



Annu. Rev. Entomol. 2003. 48:283-306
doi: 10.1146/annurev.ento.48.091801.112611
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First published online as a Review in Advance on August 28, 2002

COMPARATIVE SOCIAL BIOLOGY OF BASAL TAXA OF ANTS AND TERMITES

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Key Words Formicidae, Isoptera, eusocial evolution, colony structure, division of labor

■ **Abstract** Lacking a comprehensive fossil record, solitary representatives of the taxa, and/or a definitive phylogeny of closely related insects, comparison of the life history and social biology of basal, living groups is one of the few available options for developing inferences regarding the early eusocial evolution of ants and termites. Comparisons of a select group of basal formicid and isopteran taxa suggest that the reproductive organization of colonies and their patterns of division of labor were particularly influenced, in both groups, by nesting and feeding ecology. Opportunities for serial inheritance of the nest structure and colony population by kin may have been significant in the evolution of multiple reproductive forms and options. Disease has been a significant factor in the evolution of social organization in ants and termites, but the adaptive mechanisms of infection control differ. Evaluations of the convergent and divergent social biology of the two taxa can generate novel domains of research and testable hypotheses.

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INTRODUCTION

The study of the evolution of complex traits is greatly facilitated by the existence of phylogenetic intermediates that express gradual transitions in character states, and the comparative analysis of these transitions often provides the most compelling data for revealing patterns and developing robust hypotheses regarding selective factors that influence evolutionary change. Such stepping stone intermediates, however, are rarely present as a relatively complete fossil or living series, reflecting incomplete preservation and discovery of fossils, species extinction, the evanescence of annectant forms, and the fact that evolution is not always a gradual process. Eusociality is a highly complex trait of profound evolutionary interest because of the existence of subfertile or sterile colony members. Comparative studies of sister groups and basal taxa have been insightful in examining the evolution of eusociality in clades of bees and wasps because modern species show a cline of life histories that range from solitary to eusocial. Similar cladistic analyses are absent in ants and termites because all the roughly 10,200 species of living ants and over 2600 species of extant termites are eusocial, and solitary ancestors are sufficiently distant to obscure the linkages among selective regimes.

The structural elements of social organization in the Hymenoptera and Isoptera are highly convergent. Unlike the haplodiploid Hymenoptera, however, both sexes of termites are diploid, rendering explanations for eusocial evolution based on asymmetries in genetic relatedness generated by meiosis and fertilization inapplicable to termites. Nevertheless, the similarities and differences in the preadaptive characteristics of each group and ecological forces that impelled the evolution of social organization may offer significant sociobiological insight. Lacking the opportunity for comparative study within taxa, here we explore commonalities and contrasts in the life history, colony structure, reproductive dynamics, and socioecology of the most primitive living lineages of ants and termites. Although these phylogenetically divergent insects differ in fundamental ways (such as holometaboly in Hymenoptera and hemimetaboly in Isoptera), eusociality is based on the elaboration of family units in both groups, and eusocial evolution may be constructively discerned through focused comparative assessments. Observations on the biology of extant taxa cannot be used to definitively reconstruct ancestral states prior to the evolution of worker subfertility or sterility and thus cannot appropriately be used to test hypotheses or predictions regarding the evolution of eusociality. Once protoants or prototermites crossed the threshold of eusociality, life history constraints, especially those related to reproductive division of labor, may have

been essentially irreversible. Data that allow specific comparisons are not always available, so a collateral goal of this paper is to identify domains of research that would further advance such an approach. We begin with an overview of the phylogenetic origin of ants and termites, identify the basal taxa considered in the review, and justify the inclusions of those groups central to our comparative analysis.

ORIGIN OF ANTS AND BASAL ANT SYSTEMATICS

The origins of the formicid theme of social organization have been sought in the vespid wasps. There is a void in social behavior between basal ants and their closest vespid relatives, although the fossil record offers some evidence of how and when ants attained their morphological distinctiveness and suggests a basic timeline for the emergence of the socially advanced groups. The hypothetical ancestral vespid wasps are thought to be linked to ants through the subfamily Sphecomyrminae, the pleisiomorphic sister group to all ants, with its extinct Cretaceous fossil genera *Sphecomyrma* and *Cretomyrma* (124). *Sphecomyrma freyi*, dating from New Jersey amber of the late middle Cretaceous, exhibits a constellation of nonsocial wasp and ant traits: short bidentate mandibles, a reduced and wingless thorax, a petiolar constriction, and significantly, what appears to be a metapleural gland (33). It is considered the “nearly perfect link between some of the modern ants and the nonsocial aculeate wasps” (33, p. 23). *Kyromyrma neffi*, the first specimen of an extant ant subfamily (the Formicinae), also collected from the New Jersey amber (c. 92 million years ago, has an acidopore and is 50 mya older than *Sphecomyrma* (23). This suggests a divergence of the basal lineages of ants from the Sphecomyrminae approximately 105–110 mya. Further details of the fossil record and adaptive radiation of ants are given in Hölldobler & Wilson (33) and Crozier et al. (14), which provide molecular data dating the origin of ants to the Jurassic.

The basal division of the 17 ant subfamilies (5) separates the Myrmicinae, Pseudomyrmecinae, Nothomyrmeciinae, Myrmeciinae, Formicinae, and the Dolichoderinae from the remaining subfamilies. The Nothomyrmeciinae, Myrmeciinae, and Ponerinae include genera considered pivotal in ant social evolution because of their comparatively primitive morphology and social organization (33). The final basal group of ants is the Aneuretinae, a formicoid complex subfamily once global in distribution but today represented by a single species, *Aneuretus simoni*, found in limited areas of Sri Lanka (41).

The subfamily Nothomyrmeciinae is monotypic, known only from the single extant and elusive *Nothomyrmecia macrops* Clark from Australia. Its rediscovery in 1978 (104) was somewhat akin to finding the “Holy Grail” of myrmecology, and the collection and observation of queenright colonies made possible detailed accounts of the social organization of this relict species (31, 104). The basal characteristics of this ant include a wasp-like morphology (104), an exceptionally high level of inactivity, and low levels of social exchanges among workers in their small colonies (40). Queens do not receive food or other preferential treatment; indeed,

queens and workers rarely interact. Remarkably, queens living in intact laboratory colonies collect and feed on insect prey on their own. The subfamily Myrmicinae is represented by the Australian bulldog ants of the genus *Myrmecia*, which forms colonies of 600–900 workers (25). Colonies can be founded independently by single queens or polygynously by groups of females (12).

The Ponerinae is a large and diverse subfamily whose representatives display a mixture of basal and derived morphologies and social characters. Primitive ponerines include *Amblyopone*, an ant that exhibits morphologically and behaviorally primitive traits, although other genera in the tribe Amblyoponini show highly derivative characteristics. Because of the great diversity of ponerine ants, including numerous species with clearly derived traits (81, 82), we concentrate on the more primitive forms, using *A. pallipes* as a model, while noting that other species of *Amblyopone* may vary widely in their biology and even include queenless forms (37). In *A. pallipes*, alate queens discard their wings to establish new colonies and forage during the colony foundation stage (33). Nests, which house small colonies averaging roughly a dozen workers, are composed of simple chambers and galleries in soil and decayed wood. Populations of *A. pallipes* are patchy but can be locally abundant (112).

ORIGIN OF ISOPTERA AND INTERFAMILIAL RELATIONSHIPS

The higher-level phylogeny of termites has received considerable interest in the past decade. Although monophyly of the Dictyoptera is accepted (28, 50), relationships among the dictyopteran orders Blattaria, Mantodea, and Isoptera are not fully resolved (6, 17, 42, 44–47, 51, 57, 59, 108). Despite the topological uncertainty regarding whether cockroaches or some lineage(s) of a paraphyletic cockroach clade are the sister group to termites, there is consensus that study of the life history and social organization of the relict wood roach genus *Cryptocercus* provides constructive comparison and potential insights into the biology of prototermites and potential selective forces favoring the evolution of eusociality (10, 67, 68, 107). To date, the fossil record exposes no missing links that indicate intermediate stages between the orders, so identifying the most immediate ancestors of Isoptera, and gleaned the hints that they might reveal regarding the transition from solitary to eusocial life histories, has been impossible.

The early evolution and intrafamilial relationships of Isoptera also are not fully understood, but several lines of evidence identify the most basal lineages and provide increasing definition of their phylogeny. The earliest known fossil termites are from the Cretaceous and are representatives of the Hodotermitidae, Termopsidae, and possibly Mastotermitidae. These Mesozoic termites are distinctly primitive but reasonably diversified, suggesting an origin of the order in the Upper Jurassic (109). Hodotermitidae, represented in modern fauna by three genera (19 species) of

highly specialized “harvester” termites, has the oldest described fossil (~130 mya) (52) and a total of six genera (seven species) in the Cretaceous. Although the foraging behaviors and colony organization of extant hodotermitids are derived, they retain pleisiomorphic morphological characters (18).

Termopsidae, the sister group of Hodotermitidae [(16, 18, 73); but see (105)], is represented by at least four known genera (five species) in the Cretaceous and five modern genera (20 species, the “dampwood” termites). Termopsids, especially the relict Himalayan *Archotermopsis wroughtoni* Desneux, are considered by many to be the most primitive living termites with respect to colony size, social organization, nesting biology, and caste polyphenism (35, 71, 101, 105, 107, 108).

Mastotermitidae, apparently represented in the Cretaceous by two genera and radiating broadly by the Tertiary (4 genera with more than 20 species known from Australia, Europe, North and South America, and the Caribbean) (109), now exists as only a single species, *Mastotermes darwiniensis* Froggatt, with a natural distribution in moist, tropical regions of Northern Australia. Mastotermitidae is viewed uncontroversially as the most basal living lineage within Isoptera and as the sister taxon to all other living termites (16, 17, 43, 47, 48). *M. darwiniensis* has distinct pleisiomorphic characters, but it also features a number of highly derived characteristics. For example, *M. darwiniensis* has an early and apparently irreversible split in development of nondispersive forms, soldiers secrete a defensive chemical, male reproductives have a unique type of multiflagellate sperm, colony population sizes can be large (several million individuals), gallery construction occurs within nests, and extensive foraging tunnels connect food sources located away from the nest (21, 53, 105, 108). *M. darwiniensis* thus exemplifies a common evolutionary pattern: It retains some primitive features but also has apomorphic anatomical and life history elements.

Along with these three confirmed ancient families, some classic (48, 75) and one recent family-level phylogeny (43) place Kalotermitidae, including the “drywood” termites along with some dampwood species (53), as among the most basal clades. Kalotermitids do not appear in the fossil record until the Paleocene; there are 446 modern species in 21 genera (11). Current hypotheses of relationship among the four basal termite families Mastotermitidae, Hodotermitidae, Termopsidae, and Kalotermitidae differ only in the position of Kalotermitidae. Taxonomic sampling issues and lack of integration between morphological and molecular studies have impeded resolution of family-level phylogenies, but for the purposes of this paper we assume that Mastotermitidae, Hodotermitidae, and Termopsidae comprise the most basal living termite clades. This is in accordance with recent phylogenetic analyses that differ in topology, but include the same three families as most basal [((((((T, R), S), K), (Tp, H)), M), B)¹ (105); (((((((T, R), S), K), Tp), H), M), B)] [Donovan et al. (16) and Eggleton’s (17) “majority consensus rule” phylogeny].

¹B, Blattaria; M, Mastotermitidae; H, Hodotermitidae; Tp, Termopsidae; K, Kalotermitidae; S, Serritermitidae; R, Rhinotermitidae; T, Termitidae.

ANCESTRAL ECOLOGY OF TERMITES: FOCUS ON TERMOPSIDAE

Because social organization of living members of the Mastotermitidae and Hodotermitidae appears to be derived, we typically draw inferences regarding ancestral socioecology from life history patterns of modern Termopsidae. This interpretation has been broadly held among termitologists (18, 72, 76, 101, 107), although there is some controversy regarding whether the developmental flexibility typical of Termopsidae is an ancestral or derived characteristic of termites. The traditional view is that “true workers,” i.e., individuals that diverge early and irreversibly from the imaginal line, are a derived feature in termites (1, 70, 72, 76). According to this view, the worker caste developed at least three times independently because true workers occur in Mastotermitidae, Hodotermitidae, Serritermitidae, Rhinotermitidae, and Termitidae (3, 29, 66, 76, 77, 85, 86, 107). In Termopsidae, Kalotermitidae, and the most primitive Rhinotermitidae, helpers have marked developmental flexibility throughout their lives; all individuals except soldiers may differentiate into reproductives (70, 76, 87, 101, 107) or undergo regressive molts to revert from the nymphal line into “pseudergates” (76).

Based on hypotheses of interfamilial phylogenetic relationships, however, Thompson et al. (105) follow Watson & Sewell (118, 119) in supporting irreversible worker differentiation as an ancestral element of termite social evolution rather than a derived, phylogenetic state. It is difficult to evaluate this postulate, however, because there are so few living representatives of taxa key to this interpretation, i.e., the families Mastotermitidae and Hodotermitidae, and those species that exist are highly derived in other social attributes (18, 48, 101, 107). Nesting and feeding habits may drive the evolution of social behaviors, obscuring phylogenetic analyses based on presumed homologous traits. For example, true workers are invariably found in species that forage away from the nest exploiting multiple resources, and helpers with lifelong flexible developmental options occur in “one-piece nesting” groups that consume only the wood in which they live and therefore face eventual resource limitation and instability (1, 3, 29, 53). This correlation suggests biological significance between termite nesting biology and presence or absence of true workers in modern species. The ancestral worker hypothesis (105, 118, 119) thus carries linked implications, suggesting for example that organized foraging away from the nest is an ancestral trait and that the one-piece life type with minimal nest architecture and foraging restricted to the nest wood is secondarily derived. Eggleton (17) rationally advocates resolution of phylogenies before attempting to map social, behavioral, developmental, or biogeographic characters.

INFERENCES REGARDING ANCESTRAL LIFE HISTORIES

Considering extant basal ants and termites as “windows” into ancestral life histories, it is apparent that individual species in either taxon rarely provide an entirely credible model reflecting the biology of the group early after the evolution of

eusociality. Modern species belonging to even the most basal lineages have blended assemblages of primitive and derived traits, thus confounding interpretations. DNA sequences help resolve this issue for phylogenetic analyses, but no methodological safety net exists for evaluating social evolution because homology of behavioral traits can be difficult to verify and may be influenced by ecology or other derived life history attributes. We are thus left to draw inferences based on suites of characters considered to be primitive, compiled from a number of living taxa to yield a composite of likely traits and ancestral ecology of extinct lineages relatively close to the cusp of eusocial evolution. Our comparisons of likely ancestral character complexes from ants and termites ideally will yield productive insights regarding both commonalities and differences, and therefore potentially significant influences, favoring the evolution of eusociality in these insects. We focus on four broad and interrelated areas: reproductive plasticity, division of labor, foraging biology, and evolutionary pathobiology. We then conclude with a discussion of potential commonalities influencing the evolution of eusociality in these groups.

REPRODUCTIVE PLASTICITY IN ANTS AND TERMITES

Colony Structure, Gynes, and Replacement Reproductives

Developing a conceptual framework for the comparative analysis of reproductive variability in ants and termites has historically been impeded by the number and complexity of fertile and sterile forms, the existence of anatomical and physiological intermediates, nomenclature differences, and semantic controversy. To facilitate comparison and clarify our discussion we catalog the types of reproductives found in each group using currently recognized terminology (33, 88, 106).

In ants, reproductive division of labor presents itself in the typical dimorphic queen and worker castes: The queen is derived from the dispersing alate form, establishes a new colony, and is distinguished from her daughters by size, the extent of ovarian development and behavior. Among basal ant species, the wings may be reduced [as in the case of *Nothomyrmecia* (31)] and size differences may be limited to a somewhat broader thorax bearing the scars of the wings that are discarded following the dispersal flight. Some basal ants have fertile forms (ergatogynes) that are morphologically intermediate between independent, dealate colony-founding queens and workers and inseminated workers (gamergates). Ergatoid queens, which are found in some species of *Myrmecia* (13, 26), have a greater number of ovarioles than workers do, a filled spermatheca, and may replace a typical queen. Some ponerine ants, including *Amblyopone* (37, 83), are queenless. Reproduction by gamergates, which possess a functional spermatheca and are inseminated, occurs in these species. Colonies having gamergates occupy stressful environments, have reduced dispersal, mate within or nearby the nest, and reproduce by fission, as may colonies with ergatoid queens (83).

Recent research (96, 97) has begun to uncover unexpected and exciting details of the reproductive and genetic organization of colonies of *Nothomyrmecia macrops*. This basal ant is facultatively polyandrous; sampled queens were singly or multiply mated to unrelated males, with an overall average of 1.37 matings per queen (96). Worker nestmates are related by $b = 0.61 \pm 0.03$. Workers appear to be incapable of laying eggs. The mechanism of queen replacement in colonies of *N. macrops* is rare among ants and bears some resemblance to the pattern of colony inheritance exhibited by some basal termites. Although newly inseminated queens found *N. macrops* colonies monogynously, comparisons of worker and queen genotypes in some sampled colonies contained resident queens that were the sisters rather than the mothers of workers. Furthermore, larvae were genetically identified as the queen's progeny and not the offspring of reproductive workers. The likely explanation for this genetic structure is that the original colony-founding queen had died and been replaced by one of her daughters.

The colony life cycle of *N. macrops* has been reconstructed as follows (96, 97): New queens, one of which may inherit the parental colony, are produced from overwintering larvae that can develop from eggs laid in the autumn into gynes during the following year, even in the event of death of the queen mother. A replacement queen can produce sexual offspring in her first year. Overall, *N. macrops* illustrates a low level of serial polygyny; primarily daughters, but at least occasionally unrelated queens, are adopted by orphaned colonies. Under the condition of colony inheritance by daughters, inclusive fitness benefits extend to the original colony-founding queen (through the rearing of grand-offspring following her death) as well as to workers (through the production of nieces and nephews). The brachyptery of new queens may reflect limited dispersal and a reproductive strategy designed to favor replacement of the mother queen by her daughters. Ecological constraints such as habitat patchiness, nest site limitation, and the risk-prone foraging behavior of the partially claustral founding queens may have favored colony inheritance in *N. macrops*.

Does the presence of such reproductive flexibility in one of the most primitive extant ants accurately reflect an ancestral condition? Although it has been argued that the brachypterous queens of *N. macrops* favored the evolution of daughter replacement (97), it is also possible that brachyptery evolved concomitantly with daughter adoption under the selective pressure of dispersal-related mortality. Again, we note the difficulties inherent in analyzing the evolution of social traits in basal species whose biology may be a constellation of primitive and derived characters.

Several types of reproductives exist in termites. The terms *king* and *queen* typically refer to the colony-founding male and female. These *primary* reproductives are imagoes (alates) that drop their wings after pairing. Founding pairs in basal groups are nearly always monogamous, although there are some records of associated groups of primary reproductives (27). *Neotenics* are termite reproductives that are not derived from alates, but differentiate within their natal colony, breeding with a parent, sibling, or other inbred relative. Neotenic differentiation typically

occurs upon death or senescence of the founding reproductive of the same sex (55). Multiple neotenic of each sex develop, persisting as typically consanguineous reproductive groups in most basal termites (21) but surviving as only one pair in Kalotermitidae (72). Neoteny, literally meaning reproduction as an immature, is related to hemimetaboly, requiring one or two molts that modify morphology and produce functional sex organs (72, 106). In *Mastotermes*, neotenic may develop from workers (119); in termopsids neotenic may form from any individual in instar four or above (except soldiers or imagoes) (71), although no true neotenic are known in *Archotermopsis* (35, 89). Soldier neotenic occur in six species of termopsids (64, 107). In *Archotermopsis*, the gonads of all soldiers are as well developed as in alates (35).

All offspring helpers in termopsid families (except soldiers) retain the capacity to differentiate into fertile reproductives (in the case of termites, either alates or neotenic). They are thus poised to potentially inherit their parents' resources of a nest, food, and established family (65, 107). In such a system of serial reproductive inheritance by kin, as in the cases of ergatogyne and gamergate ants reproducing in their natal nest, all colony members gain inclusive fitness benefits and some individuals attain direct fitness advantages. These cumulative fitness components may well exceed average individual fitness prospects of dispersing, fertile offspring in a similar, solitary species, thus favoring helpers that remain in their natal colony. In *Zootermopsis*, numerous colonies may be initiated in the same log, eventually resulting in intercolony interactions, which can lead to death of reproductives and opportunities for replacement by neotenic (107).

In ancestral groups, the reproductive skew between reproductives and helpers may have been less discrete. Imms (35) reported that worker-like individuals of *Archotermopsis wroughtoni* have extensive gonad development and a fat body equivalent to alates. He observed a captive worker-like *A. wroughtoni* lay seven eggs. The eggs did not develop normally, but whether due to sterility, lack of fertilization, or laboratory conditions is unknown. Eusociality itself is viewed as a continuously varying categorization depending on the portion of progeny that reduces or foregoes reproduction (101, 103).

The possibility of merged or indistinct colonies functioning within single pieces of wood has been raised several times. Concerning *Archotermopsis*, Imms (35, p. 126) observed, "I have, on several occasions, come across three or four queens with a single large colony of ova and larvae, which probably represent several colonies which have become confluent." Fused colonies or colony complexes have also been suggested in *Stolotermes* (20, 63, 110) and *Zootermopsis* (B.L. Thorne, personal observation). These observations and their generality, context, and implications are difficult to evaluate; identification of discrete but adjacent colonies within a log is often impossible. Sufficient descriptive evidence exists, however, to encourage genetic examination of these circumstances, especially relationships among the reproductives found with the possibly merged groups. Recent work on *M. darwiniensis* (21) suggests that although neotenic within a colony are often inbred, they sometimes originate from more than two genetic

lineages, as has been indicated in some more derived termites (8). Extensive study on colony genetic structure and the possibility of merging or introduction of foreign reproductives is required for both basal ants and termites.

Reproductive Conflict

Conflict among nestmates whose fitness interests are incongruent is common in social insects. The apparent rarity of nuptial flights in some basal ant genera (13), the presence of fertile helpers in both ants and termites, and multiple replacement reproductives raise the possibility of intracolony reproductive conflict. Reproductive conflict is manifest in oophagy, the existence of inhibitory pheromones, dominance structures, mutilation, and policing behaviors (37, 62). In basal ants, larval hemolymph feeding by queens has been described in *Prionopelta* and *Amylopopone silvestrii* (38, 60) and has been interpreted as a form of queen nutrition, although the behavior could also represent a mechanism to regulate reproductive capability.

Because of the monogynous and monoandrous organization of basal termite societies, conflicts similar to those observed in ants would not be expected until colony members approach a state of reproductive competence; then policing or other related mechanisms of reproductive competition might be evident in species with flexible development because nearly all individuals have the potential to differentiate into reproductive forms. Roisin (85) cites reports of intracolony mutilation in termopsids, kalotermitids, and some rhinotermitids and proposes that competition among late instar helpers, including nymphs attempting to become alates might explain such behaviors. He suggests that siblings bite wing pads, which causes some individuals to deflect from alate development, creating "lower status" helpers with reduced chances of future dispersal. Subsequent wing bud regeneration and formation of a normal alate is possible, but with delay and additional molts (107, 118). Roisin (85) proposes that the mutilated "losers" in intracolony conflicts formed the original helpers in termites. The contexts under which primitive termites lose wing buds need to be better understood before this hypothesis, or the implications of mutilation behaviors in termites, can be rigorously evaluated (107). For example, wing bud scars in termopsids are often due to self-induced abscission rather than mutilation by colony members (35, 107). Research on complete colonies of *Zootermopsis* in the laboratory suggests that self-abscission occurs when there are opportunities to become a replacement reproductive, perhaps inducing pre-alates to shed wing pads and differentiate into a neotenic in the natal colony (107).

DIVISION OF LABOR

The primary axis of division of labor in basal ant and termite species is reproductive, but colonies theoretically may partition tasks according to the size and age of subfertile or sterile individuals. Pheromones, temperature, and nutrition direct

caste expression in both ants and termites (33, 71, 72). Historical factors, including development, cause ant and termite castes to form in fundamentally different ways and therefore potentially preadapt these two groups toward disparate mechanisms of task partitioning. In ants, morphological variation is generated through allometry within a single adult instar; size variation and polymorphism in termites is found across instars, from immature through imago. Although the caste systems of termites with true workers show a strong convergence with ants, similarities among basal species may be obscure because of the prevalence of monomorphism in ant workers. Due to hemimetabolous development, immature termites contribute to colony needs as juveniles, whereas ant larvae are seemingly unable to meet labor demands unless they are involved in food processing and nutrient distribution.

Basal ant species such as *Amblyopone pallipes* have small colonies, and activity is restricted to a limited number of nest chambers and associated tunnels where prey capture occurs (112). Workers, which hunt vermiform arthropod prey, initiate foraging soon after eclosion. Foraging and brood-care are codependent tasks because larvae are carried to freshly paralyzed prey where they feed directly. Brood-care is thus reminiscent of the direct provisioning habits of solitary wasps, and the same individual often performs both foraging and brood-care tasks. *A. pallipes* lacks age-based division of labor (111), but interspecific comparisons of polyethism in *Amblyopone* suggest that age-related division of labor might take on elements similar to that of higher ants (61), although the reasons for such differences are unclear. Colony demography, feeding specialization, and the retention of ancestral behavioral traits seem to be important determinants in division of labor in ants (40, 111, 113). The degree of sociality, which varies in ants, may also influence patterns of division of labor in *A. pallipes* and *N. macrops*, in which queen-worker and worker-worker interactions are rare and polyethism is lacking (40). In addition, some *Amblyopone* species are queenless but contain multiple inseminated gamergates that form dominance hierarchies (37), which could influence division of labor (84). Among basal ants, *Aneuretus simoni* exhibits an age-related polyethism that foreshadows the form of temporal task partitioning typical of ants of the higher subfamilies.

Like primitive ants, basal termopsid species have small colonies (35, 53), activity is limited to nest galleries, and there has been no indication of age-based division of labor (94). It has been hypothesized that termite caste systems should be fully discretized due to hemimetabolous development (79). Noirot (72, p. 9) notes that the combination of helpers of both sexes and hemimetaboly gives termites, in comparison to Hymenoptera, "many more possibilities for the diversification of polymorphism and consequently, for its adaptations." Termites may also advance, regress, or retard their metabolic development (71, 76, 87) to respond to colony needs or individual fitness initiatives. During its postembryonic development, an individual termite, especially in Termopsidae and Kalotermitidae, may "belong to different physical castes in succession" (72, p. 8), possibly terminating by becoming a soldier or reproductive. Noirot & Bordereau (74) termed this pattern *temporal polymorphism*, juxtaposed with *temporal polyethism*, or change in task

functions of a worker during its lifetime, as is characteristic in Hymenoptera and derived termites (80, 123). Flexibility in metamorphosis in basal termite species might provide a mechanism of task switching similar to, but less rapid than, the patterns of behavioral acceleration and regression seen in more advanced species of the social Hymenoptera. The multiple age (instar) cohorts generated by hemimetaboly would divide tasks along a finely graded scale, resulting in the evolution of one caste per task (79). Yet if first and second instar larvae are inactive (94), gradual metamorphosis may in essence yield a caste distribution that resembles only moderate polymorphism, although the duration between molts would seemingly provide ample time for temporal specialization. In any case, the ergonomically adaptive nature of polyethism in basal termites is virtually unknown. There is some suggestion that demography serves a function in infection control (95).

Termite soldiers are without equivalent in Hymenoptera (72); basal ants have few allometric size variants such as majors and minors, with the exception of *Aneuretus simoni* (33, 113), although large workers, possessing a disproportionately large number of ovarioles, have been described in *Myrmecia* (39). Soldier termites appear to be monophyletic (71, 76). In Mastotermitidae and Hodotermitidae, soldiers have “continuous” polymorphism because they originate from successive and numerous worker instars (72). In Termopsidae and Kalotermitidae, all except the youngest larvae [termite terminology uses “larvae” to describe apteran immatures differentiating along a nonreproductive pathway (87, 109)], all nymphs (termites with wing pads), and all pseudergates can produce soldiers with a tendency toward a later origin, and therefore larger soldiers, in older colonies (71, 72). The first termite soldiers may have had functional gonads, as in extant *Archotermopsis* (35), but it is unknown whether soldiers appeared and were selected for as a defensive caste or as replacement or supplementary reproductives as in modern neotenic soldiers (64, 86, 107).

Single-piece nest species, such as the dampwood genus *Zootermopsis*, provide an opportunity to examine the significance of the spatial organization of tasks to the evolution of division of labor. Brood-care and foraging both occur within the same piece of wood; in ants and multiple-piece nesting termites the nursery and foraging are separated inside and outside of the nest. Maturing termite larvae are likely to eclose in the proximity of the primary reproductives and egg pile and could care for reproductives early in life and transition to nonbrood-care tasks such as nest maintenance and feeding at more distal sites before they develop into reproductive forms and leave the labor force. However, *Zootermopsis* seems to show no temporal polyethism (94); third through seventh instar larvae attend to tasks with no apparent bias.

Reproductive plasticity may also influence polyethism in Termopsidae (76). The ability of larvae to achieve reproductive status in the natal nest and potential conflicts with siblings could reduce selection for behavioral schedules that enhance colony-level fitness at the expense of individual reproductive success. The reproductive plasticity of lower termites could cause individuals to remain near the egg

pile where they might deposit their own eggs or engage in oophagy, performing brood-care as they age, rather than providing labor at other work sites. West-Eberhard (121, 122) offered a similar argument concerning temporal polyethism in the social Hymenoptera, suggesting that worker reproduction should result in a brood-care bias toward newly eclosed adults that have functional ovaries. If reproductive competency in termites increases with age, older larvae could be predisposed to brood-care behavior or at least be spatially associated with brood in basal isopteran species. In any case, comparisons of polyethism among termite species indicate that worker sterility and temporal division of labor are correlated (94, 114). The loss of reproductive options among workers and foraging ecology of termites have been prerequisites for the evolution of termite polyethism. A comprehensive theory for the evolution of age-related division of labor in termites requires an understanding of how and when individuals can become reproductively competent and a species' foraging ecology.

FORAGING BIOLOGY

Striking variation is seen in the foraging biology of the basal ants; a spectrum of ancestral and derived habits has been documented (33). In some species, solitary huntresses search for arthropod prey in subterranean soil galleries and tunnels in decayed wood. In a manner reminiscent of their wasp ancestors, the sting injects paralytic venom into prey, which are subsequently transported to the nest. Feeding specialization and recruitment communication are diverse within and between genera in the tribe Amblyoponini. *Amblyopone pallipes*, for example, solitarily hunts prey such as geophilid centipedes, whereas other species may cooperate in prey capture and transport (36). Amblyoponine species, as well as species in more advanced ponerine tribes, may specialize on certain prey. *Prionopelta amabilis* workers, for example, feed exclusively on campodeid diplurans (33). Other basal ants such as *N. macrops* and *N. myrmecia* forage epigeally as solitary individuals and use the sting to paralyze prey (31, 33). *A. simoni* workers also use the sting to subdue prey, but supplement their diet with carbohydrate foods such as decaying fruit, and have well-developed chemical trail communication (113).

The foraging ecology of basal termites, like basal ants, reflects the feeding habits of their solitary and subsocial ancestors. Termopsids are one-piece nesters (2, 53, 69), living in and consuming their host log. They do not forage away from the nest wood, and colonies do not leave one stump or log to occupy another. The galleries resulting from the consumption of their host wood become nest chambers, partitioned only by fecal pellet walls. The entire life cycle of most colony members transpires within a single piece of wood. Mature colonies produce fertile offspring (alates) seasonally, and many individuals within the colony differentiate into alates and disperse when resources in the nest wood are depleted (78).

Although termites prefer nutritionally valuable food sources that are low in secondary plant compounds (114), Termopsidae appear to have a limited array of

mechanisms that could be implemented to harvest energetically rich cellulose sources. A choice mechanism exhibited by *Zootermopsis nevadensis* involves the foraging discrimination of colony-founding alates that settle on and defend nitrogen-rich wood cambium (53, 100). Whether workers in established colonies direct feeding at nutritionally rich sites in their nest log is unknown. If food selection occurs, it is likely regulated by secretions of the sternal gland, the source of trail pheromones in termites (114).

EVOLUTIONARY PATHOBIOLOGY

Many social insects nest and feed in soil and decayed-wood environments where diverse, abundant, and potentially pathenogenic microbial communities flourish. Group living may compound mortality risks through the interindividual transmission of infection (92). Adapting to disease has long been considered a major event in the evolution of sociality and the diversification of the ants (123), but only recently has the evolutionary significance of social insect pathobiology been the focus of empirical and theoretical investigation, primarily in Hymenoptera (24, 98, 99).

Ants have adapted to the constraints of living in infectious environments through the powerful antibiotic secretions of the metapleural gland (30, 33, 123). The metapleural gland is phylogenetically ancient, appearing in the extinct *Sphecomyrma* and found today in all ant subfamilies. Its evolution is considered to have been critically important to the ecological dominance of the ants (33, 123). Research on disease defenses in *Myrmecia* (58) suggests that the metapleural gland is highly significant but perhaps not the sole mechanism of infection control in basal species. Metapleural gland secretions alone, nevertheless, provide extraordinarily efficacious control of microbes.

Termites, like ants, nest and feed in areas where microbes thrive, and it is likely that pathogens have influenced their social biology. Termite life history traits (monogamy and long life span) as well as several characteristics of their host/pathogen relationships (likelihood of vertical and horizontal transmission among genetically related individuals, probability of prolonged contact with infection agents, and disease transfer through trophallactic exchanges) suggest that key aspects of termite biology could reflect adaptations to reduce pathogen virulence (19, 91). In basal isopteran species, disease resistance represents a confluence of the behavioral, physiological, and biochemical adaptations that characterized the solitary and/or presocial dictyopteran ancestors of termites and the newly adaptive mechanisms of infection control that accompanied their transition to eusociality. Although susceptibility to disease transmission was likely a cost of termite sociality, *Zootermopsis angusticollis* shows a number of infection-control adaptations such as allogrooming (92), colony demography (95), inducible humoral defenses (90), and the "social transfer" of immunocompetence (115). *Z. angusticollis* also communicates information about the presence of pathogens (90) and has antimicrobial exudates (92). In contrast to ants, termites appear to lack a metapleural gland

equivalent (22), perhaps because the evolution of potent antimicrobial defenses was compromised by the need to protect their antibiotic-sensitive cellulose-digesting symbionts (92).

The life histories of primitive termites, which feature outbreeding by alates and inbreeding by offspring, may have in part allowed these insects to escape from or adapt to pathogens and lower disease risk (91). In contrast to the hypothesis that genetic similarity fosters the spread of disease in a colony (24), Lewis (54) proposed that pathogen and parasite avoidance, operating through the preferential association of relatives, could be a driving force for sociality. In this model, the spatial association of relatives and kin-directed altruism lowers the probability of infection by an unfamiliar pathogen, favoring reproduction of group members and the maintenance of its kin structure. In basal termites, the cycle of inbreeding by offspring is punctuated by the introduction of new genes through outbreeding, which may enhance disease resistance. Genetic studies on *Z. nevadensis* support alate outbreeding (102). In light of Lewis' model, inbreeding could also be considered as having a function in the avoidance of new and unfamiliar pathogens because it would favor the continued association of relatives. Based on the observation that primary reproductives of *Z. angusticollis* have significantly lower mortality when paired with sibling rather than distantly collected, nonsibling mates, outbreeding depression could occur if infections are transferred through social contact between males and females (93). Infections can be transferred socially between mates (91).

An alternative disease-related explanation for both outbreeding and inbreeding basal termites concerns selection for genetic variation and the maintenance of adaptive genotypes. Cycles of outbreeding by founding reproductives could infuse colonies with genotypes that vary in disease resistance. As colonies mature, coevolutionary interactions could result in selection of the most resistant host genotypes and/or the least virulent pathogens. Some individuals bearing these adapted genotypes may differentiate into inbreeding reproductives, thus maintaining the resistant trait in their offspring.

DISCUSSION

Insect social systems are shaped from the inertial, phylogenetic properties of species and their interaction with environmental forces. Despite the fundamental differences between Formicidae and Isoptera, such as ploidy and holo- versus hemimetaboly, formulating comparisons between basal taxa of these two diverse and entirely eusocial clades reveal commonalities and potentially constructive insights into their early eusocial evolution. This process is not as satisfying as examining evolutionary grades in a group containing a spectrum of solitary through eusocial species such as wasps or bees (123) or in a clade with recent and repeated evolution of eusociality such as halictid bees (15), but no alternative approach exists in extant ants and termites.

Here we attempt to understand the relative contribution and significance of phylogenetic history and ecology in the evolution of colony structure in ants and termites by examining their commonalities and divergences, restricting our analysis to those species that appear to most closely approximate nascent eusocial forms. In doing so we acknowledge the inference restrictions inherent in using extant taxa to reconstruct the social past and the limitations imposed upon comparisons of analogous systems, as well as confounding issues surrounding the existence of both primitive and derived traits in modern basal species. After careful consideration of these caveats, however, we remain confident that students of both isopteran and hymenopteran societies can mutually benefit from an understanding of the predispositions and ecologies that have guided social evolution in each group, and that our preliminary attempt at a synthesis of the two literatures will encourage productive discussion and collaboration.

Reproductive Structure and Division of Labor

For basal ant and termite species, we suggest that the reproductive organization of colonies and patterns of division of labor were affected by suites of ecological factors that operated at various stages of colony life histories. We identify nesting and feeding ecology as the environmental influences that impelled the adaptive modification of reproductive organization and division of labor in both groups. In basal ants and termites, the nest (including the colony it houses) represents a resource that provides nutrition, a structured environment to rear offspring, and a labor force. In termites with the most primitive social structure, the nest and the food source are the same piece of wood. In some basal ants the nest is a collection of gallery systems and chambers from which foraging excursions are conducted over short distances within restricted areas. The nutritional aspect of the ant nest lies in the quality of its foraging territory. Nest structure is the result of prior colony labor. The nest, in the broad sense including ant foraging territory, is thus a valuable resource. Opportunities to inherit the nest and colony may have been significant in the evolution of multiple reproductive forms and options in both taxa.

Ancestral ants likely foraged relatively close to the nest and had little if any polyethism because of the sequential unity of prey paralysis, transport, and direct provisioning of larvae (33, 111). Because of small colony size, relatively synchronous brood development cycles, and large prey size, foraging excursions may have been few in number, close to the nest, and within the confines of subterranean galleries or tunnels and crevices in decayed wood. Predation rates in species such as *Amblyopone* may be low in comparison to the higher ants, which have large colony size and forage epigeally at greater distances from the nest. Our model assumes that *Amblyopone*, rather than *Nothomyrmecia*, represents a closer approximation to the biology of incipient eusocial ants. In basal termites the nest is the food source; in basal ants the distinction between nest and foraging territory is minor. The expansion of the diet, foraging away from the nest chamber, and increased colony

size in termites is correlated with the evolution of a true worker caste and division of labor (3, 53). It is a reasonable hypothesis that spatial separation of nest and feeding territory and their unambiguous discrimination was also of significance in the evolution of social organization of ants. Together with nest structure, age-related changes in the reproductive physiology of helpers, predation, and decreased reproductive competition were likely interrelated and important determinants of polyethic task schedules and division of labor, although understanding the influence of these factors requires further detailed investigation. It is a challenge, for example, to explain why *Nothomyrmecia*, which forages away from the nest, shows no division of labor (40). Perhaps ancestral social states, including limited interaction and cooperation, were retained in this relict ant.

Serial Reproductive Inheritance by Kin

Similarities in reproductive structure found in some basal ants and termites are striking and potentially revealing. Recent genetic work on the primitive ant *N. macrops* suggests colony inheritance by daughters (97). Other basal ants such as *Myrmecia* and perhaps some *Amblyopone* have life histories in which family members, even helper family members in some cases, may become reproductives within the parental nest. These dynamics and the associated resource and inclusive fitness advantages of nest inheritance in ants have similarities with the developmental plasticity and colony inheritance characteristic of replacement (neotenic) reproductives in basal termites. The common feature of serial reproductive inheritance by kin means that all colony members gain enhanced inclusive fitness benefits, and some individuals acquire direct fitness advantages. These cumulative fitness components may well exceed average individual fitness prospects of dispersing, fertile offspring in a similar, solitary species, thus favoring helpers that remain in the natal colony.

The influence of potential reproductive opportunities on the evolution of helping behavior have long been recognized and are compounded by inheritance of resources and the fitness advantages of reproducing in the natal nest. West-Eberhard (120, p. 853) observed, “. . . Michener has long insisted that helping behavior without altruism can occur if male production by ‘workers’ . . . is important enough (56). The significance of this argument has not generally been appreciated. Whether among relatives or not, as long as a female has “hope” of laying eggs—at least some small probability of future reproduction—her participation in the worker tasks can be viewed as possibly or partially an investment in her own reproductive future. . . . As long as a certain percentage of functional workers ultimately lays some eggs, then every worker—even those which never do lay eggs—can be considered ‘hopeful’ in the sense of having a certain probability of reproduction.” The “hopeful reproductive” dynamic is influenced by colony size. As colony size increases, individual workers have a lower chance of becoming replacement reproductives (7). The most primitive ants and termites have small family sizes (33, 35), thus favoring opportunities for individual offspring to become reproductives.

Disease Risk, the Evolution of Resistance, and Social Organization

In ancestral ants, the problems that disease risk posed for coloniality may have been fully solved by one key innovation: the evolution of the metapleural gland in ancestral species. This gland is well developed in all basal ants studied to date (30, 33). In basal termites, the ability to control infection with powerful antibiotic secretions biochemically similar to those secreted by the ant metapleural gland was likely compromised by the need to maintain gut symbionts (92). In contrast to the chemical mode of infection control in ants, cycles of inbreeding and outbreeding in basal termites may have resulted in the selection and maintenance of disease-adapted genotypes. We note, however, that we do not identify disease as the sole factor influencing termite life cycles and acknowledge that other factors were also significant (101, 107). Nevertheless, the dispersal of reproductive forms from the parental nest and the colonization of new food source nest sites may have involved local adaptations to pathogens that were generated and preserved by outbreeding and inbreeding, respectively.

Conclusion and Prospects

In both ants and termites, eusociality was probably fostered by a suite of contributing factors and the interacting selective pressures that they generated. Haplodiploidy, maternal care, and female-biased sex ratios have favored the evolution of eusociality in Hymenoptera [reviewed in (33, 116)]. Kin-based explanations anchored by inclusive fitness pay-offs are also the premise of the nonmutually exclusive theories explaining the evolution of eusociality in the diploid-diploid Isoptera. These include cyclic inbreeding (66), shift in dependent care (67), intra-group conflict (85), disease resistance (92, 95, 115), and predispositions related to ecological and life history attributes that favored helping behavior and reproductive skew (101, 107).

In addition to expanded study of key primitive taxa, priority domains of future research on basal ants and termites center on further understanding their mating and reproductive biology. Specifically, topics should include: (a) determination of relatedness among mates and number of mates of individuals that inherit colonies (e.g., daughter queens of *Nothomyrmecia*, ergatogynes, gamergates, and termite neotronics); (b) study of fertility or subfertility of workers and soldiers in *Archotermopsis*; (c) investigation of the possibility of foreign reproductives joining an existing colony, either through immigration or fusion; (d) further research on the circumstances surrounding policing and mutilation, and their implications for reproductive conflict; and (e) detailed studies of the mechanisms and organization of division of labor. Expanded knowledge of these subjects/areas will provide a stronger foundation for resolving reproductive patterns and their fitness implications for reproductives and helpers, thus facilitating broader synthesis of patterns of evolution in ants, termites, and other eusocial animals.

ACKNOWLEDGMENTS

We thank anonymous reviewers for constructive suggestions on the manuscript.

The Annual Review of Entomology is online at <http://ento.annualreviews.org>

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