them to reproduce high frequency sounds accurately. Although marmosets are able to hear sounds up to 30 kHz (Seiden, 1957, as cited in Coleman, 2009), a higher frequency than humans are capable of hearing, the call of interest in the present study, the chirp call, is between 5 and 8 kHz. This range is accommodated by the speakers since they reproduce sound accurately within the range of 80 Hz-20 kHz. The music management software ‘iTunes’ (Apple for Windows) was used to order stimulus tracks for playback. The chirp call is a relatively quiet within-group call so it was important to play back the call at a volume similar to that of a live call made by a marmoset so that it would be recognised and responded to as a real call. The volume of playback was determined by ear, by the experimenter and staff familiar with marmoset vocalisations, to be similar to the volume of sound produced by a single marmoset emitting a chirp call, whilst still being audible to all the marmosets in the colony room.

Short-term Playback

For short-term playback, the lap-top and speaker were connected to the mains using an extension cable and placed on a trolley with three shelves (a multi-purpose cleaning trolley of dimensions: 113 x 50 x 98 cm, Plate 5.1). For consistency of conditions, the trolley was manipulated in an identical manner during all observations (baseline, short-term, long-term and post period) although the playback track was only actually played during the short-term playback period observation. During the long-term observation period the trolley was moved, but without the lap-top and speaker, because they were being used for long-term playback in neighbouring rooms. During all observations the trolley was moved around, as the observer changed position, so that the trolley stood to one side of the home cage of the focal individual being observed, with the speaker 100 cm distance from the front middle of the cage. The speaker on the trolley was positioned and angled so that the sound was directed at the focal cage but with the trolley at the end of the cage (perpendicular to the cage).

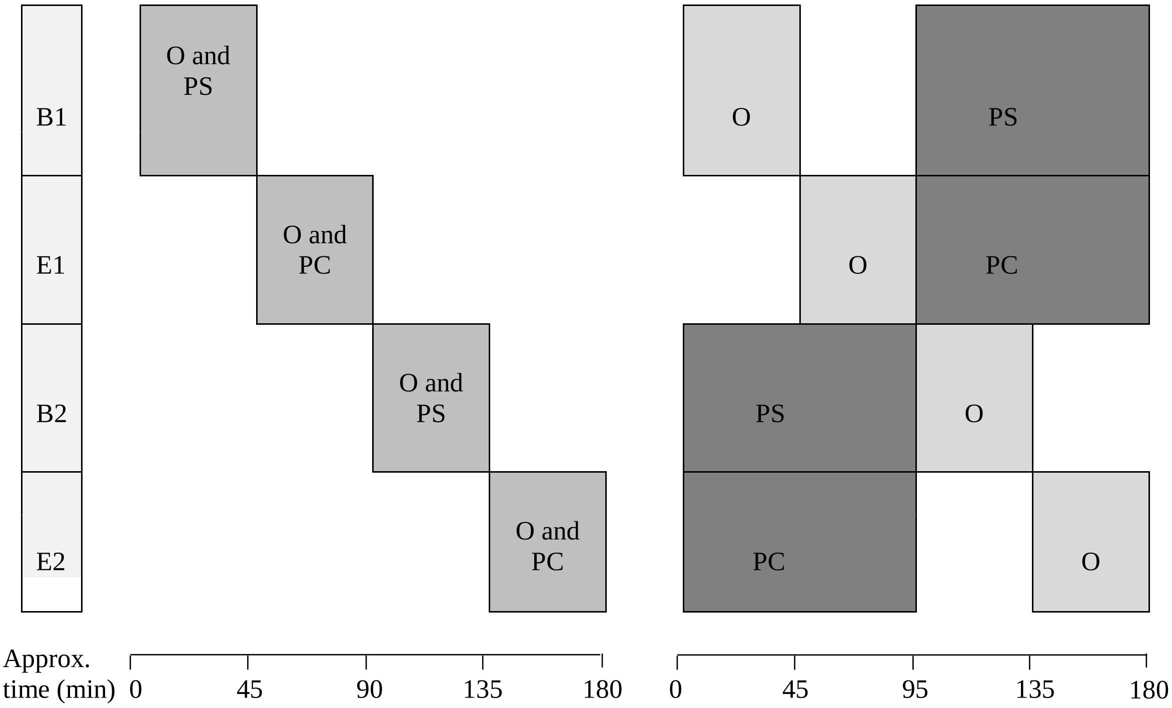
During the short-term playback period, the 5-min short-term stimulus tracks, experimental or control tracks respectively, were played back simultaneously with each 5-min observation session, in the same room. The start of the observation and of the playback track were synched manually. The accuracy of the synching was verified by checking that the 5-min track ended at the same time as the 5-min observation ended. Track playback was counterbalanced such that each room in the experimental condition heard each of the 32 chirp call exemplars repeated no more frequently than once every alternate study day.

Long-term Playback

For long-term playback, two sets of lap-top and speaker were used simultaneously, one set in a control room and one set in the matched pair experimental room, placed on one of two identical stands. Each stand was constructed from a metal bar stool with plastic back rest (Ikea Ansii bar stool: 47 x 50 x 90 cm) with an upturned plastic box (Ikea Trofast: 42 x 30 x 23 cm) attached to the seat, on which to put the speaker, and an upturned plastic box (Ikea Trofast storage box: 42 x 30 x 10 cm) attached to the bottom cross bars of the stool, on which to place the lap-top with raised screen (see Plate 5.1). The plastic boxes were secured using permanent black plastic cable ties through purpose-drilled holes in the plastic boxes and stool. The spare cable was placed into a plastic box attached below the metal cross bars of the stool to minimise the length of cable lying directly on the floor. The stand was moved between rooms by the observer and a 4-min track of silence was set to play, as the observer left the room, before the playback of the experimental track started, to ensure that the marmosets did not associate the chirp playback with any disruption. I counterbalanced the position of the stand, in each of the four the colony rooms, between the two ends of the room: the right hand side of the entrance door; and the middle of the back wall.

On experimental study days during the long-term playback period, observations were carried out in two half-rooms in succession, one pair of matched control and experimental rooms (control room two was matched with experimental room five; and similarly room four was matched with room three), whilst 90-min stimulus tracks, experimental and control respectively, were played in the two other experimental and control room simultaneously (Fig. 5.5; Table 5.3). During the 5 experimental days the order of playback was counterbalanced so that each room received 180 min/ three hr of playback: 90 min during the morning and 90 min during the afternoon. During long-term playback staff entered the rooms only if absolutely necessary. In addition to the experimental days there were 6 non-experimental days (laboratory bank holidays) during which four consecutive 90-min appropriate tracks were played back to one control room and one experimental room simultaneously for a total of 6 hr playback. Paired control and experimental rooms underwent playback simultaneously. Over the course of the 11 long-term playback study days, each room underwent a mean duration of three hr playback per day (a total of 33 hr of playback per focal individual).

Figure 5.5 An example schedule for one half of an observational study day during short-term playback (i) and during long-term playback (ii) of observation (O) and playback (P) across matched baseline and experimental rooms respectively (B1 and E1; B2 and E2). PS indicates playback of recorded silence and PC indicates playback of chirps. Time is shown approximately (for simplicity the time required to move the equipment between blocks has been disregarded).



(i) Short-term Playback **(ii) Long-term Playback**

Table 5.3 Focal subject treatments during short-term and long-term playback for focal marmosets in the control condition (B) of recorded silence (PS) and in the experimental condition (E) of a higher than average rate of chirp calls (PC). *individuals within the same room experienced 2 playbacks if in the same group as another focal individual, and therefore a total of 8 playbacks overall within the same room each day. ~ focal individual number 1 in room 4 died after the short-term playback. Focal id relates to Table 5.1.

Condition	**Room**	**Focal id**	**Short-term playback** (over 12 days: playback directed to the focal group)	**Long-term playback** (over 11 days: playback to entire colony room)
B	2	1-8	Daily playback of 150 sec of recorded silence (PS) to each focal individual* (am or pm on alternate days)	day 1 : 6 hr PS day 3, 4, 5, 6 : 3 hr PS daily: 1.5 hr in am; 1.5 hr in pm day 8, 10 : 6 hr PS day 11 : 3 hr PS daily: 1.5 hr in am;1.5 hr in pm
B	4	1-8~		day 2 : 6 hr PS day 3, 4, 5, 6 : 3 hr PS daily: 1.5 hr in am; 1.5 hr in pm day 7, 9 : 6 hr PS day 11 : 3 hr PS daily: 1.5 hr in am; 1.5 hr in pm
E	3	1-8	Daily playback of 150 sec with 4 chirp calls (PC) to each focal individual* (am or pm on alternate days)	day 2 : 6 hr PC day 3, 4, 5, 6 : 3 hr PC daily: 1.5 hr in am; 1.5 hr in pm day 7, 9 : 6 hr PC day 11 : 3 hr PC daily: 1.5 hr in am; 1.5 hr in pm
E	5	1-8		day 1 : 6 hr PC day 3, 4, 5, 6 : 3 hr PC daily: 1.5 hr in am; 1.5 hr in pm day 8, 10 : 6 hr PC day 11 : 3 hr PC daily: 1.5 hr in am; 1.5 hr in pm

Plate 5.1 Short-term playback trolley in position for short-term playback and for observation sessions (i) and in close-up; and in position for long-term playback at the wall end (iii) and in ‘close-up’ at the door end (iv).

(i) **(ii)**

(iii) **(iv)**

5.2.4 Statistical Analysis

Immediate Effect of Short-term Chirp Playback

To investigate the immediate effect of chirp call playback on focal behaviour during the 12 study days of short-term playback, only the data for the 16 focal individuals in the experimental condition were analysed. The mean proportion of focal behaviours occurring in the 15 sec before each chirp call playback was compared with the proportion occurring in the 15 sec following, using the ‘lag sequential analysis’ function in the Observer XT 8.0 (Noldus Information Technology, Wageningen, The Netherlands). The analysis was based on results from three out of the four chirps during each short-term playback observation (because the lag sequential analysis was set to ignore repeat events within each 15-sec period to avoid duplication of results). Each chirp call playback within 10 sec of the prior chirp may have added to the effect of the previous chirp but was not analysed individually. So, only three chirp calls were used for the analysis per observation, and each focal individual was recorded for 12 observations. Furthermore, since the periods of interest (from the point of view of the analyses) were restricted to 15 sec before and after each call, only 18 min of each focal individual’s behaviour contributes to the analysis (9 min of pre-call behaviour and 9 min post-call). Bearing in mind that the behaviours of interest are also very infrequent, it should be noted that it would be relatively difficult to obtain a strongly significant result. The maximum number of possible incidences per focal individual was limited to 36 (the total number of play back chirps analysed).

The 15-sec interval chosen for analysis matches that used to analyse the immediate effect of spontaneous neighbour chirp calls on focal behaviour in chapter four. Mean proportions for the intervals preceding and following chirp call stimuli were compared using permutation tests (see Chapter three for further details).

Effect of Long-term Chirp Playback

In order to determine whether the long-term chirp playback had an influence on behaviour the mean change in the mean percent time spent by each focal individual in affiliative and feeding related behaviours, both between pre-playback and mid-playback and between pre-playback and post-playback periods, was compared for marmosets in the experimental and control conditions.

Developmental Categories Analysed

The data used in this analysis constitute a unit of change within the same group over time. However, changes to the composition of focal groups in the experimental condition across the three periods of the long-term part of the study were unequal to those that occurred within control condition focal groups. A greater number of infants were born or fostered into groups containing focal marmosets in the experimental condition than to focal groups in the control condition. This difference may have important consequences for my results.

Young marmosets, and newborn infants in particular, are much more likely to receive affiliative behaviour than adults or juveniles in general. Affiliative behaviour performed towards newborns has an important cleaning as well as a social function (infants are unable to clean themselves). Any increase in the amount of time spent by focals engaged in affiliative behaviour across the data collection period may therefore be due to the confounding factor of the increase in infants alone, rather than as a result of the experimental manipulation.

One way in which to separate the effects of these two factors was to exclude from the analysis behaviour performed to, or received from, infants. However, this exclusion itself does not remove the complication of uncontrolled effects of changes in group composition across time.

Having excluded behaviours performed by and to infants, it is more likely that the behaviours of particular interest will be under-represented rather than over-represented in experimental groups relative to control groups. Focals in the experimental group may have been more likely to spend more time interacting, and affiliating, with the recently born infants than with the adults and juveniles, and, similarly, others in the group may be less likely to spend time affiliating with the focal individual, and more likely to attend to the young infants. Thus, if I analyse the behaviour to and from adults only, focal individuals in groups with increases in the number of infants may have less time to spend in affiliative behaviours towards adults due to probable time constraints imposed by very young infants.

An analysis involving behaviour to and from the remaining two developmental categories, adults and juveniles, may also be complicated by changes in group composition across time. This is because affiliative behaviours are more likely to be performed towards younger juveniles rather than towards older juveniles. Because the study was carried out across a relatively long period, those focal individuals in groups with younger juveniles, at a transitional stage, may display a decrease in affiliative behaviour towards juveniles due to the juveniles growing out of this transitional stage rather than due to the experimental manipulation.

Multiple differences in the relative changes across groups in both conditions thus complicate the analysis somewhat, with differences creating bias in different directions. For this reasons we used two categories in our analysis, adult only: and the combined adult and juvenile age groups. Examining the results across both these categories should give us an indication of real effects.

There was clearly no need to split the data for the short-term playback by developmental age group, because the experimental design was within-subjects. The comparisons for each focal were between their behaviour 15 sec before chirp playback and 15 sec after. Due to the short temporal interval between the collection of data to be compared, changes in group composition were not a problem.

I used a custom-written program in MATLAB to carry out permutation tests. The p-values are the probabilities of observing at least as great an increase in degree of change as present for the experimental group (i.e. the one-tailed probability) for a random assignment of the 31 data points into control/experimental conditions (see Chapter three for further detail).

5.3 Results

5.3.1 Immediate Effect of Short-term Chirp Playback

Table 5.4 displays the results of the statistical tests comparing the proportion of 15 second intervals before and after the playback of a pre-recorded chirp call during which affiliative behaviours were performed by the focal marmosets. I investigated the four affiliative behaviours that marmosets displayed significantly more after rather than before a neighbour chirp call in the previous chapter.

The mean probability of active affiliative contact and share food was higher immediately after chirp playback call than before, although the difference was not significant (active affiliative contact: $N = 16$, $P = 0.500$; share food: $N = 16$, $P = 0.125$, Fig. 5.6). Given the significant differences for these two affiliative behaviours in Chapter four and also due to concerns that the low rates of both behaviours might generate false negative results (i.e. type II error), I analysed a composite of share food and active affiliative contact. I found that marmosets were significantly more likely to engage in either food sharing or active affiliative contact, after a played back chirp call than before ($N = 16$, $P = 0.031$, Fig. 5.6).

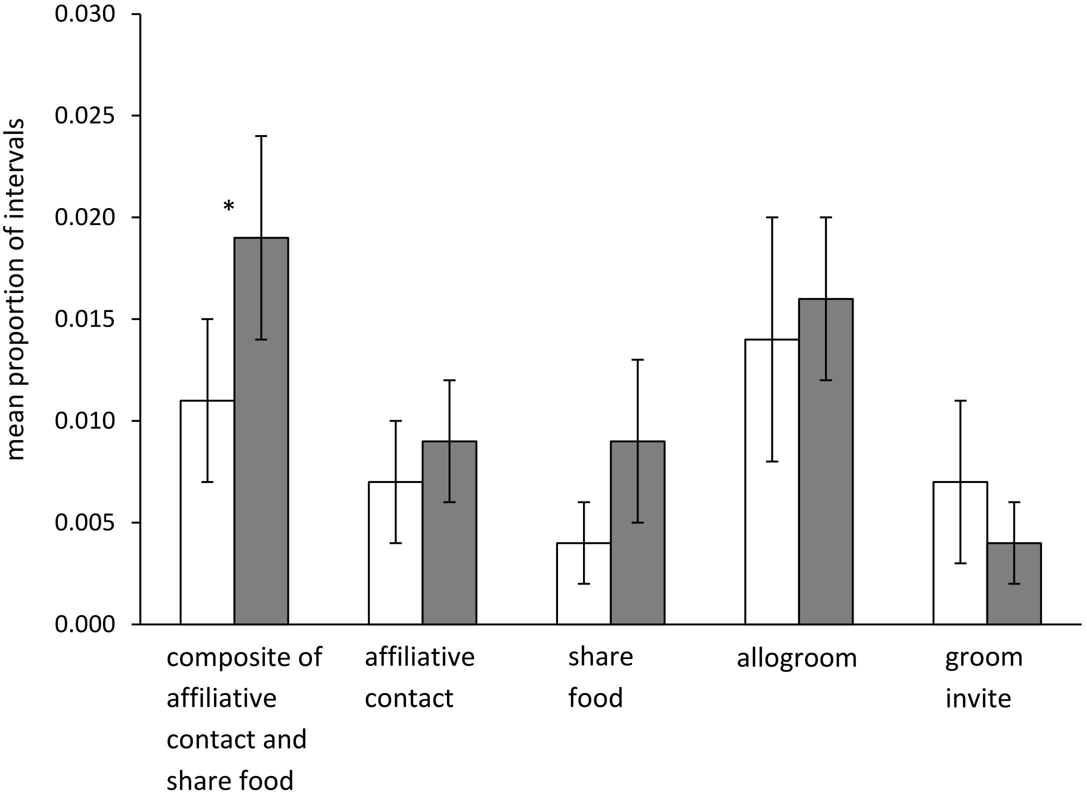
Marmosets were more likely to engage in allogrooming directly after rather than before a played back chirp call, although the difference was non-significant ($N = 16$, $P = 0.461$). They were not more likely to engage in grooming invite after compared to before a played back chirp call (direction of difference opposite to prediction).

The data were analysed, post hoc, to determine whether marmosets were more likely to feed, or to forage visually or actively, immediately before a played back chirp call or after. Marmosets were more likely to feed immediately after the playback of a chirp call

Table 5.4 Statistical test results for the analysis of the immediate effect of conspecific chirp call playback on focal marmoset behaviour; a comparison of the mean proportion of behaviours in the 15-sec pre-chirp call playback with the mean 15-sec post-chirp call playback. Asterisk (*) indicates *P* < 0.05. ns indicates a result in the predicted direction which was nonsigificant. Ŧ indicates means where the direction of difference is opposite to the predicted direction (one-tailed tests). ~ indicates two-tailed, post hoc analyses. The adjusted α-level for multiple testing is also displayed.

Focal behaviour	mean proportion pre-chirp call playback	mean proportion post-chirp call playback	*N*	*P*	adjusted α-level
Active affiliative contact	0.007	0.009	16	0.500 ns	n = 4 α = 0.0125
Share food	0.004	0.009	16	0.125 ns	
Allogroom	0.014	0.016	16	0.461 ns	
Groom invite	0.007	0.004	16	Ŧ	
Composite of share food and active affiliative contact	0.011	0.019	16	0.031 *	
Feed ~	0.049	0.066	16	0.055 ns	
Active forage ~	0.038	0.026	16	0.337 ns	
Visual forage ~	0.180	0.169	16	0.604 ns	

Fig 5.6 The immediate effect of chirp playback: mean proportion (± 1 SE) of 15-sec pre-chirp playback call (white bars) with the 15-sec interval post-chirp playback call (grey bars) in which affiliative behaviour is performed by marmosets. Asterisk (*) denotes significance.



than before, although the difference was not significant (*N* = 16, *P* = 0.055). Conversely, marmosets were more likely to forage, either actively or visually, before a chirp call than after it, although again these differences were not significant (active forage: *N* = 16, *P* = 0.337; visual forage: *N* = 16, *P* = 0.604).

5.3.2 Long-term Effect of Chirp Playback

Table 5.5 displays the results of the statistical tests comparing the mean change in time spent by focal marmosets in affiliative behaviours in the control and in the experimental conditions, between pre-playback and mid-playback, and between pre-playback and post-playback.

As predicted, between the pre-playback and the mid-playback period, the time spent by marmosets allogrooming, in the chirp playback condition increased by a larger amount, compared to the control condition (Fig. 5.8). This difference was significant for adults and juveniles combined, and it approached significance to and from adults only (adults and juveniles: *N* = 31, *P* = 0.030; adults only: *N* = 31, *P* = 0.061). Between pre-playback and post-playback however, the time spent in allogrooming by marmosets exposed to chirp playback showed a greater decrease than by those in the control playback condition, contrary to my prediction.

In contrast to the results for allogrooming, for affiliative contact our prediction was supported between pre- and post-playback, but not between pre- and mid-playback (Fig. 5.9). From pre- to post-playback the time spent by marmosets in active affiliative contact, to and from adults only, increased significantly more in the chirp playback condition than the control playback. There was a nonsignificant trend for affiliative contact to and from both adults and juveniles combined (adults only: *N* = 31, *P* = 0.048; adults and juveniles: *N* = 31, *P* = 0.073). Between pre- and mid- playback, although the relative increase in time spent in affiliative contact was greater for individuals exposed to the chirp rather than marmosets exposed to silence, the difference was not statistically significant for either category (adults and juveniles: *N* = 31, *P* = 0.396; adults only: *N* = 31, *P* = 0.432). For each of the 5 post-playback days, figure 5.10 shows the difference between the mean time spent allogrooming on these days and the mean time spent in allogrooming across the 5 pre-playback (baseline) days, by marmosets in the control and experimental conditions (thus zero on the y-axis indicated a level of allogrooming equal to the baseline level, specific to marmosets in each condition). The level of allogrooming remains elevated relative to baseline level for marmosets in the experimental condition across all five post-playback days and extrapolation of the trend-line indicated that this elevated level was likely to last somewhat beyond. However, there was a fairly high degree of inter-individual variation for marmosets in the experimental (chirp playback) condition.

For grooming invite, although the difference between the increase from pre- to mid-playback was not significant (Fig. 5.7), there was a nonsignificant trend for both categories (pre-mid-playback: adults and juveniles: *N* = 31, *P* = 0.053; adults only: *N* = 31, *P* = 0.053). For pre- to post-playback the difference was not significant for adults only, and showed a weak trend for the category of adults and juveniles combined (pre-post-playback: adults and juveniles: *N* = 31, *P* = 0.092; adults only: *N* = 31, *P* = 0.109).

Table 5.5 Statistical test results for the analysis of the long-term effect of conspecific chirp playback on focal marmoset behaviour; mean change in percent time (behaviours) and the mean frequency (calls) per observation session for focal individuals in the control and experimental condition. Asterisk (*) indicates *P* < 0.05. ns indicates a result in the predicted direction which was nonsigificant and nst indicates a nonsignificant trend (*p* < 0.100). Ŧ indicates means where the direction of difference is opposite to the predicted direction (one-tailed tests). ~ indicates two-tailed, post hoc analyses. The adjusted α-level for multiple testing is also displayed: underlining indicates that significance is retained following adjustment.

Focal Behaviour	performed to and from	pre- to mid-playback					pre- to post-playback				
		control	chirp	*N*	*P*	adjusted α-level	control	chirp	*N*	*P*	adjusted α-level
Groom invite	adults and juveniles	-0.269	0.134	31	0.053 nst		-0.289	-0.037	31	0.092 nst	
	adults	-0.334	-0.018	31	0.053 nst		-0.296	-0.058	31	0.108 ns	
Allogroom	adults and juveniles	-0.632	1.802	31	0.030 *	n = 2	0.144	-0.256	31	Ŧ	
	adults	-0.644	0.874	31	0.061 nst	α = 0.025	0.206	-0.173	31	Ŧ	
Affiliative contact	adults and juveniles	0.107	0.139	31	0.396 ns		0.051	0.256	31	0.073 nst	n = 2
	adults	0.026	0.041	31	0.432 ns		-0.005	0.135	31	0.048 *	α = 0.025
Share food	adults and juveniles	0.020	0.015	31	Ŧ		-0.018	0.014	31	0.436 ns	
	adults	-0.051	-0.106	31	Ŧ		-0.029	-0.061	31	Ŧ	
Social play	juveniles	0.032	-0.159	31	Ŧ		0.298	-0.256	31	Ŧ	
Composite of five affiliative behaviours	adults and juveniles	-0.742	1.932	31	0.037 *	n = 2	0.186	-0.279	31	Ŧ	
	adults	-1.002	0.790	31	0.046 *	α = 0.025	-0.124	-0.158	31	Ŧ	
Composite of intragroup agonism (Chase/Attack/Steal food) ~	adults and juveniles	-0.028	-0.041	31	0.899 ns		0.015	-0.096	31	0.238 ns	
	adults	-0.023	-0.027	31	1.000 ns		0.018	-0.009	31	0.832 ns	
Composite of intergroup agonism (Anog. present; Bristle) ~	n/a	-0.038	-0.370	31	0.342 ns		-0.245	-0.603	31	0.327 ns	
Composite of six anxious behaviours (inactive alert, agit., self-scratch, scent mark, self-groom, gouge) ~	n/a	-13.788	-10.269	31	0.443 ns		-7.385	-14.143	31	0.151 ns	

		pre- to mid-playback					pre- to post-playback				
Focal behaviour	performed to and from	control	chirp	*N*	*P*	adjusted α-level	control	chirp	*N*	*P*	adjusted α-level
Feed ~	n/a	0.750	0.631	31	0.966 ns	n = 3	-0.881	1.230	31	0.462 ns	
Active forage ~	n/a	2.716	-0.746	31	0.016 *	α = 0.167	0.440	1.153	31	0.776 ns	
Visual forage ~	n/a	6.124	2.743	31	0.117 ns		4.655	4.927	31	0.895 ns	

Also in the predicted direction, but not significant, was the change in time spent in food sharing, to and from adults and juveniles; this was greater for marmosets in the chirp playback condition than in the silence playback condition (Fig. 5.11), (*N* = 31, *P* = 0.436). Marmosets in the experimental condition did not display a greater positive change in time spent in sharing food than marmosets in the control condition, to and from adults only between pre- and post-playback, and between pre- and mid-playback for both age categories combined (direction of difference opposite to predicted, Fig. 5.11).

No focal marmosets engaged in social play with other adults, so the analysis was carried out on social play directed to and from juveniles only. For pre- and mid-playback, and pre- and post-playback, the positive change in time spent in social play was not greater for marmosets in the experimental condition compared to the control condition (direction of difference opposite to predicted, Fig. 5.12).

A composite of all five affiliative behaviours was analysed as a general index of social contagion of affiliation. As predicted, between pre- and mid-playback, the increase in time spent in affiliative behaviours was significantly greater for marmosets in the chirp playback condition than the control playback condition, both considering the combined category and adults only (adults and juveniles: *N* = 31, *P* = 0.037; adults: *N* = 31, *P* = 0.046). However, contrary to prediction, between pre- and post-playback the change in time spent in all of the five affiliative behaviours was more positive for marmosets in the control condition than for those in the experimental. As predicted, in the ‘matching’ analysis, there was no significant difference for marmosets in the experimental as compared to the control condition in the change in time spent in behavioural composite indices of any of the three non-matching affective categories (intragroup or intergroup aggression or anxiety) between either pre- and mid-playback, or pre- and post-playback (see Table 5.5).

I carried out a post hoc analysis of the effect of the long-term chirp playback on marmoset feeding-related behaviour (Table 5.5). Following long-term playback of chirp calls, there was no significant increase in the amount of time spent feeding, or in active or visual foraging from pre- to mid-playback or from pre- to post-playback. However, between the pre- and mid-playback period, the change in the amount of time that marmosets spent in active foraging *decreased* significantly more for marmosets in the chirp playback condition than for those in the silence playback condition. Because active foraging is a natural behaviour, a decrease in this behaviour may be considered undesirable to welfare. However, we must balance this concern with the possibility that the focal marmosets spent more time in alternative desirable behaviours incompatible with active foraging, for example: inactive rest (see below) and allogrooming (see above).

Fig. 5.7 Mean change in the mean percent time (± 1 SE) spent performing groom invite to and from adults and juveniles, and to and from adults only, between pre-playback and mid-playback, and between pre-playback and post-playback, by marmosets exposed to the long term playback: of recorded silence (white bars); and of pre-recorded chirp calls (grey bars).

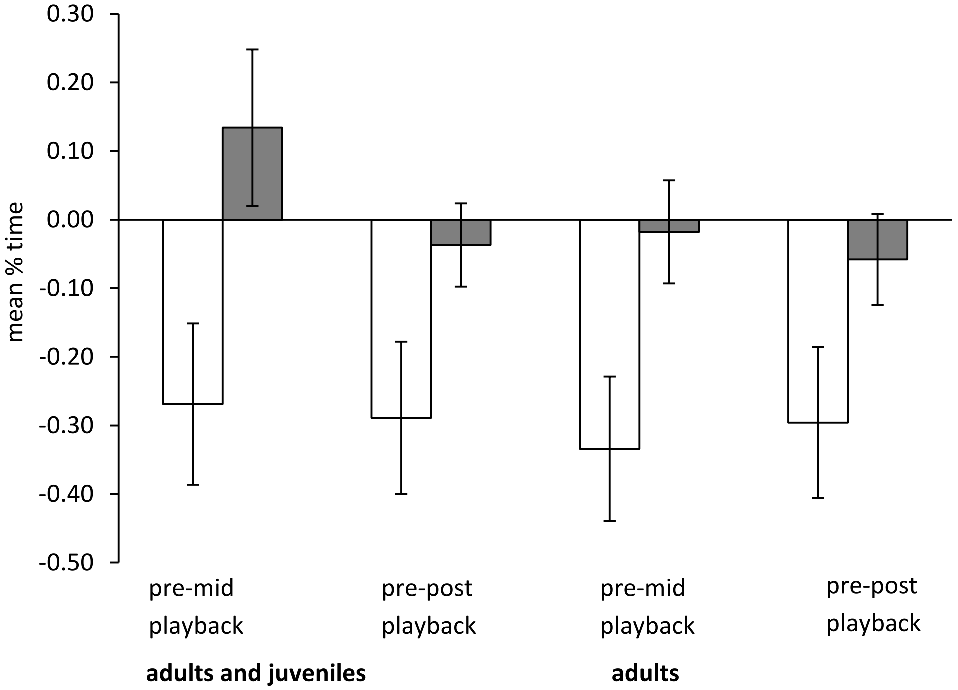


Fig. 5.8 Mean change in the mean percent time (± 1 SE) spent performing allogroom to and from adults and juveniles, and to and from adults only, between pre-playback and mid-playback, and between pre-playback and post-playback, by marmosets exposed to the long term playback: of recorded silence (white bars); and of pre-recorded chirp calls (grey bars). Asterisk (*) denotes significance.

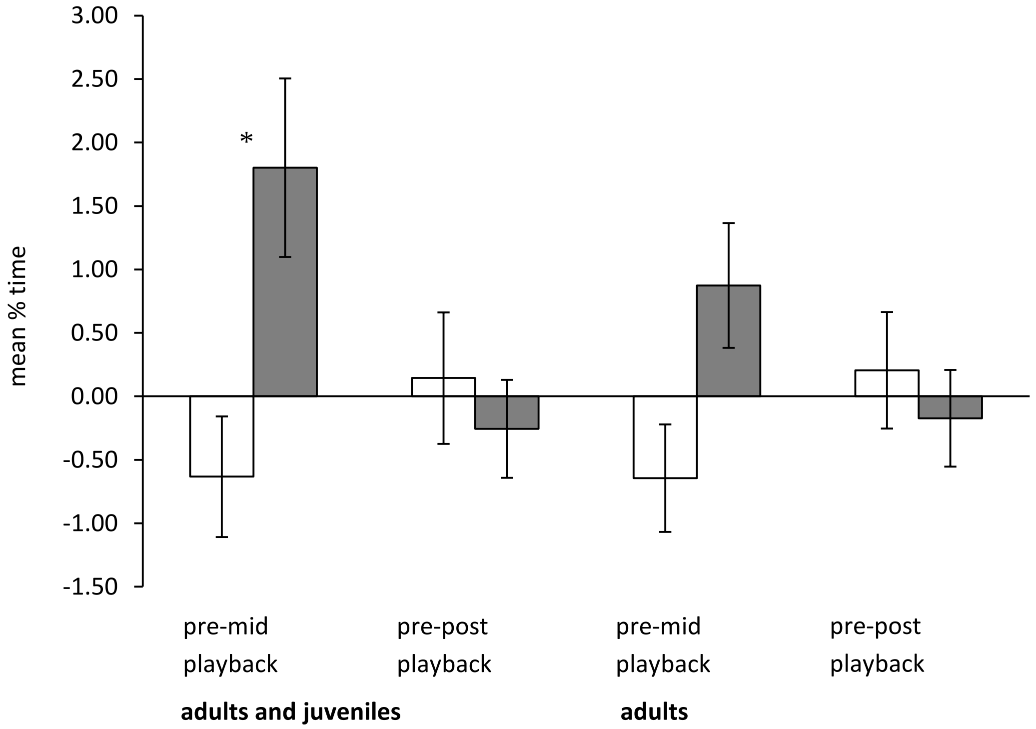


Fig. 5.9 Mean change in the mean percent time (± 1 SE) spent performing active affiliative contact to and from adults and juveniles, and to and from adults only, between pre-playback and mid-playback, and between pre-playback and post-playback, by marmosets exposed to the long term playback: of recorded silence (white bars); and of pre-recorded chirp calls (grey bars). Asterisk (*) denotes significance.

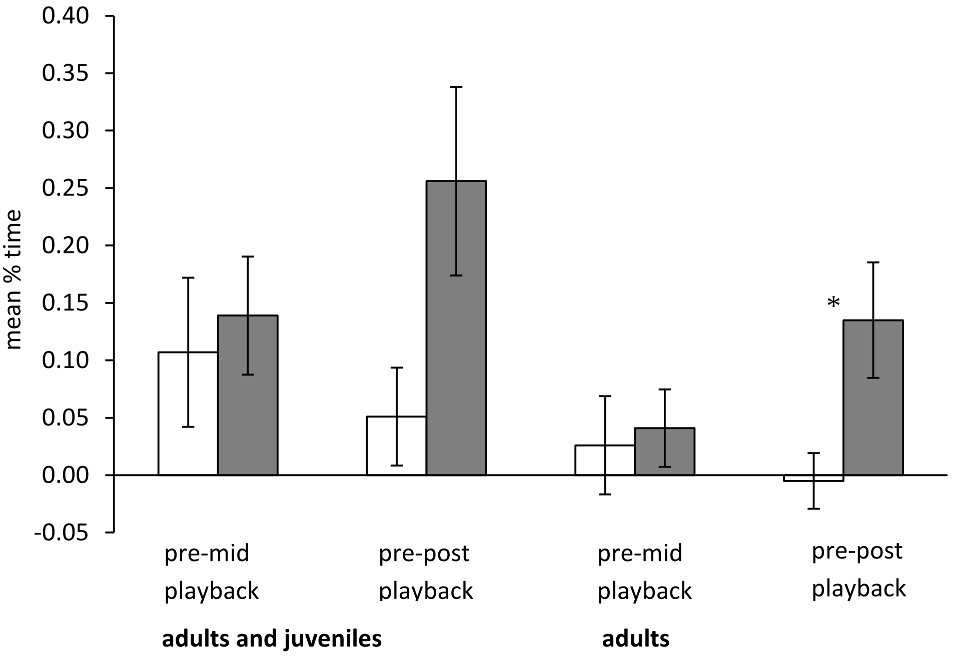


Fig 5.10 Difference between mean percent of time engaged in active affiliative contact on each post-playback day by marmosets in each condition and the baseline mean for that condition (mean for five pre-playback days) (i.e. zero indicates no change from baseline level). Marmosets exposed to the long term playback: of control (grey line); and of chirp (black line) playback. Trend lines are shown as dotted grey and black lines respectively, and have been extrapolated for the two days beyond the end of the study.

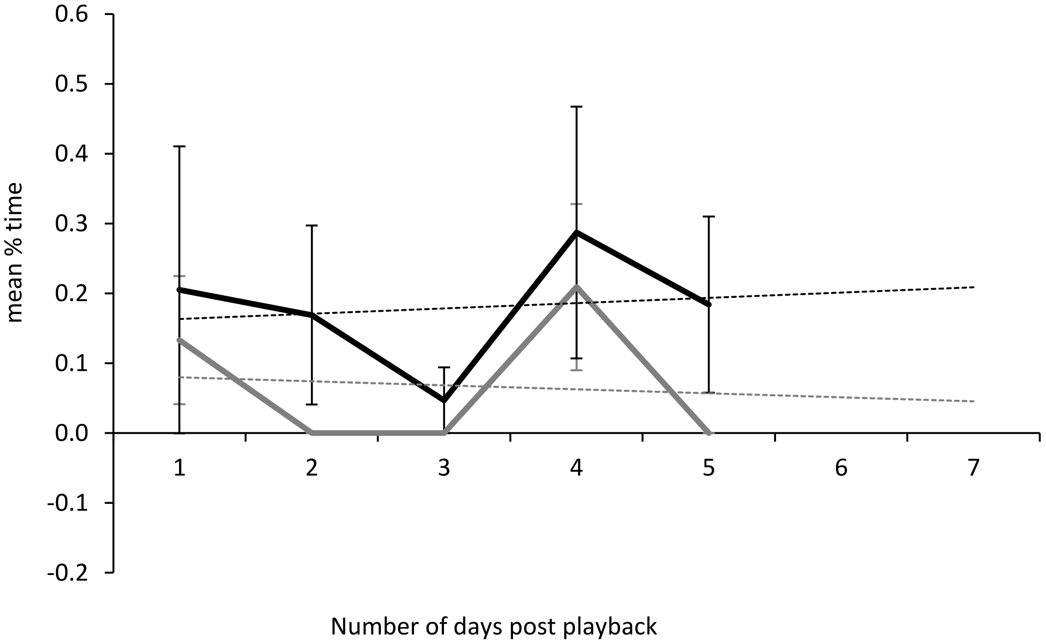


Fig. 5.11 Mean change in mean percent time (± 1 SE) spent performing share food, to and from adults and juveniles, and to and from adults only, between pre-playback and mid-playback, and between pre-playback and post-playback, by marmosets exposed to the long term playback: of recorded silence (white bars); and of pre-recorded chirp calls (grey bars).

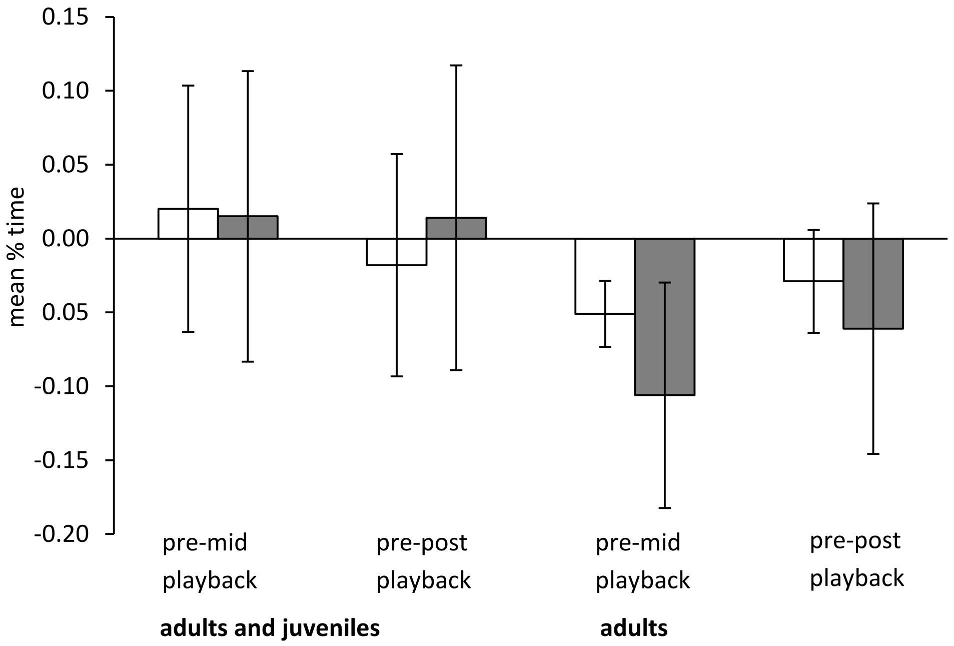
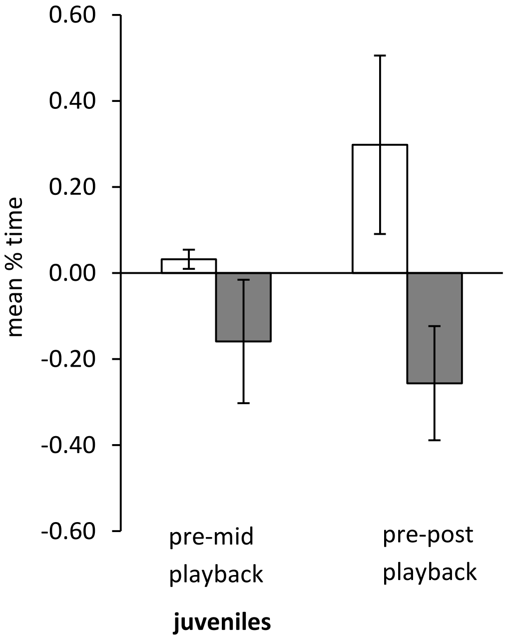


Fig. 5.12 Mean change in the mean percent time (± 1 SE) spent performing social play with juveniles (no social play engaged in by focal marmosets with other adults), between pre-playback and mid-playback, and between pre-playback and post-playback, by marmosets exposed to the long term playback: of recorded silence (white bars); and of pre-recorded chirp calls (grey bars).



5.3.3 Behavioural Welfare Indicators

Because I am interested in the possible enrichment application of the playback of affiliative vocalisations, I carried out two-tailed analyses to assess the influence of both short-term and long-term chirp playback on the welfare of captive marmosets.

Immediate Effect of Short-term Chirp Playback on Focal Vocalisation

It is possible that the playback of a higher-than-average-rate of vocalisations, especially for an extended period, may lead to a reduction in the spontaneous production of calls (a naturally expressed behaviour) by the receiving marmosets. This might be more of a concern if positive affect calls diminished. Table 5.6 displays the results of the statistical tests comparing the proportion of 15-sec intervals before and after the playback of a pre-recorded chirp call during which vocalisations, within the four main categories of affect, were produced by the focal marmosets. Because the incidence of focal vocalisations was relatively low I analysed composites of call types representative of each of the four categories of affect.

Table 5.6 Statistical results for the analysis of the immediate effect of pre-recorded chirp playback on focal marmoset vocalisation; mean proportion of behaviours in the 15-sec pre-chirp call playback with the mean 15-sec post-chirp call playback (two-tailed statistical analysis). Asterisk (*) indicates *P* < 0.05. ns indicates nonsigificant.

Focal call	Mean proportion pre-chirp call playback	Mean Proportion post-chirp call playback	*N*	*P*
Affiliative (whirr)	0.009	0.023	16	0.180 ns
Agonistic intergroup calls (composite of loud shrill and twitter)	0.012	0.011	16	1.000 ns
Agonistic intragroup calls (chatter)	0.000	0.002	16	1.000 ns
Anxiety and alarm calls (composite of ek, seep, tsik and rapid-fire tsik)	0.004	0.000	16	0.500 ns

None of the focal individuals produced chirp calls within 15 sec of a chirp playback, so the affiliative call category is represented by the whirr call only. Because the whirr call is sometimes made with a closed mouth (see Chapter three and four), the number of whirr calls that the observer detected was likely to be an underestimate. Nevertheless, I found that marmosets displayed a higher mean probability of emitting an affiliative (whirr) call directly after than before a played back chirp call, although the difference was not significant (N = 16; P = 0.180). No other differences even approached significance (Table 5.6).

Long-term Chirp Playback

Table 5.7 displays the results of statistical tests comparing the mean change in the mean time spent by marmosets in behaviours used as welfare indicators between the control and experimental long-term playback conditions: between pre-playback and mid-playback; and between pre-playback and post-playback.

I found only one statistically significant difference between the experimental and the control conditions for long-term playback. The amount of time spent in inactive rest in the long-term playback experimental condition (a positive welfare indicator) increased significantly between pre-playback and post-playback. No significant increase in behaviours indicative of negative welfare were found to be associated with the long-term playback of pre-recorded chirp calls compared to the playback of recorded silence.

5.3.4 Family-wise Error Rate Correction

Following adjustment of the α-level to correct for multiple testing, none of the previously significant results were retained.

Table 5.8 Statistical test results for the analysis of the overall effect of conspecific chirp playback on focal marmoset behaviour; mean change in percent time (behaviours) and the mean frequency (calls) per observation session for focal individuals in the control and experimental condition (two-tailed). Asterisk (*) indicates $P < 0.05$. ns indicates nonsigificant. The adjusted α-level for family-wise error rate correction is displayed at the far right of the table.

Valence of welfare indicator	focal Behaviour	Baseline to mid-playback		*N*	*P*	Baseline to post-playback		*N*	*P*	adjusted α-level
		control	chirp			control	chirp			
+ve	Calm locomotion	-0.234	-0.104	16	0.331 ns	6.027	3.488	16	0.291 ns	n = 2
	Inactive rest	2.714	4.442	16	0.398 ns	0.708	6.476	16	0.048 *	α = 0.025
-ve	Agitated locomotion	-4.196	-3.988	16	0.885 ns	-3.545	-3.770	16	0.874 ns	
	Inactive alert	-8.912	-5.560	16	0.455 ns	-3.380	-9.125	16	0.163 ns	
	Scent mark	-0.446	-0.292	16	0.493 ns	-0.383	-0.229	16	0.452 ns	
	Self-scratch	-0.030	-0.049	16	0.958 ns	-0.017	-0.394	16	0.288 ns	
	Gouge	-0.234	-0.104	16	0.706 ns	-0.134	-0.022	16	0.730 ns	

5.4 Discussion

5.4.1 Immediate Effect of Short-term Chirp Playback

Consistent with the immediate effect of spontaneous neighbour chirp calls found in the previous chapter, I found that marmosets were significantly more likely to show active affiliative contact and food sharing directly after the playback of a pre-recorded conspecific chirp call, rather just before. However, this result was only significant for these two behaviours in composite.

These results can really only give an indication of the immediate effect of chirp call playback. Affiliative behaviours are performed infrequently in captive marmosets. Our analysis was also based on a relatively small number of played back chirp calls (36 in total, giving 36 pre-call intervals and 36 post-call intervals for each individual). Thus, there were 36, 15-sec long post-call intervals per individual within which affiliative behaviours might occur, and from which the immediate effect of a non-contextual chirp call was assessed. It is likely, then, that the influence of spontaneous neighbour calls and other external noises may have interfered with the chirp playback calls. It is even possible that some of the played back calls may not have been heard by focal individuals, if nearby or external noises were particularly loud and/or distracting, since the chirp call itself is a relatively quiet, short range call. These factors give cause to treat our results with some caution, and suggest the need for repetition, but also indicate how striking the results are under the circumstances.

My predictions were based firmly on theory, and on previous empirical evidence (Chapter four). The results, thus, provide some additional support for a causal link between neighbour chirp calls and marmoset affiliative behaviour.

5.4.2 Long-term Effect of Chirp Playback

Between pre- to mid-playback, the change in the mean time spent in allogrooming was almost significantly more positive for marmosets exposed to the playback of chirp calls than for those exposed to silence, consistent with our prediction Groom invite also displayed a trend towards being more positive in the chirp calls condition. Thus, several hours of daily chirp playback appeared to have a relatively long-lasting influence on marmoset allogrooming behaviour, and to some extent on groom invite behaviour, extending beyond the specific hours of daily playback.

However, contrary to our predictions, the influence on allogrooming behaviour did not persist in the absence of continued daily exposure to chirp playback. In fact, between pre- and post-playback, the change in time spent allogrooming decreased more for experimental than control marmosets. Badihi (2006) noted that the removal of some forms of positive enrichment intervention, presented for a limited duration only, might lead to reduced welfare in captive animals. Individuals may drop, to a lower level of behavioural welfare than was evident before the exposure to the enrichment. This view is supported by the drop in allogrooming behaviour in marmosets in the experimental condition post- playback.

However, the influence of long-term chirp playback on groom invite behaviour appeared to extend somewhat longer than the effect on allogrooming. Groom invite displayed a weak positive trend for marmosets in the experimental condition relative to those in the control, between pre- and post-playback. This suggests that the effect tailed off somewhat, but not entirely, once playback ceased.

Active affiliative contact showed a significant increase between pre- and post-playback by marmosets in the chirp playback condition relative to marmosets in the control playback condition. Interestingly, although the increase approached significance for affiliative contact performed to and from adults and juveniles, the effect was only significant when adults only were considered, suggesting a stronger effect in the latter. A non-significant difference in the expected direction for the period between pre- and mid-playback indicates that the effect of long-term playback of chirp may be somewhat cumulative. In addition, the level of active affiliative contact may have been suppressed during mid-playback periods of observation. Marmosets were stimulated to perform active affiliative contact immediately after a spontaneous neighbour chirp call (Chapter four), and also following playback of chirp calls (in composite with share food, immediate effect, this Chapter).Therefore it is possible that, during the mid-playback period, marmosets were stimulated to perform more active affiliative contact immediately following playback of each chirp call during the specific hours of playback when no-one was present, but that this was reversed or decreased during the non-playback hours of observation. During the post-playback period however, no auditory playback occurred in between observation sessions, possibly meaning that during the post-playback observation hours, the behaviour of the marmosets continued to be influenced by the residual effect (positive) of having been exposed to many hours of chirp playback, but without the dampening effect of having already performed a lot of active affiliative contact in playback sessions that day.

Overall, this result suggests that the playback of chirps for several hours daily has a relatively long-term effect on marmoset active affiliative behaviour, presumably increasing during the playback period then lasting for at least several days after playback was stopped. An examination of the individual five post-playback days indicates a somewhat elevated level of active affiliative contact relative to baseline (pre-playback) for marmosets in the chirp playback condition relative to the control, across all five post-playback days and extrapolated to last at least a few days beyond that, but with much inter-individual variation for marmosets in the experimental condition.

The results of the analysis of ‘matching’ to same and different affect categories of the contagion stimulus indicate that the social contagion effect was, as predicted, specific to the affect matching that of the playback behaviour, affiliation, although it appeared to be confined to the mid-playback period. However, a possible explanation is that in the post-playback composite measure, the behaviour that showed the largest increase, active affiliative contact, is the behaviour of the shortest duration meaning that it may have been under-represented in a composite of observed times.

It is worth noting that the results here presented are, if anything, likely to provide a conservative estimate of any positive effect of chirp playback. For reasons explained above, I excluded data for behaviour performed to and from infants, and considered the results for affiliative behaviour performed to and from adults, and to and from adults and juveniles only. As anticipated, the result of analysis including all age groups together (adults, juveniles, and infants) provides much stronger results in the direction favouring the experimental condition.

All together, I have provided some evidence suggesting that the playback of affiliative chirp calls in marmosets leads to a relatively long-term change (i.e. outwith specific playback periods) in allogrooming behaviour and an even longer acting change (of 5 days) in active affiliative contact, for adults in particular, in marmosets. The long-term playback of chirp calls thus appears to initiate an increase in a range of marmoset affiliative behaviours. Such relatively long-term changes in particular affiliative behaviours, are potentially consistent with the initiation of a change in affiliative social culture in marmosets, providing some support for social contagion as a transmission mechanism. The data are (understandably) minimal because of the novelty of such research. Following adjustment for family-wise error rate, many previously significant results only approached significance. Therefore, replication is necessary before stronger conclusions can be drawn.

5.4.3 Chirp Call Function

As stated in the previous chapter, although the chirp call has been described as an affiliative call, it has also been described as a feeding call (e.g. Epple, 1968). I carried out a post hoc analysis of the data to determine whether or not the chirp call playback had an influence on the feeding-related behaviour of *Callithrix jacchus.* Consistent with the results for spontaneously produced neighbour calls (previous chapter), I found that the short-term playback had no immediate effect on marmoset feeding, or on active foraging. Contrary to my finding for spontaneous neighbour chirp calls, I did not find that marmosets spent significantly longer feeding in observations with chirp playback relative to those with the playback of silence.

I found that neither short-term nor long-term playback of chirp calls led to an increase in feeding, active or visual foraging in marmosets relative to those in the control condition. Contrary to these findings, Kitzmann and Caine (2009) played back a call that spectrographically resembles the common marmoset chirp call, and found that

Geoffroy's marmosets spent significantly longer in both feeding and active foraging for up to 20 min following call playback. My results support the view that common marmoset chirp calls function predominantly as affiliative calls, at least when heard out of context, in the absence of a highly desirable food.

5.4.4 Captive Marmoset Welfare: Chirp Playback Practical Application

As I have shown above, the playback of affiliative chirp calls leads to a significant contingent increase in the performance of certain affiliative behaviours in marmosets. Also, long-term playback appears to lead to a significant decrease in the amount of time spent resting. Further, neither the short-term nor the long-term playback of pre-recorded affiliative chirp calls led to a significant increase in any negative welfare indicators. Thus, the playback of pre-recorded conspecific affiliative calls represents a potential means of improving captive marmoset welfare. Replication of the data is necessary, due to the relatively small sample size and some limitations however, if this can be achieved economically it may lead to an improved evidence base to encourage prudent welfare improvements.

Playback of conspecific affiliative calls as environmental enrichment is likely to be both practical and economical to implement. For example, laboratory facilities, with marmosets housed in cages, may already have a system of loudspeakers within colony

Plate 5.2 Practical application for marmosets housed in large rooms: plastic box with iPod and speaker.

Plate 5.3 Chirp playback practical enrichment application: conspecific chirp calls are played to captive marmosets, housed in a large room, through a speaker attached to an iPod concealed within a small plastic box covered in white packing film to allow the sound to penetrate.

rooms. I already have acoustically clean recordings of the marmoset chirp calls. Therefore, the cost of practical application in this case is likely to be low, both in terms of initial outlay and on-going time investment.

For marmosets housed in large colony rooms a different set-up may be required. A small loudspeaker connected to an audio player could be placed in a plastic box wrapped in opaque wrapping material and placed inside the uncaged room (see Plates 5.2 and 5.3).

Many marmosets held in captivity could potentially benefit from this novel auditory environmental enrichment. Further, the playback of conspecific affiliative calls may have broader implications for improving welfare in other socially housed animals, both primates and non-primates (see Chapter seven for further suggestions).

5.4.5 Possibilities for Future Research

Social Culture

Here I have presented tentative evidence for a relatively long-lasting effect of long-term chirp playback on marmoset social behaviour. However, from the current data I cannot determine how long such a social change may continue in the absence of further playback. Practical restrictions meant that we were unable to maintain stable room compositions. I was therefore unable to observe the marmosets until any apparent effect had disappeared. The shift in social culture observed in a wild baboon population lasted for a considerable time and even following the replacement of the original demonstrators (Sapolsky and Share, 2004). Future research is needed to investigate the durability of the effect beyond 1-5 days.

If the effect of social culture is found to be durable it would be interesting to investigate whether the effect, and perhaps even its transmission, may be maintained with the removal and replacement of one, or more, original group members. A serial replacement paradigm has been used to investigate cultural transmission in chimpanzees (Menzel et al., 1972) and has also been used in humans (Jacobs and Campbell, 1961; Caldwell and Millen, 2008, 2010). Successive generations are simulated, at a micro scale, through the successive removal and replacement of individuals over a relatively short space of time, until none of the original group members remain (see Mesoudi and Whiten, 2008; Whiten and Mesoudi, 2008 for reviews of such diffusions in humans and animals respectively). Such an approach may prove fruitful for the further investigation of social culture transmission but may have ethical connotations.

Chirp Call Function

In the previous chapter I proposed that the marmoset chirp calls may be produced either specifically to solicit affiliative contact from other marmosets in their social group, or as a general expression of excitement in expectation of a desirable and pleasurable event. An interesting approach to testing whether the chirp call functions as an anticipatory call would be to condition marmosets to expect a pleasurable or desirable event on a particular cue. If chirp calls increase around such a conditioned stimulus then this would support our proposal that the chirp call is an excited, anticipatory vocalisation. The difficulty would be that the anticipated reward would have to be something other than a highly desirable food, to allow us to dissociate between the possible functions of the chirp call either as a specific desirable-food-related call and a more generic call expressive of anticipatory excitement.

Welfare

Control over their environment, or choice, is an important aspect of enhanced welfare for captive non-human primates (e.g. Badihi, 2006). It may prove illuminating to provide marmosets with a choice of auditory environment, as did McDermott and Hauser (2007). If marmosets were given the choice, would they find the playback of a high rate of conspecific chirp calls preferable to silence? In Chapter seven I discuss preference tests in relation to this subject in more detail.

Playback Extensions

I could investigate the influence of the playback of another marmoset affiliative call: the whirr call. I recorded many examples of the whirr call from marmosets, in their usual social context, during the observational study in Chapter four.

My research has, so far, been concerned exclusively with social influence in the auditory domain. It might be informative to extend our investigation of the playback of affiliative behaviours to the visual domain. In the next Chapter I follow up this proposal.

5.5 Conclusion

In summary, I have provided somewhat stronger evidence for the causality of the neighbour effect for affiliation in the common marmoset. My results also indicate that the marmoset chirp call is, indeed, an affiliative call. We found that the long-term playback of chirp calls produced a relatively long-term change in the affiliative behaviour of marmosets. My results are consistent with the successful initiation of a more affiliative social culture in marmosets through the playback of conspecific affiliative vocalisations, lending support to social contagion as a transmission mechanism for Sapolsky’s (2006) form of social culture.

Chapter 6

The Effect of the Video Playback of Conspecifics Allogrooming on Marmoset Social Behaviour

In Chapters four and five I provided evidence consistent with the social contagion of affiliation in marmosets in the auditory domain. In the current chapter I extend the investigation of social contagion from the auditory to the visual channel. In Chapter five I used the audio playback of affiliative calls in an attempt to initiate a shift to a more affiliative culture. If visual social contagion of affiliation can be demonstrated, then a further research question would be whether a more affiliative social culture can be elicited through this second modality.

6.1 Introduction

6.1.1 Visual Social Contagion

Visual social contagion in nonhuman primates has been demonstrated for: self-scratching in Japanese macaques (Nakayama, 2004), yawning through video playback in chimpanzees (Anderson et al., 2004) and in stumptail macaques (Paukner and Anderson, 2006), and through observation of spontaneous neighbour yawns in gelada baboons (Palagi et al., 2009). However, visual contagion has not yet been demonstrated, in any nonhuman primate, for an affiliative, and truly interactive, social behaviour.

Research interest in contagious yawning was initiated by anecdotal observations, followed by the empirical study of visually and cognitively mediated contagion in humans (Provine, 1986). A later study found an association between a high questionnaire score on empathy, and susceptibility to contagious yawning in humans (Platek et al., 2003). Interest in contagious yawning has been greatly increased by the apparent link between contagious yawning and empathy in humans, prompting further comparative research on contagious yawning in nonhuman primates.

Contagious yawning has now been investigated extensively in nonhuman primates (see above). However, there are good reasons to support the extension of research on visual social contagion to behaviours other than yawning.

The function of yawning is poorly understood in any species (e.g. Smith, 1999). There are many theories for the function of yawning in nonhuman primates (e.g. Deputte, 1994), some of them in direct opposition (Palagi et al., 2009). Indeed it now seems likely that the behaviour it is not a unitary phenomenon, having different contexts of use (rest and emotion yawn: Deputte, 1994), and corresponding differences in morphology (full and modified yawn: Vick and Paukner, 2010). The evidence for the contagion of yawning is so far confined to the facilitation of yawning itself, rather than a suite of related behaviours consistent with social contagion. Finally, there is little basis for supposing that any link between social contagion and empathy may be confined to yawning.

I suggest that the investigation of behaviours with a higher degree of emotional valence may be particularly illuminating with regard to a potential link with empathy. I also propose that research into the social contagion of behaviours with a clearer social function is likely to have interesting and potentially important implications, from both a theoretical and a practical point of view.

Nakayama (2004) investigated the more general contagion of negative arousal. He suggested that individuals engaged in self-directed behaviours, such as self-scratching, convey a negative emotional state to conspecific observers. He proposed that observers then experience an increase in negative arousal, mediated through a primitive form of empathy, and evidenced by a consequent increase in self-scratching behaviour. Thus, he supports the notion of social contagion, and draws links with empathy, in a behaviour other than yawning. However, his results are again consistent with a social facilitation effect (see Chapter one for the definition used for the purposes of the thesis). The evidence for the social contagion of negative arousal, so far, is confined to one behaviour only: self-scratching, rather than stemming from the influence on a range of behaviours representative of negative affect. Also, self-scratching is another behaviour without a clear social function, although as a displacement activity it apparently reveals individual anxiety (Cilia and Piper, 1997).

Both yawning and scratching are behaviours of quite short duration, neither strongly associated with positive welfare. A negative welfare indicator, self-scratching, is performed at increased rates by both Japanese macaques observing self-scratching by conspecifics (Nakayama, 2004); and also by stump-tailed macaques observing video playback of yawning (Paukner and Anderson, 2006), although, this latter effect may be confined to modified yawns, as recently found in chimpanzees (Vick and Paukner, 2010). The investigation of the social contagion of a behaviour clearly associated with positive welfare, and with a positive affective state, seems an obvious, and worthwhile new research direction.

Here I aim to investigate the potential social contagion of an affiliative social behaviour with a clear social function, which is of relatively long duration, and indicative of positive welfare. In humans social contagion of positive affective state has been investigated through the vocal medium of contagious laughter (Provine, 1992).

However, visual social contagion has yet to be demonstrated for an affiliative behaviour in nonhuman primates through experimental manipulation.

As stated above, if I establish evidence that social contagion occurs when marmosets view conspecifics performing our selected affiliative behaviour, I am interested in the possibility of initiating a social culture of increased affiliation, through observation of conspecifics engaged in the affiliative behaviour. Although there is no specific evidence for the contagiousness of the behaviour, it was allogrooming that Sapolsky and Share (2004) observed to be performed at an increased rate in the population of wild baboons that displayed a shift to a more pacific social culture. Of all the affiliative behaviours in the behavioural repertoire of marmosets, we chose to investigate allogrooming.

In comparison to the other four marmoset affiliative behaviours that I have investigated in the current thesis, allogrooming is of relatively long-term duration (as compared to groom invite and active affiliative contact). Of all the affiliative behaviours investigated in the thesis so far, social play has had effects most often contrary to our predictions, suggesting that this behaviour may belong to a separate class of behaviour, or mechanism. Social play may also be largely confined to sub-adult age groups. I rejected food sharing as the affiliative behaviour to playback following our stated aim to investigate mostly social, non-food related behaviours (see Chapter one and two).

6.1.2 Allogrooming

Allogrooming is a social, interactive, affiliative behaviour with a clear social function. Mutual grooming is considered a central social behaviour in nonhuman primates. Allogrooming relations are often used as a proximal index for the degree of affiliation, an assessment of the strength of social relationship between individuals (e.g. Cords, 1997; Fairbanks, 1980). Studies have found that the recipients of grooming show a contingent reduction in heart rate consistent with relaxation (e.g. Aureli et al., 1999), and the facial expressions and postures of groomees qualitatively support this interpretation. The benefits of allogrooming do not appear to be confined to the groomee. Aureli and Yates (2010) found evidence that allogrooming in crested black macaques results in a short-term increase in well-being for groomer as well as groomee; furthermore, a long-term reduction in physiological stress indicators for groomers has been demonstrated in Barbary macaques (Shutt et al., 2007).

Although it has been suggested for some primate species that allogrooming, acting as a tension-reduction mechanism, is indicative of increased anxiety (Schino et al., 1988), for other primate species it is clearly linked to improved welfare. Cilia and Piper (1997) found that administration of the anxiolytic (anxiety preventing or reducing) drug diazepam in marmosets resulted in a decrease in the frequency of anxious (e.g. scent marking) and aggressive behaviours (e.g. anogenital tail present), but an increase the frequency and duration of allogrooming. In marmosets allogrooming is considered a reliable behavioural indicator of positive welfare (e.g. Badihi, 2006; JWGR, 2009; Buchanan-Smith, 2010). Allogrooming behaviour in marmosets has been described in some detail (e.g. Stevenson and Poole, 1976; Woodcock, 1978). It appears to serve several functions. It maintains good health and hygiene, since groomers clean the pelage of groomees and remove ectoparasites if present. Allogrooming also plays an important social function in marmosets, in maintaining relationships, both between breeding and nonbreeding (helper) females (Lazaro-Perea et al., 2004), and between breeding pairs (Poole, 1978).

6.1.3 Use of Video in Primate Experiments: Virtual Demonstrators

Video demonstrators have been used successfully by researchers in social learning experiments: in colobus monkeys (Price and Caldwell, 2007), and more recently, in marmosets (e.g. Burkart et al., 2009b). Video playback is a useful procedure in the investigation of social behaviour, because it allows the standardisation of presentation across experimental subjects (e.g. D'Eath, 1998; Burkart, 2009b; Rieucau and Giraldeau, 2009). Video demonstrators also exclude the potential complication of interaction with the subjects. In the current study we plan to use video playback as a means of presenting the visual stimuli of conspecifics engaged in allogrooming.

6.1.4 Short-term Video Playback and Social Contagion

In the first part of the current study, I aimed to establish whether or not the video playback of allogrooming leads to social contagion of affiliation in marmosets. This represents, to my knowledge, the first investigation of the contagion of allogrooming in marmosets, and the first investigation of the social contagion of any behaviour related to positive affect in non-human primates.

I predicted that marmosets would spend significantly longer in affiliative behaviours in observation periods during which they were exposed to the experimental video footage of conspecifics allogrooming than when they were shown control footage of conspecifics near one another in inactive rest and alert. Any social influence effect was expected to be most pronounced for behaviours congruent with those being performed by conspecifics in the experimental video (allogroom and groom invite) than of more general matching behaviours.

Rationale for Choice of Control Footage

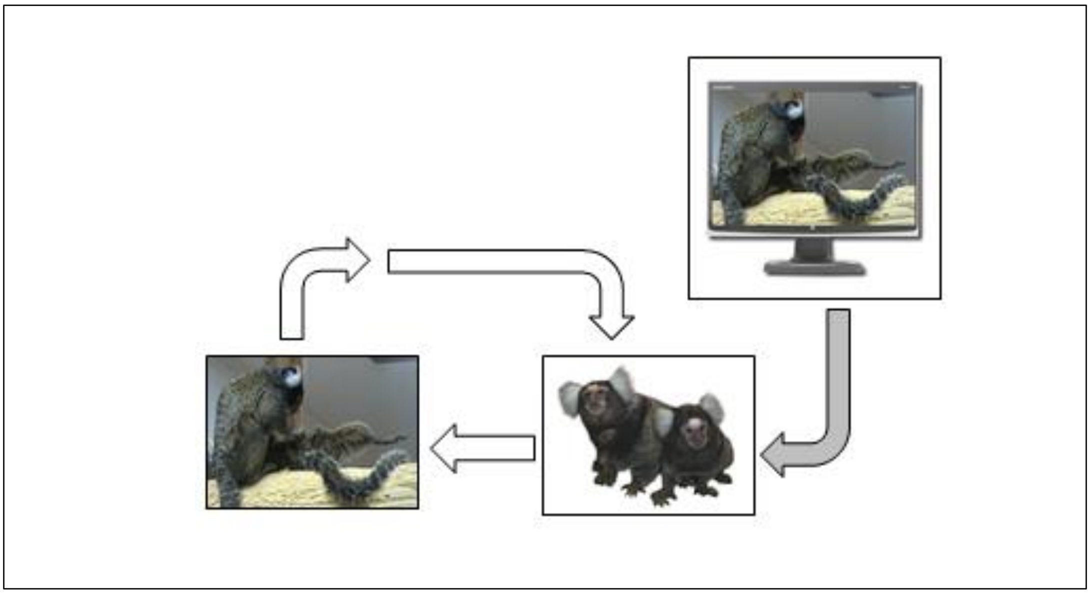
The experimental footage showed dyads of marmosets engaged in mutual grooming (with infrequent active affiliative contact and groom invite). Whilst allogrooming was the most salient behaviour, the groomee was shown sometimes resting (inactive rest) and sometimes in an alert state (inactive alert), while the groomer sometimes engaged in short periods of inactive alert. The rationale for selecting the control video was to show conspecifics engaged in as neutral a behaviour as possible, firstly to control for mere presence facilitation (i.e. an experimental effect due simply to the (virtual) mere presence of conspecifics), and secondly to be as similar as possible to the experimental footage in all aspects other than the allogrooming behaviour. For this reason, I chose to show control footage of a dyad of marmosets situated in close proximity to one another and either in inactive alert or rest (as in the experimental video).

6.1.5 Long-term Video Playback and Social Culture

I designed the second part of the experiment to investigate the potential long-term effects of video allogroom playback on marmosets. The second part was to be carried out in the event that the first part of the study provided evidence that the short-term playback of video led to an increase in the performance of affiliative behaviours, consistent with the social contagion of affiliation. As in the previous chapter, I wanted to find out whether a social culture of increased affiliation could be initiated in marmosets but, in the current study, through the visual rather than through the audio domain. Thus, I extend the investigation of a possible transmission mechanism of social culture to visual social contagion. Would the observation, of video footage showing conspecifics engaged in the affiliative behaviour of allogrooming initiate a shift to a more affiliative social culture?

In the previous chapter, I suggested a mechanism through which social contagion, through the auditory modality, might lead to the initiation of a self-perpetuating feedback loop. Fig. 6.1 displays a potential, analogous process for visual social contagion. In this process, marmosets exposed to the video playback of conspecifics engaged in allogrooming may groom each other more through social contagion. Nearby marmosets observing the allogrooming behaviour, in real time, may be influenced to spend more time allogrooming, also. Thus, a self-perpetuating positive feedback loop may become established. I predicted that the mean change in time spent in affiliative behaviours would increase significantly more for marmosets being shown the allogroom video than for those being shown the control video: both pre-playback to mid-playback, and pre-playback to post playback.

Fig. 6.1 Diagram showing potential positive feedback loop initiated by visual social contagion.



6.1.6 Visual Attention

In the previous chapter I investigated the influence of the playback of audio stimuli, whereas in the current chapter I investigate the effect of visual stimuli. An important difference between the two channels is that, while audio stimuli are difficult to avoid, visual stimuli can be selectively attended to, or ignored by gaze aversion. It was vital, then, to gauge the attention of marmosets towards the stimuli presented. If my results indicated an apparent influence of the video on marmoset behaviour, then a measure of visual attention would be essential to assess the extent to which the effect might be causally linked to the video playback itself.

As a proximal index of visual attention to the visual stimuli, I coded the time that focal individuals spent directing their gaze to one of the monitor screens during stimulus presentation. I collected this information during the first part of the study, while coding the contingent effect of short-term video playback of the experimental and control stimuli.

During the long-term study I was not present during video playback. Had it been possible to film the behaviour of the marmosets remotely during long-term video playback, then data on visual attention could have been coded from such footage. However, video recording of the marmosets was unfeasible due to constraints of cage size, lighting conditions and the relatively small width of the colony rooms.

6.1.7 Captive Marmoset Welfare: Visual Enrichment Via Video Playback

In the previous chapter I explored the possibility of applying audio playback of conspecific affiliative vocalisations to the enrichment of captive environments. Here I assess whether the video playback of conspecifics engaged in affiliative behaviour may be similarly applied to improve the welfare of captive animals.

Enrichment through visual stimuli has been approached through the use of still images, mirrors, coloured lights, and television broadcasts (for a review see: Wells, 2009). The playback of videos displays moving, coloured images, as does television, but with the advantage that ecologically relevant content can be pre-recorded and shown selectively. There is good evidence that monkeys do recognise the specific content displayed in video images (see D'Eath, 1998). However, despite the inherent advantages of the medium, and the extensive use of video in animal learning and perception research, video playback has been under-used in application to captive enrichment (Platt and Novak, 1997).

Earlier studies investigated the possible application of the playback of conspecific behaviour to enhance the welfare of singly-housed individuals (e.g. Bloomsmith et al., 1990). More recently, studies have applied video playback to entire social groups (e.g. Platt and Novak, 1997; Marquez-Arias et al., 2010). However researchers, it seems, have yet to investigate the playback of video displaying conspecifics engaged in behaviours of a specifically affiliative nature. However, Bloomsmith et al. (1990) found that chimpanzees spent longer watching videos of conspecifics performing agonistic behaviour than of chimpanzees engaged in ‘other’ behaviour. In the current study I attempt to instigate an increase in allogrooming in captive individuals, through the video playback of conspecifics mutually grooming. If successful, this may have practical application for welfare enrichment.

Behavioural Welfare Indicators

Because I was interested in the possibility of applying playback as environmental enrichment, I wanted to assess the potential impacts, positive and negative, on the welfare of captive marmosets resulting from the short- and long-term playback of videos of allogrooming. I planned to carry out a two-tailed analysis of behavioural welfare indicators not investigated in the main analysis (see Chapter three for an explanation of our choice of behavioural indicators).

6.2 Method

I carried out the current study in two parts: the investigation of the short-term effect of relatively short video playback of allogrooming conspecifics; and the investigation of the potentially long-term effect of video playback lasting several hours, over several days. Observational data collection was carried out: from 23rd July to August 11th 2010 (short-term playback); and from August 16th to September 10th 2010 (long-term playback).

6.2.1 Study Subjects

The study was conducted on common marmosets (*Callithrix jacchus*) housed in the Medical Research Council Human Reproductive Sciences Unit in Edinburgh (see Chapter three for housing and husbandry details). The study animals were 16 family groups of marmosets housed in four different colony rooms. Figure 6.1 shows the layout of the colony rooms throughout the study. Table 6.1 shows the identity, sex, and date of birth, and developmental stage, of each focal individual and for the individuals housed within the same family group, on the first day of each part of the study. The study subjects were habituated to the presence of the equipment, but were not shown any video footage until the first day of data collection.

Focal individuals in the current study that had already been subjects of previous experiments are likely to be more habituated to direct observation than those that have not (e.g. Badihi, 2006). Therefore I equalised the numbers of repeat focals as far as was possible, given practical limitations, between the control and experimental condition in the second part of the study: 8 focals in the control condition had previously been focal individuals in at least one other experiment (one had been a focal in both previous studies); 10 focals in the experimental condition had been a focal in a previous study. Half of the total number of repeat focals under each condition were also directly observed in the first part of the study, and half in the second part only (i.e. 4 focal individuals in the control and 5 in the experimental condition for the first part of the study were repeat focals).

Short-term Allogroom Video Playback

The focal individuals for the first part of the study were 16 breeding adults, 8 females and 8 males. During the first part of the study there was one change to the focal groups: a non-breeding adult (396y) was removed from group F3 in room four, on 9.08.10, due to aggression. None of the individuals present in the study rooms were involved in biomedical research studies. At the outset of the study, the mean total number of individuals per room was 36, divided among a mean number of 7 social groups, with: 6 cages out of 8 occupied in two of the rooms; and 7 out of 8 occupied in the remaining two rooms. It should be noted that the stocking density of the animals during this study was slightly lower than the previous studies reported in this thesis. This is liable to have a positive influence overall, on baseline levels of affiliative behaviour, as well as welfare indicators which, if anything, makes the findings conservative (as it is more difficult to increase already elevated welfare).

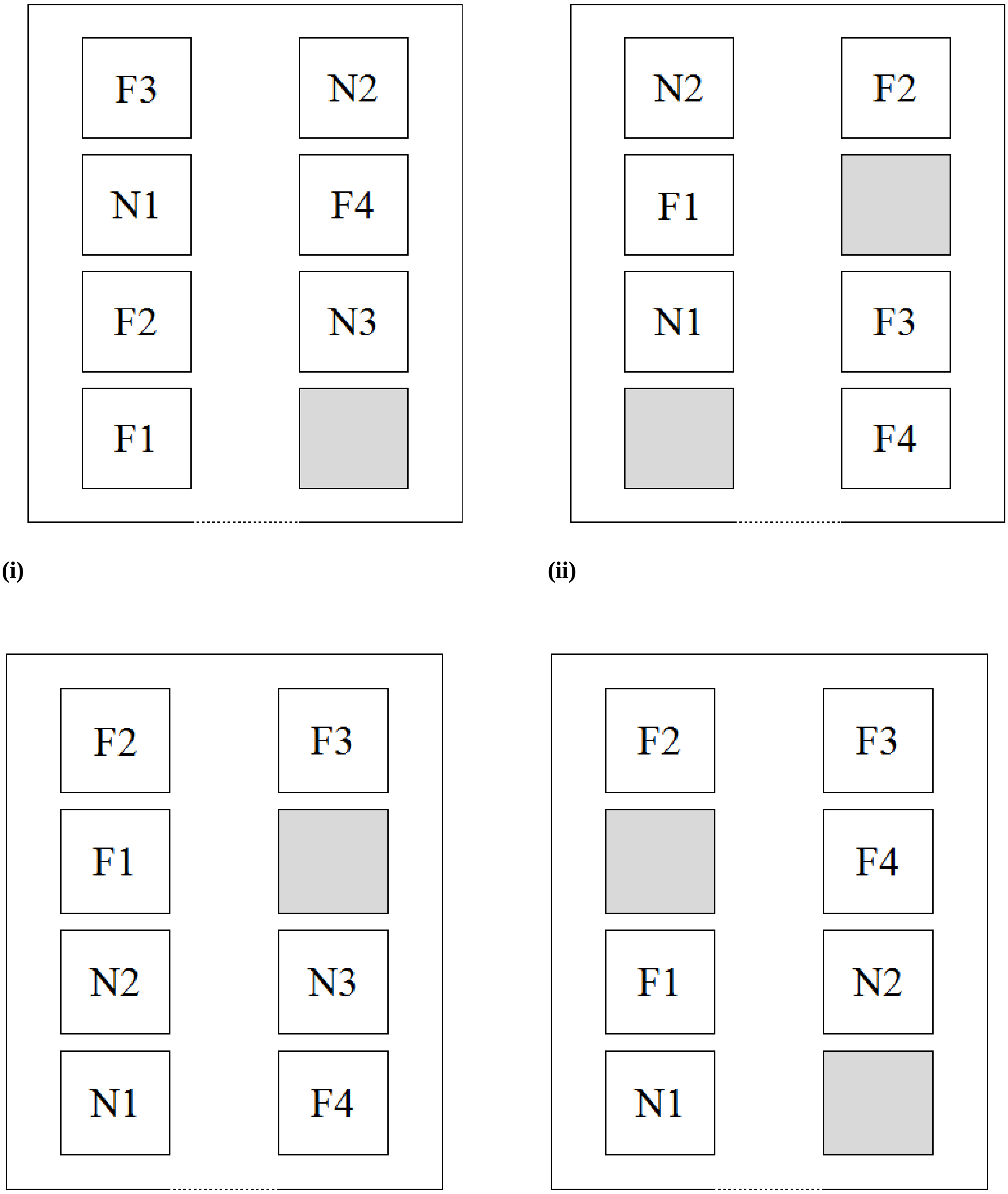
Long-term Allogroom Video Playback

Thirty-two adult marmosets were the focal individuals for the second part of the study, housed in 16 family groups in four colony rooms. The focal individuals were the original 16 individuals, used previously in part one, plus the additional breeding adult from each focal family group. There were no infants in any of the focal groups in the second part of the study.

Between parts one and two of the study a change was made to the nonfocal groups in room three: one breeding female and one non-breeding female were removed to a non-study room (for use in biomedical research). At the outset of the second part of the study, the mean total number of individuals per room was 36 (34 in the control rooms and 38 in the experimental rooms) divided among a mean number of 7 social groups (7 in the control and 7 in the experimental rooms), with one room in each of the two experimental conditions having 6 cages out of 8 occupied and 7 out of 8 occupied respectively. During the study there were no changes to the composition of the rooms.

Throughout the second part of the study several individuals were used in a biomedical study. One focal individual in experimental room 5 (339y) and one focal individual in control room three (1028) were removed for blood sampling three times per week (Mon, Tues and Wed morning, before 09.30, and prior to any observational data collection). Nonfocal breeding adult females (v007 and 324y) were also removed from experimental room five at these times. These removals may have been associated with some stress to the individuals sampled, as well as the other individuals present in the room during the removal process. The removal of marmosets for blood sampling therefore is likely to have introduced an undesirable source of noise in the data for the current experiment. However, this was unavoidable due to constraints on laboratory staff at the time of the study. All the same, the removals were considered unlikely to be a confounding factor since this applied to both the control and experimental conditions equally.

Figure 6.2 Schematic diagrams of the four colony rooms and group arrangement on study day one (23.07.10) showing the label given to each group containing focal individual(s) F1 etc. and neighbour groups N1: (i) room two; and (ii) room three (long-term part of study: control condition rooms); (iii) room four and (iv) room five (long-term part of study: experimental condition rooms). Shaded blocks indicate empty cages.



(i) **(ii)**

(iii) **(iv)**

Table 6.1 For focal individuals and, for the individuals housed within the same family group (all focal marmoset housed in family groups: Individual id, group id, sex, developmental stage (key below), date of birth and age in years and days on the first day: of the short-term playback part of the study (23.07.10); and of the long-term part of the study (16.08.10). For the long-term part of the study: rooms two and three were assigned to the control condition; and rooms four and five to the experimental condition. * indicates focal individuals used for the long-term playback part the study only; ± indicates focal individuals that are directly related to one of the breeding adults in the two rooms filmed for the stimulus video used in this study (all are progeny of 211y); † indicates individuals that changed developmental stage between first and second part of allogroom study. Key: BA = breeding adult; NBA = nonbreeding adult; J = juvenile; I =infant; n = neighbour (nonfocal population).

Room no.	Group id	Individual category	Individual id	Sex	Date of birth	Age in years and days at start of study P 1 (23.07.10)	Dev. stage P 1	Age in years and days at start of study P 2 (16.08.10)	Dev. stage P 2
2	**F1**	**focal 1**	**364y±**	**f**	**01.02.08**	**2 yr 173**	**BA**	**2 yr 197**	**BA**
		focal 2*	**158g**	**m**	**04.06.06**	**4 yr 49**	**BA**	**4 yr 73**	**BA**
		n	261g	m	04.11.09	0 yr 261	J	0 yr 285	J
		n	262g	m	04.11.09	0 yr 261	J	0 yr 285	J
	F2	**focal 3**	**118g**	**m**	**22.08.04**	**5 yr 335**	**BA**	**5 yr 359**	**BA**
		focal 4*	**355y**	**f**	**07.10.07**	**2 yr 290**	**BA**	**2 yr 314**	**BA**
		n	438y	m	01.11.09	0 yr 264	J	0 yr 288	J
		n	infant of 355y	f	02.05.10	0 yr 82	J	0 yr 106	J
		n	infant of 355y	f	02.05.10	0 yr 82	J	0 yr 106	J
	F3	**focal 5**	**326y**	**f**	**06.10.06**	**3 yr 291**	**BA**	**3 yr 315**	**BA**
		focal 6*	**188g**	**m**	**19.11.07**	**2 yr 247**	**BA**	**2 yr 271**	**BA**
		n	434y	**f**	11.10.09	0 yr 285	J	0 yr 309	NBA†
		n	infant of 326y	**m**	18.05.10	0 yr 66	J	0 yr 90	J
		n	infant of 326y	**m**	18.05.10	0 yr 66	J	0 yr 90	J
	F4	**focal 7**	**089g**	**m**	**28.08.03**	**7 yr 117**	**BA**	**7 yr 141**	**BA**
		focal 8*	**1166**	**f**	**13.02.07**	**3 yr 160**	**BA**	**3 yr 184**	**BA**
		n	416y	f	24.05.09	1 yr 60	NBA	1 yr 84	NBA
		n	235g	m	24.05.09	1 yr 60	NBA	1 yr 84	NBA
		n	infant of 1166	f	24.03.10	0 yr 121	J	0 yr 145	J
		n	infant of 1166	f	24.03.10	0 yr 121	J	0 yr 145	J
3	**F1**	**focal 1**	**365y±**	**f**	**01.02.08**	**2 yr 173**	**BA**	**2 yr 197**	**BA**
		focal 2*	**185g**	**m**	**07.10.07**	**2 yr 289**	**BA**	**2 yr 313**	**BA**
		n	246g	m	10.09.09	0 yr 316	NBA	0 yr 340	NBA
		n	247g	m	10.09.09	0 yr 316	NBA	0 yr 340	NBA
	F2	**focal 3**	**862bk**	**m**	**09.04.99**	**11 yr 105**	**BA**	**11 yr 129**	**BA**
		focal 4*	**055y**	**f**	**02.01.01**	**9 yr 202**	**BA**	**9 yr 226**	**BA**
		n	413y	f	01.05.09	1 yr 83	NBA	1 yr 107	NBA
		n	433y	f	05.10.09	0 yr 291	J	0 yr 315	NBA†
		n	256g	m	23.11.09	0 yr 242	J	0 yr 266	J
		n	infant of 055y	f	11.03.10	0 yr 134	J	0 yr 158	J
		n	infant of 055y	f	11.03.10	0 yr 134	J	0 yr 158	J
	F3	**focal 5**	**1028**	**f**	**18.12.05**	**4 yr 217**	**BA**	**4 yr 241**	**BA**
		focal 6*	**196g±**	**m**	**01.02.08**	**2 yr 173**	**BA**	**2 yr 197**	**BA**
		n	244g	m	23.08.09	0 yr 334	NBA	0 yr 358	NBA
		n	245g	m	23.08.09	0 yr 334	NBA	0 yr 358	NBA
	F4	**focal 7**	**155g**	**m**	**01.05.06**	**4 yr 83**	**BA**	**4 yr 107**	**BA**
		focal 8*	**354y**	**f**	**10.10.07**	**2 yr 286**	**BA**	**2 yr 310**	**BA**
		n	267g	m	07.12.09	0 yr 228	J	0 yr 252	J
		n	infant of 354y	f	05.06.10	0 yr 48	I	0 yr 72	J†
		n	infant of 354y	m	05.06.10	0 yr 48	I	0 yr 72	J†
4	**F1**	**focal 1**	**335y±**	**f**	**02.04.07**	**3 yr 112**	**BA**	**3 yr 136**	**BA**
		focal 2*	**177g**	**m**	**03.05.07**	**3 yr 81**	**BA**	**3 yr 105**	**BA**
		n	268g	m	25.12.09	0 yr 210	J	0 yr 234	J
		n	269g	m	25.12.09	0 yr 210	J	0 yr 234	J
	F2	**focal 3**	**150g**	**m**	**03.04.06**	**5 yr 254**	**BA**	**5 yr 278**	**BA**

		focal 4*	**286y**	**f**	**04.03.05**	**5 yr 141**	**BA**	**5 yr 165**	**BA**
		n	263g	m	10.11.09	0 yr 255	J	0 yr 279	J
		n	infant of 286y	m	18.05.10	0 yr 66	J	0 yr 90	J
		n	infant of 286y	m	18.05.10	0 yr 66	J	0 yr 90	J
	F3	**focal 5***	**276y**	**f**	**03.10.04**	**5 yr 293**	**BA**	**5 yr 317**	**BA**
		focal 6	**749bk**	**m**	**26.08.96**	**13 yr 331**	**BA**	**13 yr 355**	**BA**
		n	396y	f	16.12.08	1 yr 219	NBA	**removed 09.08.10**	-
		n	414y	f	20.05.09	1 yr 64	NBA	1 yr 88	NBA
		n	231g	m	20.05.09	1 yr 64	NBA	1 yr 88	NBA
		n	infant of 276y	f	01.05.10	0 yr 83	J	0 yr 107	J
		n	infant of 276y	m	01.05.10	0 yr 83	J	0 yr 107	J
	F4	**focal 7**	**792bk**	**m**	**01.01.98**	**12 yr 203**	**BA**	**12 yr 227**	**BA**
		focal 8*	**309y**	**f**	**28.01.06**	**4 yr 176**	**BA**	**4 yr 200**	**BA**
		n	443y	f	24.10.09	0 yr 242	J	0 yr 266	J
		n	infant of 309y	m	30.04.10	0 yr 84	J	0 yr 108	J
5	**F1**	**focal 1**	**198y**	**f**	**02.06.03**	**7 yr 51**	**BA**	**7yr 75**	**BA**
		focal 2*	**148g**	**m**	**12.01.06**	**4 yr 192**	**BA**	**4 yr 216**	**BA**
		n	224y	f	03.07.06	4 yr 20	NBA	4 yr 44	NBA
		n	248g	m	15.09.09	0 yr 311	NBA	0 yr 335	NBA
		n	249g	m	15.09.09	0 yr 311	NBA	0 yr 335	NBA
		n	infant of 198y	f	20.03.10	0 yr 125	J	0 yr 149	J
		n	infant of 198y	m	20.03.10	0 yr 125	J	0 yr 149	J
	F2	**focal 3**	**182g±**	**m**	**01.09.07**	**2 yr 325**	**BA**	**2 yr 349**	**BA**
		focal 4*	**347y**	**f**	**20.08.07**	**2 yr 337**	**BA**	**2 yr 361**	**BA**
		n	444y	f	02.01.10	0 yr 202	J	0 yr 226	J
		n	infant of 347y	f	11.06.10	0 yr 42	I	0 yr 66	J†
		n	infant of 347y	f	11.06.10	0 yr 42	I	0 yr 66	J†
	F3	**focal 5**	**159g**	**m**	**10.06.06**	**4 yr 43**	**BA**	**4 yr 67**	**BA**
		focal 6*	**334y**	**f**	**18.03.07**	**3 yr 127**	**BA**	**3 yr 151**	**BA**
		n	439y	f	02.11.09	0 yr 263	J	0 yr 287	J
		n	260g	m	02.11.09	0 yr 263	J	0 yr 287	J
		n	infant of 334y	f	06.04.10	0 yr 108	J	0 yr 311	J
		n	infant of 334y	m	06.04.10	0 yr 108	J	0 yr 311	J
	F4	**focal 7**	**339y**	**f**	**17.04.07**	**3 yr 97**	**BA**	**3 yr 121**	**BA**
		focal 8*	**160g**	**m**	**24.04.06**	**4 yr 94**	**BA**	**4 yr 118**	**BA**
		n	232g	m	20.05.09	1 yr 64	NBA	1 yr 88	NBA
		n	257g	m	20.10.09	0 yr 276	J	0 yr 300	J
		n	258g	m	20.10.09	0 yr 276	J	0 yr 300	J
		n	infant of 198y	m	20.03.10	0 yr 125	J	0 yr 149	J
		n	infant of 1166	m	24.03.10	0 yr 121	J	0 yr 145	J

6.2.2 Video Stimuli

For the experimental stimuli for both parts of the study, two family groups of marmosets (211y group and 324y group) housed in large colony rooms (see Chapter three, General Methods), were filmed over 12 full days, between May and July 2010, using a handheld camcorder (Sony DCR-SR75). We decided to film marmosets housed in this way because they spend more time grooming each other than do groups housed in cages, and also because the marmosets could be filmed from within the room without any barrier obstructing the view. Footage of 211y group only was used for the experimental and control video stimuli in the first, short-term playback, part of the study. For the second part (long-term playback) we used footage of both family groups, although mostly of the 211y group. Table 6.2 shows the identity, sex, and date of birth of each marmoset in the groups that I filmed.

Table 6.2 Individual id, group id, sex, developmental stage (key below), and date of birth of the marmosets in the two family groups, housed in large rooms, filmed for the experimental stimuli. Film footage of group 324y was used for the long-term experimental video stimuli only. Key: BA = breeding adult; NBA = nonbreeding adult; J = juvenile; I =infant.

Group id	Individual id	sex	Date of birth	Developmental stage during filming
211y	211y	f	04.08.03	BA
	816bk	m	08.06.98	BA
	208g	m	02.07.08	NBA
	209g	m	02.07.08	NBA
	398y	f	01.12.08	NBA
	227g	m	05.05.09	NBA
	228g	m	05.05.09	NBA
	254g	m	03.10.09	J
	255g	m	03.10.09	J
	432y	f	03.10.09	J
	infant of 211y	f	22.03.10	I/ J
	infant of 211y	m	22.03.10	I/ J
324y	324y	f	03.07.06	BA
	147g	m	07.10.05	BA
	373y	f	17.04.08	NBA
	388y	f	19.09.08	NBA
	408y	f	08.04.09	NBA
	409y	f	08.04.09	NBA
	427y	f	09.09.09	J
	428y	f	09.09.09	J
	infant of 324y	f	02.04.10	I/J
	infant of 324y	m	02.04.10	I/J

Five of the focal individuals were directly related to those in one of the groups (211y) filmed (see Table 6.1). Any contagion effect is may be stronger for familiar related individuals than for unrelated individuals, therefore I equalised the number of focal individuals directly related to those filmed as far as possible between the control (3 focals) and experimental (2 focals) condition. Further, the direction of the slight discrepancy (more related focals in the control condition than the experimental) was likely to bias the results against rather in favour of the direction of the hypothesis. Although it was only important to equalise the effect for the between-subjects design second part of the study, (it was unnecessary for the first part since it was a within-subjects design). It was important for the second part of the study that the focal individuals used for the second part that were directly related to filmed marmosets, within the control and experimental condition, had been exposed, respectively, to the same experience in the first part of the study, therefore all such individuals were focals in both the first and the second part of the study.

Visual attention to video playback is likely to co-vary with the rate of change, and the novelty, of the visual images. Also, the attention span of marmosets is considered to be relatively short: Range and Huber (2007) suggest an average of 6 seconds. In order to maximise the time marmosets spent attending to the stimuli, and also to minimise habituation effects, I used the intermittent presentation of relatively short stimulus clips and blank screen, in both short- and long-term video stimuli.

As stated above, each allogroom clip showed a marmoset dyad performing allogrooming (and, infrequently, groom invite and active affiliative contact) and each control clip displayed two marmosets in close proximity to each other (in inactive rest or inactive alert, only). I ensured that the video clips showed a mix of different pair combinations: of age categories; and same and mixed sex. Table 6.3 details the proportion of individual video clips, in the short-term and long-term, control and experimental, that were same-sex pairs, mixed-sex pairs, or unknown (where the sex of either or both individual could not be identified- most frequently for untagged youngsters). In terms of age categories, the table gives the percentages of such clips that are either pairs of adults, an adult and a juvenile, adult and infant or unknown (if the age category of either individual was unidentifiable from the video). The percentage of breeding pair dyads is also stated.

Table 6.3 Identity of dyads in short-term and long-term control and experimental video clips given as a percentage of the total number of video clips for each condition. The proportion of clips showing the breeding pair dyad (in parentheses) is given as a percentage of the total number of clips.

Category	Sub-category	Percentage of total number of video clips			
		Short-term		Long-term	
		Experimental	Control	Experimental	Control
Sex	same-sex	44%	39%	43%	57%
	mixed-sex	33%	30.5%	32%	14%
	unknown	22%	30.5%	25%	29%
Age Category	adult-adult (breeding pair)	50% (11%)	36% (11%)	46% (13%)	40% (3%)
	adult-juvenile	36%	50%	37%	43%
	adult-infant	0%	2%	4%	1%
	juvenile-juvenile	6%	6%	9%	7%
	unknown	8%	6%	4%	9%
Total No. video clips		36	36	97	97

Short-term Playback Stimuli

Clips of stimulus footage were edited into four control and four allogroom videos. Each video contained 95 sec of stimulus presentation; consisting of 9 clips separated by two sec or three sec, alternately, of blank black screen. The stimulus presentation was preceded by 5 sec, and followed by 205 sec of blank black screen. Each complete video was therefore 305 sec in duration.

The average length of clip was 8.3 sec (ranging from 4.0 sec to 12.0 sec). The 36 stimulus clips used were matched for length across the two conditions. Stimulus videos were edited using VideoPad Video Editor (version 2.11, © NCH Software).

Long-term Playback Video Stimuli

Video stimuli were tracks, or fixed playlists, of several hours in length (all preceded by 4 min of blank black screen). The playback stimuli tracks consisted of number of iterations of 97 clips, each iteration being first shuffled into a random order, and then saved, in sequence, as playlists (using Windows Media Player 12). Thus, I created novel tracks, with no clips repeated within each 97 clip section, lasting 2 hr (5 iterations), 2.5 hr (6 iterations) and 6 hr (17 iterations).

Each of the 97 clips, for each condition, consisted of stimulus footage (ranging from 4 to 24 sec in length), with one, two or three sec of blank black screen added to the end. Thus the total length of each clip ranged from 5 to 27 sec. The 97 sections of control stimulus footage (dyads of marmosets sitting in close proximity) were matched exactly in length to the 97 experimental stimulus footage (dyads of marmosets engaged in allogrooming). All the clips, 194 in total, were edited, as before, using VideoPad Video Editor (version 2.11, © NCH Software).

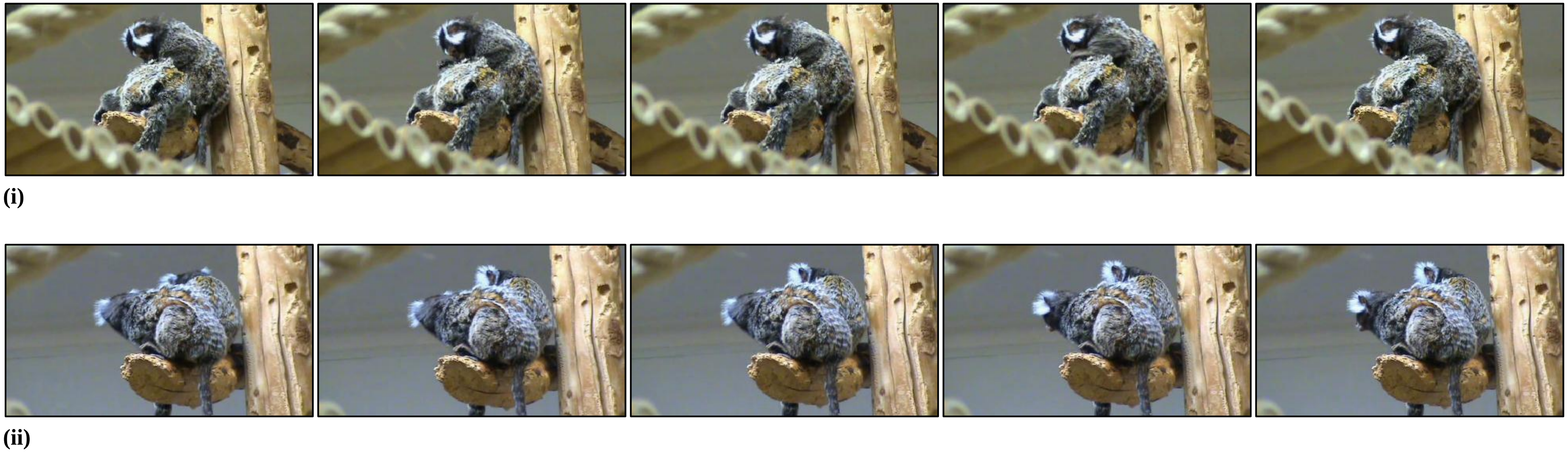
I used stimulus clips of up to 24 sec in length during the second part of the study, because marmosets were observed to maintain their gaze towards the screen for longer than I had expected during the short-term playback part of the study. Fig. 6.2 shows frames from example control and experimental video clips. Example video clips are available to be viewed in Appendix E, on the appended DVD Appendices.

Pilot Investigation of the Welfare Effect of Video Playback

I did not expect the presentation of stimulus videos to have an adverse effect on the welfare of the study marmosets. The behaviours in the video footage are not considered to be negative welfare indicators (e.g. Badihi, 2006), and video playback of conspecifics has been carried out successfully in previous research with this species (e.g. Burkart et al., 2009b) with no adverse effects reported.

If the focal marmosets (and/or surrounding cage mates) perceived the individuals in the video footage as unfamiliar, then it was possible that they might have reacted with aggressive or submissive behaviour. The relatively frequent re-organisation of the colony at the facility means that the subjects housed in cages are likely to be familiar to some degree with most of the marmosets that were shown in the videos. Most colony members are in fact inter-related to some degree. Four focal individuals in the first part of the study (and five focal marmosets in the second part) are offspring of one of the breeding individuals in the stimulus footage (Table 6.1).

Fig 6.3 Frame sequences from sample footage clips (in which there were 6 frames in between each still image shown here). Experimental condition (marmosets engaged in dyadic allogrooming): (i), (iii) and (v). Control condition (marmosets in close proximity in inactive alert or rest): (ii), (iv) and (vi). Similar compositions are shown for each pair, i.e. (i) and (ii); (iii) and (iv); (v) and (vi).



(i)

(ii)

(iii)

(iv)

(v)

(vi)

However, some subjects may be visually unfamiliar with the marmosets on the video, either because they have not been housed together in the same room at any stage or because they are familiar with these individuals only at an auditory level. For this reason I carried out a pilot investigation, using nonstudy animals, to assess whether showing video footage to the marmosets was likely to have adverse effects on their welfare. Behavioural responses indicating potential adverse effects on welfare include extended periods of mobbing or tsik vocalisation, bristle (piloerection), agitated locomotion and anogenital tail raise present (e.g. Badihi, 2006). Such behavioural responses were not observed in the pilot investigation and therefore we did not anticipate that the study would adversely affect the welfare of the study subjects.

6.2.3 Experimental Procedure

Short-term Video Playback Procedure

Each of the two conditions of stimulus video (control and allogroom) was presented to each focal individual separately in two daily trials: one trial in the morning and one in the afternoon (with the order of presentation counterbalanced). There were four trial sessions, one in each room, each half day. The only exception was a period of two days during which individuals were given both trials within the same half day, due to practical husbandry constraints. However, this was counterbalanced for each individual for morning and afternoon presentation across the two days. Also, to minimise any effect from the first stimulus video presentation, the time between successive trials involving the same focal individual was maximised within the available time (minimum = 1 hr 35 min, during the exception period of two days).

Compared to the short-term auditory playback reported in the previous chapter, there was less concern about cumulative effects caused by multiple playbacks throughout the same room in the case of video playback. The short-term audio playback although directed specifically towards the focal group, may sometimes have been audible to the entire colony room. In contrast, the short-term video stimulus playback was visible to the focal group to whom it was directed (and just possibly to the group(s) directly adjacent to them).

Stimulus videos were presented, without audio, using Windows Media Player 12, to one group of marmosets at a time, using two, colour LCD monitors (model S760A). LCD screens have pixels which are constantly lit, and therefore do not exhibit refresh flicker like traditional CRT monitors. The use of LCD screens therefore overcame the methodological problem presented by the variation in critical flicker fusion threshold across species, which can result in nonhuman subjects perceiving the screen as flickering (D’Eath, 1998).

To ensure that the marmosets displayed on screen did not appear larger than the focal marmosets (advice: personal communication, Burkart) the videos were displayed within a rectangle, 255 mm wide by 155 mm high, on a blank black screen (340mm wide by 270 mm high). The screens were placed 75 to 80cm from the cage. This distance was considered to minimise the possibility of animals perceiving pixellation (D’Eath, 1998), and to maximise the chance of the screen being within the field of view of the marmosets.

For the first five presentation days one monitor only was used. However, an additional monitor was used for the remaining eight study days. At the outset of the study one screen was considered sufficient, and indeed it did appear initially to maintain their interest. However, it seemed that as the marmosets habituated to the stimulus they spent longer foraging in the lower half of the cage, in particular in the sawdust on the cage floor. Thus it was decided that a second, lower, screen should be introduced for the remainder of this study, in order to provide the marmosets with an opportunity to view the video stimulus from lower parts of the cage.

Both monitor screens were mounted on a stand (consisting of a wooden frame built onto the base of a self-assembly Ikea bar stool). The first monitor was level with top half of cage (centre of monitor screen 1059 mm above the floor) and second was level with lower half of cage (centre of monitor screen 970 mm above the floor) (see Plate 6.1). They were connected to a Sony lap-top PC via a two-way SVGA monitor splitter (Nikkai: A93BB) and SVGA extension cable (VGA analogue monitor connection cable; 15 pin). The lap-top was positioned on a metal chest. The observer sat about 1m 40 cm from the front of the cage to one side to allow clear vision sideways, not obscured by the two monitors (custom-fitted with an extended power cable).

Short-term Playback Observational Procedure

Observational coding began after the initial 5 seconds of blank stimulus presentation. The behaviour of the focal individual was coded by continuous focal sampling (see Chapter three for further details). For a proximal index of the visual attention to the video stimuli by the focal individual, I coded the amount of time that focal individuals appeared to direct their gaze towards either of the monitor screens during stimulus presentation, by visual assessment. The order in which the 4 focal individuals were observed in each room was counterbalanced across days. The use of tracks was counterbalanced so that each track was used once each day, but played to each group only once every four study days (to minimise the risk of habituation effects).

Interval Between Part One and Part Two of Study

Between parts one and two of the study there was an interval of four days. This was considered sufficient to diminish any longer lasting effect of the 95-sec short-term playback video stimuli. Results from the short-term playback study indicated significant differences in behaviour between experimental and control conditions, despite the fact that these were run within-subjects and separated only by a matter of hours (morning/afternoon of the same day).

Long-term Video Playback Procedure

In a between subjects design, video playback, footage was shown to 8 focal groups simultaneously, 4 within each of two colony rooms assigned to different conditions. Each focal group was exposed to video playback for a daily mean duration of 2.6 hours, over a period of 9 days (a total of 23 hr per group). Table 6.4 shows the amount of time that marmoset focal groups in different rooms were exposed to video playback. Fig. 6.3 shows a typical schedule of observation and playback for a weekday, Monday to Thursday, during the mid-playback period. The first day, and last two days, of long-term playback were weekend days and the observational coding was carried out in between playback sessions during the 5 intervening weekdays.

Eight LCD monitors each mounted on a stand (a bar stool with plastic boxes bolted to the seat) by two elastic bungee straps: 800 mm Draper, allowed the presentation of footage simultaneously to eight groups, four groups in two rooms (one control and one experimental). Video footage was played to each study group, using a computer monitor with the screen directed towards the interior of the home cage and attached to a stand placed outside the home cage.

Because the playback was simultaneous to eight groups, using two monitors per group as in the short-term playback would have necessitated 16 computer monitors rather than 8 with the associated doubling of cost. Furthermore, one monitor, placed at the higher level, was considered sufficient for ensuring that marmosets noticed the visual stimuli presented in the long-term playback. The playback time was very much longer than in the short-term playback, negating the risk that the focal individual would be likely to miss the visual stimuli entirely through spending all that time foraging in the sawdust. It is very unlikely that they would not reposition themselves within the cage at all during the playback period (the shortest duration being 2hr compared with 95 sec in the short-term playback).

In both rooms during playback there was one laptop played the footage (Dell and Sony respectively) connected via a four-way SVGA monitor splitter (Nikkai: model code A94BB) and 4 SVGA extension cables (VGA analogue monitor connection cable; 15 pin) to 4 monitors duplicating the signal, mounted on stands and positioned 80cm from the front of the focal cages with the screen directed inwards. The lap-top was positioned on a low table stand at one end of the room. Plate 6.2 shows the experimental set-up. After setting-up of the equipment in each room for long-term playback, I left the room for 10 minutes before returning to initiate stimulus playback. Nobody entered the rooms during playback.

Long-term Playback Observational Procedure

Continuous focal sampling was used to record behaviours (see Chapter three for further details of the observation procedure). Daily observation periods of 5 min duration were carried out, for each focal individual, over five days during each of the three stages of the experiment: prior to video playback (pre-playback), in between video playback periods (mid-playback) and after all playback had ceased (post-playback). To maintain variation in external laboratory factors, the time of observation for each room was kept constant across each of the three weeks of the second part of the study. This consisted of: 5 days of observation pre-playback; 9 sequential days of playback, with 5 days of mid-playback observation (outwith specific playback periods); and 5 days of post-playback observation, directly after the final playback day (see Fig. 6.4 and 6.5).

Figure 6.4 An example schedule for an observational study day (Mon-Thurs), during long-term playback of observation (O) and playback (P) across matched baseline and experimental rooms respectively (B1 and E1; B2 and E2). PC indicates playback of a control track and PA indicates playback of allogroom track. Time is shown approximately (for simplicity the time required to set up equipment and to move the equipment between rooms, and for feeding, has been disregarded).

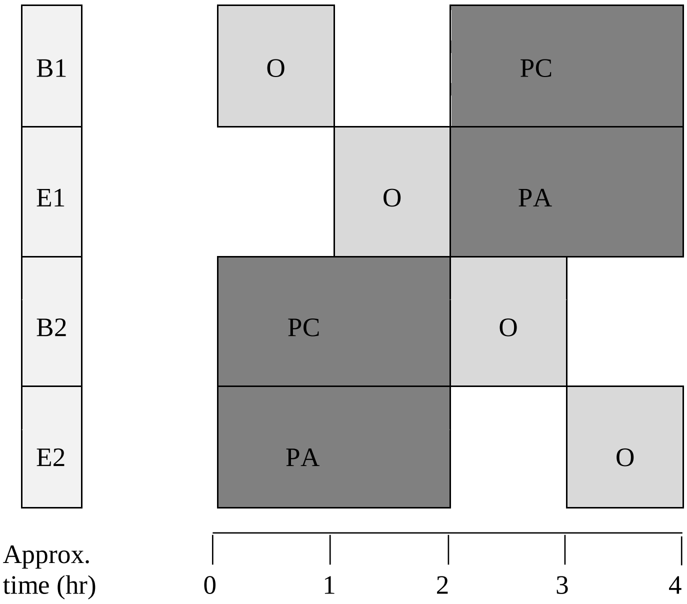


Table 6.4 Focal subject treatments during short-term and long-term playback for focal marmosets in the control and experimental conditions. Playback of silence is indicated as: (PS); and the playback of a higher than average rate of chirp calls is indicated as: (PC). Focal id relates to Table 6.1.

Condition	Room	Focal id	Long-term playback (over 9 days)
control	2	1-8	day 2 : 6.0 hr PS
			day 3,4 : 2.5 hr PS in pm
			day 5,6 : 2.0 hr PS in am
			day 7 : 2.0 hr PS in am
			day 8 : 6.0 hr PS
control	3	1-8	day 1 : 6.0 hr PS
			day 3, 4 : 2.0 hr PS in am
			day 5,6 : 2.5 hr PS in pm
			day 7 : 2.0 hr PS in pm
			day 9 : 6.0 hr PS
experimental	4	1-8	day 2 : 6.0 hr PC
			day 3,4 : 2.5 hr PC in pm
			day 5,6 : 2.0 hr PC in am
			day 7 : 2.0 hr PC in am
			day 8 : 6.0 hr PC
experimental	5	1-8	day 1 : 6.0 hr PC
			day 3, 4 : 2.0 hr PC in am
			day 5,6 : 2.5 hr PC in pm
			day 7 : 2.0 hr PC in pm
			day 9 : 6.0 hr PC

Plate 6.1 Experimental set-up of colony room for short-term video playback.

Plate 6.2 Experimental set-up of colony room for long-term video playback.

Plate 6.3 A marmoset with gaze directed at the lower monitor screen (not visible in the frame) on the stand (visible in the frame along with the bottom corner of the upper monitor screen).

6.2.4 Statistical Analyses

Focal behaviour was summarised as the percentage of time spent in each behaviour by each individual. For the short-term playback part of the study, the mean percent time for each individual was the average of the 13 trials per condition, for each behaviour. For the long-term playback part of the study, the measure used was the mean change in the mean percent time spent in each behaviour between pre-playback and mid-playback, and between pre-playback and post-playback.

There were no infants in any of the focal groups during the long-term playback part of the study, so behaviours to and from infants were excluded by default from the analysis. However, for similar reasons as stated in Chapter five, the analysis of behaviour performed by focal individual to and from both adults and juveniles involves a potentially confounding factor. Affiliative behaviour performed to younger juveniles may show a decrease over time as they pass the transitional age. This may, conversely, lead to an increase in affiliative behaviours performed to and from adults, over time, due to decreased time constraints arising from directing affiliative behaviour to younger juveniles. Thus, analysis of adult data only also entails a potentially confounding bias, but in the opposite direction. For this reason, we analysed data for adults only as well as for adults and juveniles combined.

For the short-term playback, there was clearly no need to split the data by developmental age group, because the experimental design was within-subjects. The comparisons for each focal individual were between their behaviour during a trial under one condition in the morning, and the other in the afternoon. Thus changes in group composition were not a problem, due to the short temporal interval between the collection of the data to be compared.

Permutation Analysis

The short-term playback study analysis was within-subjects, and for the long-term study was between-subjects, permutation tests were carried out (refer to Chapter three for further detail).

6.3 Results

6.3.1 Visual Attention to Video Playback

During the 95 sec of stimulus presentation time, focal marmosets were found to direct their gaze towards one of the two screens for an overall mean of 23.66% of time. They spent a larger mean percentage of the stimulus presentation time attending to the control video than to the experimental video (control 25.14%; experimental 22.17%) and this difference was statistically significant using permutation tests (*N* = 16, *P* = 0.035). However, there was high inter-individual variation (see error bars, representing ±1SE, Fig. 6.5). Fig. 6.5 shows the mean percent time of stimulus presentation time that marmosets directed their gaze towards the video screens, across the 13 days of trials. Over the 13 days of exposure to the video, mean percent visual attention did drop, though never below an average of 20% (19 sec of the total 95 sec).

Female focal marmosets spent a higher mean percentage of time directing their gaze towards one of the monitors than did males (females: 28.25%; males: 19.06%), the difference falling short of significance with permutation tests (N = 16, *P* = 0.053), which implies inter-individual variation. The pattern was also consistent across both conditions (females: control 29.51%, experimental 27.00%; males: control 20.78%, experimental 17.33%). Fig 6.6 compares the mean percent of time that female and male marmosets spent directing their gaze towards one of the monitor screens during the presentation of the control and of the allogroom video, over the 13 days of trials. Female marmosets attended to the screen for longer than males, consistently across all the trial days.

Fig 6.5 Line graph showing mean percent (± 1 SE) of stimulus presentation time spent by focal marmosets directing their gaze towards a monitor displaying control video (grey line) and the allogroom video (black line).

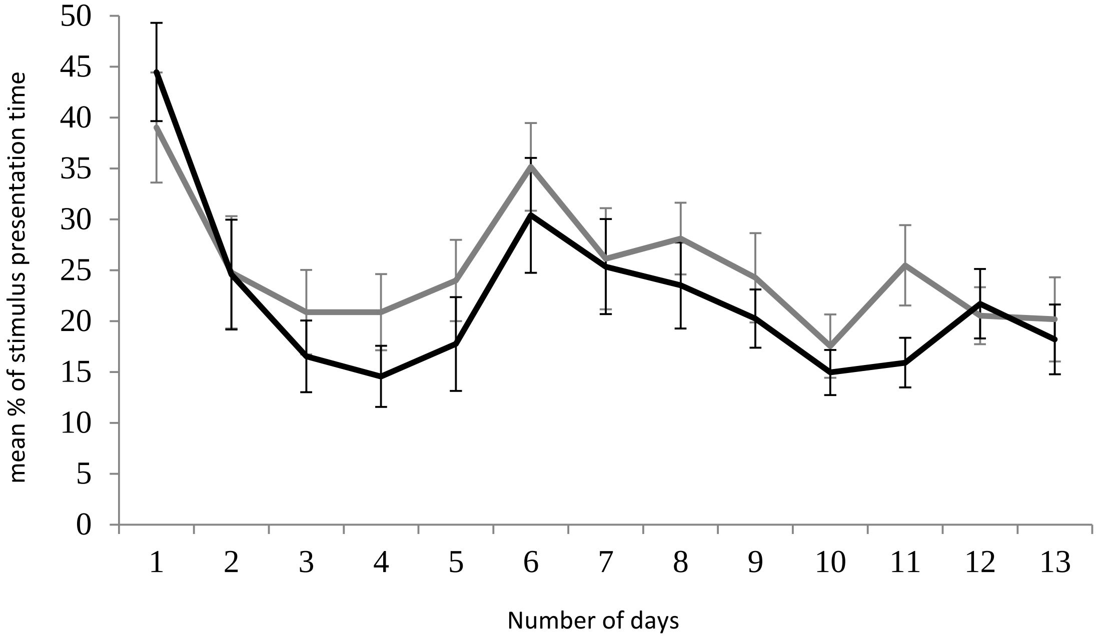
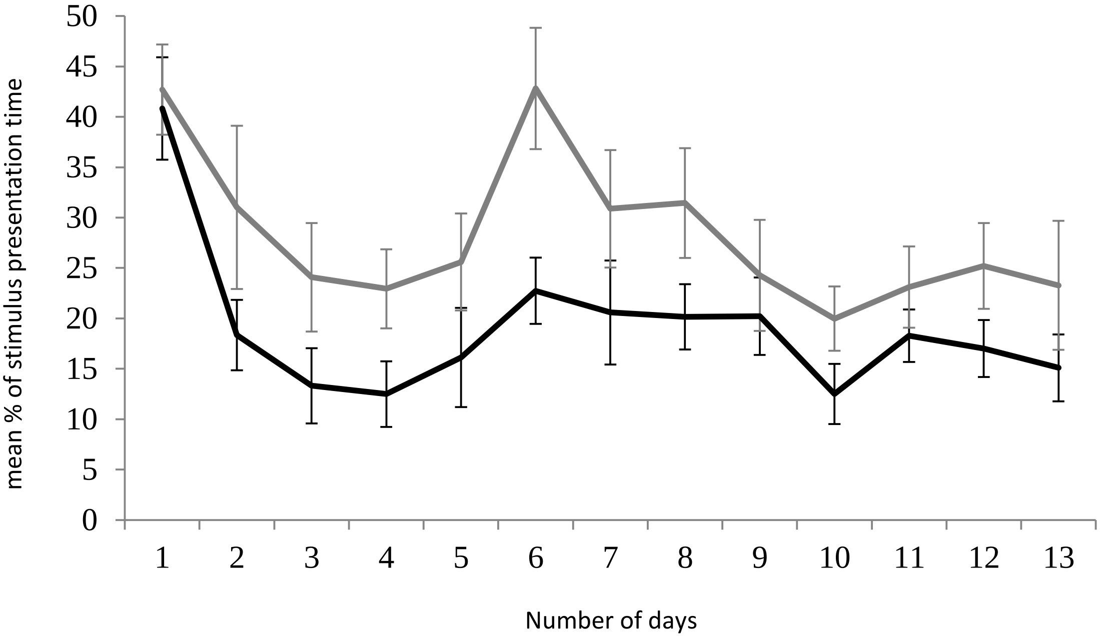


Fig. 6.6 Line graph showing mean percent (± 1 SE) of stimulus presentation time spent by female focal marmosets (grey line) and by male focal marmosets (black line) directing their gaze towards a monitor displaying the stimulus video.



6.3.2 Short-term Effect of Allogroom Playback

Table 6.5 displays the results of the statistical tests comparing the behaviour of each focal individual, between observation sessions during which a video of conspecifics engaged in allogrooming was played, and sessions in which a control video, of conspecifics in close proximity to one another, was played. The results of the main analyses are displayed graphically in Fig. 6.7.

As predicted, marmosets spent significantly longer engaged in allogrooming in allogroom video compared to control video trials ($N = 16$, $P = 0.007$). Also as predicted, the affiliative behaviour of share food was performed by marmosets for significantly longer in experimental than in control trials ($N = 16$, $P = 0.003$).

In the predicted direction, but not significant: marmosets spent more time in groom invite in the experimental condition compared with the control condition trials ($N = 16$, $P = 0.222$), and longer in social play during experimental trials than during control trials ($N = 16$, $P = 0.224$). In the opposite direction to the prediction, marmosets did not spend longer in the affiliative behaviour of active affiliative contact during experimental trials, compared with control trials.

A composite of all five affiliative behaviours was analysed as a general index of the social contagion of affiliation. Marmosets spent significantly longer in affiliative behaviour in the experimental trials compared with control trials ($N = 16$, $P = 0.005$). As predicted there was no significant difference in the time spent during control and experimental trials in behavioural composites of any of the three non-matching affective categories (intragroup aggression: *N* = 16, *P* = 0.574; intergroup aggression (anogenital present only): *N* = 16, *P* = 0.764; anxiety: *N* = 16, *P* = 0.170).

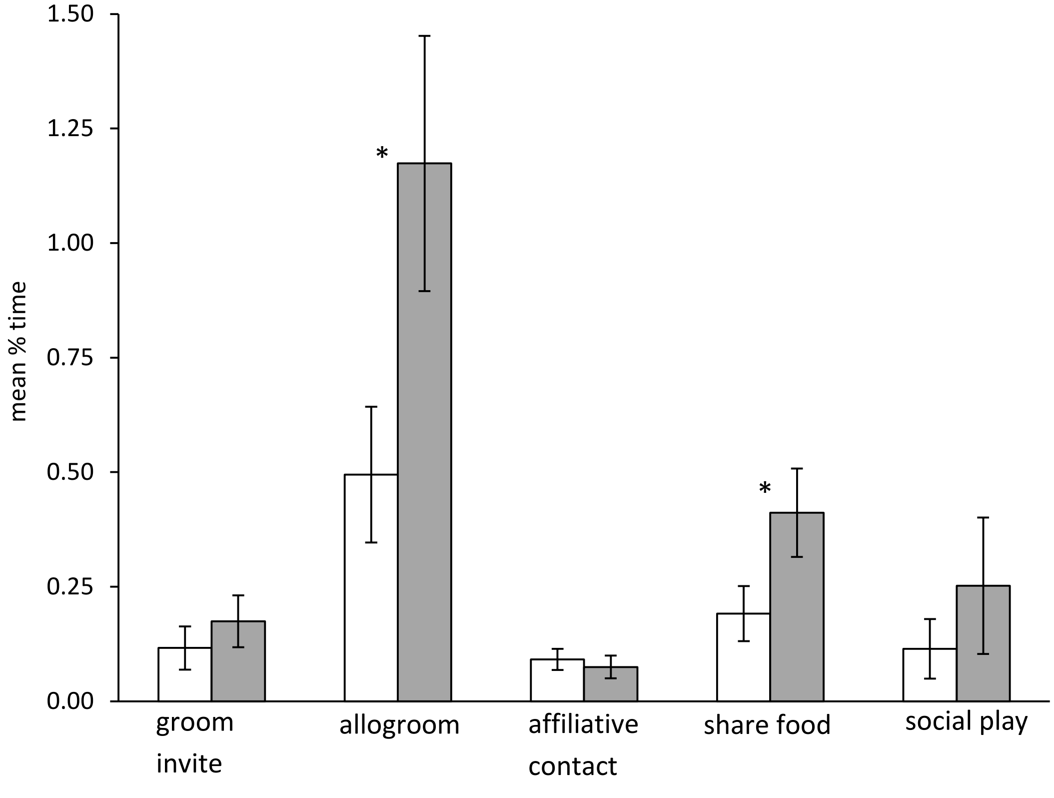
The increase in share food during experimental compared to control trials could not be explained by a general increase in feeding since, in a post hoc analysis, the amount of time spent by marmosets in feeding was very similar between control and experimental conditions and the difference was not significant (*N* = 16, *P* = 0.881). However, marmosets did spend significantly longer in active foraging during experimental than during control trials (*N* = 16, *P* = 0.024).

Table 6.5 Statistical test results for the analysis of the short-term effect of the video playback of allogrooming on focal marmoset behaviour; mean percent time per observation session spent in affiliative behaviours (to and from all) between the experimental and control condition. Asterisk (*) indicates *P* < 0.05. ns indicates nonsigificant. Ŧ indicates means where the direction of difference is opposite to the predicted direction (one-tailed tests). ~ indicates two-tailed, post hoc analyses. The adjusted α-level for multiple testing is also displayed: underlining indicates that results retain their significance following adjustment of α-level.

Focal behaviour	control	allogroom	*N*	*P*	adjusted α-level
Groom invite	0.116	0.174	16	0.222 ns	n = 5 α = 0.01
Allogroom	0.494	1.174	16	0.007 *	
Active affiliative contact	0.091	0.075	16	Ŧ	
Share food	0.191	0.411	16	0.003 *	
Social play	0.114	0.252	16	0.224 ns	
Composite of all five affiliative behaviours	1.008	2.086	16	0.005 *	
Composite of intragroup agonistic behaviours (Chase/Attack/Steal food) ~	0.120	0.099	16	0.574 ns	
Intergroup Agonism: Anog. present ~	0.215	0.200	16	0.764 ns	
Self-groom ~	0.307	0.293	16	0.930 ns	
Self-scratch ~	0.958	0.957	16	0.995 ns	
Composite of all six anxious behaviours (agitated locomotion; inactive alert; scent mark; self-scratch; self-groom; gouge) ~	0.120	0.099	16	0.170 ns	
Feed ~	5.615	5.757	16	0.881 ns	n = 2 α = 0.025
Active forage ~	1.002	2.013	16	0.024 *	

Because allogrooming involves the parting of pelage, I wanted to investigate whether showing the video of allogrooming may be associated with a general increase in self-grooming and self-scratching as well as allogrooming. This is important because self-directed behaviours are considered to be negative welfare indicators (e.g. Cilia and Piper, 1997). However, showing the allogrooming video was not found to be associated with an increase in the self-directed behaviours: self-groom (*N* = 16, *P* = 0.930) or self-scratch (*N* = 16, *P* = 0.995).

Fig 6.7 The effect of short-term allogroom video playback, and control video playback on marmoset affiliative behaviours: groom invite; allogroom; active affiliative contact; share food; and social play. Columns represent mean percent time (± 1 SE) during observations during which the control video was shown (white bars) and the experimental video, of allogrooming conspecifics was played back (grey bars). Asterisk (*) denotes significance.



6.3.3 Long-term Effect of Allogroom Playback

Table 6.6 displays the results of the statistical tests comparing the mean change in the mean percent time spent in affiliative behaviours (performed to and from adults and juveniles, and to and from adults only), between pre-playback and mid-playback, and between pre-playback and post-playback, for marmosets who were shown the control video relative to those who were shown the allogroom video. As predicted, the change between pre- and post-playback in the amount of time spent in allogrooming (to and from adults only) was significantly more positive for marmosets exposed to the long-term playback of allogroom video than the control video (N = 16, P = 0.009, Fig. 6.9). Further, the difference for allogrooming performed to and from adults and juveniles approached significance (N = 16, P = 0.083, Fig. 6.9). However, in the opposite direction to predicted, the change in the time that marmosets spent in allogrooming between pre- and mid-playback was more negative for marmosets in the allogroom condition than for those in the control condition.

The change in the time spent by marmosets in the experimental condition engaged in allogrooming did not increase gradually, over the two periods, mid- and post-playback, but increased, only after the long-term playback sessions ceased. Fig. 6.13 shows the change, in the (absolute) mean daily percent time, spent performing allogrooming by marmosets in the control and experimental conditions, across the pre-, mid-, and the post-playback periods. It is possible that the increase post-playback may be due to a factor other than the experimental condition, however this seems unlikely since the pattern is consistent across both experimental colony rooms (see Fig. 6.14). Figure 6.10 shows the difference between the mean time spent allogrooming on each of the 5 post-playback days and the mean time spent in allogrooming across the 5 pre-playback (baseline) days by marmosets in the control and experimental conditions (thus zero on the axes indicated a level of allogrooming equal to the baseline level). The level of allogrooming remains elevated relative to baseline level for marmosets in the experimental condition across all five post-playback days, despite a gradual drop indicated by the trend line. Error bars indicate fairly high inter-individual variation. The extrapolation of the trend-line indicated that the elevated level of allogrooming relative to baseline was not likely to last any longer than those five days.

Between pre- and mid-playback, the change in the amount of time spent in groom invite behaviour, to and from both adults and juveniles, was in the expected direction in the allogroom playback condition although not significantly so (*N* = 32, *P* = 0.384); for adults only, the difference was in the direction contrary to our predictions. Between pre- and post-playback there was a very high degree of dispersion for the changes in mean percent time spent in grooming invite behaviour, and the ranges for the control and experimental condition overlap (Fig. 6.8).

Between pre- and post-playback, time spent in food sharing (Fig. 6.12) was in the predicted direction but not significant and in food sharing (Fig. 6.12), (food sharing: adults and juveniles: *N* = 32, *P* = 0.466; adults only: *N* = 32, *P* = 0.354). A similar trend occurred between pre- and mid-playback for affiliative contact, to and from adults and juveniles (adults and juveniles: *N* = 32, *P* = 0.393).

Table 6.6 Statistical test results for the analysis of the long-term effect of the video playback of allogrooming on focal marmoset behaviour; a comparison of the mean difference, between pre- and mid-playback and between pre- and post-playback, in mean percent time per observation session spent in affiliative behaviours by focal marmosets in the experimental and in the control condition. Affiliative behaviours performed by marmosets to and from adults and juveniles = to and from all (no infants present in any of the focal groups). Asterisk (*) indicates $P < 0.05$; ns indicates a result in the predicted direction which was nonsigificant; and nst indicates a nonsignificant trend ($p < 0.100$). Ŧ indicates means where the direction of difference is opposite to the predicted direction (one-tailed tests); and ~ indicates two-tailed, post hoc analyses. The adjusted α-level for multiple testing is also displayed: underlining indicates that significance is retained following adjustment.

Focal behaviour	performed to and from	pre- to mid-playback				pre- to post-playback				adjusted α-level
		control	allogroom	*N*	*P*	control	allogroom	*N*	*P*	
Groom invite	adults and juveniles	0.059	0.084	32	0.384 ns	0.049	0.049	32	-	
	adults only	0.059	0.014	32	Ŧ	0.066	0.045	32	Ŧ	
Allogroom	adults and juveniles	0.593	-0.063	32	Ŧ	-1.041	0.367	32	0.083 nst	n = 2
	adults only	0.684	-0.092	32	Ŧ	-0.867	1.202	32	0.009 *	α = 0.025
Active affiliative contact	adults and juveniles	0.019	0.036	32	0.393 ns	0.016	-0.019	32	Ŧ	
	adults only	0.014	0.012	32	Ŧ	0.030	0.001	32	Ŧ	
Share food	adults and juveniles	-0.044	-0.148	32	Ŧ	-0.138	-0.113	32	0.466 ns	
	adults only	0.010	-0.069	32	Ŧ	-0.025	0.040	32	0.354 ns	
Social play	adults and juveniles	0.737	0.048	32	Ŧ	0.145	-0.363	32	Ŧ	
	adults only	0.626	0.275	32	Ŧ	0.030	0.008	32	Ŧ	
Composite of all five affiliative behaviours	adults and juveniles	1.364	-0.044	32	Ŧ	-0.969	-0.078	32	0.228 ns	n = 2
	adults only	1.392	0.141	32	Ŧ	-0.811	1.342	32	0.015 *	α = 0.025
Composite of intragroup agonistic behaviours (Chase/Attack/Steal food) ~	adults and juveniles	-0.083	0.006	32	0.660 ns	-0.162	-0.027	32	0.485 ns	
	adults only	-0.008	0.006	32	0.535 ns	0.009	0.013	32	0.922 ns	
Anog. Present ~ (intergroup agonism)	n/a	0.078	0.051	32	0.836 ns	-0.081	-0.023	32	0.435 ns	

		pre- to mid-playback				pre- to post-playback				
Focal behaviour	performed to and from	control	allogroom	N	P	control	allogroom	N	P	adjusted α-level
Self-groom ~	n/a	-0.242	0.067	32	0.396 ns	-0.319	0.233	32	0.105 ns	n = 2
Self-scratch ~	n/a	-0.257	-0.036	32	0.484 ns	-0.503	0.203	32	0.011 *	α = 0.025
Composite of all six anxious behaviours (agitated locomotion; inactive alert; scent mark; self-scratch; self-groom; gouge) ~	n/a	-6.361	-2.473	16	0.493 ns	-7.801	0.261	16	0.122 ns	
Feed ~	n/a	2.044	-0.122	16	0.528 ns	1.952	0.386	16	0.605 ns	
Active forage ~	n/a	-0.032	1.293	16	0.154 ns	-0.335	-0.093	16	0.707 ns	

However, several results were in the opposite direction to the prediction. Between pre- and mid-playback affiliative contact, to and from adults, and food sharing, increased more in the control than the experimental condition. Between pre- and post-playback active affiliative contact for both adults and adults and juveniles also increased more for marmosets in the control than the chirp playback condition. In addition, the change in mean percent time spent in social play was greater for marmosets in the control than for marmosets in the experimental condition.

Fig 6.8 Mean change in percent of time (± 1 SE) spent performing groom invite to and from adults and juveniles, and to and from adults only, between pre-playback and mid-playback, and between pre-playback and post-playback, by marmosets exposed to the long term playback: of the control video stimuli (white bars); and of the allogroom video stimuli (grey bars).

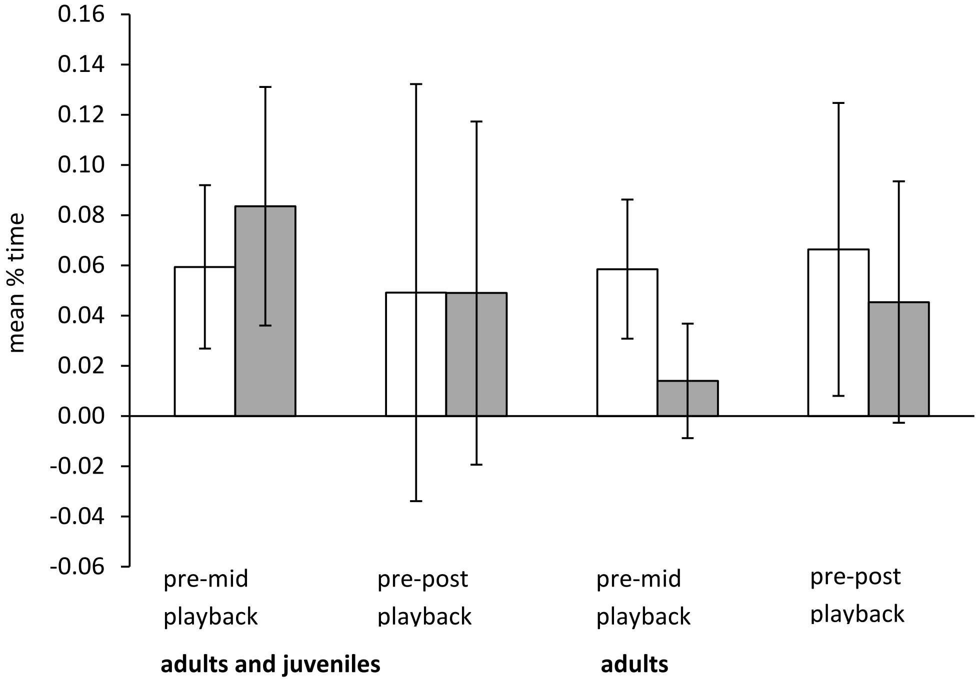


Fig 6.9 Mean change in percent of time (± 1 SE) spent engaged in allogrooming to and from adults and juveniles, and to and from adults only, between pre-playback and mid-playback, and between pre-playback and post-playback, by marmosets exposed to the long term playback: of the control video stimuli (white bars); and of the allogroom video stimuli (grey bars). Asterisk (*) denotes significance.

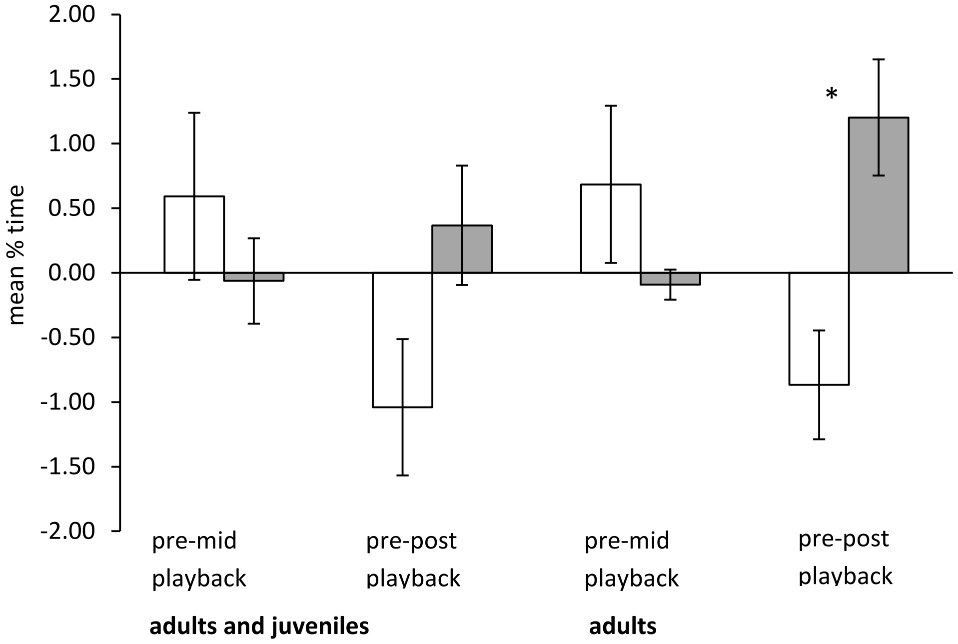


Fig 6.10 Difference between mean percent of time (± 1 SE) engaged in allogrooming on each post-playback day by marmosets in each condition and the baseline mean for that condition (mean for five pre-playback days) (i.e. zero indicates no change from baseline level). Marmosets exposed to the long term playback: of the control video stimuli (grey line); and of the allogroom video stimuli (black line). Trend lines are shown as dotted grey and black lines respectively and have been extrapolated for the next two days.

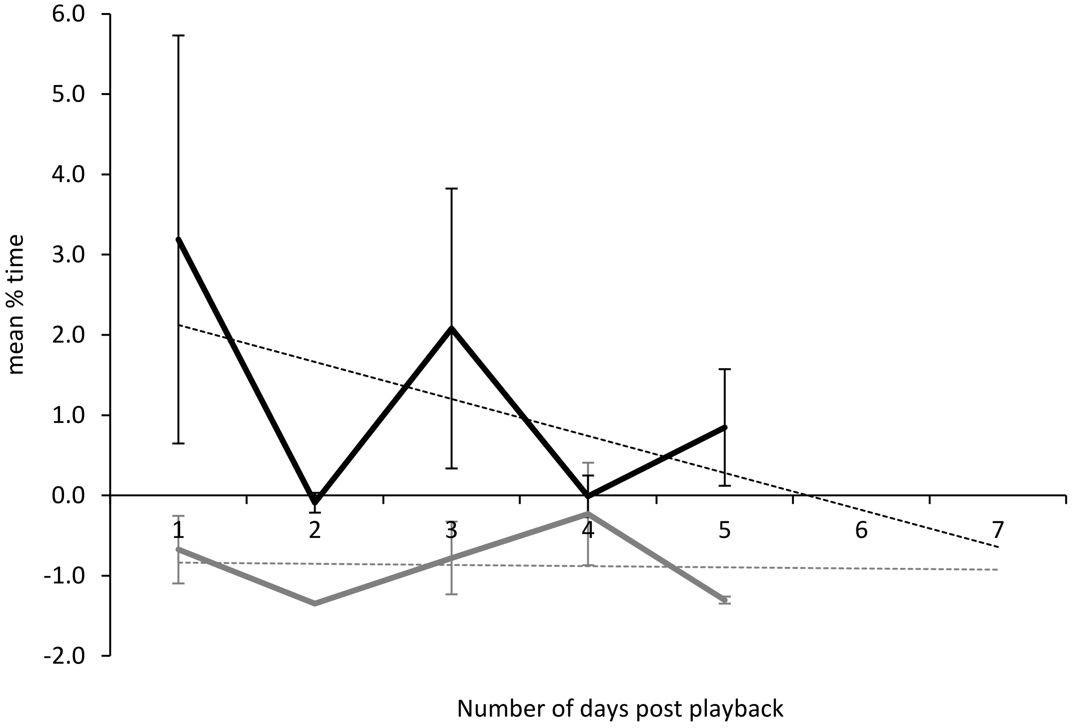


Fig 6.11 Mean change in percent of time (± 1 SE) spent performing active affiliative contact to and from adults and juveniles, and to and from adults only, between pre-playback and mid-playback, and between pre-playback and post-playback, by marmosets exposed to the long term playback: of the control video stimuli (white bars); and of the allogroom video stimuli (grey bars)

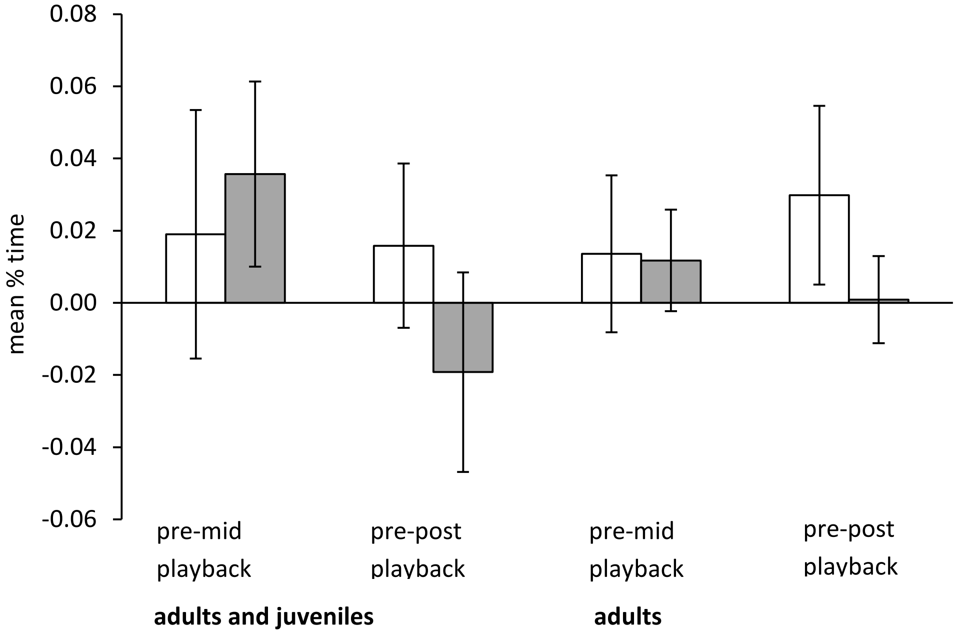


Fig 6.12 Mean change in percent of time (± 1 SE) spent sharing food to and from adults and juveniles, and to and from adults only, between pre-playback and mid-playback, and between pre-playback and post-playback, by marmosets exposed to the long term playback: of the control video stimuli (white bars); and of the allogroom video stimuli (grey bars).

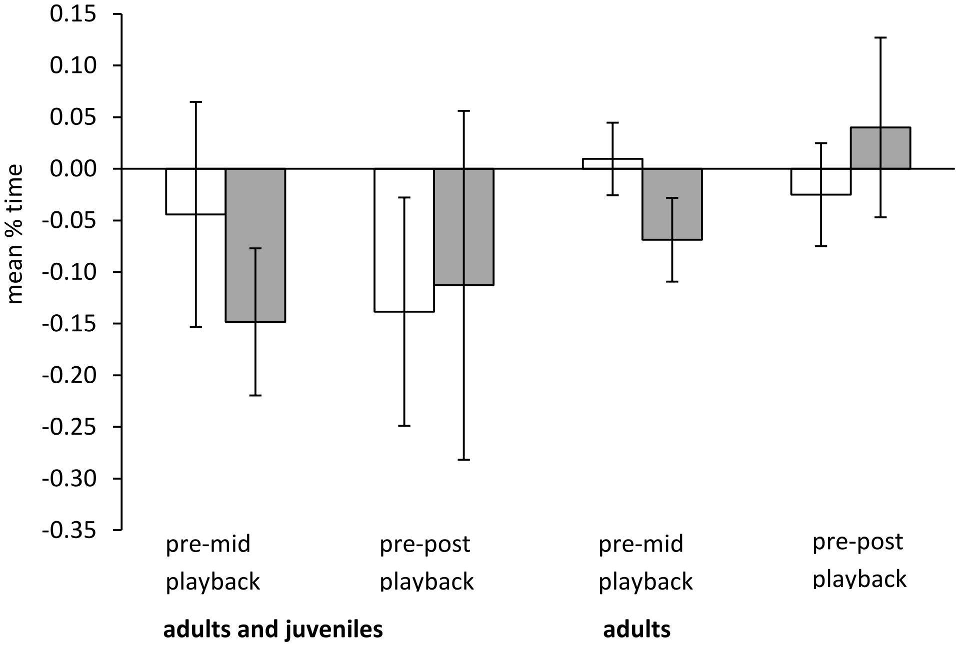
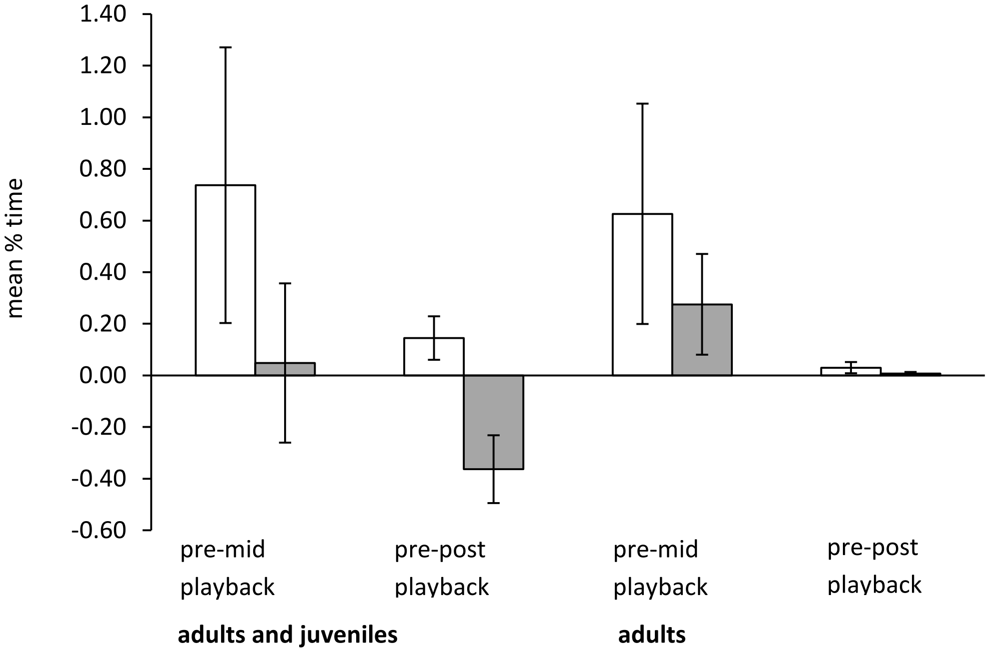


Fig 6.13 Mean change in percent of time (± 1 SE) spent in social play with adults and juveniles, and with adults only, between pre-playback and mid-playback, and between pre-playback and post-playback, by marmosets exposed to the long term playback: of the control video stimuli (white bars); and of the allogroom video stimuli (grey bars).



For the ‘matching’ analysis, a composites of all five affiliative behaviours, and composites of intergroup and intragroup agonism and anxiety-related behaviours were analysed. Between pre- and mid-playback the increase in time spent in any of the five affiliative behaviours was significantly greater in the experimental condition compared to the control for adults only, but this difference was not significant for the combined category (adults: *N* = 32, *P* = 0.015; adults and juveniles: *N* = 32, *P* = 0.228). The change in time spent in affiliative behaviours between pre- and post-playback was in the opposite to predicted direction for both age categories. There was no significant difference in the change in time spent in behavioural composites of any of the three non-matching affective categories (intergroup or intragroup aggression or anxiety) for marmosets in the experimental compared to the control condition either between pre- and mid- or between pre- and post-playback (see Table 6.6).

Fig. 6.14Mean percent of time spent allogrooming (to and from adults only) across the 15 observational days for marmosets in the control (grey line) and experimental (black line) condition.

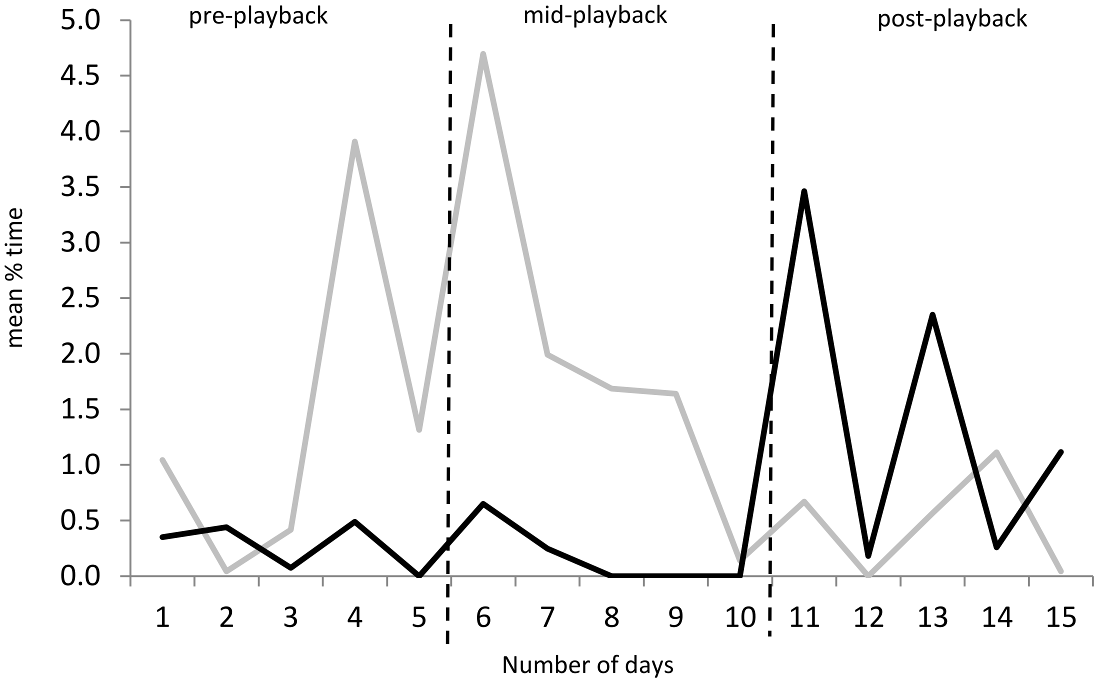
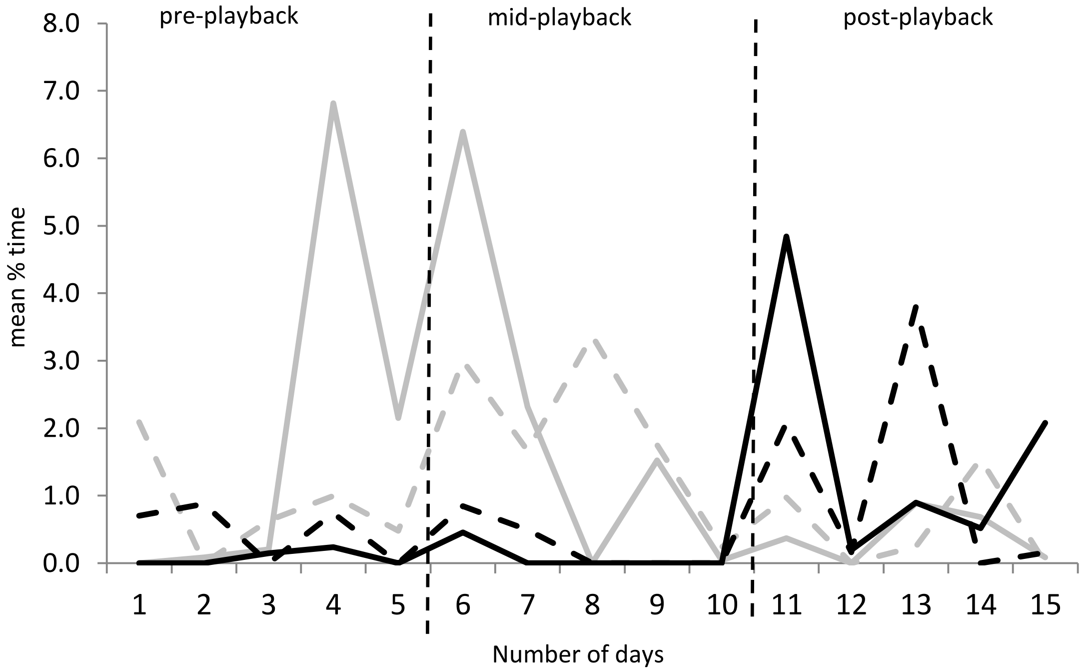


Fig. 6.15Mean percent of time spent allogrooming (to and from adults only) across the 15 observational days for marmosets in the control condition: room 2 (grey line), room 3 (dashed grey line); and in the experimental condition: room 4 (black line), room 5 (dashed black line).



A two-tailed analysis of self-groom and self-scratch, as for the first part of the study, showed that, marmosets in the allogroom video playback condition increased self-scratching between pre- and post-playback significantly more than in the control condition ($N = 32$, $P = 0.011$).

In a similar analysis of feeding and active foraging (informed by the results of the short-term study) there was no significant effect of exposure to the long-term playback of the allogroom video, relative to the control video (see Table 6.5).

6.3.4 Behavioural Welfare Indicators

Table 6.6 displays the results of statistical tests comparing the time spent and Table 6.7 the mean change in the mean percent time, between pre- and mid playback and between pre- and post-playback, in behaviours indicative of positive and negative welfare, and not analysed already for the main study predictions.

Table 6.7 Statistical test results for the analysis of the effect on focal marmoset behavioural welfare indicators of short-term video playback of allogrooming; Mean percent time per observation session spent in affiliative behaviours between experimental and control condition (two-tailed). Asterisk (*) indicates $P < 0.05$. ns indicates a result which was nonsigificant. The adjusted α-level for multiple testing is also displayed.

Focal Behaviour	Valence of welfare indicator	Control	Allogroom	*N*	*P*	corrected α-level
Calm Locomotion	+ve	4.173	4.360	16	0.308 ns	
Inactive Rest		0.183	0.353	16	0.174 ns	
Agitated Locomotion	-ve	3.457	2.758	16	0.021 *	n = 3 α = 0.016
Inactive Alert		59.689	58.173	16	0.252 ns	
Gouge		0.178	0.202	16	0.566 ns	

Table 6.8 Statistical test results for the analysis of the effect on focal marmoset behavioural welfare indicators of long-term video playback of allogrooming; mean percent time per observation session spent in affiliative behaviours between experimental and control condition (two-tailed). Asterisk (*) indicates *P* < 0.05. ns indicates a result which was nonsigificant.

Focal Behaviour	Valence of welfare indicator	pre- to mid-playback				pre- to post-playback			
		control	allo-groom	*N*	*P*	control	allo-groom	*N*	*P*
Calm locomotion	+ve	0.345	0.357	16	0.974 ns	0.599	0.136	16	0.303 ns
Inactive Rest		0.547	1.261	16	0.474 ns	2.406	2.066	16	0.881 ns
Agitated Locomotion	-ve	-0.290	0.841	16	0.350 ns	-0.031	-0.555	16	0.687 ns
Inactive alert		-5.219	-3.118	16	0.687 ns	-6.474	0.535	16	0.152 ns
Gouge		-0.279	-0.122	16	0.726 ns	-0.311	-0.103	16	0.381 ns

The only behaviour showing a significant difference between the control and experimental conditions was agitated locomotion in the first (short-term playback) part of the study, with marmosets spending significantly less time in this negative behaviour during allogroom video playback than during control playback trials ($N = 32$, $P = 0.021$).

6.3.4 Family-wise Error Rate Correction

None of the significant results were lost following adjustment of the α-level to correct for multiple testing, with the exception of the welfare indicator agitated locomotion for which there was no longer a significant difference between marmosets in the allogroom playback and control video playback between pre- and post-playback.

6.4 Discussion

6.4.1 Visual Attention to Video Playback

Marmosets spent significantly longer attending to the control video than to the experimental, allogroom video. Had the converse been true then this would have caused concern that our results may be explained by a bias in attention towards the experimental stimuli. However, I found an influence on marmoset behaviour despite the bias acting against, rather in favour of the predictions.

A small percentage of time attending to visual stimuli does not imply a small effect on behaviour. It is important to note that even when the focal marmoset was not attending to the stimulus video other members of the group might have been attending. The behaviour of nonfocal group members after attending to the stimuli also contributed to the data. For example, a juvenile marmoset attending to the video and subsequently allogrooming the focal individual would affect the results even if the focal individual paid no attention during an observation period.

Equally, the focal marmoset itself may not need to spend a long time attending to the stimulus for the visual stimulus to have an impact on its behaviour. Chimpanzees are believed to assess visual stimuli more rapidly than humans, for example visual arrays of numbers in a touch screen memory experiment (Inoue and Matsuzawa, 2007).

I found a trend towards a significant sex difference in visual attention. Females spent longer than males attending to the video stimuli. Similarly, Platt and Novak (1997) found that female rhesus monkeys showed more interest than males in video. It is not clear why female marmosets appear to attend to video images for longer, although one possible reason is the sex difference in colour perception. My study was not specifically designed to investigate sex differences and further research is required to establish whether a sex difference in visual attention does exist in marmosets, or whether such a sex difference occurs in other nonhuman primate species.

6.4.2 Short-term Video Playback and Visual Social Contagion

The results of the first part of the study provide the first evidence of social contagion of affiliation in nonhuman primates through the visual channel. Consistent with the predictions, my results show that observing video images of conspecifics allogrooming stimulates individuals to groom each other more, and this effect appears to be strong. Marmosets also tended to spend longer sharing food, suggesting that contagion is not limited simply to social facilitation, but represents instead a broader social contagion of affiliation. A ‘matching’ to same and different composite measures of affect categories provided further evidence for social contagion of affiliation, with allogrooming video stimulating ‘matching’ affiliative behaviour but not behaviours of ’non-matching’ affect, intergroup or intragroup agonism or anxiety.

The presentation of video of conspecifics allogrooming did not lead to more self-directed behaviours such as self-groom or self-scratch. This suggests that the marmosets recognise, and act on the dyadic nature of the behaviour. It also lends further support to a more general contagion of affect rather than the contagion being linked to a specific action. The marmosets also spent significantly longer in active foraging behaviour when shown the allogroom video compared to the control video, although not in feeding. This may, or may not, be associated with the increase in food sharing.

Overall, my results are consistent with the social contagion of affiliation in the visual domain in marmosets. In Chapters four and five, I presented evidence consistent with the social contagion of affiliation in the audio channel. Collectively, the results indicate that the social contagion of affiliation, at least in marmosets, is a multi-modal phenomenon.

It has been suggested that social contagion acts to improve coordination of group activity and maintenance of group cohesion in general (e.g. Clayton, 1978). I propose that the social contagion of affiliation may present an especially important mechanism for the maintenance of group cohesion, since greater affiliation between group members is thought to strengthen social bonds.

Researchers studying yawning and self-scratching, have suggested that their contagion represents a precursor to empathy. De Waal (2008) equates emotional contagion (*sensu* Hatfield et al., 1994) as a basic foundation level of empathy with cognitively mediated levels above. Over 100 years ago a researcher stated of humans that ‘the lowest common denominator of all empathic processes is that one party is affected by another’s emotional or arousal state’ (Lipps, 1903, translated from German in de Waal, 2008). The present findings appear to fulfil the basis of an empathic process proposed by Lipps. Although the definition given is admittedly rather broad and inclusive, it does point to the potential for further research into a possible precursor of empathy in social contagion.

6.4.3 Long-term Video Playback and Social Culture

The present results indicate that the long-term playback of allogrooming conspecifics may result in an increase in allogrooming by marmosets, although this effect appears to be confined to the period after all playback has ceased. This increase was also evident for a composite index of affiliative behaviours but not for composites of affect categories different to that of the playback stimulus (affiliation) indicating that the influence was not due to a general increase in activity or arousal. Intriguingly, rather than generalising to a suite of affiliative behaviours, the effect of the long-term allogroom video playback appeared specific to the identical matching behaviour, allogrooming indicating an effect consistent with social facilitation rather than social contagion.

It is puzzling that this social facilitation effect is confined to post-playback. The effect was similar across pairs of rooms in each condition. Also, the result is consistent with our stronger result for the short-term study, which reinforces the view that this is a real effect. There are several possible explanations for the effect being apparently limited to post-playback, and for the apparent negative result in mid-playback. One is that, during the mid-playback period, the effect was strong during the specific hours of playback when no-one is in the room, but that it diminished or was reversed during non-playback observation hours for some reason.

Another possible reason may result from the strength of the contingent social contagion effect via video playback of allogrooming. This effect depended on a difference between the control and experimental playbacks which occurred quite close together. It is possible that the effect would be much stronger when the grooming video is actually playing than when it is not (supported by the short-term results). If so, it is possible that the marmosets perform most of their mutual grooming for that day during video playback and are thus *less* likely to groom when the video is not playing. This could explain the apparent drop in time spent in allogrooming during mid-playback observations (in contrast, during short-term observation sessions the allogrooming video was playing during the observation). The observation sessions during the post-playback period were also conducted when the video was not playing; however, no video was played at all on those days. During the post-playback observation sessions, conceivably what remained was the residual effect of having been exposed to a lot of grooming over the previous few days (positive). This residual effect would act without the dampening effect of having already done a lot of grooming that day (or the day immediately beforehand in some cases, because sometimes they would be observed before playback, not always after).

Another possible reason is the difference in the timing of husbandry procedures between mid-playback and post-playback periods. Throughout the mid-playback period all routine husbandry tasks were compressed into the relatively short period between the long playback periods, when no-one was able to enter the rooms, and the observation sessions, during which only the observer entered the room. This meant that staff were obliged to schedule many tasks in between the specific playback hours and the observer entering to observe. Marmosets are often temporarily disturbed during husbandry tasks. This may have meant that during the observation sessions often directly following husbandry tasks, any lasting effect of the allogrooming video playback was partly supressed. The level dropped somewhat for control as well as for experimental rooms during mid-playback, providing some support for this explanation.

Regardless of the precise periods, the results provided some tentative evidence for a longer term effect of social facilitation via video playback of allogrooming. Examining the increased allogrooming of marmosets in the experimental condition across the five post-playback days, and extrapolating beyond, suggests that the elevated level did last for five days but that it was unlikely to have lasted any longer. An elevated level across five days beyond cessation of playback suggests a relatively long-lasting effect, certainly relative to contingent effects, even though it cannot be considered long-term in a general sense.

The specificity of the effect means that our results do not provide evidence for a longer-term, self-perpetuating change across a range of different affiliative behaviours. Thus my findings do not support visual social contagion as a possible transmission mechanism for social culture.

As visual attention to the screen during the long-term playback was not assessed, it is possible that attention to the stimuli diminished over time. However, this explanation does not fit well with the significant results for allogrooming between pre- and post-playback.

Given the importance of visual attention and the possibility of habituation to the video stimuli, it is possible that more infrequent and shorter exposures to the stimuli, instead of one several hour block daily, may have led to a stronger effect, including across other affiliative behaviours. However, intermittent playback of stimuli would be more difficult, and more costly to administer. Screens would need to be permanently in place and perhaps programmed to play on a timed basis, and so a larger number would be required. Such a set-up would probably be impractical in a working laboratory.

Control Video

Two perplexing aspects of the results raise opposing explanations concerning the content of the control video footage. In the coding of caged marmoset behaviours I noted that marmosets being in close proximity to each other did not necessarily imply affiliation due to the limited space and resting places (see Chapter three). However, the same reasoning does not apply to the video of marmosets in close proximity in the large rooms, where the marmosets have relatively much more space and choice of resting spots. Therefore, with this degree of choice, the close proximity of a dyad of marmosets may be considered an affiliative behaviour in itself. This may explain the lack of difference in the performance of active affiliative contact between control and experimental trials in the short-term playback, and between marmosets in the control and experimental conditions in the long-term playback, and indeed for the short-term and long-term pre- to mid-playback, differences in the opposite to predicted direction. However, it is possible that there may have been more inactive alert in the control video than the allogrooming video. If the control video showed more (anxiety-related) inactive alert behaviour (something that I tried to control for) then this may explain why marmosets spent more time attending to the control video than to the experimental video. If so, the increased active foraging in the experimental condition may be attributed to a decrease in active foraging in the control condition due to increased vigilance/anxiety in response to attending to the control video.

In an analysis of a composite of six anxiety-related behaviours (for the matching analysis), there was no significant difference in the level of anxiety-related behaviours associated with viewing the short-term control video relative to the experimental video. Similarly, there was no difference in the change in the composite of anxiety-related behaviours either between pre- and mid-playback or between pre- and post-playback, for marmosets exposed to the long-term control video playback relative to the allogroom video playback. Indeed, for the individual analysis of the anxious behaviour, self-scratch, there was a significant increase pre- to post-playback for marmosets in the experimental as compared to the control condition. For the short-term playback, marmosets spent significantly longer in the individual anxious behaviour, agitated locomotion during control trials compared to experimental trials, however this significant difference disappeared following correction for multiple testing. Overall, these analyses indicate that the first explanation is most likely to be correct, indicating that the control video was neutral or positive rather than anxiety-inducing and providing a possible explanation for the lack of influence in the experimental condition on affiliative contact.

6.4.4 Captive Marmoset Welfare: Allogroom Video Playback Practical Application

Behavioural Indicators of Welfare

Although the longer-term playback of allogrooming video over several hours per day led to an increase in allogrooming by marmosets between pre-playback and post-playback, it also led to an increase in a negative welfare indicator, self-scratching. In contrast, the short-term playback of video, showing conspecifics grooming one another, was not associated with any changes indicative of negative welfare and, in fact led to a reduction in one such behaviour: agitated locomotion. The short-term allogroom playback also stimulated more affiliative behaviours, namely allogrooming and food sharing. Therefore video playback of allogrooming behaviour for intermittent periods of several minutes may be used as enrichment to enhance the welfare of captive marmosets.

Captive Marmoset Welfare Application

Plate 6.3 shows the practical application of the short-term playback of a video showing conspecifics allogrooming to a social group of marmosets housed in an uncaged colony room. The monitor is placed in front of the internal window and the video played from a lap-top PC. The window acts as a barrier to prevent safety risks presented by moisture. Despite their spacious housing, (see Chapter three) the marmosets moved towards the monitor intermittently during stimulus presentation, and watched the images. They cling to the window sill, presumably in order to get closer to the image. The marmosets did not display any aggressive behaviours towards the images. In captive environments with several adjacent rooms or other large enclosures, video images could be played simultaneously to several different social groups at a time using a VGA monitor splitter (allowing video input to be directed to multiple monitors from one PC lap-top) and several second-hand (electrically tested) monitors, connected to a single computer. The video playback of conspecifics performing affiliative behaviours may have broader application to the enhancement of captive welfare in other socially housed animals. I discuss this further in Chapter seven.

Plate 6.4 Sensory and non-contact enrichment is provided for captive marmosets by displaying video of allogrooming conspecifics to marmosets in a large family room. Adult marmosets, and a juvenile marmoset, direct their attention towards the video image.

6.4.5 Possible Future Research

Burkart et al. (2009a; 2010) have suggested that prosociality may be especially important to cooperative rearers such as callitrichids and humans. Ought we to expect species that rear their young cooperatively to similarly have a greater tendency towards the social contagion of affiliation? It has been suggested that social contagion is a precursor to empathic processes, so might the social contagion of affiliation actually be instrumental? This suggestion is highly speculative; however, the proposition could be tested empirically. If there are species differences among primates in susceptibility to social contagion, particularly of affiliation, it should be possible to determine whether this was related to variation in prosocial tendencies.

In a study described above Platek et al. (2003) found increased susceptibility towards emotional contagion in individuals scoring high on self-reported empathy. In comparative nonhuman primate research, it may then be informative to establish whether there is individual variation in the degree of susceptibility toward social contagion, and if so to determine the characteristics of those individuals that are most susceptible. Although not directly investigating individual differences in sensitivity, Palagi et al. (2009) observed that female gelada baboons appeared to be more prone to the contagion of yawning than males. It is not clear whether or not this is due to increased attendance by females relative to males.

6.5 Conclusion

This study has provided the first evidence for the visual contagiousness of allogrooming in a non-human primate, to the best of my knowledge. .It also provides the first demonstration of visual social contagion in marmosets, and to the best of my knowledge, the first evidence for visual social contagion of any affiliative behaviour in a nonhuman primate. I found some evidence for a long-term social influence via video playback of allogrooming, although it appeared temporarily constrained (confined to post-playback) and the effect was specific to allogrooming behaviour only, consistent with an effect of social facilitation rather than social contagion.

Chapter 7

Thesis Findings, Implications, and Future Research Directions

7.1 Introduction

In this final chapter I will summarise the main findings, and place them in the context of previous research. I discuss the theoretical and practical implications of these results for social cognition, social culture, and for captive welfare. Table 1.2 gives an overview of the questions relating to each subject strand, addressed by each thesis chapter.

7.2 Summary of the Main Thesis Findings

I provided quantitative confirmation, in Chapter two, of the qualitative observation that nonfood-related behaviours are under-investigated experimentally relative to food-related behaviours, despite the significant proportion of wild cultural behaviours that are nonfood-related. Throughout the remainder of the thesis, I investigated social influence on nonfood-related social behaviours in marmosets.

In Chapter four I reported evidence for neighbour effects, of intergroup and intragroup agonism, affiliation, and anxiety, in marmosets. My results are consistent with evidence for the neighbour effects of affiliation and agonism found previously, in chimpanzees (Baker and Aureli, 1996; Videan et al., 2005). The conclusions that I drew from this study rested on the inference that the influence of neighbour vocalisations on the social behaviour of nearby marmosets was causal. Following adjustment for multiple testing, only the neighbour effect for intragroup agonism disappeared.

In Chapter five I carried out a playback manipulation, using pre-recorded affiliative (chirp) calls. The result of short-term chirp playback provided some tentative evidence supporting my inference of causality for the neighbour effect of affiliation in Chapter

Table 7.1 Overview of the questions addressed by each thesis chapter, relating to each thesis subject strand.

Thesis Subject Strand	Thesis Chapters			
	Chapter 2 Literature Survey	**Chapter 4 Spontaneous Neighbour Calls**	**Chapter 5 Audio Chirp Playback**	**Chapter 6 Video Allogroom Playback**
Social/ Communicative behaviours	Are nonfood behaviours under-represented relative to food related behaviour in social learning experiments?	Social, predominantly nonfood-related behaviours investigated	Social, predominantly non-food-related behaviours investigated and pre-recorded affiliative chirp calls used as the experimental stimuli	Social, predominantly non-food-related behaviours investigated and video of allogrooming used as the experimental stimuli
Social Contagion	–	Can audio mediated social contagion be demonstrated in marmosets through a relationship between neighbour calls and the social behaviour of marmosets in nearby groups?	If so, is the inference of the direction of causality from neighbour calls to focal marmoset behaviour supported by the results of a playback manipulation?	Can visually mediated social contagion be demonstrated in marmosets through the playback of video of conspecifics engaged in allogrooming?
Social Culture	–	–	Can a social culture of increased affiliation be initiated in marmosets through the long-term audio playback of pre-recorded conspecific affiliative (chirp) calls?	Can a social culture of increased affiliation be initiated in marmosets through the long-term playback of video of conspecifics engaged in affiliative behaviour (allogrooming)?
Captive Welfare	–	Does the influence of neighbour vocalisations on individuals in nearby groups have any implications for captive management?	Does audio playback of conspecific affiliative vocalisations (chirp calls) have the potential to improve the welfare of captive marmosets?	Does the video playback of conspecifics engaged in affiliative behaviour (allogrooming) have the potential to improve the welfare of captive marmosets?
Marmoset Vocalisations	–	What are the average call rates of the nine main marmoset call types made by marmosets housed socially? How do these rates compare to results of previous studies? Is a social and/or food function/context for the chirp call supported?	Is the affiliative function and context of chirp calls supported by the results of playback manipulation?	–

four. I also found evidence of a relatively longer-term influence of the playback of affiliative chirp calls across several affiliative behaviours. Marmosets in the chirp playback condition spent longer allogrooming between specific hours of playback, and in affiliative contact following the cessation of all playback, relative to baseline compared to individuals in the control condition. There was also a similar trend for grooming invite both between specific periods of playback and after all playback ended. Further, playback did not stimulate behaviours of different affect categories (intragroup or intergroup agonism or anxiety) to that of the playback stimulus (affiliative). However, following adjustment for multiple testing the results for the long-term playback were no longer significant, suggesting the need for caution and replication My experimental evidence then, to some degree, indicated an effect of continued influence after playback had ceased, consistent with a shift in social culture. These results provide some support for the proposal that auditory social contagion may be a transmission mechanism for social culture.

In Chapter six I turned my attention to social influence via the visual modality. I provided some tentative evidence for a longer-term effect of allogroom playback. This effect appeared specific to allogrooming behaviour itself, rather than generalising to other affiliative behaviours (i.e. consistent with social facilitation rather than social contagion). I also reported strong evidence for contingent visual social contagion of affiliation in marmosets, through the video playback of conspecifics engaged in allogrooming, both in terms of influence on various individual affiliative behaviours and a composite index. For both studies in this chapter, a test of matching to different affect categories showed that, as predicted, only behaviours of affect matching the contagion stimulus were influenced. Further, none of these results were affected following adjustment for multiple testing.

Evidence for Social Influence on Affiliative Behaviours

Table 7.2 shows the affiliative behaviours for which we found evidence for the short- and long-term effect of auditory social influence, reported in Chapters four and five. Table 7.3 shows the affiliative behaviours for which I found some evidence for the short- and long-term visual social influence, reported in Chapter six. Results following adjustment for family-wise error correction are also given in these tables.

Table 7.2 Summary of findings for auditory social contagion of affiliation in marmosets through spontaneous neighbour affiliative (chirp) calls in the short-term, and through the playback of pre-recorded affiliative (chirp) calls in the short- and long-term. A tick indicates a significant effect in the predicted direction, a cross indicates a non-significant difference, and 'nst' indicates a non-significant difference, but displaying a trend in the predicted direction. Non-adjusted α-level (N), adjusted α-level (A).

Focal behaviour	**Short-term**						**Long-term**			
	Immediate				Overall		Pre-mid		Pre-post	
	spontaneous chirp calls (Chp. 4)		playback of chirp calls (Chp. 5)		spontaneous chirp calls (Chp. 4)		playback of chirp calls (Chp. 5)		playback of chirp calls (Chp. 5)	
	N	A	N	A	N	A	N	A	N	A
Groom invite	**X**	-	**X**	-	✓	**X**	**nst**	**X**	**nst**	**X**
Allogroom	**X**	-	**X**	-	**X**	-	✓	**X**	**X**	-
Affiliative contact	✓	**X**	**X**	-	**X**	-	**X**	-	✓	**X**
Share food	✓	✓	**X**	-	✓	**X**	**X**	-	**X**	-
Social play	**X**	-	**X**	-	**X**	-	**X**	-	**X**	-
Affiliative composite (affl. contact and share food)			✓	**X**	Affiliative composite (all 5 affl. behaviours)		✓	**X**	**X**	**X**

Table 7.3 Summary of findings for visual social contagion of affiliation in marmosets through the playback of allogroom video, in the short- and long-term. A tick indicates a significant effect in the predicted direction, a cross indicates a non-significant difference.

Focal behaviour	**Short-term**		**Long-term**			
	playback of allogroom video (Chp. 6)		Pre-mid playback of allogroom video (Chp. 6)		Pre-post playback of allogroom video (Chp. 6)	
	N	A	N	A	N	A
Groom invite	**X**	**n/a**	**X**	-	**X**	-
Allogroom	✓	✓	**X**	-	✓	✓
Affiliative contact	**X**	**n/a**	**X**	-	**X**	-
Share food	✓	✓	**X**	-	**X**	-
Social play	**X**	**n/a**	**X**	-	**X**	-
Affiliative composite (all 5 affl. behaviours)	✓	✓	**X**	-	✓	✓

7.3 Implications of the Findings and Possible Future Research Directions

7.3.1 For Experimental Research on Social/Communicative Behaviours

I hope that our literature review, and survey (in Chapter two and the published version: Watson and Caldwell, 2009) will help to encourage experimental studies of nonfood-related behaviours, especially of social and communicative behaviours. Although the literature survey itself considered experimental research on social learning in particular, our review highlighted the need for experimental research on social transmission of social behaviours more generally. My thesis research work (and the published research article: Watson and Caldwell, 2010) represents a response to the need for further experimental study of social and communicative behaviours. In the following two sections I outline further suggestions for research focused on the investigation of social influences on social behaviour at both the individual and group level, in marmosets and other primate species including humans.

7.3.2 For Cognition

Cognitive Mechanisms

I do not know, and am unable to precisely determine on the basis of my present results, exactly what mechanism(s) may be underlying my findings. The empirical work reported in this thesis does, however, appear to be tapping into contagion (social contagion and in some cases social facilitation). Contagion is the most parsimonious explanation for my results, and the underlying mechanism is certainly unlikely to be anything more complex.

Here I explicitly separated my concept of social contagion, the influence on a range of behaviours associated with similar affect, from the contagion of identical behaviours only, an effect labelled here as social facilitation (see Chapter one). My results for short-term, *contingent* social influence are, without exception, consistent with my definition of social contagion. I have demonstrated social influence across an array of behaviours within the same category of affect rather than an influence on the identical matching behaviour only. Further, the results of assessments of matching to same and different affect categories of contagion stimulus for the long-term effect of auditory playback in (Chapter five), and for the short-term effect of visual playback (Chapter six) strongly suggest that the influences were specific to a particular affect (affiliation) rather than due to a more generalised increase in arousal or activity level.

Interestingly however, for the long-term effect of social contagion via video playback of allogrooming, I found that the effect appeared to be specific to allogrooming behaviour only, consistent with social facilitation rather than with social contagion.

Generality vs. Specificity of Effect:

Taxa, Categories of Affect, Sensory Modalities, and Cognitive Mechanism

Throughout the thesis I have examined the specificity of social contagion effects, and the modalities (visual and auditory) in which they might operate. In Chapter four, I provided evidence that the neighbour effect generalises, across taxa, from chimpanzees to marmosets, for affiliation and agonism. I additionally reported evidence for a neighbour effect of anxiety in the marmoset, suggesting that the neighbour effect is generalised across three categories of affect. Evidence supporting auditory social contagion in Chapters four and five, and visual social contagion in Chapter six (short-term only), indicates that the social contagion of affiliation generalises across at least two sensory modalities.

Table 7.4 shows that my thesis findings complement and extend evidence from previous studies investigating auditory and visual contagion in other species of monkey, apes and humans. Many of the studies carried out by other researchers, listed in the table, provide evidence for a contagion effect specific to one behaviour only. These examples are therefore consistent with a social facilitation effect, rather than with social contagion as we have defined it here, generalising to a range of behaviours associated with similar affect.

The Importance of Simple Cognitive Processes

As I stated in Chapter four, there is a general bias towards research on the most cognitively complex forms of social influence. Recently, however, awareness of the importance of simple social processes has grown. Certainly, our results indicate that social contagion appears to have an important and persistent effect on marmoset social behaviour.

Researchers have begun to investigate the effects of model-based social transmission bias (see Table 1.1, Chapter one) on social learning in nonhuman primates (i.e. selective copying according to the identity of the demonstrator, e.g. Laland, 2004), but not yet, to the best of my knowledge, in relation to simpler social processes. For example, van de Waal et al. (2010) found that vervet monkeys (a species with female philopatry) were more likely to learn an instrumental task (a version of the artificial fruit, Whiten et al., 1996) from a dominant female than from a dominant male demonstrator. The difference

Table 7.4 Evidence for social contagion cited, and reported, within this thesis, or of related interest, in both the auditory and visual modalities, in humans, apes and monkeys, for different categories of affect. Dark grey shading indicates no evidence of social contagion cited in this thesis (and to our knowledge currently unreported in the scientific literature); light grey shading indicates evidence cited within the thesis from previous studies; while very light grey shading indicates evidence from the current thesis findings.

Sensory Modality	**Effect of…**	**Humans; Apes; Monkeys**	**Species**	**Study**	**Influencing Behaviour**	**Category of Affect**	**Mechanism: Social Facilitation or Social Contagion?**
Auditory	Spontaneous vocalisation of neighbouring groups	**Humans**					
		Apes	*Pan troglodytes*	Baker and Aureli, 1996	Vocalisation	**Agonism**	Social Contagion
			Pan troglodytes	Videan et al., 2005	Vocalisation	**Agonism; Affiliation**	Social Contagion
		Monkeys	*Callithrix jacchus*	Chapter four	Vocalisation	**Agonism; Affiliation; Anxiety**	Social Contagion
	Playback of vocalisation	**Humans**	*Homo sapiens*	Provine, 1992	Laughter	**Affiliation**	Social Facilitation
			Homo sapiens	Bachorowski and Owren, 2001	Voiced Laughter	**Affiliation**	Social Facilitation
		Apes					
		Monkeys	*Callithrix jacchus*	Chapter five	Affiliative (chirp) call	**Affiliation**	Social Contagion
Visual	Spontaneous /provoked behaviour of nearby individuals	**Humans**					
		Apes					
		Monkeys	*Macaca fuscata*	Nakayama, 2004	Self-scratching	**Anxiety**	Social Facilitation
			Theropithecus gelada	Palagi et al., 2009	Yawning	**n/a**	Social Facilitation
	Playback of video/video games	**Humans**	*Homo sapiens*	Provine 1986; Platek et al. 2003	Yawning	**n/a**	Social Facilitation
			Homo sapiens	e.g. Black and Bevan, 1992; Anderson and Bushman, 2001	Aggressive Behaviour	**Agonism**	Social Contagion
		Apes	*Pan troglodytes*	Anderson et al., 2004; Campbell et al., 2009	Yawning	**n/a**	Social Facilitation
		Monkeys	*Macaca nemestrina*	Paukner and Anderson, 2006	Yawning	**n/a**	Social Facilitation
			Cebus apella	e.g. Visalberghi and Adessi, 2001	Feeding	**n/a**	Social Facilitation
			Callithrix jacchus	Chapter six	Allogrooming	**Affiliation**	Social Contagion Social Facilitation

appeared to be based on selective attendance to the female demonstrators rather than being attributable to greater social tolerance in females than males (van de Waal et al., 2010). Coussi-Korbel and Fragaszy (1995) drew a distinction between 'directed social learning' where the identity of the demonstrator affects the outcome of social learning, and 'non-specific social learning' that occurs independently of the identity of the active individual. Here we investigated social influences rather than direct mechanisms of social learning. Such cognitively simpler social processes may however also be subject to similar model-based biases. Should we expect social contagion of affiliation to occur independently of the identity of the sender/demonstrator or to be dependent on aspects of their identity? Might characteristics of the 'sender(s)' in relation to the 'receiver(s)' for example, the degree of familiarity of the sender to the receiver, or the perceived success of the model - prestige bias (Henrich and Gil-White, 2001) affect the strength of social influence?

It was not possible to draw any conclusions about the influence of model identity on the social contagion of affiliation on the basis of my results here. The video playback of allogrooming (Chapter six) showed a wide variety of different 'model dyads' (see Table 6.3) and the chirp calls used for the auditory playback (Chapter five) were recordings of an assortment of individuals, most whose identity it was not possible to determine beyond the colony room in which they were housed. In future research, the identity of the sender in the auditory and visual playback could be manipulated to determine empirically whether model-based biases in social contagion occur in marmosets. Would video of allogrooming exclusively among breeding pair dyads lead to more pronounced social contagion than video of mutual grooming between younger, non-breeding adults? Model-bases biases in relation to social contagion could also be investigated in other species. The chimpanzee may be a practical starting point since the neighbour effect for affiliation has been demonstrated in this species (Videan et al., 2005), and also visual contagion (yawning; e.g. Anderson et al., 2004).

Model-based biases concern characteristics of the ‘sender’ that may influence the strength of social influence exerted on the behaviour of nearby individuals. Conversely, certain characteristics of the ‘receiver’ may affect their susceptibility to the influence of social contagion (effected through playback in my empirical studies). Certainly, there appears to be relatively high inter-individual variation in susceptibility in the thesis studies. A relatively strong susceptibility towards social contagion may be adaptive.

From a functional perspective, it seems likely that social facilitation and social contagion in general, have adaptive consequences for individuals living within social groups. Social contagion especially, through spread of affect may play a valuable role in the coordination of group affect and activity. The social contagion of affiliation, in particular, may act to increase social cohesion within the group, perhaps strengthening social bonds. Coussi-Korbel and Fragaszy (1995) highlighted the influence of social dynamics on social learning, independent of the precise social learning mechanisms. They suggested that isomorphic behavioural coordination and social tolerance may support social learning. As an extension to this concept, social contagion of affect may facilitate behavioural synchrony, and in this way social learning, perhaps especially of social and communicative behavioural variants. If social contagion acts to increase behavioural synchrony then a higher susceptibility to social contagion (particularly of affiliation) may be associated with an increased rate in the spread of novel social or other behavioural variants. This is speculative, but could be empirically tested. The degree of susceptibility to social contagion of affiliation of particular groups of individuals could be measured, for example through an experimental paradigm similar to the short-term playback study in Chapter six, but perhaps using continuous behaviour sampling (Martin and Bateson, 2007) rather than focal sampling to attain a group measure for affiliative behaviours, if this proved practicable. Supposing a variation of susceptibility is found between groups, then a measure of the rate of social diffusion of a task seeded by a demonstrator in each group could also be obtained, and the rate of spread for each group compared to the degree of susceptibility to social contagion. Among nonhuman primates, chimpanzees may be well-suited to such an investigation. Visual contagion has been demonstrated already in chimpanzees through video playback for yawning (e.g. Anderson et al., 2004), and group diffusion studies have also proved successful in this species (e.g. Whiten et al, 2005).

There is growing interest in the evolutionary origins of the human capacity for empathy and altruism (e.g. de Waal, 2008; Silk and House, 2011). Platek et al. (2003) found a positive association in humans between susceptibility to social contagion of yawning and self-reported scores of empathy. It has been suggested that social contagion may form a precursor, or basis, for empathy (discussed briefly in Chapter four, 4.1, Chapter six, 6.4.2, 6.4.3: de Waal, 2008; Palagi et al., 2009; Yoon and Tennie, 2010). If social contagion in nonhuman primates does represent a precursor to empathy then we might expect it to be associated with prosociality in nonhuman primates. Under this assumption individual and species differences in susceptibility to social contagion (particularly of affiliation) may be predicted to covary with prosocial tendencies.

Humans are unusually altruistic, and a possible association with cooperative rearing has been suggested (Burkart et al., 2007). These researchers found evidence for unsolicited prosociality in the common marmoset (a species that cooperatively rears its young, as stated above) using a modified version of a ‘prosocial test’, first administered to chimpanzees by Silk et al. (2005) who found no evidence for unsolicited prosociality. In the experiment, marmosets were presented with a choice between two trays to pull (Burkart et al., 2007). No reward was gained for themselves by pulling either tray, but one tray provided a food reward to a neighbouring conspecific (0, 1), and the other resulted in no food reward to either of them (0, 0). Marmosets chose the (0, 1) tray more often when a conspecific donor was present than when they were absent, Burkart et al. (2007), indicating that marmosets will proactively work to provide food to a conspecific with no direct reward to themselves. In humans altruism is to some degree motivated by empathy (e.g. Silk, 2007; de Waal, 2008; Silk and House, 2011).

In order to test empirically the hypothesis that social contagion is a precursor to empathy, a measure or score for both degree of prosociality and susceptibility to social contagion could be recorded for individual marmosets to assess whether the scores co-vary. Prosociality could be assessed through performance on the prosocial test adapted for marmosets (Burkart et al, 2007), while susceptibility to social contagion for affiliation could be assessed using a playback study similar to the video playback experiment used in this thesis to investigate contingent social contagion, to measure individual differences in increases in affiliative behaviour during playback relative to control trials. In Chapter six, I suggested that phylogenetic differences in susceptibility to social contagion may be linked to differences in degree of prosocial tendencies. Inter-species differences could be investigated through gaining measures as described for marmosets above, for a range of other nonhuman primate species.

Possessing the capacity for empathy does not mean that humans lack the susceptibility to be influenced by cognitively simpler social influences. There appears to be at least as much contradiction within the human literature as in the animal literature over terminology for forms of social influence (see Levy and Nail, 1993 for a comprehensive review of terms and concepts of contagion in humans between 1895 and 1993). For ‘emotional contagion’ Barsade used the definition coined by Schoenewolf (1990, italics added, p. 50, cited in Barsade, 2002) as “a process in which a person or group influences the emotions or behavior of another person or group through the *conscious or unconscious* induction of emotion states and behavioral attitudes”. In contrast, Levy and Nail (1993) required that the ‘sender’ be unconscious of any intention to induce shifts in affective state in the ‘receiver’, defining social contagion as “the spread of affect, attitude, or behavior from Person A (the “initiator”) to Person B (the “recipient”), where the recipient does not perceive an intentional influence attempt on the part of the initiator.” (p. 266). Hatfield et al. (1993; 1994) however placed the onus on the ‘receiver’ rather than the ‘sender’ in their definition of emotional contagion as “the tendency to automatically mimic and synchronize expressions, vocalizations, postures, and movements with those of another person’s and, consequently, to converge emotionally” (Hatfield et al., 1992, p. 153-154, cited in Hatfield et al., 1993; 1994).

Research on social contagion in humans is complicated by the fact that we possess a definite capacity to be influenced by more cognitively mediated processes. There appears to be a similar bias in human research towards more cognitively complex forms of social influence as in the nonhuman research (Barsade, 2002). However, despite being a relatively simple cognitive process, social contagion can have pervasive consequences even in the absence of conscious cognitive processing. Barsade (2002) investigated the possible impact of emotional contagion on task performance in the workplace, and found it to be an influential effect. In a between-groups design, emotional contagion of four types of mood (positive or negative affect and high or low energy) were effected by a confederate experimenter (an undergraduate actor). Positive emotional contagion was found to reduce conflict, and to increase cooperation within work groups.

7.3.3 For Social Culture

Research into Sapolsky’s conception of “social culture”, is still in the very early stages. Here, I have presented a new approach to the study of underlying mechanisms of social transmission. In the article in which Sapolsky coined the term, he stated that “Discerning the mechanism of transmission will be particularly difficult in the case about to be considered, social culture; it will be far easier to observe the circumstances under which an individual adopts a type of tool use than to identify the performance of a pre-existing behavior to a unique extent.” (2006, p. 642). Experimental approaches provide a relatively precise means to discern underlying mechanisms. The long-term playback studies in this thesis represent the first attempt to address this challenge; directly investigating a potential transmission mechanism of social culture.

The phenomenon of ‘social culture’ described by Sapolsky (2006) refers to the performance of species typical behaviours to an atypical degree. But it is important to appreciate that the occurrence of one behaviour to an unusual degree (relative to what is considered the normative rate for the species) is not sufficient to constitute a social culture or style. Sapolsky observed groups other than the group where the shift in social culture was observed (‘Forest Troop’) with similarly high rates of grooming between females and males, but without showing unusual intensities in the performance of other behaviours. What makes the social culture or style distinctive to a particular social group is the overall ‘constellation’ of species typical behaviours performed to unusual extents “the collectivity of these extremes of behavior forms a coherent social whole” (Sapolsky, 2006, p. 647).

Overall, I have presented findings that provide some support for the thesis that auditory social contagion is a possible mechanism for the transmission of Sapolsky’s social culture. The long-term playback of chirp calls appeared to facilitate increased performance of a range of affiliative behaviours, consistent with the initiation of a change in affiliative social culture in marmosets. In as far as auditory social contagion may be a transmission mechanism for social culture, many of the theoretical implications and future research suggested for social contagion in the section above may also apply to the transmission or spread of social culture. In contrast, the evidence for a long-term effect of visual social contagion using allogrooming as a stimulus appeared limited to a behaviour-specific social facilitation effect; long-term playback of allogrooming video appeared to initiate an increase in allogrooming only. If this is so, while this result is likely to have implications for social cognition in terms of the specificity of effect, it does not appear to represent transmission of social culture. However, it is also possible that the results may represent a failure to detect social contagion which may have a small effect size.

The results of the manipulation experiment involving the relatively long-lasting effect of the long-term playback of chirp calls seem to support auditory social contagion as a possible transmission mechanism. It is however interesting to speculate as to whether this is exactly the same mechanism as that underlying the contingent, short-term influence of chirp calls (found in Chapter four through spontaneous calls, and to some degree the immediate influence of chirp playback in Chapter five). Effects longer than contingent influence may involve different behavioural changes in the individual. Coussi-Korbel and Fragaszy (1995) differentiated “momentary adjustments in behaviour” from learning “a relatively long-lasting change in behaviour” (p. 1444). The adjustments observed here in terms of social culture or style were not long-term, but neither were they momentary, suggesting a relatively-long lasting change in behaviour.

The results are tantalising but understandable minimal. There is plenty of scope for future research on the transmission of social culture. The first thing to establish, as stated in Chapter five, is whether the effect is replicable. Since the effect size is small it would be sensible to use a larger sample size, but for reasons already explained this may not practically possible. Second, the durability of the effect could be investigated, as discussed in Chapter five. Here, the evidence for a shift in social culture via auditory social contagion was limited to 5 days following the cessation of call playback. Further research is needed over a more extended time period allowing observation until the effect degrades. It is also possible that playback over a much longer period may create a longer-term change in affiliative social behaviour within groups. Comparative study of the transmission of social culture of this type (Sapolsky, 2006) across other species of nonhuman primate would provide information on the phylogenetic distribution of this phenomenon. A related question would then be what factors might influence the durability of a social culture within a population? Enquist et al. (2010) suggested that species with more numerous ‘cultural parents’ (i.e. > 2 through alloparenting and cooperative rearing) may be more likely to maintain socially cultural traits through social learning (see also Chapter three, 3.2.2). Might this also apply to the maintenance of Sapolsky’s social culture through social influence? An empirical test of this hypothesis would require comparative data on the durability of social culture within groups of species that have varying numbers of cultural parents, but that are phylogenetically related and similar in other respects. Burkart and van Schaik (2010) carried out a similar comparative analysis to assess the correlation of cooperative breeding with social cognitive ability. They compared sociocognitive skills of the cooperatively rearing common marmoset with related taxa; independently breeding squirrel monkeys; and capuchin monkeys which have an intermediate breeding system.

Sapolsky (2006) pointed out that in order to adopt the social culture of the existing population, new immigrants to the group would not need to assimilate any completely novel behaviours, but instead to alter the rate at which they perform behaviours already within their repertoire. What implications might this have for the transmission of social culture? How might this factor affect the speed and evenness of transmission in different species?

Following the research of Barsade (2002), described in section 7.3.2 above, it would be interesting to investigate whether social culture could be altered in groups of humans through simple processes of social influence. Could an entrenched culture of aggression in a particular organisation be influenced? Playback of sounds related to positive affect is likely to be too simplistic an approach. Provine found the playback of laughter to influence mood positively initially, initiating smiling and laughter in the receiver, but by the tenth playback was reported by subjects as “obnoxious” (Provine, 1992). The issue of social culture transmission is likely to be much more complex in a species with a much greater cognitive capacity, but this research avenue may prove productive. Barsade (2002) used a ‘closed-group’ method (Mesoudi and Whiten, 2008) to investigate the influence of positive contagion on the productivity of a group. The confederate effected a short-term influence on group affect that Barsade (2002) equated with mood. The groups were not established ones, having been formed specifically for the experimental task. Emotional contagion was measured through self-report and through ‘blind’ coding of video-tapes of the work-group sessions. In Chapter five I suggested the application of the serial replacement paradigm to research into the durability and transmission of social culture (Sapolsky, 2006) in nonhuman primates. It would be interesting to use a similar replacement method (Jacobs and Campbell, 1961; Caldwell and Millen, 2008; Mesoudi and Whiten, 2008) to simulate cross-generational transmission of social culture (of this type) in humans. How long would the changes in ‘group mood’ effected by emotional contagion by a confederate (as in Barsade, 2002) last after the replacement of the confederate by a subject, and the serial replacement of all the subjects in the original work group?

7.3.4 For Captive Welfare

The two forms of environmental enrichment proposed and tested in the current thesis belong to two overlapping categories: social non-contact; and sensory (Chapter one, Fig. 1.1). First, the auditory playback of conspecific affiliative calls (chirp call playback in Chapter five); and second, the video playback of conspecifics engaged in affiliative behaviour (allogrooming in Chapter six). It is important to evaluate the benefits carefully in relation to the costs of these contagion methods. Welfare budgets within research facilities are often restricted therefore it is possible that in recommending these particular enrichment options, funds may be diverted from other welfare enhancement options in consequence. A key question is whether or not the projected welfare benefits to the marmosets are likely to outweigh the costs of implementation. What are the costs likely to be, in terms of finance and time, and can they be reduced with little impact on the benefit? Any welfare improvements in the marmosets may provide ‘fringe’ benefits for research facilities, e.g. in reduced veterinarian bills (Buchanan-Smith, 2011).

Auditory Playback of Chirp Calls

Short-term exposure to a higher-than-average rate of chirp vocalisations was not associated with a reduction in the spontaneous production of calls (a naturally expressed behaviour) and led to an increase in a composite measure of active affiliative contact and food sharing (both behaviours considered positive to welfare). In between sessions of chirp playback lasting several hours per day, marmosets spent longer allogrooming (a positive welfare indicator) but less time in active foraging (which may be considered negative to welfare). After all playback had ceased, following 11 days of exposure to daily higher-than-average chirp playback of several hours, marmosets in this chirp playback condition displayed a greater increase in the time spent in inactive rest and in active affiliative contact (both considered positive for welfare) compared to marmosets in the control condition. My findings indicate that the auditory playback of a higher-than-average rate of chirp calls is likely to improve marmoset welfare through promoting an increase in time spent in affiliative behaviours and rest. The only negative welfare change associated with playback was the decrease in active foraging, which may in fact have been due to the increase in affiliative behaviours. Although affiliative behaviours are relatively infrequent they have an important positive influence on welfare. Therefore enrichment resulting in the stimulation of these behaviours is likely to enhance the well-being of captive marmosets. As detailed in Chapter five, the cost of implementing chirp playback are potentially very low. In research facilities with speakers already *in situ* the application of auditory enrichment could entail simply playing auditory recordings over these speakers, with no financial outlay and little expenditure of staff time. Even if additional speakers were required, they could be purchased at low cost and audio could be played from a re-conditioned iPod (a low memory capacity would be sufficient since the silence interspersed with a higher-than-average rate of chirp calls could be looped). Buchanan-Smith (2001) underlined the importance of enrichment being part of the routine of a working laboratory. If it becomes part of the weekly schedule to press ‘play’ on an audio CD of play back chirp calls over the speaker several times a week, or to place a stand with speakers in a room, plug it all in and press ‘play’, e.g. just prior to the staff lunch hour or over a weekend, then auditory enrichment could be executed at low cost.

Video Playback of Allogrooming Behaviour

Following exposure to several hours of daily allogroom video playback for a period of 9 days, marmosets showed a greater increase in time spent in allogrooming (a positive welfare indicator), but also a greater increase in time scratching themselves (a negative welfare indicator) relative to baseline levels, compared to marmosets in the control condition. Further research is needed in order to determine whether this increase in self-scratching following such long-term playback is a persistent problem, and if so, whether this can be alleviated in some way without weakening the positive benefits of the intervention. In the meantime, this result indicates that allogroom video playback should be confined strictly to shorter periods of playback. During 5-min trials including 1.5 min of exposure to allogrooming video playback, marmosets spent longer in affiliative behaviours allogrooming and food sharing, and longer actively foraging (all considered positive for welfare with allogroom a specific positive welfare indicator), and less time in agitated locomotion (a negative welfare indicator) than in control video trials. These findings strongly suggest that short-term playback of allogroom video for several minutes at a time (consisting of allogroom clips interspersed with blank screen) may improve welfare through stimulating allogrooming, food sharing and active foraging, and through reducing the level of agitated locomotion. Although the effect of one several-minutes-long playback may be small, the affiliative behaviours are very important in terms of welfare (see above), and the effect of implementing playback often is likely to have a cumulative benefit.

The costs of implementing this enrichment option are first of all the initial cost of creating a stand, and of purchasing a reconditioned computer monitor (to which a waterproof visor would need to be fitted) and a device from which to play the video clips, perhaps a reconditioned lap-top (see Chapter six). However, after this running costs would probably be minimal, both in terms of time and money. Once the set-up is created, staff could place the stand into a room and leave it to play through, e.g. three separate couple-of-minutes segments spaced out over a lunch hour. Alternatively, the apparatus could be set-up on a timer to play back for a couple of minutes four times throughout the day at the weekend. It is important that the playback apparatus is not present simultaneous to any potentially aversive procedures, to ensure that marmosets do not form negative associations. Placing the apparatus into the colony room only when it is unlikely to interfere with the working of the laboratory is desirable.

The video playback enrichment may be restricted to one or two groups at a time, due to the financial cost of each extra set of equipment and space and efficiency limitations of the working research facility. However, an advantage is that the social contagion effect may extend to other groups sharing the same colony room. Through a self-perpetuating feedback mechanism (see Fig. 6.1. Chapter six), marmosets with visual access to the group exposed to playback may indirectly benefit from the playback and may display an increase in affiliative behaviours in response to seeing the reaction of the primary group. Further research, involving observation of the social behaviour of nearby groups with visual access to the primary group undergoing allogroom video playback but without visual access to the video playback itself, is needed to establish whether other groups in a colony room may benefit indirectly in this way. Evidence for such a feedback effect of social contagion of affiliation would indicate greater efficacy relative to cost, thus strengthening the case for video playback as an enrichment tool.

Future Research Directions

Further Welfare Assessment

Here I have assessed the welfare effect of the playback manipulations through the observation of behavioural welfare indicators; levels of normal behaviours. The results of this evaluation are encouraging, but require replication and elaboration. Empirical evidence is tremendously important in persuading the directors of laboratories, to implement environmental enrichment (e.g. Buchanan-Smith, 2011). Therefore, it would be productive to assess the validity of the suggested welfare improvements using different, complementary approaches. It is important not to rely on a single measure of welfare (Dawkins, 2006).

Non-invasive methods for evaluating enrichment options were introduced in Chapter one. One such method, the preference test, could be used to assess individual preference for chirp playback relative to silence, in a similar manner to McDermott and Hauser (2007, see Chapter five), but in a set-up allowing more space, and voluntary participation in trials. Marmosets could be encouraged (using positive reinforcement training) to enter a mobile empty cage adjacent to their home cage through a Perspex connecting tube. Following habituation this cage through periodic exposure, a series of trials could be carried out. Within this mobile cage, presence in one half of the cage could elicit silence and in the other chirp playback, with the condition associated with each cage half counterbalanced across trials. Preference could then be measured by comparing the amount of time spent in the location associated with each condition, after McDermott and Hauser (2007).

Even supposing that a general preference for chirp playback relative to silence, or other sounds, has been established, it is important to maintain control, and so choice, in enrichment applications (see Chapter one). Individual variation is a key consideration in enrichment. Welfare is particular to each individual; different individuals will experience different welfare effects when exposed to identical conditions or enrichment manipulations (e.g. Hosey et al., 2009). Further, individual preferences may vary over time.

A set-up used to allow self-administration of call playback in rats has potential application in marmosets. Burgdorf et al. (2008) used an experimental set-up as a preference test for two rat vocal calls. Rats could self-administer one of two call types by poking their nose into either of two holes on either side of a chamber (placement was counterbalanced across trials) to elicit the playback of the loop of one call exemplar through a speaker on the roof of the chamber. Each time a nose-poke occurred, a photo beam was broken, allowing the frequency of nose-pokes for each call to be counted by a PC, and so the preference of the rat for a particular call could be assessed without a human present. This set-up could be modified for use in a marmoset home cage. Self-administration of chirp playback could be elicited by a similar nose-poke apparatus adapted for marmosets. This set-up would allow marmosets to control playback, and also a means to assess the frequency with which marmosets choose to hear chirp playback. The individual self-administering the call may also expose other nearby individuals to the playback without them having control over this exposure. However, call playback is unlikely to be too invasive since it is a relatively quiet intragroup call.

This set-up could also be modified to allow motivation-based assessment, another behavioural method for evaluating the well-being in relation to enrichment applications (see Chapter one; e.g. Mason et al., 2001). To assess motivation, an expenditure of energy could be required to self-administer the playback, for example chirp playback could perhaps be elicited by lifting a flap that in turn depresses a switch. This flap could be differentially weighted to allow an assessment of the motivation of marmoset to elicit chirp playback. The number of flap lifts could be automatically counted without the need for experimenter presence. The motivation measure could either be pooled across the social group, or the identity of individuals manipulating the flap could be coded afterwards from a remote video. A control flap which did not lead to chirp self-administration could control for motivation to lift the flap as rewarding in itself (e.g. Poole, 1992). In Chapter five, I suggested the possible extension of the auditory playback of positive calls in marmoset to another affiliative call, the ‘whirr’ call. In future studies evaluating the welfare effects of affiliative call playback in marmosets it may prove productive to investigate this call in addition to the chirp call.

Potential Application to Other Socially Housed Animals

I have so far considered the possible application of the auditory and visual playback of positive affective calls and behaviour specifically for one particular species of marmoset. Although the suggested enrichment may be applied to marmosets housed in a variety of different environments, they are likely to have most impact in more restricted environments. These new enrichment options may also generalise to other socially housed animals. The suggested contagion methods are probably most directly applicable to other species of nonhuman primates and other social animals housed in similar laboratory environments to the common marmoset (but may also be beneficial to other animals housed in different environments). Research facilities are comparatively restricted environments in relation to zoos and parks. Animals are often housed in cages with relatively restricted space and options, where the suggested enrichment options are considered most likely to maintain interest and to effect the greatest improvement relative to existing welfare levels.

Nonhuman primate species bred and used in research facilities other than common marmosets include: *Pan troglodytes* (still used in the USA), *Macaca mulatta*, *Macaca fascicularis*, and in the same family as *Callithrix jacchus*, *Saguinus spp*. (Buchanan-Smith, 2011). In a study of neighbour effect in chimpanzees, Videan et al. (2005) found that spontaneous neighbour grooming vocalisations (including lip smacking, lip-buzzing, or teeth clacking) influenced individuals in nearby groups (within full visual contact to the callers) to emit more grooming vocalisations themselves and in more distant groups (with limited or no visual contact) to spend longer allogrooming. This finding indicates potential enrichment application; the playback of such grooming vocalisations may lead to similar increases in allogrooming (a positive welfare behaviour) as do spontaneously sounds, and this deserves research attention. Chimpanzee play pants (panting during play bouts, accompanied by a play face) were also coded in their study to assess the effect on nearby individual play behaviour, but these calls were made too infrequently to allow analysis. These play pant calls may also represent a call with playback enrichment potential in chimpanzees. Similarly, playback of affiliative calls in the other nonhuman primates commonly used in laboratories, listed above, could be investigated.

Animals other than nonhuman primates may benefit from auditory playback enrichment. Rats are used extensively in research facilities. In 2009, mice, rats and other rodents constituted the vast majority (83%) of nonhuman animals that underwent the scientific procedures performed in the UK in (Home Office data for 2009). The question then is whether rodents emit positive affective vocalisations that may be manipulated to increase welfare through auditory playback? Recently, there has been an increased interest in ultrasonic vocalisations (USVs) as representing social communicative signals in rats (e.g. Takahashi et al., 2010; Browning et al., 2011). Burgdorf et al. (2008) found that rats would self-administer playback of particular sub-type of 50-kHz calls (FM 50-kHz USVs) emitted during play, and would avoid playback of 22-kHz USVs, associated with aversive behaviours such as freezing. The primary aim of their research was to directly compare the function of these two call types and they make no suggestions for the potential application of playback, self-administered or otherwise, for enrichment purposes. However, playback of the FM 50-kHz USV play call represents a potential enrichment application to enhance the welfare of rats in research facilities.

7.4 Tinbergen's Questions

Tinbergen, a founder of modern ethology, formulated a framework of four main aims of ethological enquiry to apply in attempts to understand any animal behaviour (Tinbergen, 1963). The four questions relate to the two proximal causes of behaviour: control/causation (mechanism) and development (ontogeny); and to the two ultimate causes: evolution (phylogeny), and function (adaptation). It is instructive to consider how the findings of the current thesis fit within this framework of ethological investigation.

Tinbergen's first question was the central aim. I approached the investigation of social contagion in marmosets, almost exclusively from the perspective of increasing understanding of the proximate factor of control or causation. Spontaneous neighbouring calls of anxiety, affiliation and agonism were found to influence nearby individuals to perform social behaviour of matching affect. The process of contingent social contagion was investigated through experimental manipulation, providing evidence for social contagion of affiliation in marmosets through the visual and auditory modalities (Chapters five and six). By attempting to facilitate a culture of increased affiliation in groups of marmosets through the long-term playback of conspecific affiliative calls, I directly investigated the transmission mechanism for social culture. My findings provided some evidence for auditory social contagion as one such mechanism. Future research is required to address the three other questions, for example, to empirically test whether there is indeed an adaptive function for social contagion, or whether normal developmentally early social experience is necessary for this capacity to be realised, and how and when social contagion develops normally. However, I have contributed discussion and speculation as to the ultimate causes of the phenomenon. I have discussed the potential adaptive function of social contagion. I speculated that the observed influence of neighbouring calls through social contagion of intergroup agonistic affect (Chapter four) may improve coordination of aggression towards conspecific groups encountered in the wild, and that social contagion of anxiety through vocalisation may represent a mechanism for recruitment of group members for the mobbing of predators. Quantitative evidence for the function of the ‘seep’ call as an alarm call was also provided in Chapter four. I have discussed possible adaptive functions of social contagion more generally, for example in terms of facilitating social learning through increases in behavioural synchrony.

In addition I have considered the apparent phylogenetic distribution of this phenomenon, though it remains to be seen whether social contagion should be regarded as homologous, i.e. inherited from a common ancestor with this trait, or analogous, attributable to convergent evolution across species. I have extended evidence for the neighbour effect from chimpanzees to a species of New World monkey, the common marmoset. I have also demonstrated visual social contagion of an affiliative behaviour in this species of monkey. It has been suggested that social contagion may represent a precursor to empathy. An improved understanding of the evolution of empathy and altruism in humans may be informed through comparative behavioural studies. Marmosets are cooperative rearers and show unsolicited prosociality as do humans (Burkart et al., 2007). Given this parallel it may be informative to search for phylogenetic origins of empathy in marmosets. I proposed that if social contagion was a precursor to empathy then the individual variation in degree of susceptibility to social contagion may be associated with the degree of unsolicited prosociality in nonhuman primates.

7.5 Summary and Conclusion

Summary

A systematic literature review of social learning articles provided quantitative confirmation of bias towards experimental investigation of food-related behaviours relative to nonfood-related behaviours despite the prevalence of nonfood-related behavioural traditions in wild nonhuman primates. Empirical work in the thesis was focused on investigating social influence on nonfood-related social behaviours in marmosets. In an observational study, I found evidence for neighbour effects in marmosets (the influence of spontaneous neighbour vocalisations through social contagion) of agonism (both intergroup and intragroup), anxiety and affiliation. A systematic analysis of marmoset call rates was also reported. Through playback studies, I provided evidence for the contingent social contagion of affiliation in marmosets in both the visual and auditory modalities. I directly investigated the potential transmission mechanism for social culture, as conceived by Sapolsky (2006). The long-term playback of conspecific affiliative (chirp) calls initiated relatively long-lasting increases across a range of affiliative behaviours in marmosets, consistent with a transient shift in social culture. Auditory social contagion thus represents a possible transmission mechanism for social culture. The long-term video playback of allogrooming conspecifics stimulated a post-playback increase in matching allogrooming behaviour in marmosets, consistent with a longer-term social facilitation effect. Auditory playback of affiliative conspecific calls and short-term video playback of affiliative conspecific behaviour have potential practical application to improve the welfare of captive marmosets through sensory and social non-contact enrichment.

Conclusion

Overall, the results presented in this thesis indicate that the social behaviour of marmoset monkeys influences nearby individuals to perform social behaviours associated with similar affect, and that this effect can be experimentally manipulated. My findings have interesting and important implications for our understanding of social cognition and social culture, and for captive welfare.

THE END

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Appendix A: The full list of articles reviewed for the survey in Chapter two.

1. Agostini, I. and Visalberghi, E. (2005). Social influences on the acquisition of sex-typical foraging patterns by juveniles in a group of wild tufted capuchin monkeys (*Cebus nigritus*). *American Journal of Primatology, 65,* 335-351.

2. Alvard, M. S. (2003). The adaptive nature of culture. *Evolutionary Anthropology, 12,* 136-149.

3. Aoki, K., Wakano, J. Y., and Feldman, M. W. (2005). The emergence of social learning in a temporally changing environment: a theoretical model. *Current Anthropology, 46,* 334-340.

4. Assersohn, C., Whiten, A., Kiwede, Z. T., Tinka, J., and Karamagi, J. (2004). Use of leaves to inspect ectoparasites in wild chimpanzees: a third cultural variant? *Primates, 45,* 255-258.

5. Bering, J. M. (2004). A critical review of the "enculturation hypothesis": the effects of human rearing on great ape social cognition. *Animal Cognition, 7,* 201-212.

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11. Bonnie, K. E., Horner, V., Whiten, A., and de Waal, F. B. M. (2007). Spread of arbitrary conventions among chimpanzees: a controlled experiment. *Proceedings of the Royal Society B-Biological Sciences, 274,* 367-372.

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15. Brosnan, S. F., Schiff, H. C., and de Waal, F. B. M. (2005). Tolerance for inequity may increase with social closeness in chimpanzees. *Proceedings of the Royal Society B-Biological Sciences, 272,* 253-258.

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17. Bugnyar, T. and Huber, L. (1997). Push or pull: an experimental study on imitation in marmosets. *Animal Behaviour, 54,* 817-831.

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Appendix B: Additional considerations for audio and spectrogram coding (Chapter four).

Issue	Explanation and description of guidelines used in the Neighbour effect study in Chapter four
Loud shrill calls	The difference between the categories of long phee and loud shrill created by Pook (1976) is one of degree only since the division was drawn arbitrarily according to whether or not the phee call was made with mouth closed or open, for the purposes of his experimental study. He includes all calls made with the mouth open, whether partially or wide open (loud shrills at the upper end of the spectrum represent the wide open mouth calls). However, many other studies have investigated solely open-mouth phee calls (e.g. Norcross and Newman, 1993). In the study in Chapter 4 it was possible to distinguish between focal individual calls made with mouth closed or open during live observation but it was not possible to make the same distinction for neighboring calls from the element structure in the spectrogram alone, in audio coding, therefore a criterion index was required. One distinguishing feature of loud shrill calls is their relatively high amplitude; however precise measurement of amplitude requires controlled recording conditions (Jones, 1993). Loud shrill call elements are also, on average, much longer in duration than phee calls made with a closed mouth (e.g. Pook, 1976). In order to ensure that all the calls coded as neighboring loud shrill calls did in fact represent open mouth calls, and therefore to ensure that all such calls made by the focal individual would be reliably detected, the minimum element length was set fairly high; at 1.3sec (at just above the mean for loud shrill and significantly above the mean for long phee calls, 0.89 sec). All phee calls with at least one syllable of 1.3 seconds or more duration were coded as loud shrill calls. Focal individual loud shrill calls detected in the live observation (those under 1.3 s in length) were thus discarded from the analysis. Thus the total number of loud shrill calls coded was reduced but the benefit was that the loud shrill was reliably and consistently coded in both the live and in the audio and spectrogram coding.
Infant vocalisations	Infant marmosets make certain infant-specific calls as well as calls approximating to those of adults. Infant specific calls include: cry calls; compound cry calls; and twitter hook. The cry is a long duration call covering a broad frequency range (Pistorio et al., 2006). The cry is equivalent to 'infant squeal' (Epple, 1968) and 'caw' (Pook, 1976). Compound cry calls (calls joined to cry calls: Pistorio et al., 2006), twitter calls with descents ('twitter hook') are infant-specific calls. Infant specific calls were not coded in the audio coding in the current study. Infants make highly variable call types that were not coded since they did not clearly fit any one particular adult call description. Because infants marmosets make calls approximating those of adults and call frequently but not in usual adult call contexts (Pistorio et al., 2006) it is important to try to exclude such calls from the coding since they unlikely to have an equivalent effect on focal adults as would similar calls made by mature adults. Pistorio et al. (2006) carried out a comprehensive analysis of the ontogeny of calls in infants. They showed that the parameters of the calls changed from 5 – 25 weeks (becoming more and more adult-like in particular parameters) however, the process is gradual rather than absolute so it is difficult to absolutely exclude these calls. At 3-4 months, marmosets begin to make calls in appropriate contexts and respond appropriately to adult calls (Pook, 1976). It was not possible to distinguish sub-adult calls made in isolation of cry calls. It is estimated that these calls will not greatly affect the results of the analysis. Infants are observed to make long strings of tsik calls, cry calls and twitter, phee and whirr calls to signal distress, for example when they are put down from an adult's back (Epple, 1968; Pook, 1976). Only groups of adults with young infants respond to playback of these calls (Epple, 1968). The infants also make other adult-like calls but much less frequently (e.g. ek). Pistorio et al. (2006) found that infant cry and compound cry calls disappeared entirely by 10-11 weeks in all individuals

	in their study. There were infants (aged less than 11 weeks/ 2.5 months) present in each of the four study colony rooms throughout the entire duration of the study and therefore the issue of identifying and excluding infant calls applied across all colony rooms. The duration of bouts of infant calls, as identified by cry calls and tsiks in sequence from cry calls (see below) were not coded in the audio analysis. The calls known to be most frequently uttered by infants were coded as possibly infant calls when they occurred within 2 seconds either side of known infant calls. Infants make a large number of such calls so they were considered likely to impact on the analysis of adult calls if they had been coded as such. **Infant tsik calls:** Because infant tsik calls, although more variable in structure than adult tsiks, are otherwise apparently indistinguishable in structure (Pook, 1976) it was not possible to reliably identify adult tsik calls within a bout of infant distress calls (particularly if several infants were vocalising simultaneously). Infant tsik calls could be identified when they occurred in a regular pattern of tsiks either side of a cry call (infant tsiks also often occurred in compound with cry calls). Infants use tsik calls out of the normal adult context and thus the infant tsiks cannot be considered equivalent to adult tsik calls. The author has also observed that infant distress calls appear to be largely ignored by most adult individuals. Thus if infant tsiks were included in the analysis as adult tsik calls they could be expected to largely outnumber adult calls and to have a great effect on the results. For this reason, tsik calls within infant cry bouts were not coded (including extensions of regular series of infant tsiks beyond cry calls), suspected infant tsik calls outwith cry bouts were coded as possible infant tsiks and sessions with a large percentage of infant cry bouts within them were excluded from the analysis of adult tsiks. **Infant twitter calls:** Twitter calls within infant strings (and 2 seconds either side) and those that appeared to be a continuation of twitter calls were coded as possibly infant. Twitter calls clearly overlapping infant calls when there was clearly only one infant vocalising were coded as adult calls.
Compound calls	Call elements can be made in various different arrangements, for example ‘tsik-ek’ and ‘seep-ek’ (Jones, 1993). Such combinations of different elements have been referred to as ‘compound calls’ (e.g. Pook, 1976). In the current study, the different elements of compound calls were coded separately, according to their type, for two main reasons. First, it was not always possible to establish, on the basis of the spectrogram alone, all instances in which the elements of an apparent compound call made by one individual may actually have constituted separate call elements made by different individuals that happened to occur in close temporal contiguity. Second, it was not known whether particular combinations would occur often enough to warrant a separate classification. Any elements coded as separate compound calls would reduce the number coded in any one category: excessive ‘splitting’ was thought likely to reduce the likelihood of any one category containing enough calls to allow meaningful statistical analysis. Furthermore, there is little evidence in the literature to indicate that the elements in compound calls perform different functions to the separate elements.
Transitional calls	Transitional calls are those that constitute a combination of two different call types e.g. twitter-phee (Jones, 1993) and thus do not fit the descriptive criteria for a particular individual call. Overall, transitional calls are rare in adults (e.g. Jones, 1993). Transitional calls were not coded in the audio coding in the study described in Chapter 4. Any focal individual calls coded during the live observation but found to be transitional on examination of the spectrogram were discarded from the analysis.
Ultrasonic calls	The auditory acuity of the common marmoset is around 28 kHz (Coleman, 2009). Pook (1976) stated that he detected no calls of a purely ultrasonic nature (that is, calls with a fundamental frequency starting above the audible range for humans). The equipment for the current study was carefully chosen in order to record frequencies of up to 27 kHz. Initial pilot studies showed that the marmosets occasionally made seep calls starting at around 20 kHz (concurrent with Stevenson

	and Rylands, 1988). Tests showed that the author was able to hear pure tones of up to 18 kHz but not reliably above, which probably imposes a practical limit of around 17 kHz when listening to the focal individual in a laboratory setting. It was decided to code the calls that were above the authors' hearing sensitivity (i.e. fundamental frequency is above this level) separately. This division, whilst arbitrary in relation to the marmosets, meant that all calls recorded as audible in the audio coding would have been picked up in the focal individual during the live coding.

Appendix F: MATLAB code used to generate p-values: (i) for within subjects analyses; and (ii) for between subjects analyses (Chapters four, five and six).

(i)

```
function p = prandomize(D,N);

% Approximates an exact paired test on the data by resampling N times.
% D is your input data and must consist of 2 columns, one for each
% condition.
% N determines how many trials are run, and must be an integer.
% The answer, p, is (an estimate of) the exact two-tailed probability
% of observing the difference present in the original data D.
% The algorithm orders the values in each row randomly, then
% measures the difference between the two new columns. It does this N
% times, p is the proportion of trials for which the difference is
% greater than or equal to the original observed difference.

A=[D(:,1);D(:,2)];
m=mean(A);
diff=abs(mean(D(:,1))-mean(D(:,2)));
n=size(A,1)/2;
for i=1:N;
   s=floor(2.*rand(n,1))';
   ds=s*D(:,1)+(1.-s)*D(:,2);
   d(i)=2*abs(m-ds./n);
end
p=mean(heaviside(d-diff+0.00001),2);
```

(ii)

```
function p = randomizeuneven(D,N,n);

% Approximates an exact test on the data by resampling N times.
% D is your input data and must consist of 1 column, with n values
% in the first condition (height of D - n in the other).
% N determines how many trials are run, and must be an integer.
% The answer, p, is (an estimate of) the exact two-tailed probability
% of observing the difference present in the original data D.
% The algorithm pools both columns of data and randomly draws two new
% columns, measuring the difference between the two. It does this N
% times, p is the proportion of trials for which the difference is
% greater than or equal to the original observed difference.

m=mean(D);
diff=abs(mean(D(1:n))-mean(D(n+1:size(D,1))));
s=randint(1,1,10000);
for i=1:N;
   s=s+randint(1,1,[1,100]);
   r=randintrlv(D,s);
   d(i)=2*abs(m-mean(r(1:n)));
end
p=mean(heaviside(d-diff+0.00001),2);
```