5 Sociality in Termites

Judith Korb and Barbara Thorne

Overview

Termites are biologically unique because, across all known living creatures, termites have the most diverse array of distinct body forms encoded by a single genome. These different morphologies characterize separate castes within termite societies, including up to three types of reproductives of each sex, and depending upon the species, several castes of workers and soldiers. No microbe, plant, or animal – including other eusocial taxa – rival the breadth of polyphenism found within termite species. The exceptional behavioral and physiological specializations facilitated by varying internal and external morphologies of these diversified castes, and the resulting flexibility and adaptability afforded an integrated colony, comprise one of the fundamental drivers of termites' ecological success and evolutionary radiation. Another key component of termite abundance and prosperity in many ecosystems is their exclusive niche among eusocial insects (as well as most of other animals): termites feed and often nest in or around dead plant material. Although a cellulose-based diet has its challenges, termites have evolved "clever" innovations to thrive as detritivores. Exploiting the vast and relatively uncrowded plant decomposer niche has contributed to termites' success, and has rendered their activities critical to nutrient cycles and other essential dynamics of tropical forests, savannahs, and other ecosystems.

I SOCIAL DIVERSITY

5.1 How Common is Sociality in Termites?

Termites are "eusocial cockroaches," a monophyletic clade of diploid insects (Infraorder Isoptera) within the order Blattaria (Inward *et al.*, 2007a; Lo *et al.*, 2007; Engel *et al.*, 2009; Krishna *et al.*, 2013). All of the nearly 3,000 species of modern termites (Krishna *et al.*, 2013) are eusocial, as they have sterile soldiers, a trait which is only secondarily lost in some Termitidae (Noirot & Pasteels, 1987). Termites have castes of

We thank Dustin Rubenstein and Patrick Abbot for the invitation to write this review and for all their and other contributors' efforts invested in this book. J. K. acknowledges NESCent and the German Funding Foundation for support. Both authors salute our colleagues, and fascinating termites, for exciting adventures, unexpected discoveries, and the delights of integrating field and laboratory work with comparative biology and theory.

reproductives, workers, and soldiers, but differ conspicuously from eusocial Hymenoptera in being hemimetabolous (i.e. gradual development of same body plan via molts through juvenile stages to adult) and in having morphologically versus allometrically distinct sterile soldiers. Because of hemimetabolous development, termites beyond the first instars are not helpless as are juvenile Hymenoptera larvae. Additionally, like some social vertebrates, but again in contrast to Hymenoptera, termites of both sexes are diploid and serve as helpers: female and male parents (i.e. queen and king) survive after initial mating, help rear the first brood, and continue to mate periodically.

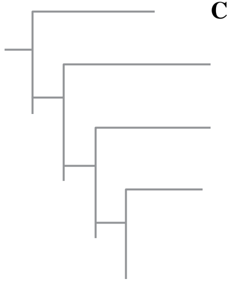
5.2 Forms of Sociality in Termites

Levels of social organization and developmental flexibility differ distinctly across termite taxa, corresponding tightly to nest and foraging habits (so called “life types”) (Tables 5.1 and 5.2). Social organization ranges from simple colonies with small colony sizes in which each individual has a high developmental plasticity, to some of the largest and most complex societies among animals in which the caste fate of each member is determined in the egg. Modern termites fall into two fundamental groups, with just a few species showing intermediate characteristics: One Piece Life Type Termites (hereafter OPT; terminology from Abe, 1987; thought to reflect ancestral life history patterns (Noirot, 1985a; Abe, 1987; Noirot & Pasteels, 1987; Noirot & Bordereau, 1988; Grandcolas & D’Haese, 2004; but see also Watson & Sewell, 1981); and Separate Type Termites (hereafter ST; Abe, 1987). This distinction in life type is reflected mainly in the worker caste (reviewed in Roisin & Korb, 2011). Soldiers do not differ as dramatically between OPT and ST species; in most species soldiers have a defensive role within the colony, but they can also serve as scouts and be involved in foraging (Traniello & Leuthold, 2000). A termite soldier is always a final (terminal) instar that develops via two molts through a presoldier intermediate. Soldiers are sterile and hence can gain only indirect fitness.

5.2.1 One Piece Life Type Termites (OPT)

OPT species (also called “single site,” Noirot, 1970; “single-site nesters,” Shellman-Reeve, 1997; or “wood-dwellers,” Korb, 2007a) spend their entire lives nesting and feeding within the same single tree, log, stump, or piece of wood where their founding queen and king first initiated the colony. They are restricted to that one resource, and do not search for or exploit nearby pieces of wood (only rare cases of “house hunting” occur, Rupf & Roisin, 2008). These termites must cope with the nutritional, moisture, thermal, competitive, predator, pathogen and parasite circumstances within their nest wood, including inevitable changes over time. When their sole resource is depleted or otherwise inhospitable, the colony dies. Their only option for relocation is for developmentally agile individuals within the colony to differentiate into winged sexuals (alates) and disperse by flight to attempt to found their own colonies.

Table 5.1 Simplified phylogeny of extant families (from Engel *et al.*, 2009) with key ecological and developmental traits of termite families and their sister taxon the *Cryptocercus* woodroaches.

PHYLOGENY[1]		Number species[2]	Distribution	Food	Build nest[3]	Foraging[4]	True workers[5]	Replacement reprod[6]
	**Cryptocercidae**		N-America, Oriental	Damp, partially decayed wood	No	No	No	No
	Mastotermitidae	1	Australia	Dead wood	Yes	Yes	Yes	Yes; ergatoids
	Hodotermitidae	15	Mainly Africa	Grass, leaves, bark	Yes	Yes	Yes	Yes; nymphoids
	Archotermopsidae	13	N-America, Oriental, Australia	Damp, partially decayed wood	No	No	No	Yes; all older instars
	Stolotermitidae	7	Mainly Australia	Damp, partially decayed wood	No	No	No	
	Kalotermitidae	~410	World-wide	Dry, sound dead wood	No	No	No	Yes; all older instars
	Stylotermitidae	34	Oriental					Unknown, but likely
	***Rhino*termitidae**	~270	World-wide	Dead wood	Yes	Yes	Yes, except 2 genera	Yes; ergatoid & nymphoid
	Serritermitidae	1	Neotropical	Unknown	Yes	Yes	Yes	Unknown
	Termitidae	~1900	World-wide	Diverse: dead wood, grass, leaf litter, humus, soil with decomposed plant material, lichen	Yes	Yes	Yes	Yes, But rare; mainly adultoids or nymphoids

OPT taxa are in *italics and underlined*. The Rhinotermitidae have both OPT and ST species.

[1] Phylogeny from Engel *et al.* (2009); only extant families

[2] Approximate number of species

[3] species construct a nest and/or build foraging galleries

[4] species forage away from the nest for separate resources

[5] workers have a reduced developmental flexibility, bifurcated pathway with workers developing from the apterous line

[6] types of replacement reproductives after Myles (1999)

Table 5.2 Major patterns of social organization within Isoptera.

One Piece Life Type Termites (OPT)	Separate Life Type Termites (ST)
Low population size per colony	Larger population size per colony
Nest excavated in one piece of wood which serves as single food source; no foraging or travel away from nest wood except for alate flights; little gallery or other construction; relatively ephemeral	Elaborately constructed, complex, stable nests
Local foraging (nest wood)	Foraging away from the nest, potentially exploiting multiple resources concurrently, and able to search for and colonize new resources
Developmental options more flexible, even in later instars	Development more rigid; largely constrained to apterous and nymphal lines in early instars
When the food source is depleted or degrades many individuals develop into alates and disperse	When a food source is depleted colony searches and moves to exploit new resource(s)
Monogamy of true (alate-derived) Queen and King (assuming no intercolony fusion)	Polygyny and polyandry of alate-derived Queens and Kings in some derived groups
Single nest 'headquarters' confined to wood in which colony was founded	Polycaly (single colony occupying multiple nest sites) in some derived taxa
Soldier caste present	Secondary loss of soldiers in Apicotermitinae
"Sex-egalitarian" castes – i.e. little morphological or behavioral specialization known between the sexes in helpers	"True worker" taxa with distinct apterous line – sexual dimorphism in castes in some species (e.g. large workers of one sex; small workers the opposite gender) and sex specialization (e.g. all soldiers are of only one sex)
Soldiers usually differentiate from 5th or 6th (or later) instar [then proceed first through a presoldier molt before final molt into soldier]	Soldiers generally develop from earlier instars, even from the 2nd or 3rd instar, although can be later (presoldier instar consistent with more primitive termites)
Soldiers may differentiate from helpers (no wingbuds) or nymphs; in the latter case soldiers have wingbuds	Soldiers differentiate almost exclusively from the apterous (worker) line
Normal soldiers are sterile; unusual fertile neotenics with soldier-like traits (of both sexes, called "reproductive soldiers" or "soldier neotenics") are known from 6 species of Archotermopsidae and Stolotermitidae.	All soldiers are sterile
Soldiers mandibulate; they generally employ physical defense, although chemical defenses are known in *Cryptotermes*	Soldiers use chemical defense in addition to, or in place of, physical defense; mandibles range from strong and elaborate to vestigial
Replacement reproductives (neotenics) can develop from any instar after the third, with and without wingbuds	Replacement neotenics, with and without wingbuds, are also known within Termitidae
Adultoids (alate-derived reproductives that stay within their natal nest, or a satellite from that original nest) unknown	Adultoids of both sexes, sometimes more than one of one or both sexes within a colony, known in some Termitidae
Merged or fused interfamilial colonies occur	Rare fusion of unrelated families into a single cooperating functional colony known in *Reticulitermes*; unknown in Termitidae

Development in OPTs is exceptionally flexible; there is no early decision point in development that determines an individual's caste fate, as there is in most eusocial Hymenoptera (e.g. Noirot, 1985b; Roisin, 2000; Korb & Hartfelder, 2008; Roisin & Korb, 2011). Offspring in these species are often referred to as helpers (analogous to helpers in cooperatively breeding vertebrates and wasps) (Roisin, 2000) or, as pseudergates, which means false workers. The use of pseudergate in the literature has been inconsistent and is therefore a confusing term. Formally (*sensu stricto*) pseudergate means an individual that has gone through a regressive or stationary molt (Grasse & Noirot, 1947; Noirot & Pasteels, 1987; Noirot & Pasteels, 1988; for an expanded discussion of the term pseudergate see Roisin & Korb, 2011). For clarity, pseudergates should refer only to such individuals. Otherwise, the extended terms *pseudergate sensu lato* and *pseudergates sensu stricto* should be used (reviewed in Roisin & Korb, 2011), or to avoid confusion, simply "helper" if the individual has not gone through a regressive or stationary molt, or "pseudergate" if it has.

In OPT species, even late instar helpers retain the capability to differentiate into reproductives, alates, or soldiers. Such developmental flexibility is achieved through an exceptional diversity of developmental options, including progressive, regressive, stationary, and saltational molts, the latter referring to molts across several instars (e.g. reviewed in Noirot, 1985b; Korb & Hartfelder, 2008). Depending upon circumstances (e.g. death of the queen and king), female and/or male helpers at a variety of developmental stages (including nymphs i.e. larvae with wing buds) may molt into reproductives, called neotenics. They remain, and inbreed, within their parents' nest. Most commonly, neotenic reproductives are replacements, succeeding a dead or senescent king or queen. In some species neotenics can differentiate as supplementary reproductives, meaning they persist as fertile reproductives in addition to a fecund king or queen of the same sex (Myles, 1999). Neotenics, alates, and soldiers are "terminal" castes, meaning no further molts or developmental changes are possible after reaching one of those castes.

Hence in OPT termites, the caste fate of an individual helper is determined by social contexts (e.g. presence/abundance of other castes, especially reproductives, colony size) and environmental factors (e.g. resource availability and quality, parasite and predation pressure, Lüscher, 1974; Lenz, 1994; Miura, 2004; Scharf *et al.*, 2007; Korb & Hartfelder, 2008; Brent, 2009). When food availability declines or colonies reach a certain size, helpers in these developmentally flexible termites predominantly develop into alates and disperse from the nest to attempt to found new colonies (reviewed in Nutting, 1969; Lenz, 1994; Korb & Schmidinger, 2004). The long-term flexibility of development of helpers is widely considered to reflect the ancestral pattern of the earliest termites (Noirot & Pasteels, 1987; Noirot & Pasteels, 1988; Inward *et al.*, 2007b; Legendre *et al.*, 2008; but see also Watson & Sewell, 1981). Modern termites fitting this pattern comprise less than 15% of extant species in 5 of 8 families: all species of Archotermopsidae, Stolotermitidae, Kalotermitidae, Stylotermitidae, as well as the genus *Prorhinotermes* within the Rhinotermitidae.

5.2.2 Separate Life Type Termites (ST)

ST species (here this comprises the "intermediate-type" where colonies are founded in a piece of wood and individuals only start foraging later in the colony cycle, and true "separate-type" nesting termites where colonies are founded in the soil, Abe, 1987; Noirot, 1970; "central-site" and "multiple site nesters," Shellman-Reeve, 1997; "foraging termites," Korb, 2007a) have a nest that is separate from their multiple food sites. They are central-place foragers that may nest within wood or soil, or build a mound or carton-like nest structure and individuals forage to one or more resources spatially separated from the nest, exploring and exploiting new resources over time. As Noirot (1970) points out, many ST nesters live early colony stages as OPTs, remaining cloistered and hidden within a single piece of wood until colony population size is sufficient to enable foraging away from the original enclave (see also Thorne & Haverty, 2000).

Developmental flexibility in ST species is more constrained due to early instar separation into two developmental pathways (reviewed in Noirot, 1985a; Roisin, 2000; Korb & Hartfelder, 2008; Roisin & Korb, 2011): (1) the wingless (apterous) line from which workers (formal term "workers" in ST species) and soldiers develop; and (2) the nymphal line (wing buds present in later instars) that culminates in alates. As with OPT species, upon death or senescence of the queen and/or king, female and/or male workers or nymphs may differentiate into neotenic reproductives (termed ergatoid neotenics if worker derived; nymphoid neotenics if they have wing buds and molt from the nymphal line, Roisin & Korb, 2011). Both ergatoid and nymphoid neotenics are common in many Rhinotermitidae; they are also known in Termitidae (reviewed in Myles, 1999). The combination of nesting, foraging, and developmental traits in ST termites are generally considered derived, but fostered diverse ecological innovations and radiations (Noirot & Pasteels, 1987; Noirot & Pasteels, 1988; Inward *et al.*, 2007b; Legendre *et al.*, 2008; but see Watson & Sewell, 1981). More than 85 percent of living species are ST termites, including the single extant species of Mastotermitidae, all Rhinotermitidae except in the genus Prorhinotermes, and all species of Hodotermitidae, Serritermitidae, and Termitidae (Kambhampati & Eggleton, 2000).

Details of development, number of castes, and task allocation vary widely across ST taxa. The most complex social systems occur among the fungus-growing termites (Macrotermitinae) and nasute termites (Nasutitermitinae). In *Macrotermes* species, two worker and two soldier castes (minor and major) are typical, each differing distinctly in morphology and in task allocation (Gerber *et al.*, 1988; Lys & Leuthold, 1991, reviewed in Traniello & Leuthold, 2000). In *Macrotermes bellicosus*, major workers forage and transport food back to the colony, while minor workers take care of the brood, the royal pair, fungus, and perform most of the mound building (Gerber *et al.*, 1988; Lys & Leuthold, 1991). Foraging major workers are protected primarily by accompanying minor soldiers while major soldiers focus on defending the nest. In Macrotermitinae caste fate seems to be predetermined at the egg stage, probably through maternal factors (Okot-Kotber, 1985). In these most socially complex species the queen can lay up to 20,000 eggs per day (Grasse, 1949; Darlington & Dransfield, 1987; Kaib *et al.*, 2001) and colony sizes range up to several million individuals (Darlington, 1984; Darlington & Dransfield, 1987; Darlington, 1990; Darlington *et al.*, 1992).

The OPT life type is broadly considered to be ancestral in termites because (1) colonies are relatively small and less socially complex, (2) individuals retain life-long flexibility in caste development (except for individuals that reach a terminal caste of reproductive or soldier), and (3) colonies nest and feed within a single piece of wood for their entire life cycle, a trait they share with their sister taxon, the woodroaches. However, Mastotermitidae is the most basal family among modern termites (reviewed in Krishna *et al.,* 2013), and its single extant species, *Mastotermes darwiniensis*, has an ST life type with large colonies, constrained developmental pathways and true workers, and foraging to multiple resources away from the nest. This paradox has fueled debate regarding whether the ST life type is derived (Noirot, 1985a,b; Grasse, 1986; Noirot & Pasteels 1987, 1988) or ancestral (Watson & Sewell, 1981) in termites. *Mastotermes darwiniensis*, the only living "relict" among many extinct genera and species of Mastotermitidae, has both ancestral and derived morphological and life history traits, featuring a common evolutionary pattern of a living member of an ancient taxon bearing a combination of ancestral and derived anatomical, developmental, and behavioral characteristics (reviewed in Thorne *et al.,* 2000; Krishna *et al.*, 2013). It seems unparsimonious that termites first evolved constrained, bifurcate juvenile development and complex foraging away from their nest, characteristics of ST, and only then evolved flexible development with long-term individual plasticity as well as smaller colonies restricted to the single piece of wood in which the colony was founded, i.e. traits of OPT.

5.3 Why Termites Form Social Groups

Termites are a monophyletic clade that evolved eusociality more than 130 million years ago (reviewed in Krishna *et al.*, 2013). The evolutionary question regarding the selective forces that favored formation of social groups, and especially sterile castes, is difficult to address because all living species are eusocial. Hence, we elaborate here which factors shape social organization in recent species. These factors differ principally between OPT and ST species, but also within each life type considerable variation exists, especially in the latter.

5.3.1 Resource Acquisition and Use

In most animals, local resource competition between parents and offspring selects for offspring dispersal (Hamilton & May, 1977). As in many social vertebrates and social insects, resource competition is mitigated in termites either by colony founding within a "bonanza-type" food source (Wilson, 1971) or by central-place foraging which can include relocation of the nest (Alexander, 1974; Alexander *et al.*, 1991; Korb, 2009). Hence, offspring can stay for prolonged periods with their parents. The established nest also provides a relatively safe haven compared to the high risk of mortality during dispersal. This, together with the low nutritional quality of wood and the necessity of offspring to re-acquire gut symbionts after each molt, are likely factors favoring an extended period of offspring staying in the natal nest and that might have been crucial in facilitating the overlap of generations, opportunities for helping, and the transition to a eusocial life (Cleveland *et al.*, 1934; Alexander, 1974; LaFage & Nutting, 1978; Alexander *et al.*, 1991; Thorne, 1997; Korb, 2008). That they might have been necessary but not sufficient prerequisites is reflected in the fact that *Cryptocercus* woodroaches live in a similar type of resource, yet never evolved eusociality (Nalepa, 2015; Korb, 2016).

Termites feed primarily on plant material (Table 5.1), a diet that has influential consequences on their life history, including the evolution of social life (Cleveland *et al.,* 1934; Waller & Lafage, 1987; Nalepa, 1994). Termites rely on gut symbionts to assist in digesting cellulose, although many species can also produce endogenous enzymes that break down cellulose directly (Lo *et al.*, 2011). Most termites harbor a diverse community of microbes (bacteria and/or protists) in their highly structured guts, facilitating termites' exploitation of many microhabitats (reviewed in Brune & Ohkuma, 2011; Ohkuma & Brune, 2011). The highly specialized fungus-growing termites (Macrotermitinae) forage for dead plant material and use it as a pre-digested substrate to culture *Termitomyces* fungi within their nests (Grasse & Noirot, 1951; Wood & Thomas, 1989; Leuthold, 1990; Rouland-Lefèvre, 2000; Nobre *et al.*, 2011). The fungus garden serves as an essential protein-rich food supplement for the termites. Fungus-growers host a lower diversity of gut symbionts probably because cultured *Termitomyces* fungi facilitate digestion of cellulose and complex plant compounds (Nobre *et al.*, 2011; Poulsen *et al.*, 2014).

Due to both their diet and hemimetabolous development, termites must reacquire obligate gut symbionts following each molt. This is accomplished by proctodeal trophallaxis, or anal feeding, among colony members, a factor proposed to have influenced termites' need for overlap of generations (Cleveland *et al.*, 1934; Nalepa, 2011). In the sister taxon of termites, the *Cryptocercus* woodroaches, symbiont loss during molting requires that immatures remain with the family through their final molt to an adult (Nalepa, 1994). In termites, typically siblings rather than parents provide proctodeal trophallaxis. However, as in OPT termites, all individuals within a termite colony act as symbiont donors as well as recipients, and reinoculation of gut fauna is a cooperative rather than altruistic act (Cleveland *et al.*, 1934; Korb, 2007b; Korb *et al.*, 2012). Altruism requires that some individuals invest more in allogrooming than others and that the behavior reduces an individual's direct fitness. This is currently unclear for OPT termites.

Termites' plant-based diet has a relatively high C:N ratio, compelling relatively slow development (Higashi *et al.*, 1992; Lenz, 1994; Nalepa, 1994). With few exceptions (e.g. fungus-growers), termites are considered protein (nitrogen)-limited. N-fixing gut bacteria in some species help moderate this constraint (Brune & Ohkuma, 2011). At present, little is known about the diversity and nutritional/developmental impacts of N-fixing symbionts across termites.

5.3.2 Predator Avoidance

In ST species, once colonies grow to a size at which workers and soldiers forage away from their founding nest, those ST castes experience different mortality risks than those of OPT species. OPT termites may share their single piece of wood with dynamic assemblages of competitors, predators, and/or pathogens, shifting in abundance and composition as the host resource decomposes (Thorne *et al.*, 2003). In contrast, ST soldiers and workers can be vulnerable to predators when searching and feeding outside the nest. Thus, predation pressure varies markedly among ST termites. Some ST species are highly protected, either underground in cryptic galleries, above ground within foraging tunnels, or as in some soil feeding Apicotermitinae that nest in and feed on carton nests. Such differences in predation risk correlate with soldier morphology and the proportions of soldiers within a colony (Haverty & Howard, 1981). For instance, the highly protected soil-feeding Apicotermitinae have secondarily lost the soldier caste completely (Sands, 1972).

5.3.3 Homeostasis

The wood nest of OPT species, and the fact that these termites never forage outside that resource, insulates them against some environmental fluctuations, probably more so in drywood termites (Kalotermitidae) that nest in sound wood than in dampwood termites (Archotermopsidae) that nest in decaying wood. The degree to which individuals and their colony in ST species are exposed to environmental fluctuations varies markedly between species, depending upon nest type, habitat, and colony size (Grasse & Noirot, 1948; Noirot, 1970; Korb & Linsenmair, 2000; Noirot & Darlington, 2000; Korb, 2011). For example, species nesting deep inside the ground may experience more consistent conditions than those nesting close to the soil surface. Occupied soil depth may be adjusted by termites moving according to environmental conditions (Lepage, 1989; Darlington, 1990).

Most studies on homeostasis focus on mound-building species (reviewed in Noirot, 1970; Noirot & Darlington, 2000; Korb, 2011). Some of these species adapt mound architecture to local environmental conditions and provide inside-nest temperatures that vary by less than 3°C daily, with a mean annual fluctuation of around 1°C, while outside temperatures can fluctuate by more than 30°C. Mounds also can have efficient ventilation systems that facilitate the input of O_2 and output of CO_2. Such impressive abilities are especially pronounced in fungus-growing termites (reviewed in Korb, 2011). Such self-organized structures are most easily implemented with relatively large colony sizes. Mounds help protect the royal chamber, nursery, and inhabiting individuals against predators and environmental perturbations, facilitating relative homeostasis for the colony. Within a species, homeostasis typically increases with mound size, which is related to colony size (Noirot, 1970; Korb & Linsenmair, 2000). Mounds also provide space for food storage in some species (and in the case of fungus-growing Macrotermitinae, for fungus cultivation) making colonies less dependent on short-term ecological conditions (reviewed in Schmidt *et al.*, 2014). Hence it is not surprising that mound-building species often have influential ecological impacts.

5.3.4 Mating

The nuptial flight of termites generally occurs during the rainy season after precipitation events, though exceptions exist (Nutting, 1969; Bourguignon *et al.*, 2009). The common pattern is as follows (Nutting, 1969; Minnick, 1973). Winged sexuals fly from their nest after a rain. Following dispersal, males are attracted to females that "call" by standing in a relatively exposed position while emitting a pheromone. When a male approaches a female he follows closely behind the female ("tandem-run"), both shed their wings synchronously, and they search for and burrow into a crack in a piece of wood or into soil. As founding primary reproductives (i.e. alate-derived king and queen), they establish a nuptial chamber where mating takes place, eggs are laid, and the first offspring are produced. During this founding period, kings and queens of some species can eat surrounding wood, or they survive by metabolizing stored resources, e.g. their now unnecessary wing muscles. After the first workers develop, these offspring start foraging, with the first broods consuming local resources.

5.3.5 Offspring Care

There are major differences in the importance of offspring brood care between OPT and ST species that correlate with their different resource acquisition types. In central-place foraging ST species, foraging for food is a most important part of brood care behavior and workers in at least some species have a high risk of dying while foraging outside the nest (Korb & Linsenmair, 2002). At the same time – and similar to social Hymenoptera – foraging workers can increase their indirect fitness by providing new diverse, distant resources for their colony. In contrast, entire OPT colonies reside inside their food. Hence, brood care in OPT colonies may, in at least some cases, be less labor intensive than in ST species, as evidence in drywood termites suggests (Korb, 2007b; Korb *et al.*, 2012). In the OPT genus *Cryptotermes*, for example, helpers are immatures that do not invest in foraging for food for the colony and mainly seem to follow a "sit and wait" tactic to try to reproduce later in life (Korb, 2007b, 2009). Correspondingly, annual growth rates of colonies and colony sizes are small in OPT species compared to those of ST species (Shellmann-Reeve, 1997), and individual body size of helpers and soldiers is often large in OPT species, although there are some exceptionally large body sized ST species such as *Syntermes* or *Macrotermes*.

In OPT species, intensity of brood care might be associated with pathogen load within the nest (Rosengaus *et al.*, 2003; Rosengaus *et al.*, 2011; Korb *et al.*, 2012). In *Zootermopsis*, which live in rotten/decaying wood, lab experiments have demonstrated that of all brood care behavior directed towards eggs and larvae, hygienic allogrooming is especially common (Korb *et al.*, 2012). This strongly contrasts with the drywood termite *C. secundus* that nests in sound wood with extremely low pathogen loads.

Workers of ST species provide extensive care of the nursery, soldiers, and reproductives (e.g. reviewed in Traniello & Leuthold, 2000). They bring food and water to the brood, reproductives, and soldiers, whose mandibles prevent harvesting food resources on their own (as is the case for OPT species). Workers construct and maintain the nest, which in some species involves elaborate albeit highly functional architecture, with heights reaching several meters (Traniello & Leuthold, 2000; Noirot & Darlington, 2000).

5.4 The Role of Ecology in Shaping Sociality in Termites

Nest and foraging ecology coincide with developmental pathways and not only distinguish OPT from ST species, but are also influential in shaping social patterns and complexity among taxa as outlined earlier. Below, we discuss how most termites share very similar habitat requirements: they are mainly tropical and subtropical detritivores with some taxonomic groups occupying more specialized niches, such as fungus-cultivating, soil-feeding, or living in temperate regions.

5.4.1 Habitat and Environment

In contrast to the differences in nest and foraging ecology, habitat and environmental requirements are similar across termites and often independent of social complexity. Among the OPT termites, dampwood and drywood species represent different termite families (Archotermopsidae and Kalotermitidae) that nest in decaying versus structurally sound wood, respectively. Comparable clear distinctions are lacking for other families. For example, Rhinotermitidae are also called subterranean termites, but they share habitat and nest type with many Termitidae. Termites are predominantly tropical decomposers that prefer temperatures above 15°C and relative high humidity. Indeed, there are only very few species that are resistant to temperatures below zero, a notable exception are the Archotermopsidae, including the only Nearctic temperate endemic genus *Zootermopsis* (Eggleton, 2000; Lacey *et al.*, 2010). Generally, termites thrive, and reach exceptional diversity, in tropical rainforests. Using exemplar assemblages, Jones & Eggleton (2011) found that tropical rainforests have a higher generic diversity than savanna woodlands and semi-deserts with least genera occurring in temperate woodlands and temperate rainforests.

5.4.2 Biogeography

Termites are mainly tropical and subtropical species, and species richness increases with latitude; some species occur in temperate regions, although with far lower diversity (Eggleton, 1994). The highest known generic richness is found in African tropical rainforests (Eggleton *et al.*, 1994; Eggleton, 2000; Jones & Eggleton, 2011). Controlling for net primary productivity, the Afrotropical region has more described endemic genera (85) than the Neotropics (63), Australasia (23) or the Oriental region (56) (Eggleton, 2000). Caveats might be that not all regions have been sampled equally for termites and that this pattern applies to generic richness, which is arguably an arbitrary classification. Termites are generally poorly studied at the species level because, among other factors, they often have few external morphological traits that reliably distinguish closely related species (Donovan *et al.*, 2000; Kambhampati & Eggleton, 2000). Use of molecular markers for species diagnosis (barcoding) suggests cryptic species diversity but also high phenotypic plasticity that risks overestimation of species richness (Hausberger *et al.*, 2011). Nevertheless, there is a dramatic drop in species richness in temperate regions, with four and three endemic genera in the Nearctic and Paleoarctic regions, respectively (Eggleton, 2000). Moreover, most of these species occur in subtropical deserts or arid grasslands rather than temperate zones with definitive winters (Eggleton, 2000). The island regions of Madagascar and Papua are also relatively depauperate with four and three endemic genera, respectively (Eggleton, 2000). This distribution pattern illustrates (1) the effect of historical biogeography and (2) that termites thrive in warm climates, from dry deserts to humid rainforests (Abensperg-Traun & Steven, 1997; Eggleton, 2000; Jones & Eggleton, 2011).

5.4.3 Niches

Termites are predominantly detritivores. Compared with other insect orders (or infraorders), Isoptera show relatively low niche differentiation, with most species preferring warm conditions and nutrition from dead, often partially decomposed plant material (e.g. wood, grass, lichen, seeds, herbivore dung; Eggleton & Tayasu, 2001). Hence, termites compete locally for the same foods. Despite niche similarities, several ecologically equivalent species coexist at the local scale in tropical and subtropical habitats (Wood *et al.*, 1977; Korb & Linsenmair, 2001; Dosso *et al.*, 2010; Hausberger *et al.*, 2011). Specialist feeders include fungus-growing termites and “soil feeders” that consume decomposing litter or humus. Fungus-cultivating termites are restricted to the paleotropics, where they occupy a niche resembling that of neotropical fungus-growing ants (Attini) except that the latter generally forage on live plants (Waller, 1988; Nobre *et al.*, 2011). Specialist humus feeders (i.e. feeding on soil-like substrates containing recognizable plant material) and soil feeding termites (i.e. consuming soil-like material with a high proportion of silica and no recognizable plant material) also belong to the Termitidae (Bignell & Eggleton, 2000; Brauman *et al.*, 2000; Eggleton & Tayasu, 2001). While soil feeders are common in humid forests in Africa (and perhaps the Neotropics, where the genus *Anoplotermes* has yet to be studied in detail), fungus-growing termites are ecologically dominant in African and Asian grasslands and savannas (Josens, 1983; Deshmukh, 1989; Bignell & Eggleton, 2000; Eggleton, 2000).

5.5 The Role of Evolutionary History in Shaping Sociality in Termites

The stem groups of all known fossil and living termite taxa originated by the early Cretaceous (135–100 Mya) on the Gondwana landmass (Thorne *et al.*, 2000; Engel *et al.*, 2009; Krishna *et al.*, 2013). Although impacted by continental drift, the primary driver of modern biogeographic distributions was an explosive Tertiary radiation followed by rapid dispersal as termites became ecologically dominant detritivores (Eggleton, 2000; Thorne *et al.*, 2000; Krishna *et al.*, 2013). The evolution of representatives of the different families was probably fast so that the ST species lifestyle radiated rapidly. *Cryptocercus* woodroaches, the sister taxon of the termites, are also one-piece nesters, but they are subsocial rather than eusocial (Cleveland *et al.*, 1934; Nalepa, 1994; Thorne, 1997; Nalepa & Bandi, 2000) implying that OPT is the ancestral life-type.

II SOCIAL TRAITS

Termites have a long history of meticulous natural history observations and careful taxonomy by early entomologists (see Snyder, 1956; many key contributors are profiled in Volume 1 of Krishna *et al.,* 2013). Their efforts provided the foundation for the modern study of termites and their diversity. New insights on the social traits of termites will emerge from modern tools, theoretical considerations, careful observations and experiments that address specific question illuminating long-standing questions and generate new avenues of research on termite social biology.

5.6 Traits of Social Species

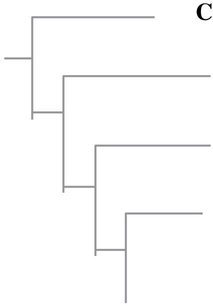
5.6.1 Cognition and Communication

The communication and cognition system of termites is fundamentally similar to that of their closest relatives, the cockroaches, although more sophisticated due to their increased social complexity. Termites, except for winged sexuals, generally lack well developed eyes. Although phototaxis plays a role during nuptial flights, the main modes of communication in termites are olfactory and tactile, with chemical, vibrational, and behavioral signals playing important roles in species recognition and within colony recognition, as well as in foraging, building, and defensive behaviors (Leuthod, 1979; Bordereau & Pasteels, 2011; Bagnères & Hanus, 2015). Convergent with eusocial Hymenoptera and many other insects, hydrocarbons on the cuticle (cuticular hydrocarbons, CHCs) provide information on identity, both within and among colonies (e.g. Haverty *et al.,* 1988; Clément & Bagnères, 1998), with long-chained CHCs indicating reproductive status (Liebig *et al.*, 2009; Weil *et al.*, 2009; Hoffmann *et al.*, 2014). Moreover, volatile compounds function for intermediate distance communication within the nest (Lüscher, 1974; Matsuura *et al.*, 2010) and species-specific trail pheromones allow efficient recruitment of nestmates to food sources (reviewed in Bordereau & Pasteels, 2011). Vibrations are known to be important in alarm communication (e.g. Rohrig *et al.*, 1999) or, in OPT termites, for measuring food availability and the presence of competing colonies (Evans *et al.*, 2005, 2009).

5.6.2 Lifespan and Longevity

There are few detailed studies revealing termite life history data (Table 5.3). As is typical for eusocial insects, there are major differences in longevity between castes

Table 5.3 Simplified phylogeny of major extant families (from Engel *et al.*, 2009) and life history traits for termite families and their sister taxon, the *Cryptocercus* wood roaches. Maximal values or ranges over different species are given. Numbers in (?) are anecdotal or unconfirmed reports.

PHYLOGENY[1]	Maximum longevity [in years][2]		Fecundity [per year]	Maximum colony size
	Reproductives	Workers/Soldiers		
 **Cryptocercidae**	6	na	1–75	2 parents + offspring
Mastotermitidae	7–17			1.1 Mio
Hodotermitidae	~20			
Archotermopsidae	4–6	>3–5	20–1000	several thousand
Stolotermitidae				
Kalotermitidae	4–5 (14?)	>5–6 (14?)	20 to few hundred	1500–3,000
Stylotermitidae				
Rhinotermitidae	9–17	>3–5		few thousand-2,750,000
Serritermitidae				
Termitidae	~20 (50?)	<1	10,000–7,300,000	10,000-several million

Given are maximal values or ranges applying to different species. Values with? = anecdotal, unconfirmed reports

[1] Phylogeny from Engel *et al.* (2009); only extant families

[2] Reviewed in Shellman-Reeve (1997)

(Wilson, 1971; Keller & Genoud, 1997; Keller, 1998). Because kings and queens typically have longer lifespans than workers or soldiers, the common life history trade-off between longevity and fecundity seems absent in termites. This may be in part due to the sheltered nests, but also because after initial phases of colony founding, eusocial insect reproductives are fed and cared for by other members of the colony (e.g. Wilson, 1971; Keller & Genoud, 1997; Heinze & Schrempf, 2008). This both reduces extrinsic mortality rates – selecting for increased longevity in reproductives – and alleviates resource allocation trade-offs (e.g. Heinze & Schrempf, 2008).

Data on longevity of termite reproductives in the field are rare (for Termitidae they are mainly restricted to fungus-growers; Table 5.3), but thus far suggest that there are no major differences among taxa. The maximum longevity of Mastotermitidae, Kalotermitidae, Rhinotermitidae and several representatives of Termitidae indicate that they commonly reach an age of between 10–20 years with average life spans of 4–5 years (reviewed in Shellman-Reeve, 1997; Keller, 1998; for Mastotermitidae, Watson & Abbey, 1989; for Archotermopsidae, Heath, 1907; Thorne *et al.*, 2002; for Kalotermitidae, Grasse, 1984; Luykx, 1993, J. Korb, *unpublished data*; for Rhinotermitidae, Nutting, 1969, Grasse, 1984; Termitidae: Macrotermitinae, Grasse, 1984; Leuthold, 1979; *personal communication*). Record holders might be some mound building species, such as *Macrotermes* or *Nasutitermes exitiosus*, for which anecdotal notes exist that mounds remained active for up to fifty and eighty years, respectively (Gay & Calaby, 1970; Grasse, 1984). However, it is unknown, and probably unlikely, if those nest structures were continuously inhabited by the same colony with the same reproductives.

For the shorter-lived worker and soldier castes, there may be a trend for a decrease in lifespan from OPT to ST termites (reviewed in Shellman-Reeve, 1997; for Archotermopsidae, Nutting, 1969; for Kalotermitidae, Gay & Calaby, 1970; J. Korb *unpublished data*; for Rhinotermitidae, Pickens, 1934; Gay & Calaby, 1970; for Termitidae: Macrotermitinae, Bouillon, 1970; Collins, 1981; Josens, 1982; Darlington, 1991; Cubitermes, Bouillon, 1970; Grasse, 1984; Table 5.3). This difference in worker longevity is in accord with life history theory (Stearns, 1992; Baudisch, 2005): a high extrinsic mortality in foraging workers in ST species is expected to result in earlier senescence and shorter lifespans compared to OPT workers that are protected within their wooden nest. Accordingly, the intra-specific difference in longevity between reproductives and non-reproductives seems to increase from OPT to ST termites and within the ST species with increasing social complexity. For instance with 4–5 years, lifespan is similar for workers, soldiers, and reproductives in *Zootermopsis* (Heath, 1907). On the other hand, the most extreme known example of lifespan occurs in *Macrotermes* where workers only live a few months while reproductives can reach ages of twenty years (Traniello & Leuthold, 2000).

Despite the high potential lifespan of reproductives, there is reasonable probability of dying each year due to ecological circumstances. Especially in OPT species with their totipotent helpers and conspecific competitors within the same limited resource, loss of founding reproductives offers opportunities for offspring to inherit the colony and differentiate into new reproductives (Thorne *et al.*, 2002, 2003; Korb & Schneider, 2007).

Cryptocercus woodroaches, the extant sister taxon of termites, are semelparous. Both parents help to raise one clutch until that monogamous pair dies. One study on *C. punctulatus* showed that roughly 15 percent of the parents die within the first year after reproducing (Nalepa, 1984). On average, parents seem to stay with the brood/offspring for three years (Seelinger & Seelinger, 1983; Nalepa, 1984). As the developmental time until the offspring reach maturity is about six years (Cleveland *et al.*, 1934), parents are often dead before offspring reach maturity.

5.6.3 Fecundity

Fecundity of primary as well as neotenic reproductives increases with age and increasing physogastry until a plateau is reached. With a maximum of a few hundred eggs per year, the fecundity of *Cryptotermes* species is low relative to most other social insects. *Cryptotermes* colony sizes with a single reproductive queen are generally only a few hundred individuals (Korb & Schmidinger, 2004; Korb, 2008; J. Korb, *unpublished data*). In *Zootermopsis,* OPT dampwood termites, fecundity is higher than in drywood species and colonies reach sizes of a few thousand individuals (Heath, 1903; Heath, 1927; B. Thorne, *unpublished data*). However, *Zootermopsis* never attain the fecundity and colony size of some of the most derived Termitidae, which can reach a few million individuals (Heath, 1927; Shellman-Reeve, 1997) (although some Termitidae retain relatively small colonies). Record holders are probably some fungus-growing Macrotermitinae with 20,000 eggs per day (reviewed in Shellman-Reeve, 1997; for Kalotermitidae, Wilkinson, 1962; Lenz, 1987; Lenz, 1994; Korb & Schneider, 2007; Neoh & Lee, 2011; for Macrotermitinae, Grasse, 1949; Darlington & Dransfield, 1987; Kaib *et al.*, 2001; Table 5.3). Often fecundity of the female and male founding queen and king is higher than that of neotenics, but this is not the case in all taxa (Myles, 1999). The cumulative fecundity of multiple neotenic reproductives within a single colony may exceed that of the monogamous founding pair.

Comparing termites with *Cryptocercus* woodroaches reveals that OPT species are similar to *Cryptocercus* with respect to the clutch size of first year adults. Unless the first brood is unsuccessful, *Cryptocercus punctulatus* produces one clutch of eggs consisting of about twenty offspring (range 1–75, Nalepa, 1984; Nalepa, 1988).

5.6.4 Age at First Reproduction

Termite colony life cycles proceed through the three stages typical of most eusocial insects (Oster & Wilson, 1978): (1) a founding stage; (2) an ergonomic stage during which the colony increases in size through production of workers and soldiers; and (3) a reproductive stage after a colony reaches maturity and produces winged sexuals. At the end of the reproductive stage, which may last over a decade, colony size and the number of sexuals produced decline. The reproductive phase of a colony is difficult to measure in the field and is often not reached before an age of several years (for Archotermopsidae, Thorne *et al.*, 2002; for Kalotermitidae, five years, J. Korb, *unpublished data*; Wilkinson, 1962; Wilkinson, 1963; for Rhinotermitidae and Termitidae, Grasse, 1982;

Shellman-Reeve, 1997) with timing strongly dependent upon environmental conditions (e.g. food quantity and quality, temperature). In the laboratory, *Zootermopsis* can produce the first mature alates after only eighteen months following pairing of a queen and king (B. Thorne, *unpublished data*). For some OPT species, it takes at least three to four years (and often much longer) until an individual can develop from an egg into an alate (for Kalotermitidae, Lüscher, 1952; Wilkinson, 1962; J. Korb, *unpublished data*). As in *Cryptotermes,* alates do not develop until certain colony sizes are reached, and the first sexuals do not occur before an age of five (J. Korb, *unpublished data*). In Termitidae (especially fungus-growers and tropical species), individual development times are considerably faster, and it often takes less than one year for alates to develop from eggs (Johnson, 1981; Grasse, 1982; Noirot, 1985a; Noirot, 1990). However, when queens actually begin to produce alate-destined eggs seems to depend upon colony size and this minimum size is reached only after several years (Grasse, 1982; Grasse, 1984; Noirot, 1990; Han & Bordereau, 1992).

5.6.5 Dispersal

In both OPT and ST species, new colonies are founded generally by alates after nuptial flights that occur seasonally. Termite alates are generally regarded as poor flyers (Nutting, 1969). Population genetic studies, however, suggest that dispersal might be less limiting and that local populations are not highly inbred (Vargo & Husseneder, 2011). Major differences likely exist between species (Schmidt *et al.*, 2013) and depending on local habitat and topography. In some species new colonies can also be founded by budding of colony parts (Nutting, 1969; Thorne 1982, 1984; Adams & Atkinson, 2007; Vargo & Husseneder, 2011). Behavioral details about how such budding occurs, and whether it is started by few individuals with scouts or by colonies breaking apart, are largely unknown (Thorne, 1982, 1984).

5.7 Traits of Social Groups

5.7.1 Genetic Structure

Unlike eusocial Hymenoptera that are haplodiploid, all termites are diploid. Genetic relatedness varies in termite colonies depending on group structure, which is largely determined by the breeding structure (reviewed by Vargo & Husseneder, 2009, 2011). In almost all termite species, new colonies are founded by a monogamous, unrelated pair of winged sexuals, the future queen and king. Hence, the default genetic relatedness among nuclear family colony members is 0.5 (parent to offspring and vice versa: $r = 0.5$; offspring to offspring: $r = 0.5$). However, within-colony relatedness can decrease in the case of colony fusions (Thorne *et al.*, 1999; Vargo & Husseneder, 2011). It can also increase due to inbreeding for instance, when an offspring inherits the natal breeding position and mates with the opposite-sex parent or sibling, or in the case of parthenogenetic reproduction, which is documented in several termite species.

5.7.2 Group Structure, Breeding Structure and Sex Ratio

Three family (colony) types are distinguished in termites (Thorne *et al.*, 1999; Bulmer *et al.*, 2001; Vargo, 2003). *Simple families* are colonies with genotypes consistent with the progeny of a monogamous pair of reproductives (monogamous colonies; a nuclear family). *Extended families* are headed by reproductives descended from the founding pair, leading to inbreeding and increased relatedness among colony/family members. These colonies can be monogamous or polygamous with several primary reproductives, and/or one or more neotenic reproductives. Finally, *mixed families* contain progeny of multiple unrelated reproductives all functioning as a social unit. Mixed family colonies can be the result of fusion of two or more neighboring colonies, nest foundation by more than one pair of unrelated reproductives (pleometrosis), or – at least in theory, although never unambiguously documented – adoption of unrelated reproductives. These elaborations on colony structure can result in polygynous and sometimes polyandrous mating systems and a decrease in average genetic relatedness among apparently cooperating individuals within a mixed colony.

Colony fusions and inbreeding, that lead to mixed and extended families, respectively, seem to be especially common in OPT species (Myles, 1999; Thorne *et al.,* 2002, 2003; Korb & Schneider, 2007; Korb & Hartfelder, 2008; Johns *et al.*, 2009; Korb & Roux, 2012; Luchetti *et al.*, 2013; Howard *et al.*, 2013). This is probably due to the common occurrence of several colonies that were founded within the same piece of wood and that meet during “nest” growth and extension while feeding (Thorne *et al.,* 2002, 2003; Johns *et al*. 2009; Korb & Roux, 2012; Howard *et al.*, 2013). High degrees of inbreeding in OPT species likely exist because of the high developmental flexibility of helpers which retain long-term flexibility to develop into neotenic reproductives (reviewed in Noirot, 1969; Korb & Hartfelder, 2008). Among ST species, *Mastotermes* and *Reticulitermes* can have large numbers of neotenics and thus inbreeding can be common too (reviewed in Vargo & Husseneder, 2011). Facultative ***thelytokous*** reproduction (i.e. a type of parthenogenesis in which females are produced from unfertilized eggs) can occur in some species from all termite families studied to date (reviewed in Matsuura, 2011).

Termitidae may take advantage of a wide variety of reproductive alternatives. For example, in addition to the typical termite pattern of colonies founded by a single king and queen (monogamy), *Nasutitermes corniger*’s reproductive options include multiple queens, multiple kings, satellite nests, and colony budding (Thorne, 1983; Roisin & Pasteels, 1986; Adams & Atkinson, 2007). This plasticity makes *N. corniger* exceptionally flexible, resilient, and equipped with the reproductive infrastructure for rapid colony growth.

In contrast to social Hymenoptera in which colonies are composed of female workers, male and female workers and soldiers (with caste gender dependent on species), occur in most termite species with varying sex ratios (Noirot, 1969; Noirot, 1985a; Roisin, 2001; Bourguignon *et al.*, 2012). There are exceptions, however, especially among the Termitidae where caste system can align with sexual dimorphism. Notably, there is no consistent phylogenetic pattern between which sex develops into which caste, although some predispositions for soldiers have been more recently proposed (Matsuura, 2006; Muller & Korb, 2008; Bourguignon *et al.*, 2012).

III SOCIAL SYNTHESIS

5.8 A Summary of Termite Sociality

Termites are the eusocial clade within the cockroaches. They can be grouped into two life types that largely differ in developmental plasticity, social complexity and ecology: the OPT and the ST species. The OPT termites in particular share several similarities with the termite's sister taxon, the *Cryptocercus* woodroaches.

In contrast to woodroaches, and especially relevant in OPT species, termite helpers can develop into replacement reproductives within their natal nest (Table 5.1). Hence, offspring of OPT species can take advantage of a nest and resource inheritance strategy (including the colony population in the case of termites), as do helpers of cooperatively breeding birds and mammals (Wilson, 1971; Thorne, 1997; Thorne *et al.*, 2003; Korb & Heinze, 2008a, 2008b). The extent to which helper or worker termites are involved in brood care, how much indirect fitness they gain, and their probability of becoming a new reproductive in their parents' colony depends upon taxon and ecological conditions (reviewed in Korb *et al.*, 2012).

Data for woodroaches and OPT species show that parents may die during the long developmental period from egg to maturity (Nalepa, 1984; Thorne *et al.*, 2002; Thorne *et al.*, 2003; Korb & Schneider, 2007; Johns *et al.* 2009; Korb & Roux, 2012; Howard *et al.*, 2013; Table 5.4). The possibility of inheritance of the nest and philopatric reproduction in OPT species also has the advantage of providing opportunities for gaining direct and/or indirect fitness benefits without risky dispersal (Myles, 1988; Thorne 1997; Thorne *et al.*, 2003; Korb & Schneider, 2007; Korb, 2007b, 2008;

Table 5.4 Key life history and morphological differences between modern woodroaches (*Cryptocercus*) and termites.

Characteristic	*Cryptocercus*	Termites
Wings	Wingless; local dispersal	Winged adults; dehiscent wings; dispersal flights
Colony size	Both parents + offspring of single reproductive event	Minimum size ~40 termites; in higher termites can reach hundreds of thousands or even a million or more individuals
Overlap of generations	Parents rarely if ever overlap in time or space with adult offspring	Parents commonly survive past maturity of adult offspring; older offspring may persist indefinitely in parental nest
Castes	Absent	Distinct castes; pronounced division of labor and reproductive skew
Body size (of adults)	Larger	Smaller (adult body size equivalent to juvenile *Cryptocercus*)
Mouthparts	Opistognathus (head facing down; mouthparts directed posteriorly)	Prognathus (head and mouthparts directed anteriorly)

Korb & Hartfelder, 2008; Johns *et al.*, 2009; Korb & Roux, 2012; Howard *et al.*, 2013). Associated with a shift to ST life histories is the emergence of true workers (Noirot 1985a; Abe 1987). The occurrence of true workers coincides with morphological differentiation (e.g. increased sclerotization), reduced developmental flexibility, and decreased lifespan in workers. These species resemble ants in many respects, and workers as well as soldiers gain mainly indirect fitness benefits during their lifetimes (Howard & Thorne, 2011). As most living termites belong to the ST category, this striking resemblance inspired the common name of termites as "white ants" in some languages.

5.9 Comparative Perspectives on Termite Sociality

Korb & Heinze (2008b) identified three "sociality syndromes" by comparing ecological and relatedness parameters across a broad range of social vertebrates and invertebrates. These traits included: food acquisition (central-place foraging/nesting inside food), nest type (inside/outside food), main type of helping (allofeeding/defense), chances to inherit the nest (yes/no), inbreeding possible (yes/no), genetic system (diploid/haplodiploid/parthenogenetic) and main altruistic caste (workers/helpers/soldiers). Strikingly, these traits, except the genetic system, grouped well into three syndromes of co-occurring traits and all social animals could be categorized accordingly. The OPT termites fit with social aphids, thrips and naked mole-rats in syndrome I. They are characterized by a "bonanza-type" food resource, and fortress defense through altruistic soldiers. Opportunities for offspring to gain direct fitness as winged sexuals and/or through nest inheritance and inbreeding by differentiating into reproductives within their parents' nest are substantial, and systems are characterized by low local competition over food (at least in recently founded resources) but potential conflict over breeding. This syndrome is broadly equivalent with the "fortress defenders" recognized by Queller & Strassmann (1998).

In contrast ST termites, along with ants and honeybees, belong to syndrome II where opportunities for offspring workers to inherit and directly reproduce in a colony are reduced, and allofeeding plays a more important role. Here, feeding typically involves progressive food provisioning, which is costly to reproductives and can be "handed over" to workers. These are the "classically" eusocial insects, largely equivalent with the "life insurers" (Queller & Strassmann, 1998). Overall, for workers there is a shift to a higher importance of indirect fitness compared to direct fitness when comparing ST species to OPT, while soldiers of both groups gain indirect fitness only.

Syndrome III comprises most cooperatively breeding vertebrates and social Hymenoptera with totipotent workers (e.g. wasps and queenless ants). It is intermediate between societies with altruistic, subfertile workers of syndrome II and those consisting of totipotent individuals of syndrome I. Helpers gain indirect fitness through potentially costly alloparental care but they can potentially also gain direct fitness through inheriting the breeding position or, in some cases, by founding their own nest. Depending upon whether brood care is costly, OPT termites might be grouped also in this syndrome. In Queller & Strassmann's (1998) categorization, this group is not described.

Contemporary viewpoints on the fundamental characteristics and dynamics driving the evolution of eusociality in termites center on ecology, behavior, and development (Shellman-Reeve, 1997; Thorne, 1997; Roisin, 2000; Thorne *et al*., 2003; Korb, 2008; Korb & Hartfelder, 2008; Johns *et al*., 2009; Korb *et al.*, 2012; Howard *et al*., 2013; see also Nalepa, 2015; Korb, 2016). Compelling insights have been advanced regarding the selective landscape favoring termite eusocial evolution compared with factors influencing eusocial origins and elaborations in other animals (e.g. Alexander *et al.*, 1991; Korb and Heinze, 2008a, 2008b; Howard & Thorne, 2011). Comprehensive, truly integrative syntheses, however, will require continued research at molecular through community levels.

5.10 Concluding Remarks

Termites are cellulose feeding social insects with distinct castes. Soldiers are sterile and are morphologically highly specialized with a fixed developmental pathway and no option for further molts. In contrast, developmental plasticity and function of helpers or workers varies, from species with totipotent immatures to morphologically and behaviorally highly specialized individuals that resemble such patterns in workers of eusocial Hymenoptera. The opportunity to inherit the local breeding position probably played an important role during the transition to eusociality. Hence, depending on caste, phylogeny and ecology, termites span a wide range of social systems observed in animals: from systems where workers are similar to helpers of cooperative breeding vertebrates, or soldiers in social thrips and aphids, to the most complex societies which share similarities with ants.

References

Abe, T. (1987) Evolution of life types in termites. *In*: Kawano, S., Connell, J. H. & Hidaka, T. (eds.) *Evolution and Coadaptation in Biotic Communities.* Tokyo: University of Tokyo Press, pp. 125–148.

Abensperg-Traun, M. & Steven, D. (1997) Latitudinal gradients in the species richness of Australian termites (Isoptera). *Australian Journal of Ecology*, **22**, 471–476.

Adams, E. S. & Atkinson, L. (2007) Queen fecundity and reproductive skew in the termite *Nasutitermes corniger. Insectes Sociaux*, **55**, 28–36.

Alexander, R. D. (1974) The evolution of social behavior. *Annual Reviews of Ecology and Systematics*, **5**, 325–383.

Alexander, R. D., Noonan, K. M. & Crespi, B. J. (1991) The evolution of eusociality. *In:* Sherman, P. W., Jarvis, J. U. M. & Alexander, R. D. (eds.) *The Biology of the Naked Mole-rat.* Princeton, New Jersey: Princeton University Press, pp. 3–44.

Abensperg Traun, M. & Steven, D. (1997) Latitudinal gradients in the species richness of Australian termites (Isoptera). *Austral Ecology*, 22, 471–476.

Atkinson, L. & Adams, E. S. (1997) The origins and relatedness of multiple reproductives in colonies of the termite *Nasutitermes corniger*. *Proceedings of the Royal Society of London B*, **264,** 1131–1136.

Baudisch, A. (2005) Hamilton's indicators of the force of selection. *Proceedings of the National Academy of Sciences USA*, **102**, 8263–8268.

Bagnères, A.-G. & Hanus, R. (2015) Communication and social regulation in termites. *In:* Aquiloni, L. & Tricarico, E. (eds.) *Social Regulation in Invertebrates.* Heidelberg: Springer, pp. 193–248.

Bignell, D. E. & Eggleton, P. (2000) Termites in ecosystems. *In:* Abe, T., Bignell, D. E. & Higashi, M. (eds.) *Termites: Evolution, Sociality, Symbiosis and Ecology.* Dordrecht, NL: Kluwer Academic Publishers, pp. 363–387.

Bordereau, C. & Pasteels, J. M. (2011) Pheromones and chemical ecology of dispersal and foraging in termites. *In:* Bignell, D. E., Roisin, Y. & Lo, N. (eds.) *Biology of Termites: A Modern Synthesis.* Dordrecht, Heidelberg, London, New York: Springer, pp. 279–320.

Bouillon, A. (1970) Termites of the Ethiopian region. *In:* Krishna, K. & Weesner, F. M. (eds.) *Biology of Termites II*. New York: New York Academic Press.

Bourguignon, T., Leponce, M. & Roisin, Y. (2009) Insights into the termite assemblage of a neotropical rainforest from the spatio-temporal distribution of flying alates. *Insect Conservation and Diversity*, **2**, 153–162.

Bourguignon, T., Hayashi, Y. & Miura, T. (2012) Skewed soldier sex ratio in termites: Testing the size-threshold hypothesis. *Insectes Sociaux*, **59**, 557–563.

Brauman, A., Bignell, D. E. & Tayasu, I. (2000) Soil-feeding termites: Biology, microbial associations and digestive mechanisms. *In*: Abe, T., Bignell, D. E. & Higashi, M. (eds.) *Termites: Evolution, Sociality, Symbioses, Ecology.* Dordrecht: Kluwer Academic Press, pp. 233–259.

Brent, C. S. (2009) Control of termite caste differentiation. *In: Gadau, J*. & Fewell, J. H. (eds.) *Organization of Insect Societies. From Genome to Sociocomplexity*. Cambridge: Harvard University Press, pp. 105–127.

Brune, A. & Ohkuma, M. (2011) Role of the termite gut microbiota in symbiotic digestion. *In:* Bignell, D. E., Roisin, Y. & Lo, N. (eds.) *Biology of Termites: A Modern Synthesis.* Dordrecht, Heidelberg, London, New York: Springer, pp. 439–476.

Bulmer, M. S., Eldridge, A. S. & Traniello, J. F. (2001) Variation in colony structure in the subterranean termite *Reticulitermes flavipes*. *Behavioral Ecology and Sociobiology*, **49,** 236–243.

Clément, J.-L. & Bagnères, A.-G. (1998) Nestmate recognition in termites. *In:* Vander Meer, R. K., Breed, M. D., Winston, M. L. & Espelie, K. (eds.) *Pheromone Communication in Social Insects: Ants, Wasps, Bees and Termites*. Boulder: Westview Press, pp. 125–155.

Cleveland, L. R., Hall, S. K., Sanders, E. P. & Collier, J. (1934) The wood feeding roach *Cryptocercus*, its protozoa, and the symbiosis between protozoa and roach. *Memoirs of the American Academy of Arts and Sciences*, **17**, 185–382.

Collins, N. M. (1981) Populations, age structure and survivorship of colonies of *Macrotermes bellicosus* (Isoptera: Macrotermitinae). *Journal of Animal Ecology*, **50**, 293–311.

Darlington, J. P. E. C. (1984) A method for sampling for populations of large termite nests. *Annals of Applied Biology*, **104**, 427–436.

Darlington, J. P. E. C. (1990) Populations in nests of the termite *Macrotermes subhyalinus* in Kenya. *Insectes Sociaux*, **37**, 158–168.

Darlington, J. P. E. C. (1991) Turnover in the populations within mature nests of the termite *Macrotermes michaelseni* in Kenya. *Insectes Sociaux*, **38**, 251–262.

Darlington, J. P. E. C. & Dransfield, R. D. (1987) Size relationships in nest populations and mound parameters in the termite *Macrotermes michaelseni* in Kenya. *Insectes Sociaux*, **34**, 165–180.

Darlington, J. P. E. C., Zimmerman, P. R. & Wandiga, S. O. (1992) Populations in nests of the termite *Macrotermes jeanneli* in Kenya. *Journal of Tropical Ecology*, **8**, 73–85.

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

Donovan, S. E., Jones, D. T., Sands, W. A. & Al., E. (2000). Morphological phylogenetics of termites (Isoptera). *Biological Journal of the Linnean Society*, **70**, 467–513.

Dosso, K., Konate, S., Aidara, D. & Linsenmair, K. E. (2010) Termite diversity and abundance across fire-induced habitat variability in a tropical moist savanna (Lamto, Central Cote d'Ivoire). *Journal of Tropical Ecology*, **26**, 323–334.

Eggleton, P. (1994) Termites live in a pear-shaped world: A response to platnick. *Journal of Natural History*, **28**, 1209–1212.

Eggleton, P. (2000) Global patterns of termite diversity. *In:* Abe, T., Bignell, D. E. & Higashi, M. (eds.) *Termites: Evolution, Sociality, Symbiosis and Ecology.* Netherlands: Kluwer Academic Publishers, pp. 25–51.

Eggleton, P. & Tayasu, I. (2001) Feeding groups, lifetypes and the global ecology of termites. *Ecological Research*, **16**, 941–960.

Eggleton, P., Williams, P. H. & Gaston, K. J. (1994) Explaining global termite diversity: Productivity or history? *Biodiversity and Conservation*, **3**, 318–330.

Engel, M. S., Grimaldi, D. A. & Krishna, K. (2009) Termites (Isoptera): Their phylogeny, classification, and rise to ecological dominance. *American Museum Novitates*, **3650**, 1–27.

Evans, T. A., Inta, R., Lai, J. C. S., Prueger, S., Foo, N. W., Fu, E. W. & Lenz, M. (2009) Termites eavesdrop to avoid competitors. *Proceedings of the Royal Society of London B*, **276,** 4035–4041.

Evans, T. A., Lai, J. C. S., Toledano, E., Mcdowall, L., Rakotonarivo, S. & Lenz, M. (2005) Termite assess wood size by using vibration signals. *Proceedings of the National Academy of Science USA*, **102,** 3732–3737.

Gay, F. J. & Calaby, J. H. (1970) Termites of the Australian region. *In:* Krishna, K. & Weesner, F. M. (eds.) *Biology of Termites II.* New York: Academic Press, pp. 393–448.

Gerber, C., Badertscher, S. & Leuthold, R. H. (1988) Polyethism in *Macrotermes bellicosus* (Isoptera). *Insectes Sociaux*, **35,** 226–240.

Grandcolas, P. & D'Haese, C. (2004) The origin of a 'true' worker caste in termites: Phylogenetic evidence is not decisive. *Journal of Evolutionary Biology*, **15,** 885–888.

Grasse, P. P. (1949) Ordre des Isopteres ou termites. *In*: Grasse, P. P. (ed.) *Traite de Zoologie.* Paris: Masson, pp. 408–544

Grasse, P. P. (1982) *Termitologia: Anatomie-Physiologie-Biologie-Systematique des Termites. Tome I*, Paris: Masson.

Grasse, P. P. (1984) *Termitologia. Fondation des Societes-Construction. Tome II*, Paris: Masson.

Grasse, P. P. (1986) *Termitologia. Comportement-Socialité-Écologie-Évolution-Systématique. Tome III*, Paris: Masson.

Grasse, P. P. & Noirot, C. (1947) Le polymorphisme social du termite à cou jaune (*Kalotermes flavicollis*) les faux-ouvriers ou pseudergates et les mues regressives. *Comptes Rendus de Academie des Sciences*, **224**, 219–221.

Grasse, P. P. & Noirot, C. (1948) La "climatisation" de la termitière par ses habitants et le transport de l'eau. *Comptes Rendus de Academie des Sciences*, **227**, 869–871.

Grasse, P. P. & Noirot, C. (1951) Nouvelles recherches sur la biologie de divers termites champignonnistes (Macrotermitinae). *Annales des Sciences Naturelles Zoologie et Biologie Animale*, **11, 13**, 291–342.

Hamilton, W. D. & May, R. M. (1977) Dispersal in stable habitats. *Nature*, **269**, 578–581.

Han, S. H. & Bordereau, C. (1992) From colony foundation to dispersal flight in a higher fungus-growing termite, *Macrotermes subhyalinus*, (Isoptera, Macrotermitinae). *Sociobiology*, **20,** 219–231.

Hausberger, B., Van Neer, A., Kimpel, D. & Korb, J. (2011) Uncovering cryptic species diversity of a termite community in a West African savanna. *Molecular Phylogenetics and Evolution*, **61**, 964–969.

Haverty, M. I. & Howard, R. W. (1981) Production of soldiers and maintenance of soldier proportions by laboratory experimental groups of *Reticulitermes flavipes* (Kollar) and *Reticulitermes virginicus* (Banks) (Isoptera: Rhinotermitidae). *Insectes Sociaux*, **28**, 32–39.

Haverty, M. I., Page, M., Nelson, L. J. & Blomquist, G. J. (1988) Cuticular hydrocarbons of dampwood termites, *Zootermopsis*: intra- and intercolony variation and potential as taxonomic characters. *Journal of Chemical Ecology*, **14**, 1035–1058.

Heath, H. (1903) The habits of California termites. *Biological Bulletin*, 4, 47–63.

Heath, H. (1907) The longevity of members of different castes of *Termopsis angusticollis*. *Biological Bulletin*, **13**, 161–164.

Heath, H. (1927) Caste formation in the termite genus *Termopsis*. *Journal of Morphology and Physiology*, **43**, 387–423.

Heinze, J. & Schrempf, A. (2008) Aging and reproduction in social insects - a mini-review. *Gerontology*, **54**, 160–167.

Higashi, M., Abe, T. & Burns, T. P. (1992) Carbo-nitrogen balance and termite ecology. *Proceedings of the Royal Society of London B*, **249**, 303–308.

Hoffmann, K., Gowin, J., Hartfelder, K. & Korb, J. (2014) The scent of royalty: A P450 gene signals reproductive status in a social insect. *Molecular Biology and Evolution*, **31**, 2689–2696.

Howard, K. J. & Thorne, B. L. (2011) Eusocial evolution in termites and hymenoptera. *In:* Bignell, D. E., Roisin, Y. & Lo, N. (eds.) *Biology of Termites: A Modern Synthesis.* Dordrecht, Heidelberg, London, New York: Springer, pp. 97–132.

Howard, K. J., Johns, P. M., Breisch, N. L. & Thorne, B. L. (2013) Frequent colony fusions provide opportunities for helpers to become reproductives in the termite *Zootermopsis nevadensis*. *Behavioural Ecology and Sociobiology*, **67**, 1575–1585.

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

Inward, D. J. G., Vogler, A. P. & Eggleton, P. (2007b) A comprehensive phylogenetic analysis of termites (Isoptera) illuminates key aspects of their evolutionary biology. *Molecular Phylogenetics and Evolution*, **44**, 953–967.

Johns, P. M., Howard, K. J., Breisch, N. L., Rivera, A. & Thorne, B. L. (2009) Nonrelatives inherit colony resources in a primitive termite. *Proceedings of the National Academy of Sciences USA*, **106,** 17452–17456.

Johnson, R. A. (1981) Colony development and establishment of the fungus comb in *Microtermes sp. nr. umbaricus* (Sjöstedt) (Isoptera: Macrotermitinae) from Nigeria. *Insectes Sociaux*, **28,** 3–12.

Jones, D. T. & Eggleton, P. (2011) Global biogeography of termites: A compilation of sources. *In:* Bignell, D. E., Roisin, Y. & Lo, N. (eds.) *Biology of Termites: A Modern Synthesis.* Dordrecht, Heidelberg, London, New York: Springer, pp. 477–498.

Josens, G. (1982) Adaptive strategies in colony foundations of two Termitidae. *In:* Breed, M. D., Michener, C. & Evans, H. E. (eds.) *IUSSI*, 1982 Boulder, CO: Westview Press, pp. 66.

Josens, G. (1983) The soil fauna of tropical savannas III: The termites. *In:* Bourliere, F. (ed.) *Tropical Savannas.* Amsterdam: Elsevier, pp. 505–524.

Kaib, M., Hacker, M. & Brandl, R. (2001) Egg laying in monogynous and polygynous colonies of the termite *Macrotermes michaelseni* (Isoptera, Macrotermitinae). *Insectes Sociaux*, **48,** 231–237.

Kambhampati, S. & Eggleton, P. (2000) Taxonomy and phylogeny of termites. *In:* Abe, T., Bignell, D. E. & Higashi, M. (eds.) *Termites: Evolution, Sociality, Symbiosis and Ecology.* Netherlands: Kluwer Academic Publishers, pp. 1–23.

Keller, L. (1998) Queen lifespan and colony characteristics in ants and termites. *Insectes Sociaux*, **45**, 235–246.

Keller, L. & Genoud, M. (1997) Extraordinary lifespans in ants: A test of evolutionary theories of ageing. *Nature*, **389**, 958–960.

Korb, J. (2007a) Termites. *Current Biology*, **17**, R995–999.

Korb, J. (2007b) Workers of a drywood termite do not work. *Frontiers in Zoology*, **4**, e7.

Korb, J. (2008) The ecology of social evolution in termites. *In:* Korb, J. & Heinze, J. (eds.) *Ecology of Social Evolution.* Berlin, Heidelberg: Springer, pp. 151–174.

Korb, J. (2009) Termites: An alternative road to eusociality and the importance of group benefits in social insects. *In:* Gadau, J. & Fewell, J. H. (eds.) *Organization of Insect Societies. From Genome to Sociocomplexity*. Cambridge: Harvard University Press, pp. 128–147.

Korb, J. (2011) Termite mound architecture, from function to construction. *In:* Bignell, D. E., Roisin, Y. & Lo, N. (eds.) *Biology of Termites: A Modern Synthesis.* Dordrecht, Heidelberg, London, New York: Springer, pp. 349–374.

Korb, J. (2016) Towards a more pluralistic view of termite social evolution. *Ecological Entomology*, **41**, 34–36.

Korb, J. & Hartfelder, K. (2008) Life history and development—a framework for understanding the ample developmental plasticity in lower termites. *Biological Reviews*, **83,** 295–313.

Korb, J. & Heinze, J. (2008a) *Ecology of Social Evolution.* Heidelberg: Springer.

Korb, J. & Heinze, J. (2008b) The ecology of social life: A synthesis. *In:* Korb, J. & Heinze, J. (eds.) *Ecology of Social Evolution.* Heidelberg: Springer, pp. 245–260.

Korb, J. & Linsenmair, K. E. (2000) Thermoregulation of termite mounds: What role does ambient temperature and metabolism of the colony play? *Insectes Sociaux*, **47**, 357–363.

Korb, J. & Linsenmair, K. E. (2001) Resource availability and distribution patterns, indicators of competition between *Macrotermes bellicosus* and other macro-detritivores in the Comoé National Park, Côte d'Ivoire. *African Journal of Ecology*, **39**, 257–265.

Korb, J. & Linsenmair, K. E. (2002) Evaluation of predation risk in the collectively foraging termite *Macrotermes bellicosus*. *Insectes Sociaux*, 49**,** 264–269.

Korb, J. & Roux, E. A. (2012) Why join a neighbour: Fitness consequences of colony fusions in termites. *Journal of Evolutionary Biology*, **25**, 2161–2170.

Korb, J. & Schmidinger, S. (2004) Help or disperse? Cooperation in termites influenced by food conditions. *Behavioral Ecology and Sociobiology*, **56**, 89–95.

Korb, J. & Schneider, K. (2007) Does kin structure explain the occurrence of workers in a lower termite? *Evolutionary Ecology*, **21**, 817–828.

Korb, J., Buschmann, M., Schafberg, S., Liebig, J. & Bagneres, A. G. (2012) Brood care and social evolution in termites. *Proceedings of the Royal Society of London B*, **279**, 2662–2671.

Krishna, K., Grimaldi, D. A., Krishna, V. & Engel, M. S. (2013) Treatise on the Isoptera of the world. *Bulletin of the American Museum of Natural History*, **377,** 1–2704.

Lacey, M. J., Lenz, M. & Evans, T. A. (2010) Cryoprotection in dampwood termites (Termopsidae, Isoptera). *Journal of Insect Physiology*, **56**, 1–7.

LaFage, J. P. & Nutting, W. L. (1978) Nutrient dynamics of termites. *In*: Brian, M. V. (ed.) *Production Ecology of Ants and Termites*. Cambridge: Cambridge University Press.

Legendre, F., Whiting, M. F., Bordereau, C., Cancello, E. M., Evans, T. A. & Grandcolas, P. (2008) The phylogeny of termites (Dictyoptera: Isoptera) based on mitochondrial and nuclear markers: Implications for the evolution of the worker and pseudergate castes, and foraging behaviors. *Molecular Phylogenetics and Evolution*, **48**, 615–627.

Lenz, M. (1987) Brood production by imaginal and neotenic pairs of *Cryptotermes brevis* (Walker): The significance of helpers (Isoptera: Kalotermitidae). *Sociobiology*, **13,** 59–66.

Lenz, M. (1994) Food resources, colony growth and caste development in wood-feeding termites. *In*: Hunt, J. & Nalepa, C. A. (eds.) *Nourishment and Evolution in Insect Societies.* New Delhi: Oxford and IBH Publishing Co. Prt. Ltd, pp. 159–209.

Lepage, M. (1989) Ecologie et adaptations des sociétés de termites en Afrique tropicale aride. *Bulletin d'Ecologie*, **20,** 59–63.

Leuthold, R. H. (1979) Chemische Kommunikation als Grundlage des Soziallebens bei Termiten. *In:* Lüscher, M. (ed.) *Insektenstaaten. Neuere Erkenntnisse.* Bern: Naturhistorisches Museum.

Leuthold, R. H. (1990) L'organisation sociale chez des termites championnistes du genre. *Macrotermes. Actes de Coloques Insectes Sociaux*, **6**, 9–20.

Liebig, J., Eliyahu, D. & Brent, C. S. (2009) Cuticular hydrocarbon profiles indicate reproductive status in the termite *Zootermopsis nevadensis*. *Behavioral Ecology and Sociobiology*, **63**, 1799–1807.

Lo, N., Engel, M. S., Cameron, S., Nalepa, C. A., *et al*. (2007) Save Isoptera: A comment on Inward *et al*. *Biology Letters*, **3,** 564–565.

Lo, N., Tokuda, G. & Watanabe, H. (2011) Evolution and function of endogenous termite cellulases. *In:* Bignell, D. E., Roisin, Y. & Lo, N. (eds.) *Biology of Termites: A Modern Synthesis.* Dordrecht, Heidelberg, London, New York: Springer, pp. 51–68.

Long, C. E. & Thorne, B. L. (2006) Resource fidelity, brood distribution and foraging dynamics in complete laboratory colonies of *Reticulitermes flavipes* (Isoptera, Rhinotermitidae). *Ethology, Ecology & Evolution*, **18,** 113–125.

Luchetti, A., Dedeine, F., Velona, A. & Mantovani, B. (2013) Extreme genetic mixing within colonies of the wood-dwelling termite *Kalotermes flavicollis* (Isoptera, Kalotermitidae). *Molecular Ecology*, **22**, 3391–3402.

Lüscher, M. (1952) Untersuchungen über das individuelle Wachstum bei der Termite *Kalotermes flavicollis* Fabr. (Ein Beitrag zum Kastenbildungsproblem). *Biologisches Zentralblatt*, **71**, 529–543.

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

Luykx, P. (1993) Turnover in termite colonies: A genetic study of colonies of *Incisitermes schwarzi* headed by replacement reproductives. *Insectes Sociaux*, **40**, 191–205.

Lys, J. A. & Leuthold, R. H. (1991) Task-specific distribution of the worker castes in extranidal activities in *Macrotermes bellicosus* (Smeathman): Observations of behaviour during food acquisition. *Insectes Sociaux*, **38**, 161–170.

Matsuura, K. (2006) A novel hypothesis for the origin of the sexual division of labor in termites: Which sex should be soldiers? *Evolutionary Ecology*, **20**, 565–574.

Matsuura, K. (2011) Sexual and asexual reproduction in termites. *In:* Bignell, D. E., Roisin, Y. & Lo, N. (eds.) *Biology of Termites: A Modern Synthesis.* Dordrecht, Heidelberg, London, New York: Springer, pp. 255–278.

Matsuura, K., Himuro, C., Yokoi, T., Yamamoto, Y., Vargo, E. L. & Keller, L. (2010) Identification of a pheromone regulating caste differentiation in termites. *Proceedings of the National Academy of Science USA*, **107**, 12963–12968.

Minnick, D. R. (1973) The flight and courtship behavior of the drywood termite, *Cryptotermes brevis*. *Environmental Entomology*, **2**, 587–591.

Miura, T. (2004) Proximate mechanisms and evolution of caste polyphenism in social insects: From sociality to genes. *Ecological Research*, **19**, 141–148.

Muller, H. & Korb, J. (2008) Male or female soldiers? An evaluation of several factors on soldier sex ratio in lower termites. *Insectes Sociaux*, **55**, 213–219.

Myles, T. (1988) Resource inheritance in social evolution from termite to man. *In:* Slobodchikoff, C. N. (ed.) *The Ecology of Social Behavior.* New York: Academic Press, pp. 379–423.

Myles, T. G. (1999) Review of secondary reproduction in termites (Insecta: Isoptera) with comments on its role in termite ecology and social evolution. *Sociobiology*, **33,** 1–91.

Nalepa, C. & Bandi, C. (2000) Characterizing the ancestors: Paedomorphosis and termite evolution. *In*: T. Abe, D. E. B. a. M. H. (eds.) *Termites: Evolution, Sociality, Symbioses, Ecology.* Dordrecht: Kluwer Academic Press, pp. 53–76.

Nalepa, C. A. (1984) Colony composition, protozoan transfer and some life history characteristics of the woodroach *Cryptocercus punctulatus* Scudder (Dictyoptera: Cryptocercidae). *Behavioural Ecology and Sociobiology*, **14**, 273–279.

Nalepa, C. A. (1988) Cost of parental care in the woodroach *Cryptocercus punctulatus* Scudder (Dictyoptera: Cryptocercidae). *Behavioural Ecology and Sociobiology*, **23**, 135–140.

Nalepa, C. A. (1994) Nourishment and the origin of termite eusociality. *In:* Hunt, J. H. & Nalepa, C. A. (eds.) *Nourishment and Evolution in Insect Societies.* Westview Press, Inc, pp. 57–104.

Nalepa, C. A. (2011) Altricial development in wood-feeding cockroaches: The key antecedent to termite eusociality. *In:* Bignell, D. E., Roisin, Y. & Lo, N. (eds.) *Biology of Termites: A Modern Synthesis.* Dordrecht, Heidelberg, London, New York: Springer, pp. 69–96.

Nalepa, C. A. (2015) Origin of termite eusociality: trophallaxis integrates the social, nutritional, and microbial environments. *Ecological Entomology*, **40**, 323–335.

Neoh, K. B. & Lee, C. Y. (2011) Developmental stages and caste composition of a mature and incipient colony of the drywood termite, *Cryptotermes dudleyi* (Isoptera: Kalotermitidae). *Journal of Economic Entomology*, **104,** 622–628.

Nobre, T., Rouland-Lefevre, C. & Aanen, D. K. (2011) Comparative biology of fungus cultivation in termites and ants. *In:* Bignell, D. E., Roisin, Y. & Lo, N. (eds.) *Biology of Termites: A Modern Synthesis.* Dordrecht, Heidelberg, London, New York: Springer, pp. 193–210.

Noirot, C. (1969) Formation of castes in the higher termites. *In:* Krishna, K. & Weesner, F. M. (eds.) *Biology of Termites Vol. 1.* New York: Academic Press.

Noirot, C. (1970) The nests of termites. *In:* Krishna, K. & Weesner, F. M. (eds.) *Biology of Termites Vol. 2.* New York: Academic Press.

Noirot, C. (1985a) The caste system in higher termites. *In:* Watson, J. A. L., Okot-Kotber, B. M. & Noirot, C. (eds.) *Caste Differentiation in Social Insects.* Oxford: Pergamon Press, pp. 75–86.

Noirot, C. (1985b) Pathways of caste development in the lower termites. *In:* Watson, J. A. L., Okot-Kotber, B. M. & Noirot, C. (eds.) *Caste Differentiation in Social Insects.* Oxford: Pergamon Press, pp. 41–58.

Noirot, C. (1990) Sexual castes and reproductive strategies in termites. *In:* Engels, W. (ed.) *An Evolutionary Approach to Castes and Reproduction.* Berlin: Springer Verlag, pp. 3–35.

Noirot, C. & Bordereau, C. (1988) Termite polymorphism and morphogenetic hormones. *In:* Gupta, A. P. (ed.) *Morphogenetic Hormones of Arthropods.* New Brunswick: Rutgers University Press, pp. 293–324.

Noirot, C. & Darlington, J. P. E. C. (2000) Termite nests: Architecture, regulation and defence. *In:* Abe, T., Bignell, D. E. & Higashi, M. (eds.) *Termites: Evolution, Sociality, Symbiosis and Ecology.* Netherlands: Kluwer Academic Publishers, pp. 121–139.

Noirot, C. & Pasteels, J. M. (1987) Ontogenic development and evolution of the worker caste in termites. *Experientia*, **43**, 851–860.

Noirot, C. & Pasteels, J. M. (1988) The worker caste is polyphyletic in termites. *Sociobiology*, **14**, 15–20.

Noirot, C. & Thorne, B. L. (1988) Ergatoid reproductives in *Nasutitermes columbicus* (Isoptera, Termitidae). *Journal of Morphology*, **195**, 83–93.

Nutting, W. L. (1969) Flight and colony foundation. *In:* Krishna, K. & Weesner, F. M. (eds.) *Biology of Termites Vol. 1.* New York: Academic Press.

Ohkuma, M. & Brune, A. (2011) Diversity, structure, and evolution of the termite gut microbial community. *In:* Bignell, D. E., Roisin, Y. & Lo, N. (eds.) *Biology of Termites: A Modern Synthesis.* Dordrecht, Heidelberg, London, New York: Springer, pp. 413–438.

Okot-Kotber, B. M. (1985) Mechanisms of caste determination in a higher termite, *Macrotermes michaelseni* (Isoptera, Macrotermitidae). *In*: Watson, J. A. L., Okot-Kotber, B. M. & Noirot, C. (eds.) *Caste Differentiation in Social Insects.* Oxford: Pergamon Press, pp. 267–306.

Oster, G. F. & Wilson, E. O. (1978) *Caste and Ecology of Social Insects.* Princeton, Princeton University Press.

Pickens, A. L. (1934) The biology and economic significance of the Western subterranean termite, *Reticulitermes hesperus*. *In:* Kofoid, C. A. (ed.) *Termites and Termite Control.* Berkeley: University of California Press, pp. 157–183.

Poulsen, M., Hu, H., Li, C., Chen, Z., Nygaard, S., *et al.* (2014) Holobiomic division of labor in fungus-farming termites. *Proceedings of the National Academy of Sciences USA*, **111**, 14500–14505.

Queller, D. C. & Strassmann, J. E. (1998) Kin selection and social insects. *Bioscience*, **48,** 165–178.

Rohrig, A., Kirchner, W. H. & Leuthold, R. H. (1999) Vibrational alarm communication in the African fungus-growing termite genus Macrotermes (Isoptera, Termitidae). *Insectes Sociaux*, **46**, 71–77.

Roisin, Y. (2000) Diversity and evolution of caste patterns. *In:* Abe, T., Bignell, D. E. & Higashi, M. (eds.) *Termites: Evolution, Sociality, Symbioses, Ecology.* Dordrecht, Netherlands: Kluwer Academic Publishers, pp. 95–119.

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

Roisin, Y. & Korb, J. (2011) Social organisation and the status of workers in termites. *In:* Bignell, D. E., Roisin, Y. & Lo, N. (eds.) *Biology of Termites: A Modern Synthesis.* Dordrecht, Heidelberg, London, New York: Springer, pp. 133–164.

Roisin, Y. & Pasteels, J. M. (1987) Caste developmental potentialities in the termite *Nasutitermes novarumhebridarum*. *Entomologia Experimentalis et Applicata*, **44**, 277–287.

Rosengaus, R. B., Moustakas, J. E., Calleri, D. V. & Traniello, J. F. A. (2003) Nesting ecology and cuticular microbial loads in dampwood (*Zootermopsis angusticollis*) and drywood termites (*Incisitermes minor*, Schwarzi, *Cryptotermes cavifrons*). *Journal of Insect Science*, **3,** e31.

Rosengaus, R. B., Traniello, J. F. A. & Bulmer, M. S. (2011) Ecology, behavior and evolution of disease resistance in termites. *In*: Bignell, D. E., Roisin, Y. & Lo, N. (eds.) *Biology of Termites: A Modern Synthesis.* Dordrecht, Heidelberg, London, New York: Springer, pp. 165–192.

Rouland-Lefèvre, C. (2000) Symbiosis with fungi. *In:* Abe T, B. D., Higashi M (ed.) *Termites: Evolution, Sociality, Symbioses, Ecology.* Dordrecht: Kluwer Academic Publishers, pp. 289–306.

Rupf, T. & Roisin, Y. (2008) Coming out of the woods: do termites need a specialized worker caste to search for new food sources? *Naturwissenschaften*, **95**, 811–819.

Sands, W. A. (1961) Foraging behavior and feeding habits in five species of Trinervitermes in West Africa. *Entomologia Experimentalis et Applicata*, **4,** 277–288.

Sands, W. A. (1972) The soldierless termites of Africa (Isoptera: Termitidae). *Bulletin of the British Museum (Natural History) Entomology*, **S18,** 1–244.

Scharf, M. E., Buckspan, C. E., Grzymala, T. L. & Zhou, X. (2007) Regulation of polyphenic caste differentiation in the termite *Reticulitermes flavipes* by interaction of intrinsic and extrinsic factors. *Journal of Experimental Biology*, **210,** 4390–4398.

Schmidt, A. M., Jacklyn, P. & Korb, J. (2013) Isolated in an ocean of grass: Low levels of gene flow between termite subpopulations. *Molecular Ecology*, **22,** 2096–2105.

Schmidt, A. M., Jacklyn, P. & Korb, J. (2014) 'Magnetic' termite mounds: Is their unique shape an adaptation to facilitate gas exchange and improve food storage. *Insectes Sociaux*, **41**, 61–69.

Seelinger, G. & Seelinger, U. (1983) On the social organisation, alarm and fighting in the primitive cockroach *Cryptocercus punctulatus* Scudder. *Zeitschrift für Tierpsychologie*, **61**, 315–333.

Shellman-Reeve, J. S. (1997) The spectrum of eusociality in termites. *In*: Choe, J. C. & Crespi, B. J. (eds.) *The Evolution of Social Behavior in Insects and Arachnids.* Cambridge: Cambridge University Press, pp. 52–93.

Snyder, T. E. (1956) *Annotated, Subject-Heading Bibliography of Termites 1350 B.C. to A.D. 1954*. Washington D.C.: Smithsonian Institution.

Stearns, S. C. (1992) *The Evolution of Life Histories.* Oxford, Oxford University Press.

Thorne, B. & Traniello, J. (2003) Comparative social biology of basal taxa of ants and termites. *Annual Reviews of Entomology*, **48,** 283–306.

Thorne, B., Breisch, N. & Haverty, M. I. (2002) Longevity of kings and queens and first time of reproduction of fertile progeny in dampwood termite (Isoptera; Termopsidae; *Zootermopsis*) colonies with different reproductive structures. *Journal of Animal Ecology*, **71,** 1030–1041.

Thorne, B. L. (1982) Polygyny in termites: multiple primary queens in colonies of *Nasutitermes corniger* (Motschulsky) (Isoptera: Termitidae). *Insectes Sociaux*, **29**, 102–107.

Thorne, B. L. (1983) Alate production and sex ratio in colonies of the Neotropical termite *Nasutitermes corniger* (Isoptera; Termitidae). *Oecologia*, 58, 103–109.

Thorne, B. L. (1984) Polygyny in the Neotropical termite *Nasutitermes corniger*: life history consequences of queen mutualism. *Behavioral Ecology and Sociobiology*, **14**, 117–136.

Thorne, B. L. (1997) Evolution of eusociality in termites. *Annual Review of Ecology and Systematics*, **28**, 27–54.

Thorne, B.L. & Haverty, M. I. (2000) Nest growth and survivorship in three species of Neotropical *Nasutitermes* (Isoptera: Termitidae). *Environmental Entomology*, **29**, 256–264.

Thorne, B. L., Traniello, J. F. A., Adams, E. S. & Bulmer, M. (1999) Reproductive dynamics and colony structure of subterranean termites of the genus Reticulitermes (Isoptera, Rhinotermitidae): A review of the evidence from behavioral, ecological, and genetic studies. *Ethology Ecology Evolution*, **11,** 149–169.

Thorne, B. L., Breisch, N. & Muscedere, M. (2003) Evolution of eusociality and the soldier caste in termites: Influence of intraspecific competition and accelerated inheritance. *Proceedings of the National Academy of Sciences USA*, **100,** 12808–12813.

Traniello, J. F. & Leuthold, R. H. (2000) Behavior and ecology of foraging in termites. *In:* Abe, T., Bignell, D. E. & Higashi, M. (eds.) *Termites: Evolution, Sociality, Symbiosis and Ecology.* Netherlands: Kluwer Academic Publishers, pp. 141–168.

Vargo, E. (2003) Hierarchical analysis of colony and population genetic structure of the eastern subterranean termite, *Reticulitermes flavipes*, using two classes of molecular markers. *Evolution*, **57**, 2805–2818.

Vargo, E. L. & Husseneder, C. (2009) Biology of subterranean termites: Insights from molecular studies of Reticulitermes and Coptotermes. *Annual Review of Entomology*, **54**, 379–403.

Vargo, E. L. & Husseneder, C. (2011) Genetic structure of termite colonies and populations. *In:* Bignell, D. E., Roisin, Y. & Lo, N. (eds.) *Biology of Termites: A Modern Synthesis.* Dordrecht, Heidelberg, London, New York: Springer, pp. 321–348.

Waller, D. A. (1988) Ecological similarities of fungus-growing ants (Attini) and termites (Macrotermitinae). *In:* Troger, J. C. (ed.) *Advances in Myrmecology.* New York: E.J. Bill, pp. 337–345.

Waller, D. A. & La Fage, J. P. (1987) Nutritional ecology of termites. *In:* Slansky, F. & Rodriguez, J. G. (eds.) *Nutritional Ecology of Insects, Mites, and Spiders*. Chichester, New York: John Wiley, pp. 487–532.

Watson, J. A. L. & Abbey, H. M. (1989) A 17-year old primary reproductive of *Mastotermes darwiniensis* (Isoptera). *Sociobiology*, **15**, 279–284.

Watson, J. A. L. & Sewell, J. J. (1981) The origin and evolution of caste systems in termites. *Sociobiology*, **6**, 101–118.

Weil, T., Hoffmann, K., Kroiss, J., Strohm, E. & Korb, J. (2009) Scent of a queen-cuticular hydrocarbons specific for female reproductives in lower termites. *Naturwissenschaften*, **96,** 315–319.

Wilkinson, W. (1962) Dispersal of alates and establishment of new colonies in *Cryptotermes havilandi* (Sjöstedt) (Isoptera, Kalotermitidae). *Bulletin of Entomological Research*, **53**, 265–286.

Wilkinson, W. (1963) The alate flight and colony foundation of *Cryptotermes havilandi* (Sjöstedt) (Isoptera, Kalotermitidae). *Symposium of Genetics and Biologie Italy*, **11**, 269–275.

Wilson, E. (1971) *Insect Societies.* Cambridge, MA: Belknap Press of Harvard University Press.

Wood, T. G. & Thomas, R. J. (1989) The mutualistic association between macrotermitinae and termitomyces. *In:* Wilding, N., Collins, N. M., Hammond, P. M. & Webber, J. F. (eds.) *Insect-fungus Interactions.* New York: Academic Press, pp. 69–92.

Wood, T. G., Johnson, R. A. & Ohiagu, C. E. (1977) Populations of termites (Isoptera) in natural and agricultural ecosystems in Southern Guinea savanna near Mokwa, Nigeria. *GeoEcoTrop*, **1,** 139–148.