Feeding strategies of the tammar wallaby (*Macropus eugenii* Desmarest).

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Roger Graham Lentle

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Abstract

The tammar wallaby (*Macropus eugenii* Desmarest) is a small, grazing, fermentative herbivore with a high digesta throughput. The strategies it uses to overcome energostatic constraints are investigated in captive and in free living specimens in a bush pasture ecotone in the Rotorua district of North Island, New Zealand. The feeding events of captive tammars have a relatively invariant crepuscular rhythm with no evidence of meal formation. The duration of feed events, but not their frequency, increases with poorer quality food. These features of ingestion may promote efficient fermentation in the stomach. The grazing events of free ranging tammars are longer than their browsing events. The efficiency of grazing by tammars may be increased by a concerted biting and chewing action of incisors and molars resulting from a lateral rotation of both lower hemi-jaws which causes the occlusive surfaces of lower dental arrays to be drawn across those of the upper dental arrays. The chewing rates of tammar wallabies are similar to those of other small herbivores. A comparison of the sizes of foregut digesta particles in tammar wallabies and in larger macropods indicates that the former may expend relatively greater masticatory effort. In tammar wallabies browsing is relatively inefficient and frequent leaf dropping during handling results in the dry matter intake of browse falling below estimated daily requirements. Analyses of the gross anatomy of tammar intestines show that the hind gut may be the site of significant 'secondary' fermentation. The colon is longer and the small intestine shorter than in browsing species of an equivalent size. There is a reciprocal variation in the weight of stomach and hindgut contents such that the mass of fermentative digesta in the hindgut is augmented during times when that of the stomach is reduced. Females have a greater amount of stomach and colon tissue with a longer caecum and colon per unit body size than males. The drinking behaviour of tammar wallabies fed dry foods may be specialised to maintain fermentative efficiency. Captive tammars fed with small, succulent, low quality food items are able to achieve dry matter compensation and never drink. When dry foods are fed, drinking is associated with feeding events and increases in frequency with lower quality food. Tammars exhibit two distinct resting behaviours which are uninfluenced by diet but resting is inhibited for a period following drinking or eating.

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Chapter 1

Introduction.

"Those who formed our species know how ungovernable our appetite for drink and food would be and how we should, out of sheer greed, consume more than a moderate or necessary amount; in order therefore to prevent our rapid destruction by disease and by the prompt and untimely disappearance of our species, they made the lower belly as it is called into a receptacle to contain superfluous food and drink, and wound the bowels around in coils, thus preventing the quick passage of food, which would otherwise compel the body to want more and make its appetite insatiable, so rendering our species incapable through gluttony of philosophy and culture, and unwilling to listen to the divinest element in us." **Plato (364 BC)**

Introduction

This study investigates the strategies by which the tammar wallaby (*Macropus eugenii* Desmarest*), a small herbivore, is able to cope with a diet consisting principally of grass (Williamson, 1986). The ability of herbivores to exploit more abundant fibrous types of food such as grass is reliant on the digestion of cellulose by microbial fermention (Van Soest, 1982). However this strategy generally requires more time to be spent both in the ingestion and the subsequent digestion of the chemically more resistant and nutritionally less dense fibrous material (Van Soest, 1982). Computer simulations indicate that with increasing restriction of diet to food items of this type, an animal's 'digestive capacity', the optimal sum of the processes of ingestion, digestion and elimination (Hirakawa, 1997), will increasingly constrain the animal's ability to balance energy intake with energy requirements (Hirakawa, 1997) i.e. to achieve caloric homeostasis (Striker, 1990) or energostasis (Hainsworth and Wolf, 1990; Blundell and Halford, 1994).

These constraints are particularly likely to occur in smaller herbivores. As body size decreases the number of herbivore species that rely on abundant fibrous plant material declines and the number relying on scarcer low fibre plant material increases (Bell, 1969; Jarman, 1974; Hume, 1984; Hofmann, 1989; Cork, 1994). This trend has been attributed to differences in allometric scaling (Parra, 1978; Demment and Van Soest, 1985) in that an animal's mass-specific energy requirement scales with body mass $^{0.75}$, whereas the maximum rate that energy can be obtained via fermentation scales to body mass $^{1.0}$, as gut capacity scales with body mass $^{1.0}$. Thus species of small body size have a higher ratio of energy requirement to gut capacity, making digestive strategies that rely primarily on the relatively slow (Mertens and Ely 1982) process of fiber fermentation less feasible. Demment and

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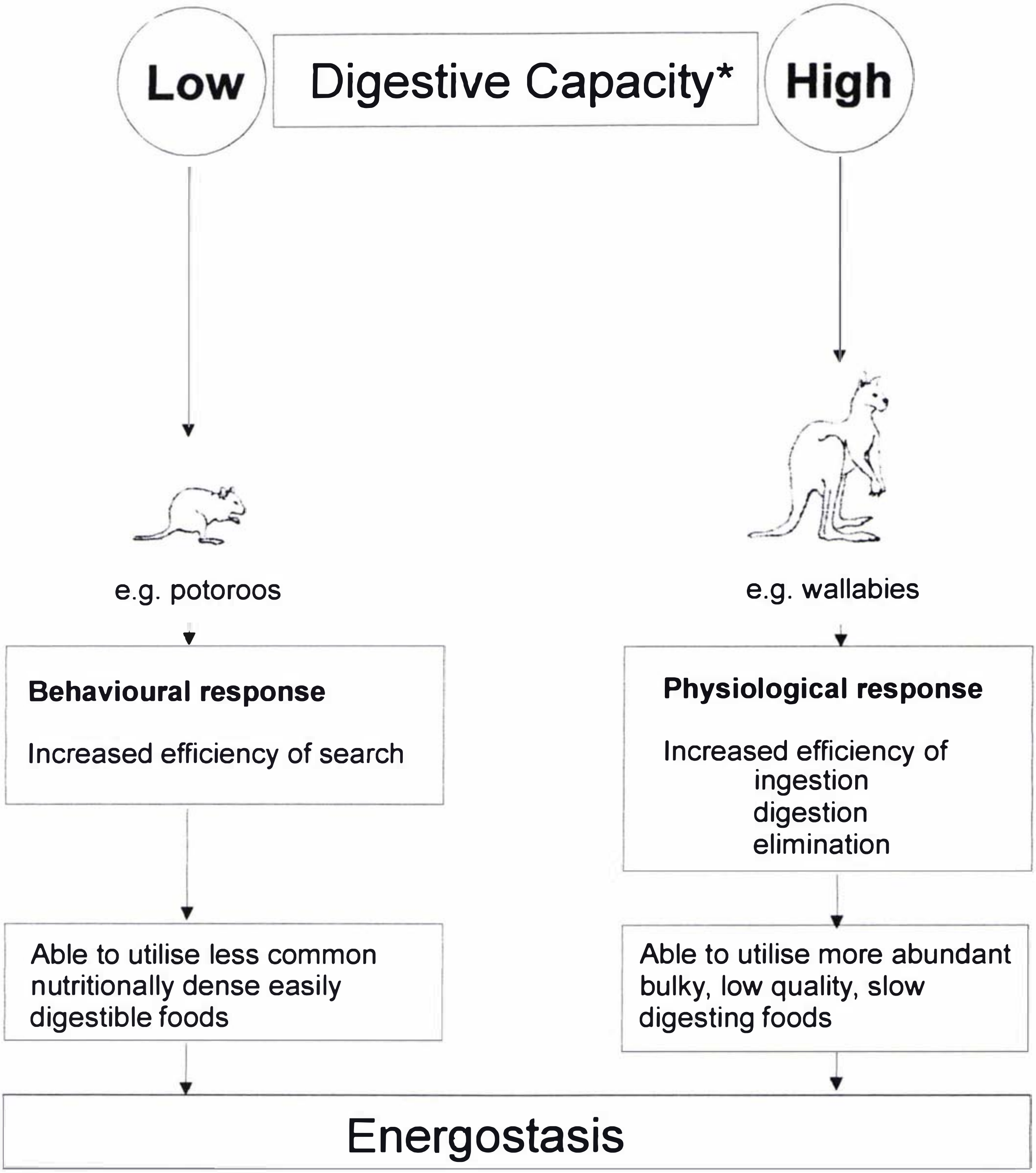
**Feral populations of tammar wallaby found in the Rotorua district of North Island New Zealand may be derived from South Australian mainland stock (Maxwell et al., 1996). This mainland population has recently re-categorised as* Macropus eugenii eugenii *(Maxwell et al., 1996) in the light of morphometric (Poole et al., 1991), allozymic (Van Oorshot et al. 1989) and genetic (unpublished findings reported in Maxwell et al., 1996) evidence.*

FIGURE 1: Possible effects of digestive capacity* on the evolution of feeding behaviour in macropods.



*The sum of the processes of ingestion, digestion and elimination (Hirakawa, 1997).

Van Soest's (1985) quantitative allometric model predicts that primary reliance on fermentative digestion becomes unfeasible in species whose liveweights are below 9 kg. It has been suggested that smaller species may lessen the constraints of body size by increasing intake so that any reduction in energy yield from reduced retention and fermentation of fibre is offset by an increase in energy yield from the more rapid digestion of cell solubles (Justice and Smith, 1992; Cork, 1994).

The strategies used by small grazing herbivores to reduce the restrictions of grazing herbivory may include those processes which influence the animal's 'digestive capacity' and those which influence the selection of food (figure 1). The changes in anatomical and physiological parameters which increase the efficiency of handling, ingestion, mastication and digestion of food may also influence the timing of feeding and eliminative behaviours and produce particular temporal patterns that optimise efficiency. The temporal characteristics of the feeding behaviour of different species (Weipkema, 1971; Baile, 1975; Panksepp, 1978; Fagen and Young, 1978; Metz, 1975; Laut et al., 1984; Le Magnen, 1992) vary according to dietary habit e.g. granivores and carnivores tend to group feed events in a different manner to herbivores. Panksepp (1978) noted that

"among the brain processes which ultimately govern food intake, behavioural differences among mammals may result from the degree to which common processes control ongoing feeding. Cats because of their dependence on energy rich sources of food may govern intake more by long term regulatory mechanisms, while intake of herbivores, with their energy poor sources of nourishment may be guided more by shorter term controls such as gastric fill and intestinal passage".

More recently Collier (1985) commented that

"meal size on any given occasion is a reflection of the animal's niche, its strategy for maximising feeding benefits relative to costs and its nutritive value and its metabolic state" and *"the morphology of an organism sets the upper limit on the meal size and frequency that it can tolerate".*

Short term changes in an animal's nutritional and metabolic requirements may be met by changes in behaviour pending physiological or anatomical compensation (McFarland, 1978). This often results in a change in the frequency of particular behaviours that entail additional energy costs (McFarland, 1978) which may undermine efficiency. Thus an animal faced with lower oxygen tensions at high altitude may temporarily increase respiration rate until such time as its red cell mass increases (McFarland, 1978). Similarly, where an animal is faced with a reduction in the quality of available food, its searching or feeding behaviour may become more protracted, until physiological or anatomical change increases efficiency and allow feeding or searching time to return to normal (McFarland, 1978). An animal with a relatively low digestive capacity is more likely to increase its search time in response to a deterioration in food quality, whereas an animal with a relatively high digestive capacity is more likely to increase the time that it spends eating (Hirakawa, 1997). In this manner, an animal's pre-existing anatomical and physiological characteristics shape the temporal aspects of compensatory behaviour and the natural selection of feeding behaviour in general (figure 1).

A knowledge of the inter-relationship between anatomical and physiological characteristics and feeding behaviour is necessary to determine the relative importance of optimal foraging strategies and to test the limitations of the optimal foraging hypothesis. Early optimal foraging theorists (Pyke et al., 1977) assumed that animals have, through the process of natural selection, developed a harvesting strategy that optimises foraging by maximising energy intake for minimum feeding time, energy, or risk of predation (Schoener, 1972). Proponents claimed that investigations based on its assumptions embraced 'proximate' as well as 'ultimate' causation (Cheverton et al., 1985). Latterly however, caution has been advised in interpreting the results of optimal foraging experiments in this manner as evolution is not a simple optimisation process (Lewontin, 1979; Gould and Lewontin, 1979). There has been greater emphasis on interpretations which consider developmental and phylogenetic 'constraints' that have been acquired during the evolution of an organism and the separation of the current utility of a particular physiological or anatomical feature from its utility in the context of the original selective forces that gave rise to it (Werner, 1981; Pierce and Ollason, 1987).

The utility of any investigation of optimality in foraging is largely dependent upon the optimal foraging paradigm being congruent with the physiological process under examination (Pierce and Ollason, 1987). Feeding behaviour is an outcome of separately integrated visceral and central nervous systems linked by adrenergic and cholinergic pathways and modulated by peptides which can act centrally as well as peripherally (Morley, 1980; Blundell and Halford, 1994). In this system the different physiological processes that mediate the commencement of feeding and its cessation may each be subject to independent selection pressure. Thus animals which are better able to vary the commencement of their feeding events or meals, i.e. their frequency, may be better able to optimise patch choice whereas animals which are better able to vary the duration of their feed events or meals may be more efficient at time allocation within patches. These views of the physiology of feeding (Morley, 1980; Blundell and Halford, 1994) are not congruent with the assumptions that are inherent in a number of functionally based optimal foraging models. Thus deterministic optimal foraging models (Schoener, 1971) implicitly assume that the processes of meal commencement and of meal termination are affected equally by environmental stochastic change. Again, a number of models which address the probabilities of meal commencement (Emlen, 1966; Rosenweig, 1966) fail to allow for differences in the probabilities of meal termination.

The present study investigates the inter-relationships between feeding and associated behaviours and various anatomical and physiological characteristics that may influence the digestive capacity of the tammar wallaby, a moderately small, foregut fermenting, non ruminant herbivore of the notamacropus subgroup of macropods (Flannery, 1989) whose feeding and digestive strategies are not completely understood. The study employs a variety of ethological, anatomical and physiological methods to undertake a broad survey of the temporal aspects of feeding, chewing, drinking and resting behaviours and relates these to known physiological constraints.

The temporal organisation of feeding behaviour is first studied in captive tammars held under controlled conditions (Chapter 3), four females of approximately equal size being maintained on a succession of feeds of differing quality with differing handling and masticatory requirements. The daily time budgets, feeding rates and temporal patterns of feeding events are assessed to determine the character of temporal organisation and the manner in which feeding behaviour is influenced by the type of food being fed. A search is made for evidence of feeding events being grouped into meals. The nature and extent of any changes in the patterns of other behaviours that may be associated with feeding is also assessed.

The temporal organisation of the feeding behaviour is subsequently studied in four free-ranging tammars by use of radiomicrophone collars. The proportion of time spent grazing and browsing, the temporal characteristics of browsing and grazing events (Chapter 4), and the frequency of chewing and biting events (Chapter 5), are determined.

Scanning electron microscopy is used in conjunction with macroscopic measurements in a study of 100 tammar skulls and jaws to determine the characteristics of incisor and molar action and tooth wear and to assess the manner and degree of molar progression (Chapter 6).

Biometric techniques are used to determine the relative capacities and physical characteristics of the various components of the gastrointestinal tract from 100 postmortem specimens with a view to assessing their functional importance (Chapter 7). The manner of variation of the gross anatomy of the various components of the gastrointestinal tract with body size and the temporal variation in the state of fill of fore and hind gut components, are both explored.

The particle size distributions of stomach digesta from postmortem specimens are determined using standard techniques (Waghorn et al., 1986). A novel graphic method based on predicted change in particle size distribution with increase in numbers of chewing cycles from computer simulations of mastication (Voon et al., 1986) is used to compare the extent of mastication with that of other macropodids (Chapter 5).

The temporal organisation of drinking and of resting and the extent to which these behaviours are temporally associated with feeding is explored in four captive tammars (Chapters 8 and 9).

The chapters covering the experimental work are preceded by a review of the literature pertaining to the physiology and ethology of feeding in small herbivores (Chapter 2) and are followed by a general discussion (Chapter 10). Appendix 1 provides more detailed discussion of some of the methods used in chapter 3. Appendices 2 and 3 cover additional experimental work that has an indirect bearing on work within the main body of the thesis.

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Chapter 2

The energostatic aspects of feeding: A literature review.

CHAPTER 2: The energostatic aspects of feeding: A literature review.

The manner in which an animal adjusts its intake of food in order to balance its energy requirements, i.e. energostasis, can be investigated by considering the physiology of ingestion, digestion and elimination and adopting a reductionist approach to elucidate factors which affect the energostatic efficiency of a particular process. An alternative is to adopt an ethological approach, relating the temporal aspects of behaviour to overall energostasis. This review considers relevant information from both disciplines on the basis that a synthesis of ethological and physiological information may increase our understanding of the factors which influence the energostatic efficiency of small herbivores.

In Justice and Smith's (1992) model of energostasis in herbivores, mass-specific energy intake for maintaining energy balance increases exponentially with decrease in body mass. Therefore small fermentative herbivores must maintain rapid intake and throughput of low quality foods in order to achieve energostasis. The ability to maintain high intake and throughput rates of low quality foods is dependent on physiological specialisations that permit optimum ingestive, digestive and eliminative efficiency rather than behavioural strategies that optimise search and thus food quality. Thus food handling and oral processing skills often become adapted to the rapid consumption and ensalivation of those particular items that form the bulk of the animal's diet (Hainsworth and Wolf, 1990).

The 'pattern' (Booth, 1990) of intake or elimination may nevertheless be important in small fermentative herbivores that rely on low quality foods. The efficiency of digestion may be affected by the spacing of feeding events (Cochran, 1987; Penry and Jumars, 1987; Sibly and Calow, 1986). Optimal foraging models which consider food within the digestive tract as a 'patch' passing through the animal predict that when cumulative gains from digestion follow a diminishing return, the patch should remain within the digestive system for an optimal length of time in order to yield a maximum rate of energy gain between meals (Cochran, 1987; Sibly, 1981; Sibly and Calow, 1986; Speakman, 1987; Taghon, Self and Jumars, 1978). Thus the timing of the feeding events (Warner, 1981a) of animals in which the stomach is an important site of digestion should permit optimal reactor performance in this organ. Similarly the timing of caecal emptying and defecation should permit optimal reactor performance in the colon and caecum.

A physiological approach

This section considers the factors which influence the efficiency of ingestion, digestion and defecation and effect feeding and eliminative behaviour, with special reference to small herbivores and to macropods in particular.

Digestion in the forestomach.

Chemical reactor theory has been used to predict 'optimality' in gut configuration for both catalytic (enzymatic) and autocatalytic (fermentative) digestion (Penry and Jumars, 1987). It is also useful in predicting the manner in which feeding behaviour may influence reactor optimality.

Three basic types of reactors may occur. Firstly, batch reactors (BRs) which process reactants in discrete batches, with perfect mixing throughout the reactor during the residence time of each batch. Secondly, plug flow reactors (PFRs) which are characterised by continuous orderly flow through consecutive small transverse segments of the (usually tubular) reactor, with perfect radial mixing within each segment. Thirdly, continuous flow stirred tank reactors (CSTRs) characterised by continuous flow of material through the reactor, with perfect mixing maintained throughout the reactor.

Proximal fermentation chambers with separate entry and exit channels such as the rumen or the forestomach of macropods can function as BRs (Penry and Jumars, 1987) under conditions where they are alternately being filled and emptied. Batch reactors are always inferior to PFRs and to CSFRs, in maintaining a maximum production rate of energy and nutrients from food, due to idle periods when the reactor is being emptied and refilled (Penry and Jumars, 1987). This conclusion is supported by Demment and Greeenwood's (1988) study which modelled energy production from fermentative digestion in a grazing ruminant and incorporated the effect of feeding behaviour as well as physiological parameters. In no case was an optimal solution for energy production based on less than maximal rumen fill. It is nevertheless possible that under some circumstances, such as when idle periods are correlated with periods when feeding is restricted by extraneous factors such as predation pressure, BRs may be superior to other reactor designs that require a more constant throughput in order to function efficiently.

CSTR designs are superior in maximising energy production from fermentation in small herbivores that occupy nutritional environments where rapid throughput (or low fermentation chamber volume) and low levels of cellulose digestion are appropriate (Penry and Jumars,1987). Conversely PFR designs are superior in situations where low flow rates and higher levels of cellulose digestion are appropriate.

A combination of a CSTR followed by a PFR is considered optimal for stomach fermenting herbivores in nutritional environments where both high levels of cellulose digestion and high rates of throughput are required (Penry and Jumars, 1987). It has been suggested (Freudenberger et al., 1989) that the layout of the macropod stomach is equivalent to this optimal configuration, the sacciform portion functioning as a CSTR, whilst the tubiform portion functions as a PFR.

However in Penry and Jumars' (1987) analysis this optimum is only achieved by each reactor in the CSTR/PFR series functioning separately. In most macropods the diameter of the junction between the sacciform and tubiform forestomach approaches the maximal diameter of the tubiform gut (Langer, 1988) and thus does not qualify as a functional sphincter in terms of Poiseuilles law (Scratcherd, 1981) i.e. the cross sectional area of the junction is too large in relation to the maximum diameter to have any significant influence on flows of material between the two compartments .

Penry and Jumars' (1987) conclusions are based on steady state reactor flows. If food transit is driven primarily by rate of intake rather than by rate of digestion, then reactor function becomes sensitive to timing of feeding events. If feeding continues in small evenly dispersed events then flow rate will approximate to a steady state and the reactor may function as a CSFR/PFR series. Conversely, if feeding events are grouped into meals and unevenly dispersed through the deil cycle, reactor function will be altered. Thus where prolonged interfeed intervals alternate with intensive feeding bouts, i.e. meals, alternate emptying and filling of both CSFR and PFR portions of the foregut may occur. In an extreme case when the whole stomach is alternately filled and emptied, the stomach will be occupied by a single meal and the extraction gradient that is essential for the tubiform forestomach to function as a PFR may be temporarily lost causing it to function as a BR until an extraction gradient is re-established.

When reactor flow becomes discontinuous there is departure from a steady state and the assumptions of Penry and Jumars' (1987) model are violated. Thus the ingestion of food in meals is difficult to model in terms of reactor theory. When previously ingested material is prematurely displaced from the assumed CSFR and PFR portions of the stomach by fresh ingesta, the mean residence time of ingesta in the CSFR and PFR will be reduced and the extraction gradient in the PFR, (i.e. the tubiform foregut) will again be compromised in proportion to the incoming volume of fresh ingesta (i.e. meal size).

The lack of an effective sphincteric division between the sacciform and tubiform portions of the forestomach may permit it to function in different reactor configurations as feeding strategy changes according to food quality and availability. Thus the gut of an animal that spends a significant amount of time searching for scarce food and retains a single large meal for a long period may function as a BR, whereas that of an animal which exploits abundant low quality food and thus takes frequent very small meals may function as a CSFR/PFR series. This hypothesis is supported by the work of Warner (1981a, 1981b) on captive tammars showing a significant variation in the retention of particulate matter and a significant variation in the digestibility of neutral detergent fibre (NDF) according to whether animals were fed continuously or once per day.

It may be expected that in species which have evolved under conditions where food abundance is spatially or temporally patchy, such as would curtail a CSFR/PFR feeding strategy, development of the tubiform portion of the forestomach would be less pronounced, because significant temporal interruptions in the flow of ingesta, would compromise extraction gradients in the manner described. Alternatively, when there is a uniform abundance of low quality food, regular events could take place, an extraction gradient may be more readily established and maintained, and stomach development would tend to emphasise CSFR/PFR configuration (i.e. the sacciform portion of the forestomach would be relatively small and tubiform portion of the forestomach relatively long).

Thus a classification of macropodine species based on the relative volume of sacciform and tubiform portions of the forestomach may be expected to be correlated with the quality and relative abundance of preferred diet. This indeed prooves to be the case (Kendalls coefficient = 1.0, p= 0.002) in table 1 which tabulates a non parametric correlation analysis between the anatomical data from ten macropod species compiled by Langer (1988) and the dietary abundance and quality data complied by Norbury et al. (1989).

Table 1: Dietary quality, food abundance and percentage volume of forestomach of sacciform and tubiform components of various macropodid species.

Species	Food quality *	Food # abundance	% Sacciform stomach@	% Tubiform stomach@
Bettongia lesueur	4.0	2.0	73	22
Potorous tridactylus	4.0	2.0	75	13
Lagorchestes conspicillatus	1.0	3.0	30	58
Macropus eugenii	2.0	3.5	26.7	60.3
Macropus giganteus	2.0	4.0	22.6	70.6
Macropus robustus	1.5	3.5	16	78
Petrogale pencilliata	2.0	4.0	27	61
Wallabia bicolor	2.0	3.0	17	76
Thylogale stigmata	2.5	3.5	47	47
Thylogale thetis	2.0	3.5	52.3	40.3

* Rank of quality from compilation by Norbury et al., (1989) 1, shrubs; 2, grasses and herbs; 3, tree leaves and fruit; 4, fungi, roots, tubers and invertebrates.

#Rank of abundance from compilation by Norbury et al., (1989) 1 - 4 (least frequent - most abundant).

@ Percentages of stomach compartment volumes, averaged from compilation by Langer (1988)

Digestion in the colon and caecum.

Penry and Jumars' (1987) analysis of reactor efficiency also applies to fermentation within the hindgut of small herbivores. Under conditions of sustained high throughput, the rate of onflow of digesta from the small gut will be consistently high and will tend to reduce the time available for fermentation in the hindgut. This time constraint may be lessened by three strategies which each increase the mean residence time of digesta particles. Firstly the development of countercurrent systems which selectively prolong the residence times of more digestible particulate matter (Bjornhag, 1994). Secondly the development of 'off line' compartments such as the caecum which function as batch reactors (BRs) in a manner that is relatively independent of throughput rate. Thirdly an increase in the relative volume of the colon, and a strategy of periodic evacuation/defecation which together result in the whole colon functioning as a batch flow reactor. In the latter two strategies digesta load is periodically increased and the timing of batch emptying may be dictated by considerations of optimality in digestion or absorbtion, rather than being at random

The hindgut is the principal site of fermentation in many marsupial species (Foley et al., 1989). Moreover, a number of marsupials (Cork and Warner, 1983; Foley and Hume; 1986) termed 'caecal fermenters'(Hume and Warner, 1980) are thought to employ a strategy of selective particle retention within the hindgut similar to that reported in rabbits (Bjornhag, 1994). Others species, termed 'colon fermenters' (Hume and Warner, 1980) also practice hindgut fermentation but have a colon which is less haustrated and does not appear to selectively retain particles.

The importance of hindgut fermentation in macropod species is less clear. The colon is not haustrated nor is there evidence of any mechanism of selective particle retention within the hindgut of these species (Hume and Warner, 1980). However, allometric studies have shown that caecal length in larger 'grazing grade' macropods (Sanson, 1980; 1989) varies as the square root (0.5) rather than the cube root (0.33) exponent of body weight i.e. in an area/volume compensating rather than isometric manner (Osawa and Woodall, 1992a). This departure from isometry may indicate a significant degree of specialisation of this gut component (Gould, 1978) for fermentative digestion or for water conservation (Osawa and Woodall, 1992a;1992b) .

The relative rate of energy production in the hindgut, and the contribution of energy produced by fermentation in the hindgut relative to that produced in the foregut, has been investigated by Hume

(1977) in macropods. Whilst the rate of production of volatile fatty acids (VFAs) in the hindgut of *Thylogale thetis* and *Macropus rufogriseus* is greater than that of sheep, the relative contribution from the hindgut of both macropod species is estimated to be less than 2% of the total VFA production within the gastro-intestinal tract due to the low volume of the hindgut compared with that of the stomach. However this assessment assumes steady state (i.e. CSTR) dynamics and does not allow for fluctuations in rates of VFA production in conjunction with the timing of feeding and eliminative behaviours. Under laboratory conditions, tammars have been shown to coordinate defecation with ingestion, moreover the neutral detergent fibre content of faeces, i.e. the residue of potentially fermentable cellulose (Prins and Kreulen, 1989), has been shown to vary with the temporal pattern of feeding and defecation (Warner, 1981a).

Ingestion

The efficiency of the feeding strategies of stomach fermenting herbivores that are adapted to conditions of high throughput may be influenced by factors such as skill in manual handling, and the speed of biting and chewing. However the extent to which overall rates of ingestion may be augmented by increases in the rate of biting or of chewing is ultimately limited by the maximum speed with which jaw muscles may contract (Hiiemae, 1978).

Studies of feeding behaviour indicate that an animal's 'functional response', the manner in which its feeding rate changes with the abundance of its food (Solomon, 1949; Holling, 1959), may ultimately determine which options of diet selection and habitat choice are feasible (Hanley, 1982; McNaughton, 1984; Fryxnell et al., 1988; Hobbs and Swift, 1988; Illius and Gordon, 1990; Spalinger and Hobbs, 1992). The functional response of herbivores feeding on uniformly distributed abundant and apparent plant sources (Spalinger and Hobbs, 1992) is determined by the interrelationship between cropping and chewing processes (Black and Kennedy, 1984; Greenwood and Demment, 1988; Spalinger et al., 1988; Penning et al., 1991; Spalinger and Hobbs, 1992) whereas that of herbivores feeding on more patchily distributed and spatially dispersed food sources such as browse is determined by the relationship between searching and cropping and by leaf size (Spalinger and Hobbs, 1992). Thus the overall rates of intake of small herbivores that depend on abundant low quality foods may be augmented by efficient coordination between chewing and biting. Conversely, the rates of intake of small herbivores that depend on more dispersed food sources such as browse may be lower, and energostasis more dependent on specialism in the efficient search for, and selection of, better quality foods.

The differences in incisor and molar tooth morphology that form the basis of Sanson's (1980; 1989) classification of macropods as browsers or grazers may be viewed as an outcome of specialism in biting or in chewing. However such morphological differences may result not only from specialism in the occlusal mechanics of particular groups of teeth e.g. chewing by molars as was suggested by Sanson (1980; 1989), but also from differences in the manner in which the actions of particular groups of teeth are integrated i.e. the extent to which the action of incisors may be dissociated from or synchronised with that of molars.

Efficient comminution is important for maintaining digestive efficiency in the face of high throughput rates. Reducing the mean particle size of food items affords a means of increasing fermentative yield without prolonging gut residence time (Dehority and Johnson, 1961; Troelsen and Bell, 1969; Robles et al.,1980; Mertens and Ely, 1982; Batzli et al., 1985; Bjorndahl et al. 1990) by providing a greater surface area for microbial attack and by reducing the viscosity of gut contents to allow more efficient dispersion of micro-organisms and salivary antitoxins.

The larger mean particle size of macropodid ingesta compared with that of ruminants (Freudenberger, 1992) does not necessarily indicate that particle size reduction is less important to macropod digestive strategy. Ruminants are able to postpone the reduction of particle size and subsequently undertake it by rumination in safer surroundings. The cost considerations i.e. the instantaneous outcome of the competitive tension between chewing and cropping (Demment and Greenwood, 1988; Spalinger and Hobbs, 1992) for ruminants thus differs from that of macropods.

Mean particle size may be reduced by a relative increase in the number of chews per bolus (Greenwood, 1991; Dryden et al., 1995), but this strategy may increase tooth wear and is problematic for macropodids whose molars have a closed root structure and finite depth of enamel (Sanson, 1980; 1989a; 1989b). The cutting surface of macropod molars is progressively reduced by wear (McArthur and Sanson, 1988). Excessive tooth wear is known to influence the survival and fecundity of a number of non-eutherian species (Pahl, 1985). Molar wear may be reduced by transferring the work of particle size reduction onto other teeth i.e. ingesting greater quantities of smaller food items that require more cutting work with incisors and less chewing with molars. The efficiency of chewing, i.e. the number of fine particles produced by a given number of chews, may be increased by maintaining mouth fill at an optimum, as overfilling is known to reduce efficiency (Lucas and Luke, 1984).

Under conditions where sustained high levels of food intake and reactor fill are necessary, feeding activity will need to continue at short intervals throughout the day. Thus feeding must take place despite lower levels of efficiency e.g. feeding on less preferred foods during prolonged periods of heat avoidance or predator avoidance. This may render optimal foraging analysis of feeding habits complex in terms of 'partial preferences' (Pyke et al., 1977).

A high daily level of feeding activity may affect the general organisation of the activity budget. Thus other activities, such as sleep, which occur less frequently and continue for more prolonged periods in larger species may tend to occur in shorter, more temporally dispersed, bouts in small herbivores with high metabolic rates (Saariko and Hanski, 1990) in order to avoid starvation.

The temporal association of post ingestive periods with behaviours that contribute to digestive efficiency may be accentuated in small animals. Sleep influences metabolic rate and modulates gastrointestinal motility in some species (Narducci et al., 1987; Furukawa et al., 1994). Therefore close interposition of sleeping and feeding periods may serve to reduce metabolic demands and allow temporary increases in gut residence time. Similarly close integration of drinking with feeding activity may also enhance overall digestive efficiency, particularly in dry environments, by promoting dispersal of microorganisms through the stomach ingesta. In the case of macropods, drinking activity may also influence the overall digestive efficiency by promoting prompt extrusion (Dellow, 1982) of soluble nutrients into the small gut where they may be digested more efficiently (Van Soest, 1982).

An ethological approach

This section considers measurements of various aspects of feeding and eliminative behaviour, with special reference to small herbivores and to macropods in particular.

Rates of ingestion

A number of vertebrate herbivores have the ability to increase their intake of food as its quality declines (Freudenberger and Hume, 1992). Such compensation may be achieved solely by an increase in the rate of ingestion, but when food quality is markedly reduced the overall time spent feeding may also increase (Laut et al., 1985). The latter increase may be achieved by adjustments either to the duration of feed events, the spacing of individual feed events or the spacing of aggregates of feed events (i.e. meals).

The ingestion rate may change with feeding conditions but the extent of this change varies with species. Thus the ingestion rate of rats remains relatively constant when they are fed *ad libitum* (Le Magnen, 1992) but increases for a short time immediately following periods of food deprivation (Le Magnen, 1992). The ingestion rate of the rabbit (Geiselmann et al., 1980) varies diurnally and is highest in the period immediately following dark. The biting rate and bite size of large domesticated herbivores remain relatively constant (sheep, Alden and Whitaker, 1970; cattle, Stobbs, 1974) over a range of conditions and only increase when feed is scarce, when body weight is below optimum or when it is unduly cold (Arnold, 1981).

It is not known whether the overall biting or chewing rates of the small fermentative marsupial herbivores that are said to employ a strategy of high throughput (Hume, 1984) are any different to those that select a diet of higher quality (Freudenberger et al., 1989) or those of larger grazing herbivores.

The timing of feeding events

In most vertebrate fermentative herbivores food intake is discontinuous and feeding events alternate with non-feeding intervals. The spacing between feeding events may be influenced either by longer term changes based on the deil cycle (Arnold, 1981; Metz, 1975; Deswysen et al., 1989;1993; Champion et al., 1994) or by short term energostatic physiological responses. Further, the operation of short term physiological responses based on palatability or satiety may result in the grouping of individual feed events into 'meals' i.e. the formation of groups of feeding events in which each event is separated from its predecessor by an inter-feed interval of shorter duration than a defined 'criterion' inter-meal interval (Fagen and Young, 1978; Le Magnen, 1992). Thus organisation of the temporal characteristics of feeding behaviour may operate at three heirarchical levels, the spacing of individual feed events, the formation of meals, and the influence of nycterohemerally induced cycles.

Temporal analyses of the spacing of meals show a significant correlation between meal size and the time interval following the meal in a number of species (Snowdon, 1969; Thomas and Mayer, 1968;

Balagura and Coscina, 1968; Duncan et al, 1970; Weipkema, 1971; Prudhon, 1972; Hirsch, 1973; Panksepp, 1978; Sanderson and Vanderweele, 1975; de Castro, 1975;1978; Davies, 1977; Wolf and Hainsworth, 1977; Hirsch et al., 1978; Ardisson et al., 1981; Kraley, 1981; Marcilloux et al. 1985; Rosenwasser et al. 1981; Le Magnen, 1992). Moreover, there are convincing correlations between circulating levels of energostatic metabolites and hormones and the duration of inter-meal intervals (Le Magnen, 1992).

Conversely, in these same species, the duration of a 'meal' is thought to be the outcome of an interaction between the palatability of a particular food and its satiating capacity (Le Magnen, 1992) and not to be directly influenced by circulating levels of energostatic metabolites i.e. the level of hunger (Le Magnen, 1992). This hypothesisis is supported by temporal analyses of feed events within meals e.g. in the satiety curves of rats there is no significant correlation of preceeding feed event duration (or size) with inter-feed interval (McCleery, 1977).

Thus, at the meal/ inter-meal interval level of temporal organisation, energostatic budgeting takes place in two distinctive respects in monogastric enzymatically digesting species (Le Magnen, 1992). Firstly the general positive relationship between the size of the meal and the duration of the interval between the current and the next meal, indicates that the timing of the start of the next meal, i.e. the spacing between meals, may depend on declining levels of energostatic metabolites (e.g glucose) obtained from the foregoing meal generating a hormonal cue (e.g. insulin) that increases the sensation of hunger. Secondly, under normal ad libitum feeding conditions, the duration of a meal is independent of the caloric deficit that was incurred in the preceding intermeal interval but driven instead by hormonal outcomes related to the palatability of the specific food that is being consumed causing changes in the relative levels of satiety.

In cattle however, meal duration and intermeal interval are 'hardly correlated' (Metz, 1975) and the pattern of meal length and intermeal interval can be 'ascribed entirely to diurnal rhythmicity in meal duration' (Metz, 1975). Again in the horse Laut et al. (1985) found no correlation between the durations of 'meals' that were based on a variety of arbitrary time criteria, and their associated intermeal intervals, and concluded that meals were 'an inappropriate term for use with grazing animals'. Similarly, other workers have failed to show any correlation between meal size and intermeal interval in sheep and cattle (de Jong, 1986), pigs (Auffrey and Marcilloux, 1983) or guinea pigs (Hirsch, 1973).

The behavioural differences between omnivores and herbivores may result from fundamental differences in the physiology of carbohydrate anabolism, and the timing of the metabolic outcome of feeding events (de Jong, 1986). Fermentative digestion, i.e. bacterial cellulolysis, is significantly slower than enzymatic digestion as a consequence of the generation time of the fermentative bacteria (Mertens and Ely, 1982). Moreover the concentration of the cellulolytic micro-organisms that 'catalyse' fermentation rises as digestion proceeds producing 'autocatalytic' (Bischoff, 1966) reaction kinetics that are significantly different from those of 'catalytic'enzymatic digestion in that reaction rate increases as substrate decreases (Penry and Jumars, 1987). These two factors together result in lower rates of change in (de Jong, 1986) the circulating digestive metabolites that may influence hunger and thus short term energostasis sensu Le Magnen (1992). Such low rates of change may impair the grouping of feeding events into meals (Weikempa, 1971) and thus inhibit the institution of any correlation between meal duration and postmeal interval (Le Magnen, 1992; Thomas and Meyer, 1968).

At the highest level of temporal organisation the timing of feeding events or meals may be influenced by the operation of nycterohemeral cycles that effect the 'utility' (McFarland, 1978) of feeding as well as that of a variety of other behaviours. At the simplest level of nycterohemeral organisation such cyclic changes may result in a simple sinusoidal change in utility through the deil cycles and lead to similar changes in feeding rate. However such cyclic changes may affect a number of behaviours and bring about more complex interacting temporal patterns. Thus for example whilst it had previously been assumed that circadian rumination patterns were a result of a single sinusoidal rhythm component of 12 h frequency (Murphy et al., 1983) recent finite Fourier transform analysis of ruminating behaviour in heifers has demonstrated complex combinations of superimposed nycterohemeral rhythm components (Deswysen et al., 1989; 1993). On the basis of this analysis Deswysen et al. (1989) concluded that eating and ruminating activities were alternate activities that 'competed' for the allocation of mastication time.

Similarly, the temporal variation of energostatic regulatory hormones that are influenced both by nycterohemeral cycles and by short term feedback mechanisms may also become complex. Thus there is evidence that insulin levels, already implicated in the short term control of food intake (i.e. in the spacing of meals) in small enzymatically digesting laboratory animals such as the rat (Le Magnen, 1992), may also be affected by longer term regulation (i.e. nycterohemeral variation in hunger) (Le Magnen, 1992). Differences in the responsiveness of hormones such as insulin to the two influences may account for differences in feeding behaviour, thus nycterohemeral variation of insulin levels may be of greater importance in fermentative herbivores (de Jong, 1986; Lesault, 1991) than in monogastric omnivores.

Under conditions where hunger drive is generated wholly nyterohemerally and not modulated by short term responses to digestive consequence, short term energostasis may nevertheless be influenced by mechanisms based on satiety and palatability (Morley, 1995). These mechanisms, though poorly developed in monogastric enzymatically digesting species (Le Magnen, 1992), may be more refined in herbivores (Farningham et al., 1993).

Concurrent analyses of the extent of meal formation, the degree of correlation between feed event (or meal) duration and following inter-feed (or inter-meal) interval (appendix 2), and the nyterohemeral distribution of feed event duration under various feeding conditions may be used to give an indication of the relative influence of the various levels of temporal organisation on the feeding schedules of small herbivores.

The timing of defecation

Defecation is a temporally discrete process whose timing may be important both to fermentative activity within the hindgut and to water conservation. The link between voiding activity and digestive strategy is particularly evident in those animals which practice caecotrophy (Bjornhag, 1994), a process in which particularly nutrient-rich material is accumulated in the caecum, periodically voided, then promptly reingested. The question remains as to whether the caecal emptying occurs randomly or in a manner that is energostatically predictable. A similar question applies to the timing of the periodic reductions in the bulk of hindgut fermenting material (i.e. caecal emptying) and defecation in non-caecotrophic hindgut fermenting herbivores.

Laboratory studies have been conducted on the timing of defecation in tammars (Warner, 1981b) but field studies of this type are precluded in many small fermentative herbivores by the fact that eliminative behaviours are not easily identifiable from a distance. Moreover such studies do not give an insight into the dynamics of caecal emptying. Provided the inflow of digesta from the small gut is relatively constant (Freudenberger and Hume, 1992) then assessment of temporal variations in wet digesta content of the hindgut gut components may give some indication of overall temporal trends of defecation, their relationship to feeding behaviour and to caecal function.

Conclusion

The strategies that are used by a small herbivore to reduce the restrictions of grazing herbivory may include changes to the efficiencies of any of those physiological processes which influence the animal's 'digestive capacity', such as the ingestion, mastication and digestion of food, as well as those behaviours which influence the selection of food and the timing of feeding. Although the overall digestive outcome that results from the sum of these strategies may be readily assessed from the *in vivo* digestibility of various diets, such estimates do not give insight into the manner that a given species adapts to its nutritional environment i.e. its ecophysiology. A wide-ranging investigation of behavioural, physiological and anatomical parameters is necessary to gain an understanding of the importance of particular strategies to particular species.

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Chapter 3

The temporal character of feeding behaviour in captive tammar wallabies *Macropus eugenii* Desmarest.

R. G. Lentle, K. J. Stafford, M. A. Potter, B. P. Springett and S. Haslett.

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The temporal character of feeding behaviour in captive tammar wallabies *Macropus eugenii* Desmarest.

R. G. Lentle [1], *K. J. Stafford* [2], *M. A. Potter* [1], *B. P. Springett* [1], *S. Haslett* [3]

[1] Department of Ecology, Massey University, Private Bag 11222, Palmerston North, New Zealand.

[2] Department of Veterinary Clinical Sciences, Massey University, Private Bag 11222, Palmerston North, New Zealand.

[3] Department of Statistics, Massey University, Private Bag 11222, Palmerston North, New Zealand.

Abstract

Four tammar wallabies, maintained in a fixed 12 h. light/ 12 h dark cycle, were fed ad libitum, one of three foods, of differing nutrient density and fibre content, consecutively, each for a period of two weeks. During the second week, food consumption was assessed daily and the temporal feeding pattern was monitored by visible and infra-red video recording. Apart from a short rest period around noon, feeding continued throughout the 24 hour cycle peaking crepuscularly. Total daily feeding time corrected to metabolic body weight was significantly longer, but dry matter intake corrected to metabolic body weight was significantly lower than that of larger macropod species, indicating greater investment in chewing. Feed event duration, inter-feed event interval, rate of feeding, and dry matter intake all increased significantly on pelleted foods of low nutritional density. Rate of feeding and feed event duration increased significantly on diced carrot such that dry matter intake was not significantly different to that on high quality pelleted food. Survivorship curves of inter-feed event intervals were predominantly linear. This and the consistently higher positive correlations between the duration of individual feed events and inter-feed event intervals, than between meals and inter-meal intervals, indicated a nibbling rather than a meal based feeding strategy. Levels of correlation of feed event duration with inter-feed event interval were generally low but there was a significant increase in positive correlation when food of lower quality was given. The duration of successive feed events tended to increase on low quality and decrease on high quality food more consistently than did successive inter-feed event intervals.

Introduction

The investigation of feeding behaviour by the analysis of temporal feeding patterns (Richter 1927; Weipkema 1971; Panksepp 1978; Le Magnen 1992), is non invasive and convenient for field application. In some species the relationship between the duration of 'meals', i.e temporally discrete (Slater and Lester 1982) groups of individual feeding events, with associated non feeding intervals, i.e the intervals separating such meals, is thought to reflect the yield of digestive product (Weipkema 1971) and to be sensitive to the cost of access to a meal i.e. the economic structure of the habitat (Collier 1985). Thus when the cost of procurement of a meal is increased for laboratory rats both the size of meals and the interval duration between them increased (Collier 1985; Johnson and Collier 1987). A positive relationship between the size of a meal and the time interval before a subsequent meal has been reported in a variety of species (Duncan et al. 1970; Prudhon 1972; Sanderson and Vanderweele 1975; Wolf and Hainsworth 1977; Ardisson et al. 1981; Laut et al. 1984; Marcilloux et al. 1985; Le Magnen 1992). This relationship is thought to be produced by a time dependant decline in the levels of circulating energostatic metabolites that are obtained from the initial meal leading to the initiation of a subsequent meal (Le Magnen 1992)

Although analysis of the temporal patterns of feeding may be unable to provide answers to complex questions of causation (Booth 1990), it is nevertheless useful in evaluating the extent to which feeding behaviour may vary in response to short term changes in energostatic metabolism. (Le Magnen 1992). Thus for example a number of studies have shown little evidence of correlation between meals and inter-meal intervals in large herbivore species (Metz 1975; Laut 1984) indicating that the formation and spacing of meals in relation to their metabolic conseqences may play little part in these animals energostatic strategies.

Differences in the allometric scalings of mass specific energy requirements and of gut capacity (Demment and Van Soest 1985) are thought to render herbivory tenuous in small herbivores (Cork 1994) and to necessitate a high throughput of food (Illius and Gordon 1992; Justice and Smith 1992) with maximal gut fill (Penry and Jumars 1987; Demment and Greenwood 1987). These conditions, in conjunction with the relative tardiness of the fermentative process (Penry and Jumars 1982; Mertens and Ely 1982), are likely to result in low rates of change in the levels of circulating digestive metabolites and thus may prevent the grouping of feeding events into meals (Weipkema 1971) necessitating a greater reliance on predetermined cycles of hunger or satiety than that reported in cattle (Metz 1975).

There are a number of problems particular to the temporal analysis of the feeding patterns of herbivores. Firstly, if feeding is viewed as any process that increases the surface area of food exposed to the action of fermentative microbial guilds (Pond et al. 1984; Wright and Vincent 1996) then this must include chewing during rumination (Mertens and Ely 1982) as well as chewing during feeding. Secondly, whilst survivorship analysis, in which the intervals between individual feeding events are plotted as a log survivor function, has been widely used to decribe the probability of meal commencement and obtain an 'objective' (Berdoy 1993) estimate of 'criterion interval' (Fagen and Young 1978) (the interval by which intra-meal intervals may be distinguished from inter-meal intervals) its applicability to the feeding patterns of small fermenting herbivores may be limited. Survivorship analysis uses a graphic configuration in which time t on the abscissa corresponds to a point on the ordinate that indicates the log of the number of intervals whose lengths are greater than t. On such a graph, randomly distributed events will plot as a straight line (Fagen and Young 1978) and it is assumed that any curved or broken stick configuration in the plot results from overall differences in the frequency of occurrance of inter and intra meal intervals (Fagen and Young 1978). However under conditions when feeding behaviour is relatively prolonged, such as in herbivores, it is probable that similar discontinuities may result from nycterohemerally induced cyclic change in hunger such as reported in the rabbit (Lesault et al., 1990). Finally, a herbivores food intake is determined not only by time spent foraging, but also by its bite rate and bite size (Mayes and Duncan 1985). The latter two variables have been found to remain relatively constant over a wide range of feeding conditions in cattle (Stobbs 1974) and in sheep (Allden and Whittaker 1970). Thus time spent feeding may give a useful measure of feed intake, particularly in herbivores whose food has relatively constant physical characteristics.

Macropod feeding behaviour is not complicated by rumination (Freudenberger and Hume 1992). Macropod digestive physiology may be relatively unsophisticated in that throughput rate does not vary with fibre content (Freudenberger and Hume 1992). Thus compensation for differences in food quality may be principally dependent on change in feeding behaviour. This is particularly likely in the tammar wallaby (*Macropus eugenii* Desmarest) whose enteric neural control is predominantly intramural there being no evidence of extrinsic modulation of myo-enteric activity by the vagus (Wyburn and Richardson 1989). Chewing rates when browsing, and when grazing, have been found. (Lentle et al. Chapter 5) to be relatively constant in free ranging tammar wallabies. Feeding patterns of tammar wallabies have been studied previously (Warner 1981a; 1981b) but only in respect of their day to day variation.

The purpose of this paper is to investigate the behavioural mechanisms which allow the tammar wallaby to respond to differences in the nutritional density and fibre content of food.

Method

Capture

Four tammar wallabies were captured at Lake Okataina Outdoor Centre (38° 06' S 176° 26' E) in the Rotorua district of North Island New Zealand using the method of Lentle et al. (1997). Tammars have inhabited the Rotorua area since their release in 1912 (Poole and Johns 1970) and the bush environs of the Outdoor Education Centre since its construction in 1976. In this latter site they have become habituated to human presence.

Housing and feeding regime

Animals were housed individually in windowless screened covered pens (4 x 2 m) with concrete floors to which they were assigned randomly. Artificial lighting was provided by two 100 watt bulbs for a fixed photo-period cycle of 12 hours dark and 12 hours light. Each pen was provided with a 400 mm x 200 mm x 10 mm feeding tray and a circular 60 mm deep drinking dish placed 2.5 m from the feeding site. All animals were fed once daily with a quantity of food which exceeded the previous days voluntary food intake by at least 50%. Tammars are messy feeders (Warner 1981a) and we were unable to find a method for obtaining ongoing temporal recordings of meal size that would not unduly influence the feeding habits of a wild caught animal. Food consumption was measured once daily by weighing food residues which included scattered feed retrieved by systematic search of the pen. In view of the disturbance caused by this procedure, feeding events and inter-feed event intervals occurring immediately prior to and after feeding were excluded from the temporal sequence analysis described below. Food residues were weighed and freeze dried.

Each animal was fed one of three food types, in a random order, consecutively, each for a two week period. Each animal was weighed at the commencement and termination of each period. Each food type was given for one week prior to the observation period in order to allow the animals to become accustomed to it. In the second week, animals were monitored by continuous video recording using a Panasonic Model AG 6730 recorder and a Panasonic WV BP 312C infra-red/ visible spectrum video recorder for one week. Dark cycle recording was augmented by infra-red illumination from two 100 watt infra-red lamps.

Food types

Two pelleted food types were given, a high calorie density low fibre food (90% milled maize and 10% milled barley), and a low calorie density high fibre food (10% milled maize 10% milled barley and 90% milled barley straw). All components were milled to a screen size of 4mm. Pellets of both food types were of identical size (7 mm x 15 mm) and colouration. A third food, fresh carrots diced to maximum dimensions of 15 mm by 15 mm, was low in calorie and in fibre content by virtue of high water content.

A previous feeding trial (Lentle and Stafford unpublished data) had demonstrated that 7 mm diameter x 15 mm long food pellets were eaten only in the quadrupedal posture regardless of formulation, whereas 15 mm diameter x 20 mm long pellets were sometimes grasped and eaten in the bipedal posture. Likewise, carrot diced to less than 15 mm x 15 mm was eaten in the quadrupedal position whereas larger portions were sometimes eaten in the bipedal posture.

Nutrient composition of freeze dried replicated samples of the three foods are shown in table 1.

Video analysis

All recordings were reviewed by the same person (R. L.). It was noted in all cases that ingestion of food took place only in the quadrupedal posture without use of forelimbs, vindicating the previous findings (Lentle and Stafford unpubl. data). For the purposes of this analysis, a feed event was defined as a period of time spent ingesting food in the quadrupedal posture. The rare event when an animal continued to chew and swallow previously ingested food after rising to the bipedal posture was not counted as part of a feed event.

Statistical analyses

Unless otherwise stated, all statistical calculations were carried out in SYSTAT (Wilkinson 1990) statistical software package. Feeding rate curves were calculated and plotted using SAS (SAS 1989) for each animal and for each seven day feed period by totalling feed event durations for consecutive half hour intervals over 24 h. Observation densities i.e the temporal frequency of occurrence of particular feed event durations and inter-feed event interval lengths during each seven day period were plotted as Epanechnikov kernel smoothed plots (Silverman 1986) in a 24 h temporal sequence. The Epanechnikov method employs a non parametric algorhythm to smooth observation densities, producing a two dimensional observation density contour plot of duration vs time of occurrence.

Daily totals of time spent feeding were calculated to run from the once daily time of food renewal. Consecutive daily totals of time spent feeding, amount eaten and feeding rate on each of the three food types were compared directly by one way repeated measures ANOVA. Log transformation of feed event durations and of inter-feed event intervals produced distributions which showed only minor departures from normality (fig. 1). However, because there were hundreds of points involved in each such regression, many of the formal tests (Lillifors tests) for non normality gave statistically significant results even though the distributions were symmetric. When log converted data were used in regression, residuals were also checked for normality with similar conclusions. Results from such parametric analyses were therefore cross checked using alternative statistical techniques that did not require distributional assumptions i.e. discriminant analyses.

Feeding data were partitioned into an 'AM' segment comprising feeding events taking place between midnight and midday and a 'PM' segment comprising events taking place between midday and midnight.

Log transformed data were assessed, by animal and by food type, for correlation between feed event duration and following inter-feed event interval. Feed event durations, meal durations, inter-feed event intervals and inter-meal intervals were compared by doubly and by triply repeated measures ANOVA of log transformed data in SAS (SAS 1994).

Whilst univariate analysis permits an overall view of changes in feed event durations and in inter-feed event intervals that are brought about by changes in food characteristics or time, these changes may not arise solely from differences in the relationship between feed events and their preceding or following inter-feed event intervals. Thus for example, the timing of the long midday resting period may influence the outcome in an analysis of differences in spacing of feeding events occurring in the 'AM' and the 'PM' feeding peak. ANOVA based on pre or post feed event ratios (Fagen and Young 1978), whilst restricting the analysis to associated events, does not permit an overview of the relative contributions of the variations in intervals and feed events to the outcome. Multivariate discriminant analysis, apart from being less sensitive to distributional assumptions, allows direct assessment of the relative contributions of various parameters including the relative durations of feeding events and their associated intervals, moreover this method may overcome the statistical difficulties associated with multiple univariate tests (Hummel and Sligo 1971).

Discriminant analyses were carried out using the following log transformed variables; first feed event duration, first post feed interval, second feed event duration, second post feed interval. Variables derived from quantity of food eaten were not included in the discriminant analysis on the basis that the effect of the significant differences in quantity of foods eaten would overshadow the effects of behavioural measurements that were based solely on time (Geiselman et al. 1980). Two analyses were run, the first based on food type, the second on temporal peak (see below).

The same analyses were also performed following the grouping of feed events into 'meals' on the basis of 'bout criterion interval' i.e the interval discriminating intra-meal from inter-meal intervals (Slater and Lester 1982). Thus 'meal duration' was the duration of a consecutive set of feed events that were each separated by an interfeed interval of lesser duration than the criterion interval.

The broad limits of bout criterion interval were derived by assuming that any broken stick profile in the survivorship curves of inter-feed event intervals results from the sum of two exponential processes, an initial steeper intra-meal segment plus a slower less steep inter-meal segment and that the criterion interval is given by the point of intersection of the two (Sibley et al. 1990). A number of studies have demonstrated sensitivity of correlations between 'meals' and 'inter-meal intervals' to small changes in this parameter (Panksepp 1978; Metz 1975). We explored the manner in which this correlation changed with increase in the value of the criterion interval and averaged the results graphically using a non parametric technique. Thus analyses based on meals were repeated using a number of different values of criterion interval. Pearson coefficients of the correlation between meal duration and inter-meal interval for various values of bout criterion interval for each animal and feed were plotted with overall 'LOWESS' smoothing (Cleveland 1979).

Results

Temporal sequence

Epanechikov kernel smoothed observation density plots of log feed event duration over a 24 h period for each animal and each food type (fig 2 a-c) showed two crepuscular peaks in feeding behaviour. (Feeding rate curves showed similar distributions but, for the sake of brevity are not shown here). The observation density plots showed little variation in the timing of early and late nocturnal crepuscular peaks either between animals or between foods and a tendency for the longer feed event durations to occur at peak observation density. This latter tendency was more evident in the curves obtained from animals on poorer quality food. There was no obvious tendency for longer feed events to occur more frequently near the commencement or termination of feeding activity as could result, for example, by prompt filling of gut after daytime emptying.

Survivorship curves

The survivorship curves of log feed event duration were predominantly linear for all animals and all food types. Similarly, with the exception of two curves from tammars maintained on high quality foods, the survivorship curves of log inter-feed event intervals (fig 3) were predominantly linear.

Univariate analyses

Total daily amounts ingested

Average daily dry matter intakes (DMIs) and DMIs corrected for metabolic body weight, for each animal maintained on each food are shown in table 2. The overall average of diced carrot consumed per 24 hrs was 712.0 ± 28.8 g. wet weight.

A one way doubly repeated measures ANOVA for six consecutive daily DMIs for the three foods of each of the four animals (table 3), showed significant differences between the daily DMIs on the two pelleted foods but no significant difference between those on high quality pelleted food and on the cubed carrot food. A graph of the daily quantities of individual nutrient components ingested calculated from the averaged DMIs of all four animals for each food type (fig 4) shows no tendency for the quantities of any given component to be similar with different food types, suggesting that nutritional compensation is not based on a single nutrient component.

Temporal budgeting

One way doubly repeated measures ANOVAs of six consecutive daily totals of time spent eating the three foods by each of the four animals (table 3) showed significant differences between the daily times spent eating the two pelleted foods and significant differences between the daily time spent eating the carrots and each of the pelleted foods. Average time spent feeding per day on diced carrots, scaled to metabolic body weight, was 7885 s./ day / $kg^{0.75}$.

Average daily eating rates.

Average daily feeding rates measured in grams wet weight per second of feed event duration (table 2) were calculated from total daily consumption and cumulative total daily feeding time. One way doubly repeated measures ANOVAs of six consecutive daily rates on each of the three foods for each of the four animals (table 3) showed the eating rate on the lower quality milled pelleted was significantly higher than that on the higher quality milled pelleted food, and that the eating rate on the diced carrot food was significantly higher than that on both pelleted foods.

Feed event duration, inter-feed event interval and correlation between feed event duration and post feed interval.

Overall averages of feed event durations and inter-feed event intervals are shown in table 4. Doubly repeated ANOVAs of log transformed feed event duration (Table 5) and of intervals (Table 6) showed that feed event duration was significantly longer on poorer quality food than on the high quality food as were (post event) inter-meal intervals i.e feeding events tended to be longer and spaced at greater distances apart. Triply repeated ANOVAs of log transformed feed event length, and (post event) inter-feed event intervals showed no overall significant differences in the duration ($F_{1,3} = 0.27$, $p = 0.638$) or in the spacing between ($F_{1,3} = 4.26$, $p = 0.104$) feed events occurring in the early morning (AM) and the late evening (PM) feeding peaks or in the duration ($F_{2,6} = 0.57$, $p = 0.595$) or spacing ($F_{2,3} = 1.16$, $p = 0.374$) of feed events on particular food types in the two peaks as evidenced by significant interaction terms between peak and food type.

Pearson correlation coefficients of the relationship between log transformed feed event duration and the associated log transformed post feed interval (table 7) were consistently positive for all animals when they were maintained on diced carrot but not on other foods. One way ANOVA of z transformed correlation coefficients showed significant overall variation with food type ($F_{2\,9} = 17.341$, $p = 0.001$) with significantly greater positive z scores when animals were maintained on diced carrot (Tukey probabilities 2/3 = 0.002 and 1/3= 0.002) than when they were maintained on either pelleted food type (Tukey probability 1/2= 0.978).

Weights of animals

The weights of the animals did not change over any of the three periods when the different types of food were fed.

Multivariate (Discriminant) analyses.

The results of three discriminant analyses, each between two of the three food types, based on duration of a single feed event and the associated (post-meal) inter-feed event interval using pooled data from all animals are shown in table 8a and 8b. The canonical discriminant functions of each analysis showed greater loading of feed event duration than of inter-feed event interval, indicating a more consistent difference with food type between feed event durations than between inter-feed event intervals.

The results of a similar analysis based on the duration of two successive feeding events and their (following) inter-feed event intervals, are shown in table 9a and 9b. The grouping into sets of two successive events with their associated inter-feed event intervals necessarily reduced the number of cases in the data set by half. Thus a further analysis of single feed events and following intervals based on a similarly reduced data set (alternate successive events) was conducted (table 10a and 10b) for the purposes of comparison. Discrimination based on the sequence of these four events is more successful than that based on only two events even when cross validation is used. The loadings of the canonical discriminant function are again based primarily on feed event duration but the loadings on both inter-feed event intervals are also significant. In comparisons between food one and two and between food one and three, i.e. comparisons between low and high quality foods, the loadings of both feeding events are higher than those of the inter-feed event intervals. Thus discrimination is again based primarily on feed event length plus a tendency for consecutive feed events to be of similar size i.e either long or short.

Discrimination between the temporal feeding patterns of the two low quality food types is less successful and little different from that based on a single feeding event and inter-feed event interval. The loadings of the inter-feed event intervals are of more or less equal value in all comparisons

Grouping of feeding events by 'criterion interval'

Any changes in the slopes of the inter-feed event survivorship curves occurred during the period between 100 and 2000 seconds (fig 3). Thus feed events were grouped into meals based on criterion intervals of either 100, 200, 300, 600, 1000, 1500 or 2000 secs and reanalysed in the manner described above. There was a generally lower degree of positive correlation between log converted 'meal duration' (the duration of a set of consecutive feed events each separated by an interfeed interval of lesser duration than the criterion interval) and log converted 'inter-meal interval' (the interval of greater duration of than the criterion interval which terminated the run of feed events and inter-feed intervals comprising the meal) than between feed event duration and inter-feed event interval, moreover the degree of positive correlations tended to decrease as criterion interval increased (fig 5). Again whilst, on doubly repeated measures ANOVA, there were significant differences, with food type, in log 'meal durations' that were derived using small criterion intervals, the results were generally less significant than those obtained with individual feed events (table 5). Again on doubly repeated measures ANOVA, there were significant differences with food type in inter-feed event intervals but not in 'inter-meal intervals' (table 6). Discriminant analyses of the types described in the previous section were consistently less successful when based on 'meal duration' and 'inter-meal interval' and canonical discriminant function loadings indicated that comparisons were based solely on meal duration.

Discussion

Time spent feeding, food consumption and feeding rate

The DMI of the poorer quality pelleted food was significantly higher than that of the higher quality pelleted food. This was achieved principally by a change in eating rate, there being no significant difference between total daily time spent eating on the two foods. The total daily wet matter intake of diced carrot was sufficiently greater than that of nutrient dense pelleted foods as to result in a similar dry matter intake to that on the higher quality pelleted food. There was a significant increase both in feeding rate and in total daily feeding time when diced carrots were fed. This suggests that, as in eutherian species, there are limits to the degree that chewing, biting and swallowing rates may be increased because of limitations in muscle contraction rates (Hiiemae 1978).

The high wet weights of diced carrot consumed demonstrate the ability of tammars to ingest large quantities of vegetable matter of low type 3 fracture propagation strength (Vincent 1990). This finding sheds some doubt on the suggestion by Fruedenberger and Hume (1992) that nutritional compensation is restricted by mastication. Their suggestion was based on the lower intake of dried chopped food intake of captive euros (*Macropus robustus erubescens*) and walleroos (*Macropus robustus robustus*) compared with that of finely ground food. Mechanical strength and mode of fracture of grass are effected by drying (Vincent 1983) and feeding dried food precludes selection on a basis of succulence, an important behavioural strategy in drought tolerant species (Nagy et al. 1990).

The total daily time spent feeding by tammars on diced carrots scaled to metabolic body weight (7885 s./ day / $kg^{0.75}$) was significantly higher than that calculated for other larger macropods (free ranging *Macropus rufus*, 2391 s./day/ $kg^{0.75}$; *Macropus giganteus*, 4929 s./ day/ $kg^{0.75}$, based on data from Southwell, 1981 and assuming an average body weight of 26.4 Kg. as reported by Norbury et al. 1989). Average DMIs corrected for metabolic body weight obtained in this study were of the same order as those reported for tammars by Dellow (1982) i.e. lower than those of most other macropod species (Hume 1982), and in line with tammars previously reported low maintenance energy requirements (White et al. 1988; Bridie et al. 1994). These results are not a consequence of low basal metabolic rate as *M. eugenii* has a BMR similar to that of captive *M. rufus* (Dawson and Hulbert 1970) and to most grazer /browser marsupial species (McNab 1978). Thus the unusually long time spent eating taken in conjunction with the low DMI may indicate that 'investment in chewing' (Batzli 1985) is particularly high in this species.

Survivorship curves

The absence of a convex 'finisher' type (Fagen and Young 1978) feed event survivorship curve configuration in which the likelihood of termination rapidly increases after an initial period of high survivorship, such as is found with tammar drinking activity (Lentle et al. in prep), suggests that tammars do not tend to prolong individual feeding events until a deterministic physiological end point, such as gastric distension (Metz 1975), is reached. Rather, the predominantly linear morphology of the survivorship curve of feeding events indicates that feeding events are terminated stochastically (Fagen and Young 1978). This not to say that longstanding effects of greater digesta mass may exert a more uniform influence on the overall probabilities of feed event termination.

Similarly the majority of the inter-feed event interval survivorship curves are almost linear and do not possess a prominent broken stick configuration that may be indicative of two (Sibley et al. 1990) or more (Berdoy 1993) populations of intervals, arising from the influence of factors which terminate intra-meal and inter-meal intervals respectively (Panksepp 1978; Sibley et al. 1990). We have therefore avoided the interpretation of our results in a manner which relies solely on the derivation of a criterion interval from survivorship curves, but have relied also on parametric analyses of ungrouped log-transformed feed event durations and inter-feed event intervals.

Feed event duration and inter-feed event interval

The significant increase in feed event duration, inter-feed event interval and correlation of feed event duration with inter-feed event interval on poorer quality foodstuffs may be viewed as findings similar to those obtained with rats (Collier 1985) which increased their meal size and decreased meal frequency when meal 'procurement cost' was higher. However under our laboratory conditions, the cost of procurement of a meal was more or less constant and any difference in overall cost must have resulted from differences in 'digestion costs' such as the carriage of greater gut loads of digesta.

Changes in feeding pattern with decrease in food quality may result either from change in the centrally integrated feeding drive (Geiselman et al. 1980) or from the local consequences of gut fill (Houpt 1984; Ralston 1984; Forbes 1985). These processes may function relatively independently in tammars as these animals exhibit little or no extrinsic vagal control of the foregut (Wyburn and Richardson 1989). The findings of Freudenberger and Hume's (1992) study of euros and eastern walleroos, where a significant increase in DMI allowed digestible dry matter intake to be maintained, but in the absence of any decrease in the mean retention time of particulate and fluid digesta markers, suggest that a decrease in food quality may bring about an increase in digesta load rather than a change in throughput. Thus, bearing in mind the fermentation times of ingesta, which may displace metabolic consequence from time of ingestion in large herbivores by as much as 60 h (Mertens and Ely 1987), the overall increase in feed event duration on poorer quality food may result from a relatively invariant change in overall feeding drive. On the other hand the more consistent correlation of feed event duration with inter-feed event interval when foods of very low nutrient density are being consumed, may result from local effects that are more evident under conditions of increased gut loading. It should be noted however that the relatively prompt on-flow of fluid phase with respect to solid phase nutrients (Dellow 1979; Warner 1981b) via extrusion from the tubiform forestomach (Dellow 1982) that is thought to occur in macropods may also influence these parameters. The greater correlation between feed event duration and inter-feed interval and greater loading of the gut on lower quality food fit in with the dynamics of Hirakawa's (1997) optimal foraging model and the general hypothesis that with increased reliance on relatively abundant low quality plant resources, herbivore intake becomes increasingly constrained by digestive processes (Westoby 1974; Belovsky 1978; Demment and Van Soest 1985; Illius and Gordon 1991).

The greater significance of differences in feed event duration rather than meal duration with food type indicate that any mechanism which relates the duration of feeding behaviour to nutrient budgeting operates at the level of feeding event rather than of meal duration. The linear survivorship curves of inter-feed event intervals of tammars maintained on low density foods indicate that the likelihood of commencement of eating behaviour is constant and does not vary in a manner that is consistent with the grouping of feeding events into meals. The greater positive correlation between feed events and their associated intervals rather than that between meal durations and their associated intervals indicates that any mechanism which relates the duration of feeding behaviour to its spacing operates at the level of feeding event rather than meal duration.

Taken together these findings support the hypothesis that nutritional strategies of tammars are based on individual feed events rather than on the organisation of feeding events into meals. This finding is similar to that obtained by Metz (1975) for cattle and Laut et al. (1984) for horses, the latter workers concluding 'meals are an inappropriate term for grazing animals'.

Small mammalian herbivores face particular problems in maintaining adequate nutrient intake in the face of higher energy losses resulting from higher surface area to body volume ratios (Demment and Van Soest 1985; Justice and Smith 1992; Cork 1994). Under such conditions a strategy of maintaining a maximal fermentation mass within the forestomach, i.e. a continuous flow reactor strategy, is more likely to be viable than one of intermittent filling and emptying, i.e a batch flow reactor strategy, that is occasioned by the grouping of feeding events into meals (Penry and Jumars 1987) particularly when the foregut is functioning as a plug flow reactor (Penry and Jumars 1987) which requires repeated ingestion of small amounts of food i.e steady flow conditions, in order to maintain a maximal extraction gradient along the length of the reactor (Penry and Jumars 1987). Under such conditions larger meals are less likely to occur and single feed events are more likely to be influenced by an inhibitory response from a full gut segment. In this respect our results support the hypothesis (Freudenberger et al. 1989) that macropod foreguts function as plug flow reactors.

The overall comparison of consecutive feeding events (or meals) and inter-feed event (or inter-meal) intervals by discriminant analysis offers a sensitive method of assessing the effect of food characteristics on the probabilities of both feed event commencement and termination in a manner which is not dependant on distributional assumptions. Thus the tendency for the duration of successive feed events to vary inversely with food quality whilst the duration of inter feed intervals is comparatively invariant, indicates that nutritional compensation as demonstrated by this and similar studies of other macropod species (Foot and Romberg 1965; McIntosh et al. 1966; Forbes and Tribe 1970; Hume 1974; Hollis 1984 reported in Hume 1984; Freudenberger and Hume 1992) is achieved principally by an appropriate adjustment of feed event size rather than short term adjustments in the spacing of feed events. Such an adjustment may be related to palatability or to nycterohemerally driven change in hunger drive. This mechanism resembles that by which feeding events become aggregated in the pattern of satiety obtained in laboratory rats feeding from a skinner box (McCleery 1977). However the mechanism differs greatly from that of energostasis in the rat (Le Magnen 1992) in which control of food intake is achieved by varying the spacing of meals consequent on short term changes in circulating levels of energostatic metabolites and hormones, and where energostasis becomes tenuous if rats are maintained under conditions that permit variation in meal size but not in spacing. This raises the question as to whether energostatic mechanisms based on meal spacing and on feed event size have separately evolved from a basal condition according to dietary habit. Grazing herbivores may lack mechanisms for efficient energostatic spacing of feeding behaviour as specialisation in the consumption of an abundant low quality food requires less responsiveness to short term fluctuations in quality.

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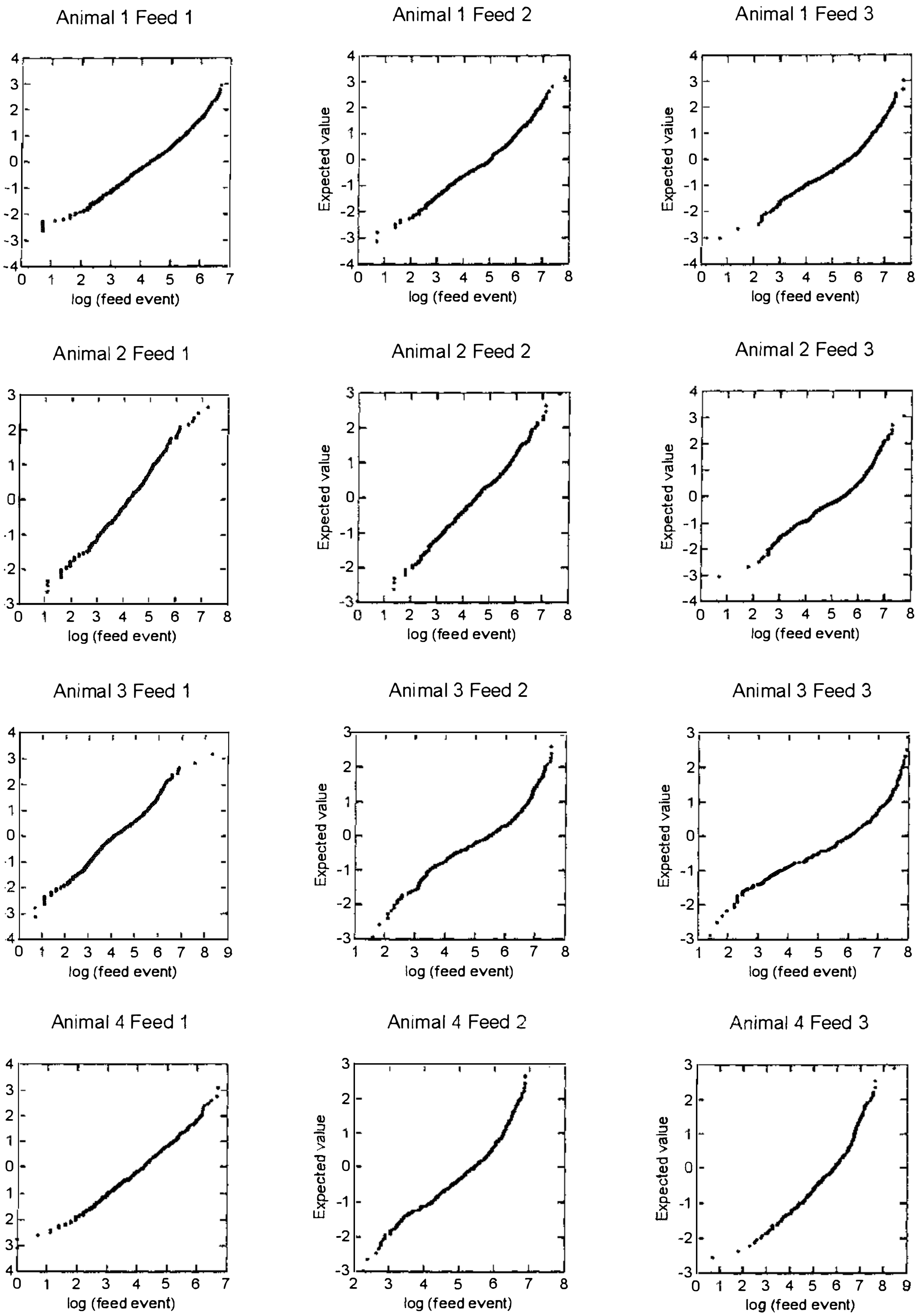
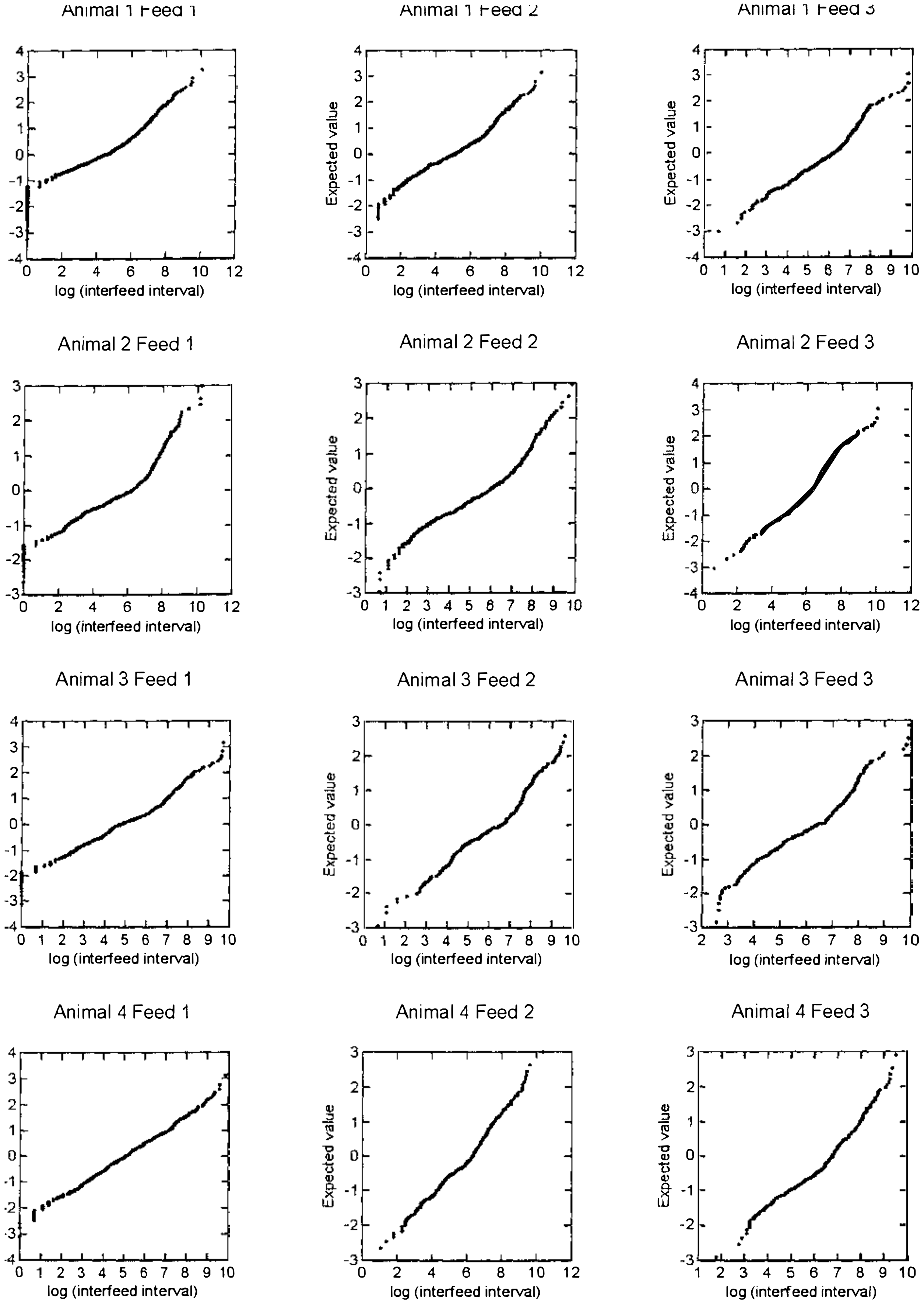
Fig 1. Normal probability plots of feed event duration and inter-feed event interval for bulked data from four tammar wallabies on three different food types. Food 1, high quality pelleted food; Food 2, low quality pelleted food; Food 3, diced carrot.


Animal 1 Feed 1
Animal 1 Feed 2
Animal 1 Feed 3
Animal 2 Feed 1
Animal 2 Feed 2
Animal 2 Feed 3
Animal 3 Feed 1
Animal 3 Feed 2
Animal 3 Feed 3
Animal 4 Feed 1
Animal 4 Feed 2
Animal 4 Feed 3
Expected value
log (feed event)



Animal 1 Feed 1

Animal 1 Feed 2

Animal 1 Feed 3

Animal 2 Feed 1

Animal 2 Feed 2

Animal 2 Feed 3

Animal 3 Feed 1

Animal 3 Feed 2

Animal 3 Feed 3

Animal 4 Feed 1

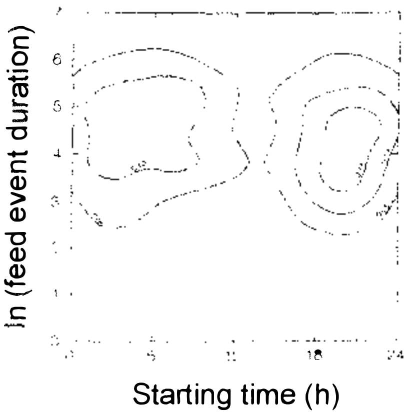
Animal 4 Feed 2

Animal 4 Feed 3

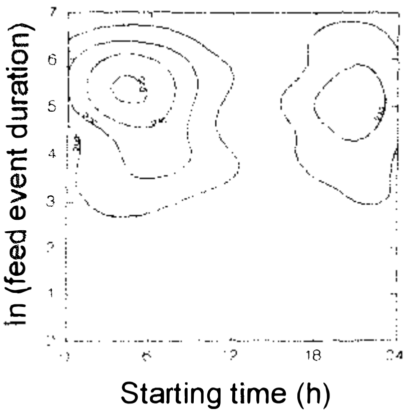
Fig 2. Epanechikov* kernel plots of feed event durations of four captive tammmar wallabies maintained on three food types. Feed 1, high quality pelleted food; Feed 2, low quality pelleted food; Feed 3, diced carrot.

*The Epanechnikov method employs a non parametric algorhythm to smooth observation densities, producing a two dimensional plot of density contours.

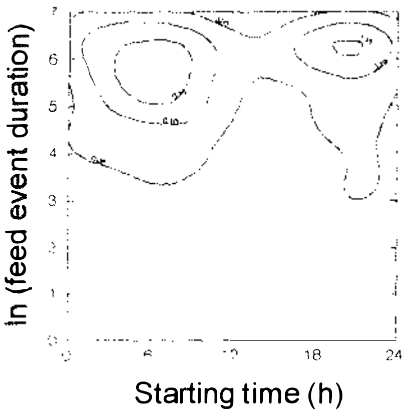
Animal 1 Feed 1



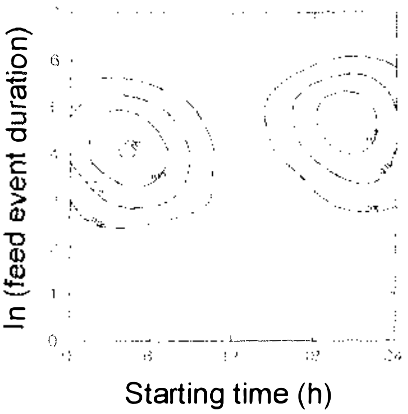
Animal 1 Feed 2



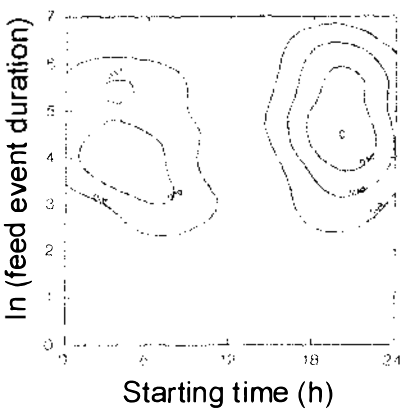
Animal 1 Feed 3



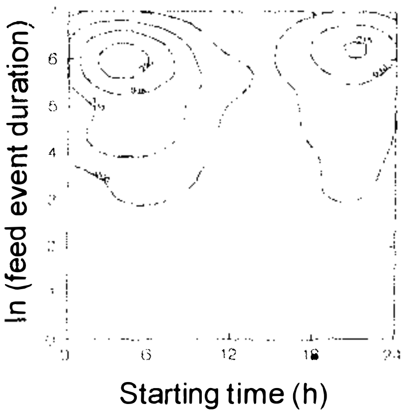
Animal 2 Feed 1



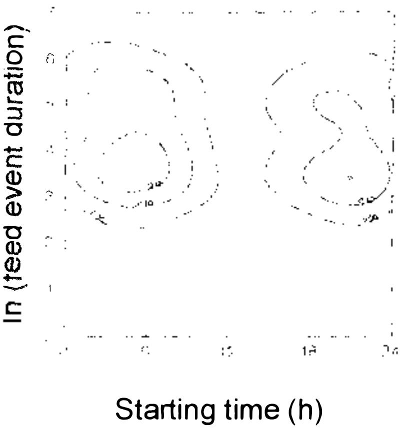
Animal 2 Feed 2



Animal 2 Feed 3



Animal 3 Feed 1



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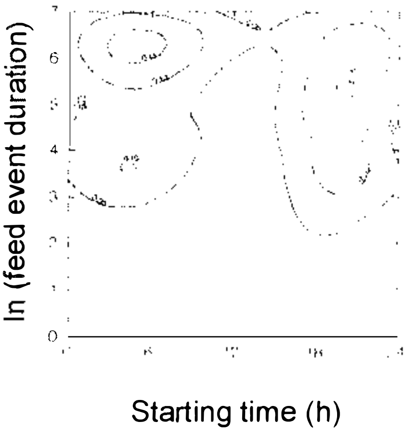
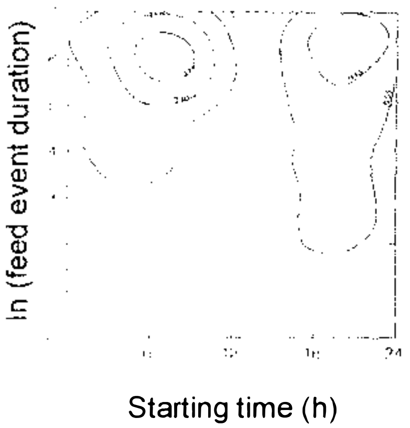
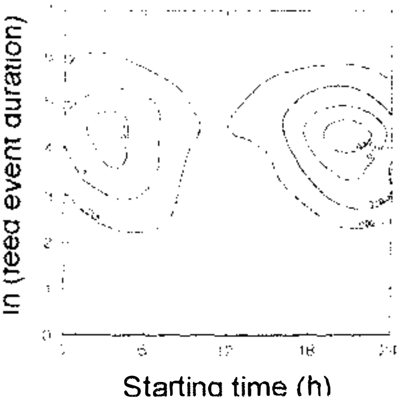


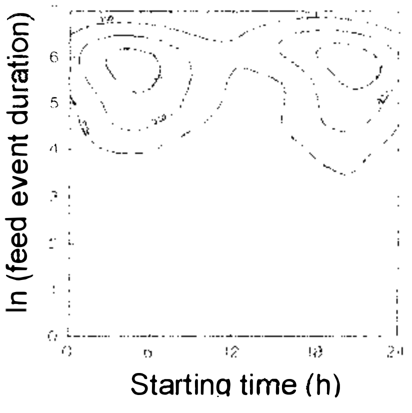
Animal 3 Feed 3



Animal 4 Feed 1



Animal 4 Feed 2



Animal 4 Feed 3

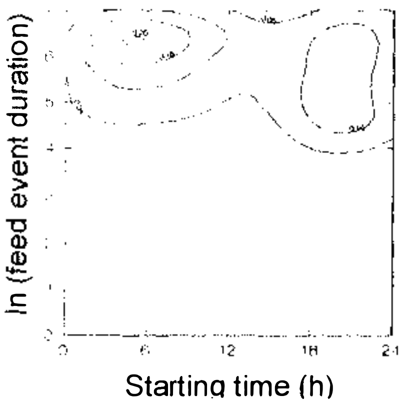


Fig 3. Survivorship curves of inter-feed intervals for four captive tammar wallabies maintained on three different food types. Feed 1, high quality pelleted food; Feed 2, low quality pelleted food; Feed 3, diced carrot.

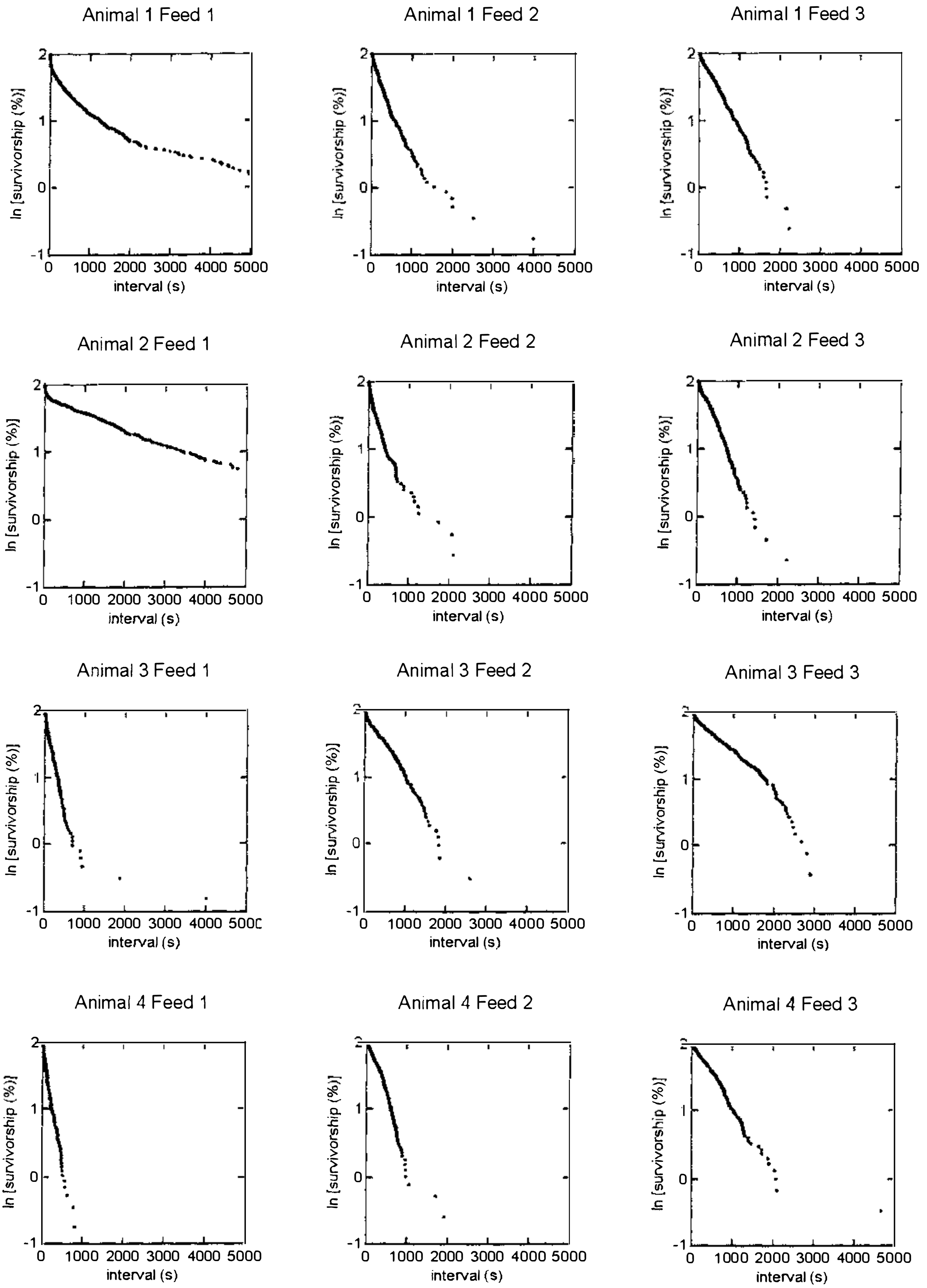

Animal 1 Feed 1
Animal 1 Feed 2
Animal 1 Feed 3
Animal 2 Feed 1
Animal 2 Feed 2
Animal 2 Feed 3
Animal 3 Feed 1
Animal 3 Feed 2
Animal 3 Feed 3
Animal 4 Feed 1
Animal 4 Feed 2
Animal 4 Feed 3
ln [survivorship (%)]
2
1
0
-1
interval (s)
0
1000
2000
3000
4000
5000

Fig 4. Histogram of average daily amounts of dry matter in grams per 24 hours consumed by four tammar wallabies showing relative proportions of reducing sugar, neutral detergent fibre and nitrogen. . Feed 1, high quality pelleted feed; Feed 2, low quality pelleted feed; Feed 3, diced carrot.

▒ , total reducing sugar; ▦ ,total cellulose; ■ , total hemicellulose; ⬚ , total lignin;

⬚ ,total nitrogen

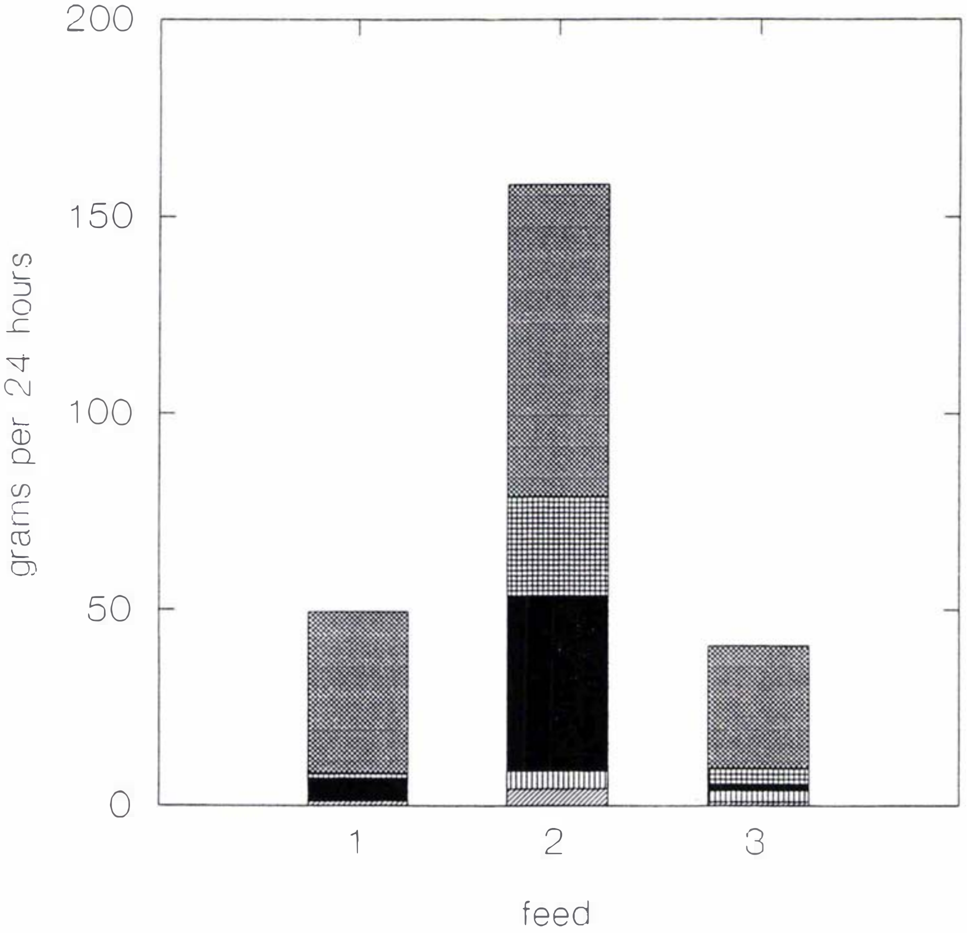
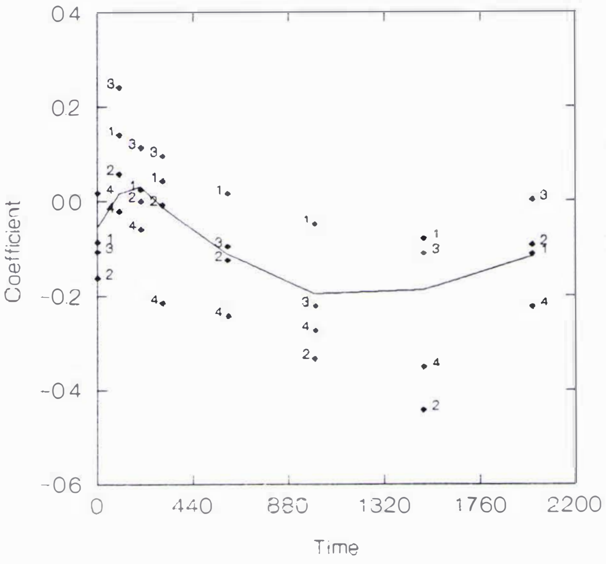
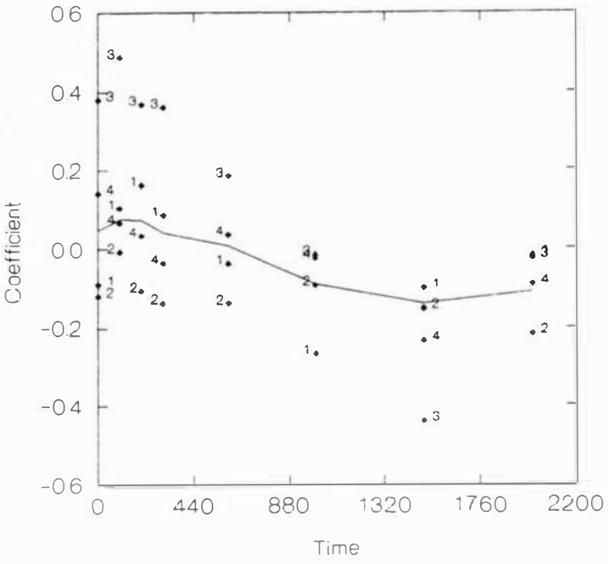

200
150
100
50
0
grams per 24 hours
1
2
3
feed

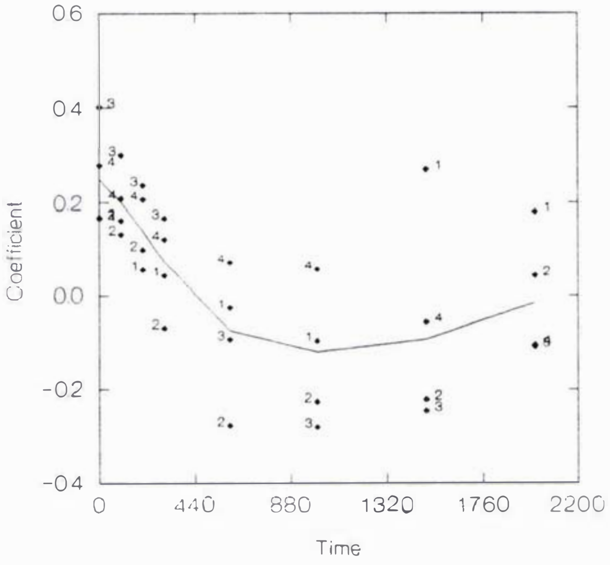
Fig 5. Plots of variation of Pearson correlation coefficient with choice of 'interval criterion'* for bulked data from four animals that were each fed consecutively on three types of food; Feed 1, high quality pelleted food; Feed 2, low quality pelleted food; Feed 3, diced carrot. Plot points are coded with animal number. *Duration of the time interval that is used as a basis for separating inter-feed from inter-meal intervals.



Feed 1



Feed 2



Feed 3

Table 1. Nutrient content of foods

	High quality pelleted food	Low quality pelleted food	Cubed carrot food
Nitrogen (g %)	1.57 ± 0.02	1.95 ± 0.01	1.27 ± 0.08
Gross energy (Kj/g)	18.48 ± 0.07	18.49 ± 0.12	17.05 ± 0.21
Neutral detergent fibre (g%)	10.12 ± 0.67	33.4 ± 0.95	11.9 ± 1.03
Acid detergent fibre (g %)	12.03 ± 0.11	13.36 ± 0.38	9.41 ± 0.87
Lignin (g %)	0.31 ± 0.03	2.09 ± 0.08	4.07 ± 1.11
Hemi-cellulose (g %)	8.09 ± 0.56	20.04 ± 0.57	2.49 ± 0.17
Cellulose (g%)	1.72 ± 0.10	11.28 ±0.30	5.33 ± 0.52
Reducing sugar (g%)	56.42 ± 4.52	35.66 ± 0.54	42.95 ± 5.13

Table 2. Cumulative daily feeding data from four captive tammar wallabies (mean ± S.E.)

a= high quality pellet food, b = low quality pellet food, c= cubed carrot food

Animal (weight in g.)	Food type	Average daily number of feeding events	Average daily dry matter intake (g)	Average daily dry matter intake (g per kg metabolic body weight)	Average daily total time spent feeding (s)	Average daily feeding rate (g wet wt /s)
1 (5500)	a	717	73.1 ± 4.0	11.3	16187 ± 2070	0.006 ± 0.002
	b	407	227 ± 7.9	35.3	20509 ± 662	0.014 ± 0.001
	c	270	81.4 ± 5.1	12.6	23455 ± 227	0.036 ± 0.002
2 (5000)	a	241	83.0 ± 6.3	13.9	6883 ± 276	0.014 ± 0.002
	b	237	213.± 8.0	35.5	9349 ± 818	0.031 ± 0.003
	c	166	79.0 ± 3.2	13.2	20010 ± 670	0.043 ± 0.003
3 (5000)	a	539	80.7 ± 3.2	13.5	14082 ± 1249	0.007 ± 0.001
	b	223	243 ± 5.4	40.5	18357 ± 1521	0.016 ± 0.002
	c	147	73.3 ± 4.2	12.2	25226 ± 991	0.032 ± 0.001
4 (3000)	a	407	54.0 ± 8.7	13.2	9749 ± 1239	0.007 ± 0.001
	b	252	208 ± 6.4	50.9	16190 ± 1299	0.016 ± 0.001
	c	176	58.7 ± 7.4	14.4	20693 ± 1706	0.035 ± 0.006

Table 3. Doubly repeated measures ANOVAs on cumulative daily totals of four captive tammar wallabies for five consecutive days on each of three different food types

Time = total daily time spent eating (s), DMI = total daily dry matter ingested (g), Rate = averaged daily ingestion rate of wet matter (g wet wt / s)

a = high quality pelleted food, b = low quality pelleted food, c = cubed carrot.

Parameter	**Food comparison**	**Results of Doubly repeated ANOVA**		
		df	**F**	**p**
Time	**all**	2/6	33.39	**0.001**
	a/b	1/3	28.74	**0.013**
	a/c	1/3	75.58	**0.003**
	b/c	1/3	13.20	**0.036**
DMI	**all**	2/6	155.91	**0.006**
	a/b	1/3	435.68	**0.000**
	a/c	1/3	0.27	0.641
	b/c	1/3	292.44	**0.000**
Feeding Rate	**all**	2/6	285.68	**0.003**
	a/b	1/3	39.32	**0.008**
	a/c	1/3	812.48	**0.000**
	b/c	1/3	81.88	**0.003**

Table 4. Means and standard errors of feed event duration and post event inter-feed intervals of four captive tammar wallabies derived from pooled raw data for five complete days on each food type.

A = high quality pellet food, b = low quality pellet food, c = cubed carrot food

Animal	Food	Feed event length			Post event interval.		
		overall	‘AM’	‘PM’	overall	‘AM’	‘PM’
1	a	125.8	125.0	126.7	472.8	555.2	377.4
		± 4.83	± 6.4	± 7.3	± 50.2	± 86.4	± 41.0
	b	230.2	198.7	290.5	693.7	688.1	704.4
		± 13.14	± 12.0	± 30.1	± 90.2	± 124.3	± 112.0
	c	392.5	401.5	379.7	975.6	984.4	963.2
		± 22.1	± 29.0	± 34.3	± 114.5	± 151.4	± 175.6
2	a	112.2	93.9	140.3	1402.0	1571.6	1143.4
		± 9.4	± 12.5	± 13.8	± 178.2	± 276.5	± 155.5
	b	172.2	114.0	230.9	1150.7	1534.0	764.3
		± 14.9	± 10.8	± 26.9	± 128.0	± 231.2	± 98.4
	c	295.9	257.9	367.9	986.5	1038.8	887.3
		± 17.1	± 17.7	± 35.3	± 118.6	± 172.5	± 105.4
3	a	126.8	141.1	107.9	671.4	726.0	599.3
		± 10.40	± 17.1	± 8.4	± 71.9	± 113.6	± 73.3
	b	353.7	382.0	322.3	1387.0	1620.0	1128.6
		± 24.7	± 34.4	± 35.4	± 168.8	± 278.1	± 176.0
	c	698.5	730.7	659.5	1669.7	2041.4	1219.5
		± 56.3	± 79.6	± 79.0	± 244.8	± 380.8	± 277.2
4	a	109.9	113.8	106.6	831.7	1104.9	601.8
		± 5.7	± 8.4	± 7.8	± 96.7	± 187.6	± 79.7
	b	281.4	253.9	307.9	1297.2	1574.5	1030.3
		± 13.9	± 18.5	± 20.4	± 180.6	± 23.5	± 167.6
	c	506.6	510.7	500.8	1595.3	1633.8	1541.2
		± 35.9	± 35.9	± 70.5	± 156.9	± 206.4	± 243.1

Table 5. Doubly repeated ANOVAs of log converted feed event durations and meal durations based on various criterion intervals for four captive tammars wallabies. Each animal was maintained on three food types in succession, and the analysis based on pooled data from five complete days

Meal Criterion (Secs)	**Food comparison**											
	All foods			**1/2**			**1/3**			**2/3**		
	F	**d/f**	**p**	**F**	**d/f**	**p**	**F**	**d/f**	**p**	**F**	**d/f**	**p**
individual events	32.39	2/6	**0.0006**	16.5	1/3	**0.027**	35.87	1/3	**0.009**	48.80	1/3	**0.006**
<100	29.80	2/6	**0.0008**	34.77	1/3	**0.010**	31.10	1/3	**0.011**	21.38	1/3	**0.019**
<200	34.24	2/6	**0.0005**	37.14	1/3	**0.009**	35.81	1/3	**0.009**	22.94	1/3	**0.017**
<300	12.55	2/6	**0.0738**	4.623	1/3	0.277	14.71	1/3	0.162	24.48	1/3	**0.016**
<600	4.89	2/6	**0.0549**	1.852	1/3	0.267	4.867	1/3	0.115	9.76	1/3	**0.052**
<1000	12.35	2/6	**0.0075**	7.698	1/3	**0.069**	14.52	1/3	**0.032**	21.02	1/3	**0.019**
<1500	6.30	2/6	**0.0336**	4.673	1/3	0.119	11.04	1/3	**0.045**	2.017	1/3	0.251
<2000	0.24	2/6	0.7963	4.383	1/3	0.127	0.074	1/3	0.804	0.090	1/3	0.783

Table 6. Doubly repeated ANOVAs of log converted inter-feed event intervals based on various criterion intervals for four captive tammars wallabies.

Each animal was maintained on three food types in succession, and the analysis based on pooled data from five complete days

Meal Criterion (Secs)	**Food comparison**											
	All foods			**1/2**			**1/3**			**2/3**		
	F	**d/f**	**p**	**F**	**d/f**	**p**	**F**	**d/f**	**p**	**F**	**d/f**	**p**
individual events	12.04	2/6	**0.008**	5.25	1/3	0.106	13.49	1/3	**0.034**	18.17	1/3	**0.024**
<100	0.051	2/6	0.623	0.307	1/3	0.618	0.501	1/3	0.530	0.704	1/3	0.463
<200	0.019	2/6	0.834	0.665	1/3	0.475	0.155	1/3	0.721	0.002	1/3	0.964
<300	0.42	2/6	0.676	0.984	1/3	0.394	0.409	1/3	0.568	0.060	1/3	0.822
<600	0.07	2/6	0.936	0.188	1/3	0.694	0.074	1/3	0.804	0.006	1/3	0.944
<1000	0.44	2/6	0.662	0.490	1/3	0.534	0.462	1/3	0.546	0.318	1/3	0.612
<1500	7.71	2/6	**0.022**	8.482	1/3	0.062	1.278	1/3	0.341	8.689	1/3	0.060
<2000	0.24	2/6	0.795	1.315	1/3	0.335	0.259	1/3	0.645	0.037	1/3	0.859

Table 7. Correlation coefficients of log feed event duration versus log postmeal inter-feed event interval for four tammars using pooled data from five day run

Food a = high quality pelleted food, b = low quality pelleted food, c = cubed carrot food

	Animal			
Food	1	2	3	4
a	- 0.086	- 0.162	- 0.107	+ 0.018
b	- 0.090	- 0.120	+ 0.380	+ 0.142
c	+ 0.168	+ 0.167	+ 0.401	+ 0.280

Table 8a. Discriminant analysis of effect of food type of log converted feed event lengths and following inter-feed event intervals, obtained from four tammars wallabies maintained on three different food types, each for six days

a = good quality pelleted food, b = poor quality pelleted food, c = cubed carrot food

Foods	Feed event		Interval		% Correct	Eigenvalue	F	p
	Loading	F to remove	Loading	F to remove				
a/b	0.846	226.57	0.562	96.17	67	0.107	163.48	0.0000
a/c	0.823	580.55	0.564	246.53	78	0.337	475.80	0.0000
b/c	0.723	72.6	0.599	49.18	62	0.070	73.089	0.0000

Table 8b. Group means

Food type	n	Feed event	Interval
a	1892	4.246	4.721
b	1166	4.890	5.513
c	931	5.437	6.182

Table 9a. Discriminant analysis of effect of food type of sets of two log converted feed event lengths and following inter-feed event intervals, obtained from four tammars wallabies maintained on three different food types, each for five days

a = good quality pelleted food, b = poor quality pelleted food, c = cubed carrot food

Food	1st Feed event		1st Interval		2nd Feed event		2nd Interval		% Correct	Eigenvalue	F	p
	Loading	F to remove	Loading	F to remove	Loading	F to remove	Loading	F to remove				
a/b	0.448	47.59	0.386	35.63	0.641	101.21	0.374	33.52	71	0.186	70.342	0.0000
a/c	0.505	144.70	0.405	90.88	0.570	189.37	0.375	77.04	82	0.601	209.876	0.0000
b/c	0.494	26.0	0.419	18.81	0.396	16.31	0.383	15.74	64	0.117	30.402	0.0000

Table 9b. Group means

Food type	n	1st feed event	1st interval	2nd feed event	2nd Interval
a	939	4.251	4.693	4.246	4.726
b	580	4.809	5.477	4.967	5.353
c	463	5.399	6.173	5.473	6.181

Table 10a. Discriminant analysis of effect of food type based on alternate values of log converted feed event lengths and following inter-feed event intervals, obtained from four tammars wallabies maintained on three different food types, each for six days for comparison with table 8

a = good quality pelleted food, b = poor quality pelleted food, c = cubed carrot food

Foods	Feed event		Interval		% correct	Eigenvalue	F	p
	Loading	F to remove	Loading	F to remove				
a/b	0.870	140.01	0.504	44.26	68	0.125	95.372	0.0000
a/c	0.841	315.47	0.531	111.12	78	0.350	246.232	0.0000
b/c	0.720	32.84	0.599	22.52	60	0.064	33.370	0.0000

Table 10b. Group means

Food type	n	Feed event	Interval
a	946	4.246	4.739
b	583	4.966	5.535
c	466	5.471	6.171

Chapter 4

The temporal characteristics of feeding activity in free ranging tammar wallabies (*Macropus eugenii* Desmarest).

R. G. Lentle, K. J. Stafford, M. A. Potter, B. P. Springett and S. Haslett.

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The temporal characteristics of feeding activity in free ranging tammar wallabies (*Macropus eugenii* Desmarest).

R. G. Lentle [1], *M. A. Potter* [1], *K. J. Stafford* [2], *B. P. Springett* [1], *S Haslett* [3]

[1] Ecology Group, Institute of Natural Resources, Massey University, Private Bag 11222, Palmerston North , New Zealand.

[2] Institute of Veterinary, Animal and Biomedical Sciences, Massey University, Private Bag 11222, Palmerston North, New Zealand.

[3] Statistics Research and Consultancy Centre, Massey University, Private Bag 11222, Palmerston North, New Zealand

Abstract

The feeding behaviour of four tammar wallabies (*Macropus eugenii* Desmarest) inhabiting a bush pasture ecotone in the Rotorua district of North Island New Zealand is described. Feeding activity, monitored by feeding sounds, was nocturnally crepuscular. Mastication effort, as daily eating time corrected for metabolic body weight and weight related change in tooth surface area, was similar to that of the red kangaroo, a species of greater equivalent dry matter intake. Grazing events were significantly longer than browsing events and feed events longer than 100 seconds comprised 66.5 % of total feeding activity. Grazing on farm pasture only took place at night during fine weather in visits that averaged 6.5 hours. The number of feed events longer than 100 seconds duration taking place within the forest were significantly increased at night and were reduced during periods of adverse weather. Overall temporal spacing of feed events did not differ significantly by day and night but there was a significant overall negative correlation between log converted feed event durations and interfeed intervals for all animals, particularly with feed events less than 100 seconds duration. This differed from that obtained in laboratory studies and may be due to grouping of feed events according to spatial distribution of food sources.

Introduction

The ancestors of macropodid marsupials underwent adaptive radiation during the Miocene (Flannery 1989) as forests gave way to increasingly arid Australian grasslands (Freudenberger *et al.* 1989). Evolutionary modifications in chewing (Sanson 1989) and gut anatomy and function (Freudenberger *et al.* 1989) permitted successful exploitation of grasses and most modern macropods eat grass when it is available. However, whilst grasses have become increasingly abundant, they are considered to be nutritionally inferior to selected browse because of their higher fibre content (Van Soest 1982). In small eutherian herbivore species which have higher mass specific energy requirements, this has led to the evolution of diverse gastro-intestinal strategies by which means retention time is increased (Cork 1995; Langer 1995) and gross fermentative yield maximised. Macropods may exhibit similar strategies of gastrointestinal delay (Langer et al 1880; Langer 1984) but they appear to be less responsive to dietary change, as an increase in dietary fibre had no effect on mean retention time of fluid or particulate markers in captive euros (*Macropus robustus erubescens*) and wallaroos (*M. r. robustus*) fed pelleted diets (Freudenberger and Hume 1992). This constraint limits the ability of macropods to compensate for short term changes in food quality, either by an increase in throughput (Kay *et al.* 1970; Hanley 1982; Hume 1984; 1989; Hume and Sakaguchi 1991) or by an increase in residence time and fermentation (Bjornhag 1995). Thus smaller macropods are less able to digest fibre than both larger macropods (Freudenberger *et al.* 1989) and other herbivores (Cork 1995).

Macropodian digestive strategies may therefore be more heavily reliant on behavioural compensation through food selection (Hungate *et al.* 1959; Bell 1970; Jarman 1974; Baker and Hobbs 1987) and on relative efficiency in food ingestion (McLeod and Minson 1969; Lanyon and Sanson 1986) in order to maintain high throughput (Hume 1984; 1989). In particular, animals must optimise the time spent in consuming abundant low quality food, i.e. grass, or in searching for and handling scarcer high quality food e.g. browse.

Quantitative studies of feeding behaviour in macropods are limited to the larger species (Caughley 1964; Grant 1974; Kaufmann 1975; Southwell 1981; Croft 1981; Priddel 1986; Clarke *et al.* 1989; 1995). Until recently, the quantification of feeding behaviour in small macropod species which inhabit dense scrub has not been possible. A development in surveillance technology (Greager *et al.* 1979) permitted us to directly and quantitatively record certain behaviours of these animals including feed event duration and chewing rate. This study aimed to determine the day to day temporal patterns of browsing and grazing in a free ranging small macropod, the tammar wallaby (*Macropus eugenii* Desmarest) in a similar detailed manner to that of a previous laboratory study conducted by us (Lentle *et al.*, in preparation).

Method

Study site

The study site was situated in the Okataina forest park in the Rotorua district of North Island, New Zealand (latitude 38° 6'; longitude 176° 24') which has been successfully colonised by tammars since their liberation around 1912 by H. R. Benn (Wodzicki and Flux, 1967). On this site tammars inhabit an ecotone between a mainly broadleaf (*Beilschmiedia tawa*, *Knightia excelsa*, *Litsea calicaris* and *Weinmannia racemosa*) forest (Nicholls, 1964) and farm pasture.

Field work and recording technique

The relatively short microphone transmitter life and long periods of continuous observation that were necessary on each animal limited the numbers of animals that could be studied in rotation.

Four tammar wallabies were captured in the Rotorua area, North Island, New Zealand using the method described by Lentle *et al.* (1997). After being tranquillised they were each fitted with a collar bearing a microphone transmitter and a small directional transmitter (Photo 1) and released. Battery life of the transmitters was sufficient to permit continuous recording for one month.

The animals were subsequently located with a TR4 (Telonics, 100 channel, 1 Mhz.) receiver and hand held Yagi aerial, and approached to within 200 m. Microphone transmissions were monitored continuously by use of a single earpiece extension from a modified A. O. R. 1500 wide range monitor (A.O.R. Ltd., Tokoyo, Japan) frequency range 500-1300 khz. The duration of each feed event i.e. the duration of each period of uninterrupted feeding noises, and of interfeed interval i.e. the duration of the interval between successive periods of feeding noises was noted and feed events recorded on a portable dictaphone recorder for later analysis. Observation periods on individual animals were continued round the clock, in 8 hour shifts, in all weathers for a total of thirty days, (each animal being observed for a minimum of 24 hours).

Disturbance from the operator approaching the animal too closely was prevented by estimating its distance using the difference in time of hearing of loud extraneous noises such as bird song via the microphone transmitter and via the operators 'free' ear. It had been found by trial and error that at distances over 500 m there was an audible difference in the timing of these two events whereas no such difference was detectable at distances of less than 200 m. In areas where topography permitted, this same disparity was used to estimate ranges, and in conjunction with a Yagi directional bearing, to obtain radio fixes using the 'offset ' feature (Trimble Navigation 1996) of a Trimble "Scoutmaster" satellite navigation compass. In sites where topography precluded satellite compass operation, traditional triangulation methods were used. Whenever possible radio surveillance was supplemented by direct observation, Swarowski NS-B- 480 night vision equipment being used during the hours of darkness. Note was made of those browsing events that were directly observed whilst being recorded.

Data analysis

Statistical analyses, unless otherwise stated, were carried out in SYSTAT (Wilkinson 1990) statistical software package. Survivorship curves were constructed using SAS statistical software package (1989; 1990).

Unless otherwise stated, all analyses were carried out on log transformed data. Log transformed feed event durations and log interfeed interval were analysed as doubly repeated measures designs with light/dark and event number as the two repeated measures for each animal. For all ANOVA's, model residuals were analysed and tested for normality. Where residuals were non-normal, significance levels were reassessed. Because of the small number of animals in the study, denominator degrees of freedom for F-tests involving light/dark (or other effects which are not event number) are necessarily small; the effect on the study conclusions of the consequent loss of statistical power is discussed as it relates to particular analyses below.

Correlation coefficients between log converted feed events and log interfeed intervals for the three females (animal 4 being excluded on the basis of relative paucity of data) were compared by one way ANOVA of their z-scores. The use of z-scores from correlation coefficients is discussed by Snedecor and Cochran (1980).

A number of the F tests which follow have low denominator degrees of freedom, due to the small number of animals available and the fact that tests of these effects do not rely directly on the repeated measures structure of the experiment. Such F statistics need to be large to be of statistical significance. All effects of biological importance may therefore not have been found in this experiment, although those that are most pronounced are also those most likely to be significant in a statistical sense.

Results

We were able to conduct a total of 431 hours of radiomicrophone collar surviellance before the transmitter batteries failed.

Animals and details of behaviour

All subjects demonstrated a high degree of site loyalty, tending to return to within 50 m of the same midday 'roosting area' after nocturnal feeding excursions.

Animal 1, an adult female (3.3 kg), inhabited a forested gully and during periods of fine weather descended to the base of the gully at dusk to graze clearings along an adjacent bush track. On calm fine warm nights the animal travelled further to graze farm pasture, a distance of 600 m, before returning to the same gully via the same route at dawn.

Animal 2, an adult female (4.2 kg), lived further up the same gully. This subject was never observed to travel widely but regularly traversed the short distance to the base of the gully at night to feed on small grassy areas in the forest.

Animal 3, an adult female (4.2 kg), inhabited an area of dense scrub 10 m from the forest/pasture ecotone for a period of four days at the start of the study before relocating to a sheltered forested gully some 70 meters from the ecotone. There was continuous wind and rain in the initial period during which the animal did not graze the pasture area but fed instead along a small sheltered track. Feeding periods were shorter during this time but followed the same nocturnally crepuscular distribution as in fine weather. Following clearing of the weather, the animal travelled to the pasture at night but returned to the deep gully site during the day.

Animal 4, an adult male (4.3 kg) was more mobile and much more difficult to follow. This animal frequented a forested ridge 500 m from the ecotone by day, travelling to the farm pasture area at night during fine weather where it was similarly highly mobile.

Temporal sequence

Two dimensional smoothed kernel observation density plots, for log converted feed event durations are shown in figs 1. All plots show biphasic, i.e crepuscular, peaks in feeding activity with nocturnal maxima. Quantitative plots of time spent feeding per half hour interval through the diel cycle showed a similar pattern. Pasture grazing commenced later and finished earlier than feeding within the forest thus the 'AM' and 'PM' feeding peaks were closer together during nights when pasture grazing took place than when feeding took place within the forest.

Survivorship curves

Survivorship plots of all available feed event durations and those for observed pasture feed events only, for each animal are shown in fig 2. The survivorship curves of observed pasture grass feed durations are consistent with a single process exponential distribution in which feed event termination is a random process. The plots of all available feed events differ from this, having a more 'broken stick' configuration indicative of two or more Poisson processes with the faster process governing feed events of smaller duration. The point of division between the two random processes occurs consistently at feed event durations of around 100 seconds.

In view of the variability of food sources, the broken stick configuration of the non pasture feed event survivorship curves and the previous laboratory findings on tammars obtained from this study site (Lentle *et al.* 1999), it was considered inappropriate to attempt the grouping of feed events into meals as has been carried out by previous field workers on other herbivore species (Mayes and Duncan 1985). Thus all analyses were based on individual feed events and their associated intermeal intervals.

Activity budgets

Estimated totals of daily feeding time obtained from day-long recordings are shown in table 1. These totals include estimations of feeding times that were missed due to small gaps in the recordings such as during observer relocation. Each gap estimation was obtained by totalling feed events which took place in the recordings immediately preceding the gap over a time span equal to half the duration of the gap, and adding this to a similar estimate obtained from the recordings immediately following the gap. The daily total of recorded time on which each estimated daily total feeding time is based is also shown in table 1. The overall average of estimated daily total feeding times obtained from all animals in all weathers was 6.05 h (21787 s) of feeding per day.

Using all available data from all animals 66.6% (60.16 h from an overall 855 feeding events) of the total recorded time spent feeding (90.5 h from an overall 4,373 feeding events) came from feed events of greater than 100 *s* duration. When the analysis was restricted to data sets with comparable day and night coverage i.e close to 24 h cover (>19h 50m), (table 1) the proportion of the daily total recorded feeding time resulting from events of greater than 100 *s* duration was again consistently greater (7 out of 7 cases)(Binomial test $p < 0.01$) than that resulting from feed events of less than 100 *s* duration. Non parametric analysis of the same data showed that there were no significant differences in the proportion of daily feeding time that resulted from feed events less than 100 s between animals (Kruskal Wallis test statistic = 4.019, $p = 0.134$). However a similar analysis showed that there were significant differences in this proportion between day and night (Mann Whitney test statistic = 42, $p = 0.025$) shorter feed events contributing a significantly lower proportion to total nocturnal feeding time than to total diurnal feeding time.

Total durations of single visits to the pasture grazing area uninterrupted by changing weather were, 424 minutes for animal 1 and 361 minutes for animal 3.

Feed events and interfeed intervals

The overall average of feed event durations was 74 ± 2 s. That of pasture grazing events was 245 ± 27 s and that of browsing events that were directly observed whilst being recorded was 46.6 ± 4.8 s. Similarly the overall average post event interval was 219.8 ± 10 s, that between pasture grazing events was 246.2 ± 38 s and that between browsing events recorded whilst being observed was 492.5 ± 98.2 s.

The means and standard errors of pasture grazing events and of browsing feed events that were simultaneously observed and recorded along with means and standard errors of associated interfeed intervals obtained from the three individual animals which grazed on pasture are shown in table 2. Changes in overall mean values with daylight and dark, AM (late night and early morning) and PM (evening and early night) feeding peak and with weather are shown in table 3.

An overall comparison of grazing events with browsing events on the basis of animal location, i.e within bush or on pasture, was precluded by the tendency of animals to graze on small clearings in the bush interior, an activity which could not always be identified by the operator. However, directly observed browsing events were significantly shorter than grazing events, on doubly repeated measures ANOVA, ($F_{1,2}$ = 21.92, p = 0.043) in the three animals which grazed on pasture. There was no significant difference in the spacing, i.e the interfeed intervals, of observed browsing and the spacing of grazing events ($F_{1,2}$ = 1.11 p = 0.402). Residuals for both analyses were accepted as normally distributed since $p > 0.01$ in both cases using the Shapiro-Wilks test.

Overall comparison, by doubly repeated measures ANOVA, of the duration and spacing of feed events taking place in the bush by day and by night, excluding animal 4, showed that feed events were significantly longer at night ($F_{1,2}$= 1291.75, p = 0.0008) but that there was no significant difference in their spacing as represented by duration of post event intervals ($F_{1,2}$ = 0.24, p = 0.67). Similarly there was no significant difference in spacing when the analysis was restricted to feed events of less than 100 s duration ($F_{1,2}$ = 0.12 and p = 0.762). Residuals from the analysis of log feed event duration were accepted as normally distributed since p = 0.74 using the Shapiro-Wilks test. The residuals from the analysis of log post event interval were symmetric but too long tailed to pass the normality test ($p<0.0001$); however even this departure from normality was insufficient to allow the possibility that a significant difference in feed event spacing had occurred. Residuals from the analysis of log post event intervals corresponding to feed events > 100 s in duration, were assessed as normally distributed (Shapiro Wilks p = 0.98).

A similar comparison, by doubly repeated measures ANOVA, of the duration and spacing of feed events according to 'AM' or 'PM' feeding peak, showed no significant difference in the duration of feed events ($F_{1,2}$ = 0.14, p= 0.7466) or in their spacing as represented by duration of post event intervals ($F_{1,2}$ = 0.19, p = 0.7067). For log feed events the Shapiro Wilks test had p = 0.57, so normality of residuals was accepted. For log post event interval the residuals were again symmetric but too long tailed to pass the normality test ($p < 0.0001$); however even this departure from normality was insufficient to allow the possibility that a significant difference in meal spacing had occurred.

For animal 3 alone, the mean overall feed event duration was significantly shorter in bad (heavy rain and gales) rather than favourable weather, on one way ANOVA ($F_{1,\ 879}$= 6.931, p = 0.009). Similarly feed event spacing as represented by post event interval was significantly greater in bad weather ($F_{1,\ 834}$ = 4.545, p= 0.033). The residuals for both log feed event and log post event interval were again symmetric but too long tailed to pass the Lillifors test for normality.

Overall correlations between log converted feed event lengths and log converted post feed (table 4) intervals were negative and significant for all animals. Consistent significant negative correlations persisted when analyses were restricted to feed events of less than 100 s. Conversely, when analyses were restricted to feed events > 100 *s* duration, there were significantly lower degrees of negative correlation (ANOVA of z scores $F_{1,4}$ = 8.090, p = 0.047). The Lillifors test on the distribution of the residuals showed no significant difference from normality (p = 0.754) in the latter analysis.

Grass and foliage analysis

Nutrient analysis of foliage samples taken from areas that were seen to be actively grazed or browsed are shown in table 5. All were composite samples, taken from 5 locations at each site and thoroughly mixed prior to analysis.

Discussion

Large macropod species differ in the degree to which their daily schedules of activities are 'constrained' by environmental factors such as daylight (Clarke *et al.* 1989). Our results showed that summer feeding activity in the tammar was relatively unconstrained by daylight but did follow the general macropodian pattern (Clarke *et al.* 1989) being broadly nocturnally crepuscular with foraging taking place least frequently in the middle of the day. The results quantitatively confirmed the observations of other workers (Inns 1980; Williamson 1986), that the feeding activity of tammars may be constrained by inclement weather, but showed also that during such periods the same general pattern of feeding activity was maintained in limited sites in forested areas, though with significant reduction in feed event duration and increase feed event spacing.

The average total daily feeding time of 363 minutes taken over all weathers is somewhat lower than the summer value for female red kangaroos (*Macropus rufus*) of 511 minutes, measured with a tilt transmitter (Priddel 1986). Assuming that the total masticatory area of the teeth of species of similar dietary habit scales isometrically with body weight (Kay 1975; Gingerich and Holly Smith 1985) and correcting these figures for differences in the relative area of the masticatory surface as well as differences in metabolic body weight (Klieber 1975), gives a value of 325 minutes for tammars and 376 minutes for red kangaroos. These values are very similar bearing in mind that data obtained using tilt transmitters may overestimate feeding times by inclusion of time spent searching for food and time tending joeys. Conversely, dry matter intakes standardised for metabolic weight (DMI) are considerably lower for tammars (29.4 g per kg $^{-0.75}$ day $^{-1}$) (Hume 1982; Dellow 1982) than for red kangaroos (53.4.1 g per kg $^{-0.75}$ day $^{-1}$) and other macropodine species (Hume, 1982). Again the DMI of tammars captured from the same population as was used in this study and maintained on cubed carrot was also low (13.2 g per kg $^{0.75}$ per day, and the average total daily feeding time (372 minutes per day) similar to that obtained in this study (Lentle *et al.* 1999). It is therefore likely that tammars spend more time eating less food than red kangaroos which may result in greater on site comminution of food prior to swallowing (Bazli 1985).

The results of direct observations taken during the course of this study and of analysis of radio-microphone chewing noises (Lentle et al in prep) show that animals continue to browse or to graze through most of the day depending on what is available. The point of inflection in the broken stick configuration of the feed event duration survivorship curve is close to the average consumption time for a mahoe (*Melicytus ramiflorus*) leaf (110 s) (Lentle *et al.*, in prep), one of the largest leaved species known to be eaten by tammars in this area (Williamson 1986).

If feed event durations longer than 100 seconds are assumed to result from grazing activity then the predominance of such events in the daily feeding budgets of tammars provides indirect evidence that Sanson's (1989) classification of tammars, along with other members of the genus *Macropus*, as grazers is broadly appropriate. Similarly, the significant reduction in the proportion of shorter feeds more typical of browsing in all four subjects during the hours of darkness, a period when mobility is generally increased, may indicate that grass is preferred to browse.

There was no significant difference in the overall spacing of feed events during daylight and darkness, even when the analysis was restricted to shorter events more typical of browsing. Thus darkness did not influence the rate of food selection. This finding contrasts with the significant decrease in the rate of food selection measured in grazing eastern grey kangaroos during the hours of darkness (Clarke *et al.* 1995). This may indicate that night vision is more refined in tammars than in more diurnally active macropod species such as the eastern grey kangaroo.

The negative correlation of feed event duration with following interfeed interval differs from the positive correlations obtained during the consumption of cubed carrot feeds by tammars in the laboratory (Lentle et al, 1999) and may be brought about by a number of alternative effects. A stress induced change in the temporal characteristics of feeding behaviour described in rats (Weipkema 1971) may cause shortening of feed event durations and lengthening of intermeal intervals when the animals are in strange surroundings. In this respect it is notable that mean pasture grass feed eventlengths in this study were very similar (245.0 ± 27.2 s) to those obtained with cubed carrot feeds (257.5 ± 30.6 s) in a laboratory study (Lentle et al.1999). A tendency of feed events to cluster temporally i.e. for feed events to increase in length and frequency at certain times may be brought about by patchiness in food availability e.g. when animals encounter shrubs or patches of grass that are particularly suitable for feeding; or as an outcome from a behavioural strategy of increasing intake during times when predation or hyperthermia are less likely (Clarke *et al.* 1995; Dawson and Denny 1969) which is analogous to the formation of meals. The former possibility is more likely in view of findings on penned tammars (Lentle *et al.* in preparation) which show that positive correlations are maximal between individual feed events and following interfeed intervals, i.e. meals do not occur (Weipkema 1971) under conditions where there is uniform availability of food. Again the significant lessening of the degree of negative correlation which occurs when only longer feed events and their associated interfeed intervals are considered, supports the hypothesis that negative correlation arises from spatial clustering of food in that such longer feed events are more likely to occur during grazing i.e. when spatial distribution of food is more uniform.

Comparison of the overall results from this study with those obtained in laboratory studies with animals from the same population fed on naturally ocurring foods (Lentle *et al.* in prep) shows that, whilst there is a marked dissimilarity of overall correlations between feed events and their associated interfeed intervals, there is close similarity of average total daily time spent eating. Viewed in the light of the similarity of the temporal distribution of feed event durations in both these experiments, this finding indicates the greater importance of nyterohemeral control of feeding and lesser importance of feed event spacing by metabolic consequence from previously ingested food (Le Magnen 1992) in tammar wallabies.

When weather conditions were favourable three of the study animals undertook considerable journeys to graze pasture grasses i.e. there was an investment in travelling to a more abundant food source in an area of higher risk from predators and from adverse thermal balance. Collier (1985) found that rats regulated their food intake by changing their meal pattern according to economic conditions of the habitat. Thus when 'cost' was higher meal size was increased and meal frequency reduced. When tammars were eating pasture grass, the duration of feed events was significantly increased, the feeding period lasted six hours, but there was no significant decrease in feed event frequency i.e. increase in interfeed interval. Thus viewed at a feed event scale Collier's (1985) cost related adjustment of meal pattern does not occur. However as the metabolic consequences of meal ingestion are less immediate in herbivores (Mertens and Ely 1982), the amount eaten during the whole six hour feeding period may be considered equivalent to Colliers 'meal' and the relative approximation of 'AM' and 'PM' feeding peaks when grazing on pasture grasses in comparison to peak positions during non pasture feeding considered the equivalent to an overall increase in 'meal' spacing over the 24 hour period.

Food analysis showed a number of differences in the nutrient value of pasture grasses, bush grasses and browsed vegetation, whose influence on food choice is equivocal. Thus the nitrogen content of grasses was consistently higher than that of browse but this difference is unlikely to form the basis of discrimination between food sources as tammars are known to have relatively low nitrogen requirements (Barker 1968; Hume 1977) due to their ability to recycle urea (Kinnear and Main 1975) and to withstand protein depletion (Kinnear and Main 1975). The greater reducing sugar content of browse may provide some nutritional advantage but this must be set against a concomitant increase in lignin content. Bearing in mind the significant differences in the length of browsing and grazing feed events, the change in patterns of use according to weather conditions and the known low efficiency of browsing exhibited by this species (Lentle *et al.* in prep.) it is more likely that a tammar's choice to browse or to graze is based on relative abundance and ease of ingestion rather than on nutrient content.

In summary a number of features of the feeding behaviour of tammars highlighted by this study suggest that whilst tammars are able to utilise browse, they rely mainly on grazing. Allowing for differences in body size, tammars spend a similar amount of time feeding per day to that of larger grazing species (Priddel 1986), moreover the temporal patterns of their feeding suggest a predominantly grazing habit. Analysis of the temporal patterns of feeding indicates that the crepuscular peaking of feeding activity that is exhibited by the tammar and is typical of macropod species (Clarke *et al.* 1989) results largely from an interaction between the spatial distribution of food resources and a nycterohemeral variation in feeding drive rather than from the grouping of feed events according to their metabolic consequence such as in the rat (Le Magnen 1992).

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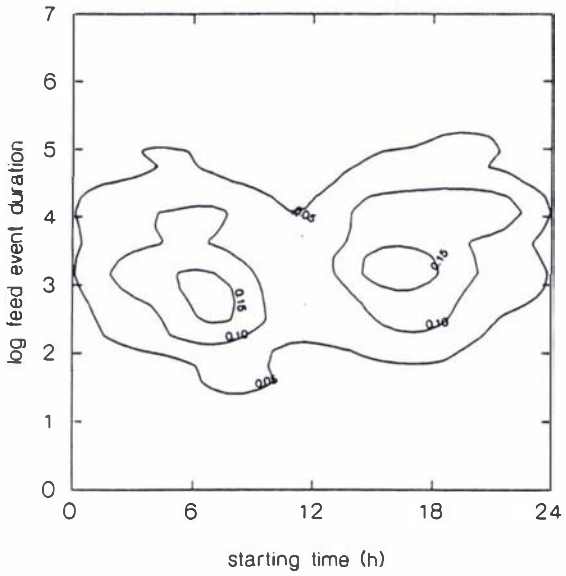
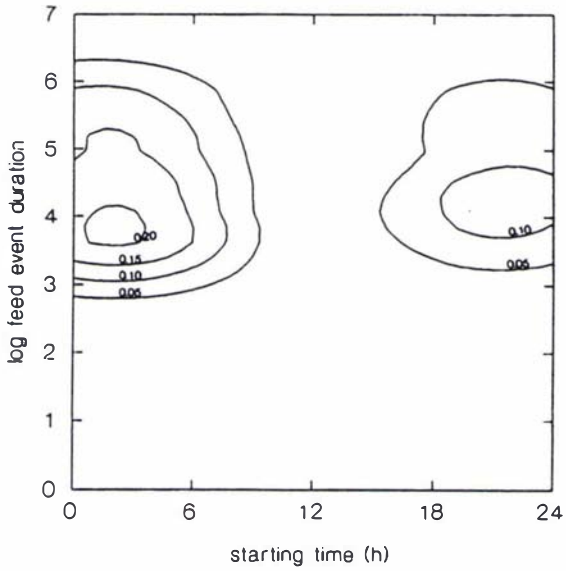
Figure 1 Smoothed kernel observation density plots of log converted feed event durations (s) of four free ranging tammar wallabies.

Abscissa, time of day in hours that feed event commenced. Ordinate, log of feed event duration in seconds. Inset contour figures are observation density values.

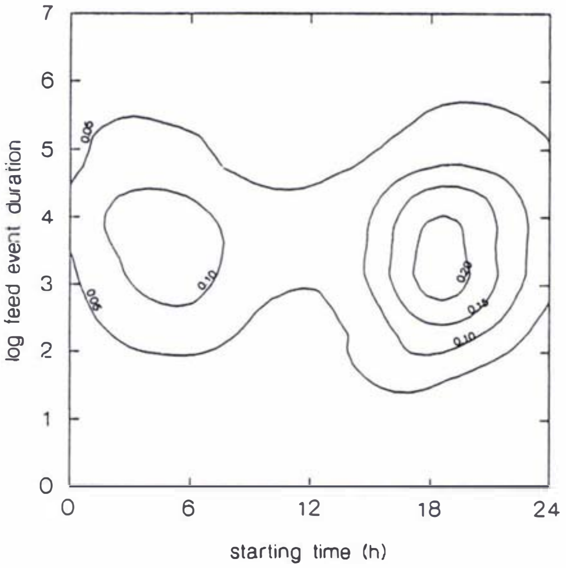
Animal 1: feeding in forest



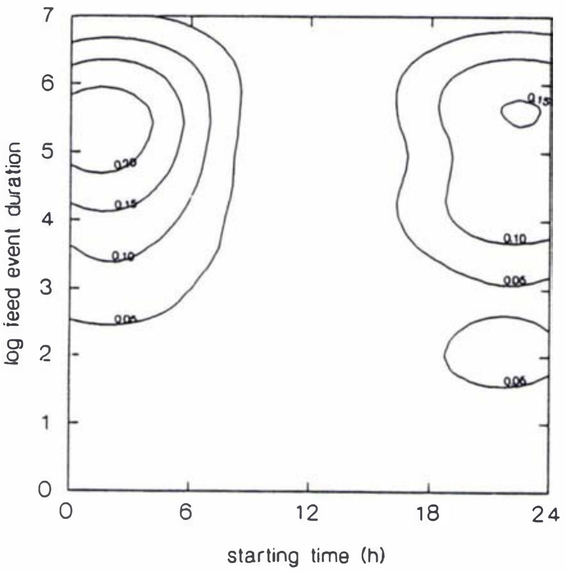
Animal 1: feeding on pasture



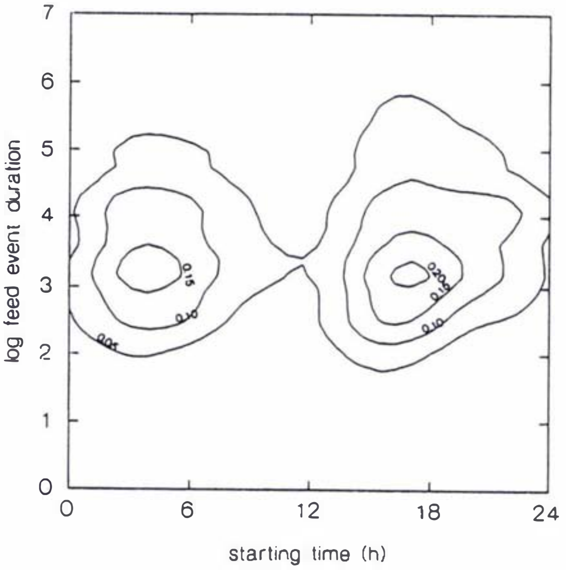
Animal 3: feeding in forest



Animal 3: feeding on pasture



Animal 2: feeding in forest



Animal 4: feeding on pasture

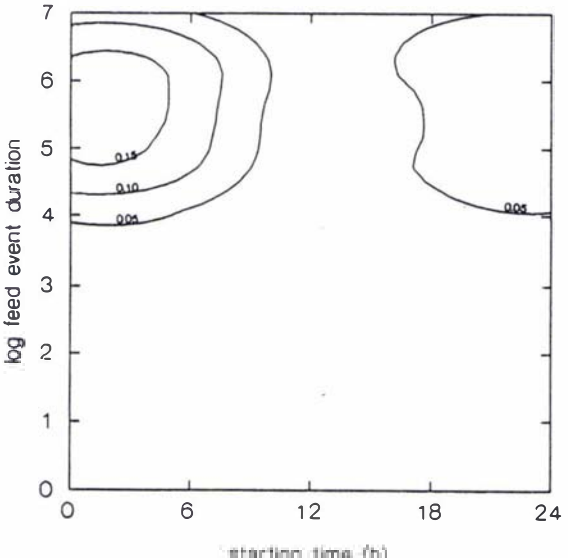
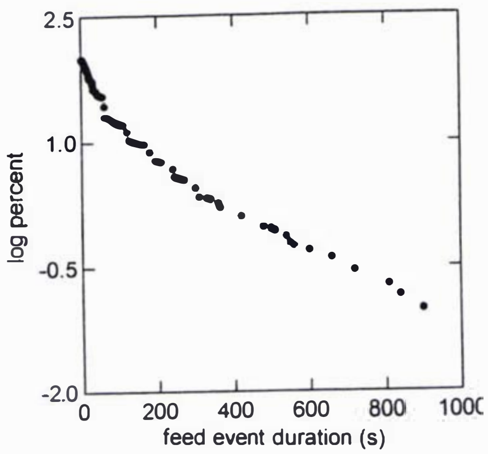


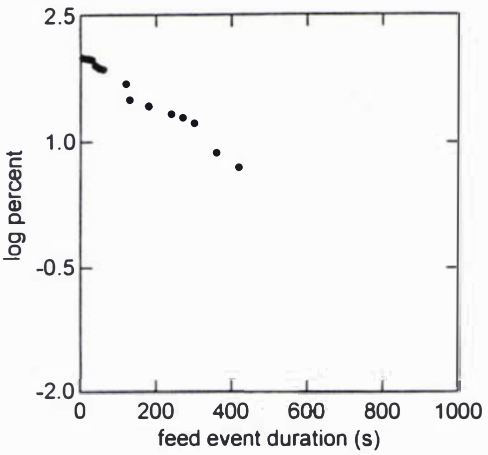
Fig 2: Survivorship curves of log converted feed event durations of four free ranging tammar wallabies.

Curves labelled 'all feed events' include all available data. Curves labelled 'observed events' include only those grazing events that were simultaneously observed and recorded. Animal 2 is not shown as an 'observed event' plot as it did not graze on the pasture site during the period of observation.

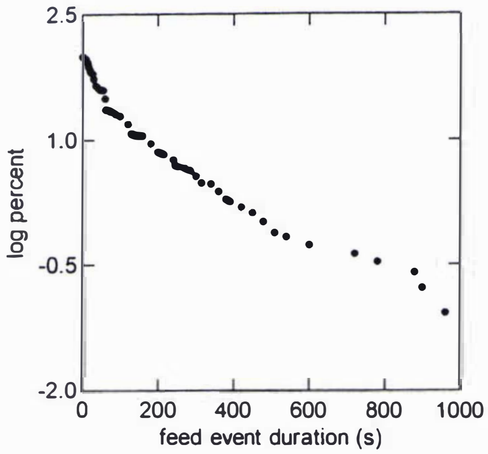
Animal 1: All feed events



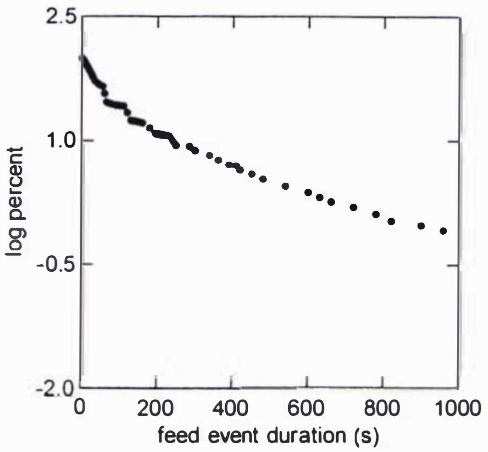
Animal 1: observed grazing events



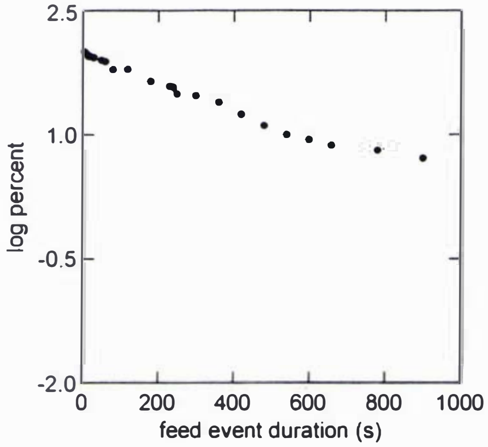
Animal 2: All feed events



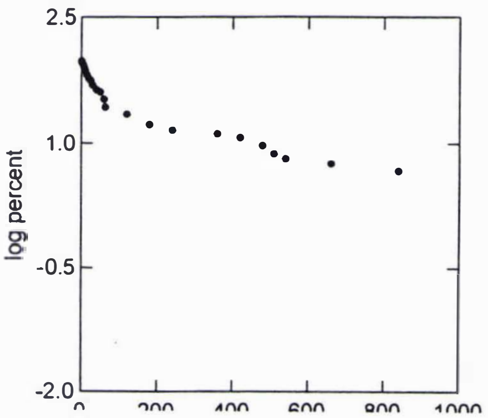
Animal 3: All feed events



Animal 3: observed grazing events



Animal 4: All feed events



Animal 4: observed grazing events

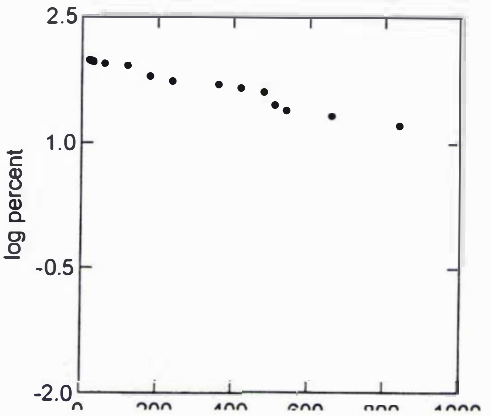


Table 1: Feeding budget for 24 h periods based on the recorded feeding noises of three female free ranging tammar wallabies in the Rotorua district of North Island, New Zealand.

*Estimated daily totals have been approximated for small gaps in records due to such technical problems as observer relocation by adding appropriate averages from succeeding and preceding segments. Sum total of continuous recordings on which each estimate is based is shown under 'Time base of estimate'. Percentage estimates are based solely on recorded (not estimated) totals.

Animal	Date	Weather	Pasture feeds	Estimated daily total* (s)	Time base of estimate	Total of recorded feed events of <100 s (s)		Total of recorded feed events of >100 s (s)	
						24 hr (% of total events)	Daytime (% of total events of <100 s)	24 hr (% of total events)	Daytime (% of total events >100 s)
1	6/7	fine	yes	20498	21h 26m	5488 (27.4)	4428 (80.7)	14540 (72.6)	9330 (64.2)
1	8/9	cloudy and cold	no	17009	22h 25m	5622 (35.2)	4647 (82.7)	10365 (60.9)	6315 (64.8)
1	26/27	fine	no	29193	19h 50m	7271 (40.7)	3699 (50.1)	10582 (60.2)	2712 (25.6)
2	13	occasional light rain	no	20206	21h 30m	8716 (46.1)	6270 (71.9)	10170 (53.9)	8310 (81.7)
3	18	High wind + heavy rain	no	11955	24 h 0m	4485 (37.5)	3687 (82.2)	7470 (62.5)	5430 (72.7)
3	22	occasional rain	yes	22986	21h 0m	4735 (26.1)	3189 (67.3)	13400 (73.9)	6610 (49.3)
3	23	occasional rain	yes	21780	22h 45m	3075 (16.1)	1960 (63.7)	15975 (83.9)	4555 (28.5)

Table 2: Means and standard errors of simultaneously observed and recorded feed events and interfeed intervals (in seconds) of three free ranging pasture grazing tammar wallabies at different sites, times and weather conditions in the Rotorua district of North Island New Zealand

	Animal 1		Animal 3		Animal 4	
	Feed event	Interfeed interval	Feed event	Interfeed interval	Feed event	Interfeed interval
Browsing	54.3 (7. 91)	280.8 (106.0)	41.8 (7.9)	549.0 (8.8)	40.2 (8.8)	797.1 (264.7)
Pasture grazing	125.4 (17.4)	248.1 (93.4)	237.5 (29. 0)	212.2 (44.2)	485.8 (124.2)	359.1 (75.4)

Overall feed event durations: Browsing = 46.64 (4.78) **Grazing** = 245.01 (27.27)

Table 3: Overall means and standard errors of feed events and interfeed intervals of four free ranging tammar wallabies at different sites, times and weather conditions in the Rotorua district of North Island New Zealand.

* Indicates mean is based only on bush site events. # animal 2 did not emerge onto pasture during the period of study.

		Animal 1		Animal 2		Animal 3		Animal 4	
		feed event	interval	feed event	interval	feed event	interval	feed event	interval
Overall		61.7 ± 2.0	178.4 ± 11.8	70.7 ± 3.0	192.5 ± 18.2	98.7 ± 5.8	316.0 ± 30.3	149.6 ± 35.3	358.4 ± 91.8
Site	**Pasture**	125.4 ± 17.4	248.1 ± 93.4	- #	- #	237.0 ± 29.0	212.3 ± 44.2	485.8 ± 124.2	359.1 ± 75.4
	Bush	59.9 ± 2.0	177.0 ± 11.9	70.7 ± 3.0	192.5 ± 18.2	83.9 ± 5.4	326.7 ± 33.1	64.2 ± 25.5	646.3 ± 114.7
Time *	**Night**	85.7 ± 5.2	154.8 ± 14.6	62.4 ± 4.1	172.0 ± 17.4	159.5 ± 13.4	273.6 ± 37.0	62.5 ± 26.9	653.4 ± 115.9
	Day	52.6 ± 1.9	187.3 ± 15.3	74.6 ± 3.9	202.4 ± 25.8	62.8 ± 4.0	340.6 ± 42.8	409.7 ± 103.1	346.7 ± 73.3
Feeding Peak	**early (PM)**	66.9 ± 3.1	174.4 ± 13.2	78.2 ± 4.4	163.1 ± 15.3	85.7 ± 6.7	292.4 ± 39.0		
	late (AM)	55.8 ± 2.6	182.8 ± 20.2	60.7 ± 3.8	231.4 ± 37.2	116.3 ± 10.2	347.5 ± 48.0		
Wind *	**Calm**	62.5 ± 2.4	165.8 ± 11.3	76.8 ± 4.9	184.0 ± 29.5	105.8 ± 6.6	303.2 ± 31.5		
	Moderate	66.3 ± 4.4	218.7± 36.6-	65.5 ± 3.6	199.2 ± 22.9	-	-		
	Gale	32.06 ± 6.9	187.9 ± 59.8	-	-	52.8 ± 5.6	404.7 ± 100.5		

Table 4: Correlation coefficients of log converted meal durations with log converted postmeal intervals for three female free ranging tammar wallabies in the Rotorua district of North Island New Zealand.

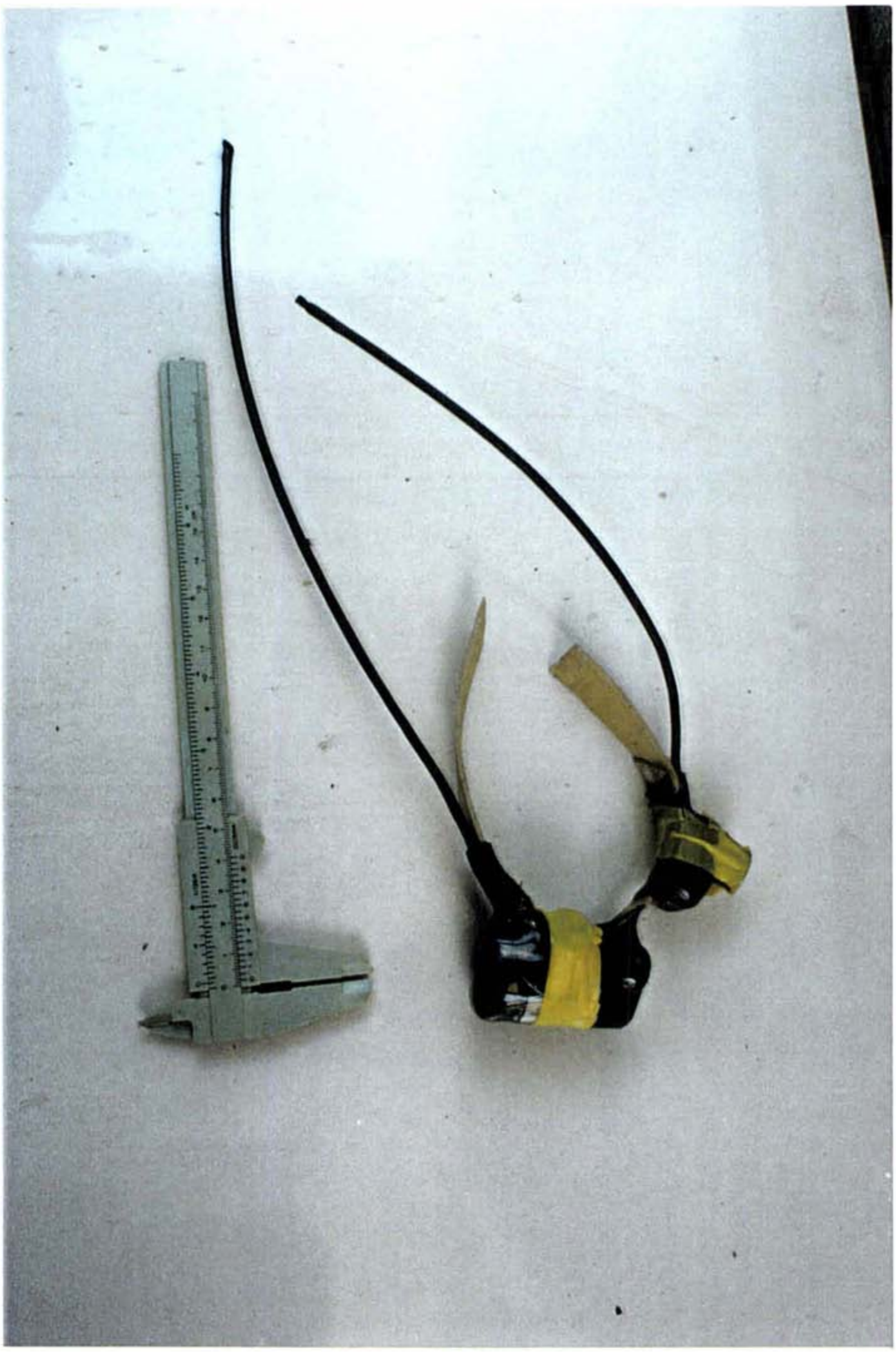
	Animal 1	Animal 2	Animal 3
Overall	- 0.101	- 0.070	- 0.215
Duration <100s	- 0.167	- 0.128	- 0.327
Duration >100s	+ 0.053	- 0.058	- 0.017
AM	- 0.142	- 0.116	- 0.241
PM	- 0.066	- 0.032	- 0.202
Light	- 0.133	- 0.090	- 0.225
Dark	- 0.009	- 0.023	- 0.212
Grass	- 0.189	-	- 0.037

Table 5: Nutrient analysis of pooled grab samples of foliage taken from known feeding sites of free ranging tammar wallabies in the Rotorua district of North Island, New Zealand.

Sample name	Bush grass	Pasture grass	Leaves
Number of grab samples in pool	**10**	**10**	**7**
Dry matter (g %)	94.53	94.46	94.56
Nitrogen (g %)	2.072	2.306	1.079
Gross energy (kJ/g)	17.76	17.87	18.75
Neutral detergent fibre (g %)	58.93	58.87	56.54
Acid detergent fibre (g %)	28.17	26.37	40.51
Lignin (g %)	3.15	3.36	21.94
Hemicellulose (g %)	30.76	32.50	16.03
Cellulose (g %)	25.02	23.01	18.56
Reducing sugar (g % of dry matter)	7.78	8.77	15.51

Photo 1: Collar showing radiomicrophone and directional radiotransmitters

The radiomicrophone transmitter (left) is mounted on the collar in such a way that the microphone (arrowed) comes to lies against the anterior region of the animal's neck and the two aerials lie dorsally along the animal's back. The collar is shown prior to removal of magnetic stoppers which are shown taped to the midpoint of each transmitter.



Chapter 5

Ingesta particle size, food handling and ingestion in the tammar wallaby (*Macropus eugenii* Desmarest).

R. G. Lentle, K. J. Stafford, M. A. Potter, B. P. Springett and S. Haslett.

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Ingesta particle size, food handling and ingestion in the Tammar wallaby (*Macropus eugenii* Desmarest)

R. G. Lentle [1], *K. J. Stafford* [2], *M. A. Potter* [1], *B. P. Springett* [1], *S Haslett* [3]

[1] Ecology Group, Institute of Natural Resources, Massey University, Private Bag 11222, Palmerston North , New Zealand.

[2] Institute of Veterinary Animal and Biomedical Sciences, Massey University Private Bag 11222, Palmerston North, New Zealand.

[3] Statistics Research and Consultancy Centre, Massey University, Private Bag 11222, Palmerston North, New Zealand.

Summary

The particle size distribution of stomach contents from 25 tammar wallabies (*Macropus eugenii* Desmarest) shot in the Okataina State Forest and adjoining farmland near Rotorua, New Zealand, were determined. There was a greater perecentage of finer and a smaller percentage of larger particles than reported in the stomach contents of larger macropods. The chewing and biting activities of four free ranging tammars fitted with radio-microphone collars were monitored. Chewing rates (Chews/ min) were similar to those of other small herbivorous vertebrates. There were significantly lower rates of chewing and higher chew to bite ratios when browsing than when grazing. Observations of browsing by three captive tammars showed inefficient handling by mutually opposed palms and digitopalmar grip resulting in low rates of ingestion. The authors suggest that tammars lower the time necessary for fermentation of food by reducing food particle size, and that their choice between graze and browse is influenced by food handling and chewing investment.

Introduction

The manner by which small herbivore species obtain their relatively high mass specific energy requirements whilst achieving the long digesta residence times required for fermentation has been the subject of considerable inquiry (Cork 1994). Interspecific comparisons of gut volume with body mass show that compensation via a relative increase in the size of fermentation compartment to body mass does not generally occur (Demment and Van Soest 1985). Whilst ruminants (Ulyatt 1983; Ulyatt et al. 1985) and some hindgut fermenting species (Bjornhag 1972; 1987; Cork and Warner 1983; Chilcott and Hume 1985; Foley and Hume 1987; Foley et al. 1989; Cork and Foley 1991; Cork 1994), possess mechanisms of selective particle retention which may help resolve this difficulty, the strategies by which macropod herbivores deal with these problems remain poorly understood. It has been suggested (Hume 1984; Hume 1989) that macropod stomach fermenters generally employ a strategy of rapid throughput of low quality herbage, but evidence for this is incomplete (Freudenberger and Hume 1992).

We have recently demonstrated (Lentle et al. Chapter 3) that weight for weight, free ranging tammar wallabies *(Macropus eugenii)*, spend more time eating (Priddel 1986) but eat less food (Hume 1982; Dellow 1982) than is reported in red kangaroos (*Macropus rufus*) a grazing species (Sanson, 1989) of significantly greater body weight. This may result in greater comminution of food by tammars, perhaps as a strategy to increase the rate of digestion by increasing the surface area available for attack by microbial guilds (Batzli 1985; Bjorndal et al. 1990). The critical role of food handling and mastication in the nutritional strategies of macropod species has been highlighted by the demonstration that pelletising low nutrient density diets permitted a relative increase in dry matter intake, apparent dry matter and acid detergent fibre digestibility, and thus a relative increase in digestible dry matter intake in eastern wallaroo *(M. robustus robustus)*, and euro (*M. robustus erubescens*) (Freudenberger and Hume 1992).

Feeding rate and thus foraging efficiency can be influenced by handling time, bite size (Vivas and Saether 1987; Spalinger and Hobbs 1992) and the manner in which biting and chewing activities are integrated (Spalinger et al. 1988; Spalinger and Hobbs 1992). These factors will vary according to whether the animal is browsing or grazing. If the final outcomes of chewing browse or graze is similar, with equal particle size distributions, then assessment of the relative effort spent in chewing and efficiency in handling the two food types may give some insight into which constitutes the optimal choice.

This paper describes the browse handling characteristics of captive tammar wallabies as well as the manner of feeding, chewing rates, digesta particle sizes and degree of stomach fill in free ranging tammar wallabies that inhabit a site in the Okataina forest park in the Rotorua district of North Island, New Zealand (latitude 38° 6'; longitude 176° 24') on an ecotone between a mainly broadleaf (*Beilschmiedia tawa*, *Knightia excelsa*, *Litsea calicaris* and *Weinmannia racemosa*) forest (Nicholls, 1964) and farm pasture.

Methods

Particle size distribution analysis

Particle size distributions in the stomach ingesta of 23 tammars shot on a single summer night in the Okataina forest near Rotorua were determined by wet sieving (Waghorn 1986) using sieves with apertures of 4, 2, 1, 0.5, and 0.25 mm. The weights of material retained on each sieve were determined after drying for 24 hr at 70° C. The weights of solid material which passed the final sieve were determined by centrifugation of the eluent and subsequent decanting, drying and weighing of solid matter.

Feeding noise recordings on free ranging animals

Four tammar wallabies were captured on a study site near Rotorua using the method described by Lentle et al. (1997). They were each fitted with a collar bearing a microphone transmitter (Greager et al. 1979) and a small radiolocation transmitter. Battery life of the transmitters was sufficient to permit continuous recording for one month.

Following release, the animals were subsequently relocated with a hand held Yagi aerial, approached to within 200 m, and microphone transmissions continuously monitored by use of a single earpiece extension (Lentle et al. Chapter 4). Feeding noises were recorded on a portable dictaphone recorder for subsequent analysis. Individual animals were monitored continuously. Whenever possible radio surveillance was supplemented by direct observation using binoculars by day and night vision equipment during the hours of darkness.

Sound analysis

Only recordings where the location of the animal had been precisely located i.e. bush or grass site were used for this analysis. Selected samples of feeding sounds from each of the four wallabies were transcribed onto a sound analysis system. Extraneous noises were edited out by use of frequency specific filters. Counts of regular (chewing) and irregular (biting) noises, were obtained from graphically displayed sounds following verification by ear and eye. Chewing rates were calculated from the duration of ten chewing cycles i.e. the time between eleven consecutive chewing sounds. Biting rates were obtained from calculating the interval between consecutive biting noises during the time when chewing rate was estimated. Chew to bite ratios were calculated from relative numbers of cropping and chewing noises during this same period.

Observations on captive animals

Two tammar wallabies were captured near Rotorua using the method described by Lentle et al. (1997). They were subsequently housed together in a windowless indoor pen (12 x 2 m). Artificial lighting was provided by two 100 watt bulbs for a fixed photo-period cycle of 12 hours dark and 12 hours light. Mahoe (*Melicytus ramiflorus*) foliage was fed as it was known to be favoured by tammar wallabies (Williamson 1986). A quantity of freshly cut mahoe branches with sufficient leaves to be in excess of the animals daily requirements was placed in the pen each night. The animals were monitored by continuous video recording using a Panasonic model AG 6730 recorder and Panasonic WV PB 312C infra-red / visible spectrum video camera for one week. Dark cycle recording was augmented by infrared illumination from two 100 watt infra-red lamps on a twelve hour light dark cycle.

The laboratory video observations were supplemented by daytime observations of a captive tammar in a 100m x 50m enclosure at 'Staglands Game Park' near Wellington, New Zealand.

Statistics

Statistical analyses were carried out in SYSTAT (Wilkinson, 1990).

Results

Stomach contents

· Particle size distributions were determined for digesta from 23 randomly chosen gut samples (table 1). These results are shown as the cumulative percentage of particles below a given size plotted against particle size (fig 1) using the method described by Voon et al. (1986). Similar plots, of the particle size distributions of the stomach contents of euros (*Macropus robustus erubescens*) and wallaroos (*M. robustus robustus*) shot whilst grazing (Freudenberger, 1992) and from brushtail possums (*Trichosurus vulpecula*) fed on natural foliage (Foley and Hume, 1987), are shown for the purposes of comparison.

Variation in the relative proportions of each particle fraction in the stomach digesta (measured as grm dry matter per grm dry matter of digesta) of the 23 animals, according to gender or 'time when shot' ('PM' or 'AM') was assessed using multivariate (discriminant) analyses. These showed no significant variation of these parameters either between the classes based on sex (Wilks' Lambda $p = 0.264$) or based on time when shot (Wilks' lambda $p = 0.522$).

Feeding behaviour

There were clear differences between the feeding position that was adopted when browsing and that adopted when grazing, both in the laboratory and in the field.

Grazing behaviour

Wild Tammars favoured grazing areas where the sward was short. They were never observed feeding in areas where tillers were longer than 50 mm. When feeding on short sward the animals adopted a typical quadrupedal posture, but often with the forelimbs tucked up. They grazed in this posture for relatively long periods (Lentle et al. Chapter 4). Grazing was characterised by continuous regular chewing movements of the jaw accompanied by intermittant biting activity that was recognisable by sudden small jerking semirotations of the head that were concurrent with irregularly spaced noises on the microphone recording (fig 2).

Browsing behaviour

Typically tammars would detach a leaf by biting through its petiole. With smaller leaves, progressive ingestion by action of teeth and lips alone would immediately follow. With larger leaves, the initial bite was maintained whilst the forelimbs gripped the leaf, most commonly by use of mutually opposed palms but sometimes by use of the flexed digits of a single forelimb in a digitopalmar grip (Markze and Shackley 1986). The application of forelimb grip using either method was often unsuccessful, the leaf being dropped and discarded on a significant number of occasions (see table 3). The use of a grip described in the phascolarctinae (Lewis 1985; 1989) in which the first and second digits are opposed with the lateral three digits in a pincer action (Lewis 1989), was never observed. The period of chewing that followed ingestion of a leaf was significantly longer than that following cropping of grass.

Oral processing

a) Mahoe leaf ingestion analysis

The mean weight of mahoe leaves used for this experiment was 0.0012 g dry weight, or 0.00385 g wet weight (n = 200). Analyses (table 2) showed remarkably consistent chewing time per bite. All three animals frequently dropped leaves prior to, and during, the process of their consumption. The percentage of leaves dropped in this manner was recorded as 'drop rate' (table 2).

b) Feeding sound analysis

Results of feeding sound analysis are shown in table 3. The average duration of one 'chewing cycle' (Hiiemae, 1978) (time from commencement of one chewing sound until the commencement of the next) was 0.394 ± 0.016 sec. Chewing rate, biting rate and number of chews per bite all varied significantly on repeated measures ANOVA (table 4) between (grazing and browsing) sites.

Note that although the denominator degrees of freedom are low due to the small number of animals, the tabulated results are nevertheless statistically significant at the 5% level.

Discussion

Particle size distributions varied little between tammar stomach samples but differed considerably from those obtained by Freudenberger (1992), for the wallero and the euro, having a consistently lower percentage of larger and a higher percentage of smaller particles. Cumulative plots of percentage dry weight against maximum size of ingesta particles are known to approach the ordinate more closely as the number of chews per mouthful increases (Voon et al. 1986). The plot obtained from the averaged particle distributions of tammar wallabies is closer to the ordinate than for the euro and walleroo (Freudenberger 1992) and close to that of the brushtail possum (*Trichosurus vulpecula*) (Foley and Hume 1987)(fig. 1).

This finding supports the hypothesis that the relative increase in time spent feeding by tammar wallabies (Lentle et al. Chapters 3 and 4) results in more extensive comminution of food and achieves particle size distributions more like those of a small 'colon fermenting' marsupial folivore (Hume and Warner 1980).

The results from previous studies on the dynamics of volatile fatty acid (VFA) production at various gut sites in different wallaby species permit some speculation as to the possible site where smaller food particle size is likely to benefit the fermentation process. The concentrations and production rates of VFAs were higher in the pademelon *(T. Thetis)* stomach (Dellow and Hume 1982b), than in the stomach of similar sized tammar wallabies maintained on the same feed (Dellow et al. 1983). Conversely, VFA concentrations were higher in the tammar hindgut than in the hindgut of pademelons (Dellow and Hume 1982b). Bearing in mind the higher intake of digestible organic matter by the pademelons (Dellow et al. 1983) and the shorter transit time of particulate phase markers in pademelons than in tammars (Dellow 1982), it seems likely that any fermentative benefit that results from greater particle size reduction and reduced throughput will accrue in the hindgut. The similarity between particle size distributions of tammars and those of the brushtail possum, a 'colon fermenting' (Hume and Warner 1980) species (Wellard and Hume 1981), adds further weight to the hypothesis that small particle size specifically aids large gut fermentation.

The tammars used for this study may be derived from Kangaroo Island stock (Van Oorschot et al. 1989) and a strategy of more extensive comminution may have evolved because of the seasonal scarcity of carbohydrates known to affect tammars living on this site (Hume 1982).

The lack of any significant difference in the relative proportion of different particle sizes between samples obtained in the early evening, when browsing was likely to have recently taken place (Lentle et al. in prep), and those obtained later in the night, when recent grazing was more likely, indicates that the particulate characteristics of ingesta are the same regardless of whether they derived from browsed or grazed material. Chewing efficiencies are known to be lower when larger leaved forages are masticated by ungulates (Dryden et al. 1996) thus this finding may indicate greater chewing investment by macropods when browsing. This conclusion is also borne out by the significantly higher chew to bite ratio during browsing which suggests that the average number of chews required to reduce a bite of browse to the requisite dimensions is higher. This conclusion applies, even if greater quantities of browse than of graze are ingested per bite, as chewing efficiencies are known to decline when mouthful increases above optimum (Lucas 1994; Lucas and Luke 1984).

The high rate of dropping of leaves may be related to the loss of sectorial premolars in this species. The Forest wallaby (*Dorcopsis luctuosa*), a species adapted to browsing, grasps leaves by biting (Menzies 1989) in a similar manner to that described here. However this species used the recessed crests of their sectorial premolars in a lateral mouth grip, rather than an anterior mouth grip with the flat crests of the incisor crowns as was observed in this study and reported in another grazing species, the agile wallaby (*Macropus agilis*) (Menzies 1989).

Using the overall average of 110.8 secs eating time per leaf and a total daily feeding time of 22346 secs per day (Lentle et al. Chapter 3 and 4), the maximum daily dry matter intake (DMI) would be 48.41 g/24 h. An average leaf dropping rate of 49 % would reduce the DMI to well below that of tammars fed chopped carrot (73.1 g/ 24 h) (Lentle et al. Chapter 4), pelleted lucerne hay (155 g/ 24 h) (Warner, 1981), chopped lucerne hay (94 g/ 24 h) (Dellow and Hume, 1982a) or freshly cut phalaris grass (115 g/24h) (Dellow and Hume, 1982b) and well short of the 115g DM/ 24 h that is necessary to maintain the field metabolic rate of a 4.4 kg. tammar (Nagy et al., 1990).

A lack of efficiency in the chewing of browse may result from limits to the maximum speed of the chewing cycle (Hiiemae, 1978). The overall average chewing cycle time (0.394 ± 0.016 secs) for tammar wallabies obtained in this study is remarkably similar to that reported for the American opossum (*Didelphys marsupialis*) (0.390 ± 0.048 secs) (Hiiemeae, 1978) and the similar sized Rhesus monkey (*Rhesus mulatta*) (0.317 - 0.360 secs) (Lushei and Goodwin 1974). This finding is in line with Hiiemae's (1978) conclusion that chewing rate does not increase with decrease in species body weight. Thus the increases in chewing investment that are required when browsing, may not be achieved by an increase in chewing rate. Indeed in this study chewing rates when browsing were significantly lower than when grazing. The loss of concurrence of cropping with chewing activity that occurs during grazing and its substitution by mutually exclusive biting and chewing activities during browsing in the manner that has been modelled by Spalinger and Hobbs (1992) may further reduce masticatory efficiency.

The results of this study suggest that tammar wallabies reduce ingested food to a smaller particle size than do other macropods of similar size, a strategy that necessitates an increased investment in chewing and a relative increase in average daily eating time (Lentle et al., Chapters 3 and 4). The inefficency in the handling of browse and the need for an even higher chewing investment when browsing may be more potent factors in this species preference for grazing (Williamson 1986) rather than any need for specific nutrients. Thus the nutritional ecology of this small herbivore may be influenced more by the physical characteristics of food plants (i.e. potential handling time), than by any variation of the anatomy in the alimentary tract, a conclusion similar to that obtained from work on African ruminants by Gordon and Ileus (1996).

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Fig 1: Cumulative distributions of percentage dry weight of stomach ingesta of tammar wallabies according to maximal particle size.

Dotted line, calculated from averaged sieving results of stomach contents of 8 euros and 8 wallcroos (Freudenberger, 1992); Solid line, calculated from averaged sieving results of stomach contents of 25 tammars (this study); Dashed line, calculated from averaged sieving results of stomach contents of 3 brushtail possums (Foley and Hume, 1986).

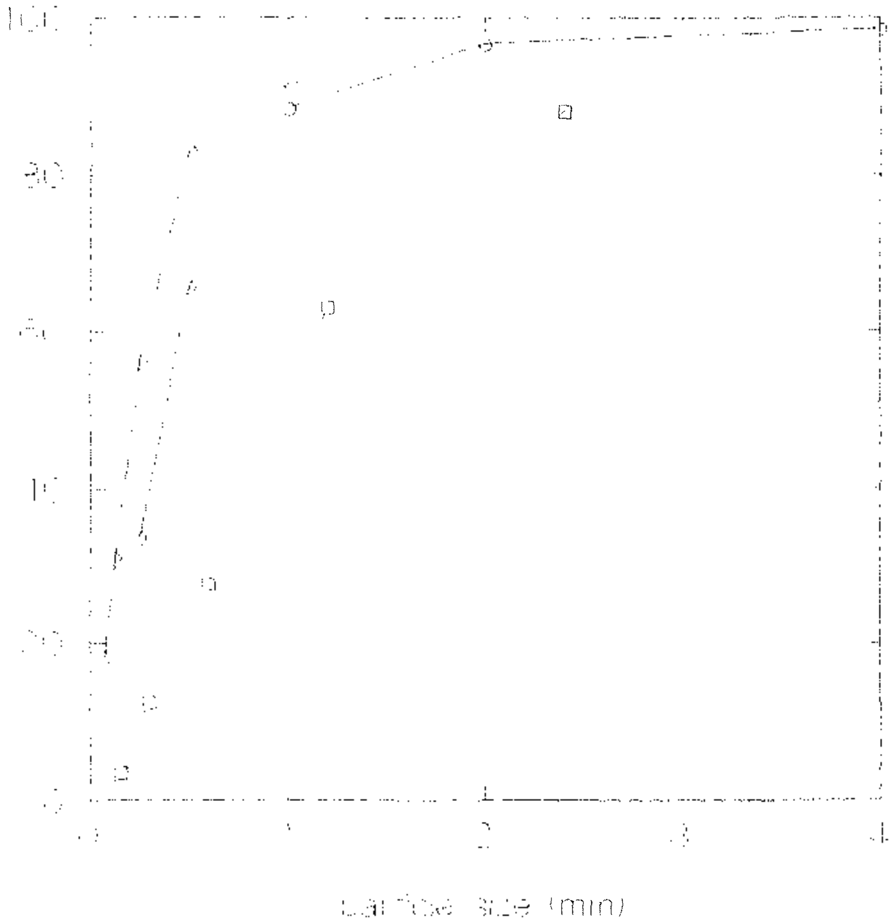
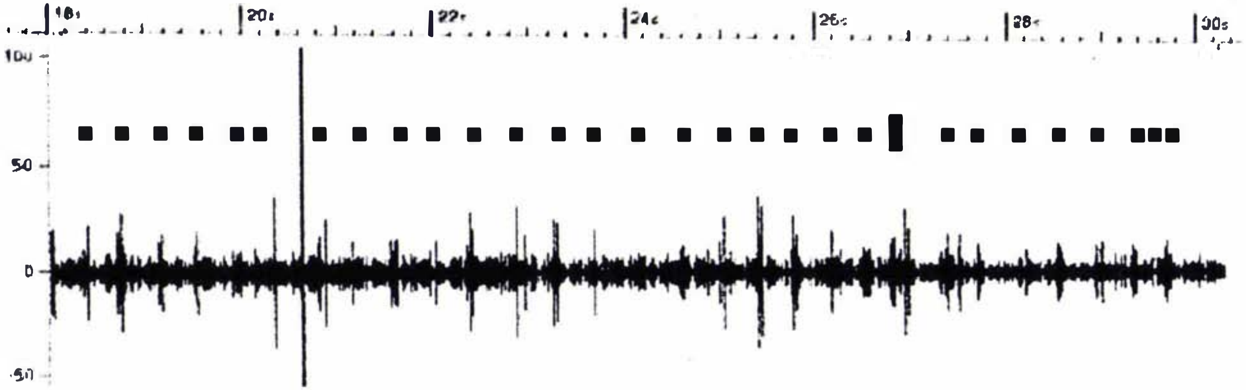

100
80
60
40
20
0
0
1
2
3
4
Particle Size (mm)

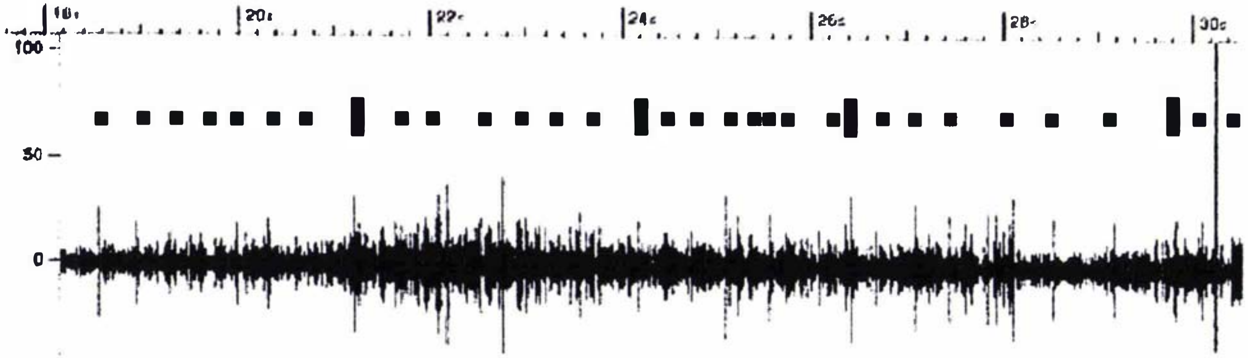
Fig 2: Audiographic recordings of the eating noises occurring during browsing and grazing activities of a tammar wallaby in the Rotorua district of North Island, New Zealand.

A, Typical browsing recording showing regular pattern of chewing sounds with comparatively few biting sounds; B, Typical grazing recording showing more frequent biting sounds and less regular chewing sounds. Accurate distinction between biting and chewing sounds is not possible without simultaneous auditory replay, particualry during grazing when there is more extraneous noise from brushing of the snout against vegetation. The concurrence of sounds with the graphic representation is indicated by the travelling cursor (shown in both plots) above. Horizontal scale is calibrated in seconds. Vertical scale is arbitrary units of amplitude.‘ ’, chewing noise; ‘ ’, biting noise.

A


18s
20s
22s
24s
26s
28s
30s
100
50
0
-50

B


18s
20s
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30s
100
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0

Table 1: Particle size distribution analysis (g dry weight/ g total dry weight recovered) in total stomach content of 23 free ranging tammars from an ecotone site in Rotorua New Zealand.

	Particle size					
	>4 mm.	**2-4 mm**	**1-2 mm**	**0.5-1 mm.**	**0.25-0.5 mm.**	**>0.25 mm.**
n	23	23	23	23	23	23
mean	0.011	0.015	0.064	0.181	0.253	0.267
se	0.003	0.002	0.006	0.008	0.010	0.012
% of DM	1.3	1.9	8.1	22.9	32.0	33.7

Table 2: Analysis of the consumption of mahoe leaves by three adult female captive tammars.

* video analysis; # direct observation.

** Percentage of leaves dropped prior to and during the process of their consumption.

Animal		Time spent eating a leaf	Time spent chewing per bite	Drop rate** %
*a	mean	116.97	55.82	60
	s. e.	34.77	8.373	
	n	14	30	18
*b	mean	103.23	55.17	58
	s. e.	44.89	3.66	
	n	7	31	17
#c	mean	112.162	52.01	30
	s. e	26.85	4.22	
	n	13	13	4
overall	mean	110.79	54.33	49

Table 3: Chewing rate, biting rates and chews per bite obtained from radio-microphone surveillance on four adult free ranging tammars (three female and one male). Chewing rates and biting rates are expressed as time in seconds between successive acts i.e duration of cycle. Chew to bite ratio is expressed as number of chews per bite.

Animal		a		b		c		d	
		Grass	Bush	Grass	Bush	Grass	Bush	Grass	Bush
Chew rate	Mean	0.350	0.44	0.338	0.44	0.35	0.44	0.35	0.45
	SE	0.008	0.008	0.013	0.010	0.008	0.005	0.042	0.036
	N	9	18	8	22	24	32	2	5
Bite rate	mean	0.83	15.82	1.80	12.67	3.79	18.07	4.49	9.57
	SE	0.16	3.34	3.77	2.517	0.63	2.50	1.20	1.5
	n	8	13	9	20	23	29	6	8
Chew/bite	mean	1.54	33.8	4.52	26.06	9.989	38.1	11.282	19.3
	SE	0.544	7.828	1.507	5.827	1.726	5.627	2.327	3.183
	n	8	13	9	20	23	29	6	8

Table 4: Repeated measures ANOVAs on radio-microphone data from three free ranging female and one male tammar showing variation of chewing rate (s per cycle), biting rate (s per cycle) and number of chews per bite with grazing and browsing

	Grazing / browsing		
	F ratio	DF	P
Chewing rate#	67.123	1/2	**0.015**
Biting rate	19.14	1/3	**0.022**
No of chews per bite	14.712	1/3	**0.031**

3 females only

Chapter 6

Incisor and Molar wear in the tammar wallaby (*Macropus eugenii* Desmarest).

R. G. Lentle, K. J. Stafford, M. A. Potter, B. P. Springett and S. Haslett.

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Incisor and molar wear in the tammar wallaby (*Macropus eugenii* Desmarest).

R. G. Lentle [1], K. J. Stafford [2], M. A. Potter [1], B. P. Springett [1], S. Haslett [3]

[1] Department of Ecology, Massey University, Private Bag 11222, Palmerston North , New Zealand.

[2] Department of Veterinary Clinical Sciences, Massey University, Private Bag 11222, Palmerston North, New Zealand.

[3] Department of Statistics, Massey University, Private Bag 11222, Palmerston North New Zealand.

Abstract

The morphology of incisor and molar teeth of tammar wallabies (*Macropus eugenii* Desmarest) is similar to that of the archetypal grazing macropod (*M. giganteus*) but there are some resemblances in the wear pattern of molars to that of grazer/browsers. Incisor wear patterns show that cutting during biting is by scissor-like action of the elevated lingual enamel edge of an attrition facet on each lower incisor being occluded with, and rotated infero-laterally across the buccal surface of the upper incisor arcade. With increase in age and body size, the cutting surface moves from anterior to lateral upper incisors, progressive wear on the inner surface of the lateral upper incisors permitting an increasing degree of incisor action coincident with medial molar movement in phase 2 occlusion which is similarly achieved by lateral rotation of the jaw.

Significant distal movement of the reference point for molar index, along the line of the upper jaw, with increase in body size, indicates that this index does not measure the absolute mesial movement of molars in the plane of occlusion. The estimated value of absolute mesial movement of the first upper premolar along the line of the jaw (2.45 mm/yr) is at the known limits of mesial drift. Studies of size related changes in the linear dimensions of various bony landmarks on jawbone and skull indicate that the high rate of movement may result from deposition of bone in the rear of the tooth row, i.e. ‘mesial shift’, as well as mesial drift. However mesial shift may not account for significant differences in rates of absolute mesial movement of upper molars with gender.

With increase in body size, the caudal insertions of the masseter and temporalis and the cranial origin of the line of action of masseter all move distally along the plane of occlusion. However a concurrent mesial movement in the cranial origin of the line of action of temporalis may act to counter any distal movement of occlusive force along the jaw-line and to decrease the relative force of the retraction component that aids phase 1 occlusion.

Introduction

The eating habits of macropodids have been categorised on the basis of their dental morphology, in particular their premolar and molar anatomy and extent of molar progression (Sanson 1978; 1980; 1989; Hume 1982). Sanson's (1978; 1980; 1989) analyses distinguished between grazing and browsing types but did not take account of the dietary differences arising intra-specifically due to age or gender. Among the macropod species classified by Sanson (1978) as grazers, several including the tammar (*Macropus eugenii)* (Williamson 1986), the agile wallaby (*Macropus agilis)* (Bell 1973) and the western brush wallaby (*Macropus irma*) (Algar 1986) are known also to consume browse.

Two factors influence the relative position of teeth in the jaws through time. Firstly, the accumulation of bone by ossification centres in the skull or mandible, a process which continues through life in a number of macropod bones including those of the skull (Jarman 1989). Secondly chewing, which is an outcome of the physical characteristics of the diet, may act via propalinal occlusion pressure (Sanson 1989) to change the position of the molar row relative to that determined by bone growth alone (Sanson 1980).

The 'index of molar progression' of upper molars has been shown to increase with age in a number of macropod species (Kirkpatrick 1964; 1965; Dudzinski *et al.* 1977; Wilson 1975; Sanson 1980) including tammars (Inns 1982) and has been subsequently employed as means of comparing age (Sanson 1980). This index, in measuring the relative movement between the upper molar row and a reference point on the zygomatic arch in units of propalinal tooth width, introduces two variables which may confound the outcome of studies that seek to assess the influence of diet on the forward movement of the molar row in the occlusal plane. Firstly as the zygomatic arch links two functionally separate bone structures, the facial and the neural skull (Vilman and Moss 1980) whose rates of growth may differ over time (Jarman 1989), and be differently influenced by factors such as sexual dimorphism (Jarman 1989) its position with respect to the maxilla may vary. Secondly, in measuring progression in multiples and fractions of propalinal molar length, Kirkpatrick's (1964) index introduces a non-linearity that varies in proportion to relative sizes of the teeth in the molar row and renders inter-species comparisons difficult. Therefore, for studies which attempt to assess the influence of diet and of bone accretion on forward tooth progression, the index of molar progression may not be meaningful and should be accompanied by an assessment of the actual rate of mesial movement along the line of occlusion. Thus while it is known that the index of molar progression may vary between sexes and between populations (Newsome et al. 1977) these findings have not been related to the degree of true forward movement of the tooth row in the occlusal plane.

Anterior (mesial) movement of erupted molars relative to the jaw is recorded in a number of species other than macropods e.g. *Macaca fasicularis* (Moss and Picton 1982) *Rattus norvegicus* (King *et al.* 1991) and *Homo sapiens* (Moss and Picton 1975) in which it is known as 'mesial drift'. Hypotheses for the mechanism of molar progression (Sanson 1989) are strikingly similar to those for mesial drift (Moss and Picton 1982). In both cases the forces that induce tooth movement are thought to be transmitted by transeptal fibres within the peridontal ligament producing forward drift of distal molars into gaps (Papandreas *et al.* 1993) such as the 'leeway space' (Araya and Savara 1977) left by deciduous teeth.

Tammars reduce the particle size of their food to unusually small dimensions (Lentle *et al.* Chapter 5) a process that may result in excessive tooth wear. Tooth wear is known to reduce the ability of *Pseudochireus peregrinus* to digest food (Gipps and Sanson 1984) and may influence dietary choice by its effect on masticatory efficiency (McArthur and Sanson 1988). Molar activity and wear may be reduced by transferring the work of particle size reduction onto incisors thus ingesting a greater proportion of the smaller food particles that result from smaller bites. It is therefore important to study wear of incisors and of molars concurrently.

The mode of action of macropodine incisors in which the lower procumbent incisors act against those of the upper incisor row was first described by Waterhouse (1845) and subsequently confirmed by Anderson (1927). However neither worker described the cutting site in detail nor the disposition of the wear facets on the incisor teeth. This is important in view of the morphological variation of macropod upper incisors according to dietary grade (Sanson 1989).

In this study the dental morphology, the extent of tooth wear and the mechanism of molar movement in the jaws of tammar wallabies (*Macropus eugenii* Desmarest), were investigated. This species has been classified as a member of the subgeneric group Notamacropus (Flannery, 1989). A number of species within this subgroup possess a tooth configuration characterised by long narrow lower incisors and short molars and premolars, the reasons for which are currently unknown.

Methods

Eighty six tammar wallabies were shot on a single night in an area of the Okataina State Forest in the Rotorua region of North Island New Zealand as part of pest control operation conducted by the Bay of Plenty Regional Council. They were measured, weighed, sexed and skull tags attached. A gross dissection of the principal muscles of mastication was performed on the heads of five male and two female tammars. The attachments of each muscle were identified and subsequently freed so that the body of the muscle could be removed and weighed. Distinction between the deep surface of the masseter and the subjacent surface of the temporalis, in the area lying deep to the zygomatic arch, was made difficult by the lack of any integument separating the two muscles. We therefore adopted the protocol used by Barbour (1963) and by Ride (1959) in allocating any muscle tissue arising from the zygomatic arch to the masseter and any arising from the temporal fossa or temporal fascia to the temporalis muscle.

All remaining skulls and mandibles were cleansed of flesh and the following measurements recorded.

1) Molar index, as described by Kirkpatrick, (1964) and Inns, (1982) i.e. the number and fraction of propalinal tooth lengths anterior to a line passing sagittally and tangentially across the anterior rims of the orbits with the skull held in a position with the palate at 90 degrees to the line of vision.

2) The length of the lower jaw (LJ), measured along a line running parallel to the line of occlusion from the anterior limit of the mandible, i.e. the leading edge of the most anterior alveolus, to the point of intersection with a line projected inferiorly at right angles to the line of occlusion from the posterior aspect of the ipsilateral craniomandibular joint facet (Fig 1a).

3) The distance (MO), measured along a line running parallel to the line of occlusion from the point where the anterior crest of the ramus of the mandible crossed the superior limit of the body of the mandible to the point of intersection with a line projected inferiorly at right angles to the line of occlusion from the posterior aspect of the ipsilateral craniomandibular joint (Fig 1a).

4) The distance of the anterior limit of the reverse curve of spee of the lower jaw from the rear of the jaw-line (CD), measured along a line running parallel to the line of occlusion, from the most anterior point of the junction of the curve of spee with the ramus of mandible to the point of intersection with a line projected inferiorly at right angles to the line of occlusion from the posterior aspect of the

ipsilateral craniomandibular joint facet (Fig 1a). This distance was more difficult to accurately assess in older and larger specimens in which the anterior face of the curve was less steep.

5) The length of upper jaw (UJ), measured along a line running parallel to the line of occlusion, from the anterior point of the pre-maxilla to the point of intersection with a line drawn sagittally from the ipsilateral craniomandibular joint (Fig 1a).

6) The distance of the anterior limit of the first upper molar from the rear of the jaw-line (UM1), measured along a line running parallel to the line of occlusion, from the anterior rim of the anterior cingulum of the tooth to a line projected sagittally from the ipsilateral craniomandibular joint facet (Fig 1a).

7) The distance (MP) from the reference point used to determine molar index (Kirkpatrick 1964; 1965; Dudzinski *et al.* 1977; Wilson 1975; Sanson 1980) to the rear of the jaw joint, measured along a line running parallel to the line of occlusion, from the most anterior limit of the internal profile of the zygomatic arch (viewed at right angles to the plane of the palate) to the posterior limit of the ipsilateral craniomandibular joint facet (Fig 1a).

8) The distance (MA) from the most anterior site of attachment of the deep fibres of the masseter to the rear of the jaw-line, measured along a line running parallel to the line of occlusion, from to the tip of the inferior zygomatic process to the posterior limit of the ipsilateral craniomandibular joint facet.

9) The distance from the most anterior point of attachment of the temporalis muscle to the rear of the jaw joint (TA), measured along a line running parallel to the line of occlusion, from the most anterior limit of insertion to the point of right-angled intersection with a line projected inferiorly from the posterior aspect of the ipsilateral craniomandibular joint (Fig 1a). The most anterior point of attachment of the temporalis muscle was distinguishable in cleaned skulls as the point at which the fine bony elevated line on the surface of the temporal fossa, coincident with the anterior attachment of the temporalis facia and associated muscle, merged with a similar fine bony line running anteriorly from the occiput to the rim of the orbital fossa (Fig 1a).

10) The distance from the most posterior point of attachment of the temporalis muscle to the rear of the jaw joint (TP), measured along a line running parallel to the line of occlusion, from the most posterior limit of insertion to the point of right-angled intersection with a line projected inferiorly from the posterior aspect of the ipsilateral craniomandibular joint (Fig 1a).

11) The index of wear of the procumbent incisors was the maximum length of the triangular wear facet on the supero-lateral side of the tooth (Fig 7 a and b) measured parallel to the long axis of the tooth.

12) Wear of upper incisors was scored using criteria devised by us (Fig 2) and that of the lower second premolar and molars was assessed using criteria similar to those of McArthur and Sanson (1988) but modified in view of the wear pattern described below (Fig 3).

13) The maximum potential contact between upper and lower incisors was determined using a method similar to that described by McArthur and Sanson (1988) by placing dental articulation paper between the opposing teeth, manipulating the lower jaw and examining the teeth for staining. This procedure was conducted on fresh intact heads and on those from which the muscles of mastication had been removed as well as on dried skulls and jaws.

The following dimensions were derived from these measurements. The length of the body of mandible anterior to the ramus (BD) was calculated as (LJ-MO). The length of the body of mandible bearing the lower premolar/molar array (LDENT) was calculated as (CD-MO). The distance (MPT) between the midpoint of the cranial insertion of temporalis and the rear of the temporomandibular joint, measured along a line running parallel to the plane of occlusion, was calculated as [{1/2(TPA+TPJ)}-TPJ]. Similarly the distance (MPM) between the midpoint of masseter and the rear of the temporomandibular joint was assumed to be MA/2 in view of the pattern of insertion that is described below.

All measurements were taken with vernier callipers and the positions of projected lines determined by the use of fixed set squares. Both sides of the skull were measured and the mean of the two readings used in subsequent calculations. Scanning electron microscopy was carried out on a Cambridge model 250 Mk 3. All specimens were coated with gold within a vacuum evaporator.

Statistics

Statistical calculations were carried out on the SYSTAT statistical software package (Wilkinson, 1990) using averaged values of right and left jaws.

Many of the analyses undertaken were simple linear regressions which indicated how one variable (the dependant variable) was best predicted from another (the independent variable). The accuracy of this prediction was indicated by the correlation coefficient between the two variables. The relationship between the variables is defined as; dependant variable equals the gradient times the independent variable plus a constant, so that the gradient equals the expected change in the value of the dependant variable for a change of one unit in the independent variable. Gradients can be positive or negative in value. Generally simple linear regressions involving ratios of variables have been used. This has been done for historical reasons. However, the alternative method of taking logarithms (in the context of multiplicative rather than linear models) yields identical conclusions about anatomical relationships. Where ANCOVA was performed the distribution of the residuals was tested for normality using Lillifors test.

Results

Wear pattern, articulation and microscopic characteristics of incisors

The first upper incisor was not greatly disproportionate in size as has been described in macropods of browsing grade (Sanson, 1989) i.e. the second and third upper incisors were well developed. A sloping concave attrition facet with centrally exposed dentine was evident on the lingual aspect of the crown of all six upper incisors in adult specimens (Fig 2). Together these formed a conjoined longitudinal concave facet that was coincident with an extensive attrition facet on each of the two procumbent incisors (Fig 7a) in adult specimens. In juvenile specimens this facet was limited to the lingual aspect of the crown of the first upper incisor (Fig 2) and was in a position corresponding to a less extensive attrition facet on the tip of the procumbent incisor (Fig 7b). Wear patterns of upper incisors demonstrated progressive extension of attrition facets, from the first to the third incisors, with increasing age and body size (Figs 2 and 4).

No attrition facet formation, such as previously described by Anderson (1927), was observed on the mutually opposed medial surfaces of the procumbent incisors. However sharply delineated, broadly planar attrition facets occurred on the anterolateral aspects of the tips of the procumbent incisors (Fig 7a and b). In larger facets, the surface enamel was breached and brown dentine interposed between a raised thicker labial enamel layer and a noticeably thinner lingual enamel layer (Fig 8a and 2d). The outer half of the labial enamel layer showed parallel striations (Rensberger 1978) which were more numerous and oriented at right angles to the long axis of the tooth (Fig 8a) in the more posterior parts of the larger facets. At the anterior limit of the larger facets the striations were reduced in number and were oriented parallel to the long axis of the tooth (Fig 8c). Flake pits (Rensberger 1978) were seen on the inner edge of the labial enamel layer which projected above the dentine (Fig 8a). The exposed surfaces of the dentine and the lingual enamel layer were polished (Rensberger 1978) (Fig 8d) and bore no striations.

The wear facets of the procumbent incisors in the largest skulls extended more posteriorly along the supero-lateral edge of the procumbent incisor as well as more ventrally to form a triangle (Fig 7a). In this case there was uniform occlusion with a conjoined curved facet on the buccal surface of the upper three incisors in the manner described above (Fig 2). Articulation tests showed that it was possible, in these larger specimens, to rotate the hemi-jaw in the manner described by Sanson (1989) and thus partially displace the lower molar row lingually from occlusion with the ipsilateral upper molar row whilst the upper and lower incisor facets remained in occlusion.

In the smallest specimens, where attrition facets were limited to the extreme antero-lateral tip of the procumbent incisor at the point of its articulation with the buccal surface of the first upper incisor (Fig 7b), the more posterior portions of the lateral edge of the procumbent incisor did not come into contact with the more laterally placed upper incisors. Articulation tests in these specimens showed that it was not possible to rotate the hemi-jaw in the manner described by Sanson (1989) and displace the ipsilateral lower from occlusion with the upper molar row whilst the upper and lower incisor facets remained in occlusion.

The LOWESS (Cleveland 1981) smoothed scatterplot (Fig 5) of propalinal length of the procumbent incisor attrition facet against jaw length shows their relationship is linear and positive above jaw length values of 5.6 cm. Given the mass of points with less than one millimeter of incisor facet length, a linear or quadratic regression has not been fitted, since either form of regression would yield negative fitted values of jaw length, which is clearly impossible.

Anatomy and wear patterns of molars and premolars

The premolar and molar row of the lower jaw was in the form of a longitudinal inverse curve of spee. The anterior face of the curve was noticeably less steep in larger specimens. Upper and lower (p2) and (p3) premolars were small in size. Both p2 and p3 were present in the upper jaw of a few larger/older animals. A planar attrition facet developed on the crown of the (p_3) lower premolar in some larger specimens (Fig 7c and e). The upper and lower deciduous premolars (Dp3) were molariform and often present in larger animals. Molars had broad anterior cingulae and a well developed link structure (Fig 7d and e). Whilst the occlusal surface of the upper premolar/molar row was inclined medially, wear fell evenly on anterior and posterior lophs of each lower molar i.e. dentine was exposed on the hypoconid and sometimes on the entoconid prior to the coalescence of exposed dentine of the protoconid and metaconid (Fig 7e). Whilst there was extensive broadening of exposed dentine on the two lophs with attendant loss of sagittally-oriented cutting edges (Fig 7c and d) as described in association with class seven of Mc Arthur and Sanson's (1988) wear index scale, the maximum wear class could not be categorised as higher than five owing to the failure of exposed dentine on anterior and posterior lophs to join along the line of the mid-link. Wear criteria defined by McArthur and Sanson (1988) were therefore modified to take account of some of these differences (Fig 3). Bar charts of averaged wear scores are shown in Fig 6. They illustrate a steady progression of wear across the molars with increase in size and relative age of the animal.

Palatal anatomy

The anterior portion of the soft palate had two transverse ridges of elevated mucosa each with a gently sloping anterior face and a sharply angulated posterior face (Fig 7f). In cadaver specimens, a flow of water directed rearwards across the line of these ridges caused them to be depressed whilst a forward flow of water caused them to become elevated.

The muscles of mastication

The insertions of the muscles of mastication were broadly similar to those described in a number of macropodine species by Abbie (1939), and by Sanson (1980) and in *Trichosurus vulpecula* by Barbour (1963) (Fig 1). The masseter (Fig 1b), the largest muscle (Table 1) of mastication was attached cranially to the infero-lateral, inferior and deep surfaces of the zygomatic arch, its fibres running caudo-ventrally to their caudal attachments on the ramus of mandible. Fibres from the superficial layer were inserted into the ventral and caudal edges of the ramus whilst fibres of the deeper layers were attached to all of the inflected lateral surface of the ramus. In the region of its cranial insertions the masseter muscle was of uniform thickness. In the region of its caudal insertions the thickness of the masseter muscle was greatest at the anterior limit of the inflected portion of the lateral ramus where fibres entered a masseteric canal that was situated just caudal to the junction of thickened anterior edge of the ramus with the body of the mandible. The anterior limit of the cranial attachment of the masseter muscle was at the inferior process of the zygomatic arch which was prominent in this species. The posterior limit of the cranial attachment of the deep masseter was at the posterior limit of the zygomatic arch at a point close to the temporomandibular joint.

The temporalis muscle, (Fig 1c) was attached cranially to the temporal fossa of the skull and the temporal fascia and was inserted ventrally onto the lateral surface of the coronoid process and the frontal border and medial surface of the ramus. The most anterior cranial attachment of the temporalis was at the posterior limit of the superior crest of the orbital fossa, at the junction point of a thin bony line marking the anterior limit of the temporal fossa with a similar line marking the superior limit of the temporal fossa. The most posterior cranial attachment was at the posterior limit of the parieto-occipital eminence. The temporalis muscle was of uniform thickness in the region of its cranial insertions and was thickest in its caudal insertion just distal to the anterior edge of the ramus of mandible.

The medial pterygoid (Fig 1d) was attached to the medial pterygoid plate and the pterygoid fossa of the sphenoid, its fibres travelling a short distance caudally and ventrally to gain attachment on the whole of the pterygoid fossa which was situated on the medial aspect of the ramus of mandible. The lateral pterygoid is not described in detail as its fibres lay more or less parallel to the long axis of the mandible and thus could not contribute significantly to occlusion of the jaw.

The weights of the principal muscles of mastication varied with body weight but the relative proportions of the masseter and temporalis muscles did not (Table 1). In view of the fact that the cranial attachments of the masseter and temporalis were of uniform thickness along their length, an indication of the cranial origin of their line of action (Badoux, 1975) of each muscle was given by the position of the midpoint of a line drawn parallel to the plane of occlusion through its cranial attachment (Badoux, 1964).

Changes in tooth position, jaw length and insertions of the masticatory muscles with body size.

1) Molar index and mesial movement of the first upper molar.

There was significant linear regression of the molar index against upper jaw length (UJ) and against indices of body size (Table 2) indicating that the length of the upper jaw increased significantly with age and that molar index increased with body size.

Regression of molar index against distance of the first molar from the ipsilateral jaw joint (UM1) was significant and positive (Table 2). As the age of the subjects was unknown, we calculated an overall value for the rate of forward (mesial) movement of the first upper molar from the jaw joint per annum using the coefficients describing the relationship between age and molar index reported by Innes (1980) ($\log_{10}$ age in days = 2.0939 + 0.4067{MP}) to determine mean annual rate of increase in molar index (0.743 MP units/yr) and applying this to the parameters obtained in our regression of molar index against UM1. This gave an overall rate of mesial movement of the first upper molar of between 2.23 and 2.67 mm/year, assuming that the relationship between molar index and age was the same in the two populations.

ANCOVA (Table 3) of the distance of the first upper molar from the rear of the temporomandibular joint (M1) against indices of body size as dependant variables showed a significant effect of gender and significant effects of the interaction term between gender and M1.

2) *Age and body size related changes in the relative position of the reference point for molar progression along the line of the upper jaw.*

There was a significant negative regression of the ratio MP/UJ both with body weight, with whole body length and with molar index (Table 2) indicating that, with increase in age and body size, the reference point from which the molar index was measured moved rearwards with respect to the upper jaw-line.

3) *Age, body size and gender related changes in the relative length of the body of mandible and in the relative length of jaw bearing the erupted premolar/molar row.*

There was a significant positive regression of the ratio BD/LJ against Body weight, whole body length and molar index (Table 2) indicating that with increase in body size and age there was an increase in the relative proportion of the body of the lower jaw.

There was a significant positive regression of the ratio LDENT/LJ against whole body length and molar index (Table 2) indicating that, with increase in body size and age, there was an increase in the relative proportion of the part of the body of mandible bearing the lower premolar/molar array.

ANCOVAs of the ratio BD/LJ (Table 4) against the dependant variables of body weight, and molar index showed no significant interaction terms with gender, indicating that there was no significant difference according to gender, in the rate of change of the ratio with body size or age.

4) Changes in the positions of the insertions of the principal muscles of mastication with body size.

The medial and lateral pterygoid muscles were of relatively low mass compared to the masseter and temporal muscles (Table 1) moreover the site of their insertion and their orientation with respect to the long axis of the premolar/molar row was such that the resultant of occlusion (Badoux, 1975) was likely to be small and applied at a relatively short distance from the temporomandibular joint. Thus their effect in modifying the position of the overall resultant of occlusal forces acting on the premolar/molar row was likely to be relatively insignificant and was not considered in this analysis.

Change in the cranial origin of the line of action of masseter and temporalis with indexes of body size and age occurred in a reciprocal manner. There was significant negative regression of the ratio MPM/UJ against body weight, body length and molar index (Table 2) indicating that, with increase in body size and age, the cranial origin of the line of action (Badoux, 1964; 1975) of the deep masseter moved nearer, i.e. distally, toward the temporomandibular joint. There was a significant positive regression of MPT/UJ against body weight, body length and molar index (Table 2) of nearly equal and opposite gradient to that of MPM/UJ with body weight (Table 2) indicating that, with increase in body size and age, the cranial origin of the line of action (Badoux, 1964; 1975) of the deep masseter moved further away, i.e. mesially, from the temporomandibular jaw joint.

Discussion

As has been suggested by Sanson and Millar (1979) relative anterior (mesial) movement of teeth within the jaw, i.e. mesial drift, induced by forces of occlusion in chewing may be an important means for countering wear in the premolar/molar rows of grazing macropods. However the slope coefficients of a regression of molar index (Kirkpatrick 1964) against body size, such as were demonstrated in this study, do not necessarily represent the accumulated total of mesial drift that has occurred through the life of the animal, as was assumed by McArthur and Sanson (1988).

The finding that the datum point from which molar index is measured, changes in position with respect to the length of the upper jaw according to body weight, indicates that measures of molar index do not yield an absolute assessment of mesial movement of molars along the plane of occlusion of the jaw-line. Further, if the relative rate of movement of the datum point with respect of the jaw-line changes between species this may preclude any meaningful inter and intra-species comparisons. This seems likely in view of the considerable variation in zygomatic width in skulls from tammar populations in different geographic locations that were reported by Poole *et al.*(1991). On the other hand, measurements of the distance of the first upper molar from the jaw joint along the line of the premolar/molar occlusion provides a means of assessment and comparison of tooth movements on a bio-mechanical basis that is comparable between species.

Rates of mesial drift obtained with continuously applied displacement forces are known to approach the maximum turnover rate for alveolar bone (King *et al.* 1991) and are of the order of 6.7 microns per day, or 2.5 mm/yr in rats (King *et al.* 1991). Thus the rates of mesial movement of tammar first upper molars (2.23 - 2.67 mm/yr) calculated from the results of this study lie at the upper possible limits of 'mesial drift'. This conclusion will hold even if the relationship between molar index and age varies with dietary characteristics (McArthur and Sanson, 1988) as the high content of fine volcanic silica in the topsoils of the study site (G, Williamsen pers. comm.) are likely to augment the abrasive qualities of the sward (Baker *et al.* 1959) and bring about greater annual rates of increase of index than those reported by Innes (1982). The high rates of mesial molar movement may indicate the operation of a mechanism additional to that of 'mesial drift'. Overall length of jaw is known to increase though life in a number of eutherian herbivore species e.g. fallow deer (Frampton and Nugent, 1992) and red deer (Challies, 1978). A similar increase in macropods with relatively localised deposition of bone in the rear of the premolar/molar row, which we shall call 'relative mesial shift', may contribute to the high overall rates of mesial movement. The existence of such a process may be detected by its specific effect on the relative length of that portion of the lower jaw that bears the erupted premolar/molar row. Thus for example the relative proportion of the lower jaw that lies anterior to the ramus will change when there is addition of bone at the rear of the molar array, i.e. mesial shift, but will not change when there is mesial drift. The results show a highly significant increase in the relative proportion of the body of mandible to the length of lower jaw with age and with indices of body size. Moreover, there are similar relative increases in that portion of the lower jaw that is occupied by the premolar/molar row which may be viewed as of equal significance, bearing in mind the difficulties in determining the anterior limit of the curve of spee given the age related changes in its profile. The finding that mesial shift may be contributing to molar index is important from an ecological viewpoint as the rate of mesial drift is likely to be influenced by change in chewing requirement (Sanson, 1989) whereas the rate of mesial shift, i.e rate of growth of bone, is likely to influenced by the general plane of nutrition as well as by genetic differences (Frampton and Nugent, 1992). Further work using surgically implanted datum points (King *et al.*1991) will be needed to determine the relative contributions of 'mesial drift' and 'mesial shift' to the overall rates of molar mesial movement and to molar index before firm conclusions can be drawn with regard to the role of molar progression in the regulation of molar wear.

The significant differences on ANCOVA in the rate of mesial upper molar movement with body size according to gender, mirror the findings of Newsome *et al.*(1977) who showed significant differences in rate of molar progression with age in the agile wallaby *Macropus agilis*. Viewed in the light of the above findings such differences may result either from differences in mesial drift or from differences in mesial shift. The failure of ANCOVA to demonstrate a significant interaction term indicative of an effect of gender on the rate of change of the ratio (BD/LJ) with body size or with age, shows that significant difference in the rates of mesial molar movement between the sexes are less likely to result from mesial shift and thus may result from differences in mesial drift, i.e. from differences in dietary chewing requirements between the two sexes.

Changes in the location of the sites of attachment of the major muscles of mastication that are consequent on mesial shift of molars have an important bearing on theories of the function of molar progression (Sanson, 1989). The corollary of a relative increase in the length of the portion of the jaw that carries the erupted dentary is a reduction in the relative length that is available for application of occlusive force to the mandible. Similarly a decrease in the relative proportions of the mandible results in a more distal positioning of the most anterior point of insertion of the occlusal musculature, a point that is said to be positioned to yield maximum mechanical advantage (Ride, 1959). If this change were accompanied by a similar distal movement in the cranial attachments of the major muscles of mastication, the resulting distal movement of the forces of occlusion along the premolar/molar row would obviate any need for molar progression. The analysis of the relative position of the cranial origin of the line of action of the two largest muscles of mastication showed that whilst that of the masseter moved distally with increase in body size, there was an equal and opposite, i.e. mesial, movement of the cranial origin of the line of action of the temporalis. Thus whilst there was no change in the relative bulk of masseter and temporalis with body size, compensatory changes in the disposition of the cranial attachments of the major muscles of mastication may result in occlusive forces remaining localised in the same region of the molar row regardless of size. However, it should also be noted that a relative anterior movement of the cranial origin of the line of action of the temporalis muscle must also result in a decrease in the retraction component (Badoux, 1979) that is associated with phase 1 molar movement (Sanson, 1980). Again, in view of the more medial disposition of the anterior position of the temporal fossa of the skull and the more lateral disposition of the distal zygomatic arch with respect to the long axis of the lower jaw, relative mesial extension of the temporalis muscle and distal extension of masseter may result in result in larger animals having greater power in phase 2 movement (Sanson, 1980) of premolar/molar rows and in the rotational movement of lower incisors which is discussed below.

Although this study demonstrated a broad resemblance in jaw and tooth structure to that of *M. giganteus* an archetypical grazing type described by Sanson (1980), the failure of exposed dentine on anterior and posterior lophs to join along the line of the mid-link with wear is more typical of *Wallabia bicolor* a browser /grazer type (Sanson 1980) and suggests that the link structure is less prominent, i.e the links are lower in relation to the height of the lophs, in tammars than in *M. Giganteus*. This morphological difference may reflect the relative importance of larger crushing surfaces for more efficient mastication of browse (Sanson 1989) which is known to be consumed on occasion by tammars (Williamson 1986). Similarly the relatively even progression of wear across the molar rows demonstrated in this study may reflect the greater depths of occlusion that result from the lower profile of the links.

The pattern of wear on the attrition facets of the procumbent incisors coupled with that of the inner surface of the upper incisors indicates that, in adult animals, cutting takes place by the thickened enamel (which runs along the labial edge of the attrition facet on each procumbent incisor) being brought into occlusion against the conjoined occlusal surface of the upper incisors and subsequently rotated infero-laterally across this surface. Thus, during jaw closure both procumbent incisors come to lie with their lateral edges on the medial aspect of the conjoined attrition facet on the upper incisors, i.e. are relatively adducted. When the lower incisors are in this position, the molars are intercuspated

(Hiiemae 1978) but with the lingual edge of the lower molar row lying more medial to that of the upper molar row. The slight concavity of the conjoined upper incisor attrition facet indicates that the adduction phase of lower incisor movement that follows cutting is accompanied by rotation of each mandible about its longitudinal axis. Moreover, articulation tests demonstrate that these movements simultaneously cause the intercuspated (Hiieme 1978) lower molar row to be drawn laterally across the upper molar row in phase 2 occlusion described by Sanson (1989). Thus there is close integration between incisor and molar action in adult tammars particularly in respect of the cutting action of incisors and that caused by relative movement of the links on upper and lower molars during 'type-G' occlusion (Sanson 1980). It should be noted that the nature of this integration does not require greater occlusive forces to act on the jaw because the conjoined cutting actions from incisor and molar action occur on lateral rotation and thus are disposed buccally and lingually at short distances from the hypomochlion (Badoux 1975) which is the longitudinal axis of the jaw. In view of the relatively poor development of pterygoid musculature shown in this study and in other macropodine species (Abbie 1939) it is probable that this rotation relies on the action of the temporalis and the masseter (Sanson, 1980) muscles. Bio-mechanical studies (Badoux 1964; 1975) indicate that, under conditions where there is relative elevation of the labial edges of the upper premolar/molar rows such as occurs in tammars, the lateral component of any vertically applied occlusive force produces a torsional force that aids the lateral rotation of the lower jaw. Moreover, the magnitude of the torsional force is directly proportional to the length of the jaw.

In younger animals with shorter jaws, the extent of rotation of each hemi-jaw is reduced, and the incisor cutting surface is confined to the area between the tips of the procumbent incisors and the buccal surface of the first incisor. With increasing wear of the occlusal aspects of the upper incisors and concurrent rearward extension of the attrition facet on the lower incisors, an increasing amount of abduction and rotation of each mandible is required in order to occlude the opposing incisor surfaces. Thus, as animals age, bite width increases, as does the amplitude of phase 2 movements between upper and lower molars (Sanson 1980). These age-related differences may be important in respect of dietary specialisation. Older animals may consume larger items of vegetation more efficiently whilst younger animals are constrained to physically smaller items. This observation fits in with that of McArthur and Sanson (1988) who showed that the cutting-edge length of molars is short in young eastern (*M. giganteus*) and western grey kangaroos (*M. fuliginosus*) and increases with wear in the first few years of life.

Dietary specialisation has been shown to vary with bite width between species in other herbivores particularly with regard to browsing and grazing (Illeus and Gordon 1987). The greater dietary versatility of older animals may permit them to range more widely. Home range size is reported to vary with body size and/or gender (Jaremovic and Croft 1987; Arnold *et al.*1992; Horsup 1994) in a number of macropod species. Lentle *et al.*(unpublished data) observed that larger tammars ranged more widely on grasslands than sub-adults, similarly Warburton (1983) noted more extensive use of tussock grass for feeding by male Bennetts wallabies (*Macropus rufogriseus rufogriseus*), a closely related species that is similarly classified as a grazer.

The close integration between biting and chewing may be a feature of specialisation in grazing species such as the tanunar. When narrow abrasive items such as grass are being eaten, the burden of particle reduction is shared between the incisors and the molars, a strategy that may be important in macropods in view of their limited supply of molars (Sanson 1989). Thus narrow items which need comparatively little subsequent mastication are cut by incisors and require limited numbers of chewing cycles (Hiiemae 1978) before swallowing. Conversely, the concurrence of molar and incisor action is not preserved during puncture/crush cycles (Hiiemae 1978) as, when molar intercuspation does not occur (Hiiemae 1978) the incisor cutting edges cannot be easily occluded. Browsing by tammars is a relatively discontinuous process characterised by relatively long periods of chewing (Lentle et al, unpublished findings) and thus is more reliant on the use of molars to reduce particle size. Synchronous molar and incisor cutting action during grazing is made possible by the relative positions of the planes of occlusion of the incisor and the molar row. This may vary with dietary specialisation, for example to allow more complete dissociation of molar from incisor action in specialised browsing species.

The dispersal of food particles away from the cutting surface of the molars during chewing decreases chewing efficiency (Voon *et al.*1986). The transverse ridging of the soft palate may help to prevent particle dispersal by impeding retrograde flow during chewing and biting. However such a mechanism will be of benefit only when mouth-fill is low. High levels of mouth-fill are known to decrease molar chewing efficiency (Voon *et al.*1986; Lucas 1994), and such transverse ridging may, by confining food to the rear of the mouth, exacerbate this effect. Thus transverse ridging may be expected to be less prominent in browsing species.

In summary, tammar wallabies exhibit a mixture of the tooth morphologies and jaw action characteristics found in archetypical browsing and grazing macropods (Sanson, 1989). Thus whilst their tooth morphologies are more typical of the grazing grade, their lateral jaw movements are relatively restricted and phase 2 movement (Sanson, 1980) between molars results from a rotational movement that is more typical of browsers. The range and power of this rotational movement may increase with body size and influence choice of diet. Further work is required to determine whether these features are typical of other small grazing species in the Notomacropus group (Flannery, 1989).

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Figure 1: Side view of tammar skull showing measurement points of lower and upper jaw.

A) Skull measurements

X', Occlusal axis; UJ, length of upper jaw-line; LJ, Overall length of lower jaw in cm; MA, Projected distance along the line of occlusion of the inferior zygomatic process from the jaw joint; TA, Projected distance along the line of occlusion of the most anterior cranial insertion of temporalis from the jaw joint; TP, Projected distance along the line of occlusion of the most posterior cranial insertion of temporalis from the jaw joint; MP, Projected distance along the line of occlusion of the reference point on the rear of the anterior zygomatic arch from the jaw joint; MO, Projected distance along the line of occlusion of the anterior limit of the ramus of mandible from the jaw joint; UM1, Projected distance along the line of occlusion of the anterior limit of the cingulum of M1 from the jaw joint;

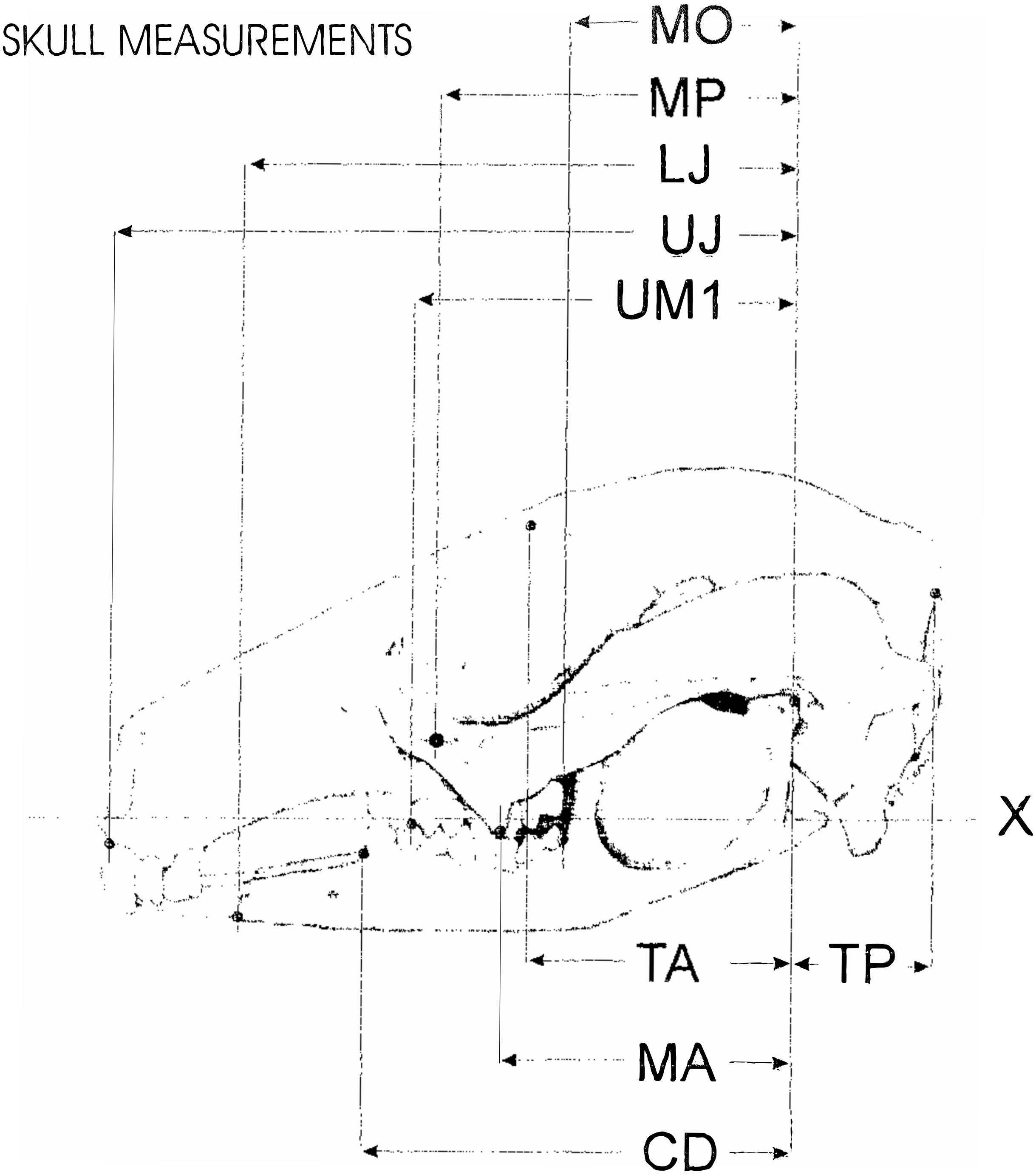
CD, Projected distance along the line of occlusion of the anterior limit of the reversed curve of spee from the jaw joint.

B) Attachments of Masseter.

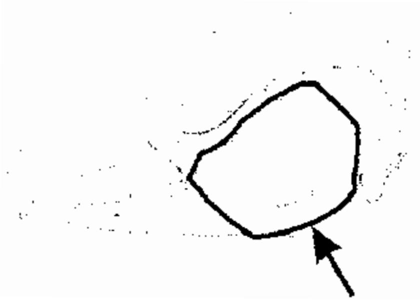
C) Attachments of Temporalis. * Zygomatic arch has been removed to allow view of ramus . Dotted line shows site of attachment to medial surface of ramus.

D) Medial pterygoid. Dotted line at anterior edge of muscle shows the side on profile of the pterygoid fossa of sphenoid

A) SKULL MEASUREMENTS



B) MASSETER



C) TEMPORALIS*

D) MEDIAL PTERYGOID

Figure 2: Criteria for assessment of the degree of wear in the upper incisors of Tammar wallabies

Score	Wear characteristics
0.5	Smooth worn surface on the anterior half of the tooth
1.0	Smooth worn surface extends over at least one quarter of the posterior half of the tooth
1.5	Some concavity over the worn surface
2.0	Continuous smooth concave surface over the entire width of the tooth
2.5	Exposure of dentine on the anterior half of the tooth
3.0	Exposure of dentine on the posterior half of the tooth
3.5	Sufficient wear to obliterate the vertical groove
4.0	A continuous concave transverse groove with uniform exposure of dentine traversing the tooth.

The illustration below shows the incisor arcades of a juvenile (Left) and an adult (Right) tammar with wear score of each tooth given alongside

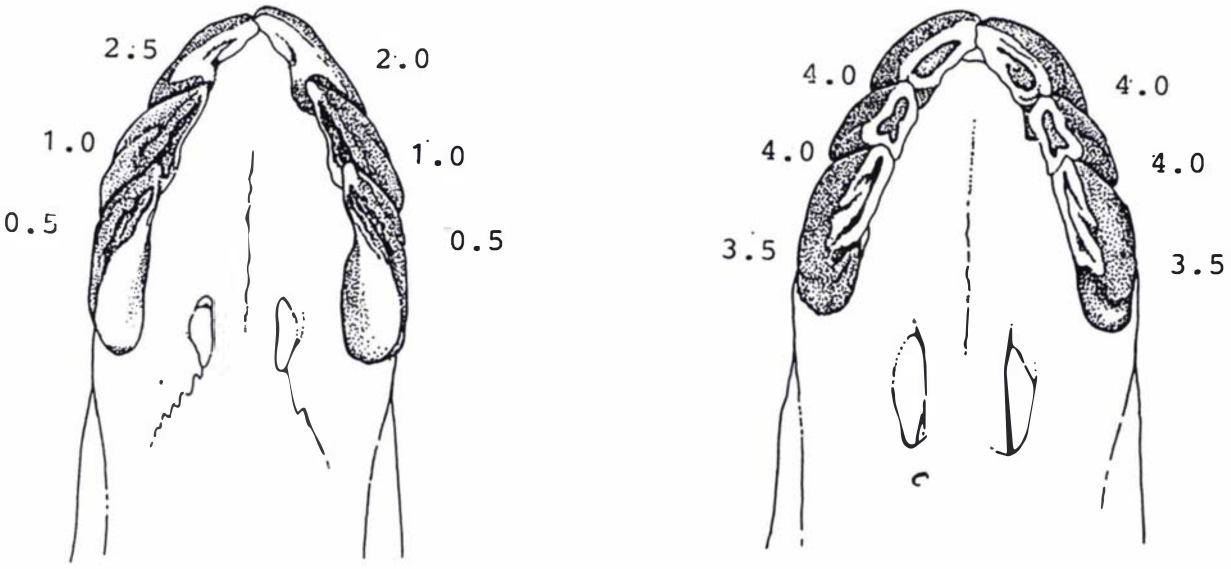
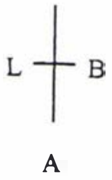


Figure 3 Criteria for assessment of 2nd premolar and molar wear in the lower jaw of tammar wallabies (after Mc Arthur and Sanson, 1988).

Score	Wear characteristics
0	No wear as tooth not in occlusal plane.
1	Facets and striae on lophids
2	Dentine exposed on either protoconid, metaconid, hypoconid or entoconid
3	Dentine exposed continuously along protolophid from protoconid to metaconid
4	Dentine exposed continuously along both lophids. Maximum height of lophids level with links. There is some extension of exposed dentine along the line of the forelink and the midlink
5	Similar to 4 but area of exposed dentine is greater.

Left molars with various wear scores are shown below. Dark shaded outer material is adherent detritus. Dark innermost areas show exposed brown dentine.

A, anterior; B, buccal; L, lingual



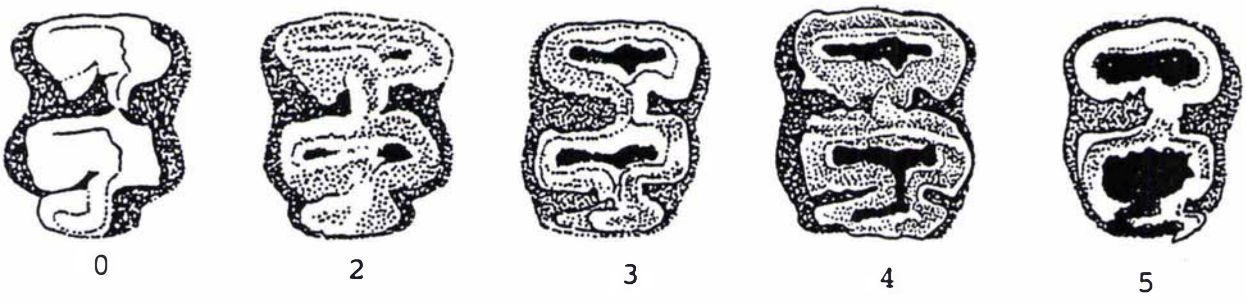


Figure 4: Bar chart showing the distribution of average wear scores of the three upper incisors according to body size

Size classes:- ‘small’ body weight < 4.0 kg; ‘medium’, body weight 4.0 -5.0 kg,; ‘large’, body weight > 5.0 kg.

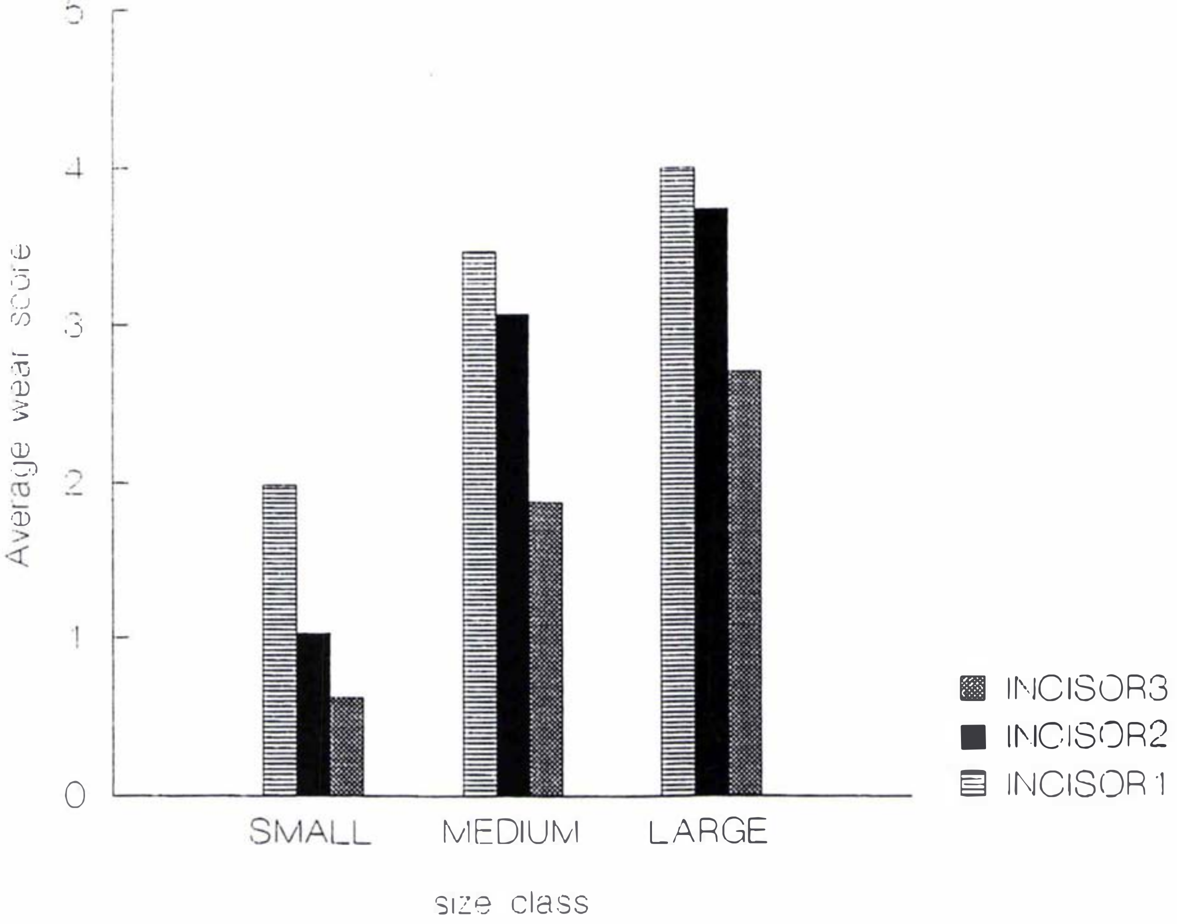

5
4
3
2
1
0
Average wear score
SMALL
MEDIUM
LARGE
size class
INCISOR3
INCISOR2
INCISOR1

Fig 5: LOWESS *# smoothed plot of the distribution of lower jaw length and average of left and right propalinal lengths of procumbent incisor attrition facet.

* Method of smoothing by weighted average of X from nearby Y values (Cleveland 1981).

Tension 0.7

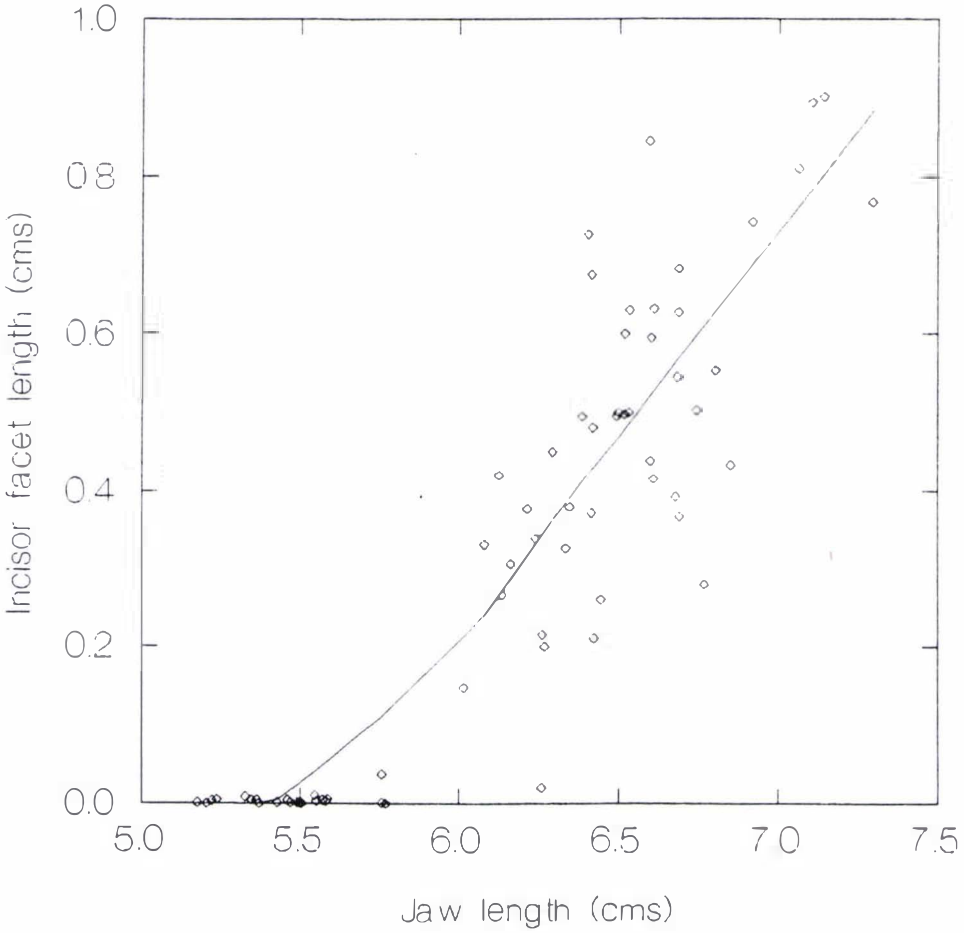

Incisor facet length (cms)
Jaw length (cms)
0.0
0.2
0.4
0.6
0.8
1.0
5.0
5.5
6.0
6.5
7.0
7.5

Figure 6: Bar chart showing the distribution of averaged wear scores for molariform deciduous premolar (Dp3) and lower molars according to body size

Size classes:- 'small' body weight < 4.0 kg; 'medium', body weight 4.0 -5.0 kg,; 'large', body weight > 5.0 kg. Shading codes for DP3, M1, M2, M3 and M4 shown on legend. SE s are shown as one sided error bars.

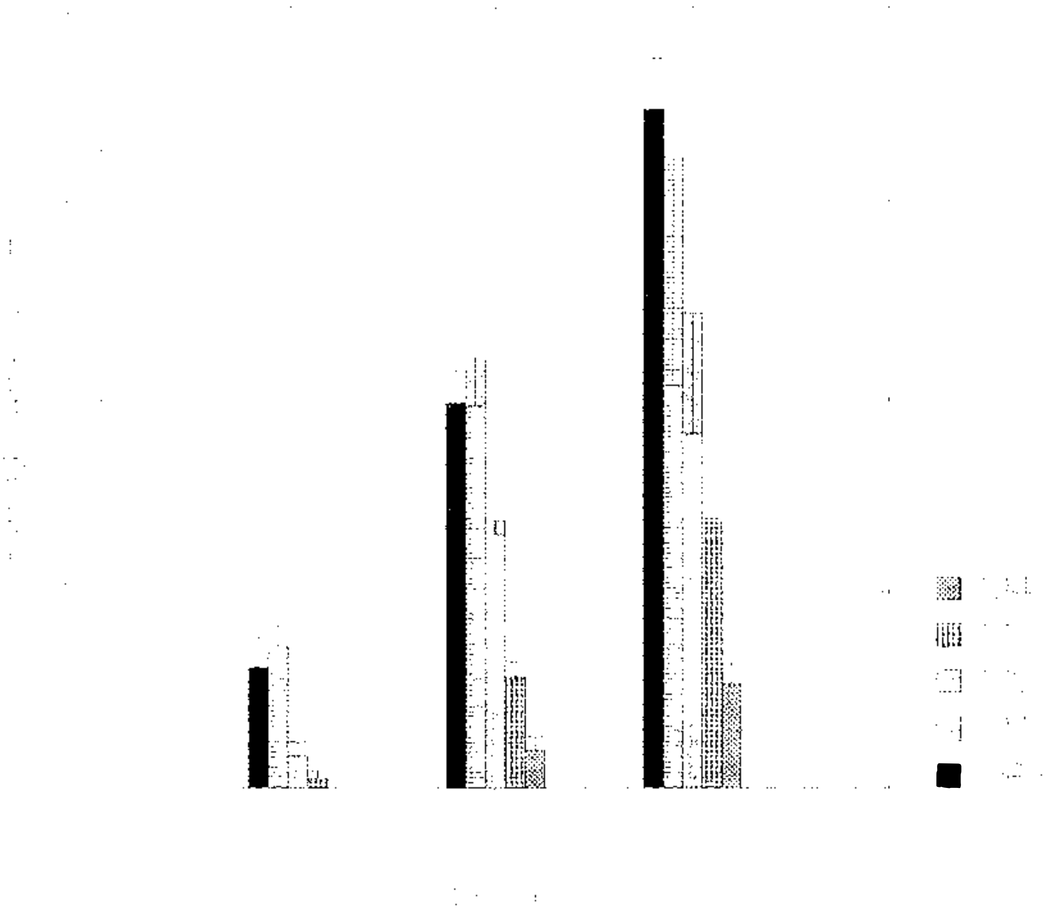


Figure 7: Macroscopic views of tammar teeth and palate.

a. Dorsal view of tip of procumbent incisor in an adult male. Attrition facet (arrowed) extends laterally and posteriorly with exposed dentine lying lingular to the thick labial enamel layer whose cutting edge lies outermost on the left.

b. Dorsal view of tip of left procumbent incisor in a juvenile male. Attrition facet (arrowed) is limited to extreme anterolateral aspect.

c. Enlarged view of anterior aspect of the lower jaw of a mature animal showing worn crown of P3 and advanced wear of adjacent M1. Relatively few mature specimens had shed DP3 and P2 was sometimes present alongside P3.

d. Lower jaw showing the molar row of a mature specimen with extensive wear on all molars. Note the lack of exposed dentine on the links.

e. Lower jaw showing the molar row of a sub-adult specimen with little wear. P2 was present in most middle sized and some larger animals.

f. View of soft palate showing transverse ridging. The more substantial ridges (arrowed) become elevated when fluid material flows postero-anteriorly across them but not when fluid flows in a caudal direction.

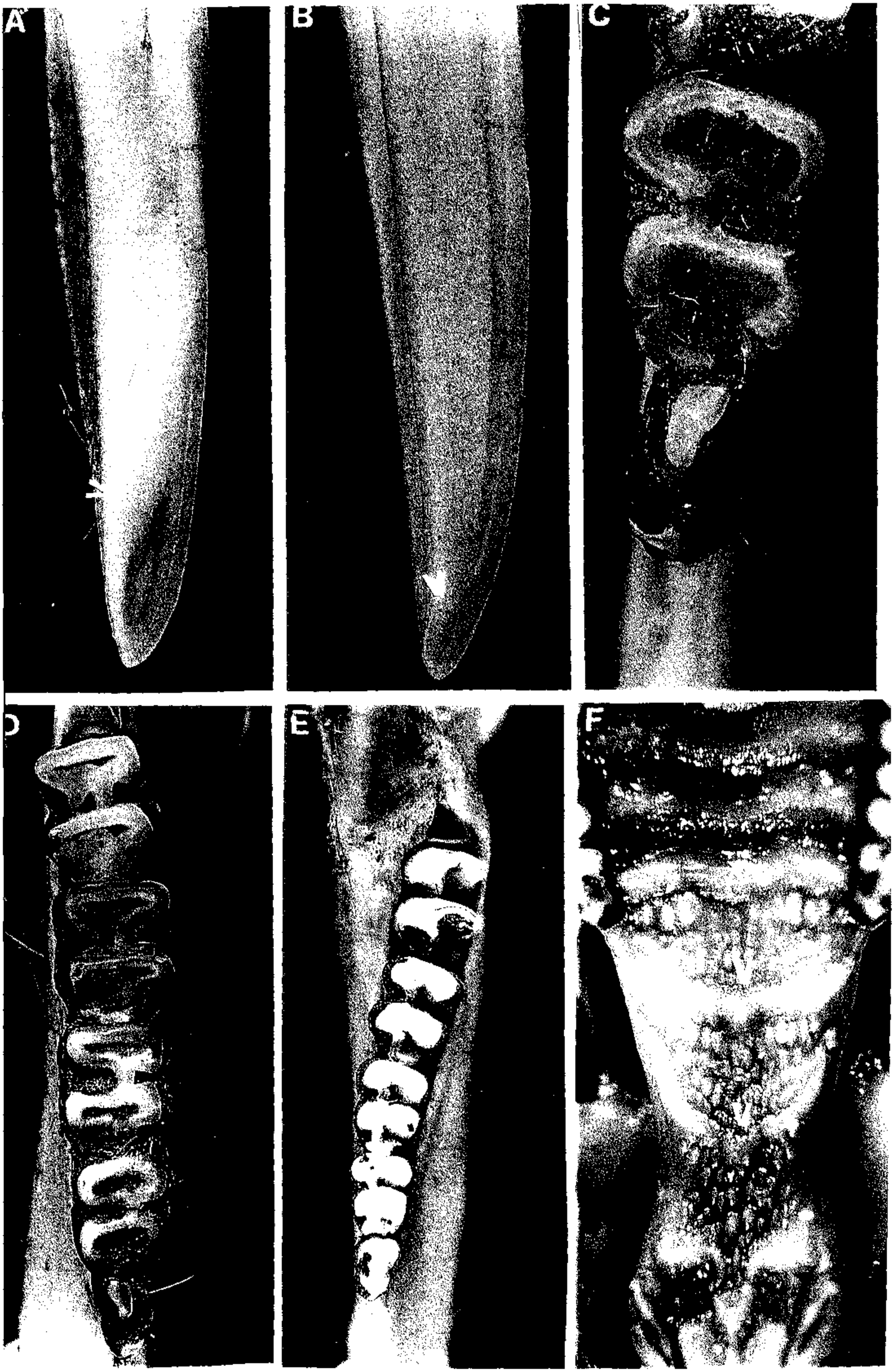

A
B
C
D
E
F

Figure 8: Scanning electron micrographs of tammar procumbent incisors.

a) View of raised labial enamel cutting edge from the left procumbent incisor of a mature specimen. Parallel striations are visible on the outer half. The long axis of the tooth runs from top right to bottom left and the labial edge is on the left.

b) Enlarged view of the striations .

c) Extreme anterior limit of the raised labial enamel cutting edge from the same left procumbent incisor. Note relative paucity of striations and striations on outer half running parallel to the long axis of the tooth which runs from top right to bottom left.

d) Surface of exposed dentine with lingual enamel edge lying to the right. Note relative lack of striations.

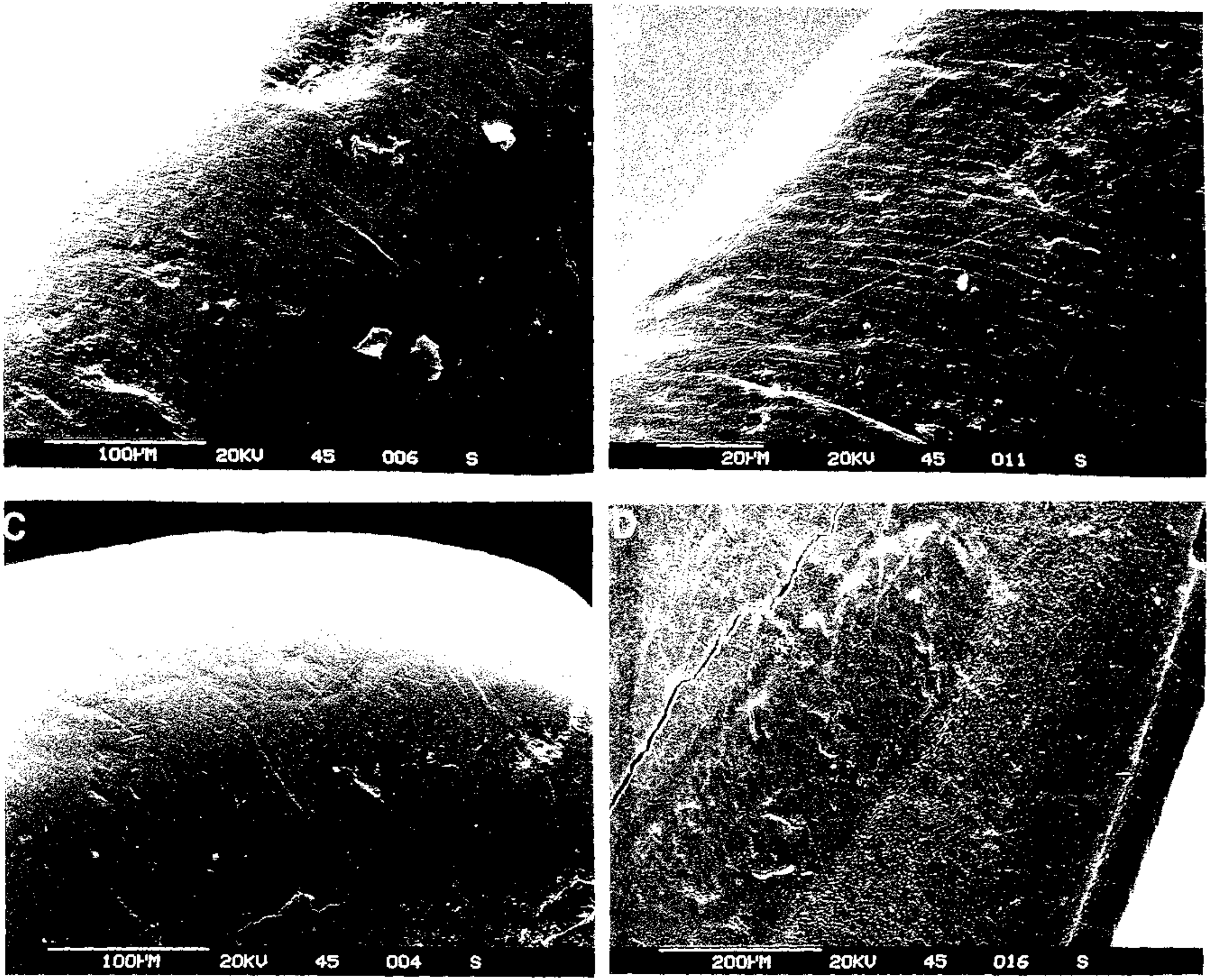

100µM 20KU 45 006 S
20µM 20KU 45 011 S
C
100µM 20KU 45 004 S
D
200µM 20KU 45 016 S

Table 1: Weights of the principal muscles of mastication in free ranging tammar wallabies. Muscle weights are averages of the wet weights of right and left sides taken immediately following dissection. The M/T ratio is the weight of masseter per gram of temporalis muscle. *The higher variability of the weights of the medial pterygoids may be due in part to the difficulty in extracting the muscle from the pterygoid fossa of the sphenoid especially in small specimens

Body weight (kg)	Sex	Masseter (g)	Temporalis (g)	Medial Pterygoid* (g)	M/T ratio
5.5	m	3.7	3.1	1.3	1.2
4.5	m	3.2	2.6	1.0	1.2
7.4	m	4.4	3.5	1.7	1.2
4.1	m	2.4	2.0	0.9	1.2
4.4	f	2.9	2.6	0.8	1.1
4.5	m	3.2	2.9	1.0	1.1
4.7	f	3.0	2.5	1.8	1.2

Table 2: Gradients* from simple linear regression analyses of various dimensional jaw parameters of tammar wallabies from the Rotorua district North Island New Zealand.

*Jaw dimensions in mm, body weight in kilograms, body length in mm and molar index after Kirkpatrick (1965); UJ, Occlusal length of upper jaw; LJ, Occlusal length of lower jaw; BD, Occlusal length of jaw mesial to the leading edge of the ramus; LDENT, Occlusal length of jaw between the anterior cingulum of M1 and the leading edge of the ramus; MA, Projected occlusal distance of inferior zygomatic process from jaw joint; MP, Projected occlusal distance of reference point on the rear of the anterior zygomatic arch from the jaw joint; MPM, Occlusal distance of the cranial origin of the line of action (mid point of the cranial attachment of masseter with respect to the line of occlusion) from the temporomandibular joint ; MPT, Occlusal distance of the cranial origin of the line of action (the midpoint of the cranial attachment of temporalis with respect to the line of occlusion) from the temporomandibular joint .

Independent variable	**Dependent variable**	**Gradient**	**DF**	**F ratio**	**p**	**R**
Molar Index	UJ	10.359	1/85	238.925	**0.000**	0.859
Molar Index	UM1	3.25	1/75	124.57	**0.000**	0.790
Molar Index	Body weight	2.057	1/68	141.13	**0.000**	0.821
Molar Index	Body length	142.61	1/67	194.28	**0.000**	0.744
Ratio BD/LJ	Molar Index	20.09	1/72	36.59	**0.000**	0.580
Ratio BD/LJ	Body weight	52.58	1/57	29.52	**0.000**	0.584
Ratio BD/LJ	Body length	3247.7	1/57	25.35	**0.000**	0.556
Ratio LDENT/LJ	Molar Index	11.80	1/72	10.14	**0.002**	0.351
Ratio LDENT/LJ	Body weight	18.17	1/57	2.94	0.092	0.221
Ratio LDENT/LJ	Body length	1516.3	1/57	5.026	**0.029**	0.285
Ratio MPM/UJ	Molar Index	- 22.66	1/78	14.01	**0.000**	0.391
Ratio MPM/UJ	Body weight	- 63.62	1/62	14.23	**0.000**	0.432
Ratio MPM/UJ	Body length	- 4221.0	1/62	15.25	**0.000**	0.444
Ratio MPT/UJ	Molar Index	24.92	1/73	23.811	**0.000**	0.496
Ratio MPT/UJ	Body weight	71.77	1/60	30.965	**0.000**	0.583
Ratio MPT/UJ	Body length	4680.9	1/60	31.93	**0.000**	0.589
Ratio MP/UJ	Molar Index	- 15.001	1/75	20.165	**0.000**	0.460
Ratio MP/UJ	Body weight	- 36.345	1/60	14.034	**0.000**	0.435
Ratio MP/UJ	Body length	- 2361.9	1/60	14.263	**0.000**	0.438

Table 3: ANCOVAs of effect of gender on rate of change in the averaged distance of the first upper molar from the rear of the temporomandibular joint (M1), measured along the occlusal axis, with body size.

Lillifors test probabilities of distribution of residuals from analysis based on wt = 0.595; from analysis based on length = 0.783

Dependent variable	Source	D/F	F ratio	P	R
Body weight	M1 distance (M1)	1/53	358.00	< 0.000	0.955
	Gender (S)	1/53	17.43	< 0.000	
	M1x S	1/53	22.28	< 0.000	
Whole body Length	M1 distance (M1)	1/53	328.27	< 0.000	0.949
	Gender (S)	1/53	9.70	0.003	
	M1x S	1/53	13.33	0.001	

Table 4: ANCOVAs of effect of gender on change in the ratio BD/LJ (the length of the body of the lower jaw to that of the whole jaw, measured along the occlusal axis, with body weight and with molar index.

Lillifors test probabilities of distribution of residuals from analysis based on wt = 0.058; from analysis based on molar index = 0.237

Dependent variable	Source	D/F	F ratio	P	R
Body weight	BD/LJ	1/55	15..636	**< 0.000**	0.649
	Gender (S)	1/55	1. 396	0.243	
	BD/LJ x S	1/55	1.553	0.221	
Molar index	BD/LJ	1/53	5.915	**0.018**	0.536
	Gender (S)	1/53	2.831	0.098	
	BD/LJ x S	1/53	2.938	0.092	

Chapter 7

Factors affecting the volume and macrostructure of gastrointestinal compartments in the tammar wallaby (*Macropus eugenii* Desmarest).

R. G. Lentle, K. J. Stafford, M. A. Potter, B. P. Springett and S. Haslett.

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Factors affecting the volume and macrostructure of gastrointestinal compartments in the tammar wallaby *Macropus eugenii* Desmarest.

R. G. Lentle [1], K. J. Stafford [2], M. A. Potter [1], B. P. Springett [1], S Haslett [3]

[1] Department of Ecology, Massey University, Private Bag 11222, Palmerston North, New Zealand.

[2] Institute of Veterinary, Animal, and Biomedical Sciences. Massey University, Private Bag 11222, Palmerston North New Zealand.

[3] Department of Statistics, Massey University, Private Bag 11222, Palmerston North New Zealand.

Abstract

We explored the factors that govern the length, wet tissue weight and wet digesta content of the gut components of 100 tammar wallabies (*Macropus eugenii* Desmarest) shot on the same night, by multivariate (discriminant) analysis and by allometric analyses based on simple linear regression (SLR), and on reduced major axis (RMA) regression. The slope coefficient of the regression describing variation of whole gut content with body weight was not significantly different from isometry. Similarly, stomach length, content and tissue weight scaled isometrically with body weight as did small intestine tissue weight and content and colon content. Colon tissue weight scaled allometrically with body weight. Length of caecum scaled to body weight was similar to that of browsing species, shorter than that of gazing species and varied with body size like that of larger species. Length of small intestine scaled to body weight was shorter and length of colon longer than that of similar sized grazing species. There was a sexual dimorphism in gut morphology, females having a relatively greater amount of tissue in the stomach and colon, and a relatively long caecum and colon. There was a reciprocal variation in the weight of digesta in stomach and hindgut suggesting that hindgut content was evacuated as feeding proceeded. The authors suggest that the hindgut may contribute to overall digestive strategy under conditions when reduction in feeding rate brings about a relative emtpying of the stomach.

Introduction

Little is known of the factors that govern the size of the gut components of macropods, particularly that of the caecum and colon. Allometric analyses which describe the manner in which the size of gut components vary with body size are a useful means of identifying special adaptations in relation to dietary habit. (Martin et al. 1985). The exponent that describes the relationship between body weight and the overall surface area of the digestive tract has generally been found to be nearly isometric (Martin et al, 1985) and close to that describing the relationship between body weight and metabolic rate (Klieber 1961). The latter exponent has been used as an 'allometric baseline' or 'criterion of subtraction' (Gould 1978) for functional equivalence and the presence of area / volume (A:V) compensation between body weight and various linear dimensions of gut components used to infer relative specialisation (Osawa and Woodall 1992a) in digestive process i.e. the presence of adaptive features that are additional to the scaling described by Kliebers law. Thus the fact that in smaller macropod species the length of the small intestine varies with body weight in a manner which is closer to A:V compensation than to isometry (Osawa and Woodall 1992a), may indicate the relative importance of enzymatic digestion. Conversely, the fact that in larger macropod species, caecal and colon length scales with body weight in a manner that is closer to A:V compensation than to isometry (Osawa and Woodall 1992a) may indicate the relative importance of hindgut fermentation or ability to absorb faecal water (Osawa and Woodall 1992a).

Apart from differences that result from particular adaptations among species, the gross anatomy of gut components may also vary in reponse to temporal variation in the quality of diet (Sibly 1981). Thus the average length of the small intestine and caecum increases significantly with change from a grain to a foliage diet in the field vole (*Clethrionomys glareolus)* and the bank vole (*Microtus agrestis*) (Lee and Houston 1994). Similarly, in the rabbit (*Oryctolagus cuniculus)* there is significant variation in average weight of stomach tissue, average volume of small intestine and average length of large intestine with soil type and with season (Sibly et al 1990). It is noteworthy that the magnitude of such responses varies considerably beween species, thus whilst the length of the small intestine of the field vole increased by 19% in response to a change from a grain to a foliage diet, that of the bank vole increased by 47% (Lee and Houston 1994). Currently it is not known whether the size of the gut components of any macropod species changes in this manner.

Apart from work carried out by Osawa and Woodall (1992a; 1992b) investigations of the gut morphology of macropods, including that of the tammar (*Macropus eugenii*), have been largely descriptive and based on limited numbers of animals (Langer 1988). The caecum of larger macropods e.g. *Macropus rufus and M. giganteus* is haustrated (Osawa and Woodall 1992a) in a manner similar to that of folivorous 'colon separator' species (Cork and Foley 1997) whilst the caecum of smaller species such as *Thylogale thetis, Wallabia bicolor* and *M. agilis* is relatively short and simple in structure with much less sacculation (Osawa and Woodall 1992a). In spite of the morphological resemblance of the caecum of larger macropods to that of folivourous 'colon separator' species which rely on hind gut fermentation (Cork and Foley 1997), post mortem studies of particle size distribution in the hindguts of a number of large macropod species have shown no evidence of selective particle retention (Freudenberger 1992).

It is difficult to envisage colon fermentation contributing substantially to the nutritional strategy of macropods as the overall transit times of food particles are generally shorter than those of non macropod species which exhibit a hindgut fermenting strategy (Wellard and Hume 1981). Nevertheless, hindgut fermentation may be used by macropods to augment the fermentative yield of the stomach, especially in those species which have somewhat longer overall mean particle retention times e.g. *Lagorchestes hirsutus* (Bridie et al 1994) or which are able to sequester significant quantities of digesta in offset compartments such as the caecum (Cork and Foley 1997). Thus, whilst 'total fermentative gut volume' as a percentage of total gut volume has been noted to be similar in feral goats, walleroos (*M robustus robustus)* and euros *(M. r. erubesens)* (Freudenberger 1992), the relative contribution from the stomach was lower, and that from the colon and caecum correspondingly higher, in the two macropod species (Freudenberger 1992). Again whilst the contribution of volatile fatty acid (VFA) production from fermentation in the hindgut of *Thylogale thetis* and *Macropus rufogriseus* was less than 2% of total digestible energy intake (Hume, 1977), the rate of production of VFAs in the hindgut was higher in the macropods than in sheep (Hume, 1977). Further, the concentrations of VFAs found in digesta from the small intestine and hindgut of freshly slaughtered captive animals that had been maintained on indentical diets of chopped lucerne hay were higher in smaller (*M. eugenii* and *T. thetis*) relatively folivorous (Dawson 1989; Williamson 1986) than in larger (*M. giganteus*) grazing (Dawson 1989) species (Dellow and Hume 1982a) and highest in tammars, perhaps in consequence of their relatively long dry matter retention times (Dellow 1982) and relatively small ingesta particle size (Lentle *et al.*, unpublished data).

Although other workers have commented on the possible importance of water absorption by hindgut components in certain macropods (Bridie *et al.* 1994) no quantitative physiological data are yet available.

The purpose of this study is to explore the anatomical relationships between hindgut and other gut compartments in tammar wallaby (*Macropus eugenii* Desmarest) and to evaluate the effect of habitat, gender and feeding time on these relationships. A number of species within the subgeneric group Notamacropus, to which the tammar has been assigned (Flannery 1989), are known to possess similar dental characteristics and to ingest significant quantities of browse (Dawson 1989; Williamson 1986) but little is known of their particular digestive adaptations. Previous work on the gastrointestinal anatomy of the tammar wallaby has been largely descriptive and performed on limited numbers of animals (Langer 1988). Tammars, probably of South Australian origin (Poole et al. 1991; Maxwell et al. 1996), were introduced into the Rotorua district of New Zealand in 1912 (Wodziki and Flux 1967) and have since so successfully adapted to the native forest and the forest/pasture ecotone that they pose a threat to conservation values and thus are now regarded as a pest (Williamson 1988).

Method

A total of 100 wallabies was shot by professional hunters as part of a pest control operation conducted by the Bay of Plenty Regional Council. The cull was carried out on a single fine night in summer (February) on two sites; a grassland site of improved farm pasture immediately adjacent to a forest ecotone, and a forest site of broadleaf (*Knightia excelsa* and *Weinmannia racemosa*) (Nicholls 1964) situated at a distance of 8 km from the ecotone. Culling commenced at 2130 hrs in the evening and continued until 0430 hrs on the following morning. All animals that were seen were shot. Hunters moved progressively onto new ground throughout the period of the cull, so animals that were shot had not been previously disturbed. A tag was attached to each wallaby carcass giving details of time and site where shot. The carcasses were transported to a field laboratory and immediately processed.

Each carcass was weighed, then the entire gastro-intestinal tract from sub-diaphragmatic oesophagus to anus was removed via a ventral incision, with as little disturbance of gut content as possible. The gastro-intestinal compartments were tied off and separated as follows; the stomach, from the commencement of the sub-diaphragmatic oesophagus, to the site of attachment to the small intestine at the pylorus ; the small intestine, from the site of attachment to the pylorus, to the site of attachment with the caeco-colonic junction; the caecum, from the site of attachment at the junction of the colon and small intestine; the colon, from site of attachment at the caeco-colonic junction to the rectum. Each gut compartment was weighed (± 0.1 g) and then laid out on a dissection board where its length was measured (± 1.0 mm) with a steel tape. The ligatures were then removed and the digesta contained within each compartment carefully evacuated, any adherent digesta was washed out, and the tissue blotted dry, and weighed (± 10 mg).

Statistics

Allometric analysis (White and Gould 1965; Gould 1966; Reiss 1989) was used to investigate the relationships between various parameters of the gut with body weight according to equation

$$y = a X^{b}$$

Where X = body weight and y = gut parameter.

Values for 'a' and 'b' were estimated by simple linear regression (SLR) and by reduced major axis (RMA) analysis of log converted values (Sokal and Rohlf 1995). More extensive discussion of measurement error models (of which RMA is a particular example) can be found in Fuller (1987) chapter 1.

Allometric analyses based on the parameters of length, weight of wet digesta and weight of tissue, were carried out for each gut compartment. The slope coefficients for gut component lengths obtained by SLR and RMA analyses were compared, by Students t test, with an exponent of 0.33 to test for isometry and 0.5 to test for A:V compensation i.e. allometry. Similarly, the slope coefficients for wet digesta content and for wet tissue weight of gut components obtained by SLR and RMA analyses were compared with exponents that were extrapolated according to the dimensions in which the effect operated. Thus the value of the exponents in analyses based on wet digesta content were 1.0 (0.33 x 3) to test for isometry and 1.5 (0.5 x 3) to test for allometry. Similarly the values of the exponents in analyses based on wet tissue weights of gut compartments were 0.66 (0.33 x 2) to test for isometry, and 1.0 (0.5 x 2) to test for allometry (Osawa and Woodall 1992a). Comparisons with these assumed values were based on the distribution of Student t values calculated from

$$t = \frac{a - b}{SE_a}$$

where a = mean slope coefficient determined by SLR or RMA analysis

b = appropriately extrapolated isometric or allometric exponent

SE_a = standard error of slope determined by SLR or RMA analysis.

Probabilities were determined for N-2 degrees of freedom where N was the number of gut samples, (number of animals) used in the reduced major axis analysis.

Direct comparisons between slope coefficients determined by RMA analyses were similarly based on the distribution of the Students t value determined from

$$t = \frac{a_1 - a_2}{SE_{a1-a2}}$$

where a_1 = mean slope coefficient determined from first analysis

a_2 = mean slope coefficient determined from second analysis

$SE_{a1\text{-}a2}$= standard error of the comparison. i.e

$$SE_{a1-a2} = \sqrt{SE_{a1}^2 - SE_{a2}^2}$$

ANCOVAs of log converted body weight against log converted values of length, of wet digesta content and of wet tissue weight of each gut component were conducted to test for the effect of gender, 'site where shot' (forested or pasture area) and time when shot (prior to or after midnight).

Repeated statistical comparisons of parameters based on various gut compartments may produce spurious correlations (Hummel and Sligo, 1971). One way of circumventing this problem and allowing assessments of the effect of one variable to be adjusted for others is by use of multivariate methods. We conducted separate discriminant analyses based on weight standardised values for gut content, gut tissue weight, and gut length. Analyses were weighted for unequal sample sizes, i.e. for prior probabilities, and carried out in SYSTAT (Wilkinson 1990).

We used simple linear regression to clarify the relationship between 'time when shot' and wet digesta content of individual gut components. In this analysis we standardised wet digesta content on a basis of metabolic body weight rather that simple weight correction as this resulted in normally distributed residuals.

Results

Tabulated data

Means and standard errors of raw data are shown in Table 1. With the exception of certain hind gut parameters, length, weight and wet digesta content of gut components were generally greater in male than female tammars in line with their significantly higher body weights (Mann Whitney U test statistic = 617, Chi sq. approx. = 98.835, d/F 1, p = 0.002). Previous workers have endeavoured to circumvent the problem of variation in body weight confounding intuitive interpretation by expressing gut parameters as a proportion of whole gut or as a weight of wet digesta per kg metabolic body weight (Dellow and Hume 1982b; Freudenberger 1992). For the purposes of comparison with the results obtained by these workers, mean digesta content, wet tissue weight, and lengths of various gut compartments expressed as a fractions of total wet digesta content, total gastro-intestinal tract wet tissue weight, and total gastro-intestinal tract length respectively are shown in Table 2. Means and standard errors of wet digesta contents of various gut compartments expressed as fractions of metabolic body weight are shown in Table 3.

Allometric analyses

The means and standard errors of slope and intercept coefficients for length, wet digesta content or tissue weight of various gut compartments obtained from SLR and RMA, and scores from their comparison with isometric and allometric coefficients by Students t test are shown in Table 4. Ln-ln scattergrams of length, wet tissue weight and digesta content of each of the four gut components, plotted against whole body weight are shown in fig 1.

The slope coefficient, obtained from RMA analysis, describing the overall variation of total gut contents with body weight (Table 4) was not significantly different from isometry ($t = 1.026$, d/f 1/94, $p < 0.1$). This result is robust in its description of a scaling value not exceeding isometry in view of the bias to higher values that is inherent in the RMA method (Sokal and Rolf, 1995).

None of the slope coefficients that described the variation of the three parameters of the stomach with body weight, that were obtained using either SLR or RMA, were significantly different from isometry. The slope coefficients, obtained by SLR, describing variation in the length, wet digesta content or tissue weight of the small intestine with body weight were all significantly below the value for isometry. With the exception of that of small intestine length, the same parameters obtained by RMA were not significantly different from isometry. This latter result is robust in its description of a scaling value not exceeding isometry in view of the bias to higher values that is inherent in the RMA method (Sokal and Rolf, 1995).

The slope coefficients obtained by RMA for all three parameters of the caecum were not significantly different from either isometry or allometry but the slope coefficients of the same parameters obtained by SLR were significantly different from both isometry, and allometry with Students t scores lower for isometry.

The slope coefficient obtained by RMA describing variation of colon length with body weight was not significantly different from allometry whilst that obtained by SLR was not significantly different from isometry. The slope coefficient obtained by RMA describing variation of colon tissue weight with body weight was significantly above allometry whilst that obtained by SLR was not significantly different from allometry. The latter finding is robust with respect to the description of allometry in view of the bias to lower values that is inherent in the SLR method (Sokal and Rolf, 1995). Neither the RMA or the SLR slope coefficients describing variation in colon content with body weight were significantly different from isometry.

The slope coefficient obtained by RMA analysis of change in stomach volume with body weight was not significantly different to that of caecal volume with body weight ($t= 0.389$ d/f 1/190 $p > 0.05$), but significantly greater than that of colon volume with body weight ($t= 2.067$, df 1/189 $p < 0.025$). Thus with increase in body weight, wet digesta volume increased at the same rate in the caecum as in the stomach, but less rapidly in the colon than in the stomach.

ANCOVA

ANCOVA of body weight against wet tissue weight of the colon (Table 5) showed a significant interaction term for the effect of gender indicating that tissue weight tended to increase with body weight more rapidly in females than in males.

Discriminant analyses

The length, tissue weight and wet digesta content of the various gut components were standardised for body weight. Separate discriminant analyses were conducted on each parameter for the effect of gender, time when shot, and place where shot. The results of those analyses which showed significant variation between groups based on the character used as a basis for discrimination, i.e significant probability of Wilkes lambda, and successful levels of discrimination (Table 6) are given below

1) Discrimination of gender.

Successful discrimination between genders was possible on a basis of weight corrected wet tissue content of each gut component and on basis of the weight corrected length of each gut component.

The canonical discriminant functions and 'F-to-remove' values of the various gut compartments in the analysis based on the weight corrected tissue content (Table 6) indicate that successful discrimination of gender was based principally on the weight corrected tissue weight of the colon but also on that of the stomach. In the analysis comparing the weight corrected length of gut compartments, the loadings and F-to-remove values indicate successful discrimination of gender was based principally on the weight corrected length of the colon but also on that of the caecum. Thus weight standardised tissue weight and length of colon were both greater in females.

2) Discrimination of time when shot.

The canonical discriminant functions and F-to-remove values of the wet digesta contents of the various gut components corrected for body weight, showed successful discrimination of 'time when shot' is based on a contrast between the relative fill of stomach and caecum.

Simple linear regression of actual time when shot (measured as hours prior to or after midnight) against stomach content corrected for metabolic body weight (Table 7) was positive and highly significant indicating that stomach content increased significantly during the period of the cull. Simple linear regression of actual time when shot against caecal content corrected for metabolic body weight (Table 7) was negative and significant, indicating that colon content declined significantly over the same period.

Discussion

The relative capacities of the gut compartments of free ranging tammars, expressed as a percentage of total gut volume, obtained in this study, were similar to those obtained from captive tammars fed chopped lucerne hay *ad libitum* by Dellow and Hume (1982b) who reported 76 ± 4 % for the whole stomach, 9 ± 1 % for small intestine and 15 ± 2 % for large gut content . However the total digesta content of the stomachs was 50% higher in this study compared to that reported by these workers. When the capacities of gastrointestinal compartments are expressed as a precentage of total volume

(Freudenberger 1992; Dellow and Hume 1982a) the results between compartments are no longer independent of each other, thus relative differences in foregut fill will influence the results from more distal compartments and may confound their meaningful comparison. The use of comparisons based on weight compensated figures of individual compartments or of allometric methods are therefore to be preferred.

The use of the somewhat controversial (Sokal and Rolf, 1995) RMA method of allometric analysis may not be necessary in view of the low levels of error in the measurement of body weight and the fact that variability in the independent variable, i.e. the gut parameter, is likely to be proportional to body weight in the untransformed data. However it does permit direct comparison of our results with the values obtained from other macropod species by Osawa and Woodall (1992a) who used the same method. As slope coefficients estimated by RMA are always higher than those estimated by SLR (Sokal and Rolf, 1995) the use of RMA methods may introduce a bias in favour of the higher exponent, i.e. allometry. We therefore carried out allometric analyses using both RMA and SLR methods and assessed comparisons of derived slope coefficients with theoretically deduced exponents (see below) in a manner which considered this bias.

Osawa and Woodall's (1992a) comparative allometric studies on macropods were based on variation in the length of a given alimentary tract component with body weight. However coefficients derived from length may vary with the shape of the component, i.e. the length to width ratio, which precludes any meaningful direct comparison of allometric trends between gut components of differing shape.

Other studies (Hoppe 1977; Parra 1978; Dellow and Hume 1982a; Demment 1983; Demment and Van Soest 1985; Demment and Greenwood 1988; Freudenberger 1992) have assumed that the mass of wet digesta within a gut component provides a reasonable estimate of its capacity. The general validity of such an assumption depends on whether the sample size is sufficiently large to offset temporal variations in wet digesta content, and on whether physiological capacity is adequately described by wet digesta content, especially in the more distal gut compartments where digesta travels in discrete boluses i.e. faecal pellets. Within the bounds of these constraints, allometric analysis of variation in wet digesta content of gut compartments with body weight may provide a more meaningful basis for the direct comparison of allometric trends in gut components of differing shape.

Allometric coefficients based on the variation of the weight of an empty gut compartment with body weight may, if it is assumed that there is uniform thickness of gut wall, also describe variation in the basal surface area of the gut component with body weight. Differences in the average wall thickness of different gut compartments will effect the 'y' intercept of the line of regression that is obtained using log converted values, i.e the value of 'a', but will not affect the slope coefficient which is the value of 'b'. In this respect, the weight of the empty gut compartment may offer a more robust index for allometric comparisons between gut components. However, when simple macroscopic measurements are used, the approximation to surface area is more likely to be valid for thin walled capacious structures such as caecum, colon and stomach.

The results of the allometric study show that the slope coefficient describing the change of total wet digesta content of the gastrointestinal tract with body weight in tammars, was close to isometry and thus similar to that reported in a large number of eutherian species (Cork 1994; Demment and Van Soest 1985). Under such conditions, in order for the rate of food intake (retention time x gut volume) (Calder, 1984) to scale with metabolic body weight (body mass $^{0.75}$), digesta retention must be augmented (body mass $^{0.25}$) relative to that of larger bodied herbivores (Cork, 1994). Thus digestive strategies which prolong particle retention in the hind gut may be important particularly in in this 'fermentatively digesting' species.

The principles of dynamic programming. (Bellman 1957) applied to digestive process, suggest that with increasing reliance on fermentation in the foregut, herbivores will minimise the proportion of gut that is subsequently used in enzymatic digestion i.e. the small intestine (Penry and Jumars 1987). The finding that the mean length of small intestine obtained from this study (242 ± 3.4 cm) was similar to that of *M. agilis* (240.5 mm) but shorter than of the browsing macropods *Thylogale thetis* (283.9 cm) and *Wallabia bicolor* (384.7 mm) in a comparison of figures corrected for a body weight of 4.52 kg, using the regression coefficients obtained by Osawa and Woodall (1992b), may therefore indicate that enzymatic digestion is of lesser importance in grazing (Sanson 1989) macropod species of the Notamacropus subgroup (Flannnery 1989) than in browsers.

The mean length of the caecum is similar to that found in *T. thetis* (11.8 ± 2.1 mm) a browsing grade (Sanson 1989) species of similar mean body weight (4.6 ± 1.0 kg) (Osawa and Woodall 1992b) and is considerably shorter than that of larger grazing species *Macropus rufus* (22.6 mm) corrected for 4.52 kg body weight using the regression coefficients obtained by Osawa and Woodall (1992b). Thus length of caecum may with vary dietary habit in macropod species, tending to be longer in grazers.

Whilst the allometric analysis does not give a clear result as to whether the scaling of caecal volume or wet tissue mass is significantly different from isometry the results do show that the caecal length of tammar wallabies, like that of larger grazing macropods (Osawa and Woodall 1992a), varies significantly with body weight. This finding contrasts with that from the small wallaby species *M. agilis, W. bicolor* and *T. thetis* in which caecal length does not change significantly with body weight (Osawa and Woodall 1992a). The significant similarity of the RMA scaling coefficients describing variation of stomach content and of caecal content with body weight may, provided the retention time of particulate matter in the two structures is similar (Calder, 1984), indicate that the control of digesta fill in these two compartments is governed by a common outcome.

The mean length of colon obtained in this study (100.0 ± 1.5 cms) is identical to that obtained from four captive tammars of similar body weight fed chopped lucerne hay by Dellow and Hume (1982b) (100.0 ± 3.0 cms) and greater than that of the similar sized browsing species (Sanson 1989) *Thylogale thetis* (73.9 cm) and *Wallabia bicolor* (61.2 cm) corrected for a body weight of 4.52 kg using the regression coefficients reported by Osawa and Woodall (1992b). A similar association between grazing habit and increased length of colon has been reported by Bridie et al (1994) in the rufus hare wallaby *Lagorchestetes hirsutus*. Thus length of colon may also with vary dietary habit in macropod species, tending to be longer in grazers.

The 'relative volume' of the caecum expressed as percentage of total large intestine volume has been shown to vary with diet in eutherian species (Langer and Snipes 1991). The value obtained for the tammar wallaby caecum in this study is 36.6%, a value remarkably similar to that calculated from data published by Freudenberger (1992) for the euro (*M. robustus erubescens*) (36.2%) and the wallcroo (35.5%) (*M. robustus robustus*), macropod species known to eat diets of low nutrient quality.

Thus whilst overall length of the colon and the caecum of macropod species changes with dietary habit, the ratio of the volumes of these two compartments may remain relatively constant.

The scaling of the length of the tammar wallaby colon with body weight is allometric and similar to that obtained from other macropod species (Osawa and Woodall 1992a) when the RMA method is used. However, this result is equivocal viewed in the light of the bias of the RMA method and the result from SLR which shows isometry. Nevertheless, the more robust result from the analyses of colon tissue weight, showing allometric scaling with body weight, indicates the influence of 'adaptive factors' such as 'the need for digestion of dietary fibre in the hindgut or for water conservation' (Osawa and Woodall, 1992).

Sexual dimorphism has been previously described in macropods but only in respect of musculoskeletal development (Jarman 1989). ANCOVA indicates a significant difference in the allometric scaling of colon tissue between the sexes, moreover the discriminant analyses also suggests sexual dimorphism in gut morphology, females having relatively heavy walls in fore and hind gut and relatively long colons. Similar differences in colon length have been reported in the rabbit *Oryctolagus cuniculus* in early summer (Sibly et al. 1990) and were attributed to an increase in digestive capacity in breeding females at this time.

The loading factors of the discriminant analysis for the effect of 'time when shot' on weight standardised wet digesta content, highlight a contrast between the content of the caecum and that of the stomach. Thus, as the evening feeding peak continued, the wet digesta content of the stomach increased whilst that of the caecum declined. This result is supported by the significant regressions of time shot on metabolic weight corrected contents of stomach and of caecum, that of the stomach increasing and that of the caecum decreasing with the passage of time. These results fit in with work on captive tammars that showed a juxtaposition in the peaks of feeding rate and defecation rate (Warner 1981a). Periodic emptying of the caecum by tammar wallabies may account for the inconsistent subsidiary peaking in the fluid and in the solid phase marker excretion profiles reported by Warner (1981b) as well as the concomitant variation in dryness and neutral detergent fibre content of the faeces (Warner 1981b). The synchronicity of events could be brought about by enteric reflex or, as has been suggested by Warner (1981a), by a process of passive displacement. The synchronicity is logical from an optimal foraging viewpoint, as 'cost' (Collier 1985) increases with weight of wet digesta carried, and voiding of older digesta as fresh digesta is acquired would offset this increase.

The increase in the wet digesta content of the stomach during the evening feeding peak ties in with reports of diurnal variation of gut fill in the quokka (Storr 1964) and in captive tammars (Warner 1981b), but runs contrary to the predictions of optimality of foregut fermentation in respect of reactor theory (Penry and Jumars, 1987), in showing that the foregut reactor is not maintained at full capacity at all times. Reciprocal variation between caecal and stomach fill may help to offset fermentative losses incurred from diurnal reduction of the wet digesta content of the stomach.

Taken together the significant interspecific variation of caecal and colonic length with diet and the similarity of scaling of caecal and stomach volume suggest that the hindgut may play a more significant part in nutritional strategy of macropods of grazing grade (Sanson, 1989) than has hitherto been recognised. The reciprocal variation of hindgut fill with that of the stomach indicates that this role may be compensatory under conditions where feeding rate is reduced.

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Figure 1; Ln-ln plots of the length, wet tissue weight and digesta content of the stomach, small intestine, caecum and colon of tammar wallabies against whole body weight, showing (SLR) linear regression lines and 95% confidence intervals.

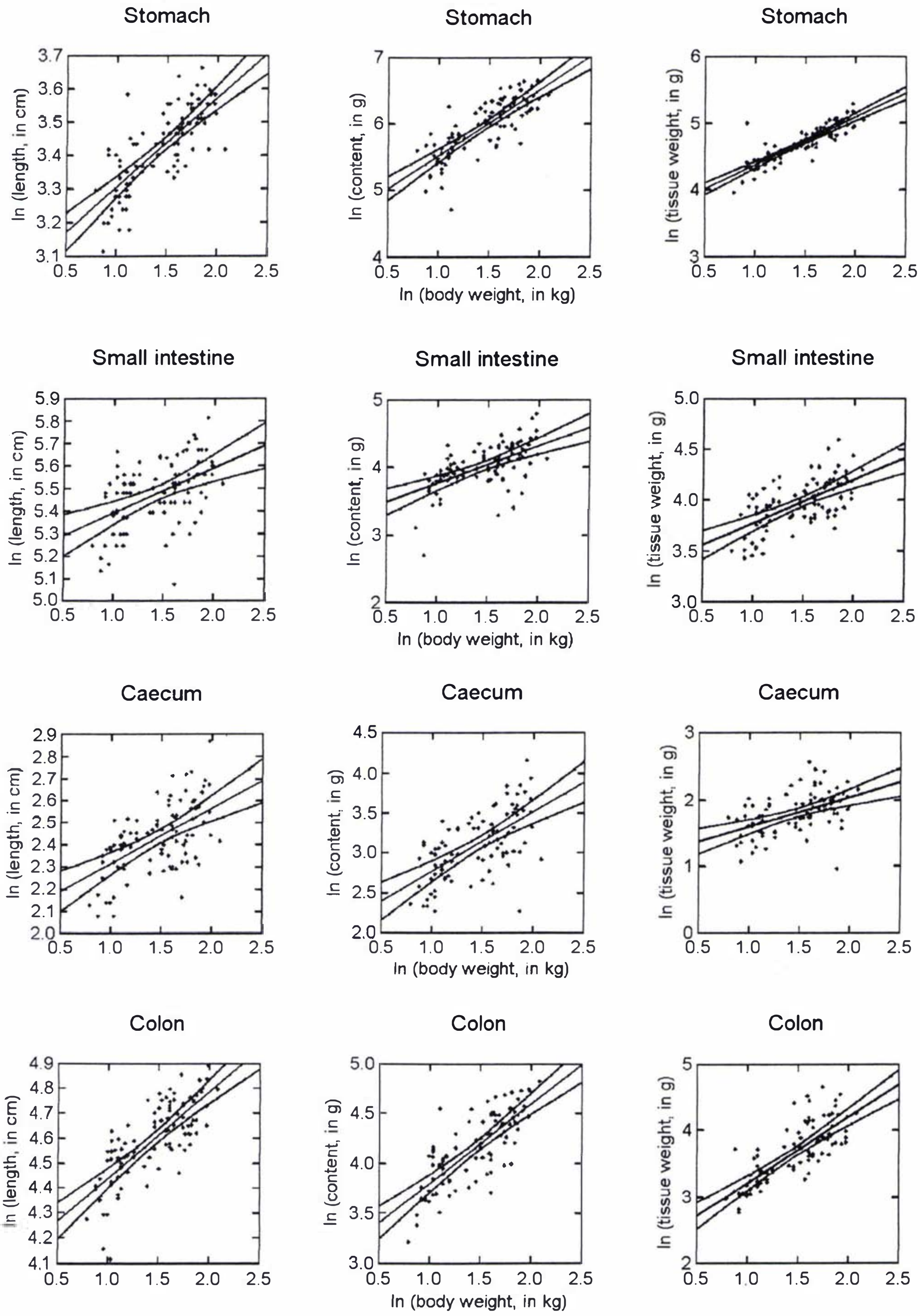
Stomach
ln (length, in cm)
3.1
3.2
3.3
3.4
3.5
3.6
3.7
Stomach
ln (content, in g)
4
5
6
7
Stomach
ln (tissue weight, in g)
3
4
5
6
Small intestine
ln (length, in cm)
5.0
5.1
5.2
5.3
5.4
5.5
5.6
5.7
5.8
5.9
Small intestine
ln (content, in g)
2
3
4
5
Small intestine
ln (tissue weight, in g)
3.0
3.5
4.0
4.5
5.0
Caecum
ln (length, in cm)
2.0
2.1
2.2
2.3
2.4
2.5
2.6
2.7
2.8
2.9
Caecum
ln (content, in g)
2.0
2.5
3.0
3.5
4.0
4.5
Caecum
ln (tissue weight, in g)
0
1
2
3
Colon
ln (length, in cm)
4.1
4.2
4.3
4.4
4.5
4.6
4.7
4.8
4.9
Colon
ln (content, in g)
3.0
3.5
4.0
4.5
5.0
Colon
ln (tissue weight, in g)
2
3
4
5
0.5
1.0
1.5
2.0
2.5
ln (body weight, in kg)

Table 1: Means and standard errors of various gut parameters and of whole body weights of 100 tammars shot on two sites in Rotorua, North Island, New Zealand in a single night.

AM, shot prior to midnight; PM, shot after midnight; m, males; f, females.

Class		BODY WEIGHT	STOMACH			SMALL INTESTINE			CAECUM			COLON		
		(kg)	length (cm)	weight (g)	contents (g)	length (cm)	weight (g)	contents (g)	length (cm)	weight (g)	contents (g)	length (cm)	weight (g)	contents (g)
Overall	n	100	98	100	100	97	96	98	99	97	98	98	98	98
	MEAN	4.52	31.00	113.44	424.59	242.32	54.62	58.20	11.47	6.33	24.33	100.01	42.328	66.465
	S.E	0.149	0.365	2.992	16.216	3.395	1.305	1.789	0.176	0.193	1.025	1.495	1.950	2.481
Male	n	71	69	71	71	68	69	70	70	69	69	69	69	69
	MEAN	4.792	31.601	116.51	454.96	249.41	55.69	60.892	11.86	6.39	25.96	101.10	40.22	72.07
	S.E	0.184	0.434	3.63	19.96	3.96	1.45	2.24	0.201	0.227	1.27	1.67	2.05	2.76
Female	n	29	29	29	29	29	27	28	29	28	29	29	29	29
	MEAN	3.855	29.55	105.92	350.23	225.69	51.89	51.46	10.53	6.20	20.46	97.39	47.33	53.13
	S.E	0.198	0.61	5.07	22.09	5.48	2.77	2.42	0.29	0.37	1.46	3.11	4.36	4.35
Grass/m	n	56	55	56	56	55	55	55	55	55	55	54	54	54
	MEAN	4.621	31.57	113.45	435.63	249.16	54.97	60.16	11.95	6.28	26.30	101.73	38.68	69.99
	S.E	0.209	0.511	4.19	22.42	4.54	1.71	2.53	0.24	0.26	1.49	1.92	2.25	2.98
Grass/f	n	23	23	23	23	23	22	22	23	22	23	23	23	23
	MEAN	3.878	29.74	104.4	337.02	229.78	51.76	50.07	10.64	6.01	19.30	98.74	48.06	53.63
	S.E	0.225	0.68	5.56	23.41	6.30	3.03	2.77	0.34	0.36	1.70	3.57	5.28	5.10
Forest/m	n	14	13	14	14	12	13	14	14	13	13	14	14	14
	MEAN	5.593	32.15	130.79	544.72	251.33	59.08	64.38	11.54	6.90	25.37	100.11	47.02	81.71
	S.E	0.342	0.70	6.24	38.42	8.75	2.50	5.22	0.38	0.49	2.44	3.47	4.80	6.75
Forest/f	n	6	6	6	6	6	5	6	6	6	6	6	6	6
	MEAN	3.767	28.83	111.72	400.86	210.00	52.44	56.55	10.13	6.90	24.92	92.23	44.55	51.23
	S.E	0.458	1.44	12.83	57.64	8.94	7.59	4.78	0.52	1.13	1.99	6.37	6.51	8.49
PM/m	n	22			22			22			22			22
	MEAN	4.736			390.17			63.19			28.95			73.68
	S.E	0.341			28.94			3.79			2.62			4.23
AM/m	n	47			47			46			45			45
	MEAN	4.847			486.31			59.38			24.50			71.37
	S.E	0.228			19.73			2.83			1.40			3.66

Table 2: Means and standard errors of various tammar gut parameters expressed as a percentage of totals for all gut components.

AM, shot prior to midnight; PM, shot after midnight; m, males; f, females; #, analysis was confined to males in order to eliminate effects of gender.

Compartment	Parameter	Overall	Male	Female	'early' #	'late'#	Grass #	Bush#
Stomach	weight (g)	52.42 ± 0.49	53.0 ± 0.50	50.93 ± 1.15	54.36 ± 1.001	52.31 ± 0.56	52.84 ± 0.57	53.88 ± 1.05
	length (cm)	8.08 ± 0.08	8.03 ± 0.085	8.19 ± 0.15	7.76 ± 0.14	8.19 ± 0.10	8.01 ± 0.09	8.19 ± 0.25
	content (g)	72.83 ± 0.64	72.84 ± 0.74	72.79 ± 0.74	69.30 ± 1.06	74.66 ± 0.90	72.16 ± 0.82	75.83 ± 1.69
Midgut	weight (g)	25.70 ± 0.47	26.12 ± 0.54	24.61 ± 0.92	25.19 ± 0.99	26.50 ± 0.67	26.39 ± 0.64	24.62 ± 0.77
	length (cm)	62.87 ± 0.31	63.20 ± 0.31	62.14 ± 0.64	64.15 ± 0.46	62.54 ± 0.45	63.13 ± 0.37	63.19 ± 1.00
	content (g)	10.66 ± 0.30	10.46 ± 0.38	11.13 ± 0.49	11.74 ± 0.50	9.75 ± 0.50	10.75 ± 0.40	9.06 ± 0.95
Caecum	weight (g)	2.98 ± 0.08	2.99 ± 0.09	2.96 ± 0.07	2.91 ± 0.14	3.04 ± 0.12	3.02 ± 0.10	2.87 ± 0.25
	length (cm)	3.00 ± 0.04	3.04 ± 0.05	2.91 ± 0.07	3.09 ± 0.05	3.01 ± 0.07	3.05 ± 0.5	2.99 ± 0.08
	content (g)	4.32 ± 0.12	4.36 ± 0.14	4.24 ± 0.23	5.15 ± 0.22	3.96 ± 0.16	4.58 ± 0.157	3.46 ± 0.28
Colon	weight (g)	18.90 ± 0.50	17.89 ± 0.46	21.49 ± 1.21	17.55 ± 0.85	18.15 ± 0.85	17.75 ± 0.50	18.64 ± 1.28
	length (cm)	26.05 ± 0.27	25.73 ± 0.30	26.76 ± 0.56	24.98 ± 0.34	26.26 ± 0.40	25.82 ± 0.316	25.63 ± 0.86
	content (g)	12.19 ± 0.39	12.34 ±0.397	11.84 ± 0.96	13.80 ± 0.69	11.63 ± 0.48	12.50 ± 0.44	11.65 ± 0.98

Table 3: Means and standard errors of tammar gut contents expressed as grams per Kg metabolic body weight (g/kg $^{0.75}$).

# Indicates that anlaysis was confined to males in order to exclude the effect of gender.

Compartment	Overall	Male	Female	'early'#	'late#'	Bush #	Grass #
Stomach	135.93 ± 3.25	139.90 ± 4.07	126.21 ± 4.78	120.77 ± 4.50	148.61 ± 5.27	151.70 ± 9.17	137.30 ± 4.57
Midgut	19.23 ± 0.47	19.35 ± 0.58	19.03 ± 0.78	20.13 ± 0.77	18.77 ± 0.78	18.25 ± 1.60	19.58 ± 0.61
Caecum	7.90 ± 0.24	8.07 ± 0.28	7.49 ± 0.45	8.92 ± 0.46	7.63 ± 0.35	7.02 ± 0.76	8.35 ± 0.30
Colon	21.75 ± 0.58	22.59 ± 0.57	19.75 ± 1.37	23.46 ± 0.87	22.11 ± 0.75	22.52 ± 1.46	22.64 ± 0.62

Table 4: Scaling coefficients of gut compartments as a function of body weight (allometric scaling) obtained from simple linear regression (SLR) and reduced major axis analysis (RMA) showing Students t values of differences of exponential scaling coefficients ('b') from that of isometry and from that of av compensation for various gut compartments of 100 tammars shot on two sites in a single night in Rotorua district of New Zealand.

* Differences in degrees of freedom due to loss of some data from gunshot damage.

In the analysis of overall totals, t scores having $p < 0.05$ are highlighted. In the analyses of individual gut components, t scores that have $p < 0.0005$ are highlighted. This results in $p < 0.01$ per individual test in a rank of 24 tests.

Gut Compartment	Parameter	d/f*	SLR scaling coefficients		RMA Scaling Coefficients		SE s*		r	SLR Students t scores # (probabilities)		RMA Students t scores # (probabilities)	
			a	b	a	b	a	b		Isometry	Allometry	Isometry	Allometry
Total	length (cm)	1/92	5.586	0.248	5.417	0.363	± 0.041	± 0.028	0.685	-2.929	- 9.0	**1.163**	- 4.908
	weight (g)	1/94	4.974	0.904	4.274	0.743	± 0.085	± 0.057	0.855	6.778	- 2.667	2.297	- 7.147
	content (g)	1/91	4.317	0.672	4.751	1.058	± 0.054	± 0.036	0.892	5.754	14.526	**1.026**	- 7.746
Stomach	length (cm)	1/96	3.037	0.269	2.922	0.348	± 0.034	± 0.023	0.770	**-2.652**	-10.043	**0.781 (NS)**	-6.611
	weight (g)	1/98	3.659	0.714	3.532	0.801	± 0.055	± 0.037	0.944	**-1.459 (NS)**	-7.73	**3.185**	-5.374
	content (g)	1/98	4.520	0.999	4.187	1.228	± 0.107	± 0.072	0.814	**-0.014 (NS)**	-6.958	**3.168**	-3.777
Small I	length (cm)	1/95	5.193	0.199	4.878	0.415	± 0.055	± 0.037	0.483	-3.541	-8.135	**2.303**	**-2.292**
	weight (g)	1/95	3.349	0.426	2.980	0.684	± 0.083	± 0.056	0.636	-4.179	-10.25	**0.485 (NS)**	-5.587
	content (g)	1/96	3.216	0.550	2.649	0.942	± 0.116	± 0.077	0.587	-5.844	-12.338	**0.759 (NS)**	-7.253
Caecum	length (cm)	1/97	2.065	0.250	1.787	0.422	± 0.054	± 0.037	0.571	**-2.162**	-6.757	**0.301 (NS)**	**-0.158 (NS)**
	weight (g)	1/95	1.151	0.446	0.528	0.877	± 0.116	± 0.077	0.501	**-2.779**	-7.195	**0.282 (NS)**	**-0.160 (NS)**
	content (g)	1/96	2.022	0.748	1.382	1.190	± 0.140	± 0.094	0.632	**-2.681**	- 8.0	**2.022**	**-3.297**
Colon	length (cm)	1/96	4.095	0.345	3.940	0.450	± 0.044	± 0.030	0.767	**0.500 (NS)**	- 5.167	4.010	**-1.657 (NS)**
	weight (g)	1/96	2.220	0.989	1.803	1.272	± 0.121	± 0.081	0.778	4.062	**-0.136 (NS)**	7.555	-3.570
	content (g)	1/95	3.004	0.795	2.663	1.026	± 0.097	± 0.066	0.779	**-3.106**	-10.682	**0.399 (NS)**	-7.177

Table 5: ANCOVA of the variation in colon tissue with log (log n) converted whole body weight (kg) for factors of sex, 'time when shot*' and 'site where shot#'

Only significant interaction terms are shown;*, time when shot classified as either prior to or after midnight; #, site where shot classified as either forested or pasture area; n= 96 r = 0.878

Source	**f-ratio**	**p**
log n body weight	87.184	**0.000**
sex	3.482	0.065
time when shot	2.097	0.151
site where shot	0.181	0.671
log n body weight x sex	11.481	**0.001**

Table 6: A collection of separate discriminant function analyses of various gut parameters of 100 tammar wallabies shot on a single night in the Rotorua district of North island New Zealand, showing loadings of canonical discriminant functions, F-to-remove values and % success of jackknifed classification matrices for discrimination based on body weight, gender, time when shot and site where shot.

Wilk's lambda	Provides a test of whether groups based on character for discrimination are significantly different.
% Correct	Indicates the % correctly classified after suitable weighting for prior probabilities.
F-to remove.	For each gut component indicates the importance of that component to the discrimination (higher values indicate greater importance).
Loading	Indicates the contribution of that standardised variable to the discriminant function. (higher values indicate greater importance.)

a1) Discriminant analyses based on gender

	Gut tissue (g/g)		Compartment length (cm/g)	
Probability of Wilks lambda	0.0000		0.0033	
% Correct	82		72	
	loading	**F to remove**	**loading**	**F to remove**
stomach	0.457	6.04	0.880	1.46
midgut	-0.218	0.98	- 0.649	0.98
caecum	0.413	3.77	- 1.449	5.51
colon	0.931	38.02	- 1.652	7.74

a2) Means based on gender

Gut Component	Tissue g/g		Length cm/g	
	female	male	female	male
stomach	0.028	0.025	0.008	0.007
midgut	0.014	0.013	0.063	0.058
caecum	0.002	0.001	0.003	0.003
colon	0.012	0.008	0.026	0.023
n	26	67	29	65

c) Discriminant analysis based on time when shot

	Gut fill (g/g)	
Probability of Wilks lambda	0.0000	
% Correct	79	
	loading	**F to remove**
stomach	1.052	32.93
midgut	- 0.140	0.32
caecum	- 0.567	6.38
colon	- 0.379	3.13

b2) Means based on time when shot

Gut Component	**Gut fill (g/g)** **late**	 **early**
stomach	0.080	0.100
midgut	0.014	0.013
caecum	0.006	0.005
colon	0.017	0.015
n	30	64

Table 7: Simple linear regressions of time when shot against wet digesta content of certain gut segments corrected for metabolic body weight.

	Stomach	Caecum
Coefficient		
a	131.72	22.00
b	8.071	- 0.593
F	26.944	3.766
d/f	1/96	1/94
p	0.000	0.055
r	0.468	0.196
p of residuals (Lillifors test)	0.436	0.101

Chapter 8

Temporal patterns of drinking in the tammar wallaby (*Macropus eugenii* Desmarest).

R. G. Lentle, K. J. Stafford, M. A. Potter, B. P. Springett, S. Haslett.

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Temporal patterns of drinking in the tammar wallaby (*Macropus eugenii* Desmarest).

R. G. Lentle [1] , *K. J. Stafford* [2] , *M. A. Potter* [1] , *B. P. Springett* [1] , *S. Haslett* [3]

[1] Ecology Group, Institute of Natural Resources, Massey University, Private Bag 11222, Palmerston North, New Zealand.

[2] Institute of Veterinary Animal and Biomedical Sciences, Massey University Private Bag 11222, Palmerston North, New Zealand.

[3] Statistics Research and Consultancy Centre, Massey University, Private Bag 11222, Palmerston North New Zealand.

Abstract

The temporal association between drinking and feeding in four captive tammar wallabies (*Macropus eugenii* Desmarest) maintained on various foods is examined. Tammars maintained on cubed carrots never drank. In tammars fed pellets food associated drinking took place and 77.5 (s.e. ± 7.4) % of drinking episodes commenced within 60 seconds of the beginning or end of a feeding event. Drinking events occurred singly, were of short duration and increased in frequency but not duration, when low quality pellets were fed. The authors propose that food associated drinking in the tammar may result from the induction of drinking episodes of relatively fixed duration by an oropharyngeal reflex.

Introduction

The Tammar wallaby *Macropus eugenii* is well adapted to its semiarid island habitats (Kinnear *et al.* 1968; Barker *et al.*, 1970; Dellow and Hume 1982). The remarkable ability of Albrolhos tammars to maintain body mass and water balance on a low-protein food and seawater diet for periods of up to 30 days (Kinnear *et al.* 1968; Hume and Dunning 1979; Purohit 1971; Bakker *et al.* 1982) has been related to enhanced renal efficiency (Kinnear *et al.* 1968). Water flux rates of free-ranging Garden Island tammars are such that positive body water balance may be sustainable solely by the consumption of succulent plant foods without recourse to the drinking of seawater (Nagy *et al.* 1990). This strategy may be preferable to the ingestion of salt water which might lower the levels of fermenting micro-organisms and volatile fatty acids (VFAs) (Garg and Nangia 1993) and may not be tenable in view of the lower urine-concentrating ability of Garden Island tammars (Kinnear *et al.* 1968).

In arid-zone species, regulation of water intake has been shown to be important for efficient digestive function (Freudenberger *et al.* 1989). Thus, euros (*Macropus robustus erubescens*) are thought to maintain gut water at the expense of interstitial water during periods of drought (Denny and Dawson 1975) and a failure to maintain water intake produces an immediate decline in food intake in this species (Freudenberger and Hume 1987).

When dry foods are ingested by macropods, a source of fluid is required to maintain efficient fermentation and for the ongoing separation of fluid and particulate phases of digesta (Dellow 1979, Hume 1982) as well as food ingestion. Lubrication for deglutition can only come from water content of food, efficient ensalivation, or concurrent drinking (Kisseleff 1969). Stomach fluid may come from water content of food, from saliva swallowed during deglutition (Dellow, 1982), from transudation across the gut mucosa via the osmotic effect of ingested foods (Warner 1981), or from frequent drinking. The lack of difference in the rates of flow of the fluid phase of digesta through the sacciform and the tubiform forestomach (Dellow, 1982) shows that relatively little fluid enters these fermentative compartments by transudation. A review of studies of macropodine salivary gland anatomy and function suggests that the secretory capacity of salivary glands may be reduced with respect to that of eutherian species. Thus, whilst parotid gland weights of red (*Macropus rufus*) and grey (*M. giganteus*) kangaroos, when standardised for body weight, are twice as heavy as those of sheep (Forbes and Tribe 1969) the weight standardised production of saliva by red kangaroos is lower than that of sheep (McArthur *et al.*, 1995). Again the salivary production rates of the red necked pademelon (*Thylogale thetis)* (McArthur *et al.*, 1995), when standardised for body weight are lower than those of sheep and cattle.

Where drinking aids deglutition, its pattern may resemble that of desalivate rats (Kissileff 1969) which take large numbers of single short drinks interspersed with short feeding events, in a characteristic pattern described as ' prandial drinking'(Kisseleff 1969). Similarly where drinking contributes to the regulation of stomach water content, it may be temporally associated with feeding events and change in frequency or duration according to the quality of food supplied, as does the pattern of 'food associated drinking' (Kisseleff 1969; Fitzsimons and Le Magnen 1969; Le Magnen 1992) reported in ruminants, equines (Sufit et al 1985), pigs (Houpt *et al.* 1983), and rats (Kissileff 1969). Both 'prandial' and 'food associated drinking' have been classified as secondary drinking (Fitzsimons 1972) in that drinking activity is not brought about by fluid deficit (Le Magnen 1992) but by local conditions relating to feeding events (Fitzsimons 1972). Under such conditions the volume ingested per drinking event is likely to be limited in order to prevent drinking from 'overshooting the needs of the animal' (Toates and Oatley 1970). Conversely, when water is in short supply and situated some distance from feeding sites, or when drinking arises solely in response to whole body water needs, optimal foraging strategies may result in drinking becoming dissociated from feeding behaviour and controlled by 'feed forward' physiological mechanisms that maximise water intake per drinking event (McFarland 1970). Under such conditions it is likely that drinking bouts will be fewer and more prolonged.

Rotorua tammar populations may be derived from South Australian mainland stock *Macropus eugenii eugenii* (Poole *et al.* 1991) which is extinct in the wild (Maxwell *et al.* 1996). Previous work by us (Lentle *et al.* unpublished data) showed that captive Rotorua tammars always preferred carrot to high quality pelleted feeds. The purpose of this study was to investigate the temporal character of drinking behaviour and its relationship to feeding behaviour in captive Rotorua tammar wallabies maintained on pelleted and on carrot diets.

Methods

The activities of three adult (body weights 5.5 kg , 5.0 kg and 5.0 kg) estimated age 2.5 yrs (Sadlier 1984) and one subadult (body weight 3.0 kg) estimated age 1.5 yrs (Sadlier 1984) female wallabies kept in separate pens were recorded using infra-red and daylight video recording (Lentle *et al.* in press). The time spent drinking was estimated and it was assumed that this gave a good indication of the quantity of water ingested as shown for other species (Stellar and Hill 1952). Water was provided in a flat 20 cm diameter circular dish placed 2.5 m from the food dish, a position which required that the animal move away from the food dish in order to drink.

Three foods were fed, each for a period of two weeks, to allow for eight days familiarisation followed by six days monitoring. The foods were, fresh carrot diced to maximum dimensions of 15 mm x 15 mm, a high calorie density pelleted food composed of 90% milled maize and 10% milled barley, and a low calorie density pelleted food composed of 10% milled maize 10% milled barley and 90% milled barley straw. All pelleted food components were milled to a screen size of 4 mm. Pellets of both food types were of identical size (7mm x 15mm) and colouration. The dry matter content of high quality pelletised food was 90.5 s.e.. ± 0.45 % poor quality pelletised food , 90.4 s.e ± 1.786 % and cubed carrot 10.3 s.e ± 0.90 %.

All video recordings were reviewed by a single operator (R. L.). Drinking event duration was recorded as the time during which the subject maintained a quadrupedal position with its muzzle in the water dish and lapped continuously.

Statistics

Survivorship curves were calculated in SAS (1989; 1990). Log converted drinking event durations were normally distributed (2 tail Lillifors probability p = 0.101). Thus repeated measures ANOVA of log converted drinking events was carried out in SYSTAT version 5.03 (1992) and SAS (1989; 90).

A number of the F tests which follow have low denominator degrees of freedom, due to the small number of animals available and the fact that tests of these effects do not rely directly on the repeated measures structure of the experiment . Such F statistics need to be large to be of statistical significance. All effects of biological importance may therefore not have been identified in this experiment, although those that are most pronounced are also those most likely to be significant in a statistical sense.

The qualitative relationship between drinking and other activities was assessed by Markov chain analysis. Activity sequences were prepared for each of the six day study periods during which each animal was maintained on one of the two pelleted feed types. Activities were classified either as eating ('e'), drinking ('d') or other activity ('o') during which the animal was either resting, standing still or hiding. A changeover time of up to 120 seconds was allowed between each activity as this was the maximum time taken to traverse the pen. Thus an interval between successive acts of eating and/or drinking activity longer than 120 s was classified as 'o'. Randomness of association between alternate successive pairs of activities was tested by chi squared analysis of bulked data sets of the three adult animals.

The quantitative temporal relationships between drinking and feeding activities were calculated using the method employed by Kissileff (1969). The time intervals between successive drinking and eating events was calculated. Subsequent calculations were based on the shorter of the preceding and succeeding intervals e.g. if the pre-drink interval was the shorter, then the drink was considered to have taken place after eating. The durations of the drinking events associated with various pre and post feeding event time interval limits were each then totalled. In the rare cases where both the intervals were of the same length, drinking time was divided equally between pre and post feed intervals. A similar procedure was used to total the number of drinking events falling within each pre or post feed interval category.

Results

None of the four animals were observed to drink during the periods when they were maintained on cubed carrot. The mean daily drinking times, number of drinking events per day and mean duration of drinking events obtained on each of the two pelleted food types are shown in table 1. The overall mean drinking event duration was 68.4 ± 1.4 seconds and the longest drinking event duration was 250 seconds. The overall ratio of drinking events to eating events was less than one for both pelleted food types (food 1 mean = 0.128 ± 0.018, food 2 mean = 0.245 ± 0.028).

Of the total number of drinking events that were observed when pelleted food was fed 77.5 ± 7.4% commenced within 60 seconds of the beginning or end of a feeding event. Similarly 78.45 ± 6.7% of the total time spent drinking resulted from events that commenced within 60 seconds of the beginning or the end of a feeding event.

Doubly repeated measures ANOVA of the effect of pelleted food type on log converted total daily number of drinking events of adults female tammars was statistically significant ($F_{[1,2]} = 18.1$, $p = 0.05$), in spite of low statistical power, indicating that the number of drinking events increased significantly when adult animals were maintained on the poorer quality food type which was consumed in significantly greater quantity (Lentle *et al.* in press). Similar doubly repeated measures ANOVAs on total daily drinking time ($F_{[1,2]} = 6.88$, $p=0.08$) and on log converted duration of drinking events ($F_{[1,2]} = 1.21$, $p= 0.38$) showed that neither of these parameters were significantly effected by food type. The subadult animal maintained a high rate of drinking events on both food types. Doubly repeated measures ANOVA showed that changing to the poorer quality food type brought about a significant increase in the ratio of drinking to eating event numbers in all animals ($F_{[1,3]} = 10.676$, $p = 0.047$). However regression of daily numbers of drinking events against numbers of eating events using pooled data from all four animals showed no significant correlation with either feed 1 ($F_{[1,24]} = 0.655$, $p = 0.427$) or feed 2 ($F_{[1,22]} = 0.073$, $p = 0.789$)

Survivorship curves of drink events on pelleted foods

The survivorship curves of drink event duration of the three adult females on both feed types (fig 1) showed significant non linearity i.e. a broken stick configuration comprising a flatter initial segment where the likelihood of event termination was relatively low and a steeper secondary segment where the likelihood of termination was relatively high. Such configuration indicated that drinking activity tended to continue for a defined period and was more likely to terminate when this threshold had been exceeded. The threshold point, i.e. the inflection point on the curve, was similar in all non linear curves and did not change with feed type.

Markov chain analysis

The Markov chain analysis of the association between consecutive drinking and eating events (table 3) showed significant departure from an overall random association between these events both when either feed 1 (Chi sq = 15.36, df = 1, p = 0.001) or feed 2 (Chi sq .= 43.39, df 1, p = 0.001) was given. The results showed that this was due primarily to the significant tendency for feed events to occur singly, i.e. negatively associate, and partly to a less significant positive association between drinking and eating events, when the poor quality food type, that was eaten in greater quantities, was being fed.

Discussion

The results, showing complete absence of drinking activity in Rotorua tammars fed carrot cubes, confirm Nagy *et al.*'s (1990) hypothesis, based on garden island tammars, that this species does not need to drink when eating relatively succulent vegetable material. These results also show that any ongoing (Warner 1981) extrusion of liquid phase through the solid phase of digesta (Dellow 1979; Hume 1982) is not dependent on acts of drinking. Thus in relatively dry habitats, a foraging strategy of location and consumption of relatively succulent plants, which may include those of lower overall nutrient density, may be more viable than a strategy of selecting drier more nutrient dense material coupled with temporally discrete drinking.

The temporal pattern of drinking behaviour of tammars fed dry pelleted foods closely resembled that of 'food associated drinking' reported in the rat (Fitzsimons and Le Magnen 1969; Kissileff, 1969) in that the majority of drinking activity resulted from events which commenced within one minute of a feeding event and that drinking was influenced by feeding conditions. As mentioned hitherto, food associated drinking is widely reported in eutherian species, but as far as we are aware this study is the first to formally report this behaviour in a non eutherian species.

It is unlikely that food associated drinking results from humeral stimuli as reduction in plasma volume takes 15 minutes to occur in the sheep following ingestion of dry food (Blair-West and Brook, 1969). Similarly work on pigs (Houpt and Anderson, 1990) and rats (Fitzsimons and Le Magnen, 1969) has shown no association between the commencement of food associated drinking and changes in blood osmolarity or volume. Thus in tammars, as in rats (Lucas et al. 1989; De Castro, 1989), oropharnygeal 'cues' that result from the relative dryness or succulence (Nagy , 1990) of a new diet may directly induce an appropriate adjustment in food associated water intake. The results of this study show that in tammars, such adjustments result from changes in the number rather than the duration of drinking events. The survivorship analysis, showing a significant tendency of all drinking events to finish after a few seconds with close similarity of the inflection points on the survivorship curves regardless of pelleted feed type, further supports this conclusion. Given these findings, appropriate adjustments could arise equally well from oropharyngeal reflexes as from the 'learnt associations' (Fitzsimons 1972) that are thought to bring about 'anticipatory' (Le Magnen 1992) changes of drinking behaviour in the rat. The significant tendency for drink events to occur singly supports the existence of an orophamygeal reflex rather than an anticipatory mechanism but further study of changes in food related drinking in response to short term change in food quality is needed to distinguish more completely between these two possibilities.

Food associated drinking may allow whole body water requirements to be adjusted according to dietary moisture content but may also provide a means by which foregut water content is optimised. Indeed the persistence of food associated drinking in a non ruminant foregut fermenting species, such as the tammar, that is adapted to drought conditions, may indicate its particular importance in the control of foregut water content when ongoing re-ensalivation, i.e rumination, is not an option.

The low ratio of drinking to eating events and the lack of any overall correlation between numbers of drinking and eating events indicate that the timing of drinking differs from the classical 'prandial' pattern (Kissileff 1969; Fitzsimons 1970) in which drinking affords the principal means of deglutition. The food associated pattern of drinking may nevertheless act as a aid deglutition particularly under conditions where acts of drinking are triggered by local reflexes based on oropharyngeal dryness.

In summary the temporal pattern of drinking that is elicited when tammars are fed dry foods may function as an aid to digestion and to deglutition. The limitations of such a pattern of behaviour may influence food choice in an arid environment and in laboratory conditions. This finding has an important bearing not only on the field ecology of this species but also on the use of dried and pelleted foods in laboratory based experiments.

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Table 1: Mean (± SE) total daily drinking time, daily number of drinking events, daily number of feeding events and drinking event duration in four captive female tammars maintained ad libitum on high and low quality milled pelleted foods of identical appearance, dimension, and particle size for six days. Water was available ad libitum.

Feed 1, high nutrient density pelleted feed; Feed 2, low nutrient density pelleted feed; *.subadult

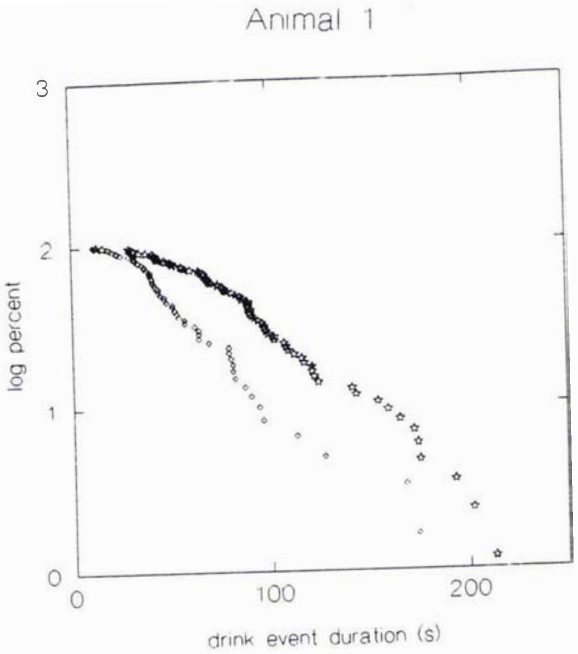
Animal	**Feed**	**Total daily drink event duration (mins)**	**Total daily number of drink events**	**Total daily number of feed events**	**Mean drink event duration (secs)**
1	1	7.81 ± 0.74	9.5 ± 0.99	123.3 ± 20.2	55.13 ± 4.21
	2	18.99 ± 1.04	12.5 ± 1.18	72.9 ± 11.8	85.58 ± 4.68
2	1	8.07 ± 0.58	5.8 ± 0.60	47.4 ± 6.1	81.36 ± 5.34
	2	11.13 ± 0.79	8.0 ± 0.82	47.4 ± 4.3	85.51 ± 5.47
3*	1	19.37 ± 2.79	22.0 ± 3.1	85.9 ± 10.7	53.05 ± 1.80
	2	17.1 ± 1.43	18.0 ± 1.23	39.9 ± 7.3	59.16 ± 2.09
4	1	10.69 ± 1.26	9.0 ± 1.09	75.7 ± 7.6	77.15 ± 5.41
	2	15.71 ± 2.99	12.5 ± 1.98	47.3 ± 6.3	73.13 ± 3.76

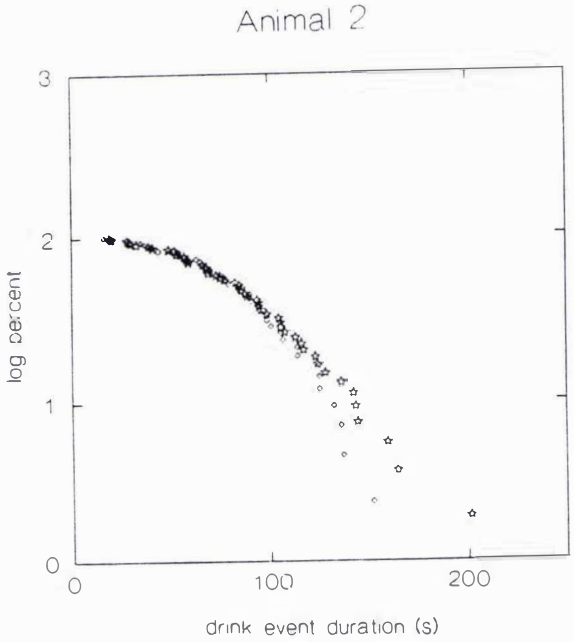
Table 2: Markov chain analysis of the temporal association between drinking and eating events on high and low quality pelleted foods.

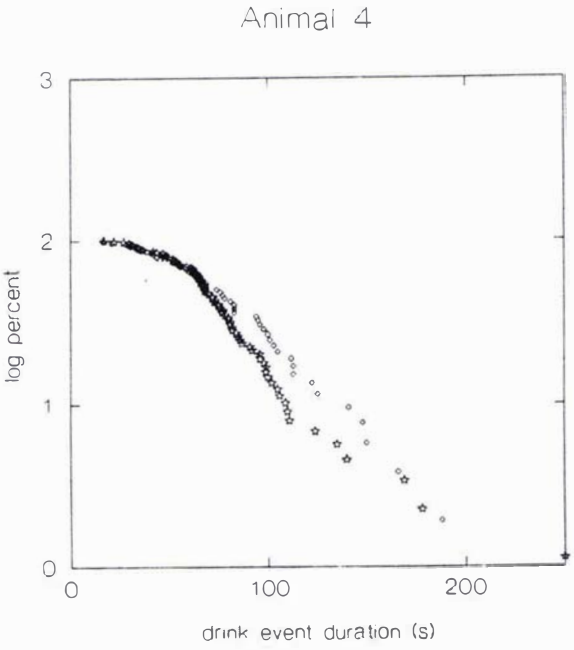
	High quality feed		Low quality feed		
Following event	**Prior event**		**Prior event**		
	drink	**eat**	**drink**	**eat**	
drink	0	111	2	147	**Actual (n)**
	11.93	99.07	30.14	118.86	**Expected (n)**
	11.93	1.43	26.27	6.66	**Chi sq**
eat	92	653	123	346	**Actual (n)**
	80.07	664.93	94.86	374.1	**Expected (n)**
	1.78	0.21	8.35	2.12	**Chi sq.**

Figure 1: Survivorship curves of drinking events of three captive adult female tammar wallabies over a six day period maintained on two pelleted feed types.

High quality food pellets (food type 1), diamond; low quality food pellets (food type 2), star.


Animal 1
3
2
1
0
log percent
0
100
200
drink event duration (s)


Animal 2
3
2
1
0
log percent
0
100
200
drink event duration (s)


Animal 4
3
2
1
0
log percent
0
100
200
drink event duration (s)

Chapter 9

The integration of resting with other activities in the tammar wallaby (*Macropus eugenii* Desmarest).

R. G. Lentle, K. J. Stafford, M. A. Potter, B. P. Springett, S Haslett.

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The integration of resting with other activities in the tammar wallaby (*Macropus eugenii* Desmarest).

R. G. Lentle[1] ,*K. J. Stafford*[2] , *M. A. Potter*[1] , *B. P. Springett*[1] , *S Haslett*[3]

[1] Ecology Group, Institute of Natural Resources, Massey University, Private Bag 11222, Palmerston North , New Zealand.

[2] Institute of Veterinary Animal and Biomedical Sciences, Massey University Private Bag 11222, Palmerston North, New Zealand.

[3] Statistics Research and Consultancy Centre, Massey University, Private Bag 11222, Palmerston North New Zealand

Abstract

The temporal structure of resting periods and correlation with body position are examined in captive tammar wallabies. Resting periods in the sitting position are relatively long and are favoured by day whilst resting periods in the lying position are relatively brief and favoured at night. The duration of each type of resting was uninfluenced by deil cycle and, unlike that of rats, uninfluenced by nutrient density of food. The authors hypothesise that the sitting resting behaviour of tammars may result either from a need to avoid heat or for a greater alertness during the day rather than from any digestive requirements. Mericism was observed only when the animal was standing and occurred more frequently on poor quality food.

Introduction

A number of factors including climate (Dawson and Denny 1969) and predation (Clarke et al. 1995) can influence the timing of macropodid activity. The relative influence of these factors in shaping the day to day temporal patterns of behaviour are largely unknown. The timing and mechanism of sleep may be shaped by the selective pressures of temporally varying environmental factors (Webb 1970; 1975; Heller et al. 1996). Insight into the forces shaping the temporal allocation of sleep may be obtained by studying its temporal structure and the manner in which it is integrated with other activities.

Two factors, feeding and defence, are thought to influence sleep form. Heidiger (1959; 1969) suggested that differences in rapid eye movement (REM) sleep were due to solely to 'security'. Karmanova (1977) considered that whilst periodicity of illumination acted as a 'zeitgeber' the circadian rhythm of wakefulness of an animal may ultimately be determined by both 'alimentary and defensive activities'. Danguir et al (1979) showed a significant correlation between meal size and sleep in rats. The manner of integration of sleep with feeding activity is particularly important in small animals with high energy requirements, especially if they employ a digestive strategy of high throughput of low energy materials. Thus shrews (*Sorex*) known to have an exceptionally high metabolic rate (Vogel 1976) integrate short 'rest periods' with foraging activity because they would starve if they slept for an entire day or night (Saarikko 1990). A similar integration of feeding and resting behaviour has been shown in humming birds (Karasov et al. 1986).

In humans the coordination of central nervous system and enteric nervous system changes with sleep state (Kumar et al. 1994), effecting motility and digestive processing (Narducci et al. 1987; Furukawae al. 1994). Rapid eye movement (REM) sleep is reported to increase colonic activity and throughput (Narducci et al. 1987), whereas slow wave (SW) sleep brings about a general reduction of migrating motor complexes (Furukawae et al. 1994) with concomitant reduction in colonic activity (Narducci et al. 1987). Thus, in animals in which a high gastrointestinal throughput must be maintained, it may be advantageous to take rest as short periods of REM sleep.

Rest/sleep patterns of macropods are likely to have been influenced by the selective forces of predation and digestion suggested by Karmanova (1977). Macropods may have been subject to predation pressure (Jarman and Coulson 1989; Croft 1989), and often forage nocturnally in groups (Caughley 1964;

Kaufmann 1974; Croft 1981; Jarman and Southwell 1986; Jarman and Coulson 1989; Clarke et al. 1995). Macropods are said to be specialised for rapid throughput of low quality herbage (Hume 1982).

In the same manner that visceral anatomical differences in ruminants may predispose to bloat (Waghorn and Reid 1984) anatomical factors may impede the efficient eructation of methane or mericism in macropods. Thus the relatively long intra-abdominal oesophagus (Richardson 1980) may preclude the close functional association between diaphragm and cardia that is seen in ruminants (Phillipson 1977). Again, the lack of anchorage of the roof of the foregut may permit greater degrees movement of the fermentation chamber in relation to the diaphragm than occur in ruminants (Waghorn and Reid 1984). In certain postures such movement may obstruct the transfer and release of gas. These interactions may be important in a species in which mixing of digesta in the foregut may be influenced by the relative movements of the 'visceral piston' associated with locomotion (Baudinette et al., 1987)

In this study the temporal characteristics of rest, in tammar wallabies (*Macropus eugenii* Desmarest) maintained on various food types, and its timing in relation to other behaviours, particularly eating, drinking, and regurgitation are examined. This species is appropriate for such a study as tammars have been noted to rest in two distinctive postures (Kinloch 1973; Russell 1973; M Vujcich 1979). Thus the temporal distribution of the two postures may yield information on the temporal aspects of predation.

Methods

Rest patterns of captive tammars

Two adult females without pouch young and one juvenile, captured in the Rotorua district of North Island, New Zealand, using the method described by Lentle et al. (1996), were held and monitored using infra-red techniques (Lentle et al., in preparation). Each animal was maintained at different times on one of two food types, a high quality pelleted food or a low quality pelleted foods (Lentle et al., in preparation).

Resting behaviour was classified either as the 'sitting tail forward' or the 'lying' posture described by Russell (1973) (fig 1). Only non-cryptic resting behaviour was recorded i.e any resting that took place when tammars were hiding in a small enclosed box, following disturbance, was not recorded.

The video records of the three animals maintained on the two food types were reviewed by a single operator (RL) and the duration and type of each resting event noted. Log survivorship curves (Fagen and Young 1978) of the durations of each type of resting event that took place when each animal was fed each pelleted food type were plotted using SAS (1989; 90). Repeated measures ANOVA of log converted resting events duration of both types was carried out in SYSTAT version 5.03 (1992) and SAS (1989; 90).

Markov chain analysis

A Markov chain analysis was conducted on the relative frequencies of sequences of two consecutive behavioural events in the bulked data obtained from the three animals taken over six days on each of the two pelleted food types. Behaviour was classified as eating, drinking, resting in tail prop posture, resting in lying posture or 'other behaviour' the latter category comprising crypsis, standing alert, or travelling for periods of greater than two minutes. Periods of travelling between drinking, feeding, resting and hiding activities that were of less than two minutes duration were not included in the analysis.

Regurgitation

The occurrence and timing of regurgitation was monitored in the wallabies fed pelleted food. In addition video records of two trials in which these animals were fed a daily ration of three square meters of ryegrass (table 1) turves with 2.5 cm of sward depth, or 0.5 cm cubed carrot *ad libitum*, were reviewed and the occurrence and timing of regurgitation noted.

Results

Behavioural observations

Resting postures

In 'lying' the animals lay on one side with thorax and abdomen in contact with the ground and tail projecting posteriorly i. e. not brought forward between the legs (fig 1). In contrast to the observations of Russell (1984), which were taken during a constant three hour daily time period of artificial illumination, it was noted that the head was also rested side on and rarely elevated, particularly during the hours of darkness. During periods of rest in this position, there was notable absence of body movements. Termination of a 'lying' resting period was generally abrupt, sometimes with elevation of the head for a few seconds prior to rising. Rising from a lying position was achieved by jumping with the hind legs and was often accompanied by a thumping sound.

In 'sitting tail forward' the animals adopted the posture described by Russell (1973) with the tail brought forward between the legs and the hindquarters in contact with the ground. This position was often adopted in a situation where the back was supported by a vertical surface. Generally the shoulders were hunched forward and the spine flexed anteriorly. However from time to time, and when startled, the spine was straightened and the head held higher. This movement often preceded locomotion and was silent. On occasion an animal in the 'sitting tail forward posture' changed suddenly to lying posture, this change being effected by a sideways fall accompanied by a lateral and posterior movement of the tail. The reverse sequence, a transition from lying to sitting, was never observed.

Regurgitation

No episodes of regurgitation were identified during the period when animals were maintained on pelleted and cubed carrot feeds. However, during the periods when grass was fed and the sward denuded, causing the animals to consume more fibrous low quality residues, five episodes of projectile regurgitation of dark liquid material were recorded, one by an adult female and the other four by a juvenile female (two episodes on each of two nights). All took place during the hours of darkness (between 2347 hrs and 0449 hrs), in the standing position, the animal having been being restless and ambulant immediately prior to the behaviour.

Statistical analyses

A number of the F tests which follow have low denominator degrees of freedom, due to the small number of animals available and the fact that tests of these effects do not rely directly on the repeated measures structure of the experiment. Under such conditions F statistics need to be large to be of statistical significance. All effects of biological importance may therefore not have been found in this experiment, although those that are most pronounced are also those most likely to be significant in a statistical sense.

Numbers of resting events.

Variations, due to incidental disturbance, in the relative proportion of time spent in the enclosed box by each animal, rendered direct comparison of total numbers of the two types of resting events between animals less meaningful. Thus the relative proportions of each type of resting event taken over a six day period (table 2) on each feed (which were distributed normally, Lillifors probability = 0.945) were compared by doubly repeated measures ANOVA. There was a barely significant greater overall proportion of 'lying' resting than ' sitting tail forward' events (F = 4.141, df = 1/24 , p = 0.054). The relative proportion of the number of times each of the two types of rest was seen varied significantly with daylight ($F_{1,2}$ = 156.42, p = 0.006), the 'sitting tail forward' posture being used more frequently during the hours of daylight and the 'lying' posture being used more frequently during the hours of darkness. The relative use of the two resting postures was not significantly influenced by the type of food being fed ($F_{3,6}$ = 3.964, p = 0.071) There was no significant interaction between 'food type' and 'daylight/darkness' terms ($F_{3,6}$ = 0.435, p = 0.736) i.e the relative use of the two resting positions by day or night did not not vary significantly with food type.

Duration of resting events

Survivorship curves of the durations of resting events for the three tammars on both feeds (fig 2) with one exception (animal 2 on low quality feed) all exhibited a concave broken stick conformation indicating an initial process in which the likelihood of termination of shorter resting events is high and a second process in which the likelihood of termination of longer resting events is lower.

Means (± s.e.) of durations of the two types of resting events for the three tammars are shown in table 3. Analyses of resting event durations were carried out on log transformed values. Log transformations of rest event durations produced a distribution which showed only minor departures from normality (fig 3). However, because there were hundreds of points, many of the formal significance tests (Lillifors tests) for non normality were statistically significant even given that the distribution was symmetric.

There were significant differences ($F_{1,2}$ = 23.46, p = 0.04) in the duration of rest in the two postures on repeated measures ANOVA. Resting in the 'sitting tail forward' posture tended to continue for longer periods than resting in the 'lying' posture. However darkness had no significant influence on the duration of rest either in the lying ($F_{1,2}$ = 1.42, p = 0.356) or the ' sitting tail forward' ($F_{1,2}$ = 0.14, p = 0.744) posture. Again the duration of 'lying' ($F_{1,2}$ = 0.05, p = 0.846) and 'sitting tail forward' resting events ($F_{1,2}$ = 4.72, p = 0.17) did not vary according to which of the two feeding peaks (evening/ early night or late night/morning) in which they occurred. Similarly the nutrient density of the pelleted feeds did not influence the duration of rests either in the 'lying' ($F_{1,2}$ = 0.28, p = 0.649) or in the 'sitting tail forward' ($F_{1,2}$ = 4.81, p = 0.159) posture.

Association with other behaviours

The Markov chain analysis (table 4) showed a general negative association of resting with drinking activity with animals maintained on either of the two pelleted feed types i. e. drinking tended to occur less frequently in association with either type of non-cryptic rest than would occur if both were distributed randomly, particularly for periods of 'lying' rest and when the animals were maintained on high quality food. A similar analysis (table 5) showed that resting events were less likely to follow an eating event than would occur if both were distributed randomly.

Discussion

The results of the survivorship analysis indicate that the termination of rest periods in this species (Russell 1973) is generated by at least two stochastic processes, causing them to be of significantly different duration i.e that there are two types of resting behaviour each with a different probability of termination. The significant differences in the duration of lying and sitting tail forward resting indicates that these two types of resting behaviour are characterised by posture.

The choice of resting type is not made on a random basis, 'lying' rest being used more frequently during the hours of darkness and 'sitting tail forward' rest being used more frequently during the hours of daylight. However the duration of each resting type is not influenced by the deil cycle and thus adjustments in quantity of rest must be achieved principally by frequency of choice between the significantly longer 'sitting tail forward' rest and the shorter 'lying' rest.

It is possible that the choice of daytime rest type may represent habitual daytime avoidance of direct solar radiation in that greater surface area is exposed in the lying than in the sitting tail forward rest.

It is difficult to assess state of arousal or alertness without electro-encephalography. However, difference in height of head has been used as a measure of vigilance in free ranging eastern grey kangaroos, *Macropus giganteus* (Clarke et al 1995) and on this basis, vigilance is lower in 'lying' compared to 'sitting tail forward' rest. Moreover the presence of episodic head raising in the 'sitting tail forward' and relative absence of movement during 'lying' rest, again suggest that the 'sitting tail forward' position is associated with greater vigilance. Thus the greater use of the tail forward position in the day may indicate greater vigilance by day, a hypothesis that is supported by Clarke et al.'s (1995) findings that eastern grey kangaroos group size was smaller and the time they spent surveying was lower at night than during the day. Both findings are contrary to Clarkes (1995) general hypothesis of a greater nocturnal than diurnal anti-predator effort by macropod species.

As noted hitherto in certain eutherian monogastric species feeding conditions may influence sleep type (Lorenz 1986; Macfayden et al. 1973). Marsupial species are known to exhibit both SW and REM sleep (Van Twyver and Allison 1970) and the two resting positions may characterise these two types of sleep. The results showing that both the frequency of occurrence and the duration of both types of resting posture are uninfluenced by the caloric density of food do not support the existence of a link between resting behaviour and feeding conditions in marsupials. Thus when lower quality food is being consumed, neither the physical bulk of food consumed per feeding event (Lentle et. al. In prep.), nor the increase in gut load that must result from such an increase, given that macropod throughput rates are relatively fixed (Freudenberger and Hume 1992), influence resting behaviour. This is not to say that the metabolic outcome of feeding events does not influence these parameters. It is conceivable that, under conditions of adequate nutritional compensation, fermentation of a larger gut load of lower quality food may have a similar metabolic outcome as a smaller gutload of higher quality food. However in view of the relatively slow process of fermentation (Mertens and Ely 1982) it seems unlikely that meal frequency, sleep frequency or sleep duration in herbivores are regulated by mechanisms that depend on the prompt metabolic outcome of a meal such as occurs in the rat (Danguir 1979; Le Magnen 1992).

The higher incidence of regurgitation with poorer quality food has been commented on by other workers (Hume, 1982). The lower than random association between drinking and resting events and between resting and feeding events may indicate that the adoption of a resting position is inhibited for a time following a drinking or an eating episode. This may allow regurgitation or eructation to take place more readily when the animal is in a standing position.

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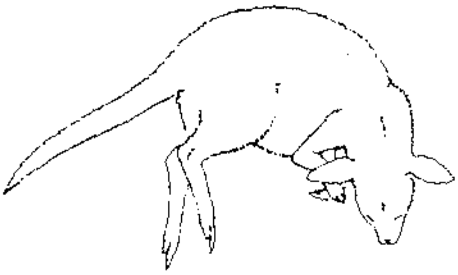
Figure 1: Showing the 'lying' and 'sitting tail forward' postures in the tammar wallaby (*Macropus eugenii* Desmarest).

A, sitting tail forward position; B, lying position from above; C, lying position form the side. Views are drawn from infra-red video stills.

A

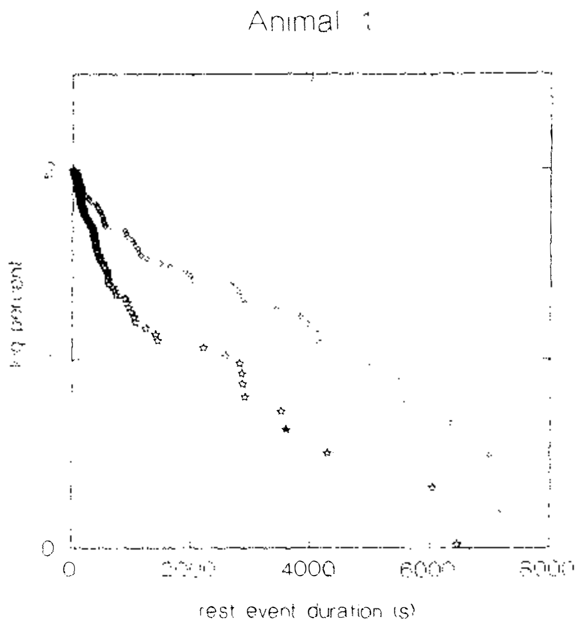


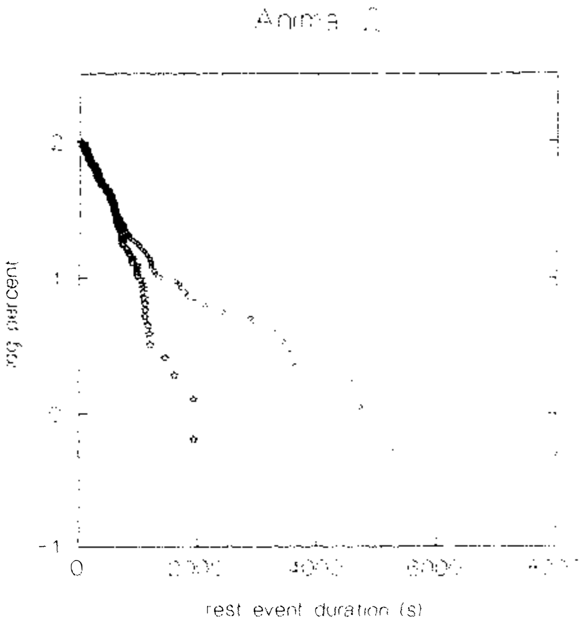
B

C

Figure 2: Survivorship curves of pooled resting events in three captive female tammar wallabies maintained on two food types of differing nutrient density density each for a period of six days.

High quality milled pelleted food (Feed 1), diamond; Low quality milled pelleted food (Feed 2), star.


Animal 1
log percent
2
1
0
0
2000
4000
6000
8000
rest event duration (s)


Animal 2
log percent
2
1
0
−1
0
2000
4000
6000
8000
rest event duration (s)

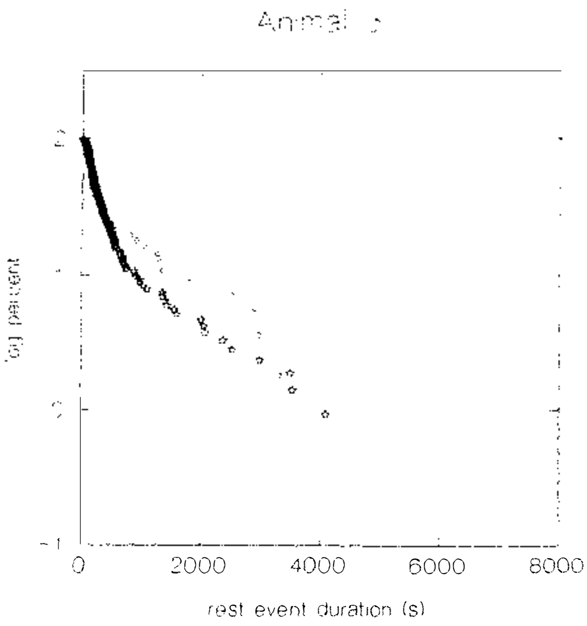

Animal 3
log percent
2
1
0
−1
0
2000
4000
6000
8000
rest event duration (s)

Figure 3: Normal probability plot of pooled log converted resting event durations of three captive female tammars maintained on two feed types types of differing nutrient density.

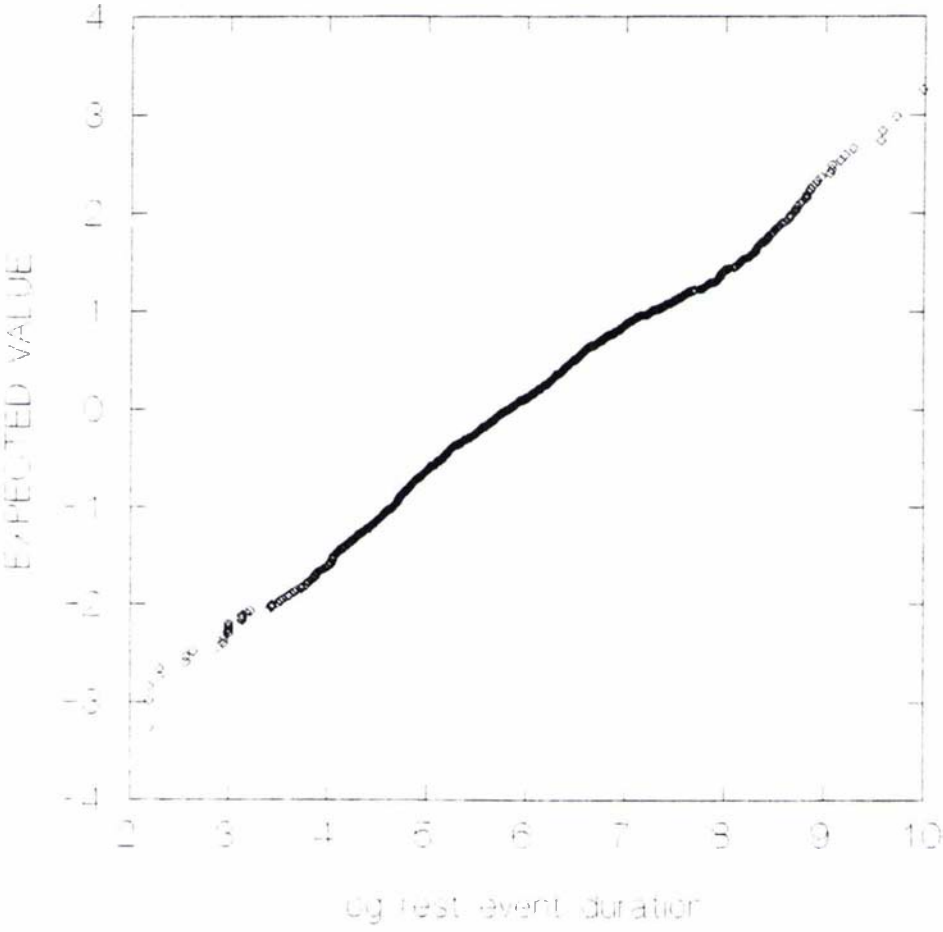

EXPECTED VALUE
4
3
2
1
0
-1
-2
-3
-4
2
3
4
5
6
7
8
9
10
log test event duration

Table 1; Nutrient analysis of rye grass sward.

	Dry matter %	Nitrogen %	Gross energy kJ/g	Neutral detergent fibre %	Acid detergent fibre %	Lignin %	Hemi-cellulose %	Cellulose %	Reducing sugar %
mean	94.3	4.06	18.40	47.8	23.1	2.49	24.69	20.61	8.830
se	0.38	0.49	0.035	3.04	1.23	0.28	1.81	0.945	0.650

Table 2: Means and standard errors of the relative percentages of numbers of resting events taken in 'tail prop' and 'sitting tail forward' resting posture by three captive female tammar wallabies maintained on two feed types of differing nutrient density each for a period of six days.

Resting posture	overall	light	dark	feed1	feed2
lying	42.4	14.8	70.1	38.2	62.8
	± 8.77	± 3.46	± 13.06	± 17.41	± 25.08
sitting	21.51	29.8	13.2	11.7	14.7
	± 4.60	± 8.42	± 2.42	± 2.56	± 2.58

Table 3: Means and standard errors of duration of rest events (minutes), in 'lying' (l) and in 'sitting tail forward' (s) posture taken by three captive female tammar wallabies maintained on two food types of differing nutrient density each for a period of six days.

Feed 1 = high quality milled pellet; Feed 2 = low quality milled pellet.

	Feed type			
Animal	**1**		**2**	
	Resting posture		**Resting posture**	
	l	**s**	**l**	**s**
1	6.78	56.25	4.90	26.23
	± 0.90	± 6.50	± 0.63	± 5.15
2	6.71	30.56	7.62	8.34
	± 0.56	± 4.16	± 0.52	± 1.73
3	3.19	22.65	3.68	25.23
	± 0.72	± 5.08	± 0.25	± 5.48

Table 4: Association of resting events with drinking events. Results of Markov chain analysis of pooled event numbers from three captive female tammar wallabies maintained on two feed types of differing nutrient density each for a period of six days.

Feed 1 = high quality food. Feed 2 = low quality food

		First event			
		Feed 1		**Feed 2**	
Rest posture		**drinking**	**resting**	**drinking**	**resting**
sitting	**actual**	0	0	1	1
	expected	2.39	2.52	5.40	5.375
	Chi sq	2.39	2.52	3.58	3.56
lying	**actual**	0	2	2	3
	expected	7.65	7.82	24.89	24.78
	Chi sq	7.65	4.33	21.05	19.15

Table 5: Association of resting events with eating events. Results of Markov chain analysis of pooled event numbers from three captive adult female tammar wallabies maintained on two feed types of differing nutrient density each for a period of six days.

Feed 1 = high quality food. Feed 2 = low quality food

		First event			
		Feed 1		Feed 2	
Rest posture		**eating**	**resting**	**eating**	**resting**
tail prop	**actual**	9	22	13	22
	expected	21.53	22.69	26.16	26.18
	Chi sq	7.29	0.021	6.62	0.669
lying	**actual**	27	49	59	94
	expected	69.00	70.28	120.61	120.7
	Chi sq	25.56	6.45	2.24	5.91

Chapter 10

General discussion.

General discussion

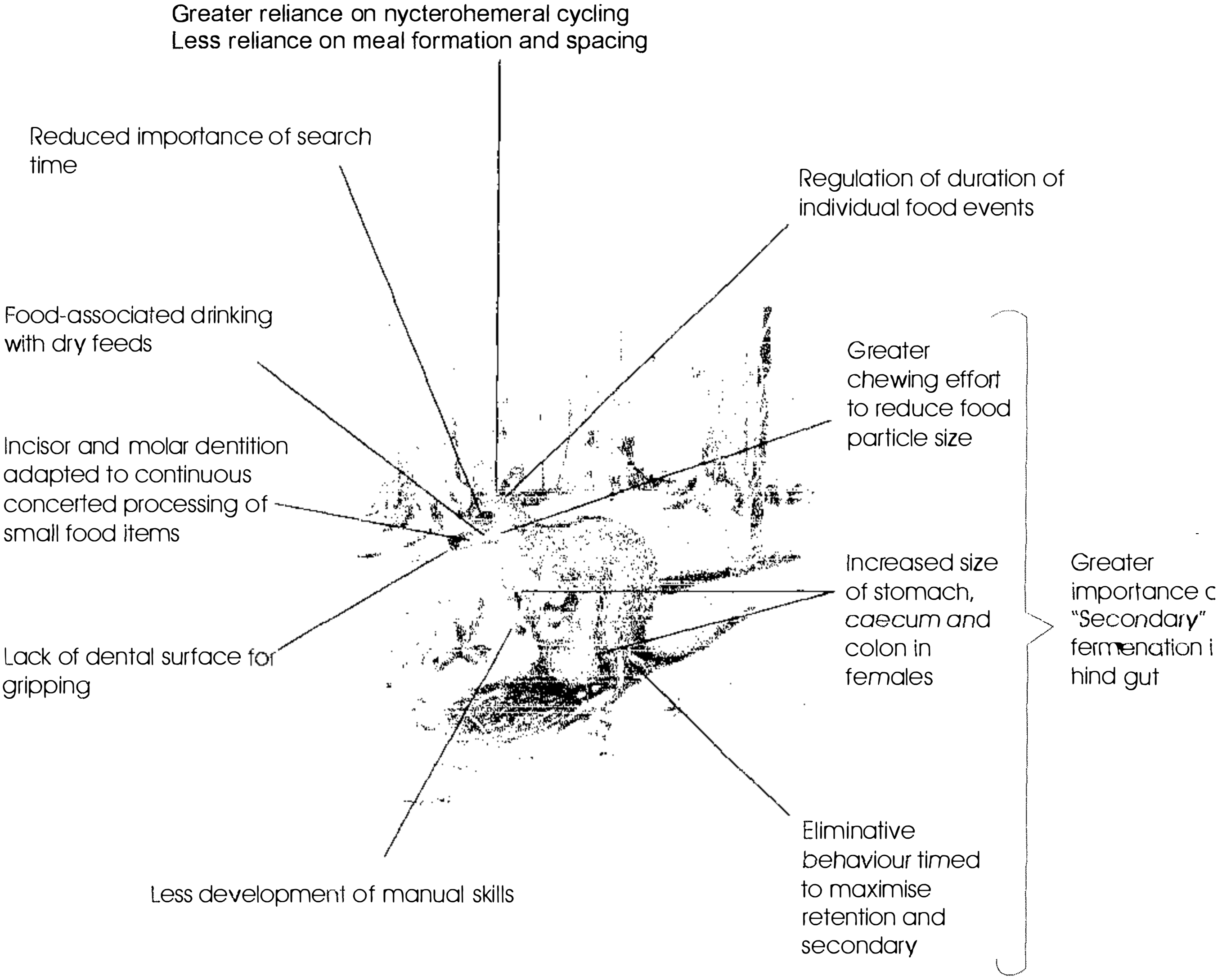
Macropods have been broadly classified as grazers (Sanson, 1980; 1989) and their general feeding strategy has been summarised as the rapid throughput of low quality material (Hume, 1984; 1989). Specialism in the consumption of relatively abundant poor quality foods i.e. grazing herbivory increases the probability of an animal encountering food, but also results in constraints on energostasis resulting from the relatively longer times spent ingesting and digesting greater quantities of more chemically resistant material (Van Soest, 1982). These time constraints are particularly likely in small herbivores where disparity between the scaling of gut volume and of energy expenditure with body weight will exacerbate energostatic difficulties (Demment and Van Soest, 1985; Cork, 1995).

In tammars (*Macropus eugenii* Desmarest) the existence of such a disparity is demonstrated by the near isometric scaling of total fermentative gut volume with body weight shown in this study, and the known allometric scaling of the basal metabolic rate with body weight (Hulbert and Dawson, 1974). Small grazing herbivores such as the tammar may lessen the time constraints either by increasing digestive capacity i.e. increasing the efficiency of intake and processing of food, or by using behavioural strategies to search out better quality foods. The present multifaceted study of the dynamics of feeding in the tammar wallaby reveals a number of ingestive, digestive and eliminative strategies which this small grazer (Norbury et al., 1989; Williamsen, 1986) uses to lessen the energostatic constraints of herbivory (figure 1).

The temporal distribution of feeding behaviour

The feeding events of tammars are dispersed throughout the day with a period of reduced activity around midday. Their duration and incidence varies in a crepuscular pattern with feeding events tending to occur most frequently, and to be longest, in the four hours around sunset and sunrise. The similarity between the temporal incidence of feed events of tammars in the laboratory and in the field indicates that the underlying nycterohemeral rhythm is relatively invarient. A search for the existence of a temporal pattern in which the time interval between successive groups of feeding events is proportional to the duration of the initial group shows low levels of correlation over a wide range of

FIGURE 1: Adaptations of the tammar wallaby to grazing.



Greater reliance on nycterohemeral cycling
Less reliance on meal formation and spacing

Reduced importance of search time

Regulation of duration of individual food events

Food-associated drinking with dry feeds

Greater chewing effort to reduce food particle size

Incisor and molar dentition adapted to continuous concerted processing of small food items

Increased size of stomach, *caecum and* colon in females

Greater importance c "Secondary" fermenation i hind gut

Lack of dental surface for gripping

Eliminative behaviour timed to maximise retention and secondary

Less development of manual skills

Tammars are specialists in the consumption of food items that are:

Abundant/ Temporally predictable
Low Quality
Small

criterion intervals. The decrease in levels of correlation with increase in criterion interval indicates that tammars do not achieve nutritional compensation by the appropriate spacing of aggregates of feeding events i.e. meals. The significant change in the duration of feeding events that occurs when less nutrient-dense foods are being fed indicates that compensation for dry matter intake is accomplished instead by factors acting at the level of individual events.

An intake strategy based on the duration of individual feeding events circumvents a number of physiological difficulties which may render nutritional compensation based on changes in the spacing of meals relatively inefficient in herbivores. Appropriate adjustments to the spacing of meals are dependent upon prompt metabolic feedback from digestive products (Le Magnen, 1992) and the relative slowness of fermentative digestion (Mertens and Ely, 1982; Demment and Van Soest. 1985) makes such feedback tenuous. Further, the efficiency of the tammar fermentative reactor may be augmented by strategies based on temporal dispersal rather than clustering of individual feed events. Chemical reactor theory indicates that optimum energy yields are best achieved by maintaining the digesta content of continuous flow reactors, such as the stomach of tammars, at or near to maximum capacity (Penry and Jumars 1987) with regular small 'top ups' from individual feeding events. A strategy based on the formation of meals, where longer feeding periods occur at greater intervals, would result in periodic partial emptying of the reactor causing dynamics to approach those of the less efficient batch flow reactor type (Penry and Jumars 1987).

The dynamic properties of a system based on the duration of individual feeding events in a herbivore may differ from those of omnivores such as the rat (Le Magnen, 1992). The rat's ability to achieve nutritional compensation by the formation and appropriate spacing of meals (Le Magnen, 1992) may be advantageous for the rapid adjustments to intake that are necessary in the face of the large variations in quality of food faced by generalists. Thus when rats change from higher to lower caloric density foods, this mechanism permits an immediate increase in meal frequency which maintains energostasis until such times as longer term compensation by change in meal size can take effect (Le Magnen, 1969; Kanerek, 1976). Such mechanisms of short term energostatic compensation may confer less advantage to grazing herbivores such as the tammar which are specialised in the consumption of abundant foods of more uniformly low quality.

In the absence of any mechanism by which feed events are grouped into meals and spaced energostatically (Le Magnen, 1992), nycterohemeral variation may account for the bulk of non-stochastic variation in feed event frequency as was suggested in the case of domestic cattle by Metz (1975). Nycterohemeral variation in the temporal dispersal of feeding events has been reported in other small herbivore species (Jolivet et al., 1983; Geiselman et al., 1980) and is thought to result from photoperiodically induced change in responsiveness to satiety-inducing hormones (Morley, 1980). Under conditions when there is a relative abundance of food, the predominance of nycterohemeral rhythms of feeding behaviour permits the more successful avoidance of predictable environmental hazards such as thermal stress.

The temporal distribution of non feeding behaviour.

Tammars do not drink when maintained on succulent food but, when dry pelleted foods are fed, they exhibit 'food-associated drinking'. This form of 'secondary' drinking is not accompanied by body fluid deficit (Fitzsimons, 1972), and has been reported in a variety of eutherian species including ruminants (Sufit et al., 1985), equines (Sufit et al., 1985), pigs (Houpt and Anderson, 1990), and rats (Kissileff, 1969). The prominence of food associated drinking in tammars, a drought adapted species, and the absence of relatively prolonged drinking events which would allow water intake to be maximised (Mc Farland, 1970), may indicate the importance to fermenting macropod herbivores of regulating stomach water content (Freudenberger et al., 1989).

Food-associated drinking is likely to influence reactor performance, especially in non-ruminant herbivores where ongoing re-ensalivation is not an option. Further work is needed to quantify the extent to which food-associated drinking is able to influence fermentative efficiency.

The statistical analysis of the drinking behaviour of tammars suggests that acts of food-associated drinking are of relatively fixed duration and that a change in food type chiefly affects the number rather than the duration of drinking events. In view of the relative slowness of fermentative digestion it is difficult to envisage that such a change results from the 'learnt digestive associations' (Fitzsimons 1972) which for example condition 'anticipatory' (Le Magnen, 1992) adjustments to drinking behaviour in the rat. The appropriate adjustments of drink events could arise from the conditioning of oropharyngeal reflexes to the physical characteristics of the diet. Further comparative studies which examine short term drinking responses to change in food quality are needed to enable a distinction to be made between these two possibilities.

The temporal association between drinking and feeding activities constitutes evidence of an interaction between two behaviours (see page 25 Chapter 2) where the temporal distribution of one influences that of the other. Thus the greater tendency for shorter interfeed intervals to be terminated by an act of drinking may steepen the survivorship curve of shorter compared with that of longer interfeed intervals and introduce a broken stick configuration. This phenomenon may complicate studies which assume that meals are formed, and which derive interval criteria from discontinuities in interval survivorship slopes (Fagen and Young, 1978), as well as those which evaluate overall nycterohemeral feeding rhythms by Fourier transform (Deswysen et al., 1987).

The foregoing conclusions assume a causal association between drinking and feeding, however it is important to note that the drinking behaviour of rats has been shown to vary nycterohemerally under experimental conditions when food is not available (Morrison, 1968; Fitzsimons and Le Magnen, 1969; Lucas et al., 1989). A repetition of these workers' experiments, with feeding of dry pellets restricted to a brief period during daylight hours but with water available *ad libitum*, would clarify the extent to which drinking and feeding are causally associated, and whether the character of drinking and feeding change when they are dissociated from each other.

Tammars have two distinctive types of resting behaviour which are characterised by different body positions: one where the animal lies in a lateral prone position and the other where the animal sits upright with the tail brought forward between the hind legs. Greater use of the 'sitting tail forward' resting position during the day results in greater vigilance and a reduction in body area exposed to the sun. Electroencephalographic studies are required to determine whether the two resting behaviours are associated with different types of sleep.

Diet quality does not influence either the duration of resting events nor the spacing between them. However, the lower than random association between drinking and resting events and between resting and feeding events indicate that adoption of a resting position is inhibited for a period of time following a drinking or feeding event, possibly to permit regurgitation which was only observed when tammars were in a standing position. This period of latency suggests that there are interactions between ingestive and resting behaviours which are of a more subtle nature than have been previously reported in other species (Saarikko and Hanzki, 1990). These interactions may be important in a species in which the mixing of digesta may be influenced by the relative movements of the 'visceral piston' associated with locomotion (Baudinette et al., 1987)

The dynamics of ingestion.

The radio-microphone study supports the classification of tammar wallabies as grazers (Sanson, 1980; 1989) by showing that they spend more time grazing than browsing (66.5% of daily time spent feeding) with feeding events whose durations are significantly longer when grazing than when browsing.

Animals that are specialised grazers may be expected to show a greater efficiency in consumption of smaller food items such as grass than of larger leaved food items such as browse (Hainsworth and Wolf, 1990). However although a number of grazing macropods are able to vary their intake according to the quality of the processed food that is fed, and thereby achieve a degree of nutritional compensation, doubt has been expressed as to whether such compensation can be achieved with unprocessed feeds (Freudenberger and Hume, 1992). We showed that tammars are able to ingest large quantities of unprocessed vegetable material and maintain a dry matter intake similar to that when they are fed high quality pelleted feeds, provided the food is presented in a form that does not require manual handing. However, we also showed that tammars have relatively low consumption rates and poor handling skills when larger food items such as browse are being fed. These findings indicate that tammars are relatively specialised in the consumption of small discrete food items such as grass. If similar difficulties in the handling of larger items accompany a specialism in grazing by euros (*Macropus robustus erubescens*) and walleroos (*Macropus robustus robustus*), this may account for the failure of these species to achieve dietary compensation when they are fed chopped unpelleted diets (Freudenberger and Hume, 1992).

The relatively primitive (Lewis, 1985; 1989) manual techniques employed by tammars when handling larger food items i.e. the use of mutually opposed palms or 'digitopalmar' grip (Marzke and Shackley, 1986), may impair browsing efficiency. Other marsupial species such as the Phascolarctines are, as a result of an anatomical specialisation of the proximal carpal row known as zygodactyly (Lewis, 1989), able to grip small items by a pincer action of the first and second digits acting against the lateral three digits (Lewis, 1985). It remains to be seen whether such anatomical features are more evident in browsing and arboreal macropodine species and whether they are entirely absent in tammar wallabies.

A number of factors may influence the efficient handling of larger food items by tammars. Tammars use their frontal incisors in a manner similar to that reported in another grazing species, the agile wallaby (*Macropus agilis*) (Menzies, 1989), whereas the forest wallaby (*Dorcopsis luctosa*), a browsing species, employs the more angulated edges of the sectorial premolars (Menzies, 1989) which may permit a better grip. Tammars grip food items using the same incisor surfaces that are the sites of cutting action, which suggests that the dropping of leaves and leaf fragments may sometimes result from accidental cutting.

Currently, specialism in grazing by macropod species has been associated solely with the presence of certain morphological characteristics in the incisor and molar teeth (Sanson, 1989). The concurrence of biting and chewing sounds during grazing (as found in the field microphone transmitter studies), when considered in conjunction with the jaw studies, indicate that other specialisms in the dynamics of oral food processing may also be operating. Thus, infero-lateral rotation of the jaw following closure results not only in mastication from relative movement between the occluded and transversely ridged upper and lower molar arrays (Sanson, 1980; 1989), but also in a concurrent biting and cutting action from the simultaneous occlusion of the conjoined facets of the upper and the elongated facets of the lower incisors. Moreover the relative movement with growth of the insertions of the masseteric musculature that is shown in this study may act to increase rotational power with body size. Thus concurrent and ongoing biting and mastication during grazing may, by generating a steady onflow of ingested material, produce higher ingestion rates than when biting and mastication operate alternately such as in browsing. Such an hypothesis is in line with previous studies of the functional response of herbivores feeding on uniformly distributed abundant and apparent plant sources which showed that ingestive efficiency is determined by the interrelationship between cropping and chewing processes (Black and Kennedy, 1984; Greenwood and Demment, 1988; Spalinger et al., 1988; Penning et al. 1991; Spalinger and Hobbs, 1992). Moreover, the work of cutting and of particle size reduction is then shared between the incisor and the molar array. Strategies which reduce molar wear are important for the long term fitness of macropods (Lanyon and

Sanson, 1985; 1986) particularly when abrasive siliceous grasses are being consumed (Sanson, 1980; 1989). Thus the sharing of tooth work in this manner may be an important strategy for reducing wear on cutting surfaces which, because of closed root structure (Sanson, 1989), have a finite working life.

Non-ruminant species must masticate 'on site' when feeding and the development of such strategies by grazing species may also have been driven by a need to reduce time spent in more open areas. In this respect it is interesting to note that ruminant herbivores are able to postpone fine mastication but, as a consequence of their longitudinally ridged molar array and lack of upper incisor arcade, are unable either to carry out fine cutting with their incisors, or to concurrently bite and chew.

Further work is needed to compare the relative positions of cutting and incisor surfaces in a range of grazing and browsing macropod species and to evaluate their relative efficiencies during browsing and grazing activities. Such work, in conjunction with more detailed study of carpal and phalangeal morphology and of dexterity in the handling of browse, may permit a greater understanding of the dietary specialisms and requirements of various macropod species. In tammar wallabies the work may permit evaluation of the manner in which those tammar subspecies (Maxwell et al., 1996) that have been subject to island isolation since the passing of the last ice age have broadened their dietary niches.

It has been suggested that molar progression in macropod species results from a direct effect of the physical properties of the diet on molar movement i.e. mesial drift, and may afford a mechanism for limiting wear (Sanson, 1980; 1989). However it is difficult to envisage mesial drift in the upper and lower jaw being so perfectly coordinated that attrition facets on both type B lophs and type G links (Sanson, 1980) are always maintained in perfect congruence and occlusion, particularly as rates of mesial drift have been related to propalinally-oriented forces (Picton, 1980) which may vary according to the differing longitudinal profiles in the upper and lower jaws of grazing macropods. Such incongruence between opposing lophs and links would constitute an impediment to any hypothesis of specialisation toward maximal oral efficiency.

This study demonstrated that there is significant distal movement of the reference point from which molar index is measured, i.e. the rearmost point of the inner aspect of the zygomatic arch, along the line of the upper jaw with increase in body size, showing that this index does not measure the absolute mesial movement of molars in the plane of occlusion. Further, the estimated value of absolute mesial movement for the first upper premolar along the line of the jaw (2.45 mm/yr) is at the upper known limit of mesial drift. The studies of size-related changes in the linear dimensions of various bony landmarks on jawbone and skull indicate that the high rate of movement in molar progression may result more from deposition of bone in the rear of the tooth row, i.e. 'mesial shift', than from mesial drift.

The weight-corrected time spent feeding per 24 h period was higher in tammars than in a number of other macropod species (Southwell, 1981; Pridell, 1986) whilst dry matter intake was lower than that of other grazing macropod species (Bridie et al., 1994), even with foods that were eaten solely in the quadrupedal position. Thus, regardless of the specialisations in oral processing mentioned hitherto, tammars spent more time eating less food. The chewing speeds obtained in the microphone studies were similar to those reported in other small eutherian and non-eutherian species and may approach the upper physiological limits to the speed of mastication (Hiiemae, 1978). Thus the increase in time spent eating may result from an increase in chewing effort i.e. longer time spent chewing per mouthful. This conclusion is supported by the results from the novel application of a method of graphic analysis to the data on particle size distributions (Voon et al., 1986) of foregut digesta that were obtained in this study. Voon et al. (1986) showed by computer simulation and by experimentation that increases in the number of chewing strokes per mouthful result in a progressive shift in a cumulative distribution plot of the proportion of particles less than a given particle size against particle size towards the ordinate. Thus the fact that the curve of such a particle size distribution plot for tammar foregut digesta lies closer to the ordinate than that of other macropod species, shows that tammars chew more per per unit mouthful than these species.

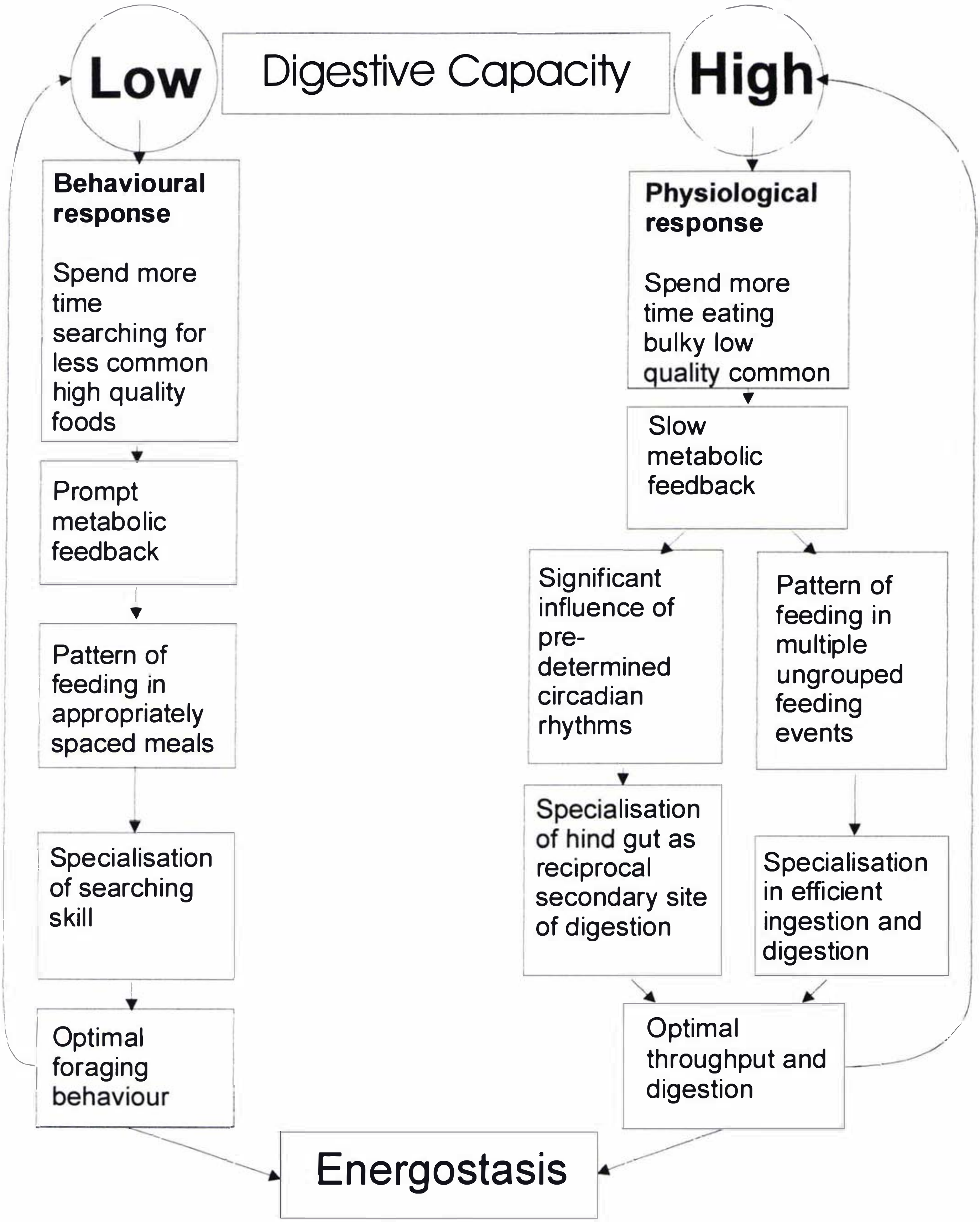
It has been suggested (Batzli, 1985; Mc Leod and Minson, 1969) that a decrease in particle size may increase the surface area of ingesta and thus the number of sites which are available for attachment of fermentative bacteria. Further, it has been demonstrated that reduction in particle size augments in vivo and *in sacco* digestion in ungulates (Bjorndal et al., 1990). It remains to be seen whether a difference in particle size has any discernible in vivo effect in species with higher throughput rates such as macropods. Judged on the basis of the relatively low concentrations of volatile fatty acids (VFAs) found in the foregut and the relatively high concentrations of VFAs that were found in the distal hind gut of tammars in comparison with those of other macropod species that were fed on the same diet (Dellow and Hume, 1982a), fermentation in the hindgut seems more likely to benefit from smaller particle size.

Digestion.

If, as suggested by Penry and Jumars (1987), the principles of dynamic programming (Belman 1957) apply to the digestive process then the relative sizes of the portions of the gut that are concerned with enzymatic or with fermentative digestion may vary with dietary habit. The finding that the mean length of the small intestine corrected for differences in average body weight is shorter in tammars than in browsing macropods and similar to that of *M. agilis* may indicate the lesser importance of enzymatic digestion. Similarly the finding that the mean length of the colon corrected for differences in body weight is longer than that of these same browsing species may indicate the greater importance of hindgut function in tammars.

Whilst the results of a study by Hume (1977) quantifying the VFA production in the foregut and hindgut components of *Thylogale thetis* and *Macropus rufogriseus* show a relatively low contribution from the hindgut, this contribution may nevertheless be of importance in marginal conditions. Hume's (1977) quantification assumes steady state conditions in the two gut segments, whereas the present study shows a reciprocal association between hindgut and foregut fill and suggests that filling and voiding of the hindgut may be relatively independent of onflow from preceding segments, two conditions which may invalidate Hume's (1977) calculations. The similarity in the scaling of caecal length with body weight in tammars to that of larger grazing species (Osawa and Woodall, 1992a; 199b), coupled with the allometric, rather than isometric, scaling of colon length and colon tissue weight with body weight together suggest that the hindgut may have a more significant role in smaller grazing species than has hitherto been realised, perhaps in scavenging by 'secondary' (Hume, 1982) fermentative digestion during periods of lower throughput. The significant sexual dimorphism of gut morphology in which females have heavier foregut and colon tissue components resembles the seasonal differences reported in rabbits *Oryctolagus cuniculus* by Sibly et al. (1990) which was attributed to the greater nutritional requirements of breeding females.

FIGURE 2: The effect of digestive capacity and other temporal factors on the evolution of feeding behaviour in macropods.



Future research.

The findings of this study suggest that grazing herbivores rely on a series of interrelated strategies (figure 1) that maximise digestive capacity in order to achieve energostasis. The corollary of this is that herbivores with relatively low digestive capacity may rely to a greater extent on behavioural strategies to achieve energostasis. Thus smaller macropodoids such as the potoroo (*Potorous tridactylus*) and the brush tailed bettong (*Bettongia pencilliata*) may be more reliant on specialist optimal foraging strategies such as the searching out of more nutritive hypogeal fungi (Guiler, 1971; Christensen, 1977; Freudenberger and Hume, 1989).

I propose that natural selection may amplify the division of such strategies (figure 2). In the face of such an adaptive dichotomy, those species that rely on optimal digestive strategies may be expected to exhibit greater plasticity of gut morphology according to seasonal variations in food supply and nutritional demands, whilst those that rely on optimal foraging strategies exhibit greater degrees of behavioural compensation. Such a dichotomy provides an explanation for the solitary nature of small macropodids with highly selected diets (Norbury et al., 1989) and the seasonal variation of gut morphology in more gregarious herbivores such as the rabbit (Sibley et al., 1990). Further validation of this hypothesis requires more detailed work on the interrelationship between various aspects of small herbivores digestive physiology and their feeding ethology as outlined in figure 2. Marsupial species are particularly suitable for such work as their digestive anatomy and physiology is well described (Hume, 1982) and exhibits an orderly progression of complexity over a range of body sizes (Langer, 1988). A comparative study of marsupial species, in contiguous home ranges, may help to shed light on the relative importance of physiological and behavioural strategies in animals of various body sizes and relative gut volumes. Further requirements for more detailed physiological and ethological experimentation are described below.

Physiological studies

Laboratory investigations are required to evaluate the factors which determine nycterohemeral variation in the temporal pattern of feeding events, the processes that govern feed event termination, and the manner in which both may respond to changes in food quality. The lack of modulation of the myoelectrical activity of the foregut of tammars by the vagus (Wyburn and Richardson, 1989) may be viewed as an 'anatomical property' (Mc Farland, 1985) indicating a greater autonomy of the enteric nervous system, the primary arbiter of satiety (Morley 1980) and the means by which the duration of individual feed events may be varied. Thus research on the physiology of satiety in tammars, apart from shedding light on certain physiological aspects of phylogeny, may provide a means of assessing responsiveness to satiety-inducing hormones under conditions where there is no opportunity for vagal axonal transport (Farningham et al., 1993) and where rumination does not occur. In addition to its physiological importance, such empirical work is a necessary prerequisite for the application of dynamic programming methods to optimal foraging studies on tammars and other herbivore species.

Optimal foraging studies

Any algorithm that seeks to investigate optimality in tammar foraging behaviour should be based soundly on the physiological mechanisms that govern the processes of feeding. A number of optimal foraging outcomes (Reed-Hainsworth and Wolf 1990) including search intensity (Dethier, 1957; Nelson, 1977) patch use (Caraco, 1981) and food choice (Edgecomb et al., 1987) have been shown to be influenced by a change in the level of hunger or of satiety. If the strong nycterohemeral variation in the incidence and duration of the feeding events of tammars that was found in this study reflects cyclical changes in levels of hunger or of satiety then this may similarly influence the thresholds of dietary selection, resulting for example in a change in the principal site of feeding. A number of optimal foraging studies have considered hunger as a variable internal state or tried to control for changes in this state (Hainsworth et al., 1981; Krebs et al., 1977; Molles and Petruska, 1987; Perry, 1987; Sih, 1982) but few have addressed the problem in herbivores. Dynamic programming methods (Houston and McNamara, 1988; Mangel and Clark, 1986) may be required to model these complex situations.

If the separate mechanisms that control the spacing and the size of feed events or meals (Le Magnen, 1992) are refined to differing extents according to the dietary habit of the species, herbivores such as the tammar may be better able to modulate feed event size in response to short term changes in the nutritional environment than do generalists such as the rat. This may affect the validity of those tenets of classical optimal foraging theory based on the assumption that the commencement and the termination of feeding are equally susceptible to variations in the nutritional environment (Pyke et al., 1977) and such differences must also be incorporated into the model.

An understanding of the principles that govern a species feeding strategies can only be obtained from a model that is based on a sound knowledge of the underlying physiological, morphological and behavioural factors. The present study indicates that the feeding strategies of the small grazing herbivore *Macropus eugenii* Desmarest depend on physiological and morphological, rather than behavioural traits. This points to a dichotomy in the evolution of particular traits which is influenced by the abundance of the preferred diet.

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Appendix 1

Practical aspects of the temporal analysis of feeding behaviour

Appendix 1: Practical aspects of the temporal analysis of feeding behaviour

Methods for detecting the organisation of feed events into meals.

Theoretically, it is possible to detect the formation of meals by two methods.

i) The contour of log survivor functions

Where events of a single type are randomly distributed in time, the intervals between them follow a negative exponential (Poisson) distribution. Such a distribution, when plotted as a log survivor function, appears as a straight line whose slope is proportional to the probability of a new event occurring with the passage of time since the last event (Nelson, 1964; Slater, 1974a; 1974b; Slater and Lester, 1982).

When the intervals between behavioural events occur in 'bouts' the log survivor functions of intervals will not follow such a simple distribution and instead become concave with an initial steeply descending segment (higher probability of a further event) followed by a more slowly descending portion (lower probability of a further event) (Slater and Lester, 1982). On a basis of this logic the 'broken stick' morphology found in log survivor plots of real interval data has commonly been assumed to indicate the formation of bouts, and the point where the slope changes 'most dramatically' (Slater and Lester, 1981) has been used as a basis for separating intra-bout from inter-bout intervals i.e. the 'bout criterion'. The technique has been widely employed (Slater, 1974a; 1974b; Peterson, 1976; Clifton, 1979; Culshaw and Broom, 1980; Sibly et al., 1990, Burdoy, 1993) albeit with modifications to the mathematical method by which the bout criterion is derived from the change in slope (Sibly et al., 1990; Burdoy, 1993). There are however serious problems with the assumption that any discontinuity in slope indicates the formation of bouts. These are discussed in a later section.

Survivorship analysis may equally be applied to the durations of particular behaviours (Fagen and Young, 1978), the slope of the log survivor function describing in this case the probability of the termination of a behavioural act. Thus if an act terminates independently of the time at which it begins i.e. was prone to random interruption, then the durations of that act will be negatively exponentially distributed and a graph of the log survivorships of the act will be linear. Alternatively if the duration of the act tended to be terminated with increased probability as performance time increased i.e. the act was 'finished' then its temporal distribution would be relatively skewed and the graph of the log survivor function would assume an upwardly convex configuration. The use of such a technique is equally vulnerable to the criticisms levelled against interval survivorship curves.

b) Change in the temporal correlations between feed events and intervals within and between meals.

A potential second method that has not previously been used for detecting the formation of meals is by searching mathematically for the shift that occurs between the lower levels of correlation existing between feed event durations and following inter-feed intervals within the meal, and the higher levels of correlation that occur between meal durations and their following inter-meal intervals. Under conditions where meal formation occurs and spacing of meals is regulated by hunger (Le Magnen, 1992) then correlations will tend to increase as the chosen 'criterion interval' approaches the mean time taken for energostatic metabolites to fall below the concentration needed to initiate feeding (Weipkema, 1971) i.e. the true mean inter-meal interval.

This is not to say that some degree of correlation between feed event duration and inter-feed interval may not occur as a result of gut distension, indeed digestive constraint has been suggested to be the primary energostatic regulator in many herbivore species (Hirakawa, 1997: Forbes, 1978). However the temporal duration of action of the factors involved in short term regulation via change in circulating levels of energostatic metabolites differs from that based on gut distension in one important respect, it is continuous in the former but intermittent in the latter. This feature permits a test based on differences in the correlation of feed events and following inter-meal intervals in the two scenarios.

The physiological rationale of this test is as follows. Under conditions where an animal maintains a maximal gut load of digesta (which is desirable in small fermentative herbivores from a viewpoint of maintaining maximal reactor efficiency), gastric distension may limit the duration of individual 'top up' feeding events and there may be a correlation between an individual feed event and the associated inter-feed interval. However where stochastic environmental change occasionally results in an unduly large inter-feed interval, then a group of feed events will be required in order to re-establish gastric fill, (which on superficial examination may be interpreted as the taking of a 'meal'). Under such conditions the intervals between each feeding event will not be governed by gastric constraints and the sum of such intervals will represent a random amount of time during which further gastric emptying can occur, necessitating additional feed events in order to achieve a top up. Thus the 'meal's duration will contain a random component that adversely influences correlation with inter-meal interval. Therefore as chosen criterion interval is increased so meal duration and length of the random component are increased and the correlation between meal duration and inter-meal interval will decline. Thus when short term regulation is by gastric distension, the correlation of meal duration with inter-meal interval will fall away monotonically with increasing criterion interval. Conversely when regulation is by the circulating levels of energostatic metabolites their concentrations will continue to increase throughout the duration of a meal regardless of any gastric emptying that occurs during intervals between individual feed events and will only fall during the subsequent inter-meal interval.

Practical difficulties in survivorship analyses

In the method described by Slater and Lester (1982) the maximum discontinuity in the slope of survivorship curve is assumed to result from the transition between intra and inter-meal intervals. However such discontinuity may equally well arise from nycterohemeral changes. For example, if a significant time period exists when the risks associated with the performance of a particular act decrease relative to the rest of the day, then the probability of survival of intervals between acts may be decreased and the probability of survival of acts may be increased during this period. Under such conditions, a survivorship profile of intervals between that behaviour based on data for the whole day will be skewed and have an upwardly concave broken stick profile. Similarly the survivorship profiles based on the duration of acts will be skewed in an upwardly convex broken stick profile.

Nycterohemeral and physiological cycling in the 'utility' (McFarland, 1978) of other non related acts may also indirectly influence the grouping of behaviours into bouts and thus their survivorship profiles. Thus for example shrews (*Sorex*) have such a high metabolic rate that they would starve if they slept an entire day or night, and laboratory studies show that their foraging is frequently 'interrupted by' short periods of rest (Saariko and Hanski, 1990). If the utility of such rests varies on a cyclical basis, survivorship analysis profile of inter-feed intervals would presumably show a change consequent on this interruption and indicate grouping of feed events for 'extraneous' reasons i.e. a change in inter-feed interval survivorship profile due to variation in the timing of a behaviour other than feeding.

These 'extraneous' influences may be identifiable by the second method of meal discrimination detailed above. In an animal whose short term energostasis is controlled by the spacing of meals. an increase in the degree of positive correlation between feed event duration and associated inter-feed interval as chosen criterion intervals approach the length of the sleep cycle will only occur if the duration of sleep correlates with 'meal' size i.e. the animal is woken by hunger.

Practical difficulties in the analysis of nycterohemeral cycles

Most published Fourier analyses of nycterohemeral cycles are based on averages of specific behaviours such as time spent eating per hour (Murphy et al., 1983; Deswysen et al., 1993) or time spent grazing per hour (Champion et al., 1994). Such measures take no account of short term changes i.e. the ongoing relationships between individual feed event or meal durations and their following intervals. Thus. whilst these analyses assess the relative contribution of different relatively fixed nycterohemerally induced cycles, they do not quantify the relative contribution of any short term variation i.e. the effects of hunger and satiety.

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Appendix 2

A trapping and immobilisation technique for small macropods.

R. G. Lentle, M. A. Potter, K. J. Stafford, B. P. Springett, S Haslett

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A trapping and immobilisation technique for small macropods.

Roger G. Lentle[A], *Murray A. Potter*[A] ,*Brian P. Springett*[A] ,*and Kevin J. Stafford*[B] .

[A] Department of Ecology, Massey University. Private Bag 11222, Palmerston North, New Zealand.

[B] Department of Clinical Veterinary Sciences, Massey University, Private Bag 11222, Palmerston North. New Zealand

Abstract

A technique for trapping and immobilising small macropods is described and trialed on forest-dwelling Tammar wallabies (*Macropus eugenii* Desmarest) The trapping method uses wire fencing and a monofilament nylon drop-net. The animals were immobilised with ketamine hydrochloride and zylazine. Tammar wallabies are reputedly hard to catch but our technique produced higher trapping rates, lower trap avoidance rates and lower death rates than other methods. Forty-six Tammars were captured in 29 trap-nights. No deaths occurred during, and in the 4 weeks following trapping.

Introduction

Early reports stated that small macropod species could be readily caught in box traps, hand nets and long nets (Dunnet 1956), but Vernes (1993) and Vujcich (1979) commented on the difficulty of using these methods. Andrewartha and Barker (1969) found that *Macropus eugenii* Desmarest was "too wary to be netted easily and can run much faster than a man pursuing it with a hand net". Vernes (1993) noted that "small forest-dwelling macropods can be difficult to catch using conventional methods". Most trapping techniques have limitations when there is a need to capture large numbers of a nocturnal animal in a short time and with a minimum of bias introduced into the sample by the trapping method. "Stunning", when an animal was immobilised by the effect of a rifle shot passing just above the vertex of its skull, had a significantly different success rate for males and females in large kangaroos and comparatively high death rate (Robertson and Gepp 1982). Alpha chloralose baits (Arnold et al. 1986; Marlow 1956; Oliver 1986) caused both high loss rates, because the animals disperse before being immobilised by the tranquillising agent (Higginbottom 1989), and high mortality (Arnold et al. 1986; Oliver 1986). Darting with a slow-acting immobilising agent is likely to result in the loss of animals when employed at night (Higginbottom 1989).

Box-trapping produced "differential trappability" according to species, sex and degree of "trap addiction" (Vujcich 1979), and was noisy enough to disturb other animals nearby (Pollock and Montague 1991). Methods that employed drive fence/ trap combinations had low loss rates and captured larger numbers of animals (Andrewartha and Barker 1969; Poole and Brown 1988, Vernes 1993). However, the method described by Vernes (1993) may be noisy (Pollock and Montaque 1991) unless the traps are widely spaced. Vujcich (1979) reported that both Tammar and Parma (*Macropus parma* Waterhouse) wallabies exhibited strong avoidance of trap entry points.

We, like previous workers (Andrewartha and Barker 1969) found that repeated trapping drives in an area can rapidly induce trap avoidance in animals resident in the neighbourhood. Thus a method that caused minimal disturbance during the trapping process, which captured all animals inhabiting the trap area, and which did not depend on habituation to narrowed entry points was needed. These characteristics are particularly desirable when trapping areas with a low animal density or animal populations with a high degree of trap suspicion.

The trapping method described in this note was developed for use on an introduced population of Tammar wallabies in the Lake Okataina scenic reserve in central North Island, New Zealand where they are regarded as a threat to conservation values. The wallaby density in the trapping areas was low as a result of extensive 1080 poisoning (G. Williamson *pers. comm.*) and continued hunting pressure (D. Williams *pers. comm.*). We believe the methods described here should have general application for the capture and immobilisation of small macropods.

Method

Trap construction

Trap sites were chosen on the basis of track usage, faecal pellet density and the presence of high quality grazing areas. Ecotone margins that encompassed numbers of well-used trails were chosen for the drop net site.

A 60 m long, 117 mm mesh size, 25 mesh deep, monofilament nylon flounder net was employed as a "drop" net. This was set up by tying the upper net edge at a height of 2 m at 10 m intervals to tree trunks along the ecotone in a roughly straight line. Fifty metre long, 2 m high, wing fences of 70mm mesh galvanised chicken wire were set up. The fences were fashioned of unstrained chicken wire loosely tied to upright stakes and pegged to the ground along its lower edge. Experience had shown us that fences constructed in this manner were strong enough to contain an entrapped animal, rigid enough to prevent its inadvertent entanglement, yet had sufficient give to cushion the impact of any animal running into them thus preventing its injury. (The use of synthetic mesh, such as was described by Vermes (1993), in the construction of wing fences was trialled but found to be more prone to entangle tammars and more diffult to install, requiring more extensive pegging of the less rigid lower edge.) The end of each wing fence was positioned at such an angle that animals emerging from the forest would view it end on (fig. 1).

On one site, the trap was sited such that the area between the far ends of the two wing fences was closed by a natural water barrier (fig 1). On the second site a third chicken wire fence was placed on lower ground in a position unable to be sighted from the drop net area. The weighted lower edge of the drop net was lifted and hooked approximately 2 m high to the same trees as the upper edge. The side branches of these trees were pruned so that the weighted edge of the net would, when released, drop to the ground. The siting of the drop net within the bush edge was carefully chosen so that when raised it was screened by vegetation from the view of animals within the bush. The weighted edge was secured to the tree trunks so that it could be easily released by a trapper walking along the net line.

At the commencement of trapping, the weighted edge of the drop net was released and secured to the ground by pegs. The pegs were located so that the lower edge of the net was pulled slightly inwards so that animals attempting to escape would tread over the net edge before encountering the vertical mesh. Before trapping, pegs were set in place in such a manner that the lower edge of the net could be readily hooked onto to them. This allowed the trap to be closed swiftly and silently. Experienced operators were able to lower and secure a 100 m. net within five minutes disturbing only such animals as were encountered within a few metres the net. Following closure of the trap, wallabies attempting to return to the forest encountered the net and moved along it. An approach by the trapper at right angles to their route was sufficient to drive them into the net, enabling them to be captured by grasping the tail.

The trap was closed between two and four hours after sunset which gave sufficient time for Tammars to emerge into the trap area to feed. Trapping was carried out on dry calm nights for a maximum of two consecutive nights followed by a minimum of five non trapping nights. The trap setting, capturing and handling was carried out by two persons. Typically, operators stayed in the vicinity of the net line capturing only those wallabies that approached them, allowing any animals that were still feeding within the trap enclosure to remain undisturbed until they too approached the net area. With this method, capture of all wallabies within the enclosure could take up to two hours. A more expedient alternative, where up to six operators traversed the trap driving the animals into the net, caused greater stress as evidenced by higher pulse and respiration rates. Using the latter method in a trap with a water frontage, it was notable that driven animals made strenuous attempts to avoid entering the water.

Post capture handling

Immediately following capture, the animals were placed in light-proof hessian bags and weighed. They were given an intramuscular injection of xylazine (20 mg per ml, Phoenix Pharmaceutical Co.) and ketamine hydrochloride (100 mg per ml, Parnell Pharmaceutical Co.) based on weight (Table 1), plus 0.2 ml of a vitamin E and selenium injection (2.5 mg selenium and 50 mg vitamin E per ml, E-

SE injection, Schering Plough) to compensate for the possibility of capture myopathy and local selenium deficiency. Sex was readily distinguishable by physical examination but it is noteworthy that males were also identifiable by their hissing and generally more aggressive behaviour .

It was possible to give the injection intramuscularly whilst the animal was contained in the bag by grasping the base of the tail and injecting into the gluteal region. The combination of drugs, xylazine to secure rapid immobilisation and ketamine to prolong immobilisation and reduce excitability during spontaneous recovery phase, was chosen on the basis of previous reports of zero mortality by Higginbottom (1989).

Animals were left undisturbed in the capture bags for 10 minutes following injection and subsequently inspected regularly until judged on the basis of relative immobility and slowing respiration rate (60 slowing to 14 bpm) to be adequately sedated.

After each animal was examined physically, a blood sample taken and a radio collar attached, it was placed in the forested area clear of the trap, thus preventing re-entry into the trap area following recovery. No attempt was made to reverse anaesthesia. The animals were placed on their sides with head downhill on sloping ground and left to recover. This procedure was adopted to guard against airway obstruction as a number of animals exhibited hypersalivation and masticatory movements during sedation. Hypersalivation was attributed to ketamine as reported by the manufacturer (Delta Veterinary Laboratories). The righting response occurred within an hour in all but those specimens where, owing to logistic delays, repeated dosing was required.

A total of 36 animals were captured and processed over 29 trap nights. There were also 10 retrappings of previously processed animals over the same time period. There were no immediate deaths and at four weeks after the end of the trapping period no deaths had occurred.

Discussion

These trapping results indicate a higher degree of success compared with those using double ended, treadle operated box traps on the Kawau Island Tammar populations by Kinloch (1973) and Vujcich (1979). The use of these box traps was favoured by commercial trappers on Kawau, yet Kinloch

(1973) reported 16 captures during 1079 trap "half days" of which 565 were nights whilst Vucich (1979) captured only 12 Tammar for her total trapping effort (trap night figures not given in her report).

Some of the success of our method was attributable to the technique of securing the lower edge of drop net to the ground with pegs. Prior to its inception, animals had been observed to escape by adopting a quadrupedal mode of locomotion and running under the net.

The drug dosage schedule was based on weight and was derived from that of Higginbottom (1989) for red necked wallabies (*Macropus rufogriseus* Banksianus) by trail and error. It is notable that our dosage schedule (Adult: xylazine range 4.3 - 6.4 mg per kg; ketamine Hydrochloride range 15.5 - 32. 2 mg per kg) differed considerably from his (xylazine 11.25 mg per kg and ketamine 9.0 mg per kg). This may reflect species differences. Moreover our regime used higher dosages than recommended by Lumb and Jones (1973) for zoo and laboratory animals (8 mg per kg ketamine and 8 mg per kg xylazine). Neither Higginbottom (1989) nor Lumb and Jones (1973) reported differences in sensitivity to xylazine and ketamine in male and female macropods.

Our method induced lower rates of trap avoidance than reported by Kinloch (1973) and Vujcich (1979) on Kawau Island. These workers, using 14 box traps spaced at intervals along a 300 m. fence, obtained no recaptures of previously processed Tammars. The low trap avoidance rates may be due to many factors including low stress induction by trap layout, appropriate post capture handling procedures, relative trap naivety of Okataina Tammar populations compared to those of Kawau Island and/or from beneficial side effects of the drugs used (stress reduction or short-term amnesia). With respect to drug side effects, whilst Kinloch (1973) did not use drug-induced immobilisation techniques for the bulk of his study, Vucich (1979) did employ ketamine immobilisation at a dosage of 10 mg per kg.

The use of intramuscular diazepam was considered inappropriate as, in macropods, it is known to induce sedation for up to 6 h (Blyde 1994) during which period animals recovering in the wild would be vulnerable to hypothermia and predation. The routine administration of selenium and vitamin E, the short chase times prior to capture, and the immediate post-capture transfer to a light-proof capture bag where intramuscular sedation was given, may have reduced the incidence of post-capture myopathy. The efficacy of the light-proof bags in stress reduction was attested by the rapid cessation of struggling which occurred once animals were placed within the bags.

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TABLE 1: Dosage rates of Xylazine and Ketamine for wild Tammar wallabies (*Macropus eugenii* Desmarest) based on sex and approximate body size.

Juveniles up to 3 kg weight (both sexes)	Xylazine 10mg. (0.5 ml) Ketamine 50 mg (0.5 ml)
Adult females up to 4.5 kg weight	Xylazine 20 mg.(1.0 ml) Ketamine 70 mg (0.7 ml)
Adult males up to 4.5 kg weight	Xylazine 20 mg (1.0 ml) Ketamine 100 mg (1.0 ml)
Adult females over 4.5 kg weight	Xylazine 20 mg. (1.0 ml) Ketamine 100mg (1.0 ml)
Adult males over 4.5 kg weight	Xylazine 26 mg. (1.3 ml) Ketamine 100mg(1.0 ml)

Figure 1. Plan of lake edge trap showing method of securing drop net in raised and lowered positions.

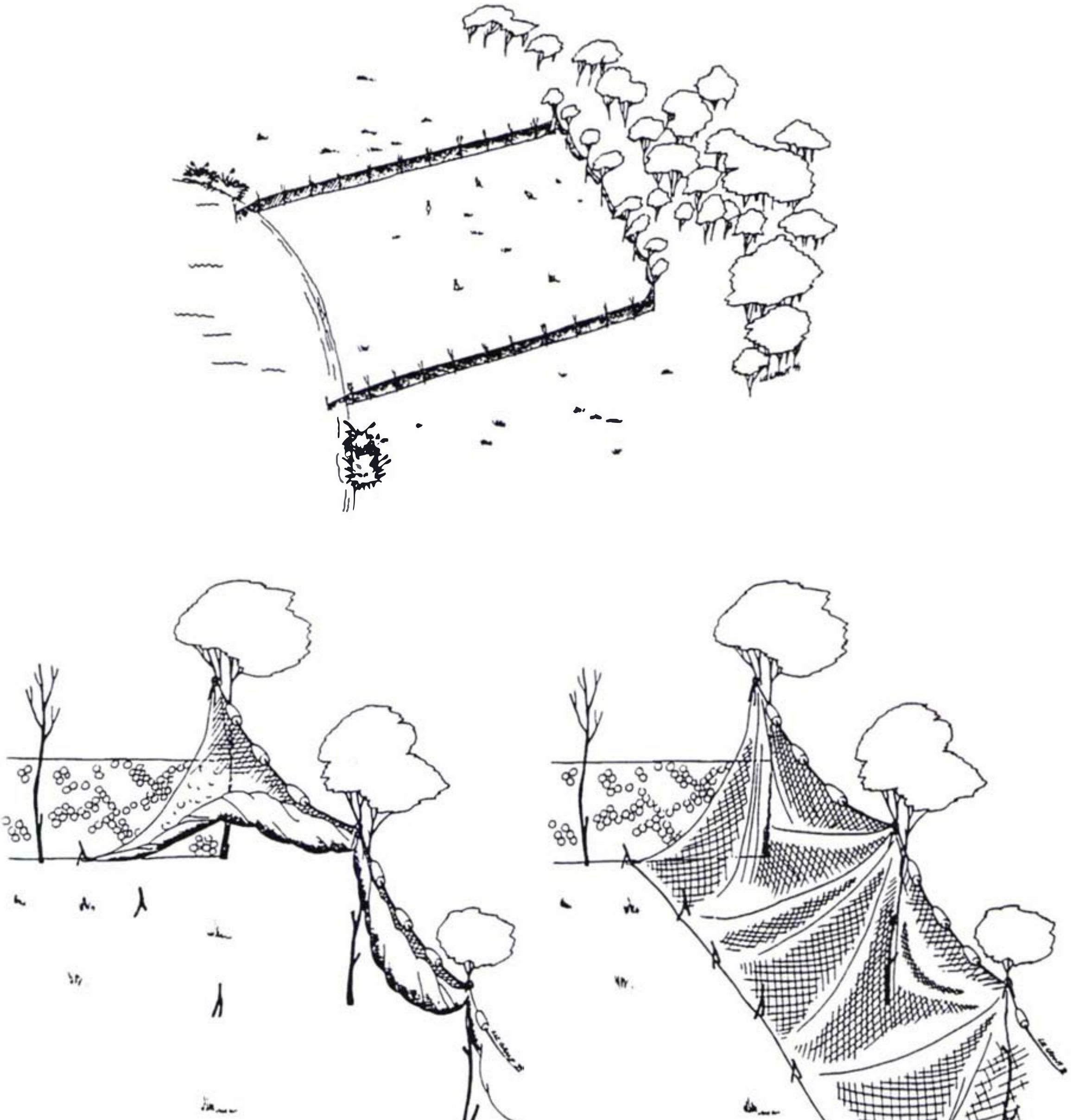

Fig. 1. Lake-edge trap, showing secured drop net in raised and lowered positions.

Appendix 3

Home range size and social interactions of Tammar wallabies (*Macropus eugenii* Desmarest) in the Rotorua district of New Zealand.

Roger G. Lentle, Murray A. Potter, Brian P. Springett and Kevin J. Stafford.

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Home range size and social interactions of Tammar wallabies (*Macropus eugenii* Desmarest) in the Rotorua district of New Zealand.

Roger G. Lentle [A], Murray A. Potter [A], Brian P. Springett [A] and Kevin J. Stafford [B]

A: Ecology, Institute of Natural Resources, Massey University, P.O. Box 11222, Palmerston North, New Zealand.

B: Institute of Veterinary, Animal and Biomedical Sciences, Massey University, P.O. Box 11222, Palmerston North, New Zealand.

Abstract

The home range size and static and dynamic interactions of five male and nine female tammar wallabies (*Macropus eugenii* Desmarest) were determined in an introduced population near Rotorua in the North Island of New Zealand. Overall home ranges (100% convex polygon areas: 9.0 - 39.0 ha) were similar to those reported on Kangaroo Island, Australia. Fifty percent core area kernels, determined over identical time periods, were positively correlated with live weight but did not vary significantly between animals living in the bush interior and those living close to an ecotone with farm pasture. There was significant diurnal positive dynamic interaction between all tammars on the ecotone site, particularly between an adult male and juvenile females. Tammars occasionally made rapidly repeated screeching calls, mainly of type IV frequency morphology. Call frequencies were highest crepuscularly during the period when animals were journeying between day-time and nocturnal feeding areas and lowest during the night-time feeding period.

Keywords *Macropus eugenii*: tammar: home range; static and dynamic interaction; radio-microphone; call sonography and frequency;

Introduction

McNab (1963) demonstrated a positive interspecific allometric correlation between home range size and body weight in various eutherian species and concluded that an animals home range size was influenced by its energetic needs and the availability of food. This interspecific relationship holds true for macropod species (Vernes *et al.* 1995) although attempts to derive a formal mathematical relationship have been unsuccessful (Croft 1989). Home range size has also been shown to vary intraspecifically with body size in the red necked wallaby, *Macropus rufogriseus* (Johnson 1987).

An animal's territory and home range size may also be influenced by the availability of resources other than food (Schoener 1983), such as the supply of mates, and by social factors such as dominance position in a group (Kaufmann 1983; Gosling 1986). The existence of social interaction cannot be inferred from an overlap in home ranges i.e. static interaction (McDonald *et al.* 1980). Thus whilst the home ranges of groups with long-term positive associations will overlap, similar overlaps may result from 'chance aggregations' *sensu* Jarman and Coulson (1989) or 'survival groups' (Brown 1975) forming on favourable sites, as has been reported in red-necked pademelons (*Thylogale thetis*) (Johnson 1977). Moreover the degree of static interaction may be influenced by non social factors such as body size. Thus, irrespective of the type of association, larger animals may have larger home ranges which are more likely to overlap the home ranges of others. Statistical inference of 'temporally cohesive group' interaction from the radio fixes of cogeners thus requires concurrent demonstration of significant positive 'dynamic interaction' (McDonald *et al.* 1980).

Significant positive dynamic interaction has been demonstrated in the allied rock wallaby (*Petrogale assimilis*) but only between consort pairs (Horsup 1994) i.e. type 'c' social dispersion (Russell 1984). Whilst male/female interactions within groups of island wallabies have been described as 'hierarchically promiscuous' (Russell 1984) by Croft (1989), it is not known whether such groups are temporally cohesive or form by chance aggregation.

Apart from inferences based on locational data, the existence of ongoing social interactions between animals may be inferred from the occurrence of events that are known to accompany such interactions.

Tammars have a limited auditory vocabulary (Russell, 1984; M. Vujcich, 1979) but are known to emit a low pitched hiss when approaching a lost young (Russell, 1973). Although tammar calls have not been sonographically classified according to the system of Eisenberg *et al.* (1975) analysis of their occurrence and timing may provide useful information on variations in intensity of 'cohesive pair interactions' between mother and young at foot (Jarman and Coulson, 1989) when foraging and travelling. Again both 'island' wallaby species (Hume 1982), the quokka (*Setonix brachyuris*) (Holsworth, 1967; Nicholls, 1971) and the tammar wallaby (*Macropus eugenii*) (Inns 1980; M. Vujcich 1979; V. Vujcich 1979), have a bipartite home range structure comprising a smaller daytime 'roosting area' (Nicholls, 1971) situated in cover, and a larger nocturnal grazing area, linked by a corridor. It is not known whether the intensity of 'cohesive pair interactions' between mother and young at foot (Jarman and Coulson, 1989) varies within this structure.

The purpose of this paper is to evaluate whether movements of an introduced population of tammar wallabies within their home range are influenced by body weight or habitat, to determine the nature and extent of any static or dynamic interactions that occur, and to study the timing of calls and the locations at which they are made.

Study sites

Tammar wallabies were introduced into the Rotorua district of New Zealand around 1912 by H. R. Benn (Wodzicki and Flux, 1967). The two areas chosen for the study were close to the original site of liberation and were sites where tammar diet had previously been evaluated (Williamson, 1986). The 'lake site' (latitude 38° 9', longitude 176° 27'), was an extensive area of broadleaf (*Knightia excelsa* and *Weinmannia racemosa*) forest with little understorey and little available grazing (Nicholls 1964), that bordered a freshwater lake. Tammars that inhabited this site were known to consume significant quantities of browse (Williamson 1986). Tammar density, as estimated by our capture rate (1.7 per trap night), was lower on this site than on the second or "farm site" (latitude 38° 6'; longitude 176° 24').

Farm site tammars inhabited an ecotone between a mainly broadleaf (*Beilschmiedia tawa*, *Knightia excelsa*, *Litsea calicaris* and *Weinmannia racemosa*) forest (Nicholls, 1964) and 'improved' grassland where Williamson's (1986) study had shown a significant dietary predominance of grass. Tammar capture rate was 3.4 per trap night on this site.

Methods

Radio location study

Data collection

A total of 36 tammars were captured using the technique and drug dosage regime described by Lentle *et al.* (1997). Each tammar was fitted with a 52 g collar-mounted radio transmitter supplied by SIRTRACK New Zealand. Seventeen tammars were captured on the farm site and 19 on the lake site.

Collared wallabies were tracked from three fixed locations using a hand held, four element, yagi directional antenna. Radio bearings were taken from any of four fixed stations at both sites by day and by night, in all weathers, at two to three week intervals over the period from March to November in 1995. On the farm site three fixed stations were spaced at 500 m intervals parallel to the fenced bush/pasture ecotone adjacent to the area inhabited by the study animals and set 100 m back in the pasture to avoid disturbing wallabies when they emerged onto the grassland. A fourth station was sited in the bush 1000 m from the ecotone at the rear of the area inhabited by the study animals. On the lake site three stations were placed at 500 m intervals along the lake edge perimeter of a flat area inhabited by the study animals whilst a fourth was situated 800 m to the rear of this area on a rock bluff. When the animals were in locations from which three bearings could be obtained their position was determined using the maximum likelihood method of Length (Length, 1981a; 1981b). However at certain locations on both sites the nature of the topography prevented us from obtaining more than two bearings. This problem affected 35 % of the fixes. In such cases the animal's position was subsequently verified with a GPS bearing following close approach by the operator. These fixes were included in order to avoid biasing our estimates of home range by exclusion of certain specific locations where the signal was heavily shielded. Fixes on each study animal were taken at least 8 h apart. Analysis using Ranges V software (Kenward and Hodder, 1966) indicated that there was no significant autocorrelation between successive fixes at this interval.

Data analysis

Transmitter locations (or 'fixes') were estimated from bearings by the Lenth (1981a; 1981b) maximum likelihood method in LOCATE 2 (Pacer, 1990). Home range areas were estimated from bearings using the adaptive kernel method of Worton (1989) in the RANGES V suite (Kenward and Hodder, 1996). This density contouring method is able to give stable area estimates with comparatively low numbers of fixes (Kenward and Hodder, 1996) and allows for multinuclear fix distributions such as are likely in species that exhibit temporal shifts in centres of activity. We used Worton's (1989) adaptive kernel method in which the density gradient in the tail of the fix distribution is smoothed. Minimum area convex polygon (MCP) home range areas were also calculated (Voigt and Tinline, 1980). Although this method requires comparatively larger samples of fixes to stabilise area estimates, it has been widely used in the past (Kenward and Hodder, 1996) and forms a useful basis for comparison. MCP core area calculations were based on the harmonic mean range centre, that point where the inverse reciprocal mean distance to all other fixes is at a minimum. The method has been demonstrated to provide more robust estimations of MCP core areas than calculations based on an arithmetic mean range centre (Spencer and Barrett, 1984).

Nocturnal and diurnal location data were combined to calculate overall home range areas. Comparative analyses were restricted to data sets with comparable numbers of fixes obtained over identical time spans i.e. based on 13 fix data sets, spanning 2/6/95 - 6/10/95 for comparisons between the two sites (8 wallabies in the farm site and 6 wallabies in the lake site).

Range overlap analysis was carried out in RANGES V, in which percentage overlap of range areas is calculated from pixel screen area (Kenward and Hodder 1996). This analysis was restricted to animals from the farm site and was based on diurnal core areas calculated as 50% adaptive kernels. This restriction permitted the use of larger contiguous 20 fix data sets spanning 2/6/95 - 6/10/95.

Dynamic interaction analysis was by the method of Kenward *et al.* (1993) in which observed and possible distances between animals were compared using Jacobs index (Jacobs 1974). Results based on arithmetic mean, median and geometric mean gave similar results but, for the sake of brevity, only median distances between pairs are listed.

Radio-microphone study

Three adult female tammars were captured in late October 1996 and fitted with microphone radio collars as described in Lentle *et al.* (1998). The animals were monitored intermittently over a period of four weeks in November 1996 for a total of 350 hours. The operators followed, located and approached the animals to within 100meters in order to maximise signal quality. The locations of points where animals were visible to the operator were subsequently determined by determined by GPS. All calls were recorded on a portable dictaphone tape recorder and their timing noted. Sonographic analysis of recorded calls was subsequently conducted using 'Canary 1.2' (Charif et al. 1995).

Results

Radio-location study

All radio transmitters failed within three months, far short of their advertised life of 18 months. This greatly restricted the amount of locational data we were able to obtain. However, incremental area analysis showed that overall home range size of individual tammars appeared to stabilise with 12 to 15 fixes obtained 8 h or more apart (fig 1), enabling us to salvage biologically informative data from this study. All fixes that were located on the farm pasture or on clearings were obtained at night.

Overall home range and core areas are shown in Table 1. Ninety percent and 50 % adaptive kernel areas (Worton, 1989) as well as 50% and 100% convex polygon areas based on exclusion from harmonic mean centre (Spencer and Barrett, 1984) for 13 point data sets of comparable time span are shown in Table 2. Means and standard deviations of various groupings of comparable 13 point 50% and of 90% adaptive kernel areas are shown in Table 3. Results of a three way ANOVA for body weight, gender and site on the 50% adaptive kernel home range areas obtained from comparable 14 fix data sets with JM18 (which relocated in a pine plantation following disturbance) deleted as an outlier, are listed in Table 4. The results indicate that body weight is the only factor amongst those we measured that significantly influences overall home range size.

Linear regression of comparable 50% adaptive kernel areas based on 13 fix data sets with JM18 removed as an outlier, versus body weight at the time of capture was significant ($R^2 = 0.481$, $p = 0.009$) but there was separation of classes by age and by gender along the regression line (fig 2). A similar less significant regression ($R^2 = 0.252$, $p = 0.039$) was obtained using metabolic body mass, i.e. kg.$^{0.75}$. Linear regression of comparable 90% adaptive kernel areas based on 13 fix data sets was not significant using either weight ($R^2 = 0.118$, $p = 0.251$) or metabolic body mass ($R^2 = 0.000$, $p = 0.422$).

Overlap analysis was restricted to the more densely distributed diurnal fixes which were all located within the bush at the farm site. The results of an overlap area analysis based on 50% kernel isopleths of diurnal locations from 20 fix farm data sets (table 5) showed overlap of all but one of the female diurnal home range core area pairs. The diurnal core area of an adult male extensively overlapped two juvenile female core areas as well a juvenile male core area. Low numbers of fixes precluded a meaningful overlap analysis of lake site data.

Median Jacobs index values from dynamic interaction analysis (Kenward *et al.*, 1993) in RANGES V based on 20 fix farm data sets are shown in Table 6. Of 15 values 14 were positive (Binomial probability = 0.0005) indicating a significant predominance of positive values. Of the 14 positive values, the three with values greater than + 0.5 all related to interaction between a male and a female.

Radio-microphone study

The signal clarity was such that we were able to monitor the sounds of biting, chewing, calling and use of bipedal gait by each subject along with its location.

The overall home range areas of the three adult female tammars were of a similar order of magnitude to those of the subjects in the home range study (11.0, 13.8, and 19.2 ha. using the 100% convex polygon method). The diurnal and noctural movements of the three animals were in line with the findings of the radiolocation study. The animals remained in the bush, within 800-1000 m of the bush/pasture ecotone, throughout the day, moving relatively small distances and using the bipedal gait only rarely. Around dusk, the animals moved closer to grassy tracks that led to the ecotone. With the advent of darkness, on fine nights, they travelled rapidly along these tracks by prolonged periods of bipedal locomotion, covering the distance to the ecotone in 10-15 minutes. Subsequently they stayed close to the ecotone during the hours of darkness, frequently emerging onto farm pastures, before returning slowly by the same route to reach the same daytime 'roosting' area just prior to dawn. The timing of feeding activity is described in detail elsewhere (Lentle; 1998).

Fortyfive calls were heard during the 350 hour observation period. All were low pitched screech/ hiss noises similar to that reported by Russell (1973). The noise was always repeated rapidly sometimes for periods up to 30 sec (fig 3). In terms of Eisenberg *et al.'s* (1973) classification of the sounds produced by Marsupialia, the sonogram (fig. 3) shows category IV frequency morphology with some type II features. The temporal distribution of calls (fig. 4) shows crepuscular peaking at times when the animals are travelling between roosting and feeding sites.

Discussion

While widespread premature transmitter failure greatly restricted the amount of locational data we were able to obtain, our overall home range area estimates for tammar wallabies were of a similar order to those obtained by Inns (1980) for Kangaroo Island tammars even though climate and vegetation at that site differed considerably from the current study sites. Moreover, the variability in overall home range area found by Inns (1980) (100% convex polygon home range areas 11.2 - 91.3 ha from 12 - 61 fix data sets) was broadly similar to the variation of our data. Inns (1980) concluded that variations in overall home range area on his study site were secondary to seasonal fluctuations in the abundance of food. However, in our study, tammar density was below carrying capacity and the data sets were of contiguous time span so such an explanation is unlikely. Viewed in conjunction with the observations from the radio-microphone study it seems more likely that this variation is a consequence of the bipolar nature of home range with different animals having 'roosting sites' at differing distances from nocturnal grazing sites.

Whilst the number of fixes are low in the comparisons based on 13 point data sets, the incremental area analysis indicates that this number of fixes provides a meaningful basis for comparisons of overall home range size. Viewed in the light of Williamson's (1986) dietary findings, the lack of significance of the effect of 'site' on overall home range demonstrates that the home ranges of tammars that rely principally on grazing are not significantly different from those that consume mainly browse. This may be a consequence of a similar bipartite range structure at both sites with separation of diurnal from nocturnal feeding areas, rather than spatial distribution of foods, being the principal determinant of core area size.

The significant influence of 'body weight' on core areas based on 13 point data sets is in line with the relationship of body weight to home range predicted by McNab (1963). However in species such as macropods that exhibit sexual dimorphism of weight (Jarman, 1989), it is difficult to separate the influences of weight and gender. Thus whilst home ranges of male macropods tend generally to be larger than, and to overlap those, of females (Croft, 1989; Vernes *et al.,* 1995; Horsup, 1984) the mean body weights of male macropods are typically greater than those of females (Vernes *et al.,* 1995). The overall ratio of male to female 50% kernels based on 13 fix data sets in our study was 1.5, close to the value of 1.4 given by Croft (1989) for total home ranges of tammars in Australia.

The highly significant predominance of positive indices of dynamic 'group' interaction rather than a predominance of negative values (repulsion) or an even spread of negative and positive values around zero (chance 'aggregation') coupled with close overlap in diurnal home range core areas together indicate type 'E' grouping (Russell, 1984) such as has previously been reported in Kangaroo Island (Inns, 1980) and Kawau Island (M. Vujcich, 1979; V. Vujcich, 1979) tammar populations on the basis of less formal studies. The fact that such grouping persisted in a tammar population whose densities were below carrying capacity indicates a significant site loyalty consistent with the findings of Johnson (1989) for macropods in general. The significant positive dynamic interactions between adult males and juveniles indicates that males will tolerate the presence of juveniles and supports observations (Christensen, 1980) that tammars associate in family groups.

The diurnal crepuscular distribution in the frequency of vocalisations with comparatively low frequencies of calling at night may indicate lower levels of social interaction during the hours of darkness and thus adds weight to an hypothesis of lower level nocturnal group vigilance in this species (Lentle, 1998). The peaks in calling frequencies that occurr during the period when tammars are journeying between day-time roosting sites and night-time feeding sites presumably indicates more intense mother/young interactions (Russell, 1973) during times of rapid travel. Juveniles would have had an average age of 40-43 weeks during the period of this study, assuming a mean birth date of late January

(Murphy and Smith, 1970). Thus, in free ranging tammars, mother young interactions may continue beyond the 36 week period reported in captive specimens by Russell (1973).

Taken together the findings of this study indicate that tammars live in temporally cohesive groups and have home ranges with a bipartite structure that is linked by a communal corridor as was proposed by Nicholls (1971). Whilst overall home range areas scale with body size, variations in the spacing between daytime roosting and nocturnal grazing areas may be sufficent to obscure any effects from differences in the spatial dispersion of available food i.e. reliance on grazing or browsing.

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Table 1: Overall home range and core areas (ha) (diurnal and nocturnal locations combined), calculated as adaptive kernels and as convex polygons with exclusion on the basis of distance from harmonic mean for tammar wallabies at two sites in the Rotorua district.

Wallaby	Number of fixes	50% Kernel	90% Kernel	50% Polygon	100% Polygon
Farm site					
JF14	25	3.0	24.6	2.0	21.0
JM18*	20	9.5	162.5	6.0	68.0
JF22	25	5.0	21.4	7.0	18.0
JF30	20	4.0	12.0	1.0	12.0
JF40	27	6.1	41.4	7.0	39.0
AM52	21	8.5	50.0	6.0	23.0
JF74	26	3.3	8.6	2.0	10.0
Lake site					
JM24	20	7.2	47.6	7.0	32.0
AF78	22	5.9	23.1	2.0	22.0

(J= juvenile, A= Adult, F= female, M= male. * changed home range substantially during the study)

Table 2: Live body weights and adaptive kernel areas (ha) based on 13 fix data sets of tammar wallabies taken over the same time period at two sites in the Rotorua district.

	Weight (kg)	Area	
Farm site		**50%**	**90%**
JF14	2.8	2.38	40.99
JM18*	2.8	7.47	184.0
JF22	2.5	6.73	17.01
JF30	2.6	1.24	18.33
JF40	2.6	2.77	30.74
AM52	8.4	9.14	34.63
JF74	2.6	1.45	8.76
AF76	5.0	2.79	9.45
Lake site			
JM12	3.2	2.30	21.68
JM24	3.1	4.03	35.73
JF28	2.6	1.21	15.14
JM68	3.0	6.13	32.56
AF78	4.5	5.12	27.26
AF80	5.5	9.61	56.04

*Changed home range substantially during the study.

Table 3: Home range sizes (ha), calculated as 50% and 90% adaptive kernels, of various groupings of comparable 13 fix home range areas (excluding JM18) for tammar wallabies in the Rotorua district.

Kernel	Group	No. of wallabies	Mean	SD
50%	Lake site	6	4.7	3.0
	Farm site	7	3.8	2.9
	Male	4	5.4	2.9
	Female	9	3.7	2.8
	Adult	4	6.7	3.3
	Juvenile	9	3.1	2.1
90%	Lake site	6	31.4	14.2
	Farm site	7	22.8	12.7
	Male	4	31.5	6.4
	Female	9	24.8	15.6
	Adult	4	31.8	19.3
	Juvenile	9	24.5	10.8

Table 4: Three way ANOVA* of comparable 13 fix overall 50% and 90% adaptive kernel home range areas of tammar wallabies (excluding JM18) on farm and lake sites in the Rotorua district. Significant probabilities are in bold.

	50% Kernel			90% Kernel		
	DF	F-Ratio	P	DF	F-Ratio	P
Body weight	1	6.036	**0.036**	1	2.225	0.418
Sex	1	1.485	0.254	1	0.187	0.670
Site	1	0.002	0.967	1	0.165	0.450
Mean sq error	10	6.148		10	199.8	
R sq.		0.452			0.184	

*(Simplified model as interaction terms were not significant)

Table 5: Overlap analysis of 50% isopleth areas obtained from diurnal locations in farm site 20 fix data sets for tammar wallabies.

Range areas in rows are overlapped by range areas in columns.

	JF14	JM18	JF22	JF40	AM52	JF74
JF14	------	5.7	24.9	26.1	50.8	3.9
JM18	3.0	------	0.8	0.0	40.5	0.0
JF22	49.4	3.2	------	0.0	78.1	27.2
JF40	80.3	0.0	0.0	------	6.4	0.0
AM52	34.6	54.9	27.1	1.5	------	5.8
JF74	8.8	0.0	41.7	0.0	19.5	------

Table: 6. Jacobs indices* of dynamic interactions on comparable farm site 20 fix data sets (* based on median values) for tammar wallabies in the Rotorua district.

Values of + 0.5 or greater, indicating strong positive association, are presented in bold.

Interacting animals	**Jacobs index**
JF14 / JM18	+ 0.19
JF14 / JF22	+ 0.39
JF14 / JF40	- 0.08
JF14 / AM52	**+ 0.52**
JF14 / JF74	+ 0.41
JM18 / JF22	**+ 0.55**
JM18 / JF40	+ 0.18
JM18 / AM52	+ 0.16
JM18 / JF74	+ 0.25
JF22 / JF40	+ 0.23
JF22 / AM52	**+ 0.50**
JF22 / JF74	+ 0.07
JF40 / AM52	+ 0.08
JF40 / JF74	+ 0.08
AM52 / JF74	+ 0.10

Fig 1: Incremental area analyses of the home ranges of 11 tammars in the Rotorua district of New Zealand.

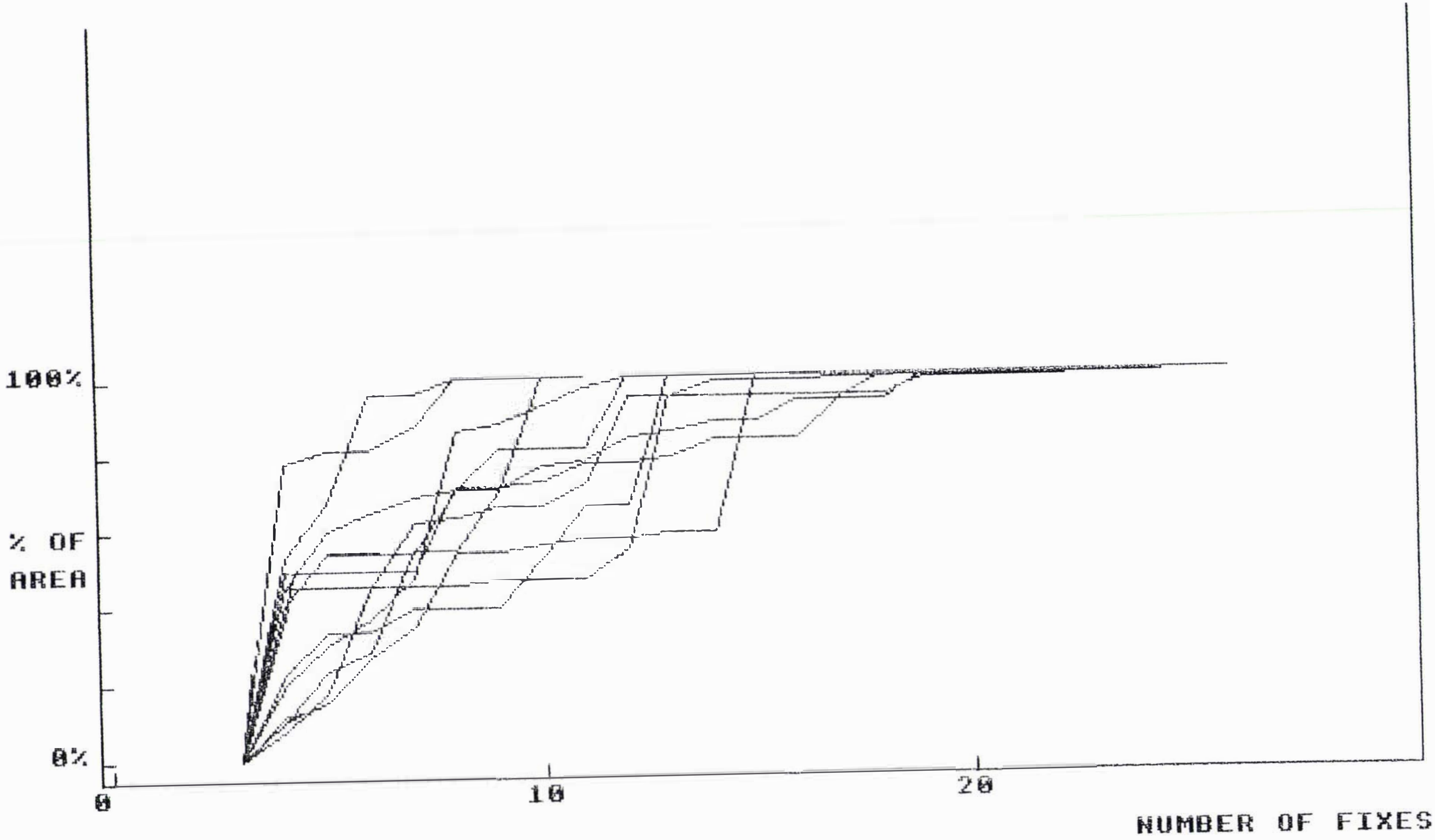

100%
% OF
AREA
0%
0
10
20
NUMBER OF FIXES

Fig 2: Linear regression of comparable 50% adaptive kernel home range core area (ha) against body weight (kg) at time of capture.

A, juvenile female; B, juvenile male; C, adult female; D, adult male. Curved lines are 95% confidence intervals

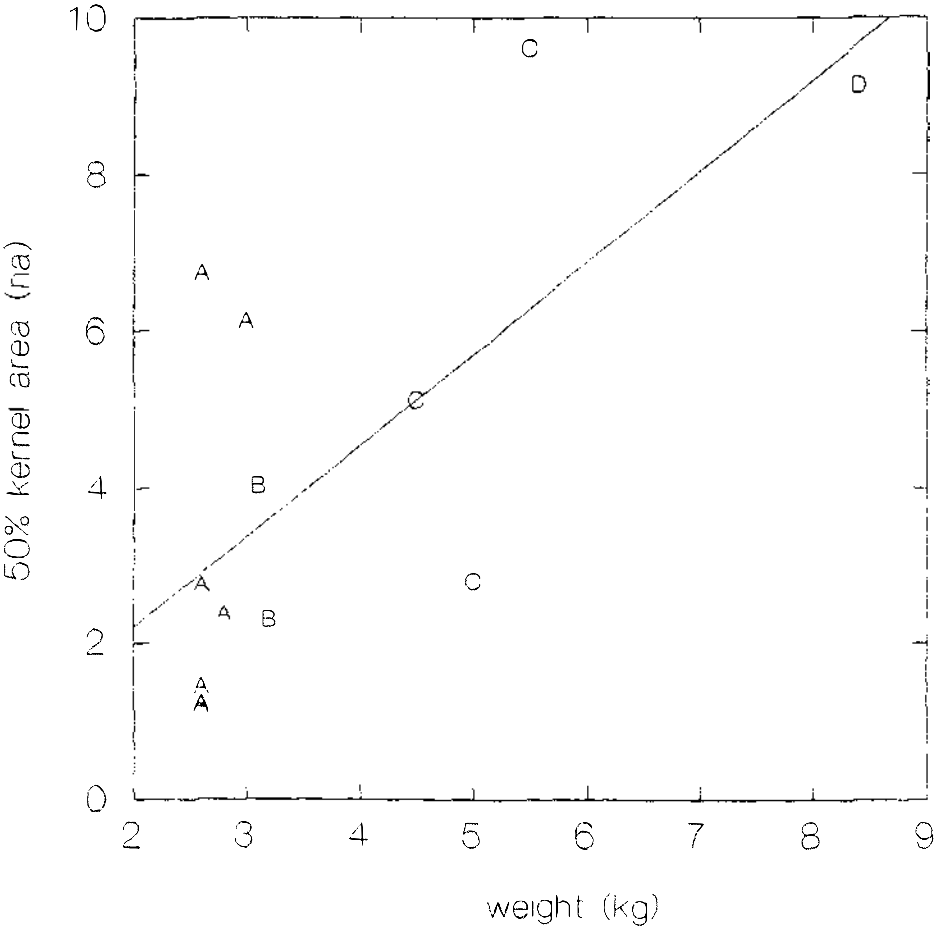
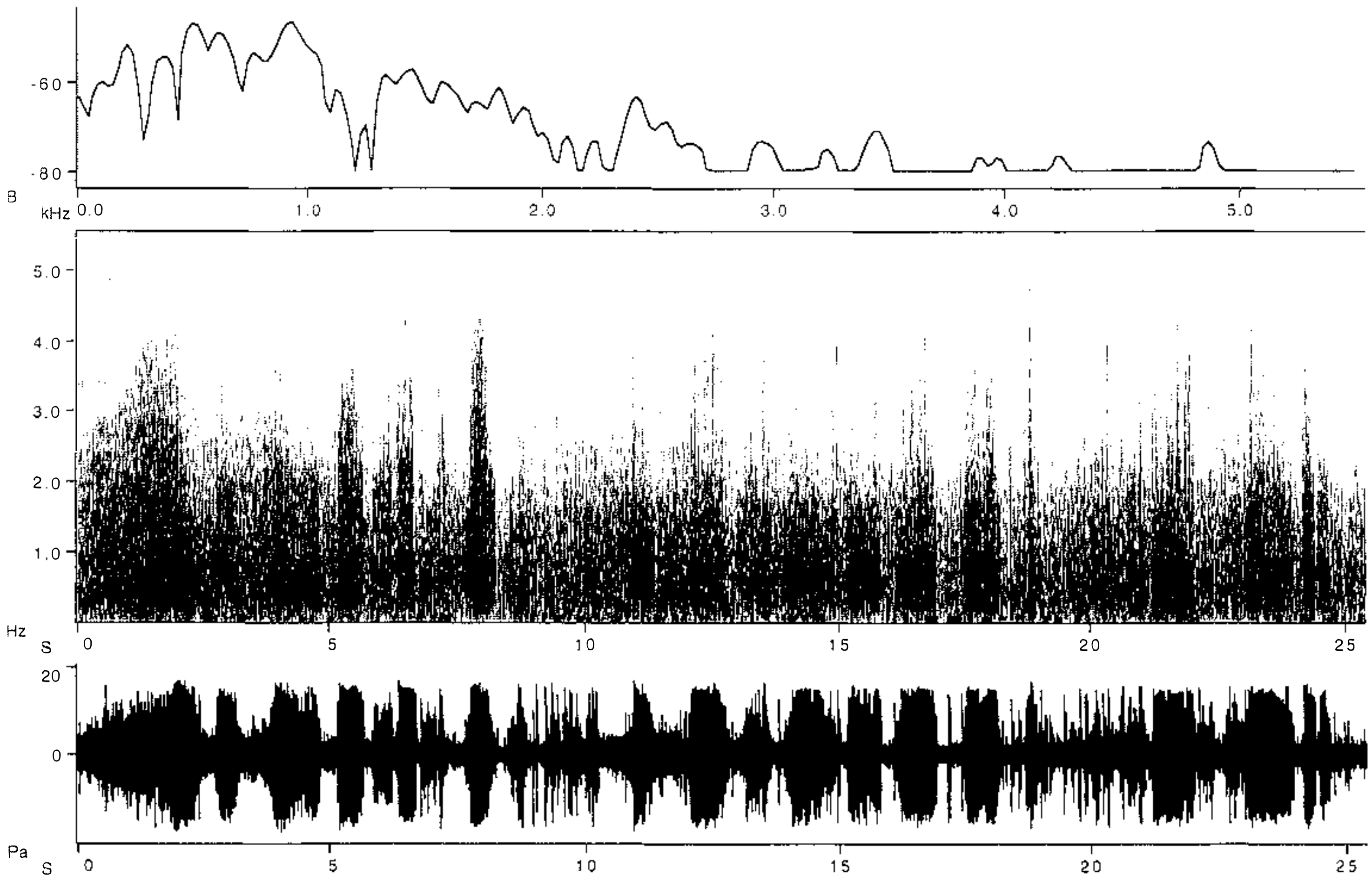
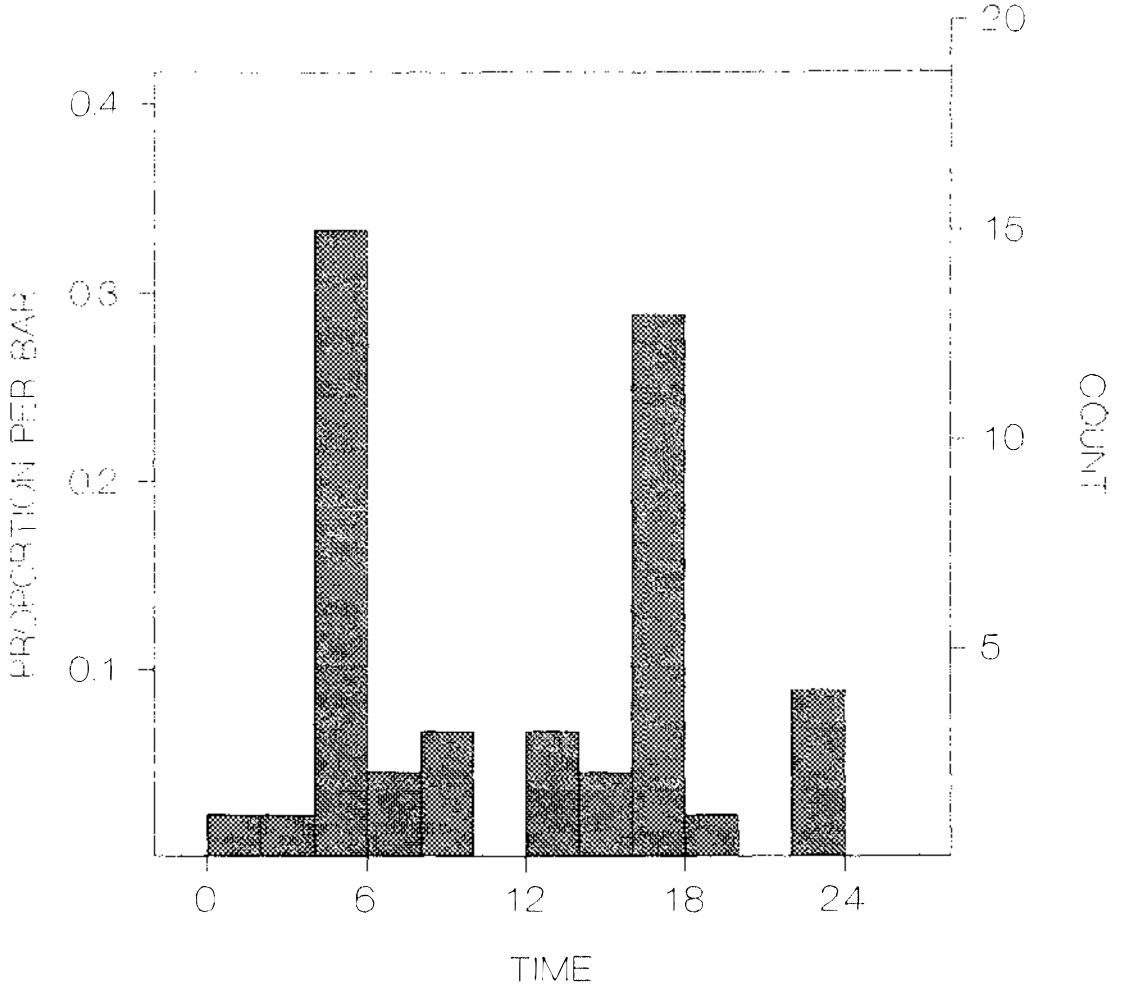

50% kernel area (ha)
10
8
6
4
2
0
2
3
4
5
6
7
8
9
weight (kg)
A
B
C
D

Figure 3: Sonogram of the typical call of a free ranging female tammar recorded using radio-microphone collar.



-60
-80
B
kHz
0.0
1.0
2.0
3.0
4.0
5.0
5.0
4.0
3.0
2.0
1.0
Hz
S
0
5
10
15
20
25
20
0
Pa
S
0
5
10
15
20
25

Figure 4: The temporal distribution of 45 calls made by three free ranging female tammar wallabies during a 350 hour surveillance period.


PROPORTION PER BAR
0.4
0.3
0.2
0.1
20
15
10
5
COUNT
0
6
12
18
24
TIME