Chapter 7
The Ecology of Social Evolution in Termites

Judith Korb

Abstract Termites (Isoptera) belong to the classical eusocial insects and their resemblance to ant colonies is so striking that they are commonly known as 'white ants'. However, the termites evolved social life independently, long before the ants. Their different ancestry also is reflected in several fundamental differences in the organization of the colonies. This chapter aims at summarizing the state-of-the-art in termite research and comparing the results with other social invertebrate and vertebrate systems in an attempt to reveal common principles underlying social evolution. First, I provide an overview of termites' biology and classification. I continue with a summary on the 'hunt' for a genetical explanation of the evolution of termite' eusociality. Using a case study, I summarize ecological factors favoring cooperation in a lower termite and show the relevance of these results for other termite species. Based on these results I outline the potential evolutionary transitions in termite eusociality. Finally, I compare the driving forces in termites with those in cooperatively breeding vertebrates and offer a potential explanation why eusociality rarely evolved in vertebrates, despite often strikingly similar ecological pressures in both groups.

7.1 Introduction: An Overview of Termite Classification and Biology

Termites (Isoptera) are the oldest social insects with a social life that dates back to the Cretaceous when they had dinosaurs as their contemporaries. In the oldest fossils from the Cretaceous (130 Mio), it is clear they were already social with characters strikingly similar to modern basal species (Thorne et al. 2000). Although

---

Judith Korb
Department Biology I, University of Regensburg, 93040 Regensburg, Germany
judith.korb@biologie.uni-regensburg.de

J. Korb and J. Heinze (eds.), *Ecology of Social Evolution*.

their morphology was primitive, the Cretaceous termites were already reasonably diversified suggesting an origin in the upper Jurassic. Non-social termites, either fossil or recent, are unknown but termites, cockroaches (Blattaria) and mantids (Mantodea) form a natural assemblage (Walker 1922) and are commonly grouped as suborders of the Dictyoptera (Kristensen 1991). The relationship among the three lineages is controversial (Nalepa and Bandi 2000; Eggleton 2001). Some authors contend that the primary dichotomy lies between the Isoptera and (Blattaria + Mantodea), and others that Mantodea diverged first, with Blattaria and Isoptera either as sister groups, or with Isoptera nested within the Blattaria (Hennig 1981; Thorne and Carpenter 1992; Grandcolas 1994; Klass 1995; Kambhampati 1995). The weight of evidence now suggests the latter (Inward et al. 2007). Most likely, they form the sister group of the Cryptocercidae (woodroaches) (Eggleton 2001; Inward et al. 2007a). It is generally accepted that eusocial termites evolved from a subsocial ancestor (Thorne 1997; Shellman-Reeve 1997). Fossil and molecular data both suggest that eusocial termites evolved relatively rapidly from their non-eusocial ancestors, and with no intermediates in the fossil record, it difficult to resolve the phylogenetic relationships (Nalepa and Bandi 2000).

The termites form a diverse group with over 2600 described species that range across 281 genera and seven families: Mastotermitidae (only 1 species: *Mastotermes darwiniensis*), Hodotermitidae, Termopsidae, Kalotermitidae, Rhinotermitidae, Serritermitidae, and Termitidae (Kambhampati and Eggleton 2000; Eggleton 2001; Inward et al. 2007b). Classically, they are grouped into the lower termites (all families except the Termitidae) and the higher termites (Termitidae), the latter constituting about 75% of all termite species (Kambhampati and Eggleton 2000). The phylogenetic relationship among the families is not completely resolved (Eggleton 2001; Lo et al. 2004) but Mastotermitidae is now generally accepted to be the most basal termite group (Fig. 7.1). Termopsidae, Hodotermitidae and Kalotermitidae are all basal to (Termitidae + Serritermitidae + Rhinotermitidae), although their relative positions within that part of the tree are disputed (Eggleton 2001). Most recent studies support a sister group relationship for Serritermitidae and (Termitidae + Rhinotermitidae). Recent molecular studies indicate that there is need for a major revision of the Rhinotermitidae that seem to be paraphyletic with the Termitidae nesting within this family (Lo et al. 2004).

Based on their ecology, and particularly their nesting and feeding habits, termites can be grouped into two life types (Abe 1987, 1990): (i) One-piece type termites (Termopsidae, Kalotermitidae and *Prorhinotermes* within the Rhinotermitidae; hereafter called OP termites): These species live in their food and spend their entire colony life in a single piece of wood that serves as both food source and shelter. As these termites do not forage for new resources, the availability of wood in the nest is of prime importance for the maximum longevity and the stability of the colony. (ii) Multiple-pieces type termites (including Abe's intermediate type; hereafter called MP termites) (Mastotermitidae, most Rhinotermitidae, Serritermitidae, Termitidae): These species live in a well-defined nest that is more or less separated from the foraging grounds. The fact that workers can explore new food sources outside the nest typically means that the nest's longevity is less limited by food availability than in the OP species

(Fig. 7.1). This ecological classification is also reflected in the social organization of the colonies. Wood-dwelling OP termites have a flexible development in which workers are totipotent to explore all caste options (Lüscher 1974; Roisin 2000). In order to reflect this distinction, they have also been called false workers, pseudergates or helpers (Thorne 1996; Roisin 2000). However, the utility of these extra terms is unclear, the term pseudergate is confusing and should be avoided. Pseudergate was originally defined for individuals that develop regressively from nymphs (in termite terminology: instars with wing buds) into workers (Grassé and Noirot 1947; Noirot and Pasteels 1987). In practice, it is difficult to separate pseudergates sensu stricto from younger individuals as the former can regain the morphological appearance of the latter. These pseudergates sensu stricto are also not the only 'workers' in the nest, but the work force also consists of late instar larvae (in termite terminology: instars without wing buds) and nymphs (Noirot and Pasteels 1987; Thorne 1997). In contrast to the OP termites, all species of the MP type have a true, morphologically differentiated worker caste with reduced reproductive potential. This reaches its extreme in the higher termites where workers are terminally differentiated and cannot proceed to the alate stage (Noirot 1990). In these species, a bifurcation into the neuter (workers and soldiers) versus the sexual line exists that is set at an early instar (Roisin 2000). In some species of the Termitidae, caste fate appears to already be determined in the egg (Roisin 2000).

Several other life-history traits correlate with this classification by nesting habit (see also Shellman-Reeve 1997). OP termites with their non-replenishable food source, have generally rather short-lived colonies (4–15 years in most species; Abe

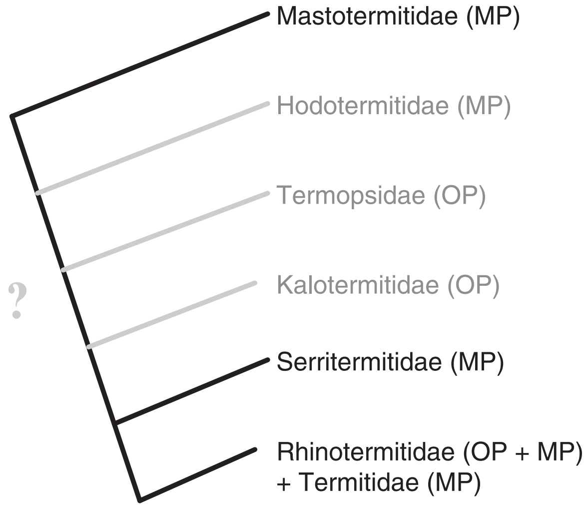

Fig. 7.1 Family-level phylogeny for termites after Eggleton (2001) and Lo et al. (2004). The relative position of the three *grey* families is not clearly resolved. *OP* Wood-dwelling, one-piece nester termites, in which food and nest are identical; *MP* Multiple-pieces nester termites, in which nest and food are separated (for more information see text)

1987; Lenz 1994) of small sizes (600–8,000; Lenz 1994). In contrast, MP termites are relatively long-lived (up to several decades; Roonwal 1970; Grassé 1984; Shellman-Reeve 1997; but see Soki et al. 1996 for short life-span of some Termitidae) and can reach large colony sizes (up to 1–5 million; Nutting 1969; Darlington 1979; Darlington et al. 1992; Lenz 1994). There, the life-span of a colony seems to be chiefly limited by predation (Bodot 1961; Longhurst and Howse 1979; Longhurst et al. 1979; Levieux 1983; Abe and Darlington 1985; Darlington 1986; Gotwald 1995; Korb 1997; Korb and Linsenmair 1999, 2001; Noirot and Darlington 2000) and sometimes competition (Leponce et al. 1997; Lepage and Darlington 2000; Korb and Linsenmair 2001), while the availability of nesting space and the fecundity of the reproductives sets the maximum colony size (Grassé 1984; Lenz 1994). There is a high degree of task specialization within colonies, reaching its peak in the Termitidae in which four morphological castes can often be distinguished that additionally exhibit age polyethism (Gerber et al. 1988; Veeranna and Basalingappa 1990; Lys and Leuthold 1991; Traniello and Leuthold 2000).

The division into OP and MP termites is not identical with the classical division in lower and higher termites (Fig. 7.1). The higher termites are confined to the family Termitidae, which are MP termites, but there are also other MP termites (i.e., Mastotermitidae, Hodotermitidae, Serritermitidae and the Rhinotermitidae with the exception of *Prorhinotermes*) that belong to the lower termites. On the other hand, however, all OP termites are lower termites.

7.2 Evolution of Sociality in Termites: the Hunt for a Genetic Explanation

The correspondence between life type (log and nest) and social organization in the termites highlights the central importance of ecological parameters in their evolution (Higashi et al. 1991, 2000). Yet, like in other social insects, explanations for the evolution of termites' sociality has mainly focused upon genetics and specifically kinship relatedness, which has become relatively easy to quantify with the advances in genetic techniques in the last 20 years. The altruistic behavior seen in insect workers, in which they reduce their lifetime reproductive success (direct fitness) in order to increase the fitness of the reproductives, can be explained by kin-selection theory: the propagation of genes via closely relatives (Hamilton 1964; Maynard Smith 1964). According to Hamilton's rule, altruism will be favored when $rb > c$, where r is relatedness between the recipient and actor and b and c are the benefit and cost of the action to the actor and recipient respectively (Hamilton 1964). The unusually high relatedness between sisters in the social Hymenoptera that occurs due to their haplodiploid genetics (males derive from haploid unfertilized eggs and females from fertilized diploid eggs) was initially thought to explain the multiple origins of eusociality in this insect order and the female preponderance in these colonies (Hamilton 1964, 1972; for a recent discussion: Bourke and Franks 1995; Crozier and Pamilo 1996; Queller and Strassmanm 1998; see Chap. 1 and

Chap. 6). In the diploid termites, no such easy genetic explanation was at hand to explain their resemblance to ant colonies, which is so striking that they are commonly known as ‘white ants’. The discovery of chromosomal translocations, in which a tight linkage of genes to the sex chromosomes occurs, seemed to provide a welcomed haplodiploidy analogy (Luykx and Syren 1979; Lacy 1980). However, chromosomal translocations are not common in the clades thought to be closest to the non-eusocial ancestor of termites and the species in which translocation occurs do not show the predicted sex-discriminative behavior (Crozier and Luykx 1985; Hahn and Stuart 1987; Leinaas 1983; Vinque and Tilquin 1978; Roisin 2001). Another candidate genetic explanation was that of inbreeding-outbreeding cycles (Bartz 1979). Bartz suggested that unrelated alates found new colonies but are later replaced as king and queen by their offspring, which remain in the colony and breed together. After several cycles of such replacement, highly inbred and therefore highly homozygous, alate offspring are produced. Assuming that such inbred alates mate with unrelated, but also inbred partners, relatedness asymmetries comparable to those of the Hymenoptera could arise: offspring from the colony founders are more related to each other than they would be to their own offspring and raising full siblings could become selectively favored. However, although inbreeding does frequently occur in termites, neither are the alates only produced by inbred reproductive nor is the number of inbreeding cycles high enough to produce highly inbred offspring (Myles and Nutting 1988; Atkinson and Adams 1997; Thompson and Herbert 1998; Husseneder et al. 1999; Shellman-Reeve 2001).

Thus, the hunt for a special genetic explanation for the evolution of eusociality in termites faltered and seemed to ultimately fail. A similar situation emerged in the eusocial Hymenoptera where the perceived importance of the haplodiploidy hypothesis faded as it became clear that haplodiploidy will only promote altruism relative to diploidy under rather restricted conditions, and eusociality was discovered in more and more non-haplodiploid species (Queller and Strassmann 1998). The costs and benefits terms in Hamilton’s rule have at last gained the equal footing that they deserve alongside relatedness in explanations of altruism. As a result, explanations for why eusociality has evolved so often in certain insect groups have taken on a distinctly ecological flavor. However, studies that quantitatively tested any factors either ecological or genetic are scarce in the termites. In the next section I will present a case study that tried to fill this gap.

7.3 A Case Study: *Cryptotermes secundus*

7.3.1 Workers

The Australian drywood termite *Cryptotermes secundus* (Kalotermitidae) occurs in dead mangrove trees that have a patchy distribution (Miller and Paton 1983; Korb and Lenz 2004). As is typical for OP termites, the workers are totipotent and able to develop into all possible castes (Fig. 7.2): (i) sterile soldiers, (ii) replacement reproductives via one neotenic molt when the same sex reproductive of the colony dies, or (iii) winged reproductives, which leave the nest to found a new colony, via several nymphal instars (Korb and Katrantzis 2004). In contrast to eusocial Hymenoptera or MP termites with morphological castes, therefore, being a worker is not a lifetime strategy but rather a developmental tactic that can be abandoned if conditions change. The basis for this developmental flexibility are progressive (increasing body size and/or wing buds), stationary (no morphological change), and regressive (decreasing body size and/or wing buds) molts (Korb and Katrantzis 2004). Regressive molts are a particularly unusual and important feature of their development because it allows individuals that have already started to develop towards sexuals to partially regress their development and become again a worker (pseudergates sensu Grassé and Noirot 1947) lacking any signs of wing buds.

Collections of natural field colonies together with laboratory and field experiments have revealed that caste development in *C. secundus* workers is influenced by internal (e.g., colony size) as well as external factors (Korb and Lenz 2004; Korb and Schmidinger 2004; Korb and Katrantzis 2004; Korb and Fuchs 2006). The development into winged sexuals is largely regulated by season (Korb and Katrantzis 2004). Over a 7-month period, individuals gradually progress through five successive nymphal instars to become alates by August when the annual nuptial flight takes place. During this developmental period there appear to be deadlines for each successive nymphal instar on the way to becoming a winged

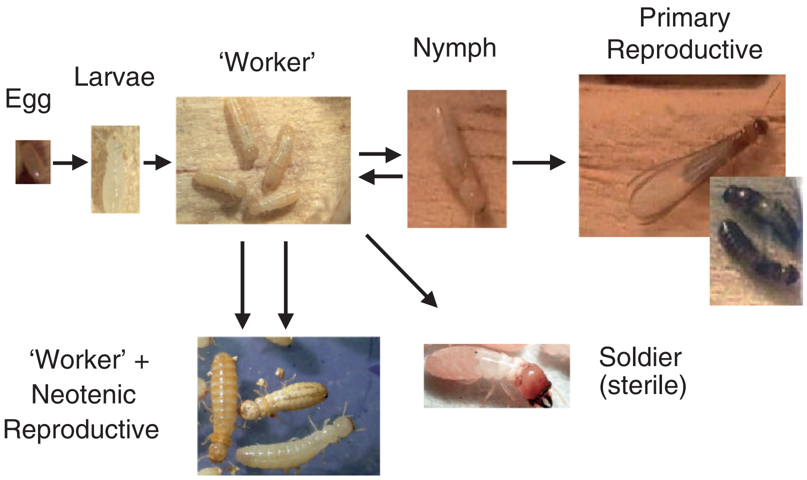

Fig. 7.2 Simplified developmental pathway of *Cryptotermes secundus* (Kalotermitidae). Eggs develop via larvae into workers. Then workers can develop (i) progressively via nymphal instars into winged sexuals (alates) that leave the nest to found a new colony as primary reproductives, (ii) into sterile soldiers, or (iii) via one neotenic molt into a replacement reproductive. The development from nymphs to workers is reversible via regressive molts. Photos: J. Korb

reproductive. Those individuals that do not reach a certain instar by a certain date (week) will regress their development and molt back into workers without wing buds (pseudergates sensu Grassé and Noirot 1947). Deadlines for earlier instar nymphs occur sooner than for older instars, which may be indicative of a reduced investment in progressive molts in response to the reduced likelihood of making the final deadline. These deadlines probably function to ensure that only individuals that are competent and well nourished to successfully disperse, fully develop into alates. This developmental strategy is in line with a mechanism suggested by Roisin (1994) for the evolution of workers in termites: According to the loser hypothesis, the termite worker caste evolved from individuals incapable of developing into sexuals. However, the 'loser' phenotype in *C. secundus* was not associated with aggressive manipulation by siblings or parents (Korb 2005) as suggested by Zimmerman (1983) and Myles (1986). Being a worker rather seems to be a conditional strategy (sensu Gross 1996) where individuals less competent for founding their own nest stay in the natal colony. Data for *C. secundus* show that this development can be reversed again and that regressed workers can later resume alate development (Korb, unpubl. data).

In addition to this seasonal regulation, alate development is also influenced by food availability in the nest (i.e., size of the wood the colony is nesting in) that adjusts the number of remaining workers versus dispersing sexuals (Korb and Katrantzis 2004). When the wood size reaches a certain threshold (< c.a. $2.5\,\mathrm{cm}^3$ per termite), individuals begin progressive nymphal development earlier in the year. Placing colonies 2 months after the nuptial flight into wood blocks below the threshold size immediately elicits progressive development, meaning that the first nymphal instars occur 3 months earlier than under abundant food conditions. As a result, more individuals reach the molt deadlines and mature into winged sexuals than in colonies with abundant food (Korb and Katrantzis 2004). Despite the precocious start to progressive development, the sexuals in these food limited colonies still leave the colony at the annual nuptial flight because their development slows down as they reach late instar nymphs (Korb and Katrantzis 2004).

This increase in dispersal as sexuals makes adaptive sense for log dwelling termites like *C. secundus* because as the log diminishes, so too does the probability they will be able to reproduce in the natal colony before the wood runs out (see below). A central component of this response is the termites' impressive ability to detect changes in the size of their log and so predict colony longevity (Korb and Katrantzis 2004). In *C. secundus* the loss of wood from the log occurs gradually by the termites own consumption of the wood but also suddenly when cyclones or heavy thunderstorms fragment their trees (Korb and Lenz 2004). Correspondingly, the termites cannot rely on extended excavations to measure wood availability. Instead, the termites continually sense the amount of wood from the vibrations generated during wood gnawing (Lenz 1994; Evans et al. 2005). These vibrations constitute reliable and fast cues of food availability. This predictable variation in food availability/colony longevity probably selects for the flexible development of workers in OP termites (Korb and Katrantzis 2004). This situation contrasts with the MP termites that leave their nest to exploit resources. They reduce the long-term food variability but experience short-term variation in food supply that lacks predictable cues allowing a plastic developmental response.

The obvious importance of ecology in the reproductive development of *C. secundus* contrasts sharply with variation in relatedness, which appears to have little effect. Colonies are founded monogamously (mainly by outbred pairs) resulting in a within-colony relatedness of $r=0.5$. However, variation in between- and within-colony relatedness is common due to two key processes, (a) reproductive replacement: the primary reproductives die and are replaced by inbred neotenic reproductives (increase in relatedness; c.a. 16% of colonies) and (b) colony fusion: colonies that were independently founded in the same tree meet and mix during colony expansion (decrease in relatedness; >c.a. 25% of colonies) (Korb and Schneider 2007). Fusion creates a single colony containing related and unrelated nestmates, and often, both reproductives of one of the original colonies are killed during fusion, which means that the workers of this colony are unrelated to the offspring produced after colony fusion. The decrease in relatedness resulting from fusion might be expected to cause more workers to leave the colony as dispersing sexuals. This is because the reduced relatedness means that the inclusive fitness benefits that they can get from helping other members of the colony will also reduce. However, there is no evidence that this occurs (Korb and Schneider 2007). This is not because the termites cannot detect the fusion event: workers can be observed do change certain behaviors (Korb and Schneider 2007) and seem to have the ability to even recognize kin (Korb 2006; Fuchs and Korb, unpubl. data). Also the developmental response of workers in inbred colonies does not seem to be linked to their increased relatedness, but to a higher likelihood of inheriting the natal colony (Korb and Schneider 2007).

The discovery that the workers stay in the colony even when they are not related to the king and queen can be explained by data that suggest they are not workers at all (Korb 2007). If the workers stay in the colony in order to help rear the colony's offspring, then increasing the number of offspring should increase the benefits of working and decrease the likelihood that a worker develops into a dispersing sexual. However, an experiment that added young instars to nests showed the number of offspring to raise did not affect the number of worker individuals developing into dispersing sexuals. Furthermore, the additional young instars nevertheless survived, although worker individuals left the colony (Korb 2007). Detailed behavioral observations further confirmed that the workers were not helping to rear offspring (Korb 2007). There is no brood care, and foraging, an important and risky task normally carried out by workers of social insects, is unnecessary as the colony lives within its food. Interactions between individuals in general are rare and proctodeal trophallaxis (= anal feeding) and allogrooming are not altruistic because each individual receives as much as it provides.

So why do workers remain in the colony if they gain no indirect benefit from raising siblings? It appears that they are hopeful reproductives. A model based upon long-term field data revealed that the number of individuals staying at the nest can be explained by the probability of inheriting the nest *versus* founding a new colony (Korb and Pirow, in prep). The probability of founding and inheritance are both very low (<1%) and certainly within the same order of magnitude (Korb and Schneider

2007). The exact values depend on the colony size, the age of the reproductives, and the potential longevity of the nest and these three variables can be used to accurately predict the number of individuals developing into dispersing sexuals in field colonies (for similar results in a stenogastrine wasp see Chap. 4). In summary then, it appears that *C. secundus* workers should be regarded as hopeful reproductives rather than true altruistic workers that stay for kin's sake. This explains why ecological factors like food availability, i.e., the potential longevity of the nest which determines the value of inheriting it, influences the development of individuals, whereas variation in relatedness among colony members has no effect.

7.3.2 Soldiers

In contrast to the workers, *C. secundus* soldiers that make up less than 5% of all colony members, are a true altruist caste that gains indirect fitness benefits (Roux and Korb 2004). They are sterile and represent a developmental endpoint as they lost their capability to molt. They are morphologically highly specialized with large mandibles and a plug-shaped head that is heavily sclerotized and used to effectively block the wooden nest galleries (Fig. 7.3). An experiment in which soldier development was inhibited has shown that soldiers increase the reproductive success of their colony and therefore gain indirect fitness benefits (Roux and Korb 2004). However, in contrast to general assumption, their function does not seem to lie in the defense of the colony against predators. Predators are extremely rare in *C. secundus* because the wooden nest structure is a very effective protection preventing predators from entering the nest. Indeed, over 5 years of fieldwork involving more than 600 studied colonies no predators or traces of predation were found (Korb and Roux, in prep.). The main threat for *C. secundus* colonies seems to be competitors

Fig. 7.3 Phragmotic head of a *Cryptotermes secundus* soldier. Photo: Birgit Lautenschläger

that live in the same tree and consume the non-replenishable wood. Beetle larvae (especially Buprestidae) are very common (in c.a. 25% of all trees) that consume considerable quantities of wood and render contacted wood unpalatable to termites. However, these are not repelled by the soldiers (Korb and Roux, in prep.). Beetle larvae are attacked by workers as well as soldiers but with little effect. Often the beetle larva is sealed off and continues to consume the wood from its sealed cavity. The main colony benefit provided by soldiers seems to occur through attacks on other termites, either of the same species or of the congeneric species *C. domesticus* that has very similar habitat requirements like *C. secundus*. As mentioned earlier, intraspecific encounters are quite common and arise when colonies founded in the same tree meet. When this occurs, the number of soldiers per worker present in a colony is a key factor that determines the survival success of a colony's reproductives (Korb and Roux, in prep.). Thus, intraspecific competition (and probably also congeneric competition with *C. domesticus*) seems to be the prime factor selecting for the maintenance of soldiers in *C. secundus*.

That there is selection on the occurrence of soldiers, despite a lack of predation, is supported by a morphometrical study (Roux et al., in prep.). The dimensions of the plug-shaped soldier heads vary among colonies, but this variation correlates with the variation in gallery dimensions. Colonies with soldiers that have larger head widths inhabit nests with larger gallery dimensions, while this does not hold, for example, for soldier body size. This correlation is also not just a consequence of soldiers being the constructors of the galleries because they are excavated by the workers. Furthermore, the variability in the dimensions of defensive traits of soldiers' morphology is consistently lower than those of non-defensive traits. This together with negative allometric slopes of defensive traits suggests that the defensive morphology of soldiers is indeed under stabilizing selection.

7.4 Relevance of the Case Study: Comparison with Other Termites

7.4.1 Workers

Many of the features of *C. secundus* sociobiology are likely to apply to other log termites that live in a confined piece of wood (about 17% of all termite species; Kambhampati and Eggleton 2000) because, like *C. secundus*, they all have the following traits:

(a) *Flexible development*: workers seem to be able to explore all caste options (see above) (Shellman-Reeve 1997; Roisin 2000; Thorne and Traniello 2003) and all these species are characterized by a high potential of workers to develop into neotenic replacement reproductives (Myles 1999), thus having the chance to inherit the natal breeding position.

(b) *Well-protected nest*: individuals are well sealed off against predators and extremes of climatic variation. Thus, survival rates in the nest are high.
(c) *No foraging trips*: living inside their food again improves survival and also reduces the value of care for other nestmates as all individuals have easy access to food.
(d) *Predictable resources*: the quality of the nest can be quickly and reliably measured. Vibrations generated by wood gnawing are the cues used to assess food availability (Lenz 1994; Evans et al. 2005). Thus, individuals have the information necessary to adaptively adjust their development to potential reproductive opportunities.
(e) *Predictable change in resource availability*: the quality, and thus the breeding opportunities, in the natal nest changes predictably. All colonies inevitably experience a shortage of the non-replenishable food source and thus the disappearance of their nest. This together with the reliability of the cues to measure nest size seems to select for a high developmental plasticity, because both reliable cues and predictability are parameters selecting for plastic development (Nijhout 2003). This may explain the correlation between the wood-dwelling life type in OP termites and their flexible caste development (Korb and Katrantzis 2004).

These shared features suggest that the workers of all wood-dwelling termites are in a similar situation to those in *C. secundus* that do not seem to be true workers at all. In support of this, reports exist for many species that colonies with low food availability produce more alates than colonies with high resources (Buchli 1958; La Fage and Nutting 1978; Lenz 1976, 1994; Korb and Lenz 2004).

7.4.2 Soldiers

The results from *C. secundus* also seem to apply more widely to the soldiers in other termites. Intraspecific competition seems to form a major threat to many lower termites with evidence from genetic studies that colony fusion is common in several species (Clement 1986; Bulmer et al. 2001; Goodisman and Crozier 2002; DeHeer and Vargo 2004). This suggests that colonies do not necessarily consist of closely related nestmates, as has generally been assumed and that competition both within and between termite species is very important. Support for the role of intraspecific competition in the occurrence of soldiers was recently provided by Thorne et al. (2003), who found that reproductive soldiers in *Zootermopsis nevadensis* are more common in colonies with a fusion history. These reproductive soldiers are a peculiarity of the family Termopsidae and are unlikely to be representative for termite soldiers in general (Roisin 2000). They are not individuals with a reduced reproductive capacity such as the sterile soldiers of other termites. Rather they are neotenic reproductives with soldier-like traits and should therefore better be called soldier-like neotenics/reproductives (Thorne 1997; Roisin 2000). Nevertheless, the *Zootermopsis* study shows the importance of intraspecific encounters as a selective force for the development of defensive traits; in this case of reproductives which after a fusion event seem to have a higher chance to inherit the colony as replacement reproductive (Thorne et al. 2003). This links back to the occurrence of workers in *C. secundus*: in both cases, in *C. secundus* and *Z. nevadensis*, inheritance opportunities, and thus direct breeding benefits in the nest, seem to be the driving forces for their occurrence (Myles 1988). Indeed, such selection for the soldier caste was probably also important ancestrally because conspecific competition is likely to predate the major termite predators of extant termites (ants and mammals).

7.5 Outline for the Evolutionary Transitions in Termites Eusociality

The view that OP termites with their flexible development reflect the ancestral state in termite evolution has been challenged (Thompson et al. 2000) but the molecular data currently still fail to resolve the relevant phylogenetic relationships (Fig. 7.1; Grandcolas and D'Haese 2002; Thompson et al. 2004; Inward et al. 2007b). Yet, other results leave less doubt about the basal position of the wood-dwelling life type (Parmentier and Roisin 2003; Parmentier 2006; Korb, in press). Therefore, I use it here to develop a tentative outline for the evolutionary transitions of eusociality in the termites (Fig. 7.4).

The hemimetabolous subsocial termite ancestor, like the woodroach *Cryptocercus punctulatus*, most likely lived inside wood that served as nest and food (e.g., Nalepa 1994; Thorne 1997; Fig. 7.4 Ancestor). Such a nesting type provided (a) a long-lasting stabile, but non-replenishable food source, (b) a safe nest that is largely protected against predators and hostile environmental conditions, and (c) low-quality food that results in slow development and which can only be exploited with the help of symbionts. Thus the nest represented a safe haven compared to the hostile and uncertain environment encountered during dispersal. Such conditions select for alternative reproductive tactics, namely staying in the nest to inherit the colony, as is also found in many aphids and thrips (see Chaps. 2, 3, 12; Stern and Foster 1997). These conditions also favor a flexible development (Fig. 7.4, stage I: Evolution of staying immatures): Firstly, it is important to be able to replace the reproductives immediately after their death (evolution of neoteny) and, secondly, to react to changing nest conditions that will inevitably occur when the food is exploited or when environmental hazards like thunderstorms suddenly destroy the nest (evolution of different molting types). Functional reproductives should not be killed as they are the parents of staying individuals; so kin selection is a very important component in this system as it reduces conflicts and guarantees group stability. Thirdly, as group size increases the chances to inherit decrease and competition among siblings for the breeding position increases. This should select for some

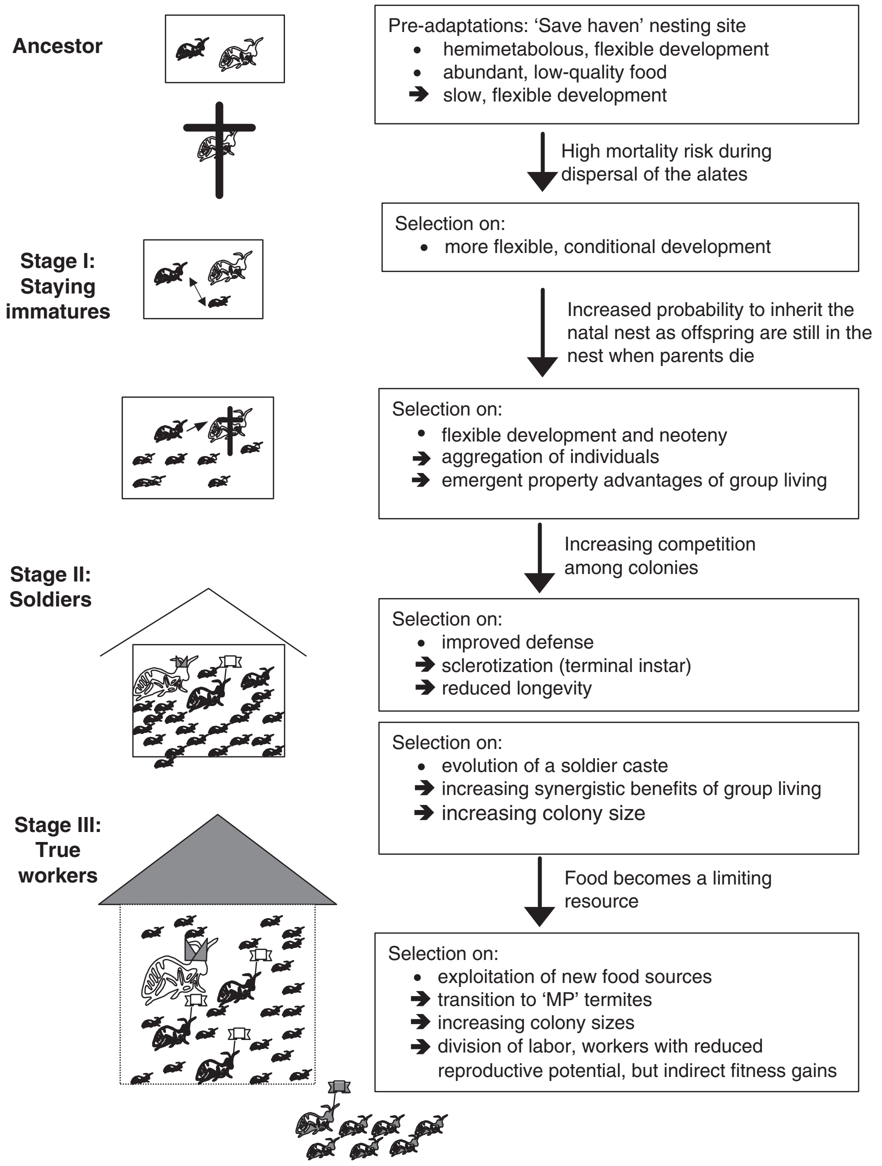

Fig. 7.4 Scenario for the evolution of termite eusociality. For further information see text

individuals leaving the nest even if it is still long-lasting. Those leaving individuals should be the most competent to do so (for a detailed discussion see Korb and Schmidinger 2004). The competence of different individuals may be 'tested' by developmental deadlines; individuals failing to reach them in time have to develop back to be 'tested' again for the next nuptial flight (see above). Thus, this evolutionary stage (Fig. 7.4, stage I) would largely correspond to the 'worker' stage in *C. secundus*. Note that at this stage there is no help in raising siblings because this is unnecessary; as hemimetabolic insects, the young larvae are quite independent and food is easily accessible to everybody.

The result of this evolutionary step would be family groups, with group sizes depending on wood size and inheritance opportunities. At this stage, living in a group may offer additional advantages such as improved thermoregulation, parasite resistance, or construction capacities (Rosengaus et al. 1998; Rosengaus and Traniello 2001; Traniello et al. 2002; Korb 2003; Korb and Heinze 2004). Also division of labor may evolve. All these advantages may offer further incentives for staying at the nest. On the other hand, intraspecific competition with colonies that had been founded in the same tree will increase as the groups are long-lived, and the likelihood increases that they will meet because of nest expansion. This would strongly select for a defensive morph, which may have a reproductive potential, like the soldier-like neotenics in the Termopsidae (Thorne et al. 2003), or which may not, like soldiers in all other termites and in the aphids and thrips (see Chaps. 2 and 3) (Fig. 7.4, stage II: Evolution of soldiers). As there is strong selection for a defensive morph to be sclerotized, these individuals lose the capability to molt. Therefore the defensive morph presents a terminal stage, again either a fertile soldier-like neotenic or a sterile soldier. Why soldier-like reproductives are limited to the Termopsidae and soldiers of all other termites are sterile remains an open question. Defenders, however, make up only a low proportion of the group as the main protection against predators is provided by the nest (Noirot and Darlington 2000). In the case of soldiers, these groups can now be considered eusocial insect colonies similar to those represented by the recent wood-dwelling termites in which soldiers make up $<5\%$ of all colony members (Haverty 1977; Henderson 1998). Due to their small numbers, the indirect fitness gains of sterile soldiers are high (Roux and Korb 2004), compensating for the high costs of the defensive task.

At this evolutionary stage (Fig. 7.4, stage II), the limiting factor for the colonies becomes the restricted amount of food, set by the nest size, and resulting in increasing intraspecific competition. This constitutes a strong selection pressure to exploit new food sources, also offering the possibility to choose higher-quality food that allows faster development (e.g., selection of partly decayed wood that is easier to digest and where the inhabiting microorganisms present an additional nitrogen-source). However, along with the exploitation of new food sources comes the cost of increased predation pressure during foraging. This has the consequence that getting food is no longer cost-free and not easily accessible for all termites, especially for the young instars and the reproductives. Now brood care becomes obligatory and it is associated with increased mortality costs during foraging. These costs are compensated by the indirect fitness gains of raising siblings (Fig. 7.4, stage III: Evolution of true worker). Whether the step to sibling brood care only evolved at this late stage or whether some OP termites already show brood care, because it enhances development, needs to be investigated. With the exploitation of new, better-quality resources colony size could increase, leading to an effective division of labor with several castes specializing on different colony tasks. The highest sophistication in recent termites occurs in the Termitidae, and especially in the fungus-growing termites (Macrotermitinae), where up to four different sterile castes exist in addition to temporal polyethism within castes (Traniello and Leuthold 2000). The Termitidae represent those termites that are evolutionary and ecologically the most successful, constituting about 75% of all recent species (Eggleton 2000) and being the most important decomposers in many tropical ecosystems (Deshmukh 1989; Bignell and Eggleton 2000).

In summary, current studies suggest that, in contrast to previous assumptions, the first critical step to eusociality in termites was probably not offspring staying at home to raise siblings but rather individuals staying to inherit the colony because the nest is a safe haven (see also Myles 1988). From there, the evolution of soldiers rather than workers may have marked the initial transition to eusociality. Furthermore, it seems that intraspecific competition rather than predation pressure was the prime factor favoring the evolution of these soldiers.

7.6 Comparison with Cooperatively Breeding Vertebrates

The potential importance of the role of inheritance in the evolution of termite eusociality draws comparison with data from cooperatively breeding vertebrates. Here, the role of ecological factors has also been emphasized. The three most influential hypotheses to explain the evolution of helping behavior in vertebrates are: (a) ecological constraint hypothesis which argues that helping occurs because opportunities for independent breeding are limited or risky because of low availability of nesting sites or a high risk of mortality during dispersal (Emlen 1991, 1997); (b) life-history hypothesis that emphasizes that certain life-history characteristics of a species limit the opportunity for independent breeding (Arnold and Owens 1998); (c) benefit of philopatry hypothesis that stresses the long-term direct benefits of staying at the natal nest, such as inheritance of the natal territory (Stacey and Ligon 1991). In vertebrates, the life-history hypothesis seems to be most successful in explaining interspecific variation in the occurrence of cooperative breeding, while the ecological constraint hypothesis is strongly supported by intraspecific studies (Hatchwell and Komdeur 2000). Besides, however, several examples also show the importance of long-term direct benefits of nest inheritance (Heinsohn and Legge 1999).

The termite studies support the benefit of philopatry hypothesis and the ecological constraints hypothesis, the latter however with restrictions (see below). According to the results for *C. secundus*, in wood-dwelling termites the opportunity of the workers to become neotenic replacement reproductives that inherit the nest seem to be the major driving force for staying at the nest as the opportunities for successful independent founding are difficult. Similar to some birds in which individuals stay at the nest and either do not help (Veltman 1989; Magrath and Whittingham 1997; Boland et al. 1997) or help, but raise unrelated offspring (Reyer et al. 1986; Dunn et al. 1995), *C. secundus* workers stay to gain direct fitness benefits. Why the termite workers do not work, although they would have the opportunity to help relatives and increase their inclusive fitness, could be explained by several factors, some of which are also proposed for the bird examples (Heinsohn and Legge 1999): (a) The costs of helping may be too high compared to the indirect benefit gains. Here a recently developed model provides interesting results (Jeon and Choe 2003). Totipotency delays the evolution of costly helping, as the costs in direct reproduction are high. This model's predictions match with the findings in termites with altruistic helping occurring in MP species. (b) There might be no need to help (Heinsohn and Legge 1999). Probably this applies to wood-dwelling termites. They live inside their food, so costly foraging and food provisioning is not necessary. Being hemimetabolous insects, the young instars are quite independent and do not need to be cared for, except for infestation with gut symbionts which is not costly. Similarly in some cooperatively breeding birds it has been shown that helping is associated with the need for help and that it can be a flexible response (Reyer and Westerterp 1985). A lack of need for help in wood-dwelling termites ultimately means a low benefit of helping and may explain why it is not evolutionary favored. (c) Under some conditions individuals may have to pay through helping in order to be allowed to stay at the nest (Kokko et al. 2002). This can be selected even if it is not optimal for the helpers to help, but when 'pay to stay' is better than not paying and leaving the nest. Such conditions occur when the nest is a very valuable resource and staying of individuals causes costs to the dominant breeders, especially when relatedness among helpers and breeders is low. In wood-dwelling termites this would be the case for fused colonies in which unrelated individuals stay and consume the non-replenishable food resource. Yet, I do not have any indications that *C. secundus* workers have to pay under such conditions (Korb, unpubl. data).

The ecological constraint hypothesis applies to *C. secundus* as well because dispersal is very costly. However, appropriate nest sites are not in limited supply. The stochasticity of the habitat (e.g., thunderstorms that suddenly and with a sufficient frequency create new patches of dead wood) prevents habitat saturation. Furthermore, in contrast to cooperatively breeding vertebrates, wood-dwelling termites have no opportunity to check the availability of nesting/breeding vacancies as they never leave the nest before the nuptial flight (Roisin 1994, 1999). Thus, perceived ecological constraints are constant for termites. Apart from these confinements, however, ecological constraints are important as they determine the costs of philopatry. Other factors being equal, if ecological constraints on founding a new colony are not very restrictive, then the benefits of philopatry need to be high to favor staying at the nest (Koenig et al. 1992; Kokko and Lundberg 2001). So the ecological constraints and the benefits of philopatry hypotheses reflect two sides of one coin. Hence, a combined approach that considers all factors is necessary to understand the evolution and maintenance of social life (Hatchwell and Komdeur 2000; Pen and Weissing 2000; Kokko and Ekman 2002). Such a unifying approach could be provided by reproductive skew theory, which aims to explain the extent to which reproduction is biased within animal societies by identifying the role of ecological, genetic, and social factors (Vehrencamp 1983; Reeve and Ratnieks 1993; Keller and Reeve 1994; Johnstone 2000). The tremendous development of skew theory has lead to many new models in recent years, but their relevance in nature still needs to be tested.

7.7 Conclusions

Ecological factors play a central role in the evolution of group nesting in termites as well as in vertebrates. This suggests that rarity of eusociality outside the insect world is not explained by differences in relatedness but rather the tendency to become eusocial might be linked to life-history traits that differ fundamentally between groups. Of course, however, this is not to say that relatedness, which is a requirement for altruism and eusociality, is not important. It simply means that *differences* in relatedness between different groups may not be the key factor in determining a predisposition to eusociality.

To the extent that it resembles the wood-dwelling termites, the first step in the scenario for the evolution of termite eusociality was very similar to many cooperative breeding vertebrates. Ecological constraints and benefits of philopatry favor staying at the nest. One fundamental difference though is the larger group sizes in the termites. This may, therefore, represent a key prerequisite for the evolution of eusociality as a loss in direct reproduction can be offset by indirect fitness gains through: (a) defending a large group of relatives instead of few siblings; (b) helping to raise many siblings which is only possible if the mother has a high fecundity; (c) the occurrence of emergent properties that add further incentives for staying in the group (Fig. 7.5).

Accordingly, two prerequisites, which birds and mammals usually lack, are necessary for the transition to eusociality: (a) a high fecundity and (b) large numbers of offspring that can stay at the nest and are not ‘forced’ to leave because there is no competition at the nest for food (no local resource competition) (Fig. 7.5). Under most conditions, offspring are selected to disperse from the nest to avoid competition among siblings (Hamilton and May 1977). Two mechanisms can overrule this: a high abundance of food at the nest that lasts reasonably long (i.e., for at least two generations that can co-exist) and/or high ecological constraints which make dispersal difficult. The latter is commonly included in many models on the evolution of sociality (e.g., see above ecological constraint hypothesis, reproductive skew models; Johnstone 2000), while the former is often only implicitly assumed. The comparison with termites, therefore, suggests that the general lack of eusociality in vertebrates might be because they can only achieve small families due to their low fecundity and the difficulty to have enough food to overcome local resource competition for more than two generations to coexist as individuals are large and rather long-lived compared to their food source (Fig. 7.5). Thus, the finally limiting trait accounting for the rarity of eusociality in birds and mammals would be their body size. Correspondingly, the only groups in which eusociality occurs are rodents, which are comparatively small mammals with a short generation time, high fecundity and long-lasting food sources (see Chap. 10).

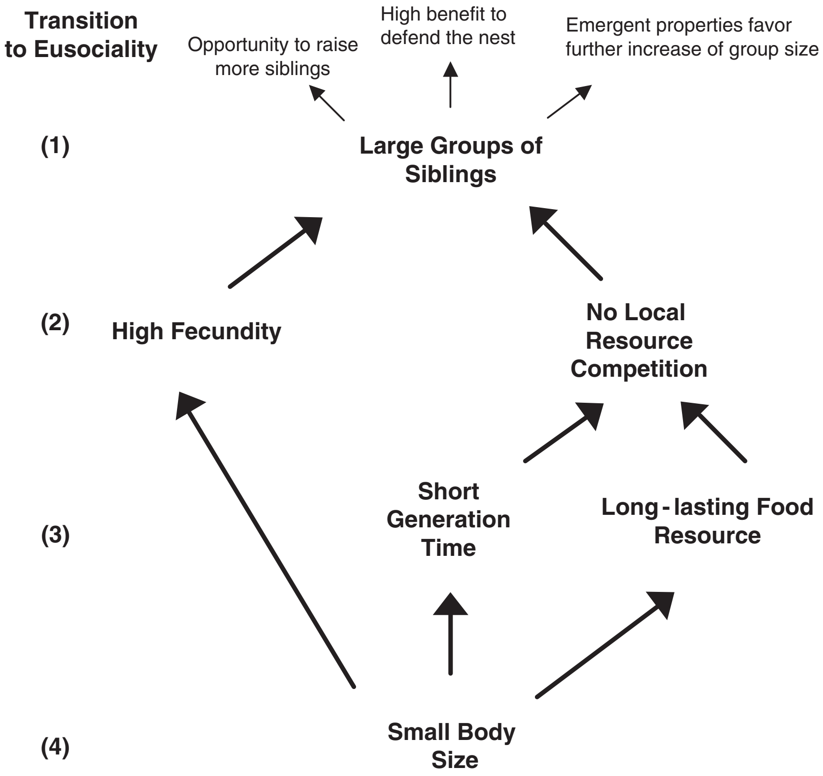

Fig. 7.5 Supposed life-history prerequisites for the evolution of eusociality. The transition to eusociality can only evolve if large groups of siblings can co-exist in the natal nest (*1*). However, for the co-existence of many individuals in large groups several life-history traits and conditions are necessary: high fecundity and a lack of local resource competition (*2*) which depends on a short generation time in relation to a long-lasting food source that provides enough food for at least two generations (*3*). All these traits link back to a small body size (*4*). In mammals and birds, their comparatively large body sizes cause low fecundity, long generation times and a high demand for food (the latter two resulting in local resource competition and dispersal from the natal nest) which prevents the occurrence of large groups of siblings, a necessary prerequisite for the transition to eusociality

Acknowledgements I wish to thank K. Foster and J. Fields for helpful comments on the MS and improvements of the English. I gratefully acknowledge an Emmy Noether fellowship from the German Science Foundation (DFG, KO1895/2) and the Institute for Advanced Studies in Berlin for funding.

References

Abe T (1987) Evolution of life types in termites. In: Kawano S, Connell JH, Hidaka T (eds) Evolution and coadaptation in biotic communities. University of Tokyo Press, Tokyo, pp 125–148

Abe T (1990) Evolution of the worker caste in termites. In: Veeresh GK, Mallik B, Viraktamath CA (eds) Social insects and the environments. Oxford & IBH, New Delhi, pp 29–30

Abe T, Darlington JPEC (1985) Distribution and abundance of a mound-building termite, *Macrotermes michaelseni*, with special reference to its subterranean colonies and ant predators. Physiol Ecol Jpn 22:59–74

Arnold KE, Owens IPF (1998) Cooperative breeding in birds: a comparative analysis of the life-history hypothesis. Proc R Soc Lond Ser B 265:739–745

Atkinson L, Adams ES (1997) The origins and relatedness of multiple reproductives in colonies of the termite *Nasutitermes corniger*. Proc R Soc Lond B 264:1131–1136

Bartz SJ (1979) Evolution of eusociality in termites. Proc Natl Acad Sci USA 76:5764–5768

Bignell DE, Eggleton P (2000) Termites in ecosystem. In: Abe T, Bignell DE, Higashi M (eds) Termites: evolution, sociality, symbioses, ecology. Kluwer Academic Publishers, Dordrecht, pp 363–388

Bodot P (1961) La destruction des termitiéres de *Bellicositermes natalensis* par une fourmi: *Dorylus (Typhlopone) dentifons* Wasman. C R Acad Sci 253:3053–3054

Boland CRJ, Heinsohn R, Cockburn A (1997) Experimental manipulation of brood reduction and parental care in cooperatively breeding white-winged choughs. J Anim Ecol 66:683–691

Bourke ARG, Franks NR (1995) Social evolution in ants. Princeton University Press, Princeton

Brown JL (1987) Helping and communal breeding in birds. Princeton University Press, Princeton

Buchli HR (1958) L'origine des castes et les potentialités ontogéniques des termites européens du genre *Reticulitermes* Holmgren. Ann Sci Nat Zool 11:267–429

Bulmer MS, Adams ES, Traniello JFA (2001) Variation in colony structure in the subterranean termite *Reticulitermes flavipes*. Behav Ecol Sociobiol 49:236–243

Clement J-L (1986) Open and closed societies in *Reticulitermes* termites (Isoptera, Rhinotermitidae): geographical and seasonal variations. Sociobiology 11:311–323

Crozier RH, Luykx PD (1985) The evolution of termite eusociality is unlikely to have been based on a haplodiploid analogy. Am Nat 126:867–869

Crozier RH, Pamilo P (1996) Evolution of social insect colonies. Oxford University Press, Oxford

Darlington JPEC (1979) Populations of nests of *Macrotermes* species in Kajiado and Bissell. Annual Report of the International Centre of Insect Physiology and Ecology 6:22–23

Darlington JPEC (1986) Attacks by doryline ants and termite nest defences (Hymenoptera; Formicidae; Isoptera; Termitidae). Sociobiology 11:189–200

Darlington JPEC, Zimmermann PR, Wandiga SO (1992) Populations in nests of the termite *Macrotermes jeanneli* in Kenya. J Trop Ecol 8:73–85

DeHeer CJ, Vargo EL (2004) Colony genetic organization and colony fusion in the termite *Reticulitermes flavipes* as revealed by foraging patterns over time and space. Mol Ecol 13: 431–441

Deshmukh I (1989) How important are termites in the production ecology of African savannas? Sociobiology 15:155–168

Dunn PO, Cockburn A, Mulder RA (1995) Fairy-wren helpers often care for young to which they are unrelated. Proc R Soc London Ser B 259:339–343

Eggleton P (2000) Global patterns of termite diversity. In: Abe T, Bignell DE, Higashi M (eds) Termites: evolution, sociality, symbioses, ecology. Kluwer Academic Publishers, Dordrecht, pp 25–52

Eggleton P (2001) Termites and trees: a review of recent advances in termite phylogenetics. Insectes Soc 48:187–193

Emlen ST (1991) Evolution of cooperative breeding in birds and mammals. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Blackwell, Oxford, pp 301–337

Emlen ST (1997) Predicting family dynamics in social vertebrates. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Blackwell Scientific, Oxford, pp 228–353

Evans TA, Lai JCS, Toledano E, McDowall L, Rakotonarivo S, Lenz M (2005) Termite assess wood size by using vibration signals. Proc Natl Acad Sci USA 102:3732–3737

Gerber C, Badertscher S, Leuthold RH (1988) Polyethism in *Macrotermes bellicosus* (Isoptera). Insectes Soc 35:226–240

Goodisman MAD, Crozier RH (2002) Population and colony genetic structure of the primitive termite *Mastotermes darwiniensis*. Evolution 56:70–83

Gotwald WH (1995) Army ants: the biology of social predation. Cornell University Press, Cornell

Grandcolas P (1994) Phylogenetic systematics of the subfamily Polyphaginae, with the assignment of *Cryptocercus* Scudderm 1862 to this taxon (Blattaria, Blaberoidea, Polyphagidae). Syst Entomol 19:145–158

Grandcolas P, D'Haese C (2002) The origin of a 'true' worker caste in termites: phylogenetic evidence is not decisive. J Evol Biol 15:885–888

Grassé PP, Noirot C (1947) Le polymorphisme social du termite a cou jaune (*Kalotermes flavicollis* F.). Les faux-ouvriers ou pseudergates et les mues regressives. Compt Rend Acad Sci 214:219–221

Grassé PP (1984) Termitologia, vol. 2. Masson, Paris

Gross MR (1996) Alternative reproductive strategies and tactics: diversity within sexes. Trends Ecol Evol 11:92–98

Hahn PD, Stuart AM (1987) Sibling interactions in two species of termites: a test of the haplodiploid analogy (Isoptera: Kalotermitidae; Rhinotermitidae). Sociobiology 13:83–92

Hamilton WD (1964) The genetic evolution of social behavior I, II. J Theoret Biol 7:1–52

Hamilton WD (1972) Altruism and related phenomena, mainly in social insects. Ann Rev Ecol Syst 3:192–232

Hamilton WD, May RM (1977) Dispersal in stable habitats. Nature 269:578–581

Hatchwell BJ, Komdeur J (2000) Ecological constraints, life-history traits and the evolution of cooperative breeding. Anim Behav 59:1079–1086

Haverty MI (1977) The proportion of soldiers in termite colonies: a list and a bibliography (Isoptera). Sociobiology 2:199–216

Heinsohn R, Legge S (1999) The cost of helping. Trends Ecol Evol 14:53–57

Henderson G (1998) Primer pheromones and possible soldier caste influence on the evolution of sociality in lower termites. In: Vandermeer R, Breed KMD, Espelie KE, Winston ML (eds) Pheromone communication in social insects. Westview Press, Boulder, pp 314–330

Hennig W (1981) Insect phylogeny. Wiley, New York

Higashi M, Yamamura N, Abe T, Burns TP (1991) Why don't all termite species have a sterile worker caste? Proc R Soc Lond Ser B 246:25–30

Higashi M, Yamamura N, Abe T (2000) Theories on the sociality of termites. In: Abe T, Bignell DE, Higashi M (eds) Termites: evolution, sociality, symbioses, ecology. Kluwer Academic Publishers, Dordrecht, pp 169–187

Husseneder C, Brandl R, Epplen JT, Kaib M (1999) Within colony relatedness in a termite species: genetic roads to eusociality? Behaviour 136:1045–1063

Inward D, Beccaloni G, Eggleton P (2007a) Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. Biol Lett 3:331–335

Inward D, Vogler AP, Eggleton P (2007b) A comprehensive phylogenetic analysis of termites (Isoptera) illuminates key aspects of their evolutionary biology. Mol Phyl Evol 44:953–967

Jeon J, Choe JC (2003) Reproductive skew and sterile castes. Am Nat 161:206–224

Johnstone RA (2000) Models of reproductive skew: a review and synthesis. Ethology 106:5–26

Kambhampati S (1995) A phylogeny of cockroaches and related insects based on DNA sequence of mitochondrial ribosomal RNA genes. Proc Natl Acad Sci USA 92:2017–2020

Kambhampati S, Eggleton P (2000) Taxonomy and phylogeny of termites. In: Abe T, Bignell DE, Higashi M (eds) Termites: evolution, sociality, symbioses, ecology. Kluwer Academic Publishers, Dordrecht, pp 1–23

Keller L, Reeve HK (1994) Partitioning of reproduction in animal societies. Trends Ecol Evol 9:98–102

Klass K-D (1995) Die Phylogenie der Dictyoptera. PhD Thesis, Fakultät für Biologie, Ludwig Maximilians Universität München, München

Koenig WD, Pitelka FA, Carmen WJ, Mumme RL, Stanback MT (1992) The evolution of delayed dispersal in cooperative breeders. Q Rev Biol 67:111–150

Kokko H, Lundberg P (2001) Dispersal, migration, and offspring retention in saturated habitats. Am Nat 157:188–202

Kokko H, Ekman J (2002) Delayed dispersal as a route to breeding: territorial inheritance, safe havens, and ecological constraints. Am Nat 160:468–484

Kokko H, Johnstone RA, Wright J (2002) The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay? Behav Ecol 13:291–300

Korb J (1997) Lokale und regionale Verbreitung von *Macrotermes bellicosus* (Isoptera; Macrotermitinae): Stochastik oder Deterministik? W&T Verlag, Berlin

Korb J (2003) Thermoregulation and ventilation of termite mounds. Naturwissenschaften 90:212–219

Korb J (2005) Regulation of sexual development in the basal termite *Cryptotermes secundus*: mutilation, pheromonal manipulation or honest signal? Naturwissenschaften 92:45–49

Korb J (2006) Limited food induces nepotism in drywood termites. Biol Lett 2:364–366

Korb J (2007) Workers of a drywood termite do not work. Frontiers Zool 4:7

Korb J (in press) Termites. Curr Biol: in press

Korb J, Fuchs A (2006) Termites and mites - adaptive behavioural responses to infestation? Behaviour 143:891–907

Korb J, Heinze J (2004) Multilevel selection and social evolution of insect societies. Naturwissenschaften 91:291–304

Korb J, Katrantzis S (2004) Influence of environmental conditions on the expression of the sexual dispersal phenotype in a lower termite: implications for the evolution of workers in termites. Evol Dev 6:342–352

Korb J, Lenz M (2004) Reproductive decision-making in the termite *Cryptotermes secundus* (Kalotermitidae) under variable food conditions. Behav Ecol 15:390–395

Korb J, Linsenmair KE (1999) Reproductive success of *Macrotermes bellicosus* (Isoptera, Macrotermitinae) in two neighbouring habitats. Oecologia 118:183–191

Korb J, Linsenmair KE (2001) The causes of spatial patterning of mounds of a fungus-cultivating termite: results from nearest-neighbour analysis and ecological studies. Oecologia 127:324–333

Korb J, Schmidinger S (2004) Help or disperse? Cooperation in termites influenced by food conditions. Behav Evol Sociobiol 56:89–95

Korb J, Schneider K (2007) Does kin structure explain the occurrence of workers in a lower termite? Evol Ecol 27:817–828

Kristensen NP (1991) Phylogeny of extant hexapods. In: The insects of Australia. CSIRO & Melbourne University Press, Carleton, pp 125–140

Lacy RC (1980) The evolution of eusociality in termites: a haplodiploid analogy? Am Nat 116:449–451

La Fage JP, Nutting WL (1978) Nutrient dynamics of termites. In: Brain MV (ed) Production ecology of ants and termites. Cambridge University Press, Cambridge, pp 165–232

Leinaas HP (1983) A haplodiploid analogy in the evolution of termite eusociality? reply to Lacy. Am Nat 121:302–304

Lenz M (1976) The dependence of hormone effects in termite caste determination on external factors. In: Lüscher M (ed) Phase and caste determination in insects: endocrine aspects. Pergamon Press, Oxford, pp 73–89

Lenz M (1994) Food resources, colony growth and caste development in wood-feeding termites. In: Hunt JH, Nalepa CA (eds) Nourishment and evolution in insect societies. Westview Press, Boulder, pp 159–209

Lepage M, Darlington JPEC (2000) Population dynamics of termites. In: Abe T, Bignell DE, Higashi M (eds) Termites: evolution, sociality, symbioses, ecology. Kluwer Academic Publishers, Dordrecht, pp 333–362

Leponce M, Roisin Y, Pasteels JM (1997) Structure and dynamics of the arboreal termite community in New Guinean coconut plantations. Biotropica 29:193–203

Levieux J (1983) Feeding strategies of ants in different West African savannas. In: Jaisson P (ed) Social insects in the tropics, vol.2. Université de Paris-Nord, Paris, pp 245–252

Lo N, Kitade O, Miura T, Constantino R, Matsumoto T (2004) Molecular phylogeny of the Rhinotermitidae. Insectes Soc 51:365–371

Longhurst C, Howse PE (1979) Foraging, recruitment and emigration in *Megaponera foetens* (Fab.) (Hym., Formicidae) from the Nigerian Guinea savanna. Insectes Soc 26:204–215

Longhurst C, Baker R, Howse PE (1979) Termite predation by *Megaponera foetens* (Fab.) (Hymenoptera: Formicidae): coordination of raids by glandular secretions. J Chem Ecol 5:703–719

Lüscher M (1974) Kasten und Kastendifferenzierung bei niederen Termiten. In: Schmidt GH (ed) Sozialpolymorphismus bei Insekten. Wissenschaftliche Verlagsgesellschaft, Stuttgart, pp 694–739

Luykx PD, Syren RM (1979) The cytogenetics of *Incisitermes schwarzi* and other Florida termites. Sociobiology 4:191–209

Lys JA, Leuthold RH (1991) Task-specific distribution of the two worker castes in extranidal activities in *Macrotermes bellicosus* (Smeathman): observation of behaviour during food acquisition. Insectes Soc 38:161–170

Magrath RD, Whittingham LA (1997) Subordinate males are more likely to help if unrelated to the breeding female in cooperatively breeding white-browed scrubwrens. Behav Ecol Sociobiol 41:185–192

Maynard Smith J (1964) Group selection and kin selection. Nature 201:1145–1147

Miller LR, Paton R (1983) *Cryptotermes* in mangroves in the Northern Territory (Isoptera: Kalotermitidae). J Aust Ent Soc 22:189–190

Myles TG (1986) Evidence of parental and-or sibling manipulation in three species of termites in Hawaii USA Isoptera. Proc Hawaiian Ento Soc 27:129–140

Myles TG (1988) Resource inheritance in social evolution from termite to man. In: Slobodchikoff CN (ed) The ecology of social behavior. Academic Press, New York, pp 379–423

Myles TG, Nutting WL (1988) Termite eusocial evolution: a re-examination of Bartz's hypothesis and assumptions. Q Rev Biol 63:1–24

Myles TG (1999) Review of secondary reproduction in termites (Insecta: Isoptera) with comments on its role in termite ecology and social evolution. Sociobiology 33:1–88

Nalepa CA (1994) Nourishment and the origin of termite eusociality. In: Hunt JH, Nalepa CA (eds) Nourishment and evolution in insect societies. Westview Press, Boulder, pp 57–104

Nalepa CA, Bandi C (2000) Characterizing the ancestors: a paedomorphosis and termite evolution. In: Abe T, Bignell DE, Higashi M (eds) Termites: evolution, sociality, symbioses, ecology. Kluwer Academic Publishers, Dordrecht, pp 53–75

Nijhout HF (2003) Development and evolution of adaptive polyphenisms. Evol Dev 5:9–18

Noirot C (1990) Sexual castes and reproductive strategies in termites. In: Engels W (ed) Social insects: an evolutionary approach to castes and reproduction. Springer, Berlin Heidelberg New York, pp 5–35

Noirot C, Darlington JPEC (2000) Termite nests: architecture, regulation and defence. In: Abe T, Bignell DE, Higashi M (eds) Termites: evolution, sociality, symbioses, ecology. Kluwer Academic Publishers, Dordrecht, pp 121–140

Noirot C, Pasteels JM (1987) Ontogenetic development and the evolution of the worker caste in termites. Experientia 43:851–860

Nutting WL (1969) Flight and colony foundation. In: Krishna K, Weesner FM (eds) Biology of termites, vol. I. Academic Press, New York, pp 233–282

Parmentier D (2006) Developmental flexibility and evolution of the worker caste in termites. PhD Thesis, Université Libre de Bruxelles

Parmentier D, Roisin Y (2003) Caste morphology and development in *Termitogeton* nr. *planus* (Insecta, Isoptera, Rhinotermitidae). J Morph 255:69–79

Pen I, Weissing FJ (2000) Towards a unified theory of cooperative breeding: the role of ecology and life history re-examined. Proc R Soc Lond Ser B 267:2411–2418

Queller DC, Strassmann JE (1998) Kin selection and social insects. Bioscience 48:165–175

Reeve HK, Ratnieks FLW (1993) Queen-queen conflict in polygynous societies: mutual tolerance and reproductive skew. In: Keller L (ed) Queen number and sociality in insects. Oxford University Press, Oxford, pp 45–85

Reyer H-U, Westerterp K (1985) Parental energy expenditure: a proximate cause of helper recruitment in the pied kingfisher (*Ceryle rudis*). Behav Ecol Sociobiol 17:363–369

Reyer H-U, Dittami JP, Hall MR (1986) Avian helpers at the nest: are they psychologically castrated? Ethology 71:216–228

Roisin Y (1994) Intragroup conflicts and the evolution of sterile castes in termites. Am Nat 143:751–765

Roisin Y (1999) Philopatric reproduction, a prime mover in the evolution of termite sociality? Insectes Soc 46:297–305

Roisin Y (2000) Diversity and evolution of caste patterns. In: Abe T, Bignell DE, Higashi M (eds) Termites: evolution, sociality, symbioses, ecology. Kluwer Academic Publishers, Dordrecht, pp 95–119

Roisin Y (2001) Caste sex ratios, sex linkage, and reproductive strategies in termites. Insectes Soc 48:224–230

Roonwal ML (1970) Termites of the oriental region. In: Krishna K, Weesner FM (eds) Biology of termites, vol. II. Academic Press, New York, pp 315–391

Rosengaus RB, Maxmen AB, Coates LA, Traniello JFA (1998) Disease resistance: a benefit of sociality in the dampwood termite *Zootermopsis angusticollis* (Isoptera: Termopsidae). Behav Ecol Sociobiol 44:125–134

Rosengaus RB, Traniello JFA (2001) Disease susceptibility and the adaptive nature of colony demography in the dampwood termite *Zootermopsis angusticollis*. Behav Ecol Sociobiol 50:546–556

Roux EA, Korb J (2004) Evolution of eusociality and the soldier caste in termites: a validation of the intrinsic benefit hypothesis. J Evol Biol 17:869–875

Shellman-Reeve JS (1997) The spectrum of eusociality in termites. In: Choe JC, Crespi BJ (eds) The evolution of social behaviour in insects and arachnids. Cambridge University Press, Cambridge, pp 52–93

Shellman-Reeve JS (2001) Genetic relatedness and partner preference in a monogamous, wood-dwelling termite. Anim Behav 61:869–876

Soki K, Josens G, Loreau M (1996) Growth and demography of *Cubitermes speciosus* mounds (Isoptera, Termitidae). Insectes Soc 43:189–200

Stacey PB, Ligon JD (1991) The benefits of philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size. Am Nat 137:831–846

Stern DL, Foster WA (1997) The evolution of sociality in aphids : a clone's-eye view. In: Choe JC, Crespi BJ (eds) The evolution of social behaviour in insects and arachnids. Cambridge University Press, Cambridge, pp 150–165

Thompson GJ, Herbert PDN (1998) Population genetic structure of the neotropical termite *Nasutitermes nigriceps* (Isoptera: Termitidae). Heredity 8:48–55

Thompson GJ, Kitade O, Lo N, Crozier RH (2000) Phylogenetic evidence for a single, ancestral origin of a 'true' worker caste in termites. J Evol Biol 13:869–881

Thompson GJ, Kitade O, Lo N, Crozier RH (2004) On the origin of termite workers: weighing up the phylogenetic evidence. J Evol Biol 17:217–220

Thorne BL (1996) Termite terminology. Sociobiology 28:253–263

Thorne BL (1997) Evolution of eusociality in termites. Annu Rev Ecol Syst 28:27–54

Thorne BL, Carpenter JM (1992) Phylogeny of Dictyoptera. Syst Entomol 17:253–268

Thorne BL, Traniello JFA (2003) Comparative social biology of basal taxa of ants and termites. Ann Rev Entomol 48:283–306

Thorne BL, Grimaldi DA, Krishna K (2000) Early fossil history of the termites. In: Abe T, Bignell DE, Higashi M (eds) Termites: evolution, sociality, symbioses, ecology. Kluwer Academic Publishers, Dordrecht, pp 77–93

Thorne BL, Breisch NL, Muscedere ML (2003) Evolution of eusociality and the soldier caste in termites: Influence of intraspecific competition and accelerated inheritance. Proc Natl Acad Sci 100:12808–12813

Traniello JFA, Leuthold RH (2000) Behavior and ecology of foraging in termites. In: Abe T, Bignell DE, Higashi M (eds) Termites: evolution, sociality, symbioses, ecology. Kluwer Academic Publishers, Dordrecht, pp 141–168

Traniello JFA, Rosengaus RB, Savoie K (2002) The development of immunity in a social insect: evidence for the group facilitation of disease resistance. Proc Natl Acad Sci 99:6838–6842

Veeranna G, Basalingappa S (1990) Population density in different parts of the mound nests of the termite *Odontotermes obesus* Rambur and their functional behavior. Entomol 15:59–62

Vehrencamp SL (1983) A model for the evolution of despotic versus egalitarian societies. Anim Behav 23:327–335

Veltman CJ (1989) Flock, pair, and group living lifestyles without cooperative breeding by Australian magpies, *Gymnorhina tibicen*. Ibis 131:601–608

Vinque PP, Tilquin JP (1978) A sex-linked ring quadrivalent in Termitidae (Isoptera). Chromosoma 67:151–156

Walker EM (1922) The terminal structures of orthopteroid insects: a phylogenetic study II. The terminal structures of the male. Ann Entomol Soc Am 15:1–87

Zimmerman RB (1983) Sibling manipulation and indirect fitness in termites. Behav Ecol Sociobiol 12:143–145