

EVOLUTION OF EUSOCIALITY IN TERMITES

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KEY WORDS: termite, Isoptera, Dictyoptera, social insects, eusocial evolution

ABSTRACT

Eusociality in Isoptera (termites) converges along many lines with colony organization and highly social behavior in the phylogenetically distinct insect order Hymenoptera (ants, bees, wasps). Unlike the haplodiploid Hymenoptera, however, both sexes of Isoptera are diploid. Termite families thus lack asymmetric degrees of genetic relatedness generated by meiosis and fertilization, so explanations for eusocial evolution based on such asymmetries are not applicable to Isoptera. The evolution of eusociality in termites likely occurred in small families in which most helpers retained developmental flexibility and reproductive options. A suite of ecological and life-history traits of termites and their ancestors may have predisposed them toward eusocial evolution. These characteristics include familial associations in cloistered, food-rich habitats; slow development; overlap of generations; monogamy; iteroparity; high-risk dispersal for individuals; opportunities for nest inheritance by offspring remaining in their natal nest; and advantages of group defense. Such life-history components are particularly persuasive as fostering social evolution because many are present in a broad group of eusocial taxa, including Hymenoptera, beetles, aphids, thrips, naked mole rats, and shrimp. The evolution of eusociality in Isoptera likely evolved in response to a variety of contributing elements and the selective pressures that they generated.

INTRODUCTION

The evolution of eusociality in termites has been a classic evolutionary conundrum since Darwin (25) recognized that the life histories of individuals in social insect colonies posed “special difficulties” to his theory of natural selection because the majority of individuals in a colony never reproduce. The perplexing

case of eusociality in the termites is rendered even more conspicuous by the abundance of work on the social evolution of Hymenoptera that emphasizes the haplodiploid genetic system of that group (42, 43, 45). Both male and female termites are diploid: Hence, the asymmetric degree of relatedness inherent between hymenopteran brothers and sisters, and between their sisters and their offspring, is not generated by meiosis and fertilization in termites. The discovery and investigation of eusociality in other diploid animals such as aphids (4, 5), beetles (57), naked mole rats (2), and shrimp (30) have escalated interest in mechanisms of eusocial evolution in taxa that do not have skewed degrees of genetic relatedness within families.

There is active discussion over the precise definition of the term eusocial, and over which species have life-history patterns that fit within this “most highly social” category (e.g. 18, 20, 119). Despite differences and nuances of opinion with regard to some other taxa, all extant termites (Isoptera) are considered eusocial. By the conventional definition (75, 139), the key element of eusociality is markedly skewed reproduction among members of the society (a distinct reproductive division of labor). In eusocial groups, a limited number of individuals are fertile and fecund, but most have reduced reproductive capacities or, in the extreme, are completely and permanently sterile. The other defining components of eusociality are cooperation in the care of brood within the group, and overlap of adult generations. These features taken together result in workers helping to rear their siblings and/or the offspring of reproductives in their parents’ generation.

Comparative studies of the social biology of a spectrum of solitary through eusocial species of bees and wasps have elucidated the evolution of complex societies, but parallel research on termites (or ants) is impossible because all living species are eusocial. Observations on the biology of extant taxa cannot be used to convincingly reconstruct ancestral states prior to the evolution of worker subfertility or sterility. Crozier (22, p. 8) states, “Many aspects of the biology of forms such as ants, honey bees, and termites seem scarcely relevant to evaluating theories on the origin of eusociality, because for them (especially those ants with sterile workers) there is no option open to workers for selfish behavior. . . .” Once prototermites evolved through the “bottleneck” of eusociality, life-history constraints, especially reproductive division of labor, are presumed to have been essentially irreversible. The new evolutionary dynamic involving the respective fitness interests of reproductives and workers likely shifted the adaptive pathway to a very different trajectory because the selective influences would be altered markedly once workers evolved lowered reproductive potential. Thus studies of living termite species can be used to generate ideas of possible evolutionary pressures and scenarios but cannot appropriately or convincingly be used to test hypotheses or predictions regarding the evolution of eusociality in Isoptera.

Thus a definitive, testable evolutionary scenario for the evolution of highly social behavior in termites is unrealistic. The best that can be developed is a comprehensive hypothesis, or set of hypotheses, each consistent both with the biology of termites and with principles of evolution. In this review I describe aspects of the biology of primitive termites, and insights that they provide into early social evolution in ancestral groups. I then present a synopsis of the major hypotheses previously presented to explain the evolution of eusociality in Isoptera. Ecological and life-history correlates of preconditions of eusociality are then discussed in a section that emphasizes general patterns recognized across phylogenetically disparate eusocial animals, including insects, naked mole rats, and shrimp. Termites have a striking number of these characteristics, and specific ecological factors are discussed as compelling forces fostering eusocial evolution in Isoptera. The ecological and life-history characteristics are then integrated into a hypothetical evolutionary scenario describing termite ancestors and possible selective influences in the transition to eusociality.

The Biology of Primitive Living Termites

Although extant termites cannot appropriately be used to test theories or predictions regarding the evolution of eusociality in Isoptera, knowledge of the biology of primitive living groups may be constructively used to generate insights and constructs regarding social evolution in their ancestors. In this section I present a synopsis of what is known about the habitat, castes, and reproductive biology of living termites considered to have retained the most primitive social organization and developmental traits. A robust phylogeny of the Isoptera has not yet been established (54, 59, 130). *Mastotermes darwiniensis* Froggatt (Mastotermitidae) is generally considered, based on morphological criteria, the most primitive living termite, but the Termopsidae, particularly the relictual himalayan termite *Archotermopsis wroughtoni* Desneux, are recognized as the most primitive socially and with respect to caste differentiation (37, 51, 95, 130). The following discussion is based on the biology of termopsids, detailing the relatively scant information available on *Archotermopsis*, supplemented by references to the more intensively studied genus *Zootermopsis*.

Termopsids live in decaying wood. *Archotermopsis wroughtoni* lives in small colonies (30–40 individuals) under the bark and within dead stumps and logs of fallen conifers (51, 108). Termopsids are “one piece” nesters (1, 93), living in and consuming their host log. They do not forage away from the nest, and colonies do not leave one log to colonize another. When the nest log, food, or space resources are depleted, many individuals within the colony differentiate into alates and disperse (102).

A soldier differentiates within the first brood of all termites in which development of incipient colonies has been studied (including *Zootermopsis*, but

not yet *Archotermopsis*) (68). In *Z. angusticollis*, the first soldier in a young colony inhibits the differentiation of additional soldiers, but if it is removed, a replacement soldier develops (15, 68). Termopsid soldiers may be of either sex; females are distinguished from males by the enlarged 7th sternum as in imagoes (51, 126). In *Archotermopsis*, all soldiers have gonads that are as well developed as those of mature alates (51). Because there is no indication of inhibition or degeneration of soldier reproductive organs, Imms (51, p. 142) suggested that they may frequently be functional; however, this has not yet been demonstrated. Fertile soldier-like males and females with mature gonads (“reproductive soldiers” or “neotenic soldiers”) are known in six species of the Termopsidae (reviewed in 78). Normal female pre-soldiers (callow soldiers that will molt into soldiers) of *Z. angusticollis* have oviducts, eggs, and a seminal receptacle. Mature female soldiers, however, are clearly infertile, with arrested development of various portions of the reproductive organs. The testes of mature male soldiers produce apparently normal sperm, but they have nonproductive seminal vesicles that probably render the sperm nonfunctional (126). Thompson (126, p. 524) concludes that normal male and female soldiers of *Z. angusticollis* are sterile, “although near the ancestral state of fertility.”

Imms (51) reports that the “worker-like forms” (presumably 4th instar or older apterous individuals) of *Archotermopsis* have extensive gonad development, and that their fat body development is equivalent to that of alates. Imms (51) observed a captive “worker-like” *A. wroughtoni* lay seven eggs. The eggs did not develop, but whether due to sterility, lack of fertilization, or laboratory conditions is unknown.

The term neotenic reproductive refers to any termite reproductive that is not derived from an alate (129). Neotenic reproductives differentiate within their natal colony, never dispersing to outbreed. They can develop from a variety of instars from individuals with or without wingpads. True neotenic reproductives have not been reported in *A. wroughtoni* (51, 108). Neotenic reproductives of both sexes, up to several hundred per colony (68), are found in the field in *Zootermopsis* colonies that have lost the original king and/or queen. When the primary (alate-derived) founding pair is present, neotenic reproductives are normally absent (68). Healthy primary reproductives produce pheromones, distributed via the anus, that inhibit the differentiation of neotenic reproductives (69). If only the queen is present, only male neotenic develop, and vice versa (15, 68). When isolated from functional reproductives, neotenic differentiate in as little as 3–4 weeks in *Z. angusticollis* (39, 141). In some kalotermitids, neotenic develop in isolated groups in as little as 8–10 days (71, 83). Multiple neotenic function together in Mastotermitidae, Termopsidae, and Rhinotermitidae colonies (65), but excess neotenic are eliminated by fighting in Kalotermitidae, leaving only one of each sex (66, 81, 110). Alates remaining in their natal nest to replace dead

or senescing primary reproductives (“adultoid” reproductives in the Termitidae) are not known to occur within the basal families of Isoptera (92, 97).

Thus colonies of living species of primitive termites differ from the general portrayal of termite societies. The king and queen do not live with a group of sterile helpers. Some individuals are near a state of fertility, and most colony members (all but soldiers) have options to differentiate into functional reproductives under certain circumstances. Developmental flexibility and retained reproductive options appear to be prominent components of the society.

Primitive Termite “Workers” Retain Developmental and Reproductive Options

In all species of termites there is a separation into two developmental pathways, the sexual (imaginal or nymphal) line identified by the presence of wing buds, and the apterous path, leading to individuals that function as workers. Distinction of these two lines appears at various instars, depending on the group (95, 96). Plasticity of developmental options also varies. Pathways are relatively more plastic in the Termopsidae, Kalotermitidae, and some Rhinotermitidae, and are relatively more rigid in *Mastotermes darwiniensis* (the single extant species of the Mastotermitidae), Hodotermitidae, some Rhinotermitidae, and Termitidae (95, 96, 99, 100). Termite castes are not genetically determined. All individuals carry developmental instructions for all castes such that hormonal and other stimuli induce particular pathways of differentiation (63, 96).

Several morphologically and/or developmentally distinct groups function as helpers or “workers” within termite colonies. In the Termopsidae, Kalotermitidae, and some Rhinotermitidae (e.g. *Prorhinotermes*), later instar “larvae” (individuals without wing pads) and nymphs (individuals with wing pads) perform “worker” tasks within their colonies. Apterous larvae may molt into nymphs, thus “switching” to the imaginal developmental path (95) (Figure 1). In these same termite groups (and in the rhinotermitid genus *Reticulitermes*), there may also be pseudergates, first defined by Grassé & Noirot (38). Pseudergates are nonreproductive, helper individuals that diverge from the imaginal line via a regressive or stationary molt at a relatively late instar (99). The principal morphological difference between a pseudergate and a nymph is the absence or regression of wing pads in the pseudergate; neither the brain nor the sex organs regress (95). Pseudergates retain the capacity to revert to the nymphal and then imaginal stages, or they can differentiate into soldiers or neotenic reproductives.

Thus larvae, nymphs, and pseudergates all function as helpers within colonies of termopsids, kalotermitids, and some rhinotermitids, and all of these individuals retain the capacity to differentiate into fertile alates or neotenic reproductives (or soldiers). Unfortunately, the circumstances that induce or contribute toward

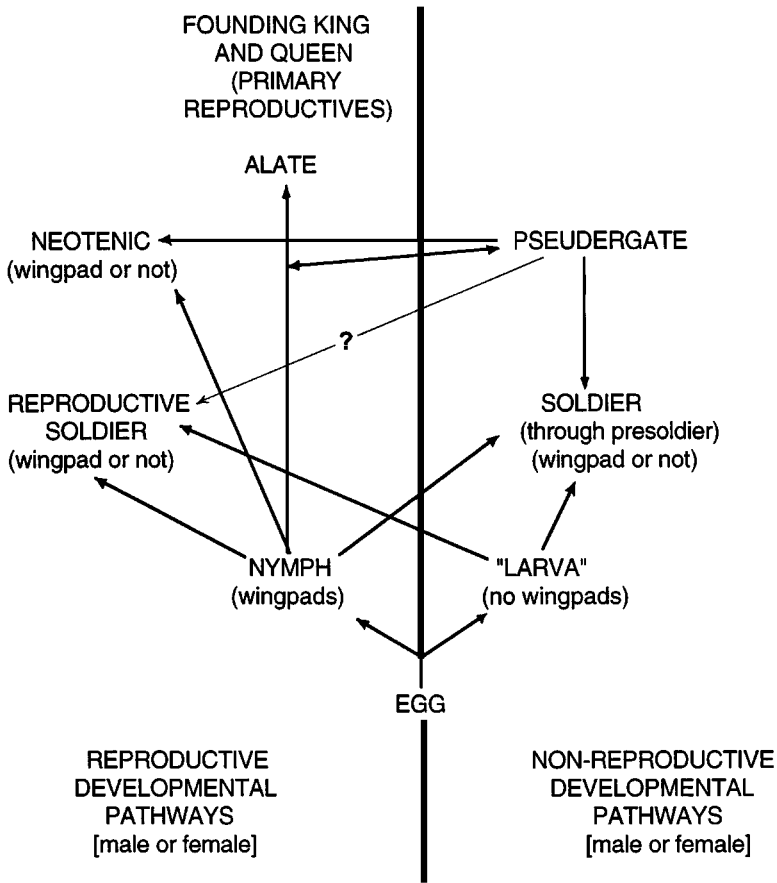


Figure 1 Developmental pathways in a primitive termite with flexible developmental options (e.g. *Zootermopsis*). Transitions can occur at various instars. Terminology as in Thorne (129).

differentiation along a particular pathway, and those that govern shifts from one path to another, are not fully understood (95).

A true *worker* termite is a nonreproductive, nonsoldier individual of the third or fourth (depending on the taxon) or a later instar that has diverged early and irreversibly from the imaginal line (94, 96, 99; irreversibly except in the rare cases that workers differentiate into replacement (ergatoid) reproductives—92, 97). True workers, a derived caste, are found in all living species of Mastotermitidae, Hodotermitidae, Serritermitidae (suggested, but not confirmed), and Termitidae, and in most species of Rhinotermitidae (*Prorhinotermes* is the only

known rhinotermitid genus without true workers) (99, 100). Termites that forage away from their nest have a true worker caste (1, 50).

We lack a robust phylogeny of termite families but it appears that true workers evolved at least three times in the Isoptera (1, 50, 79, 82, 99, 100). Considering this along with the evolution of a monophyletic, nonreproductive soldier caste, Bourke & Franks (12) state that there is a minimum of four origins of reproductive altruism in termites (see also 32). A more parsimonious interpretation is that reproductive altruism in the form of a helper caste evolved only once in ancestral termites. The initial helpers directed some of their time and energy toward assistance within the colony (family), thereby at least delaying their own reproductive maturity and potential dispersal. The soldier caste evolved from the helper line with individuals first working and then in some cases becoming soldiers (98). Eventually, the highly constrained and essentially sterile true workers evolved, probably in several independent lines (as inferred from current phylogenetic hypotheses) (54) from species with developmentally and reproductively flexible helpers. Thus, eusociality in termites, characterized by reproductive altruism and division of reproductive labor, apparently evolved once. Evolution of sterile castes from already highly social ancestors followed.

A number of hypotheses have been proposed to explain the evolution of eusociality in termites. Five of the major hypotheses are summarized below along with an assessment of their merit as comprehensive evolutionary explanations.

PREVIOUS HYPOTHESES OF TERMITE SOCIAL EVOLUTION

Consensus on Subsociality

Two paths are recognized for the origin of social groups characterized by helpers and a reproductive division of labor. By the subsocial route societies originate from familial units initially composed of parents and offspring. Social groups may also form along the semisocial route as an association of individuals, related or not, from the same generation. Both pathways have been proposed for the Hymenoptera and vertebrates, although parental care may be a universal precursor of eusociality (2). In termite societies, however, both workers and soldiers are specialized juveniles, and there is no evidence for exchange of reproductives between different established colonies. Thus there is little doubt that termite sociality evolved via the subsocial route (2, 31, 56, 88, 106, 138). The wood diet of termites (and cryptocerid roaches), and reliance on cellulolytic protozoan symbionts rendered overlap of generations a necessity in these insects (17), thus providing opportunity for parental care and subsociality.

The Symbiont Transfer Hypothesis

Termites in the families Mastotermitidae, Kalotermitidae, Termopsidae, Hodotermitidae, and Rhinotermitidae (families collectively called the lower termites) (58) harbor distinctive groups of flagellate protists in their hindguts (13). These intestinal protozoa exist in mutualistic symbiosis with their hosts. The termites provide a habitat and mode of dispersal for the flagellates, and the protozoa digest cellulose consumed by the termites. Lower termites are thus obligately dependent on the intestinal symbionts for nutrition.

Each termite must acquire symbionts after hatching, and again following each molt. An initial inoculum of protozoa is passed to newly eclosed termites by feeding on the hindgut fluids of a nestmate. The gut and intestinal linings are shed during molts, and the symbionts are cast along with the exuvia (the protozoa do not encyst as occurs, for example, in the woodroach *Cryptocercus*) (17). Freshly molted termites may receive a new assemblage of symbionts by transfer via the hindgut fluids of a nestmate, or individuals may eat a freshly cast exoskeleton and reinstate the protozoa therein.

The impact of the intestinal symbionts on termite life history is fundamental because they are required for nutrition in all but the most derived family (Termitidae), and dependence on the protozoa precludes the option of solitary living in these hemimetabolous insects. Many authors, beginning with Cleveland et al (17) have noted that reliance on the intestinal flagellates predisposes termites to parental care and a social life, and that this symbiosis may have been one driving force in the evolution of sociality in this group (70, 84, 88). There is a broad consensus, however, that although the intestinal protozoa are a fundamental adaptation that requires group living and overlap of generations, this symbiotic relationship in termites does not by itself select for advanced components of eusociality such as reproductive division of labor (e.g. 3, 8, 60, 84, 121). Extended parent-offspring contact alone would facilitate transfer of symbionts. A similar symbiotic relationship with protozoa occurs in cryptocerid roaches within the context of a much simpler social system of extended parental care (84, 111). The symbiont transfer hypothesis, which has never been strongly advocated as a theory for the evolution of eusociality, is thus not persuasive except as an element predisposing termites to social living.

Hypotheses Based on Asymmetric Degrees of Relatedness

Many discussions regarding the evolution of eusociality in Hymenoptera are linked to the fact that their haplodiploid genetic system renders relatedness higher among sisters than between a queen and her female offspring. The high average degree of genetic relationship between sisters is seen as an explanation for the evolution of worker behaviors. Workers in ant, bee, and wasp colonies are female. By helping their mother raise their sisters (some of which will be

fertile reproductives), workers likely increase their fitness (through inclusive fitness) over that which would be possible if they were solitary parents (45). Employing parallel reasoning, the cyclic-inbreeding and chromosome-linkage hypotheses have been proposed for the diplodiploid termites as mechanisms to generate similarly skewed degrees of relatedness among sibs in comparison to relatedness between parents and offspring. This would yield the consequences of haplodiploidy and, according to theory, facilitate kin selection as the driving force toward eusociality in termites.

CYCLIC-INBREEDING THEORY Bartz (8, 9) constructs a hypothetical breeding pattern that would result in protermite workers being more closely related to siblings than to offspring, thus favoring reproductive division of labor as reasoned for the Hymenoptera. This regime involves inbreeding, a condition that increases relatedness among family members and is therefore predicted to discourage selfishness within kin groups (45, 46, 77, 134). Bartz recognizes that although inbreeding increases an individual's relatedness to its siblings and to their offspring, it also boosts relatedness between individuals and their own offspring. Thus, if inbreeding continues, the extent to which inclusive fitness is increased by helping to raise siblings over offspring becomes limited, if present at all, and the selective force for such behavior is weakened (see also 60).

Bartz (8, 9) cleverly reasoned a pattern of cyclic inbreeding and outbreeding, staggered to generate and maintain asymmetries in relatedness that would favor helping behaviors. If new colonies are founded by a king and queen that are unrelated to one another but which each comes from inbred colonies, then their offspring will be relatively homogeneous and thus more closely related to one another than they would be to their own (outbred) offspring. If subsequent generations within the colony were inbred (products of parent-offspring or sib-sib matings within the nest), progeny would also be more closely related to siblings than to (outbred) offspring (see also 33, 104, 132). Hamilton (45, 46) noted that the ancestors of termites were likely restricted to the specialized habitat of decaying wood, leading to further opportunities for and predispositions toward inbreeding.

It is impossible to evaluate the reality of this type of breeding regime by studying extant termites because the model examines the case before establishment of a eusocial system, and evolutionary dynamics likely changed considerably once termites passed through the "bottleneck" of eusocial evolution. It is common, however, for termite colonies to replace a dead or senescing king or queen with one or more neotenic or adultoid reproductives that mature within the nest (95, 97, 129), thus providing opportunities for parent-offspring matings. If both original reproductives are gone, replacement reproductives often differentiate within the colony, leading to sibling-sibling, cousin-cousin, or other

inbred matings. Fertile, dispersive progeny (alates) produced during this period would be inbred (and therefore relatively homozygous), and would fly to found a colony with a mate (potentially an outbred union). Thus, the fundamental life-history aspects of the model are plausible, but it is not possible to determine the extent to which ancestral termites fit the premises of the hypothesis. Kings and queens in extant species often live long enough to produce alates themselves (82). If at least some of the kings and queens are from inbred lineages, the asymmetries in relatedness will exist, but the degree of asymmetry will subside as the proportion of outbred reproductives increases (113).

CHROMOSOME-LINKAGE HYPOTHESIS In some species of termites, a deviation from the expected relatedness structure of autosomal genes is caused by multiple reciprocal translocations among some of the chromosomes in males, apparently including the Y chromosome (73, 74, 122, 123, 133). These translocations result in the chromosomes forming rings instead of bivalents during meiosis, and segregating to the respective poles in linked clusters. Thus an entire set of translocated chromosomes moves together into Y-bearing gametes. In some species over half of the termite genome is involved in the translocation complex, and because it moves as a unit during meiosis and segregates like a single giant chromosome, the result may approach relatedness patterns typical of haplodiploidy. Lacy (60, 61) argued that these higher degrees of relationship could favor the evolution of altruistic behavior among siblings of the same sex.

In principle this “haplodiploid analogy” seems intriguing, but the translocations are absent in studied members of the primitive Mastotermitidae and Termopsidae, and the chromosome rearrangements appear to have arisen independently as a derived rather than ancestral condition (11, 23, 34). Further, no evidence has been found of sex-biased behaviors within termite colonies (41, 72). Leinaas (64) noted that if any move were made toward manipulation of the sex ratio of the brood, the male and female reproductives would generate a conflict of interest due to the linked genes within the translocation complex. In short, there is widespread consensus that multiple sex-linked reciprocal translocations were not a major factor, if any, in the evolution of eusociality in termites (23, 24).

The other two major hypotheses to explain eusocial evolution in termites involve intrafamilial dynamics and kin selection but do not depend upon generation of asymmetric degrees of genetic relatedness within a colony.

Shift-in-Dependent-Care Hypothesis

Nalepa (85, 88) discusses a possible scenario for describing how a prototermite familial group might make a transition to cooperative brood care and reproductive division of labor. The need for symbiont transfer to neonates, the relatively

poor nutritional quality of wood, and life within a log habitat together selected for subsociality, monogamy, and slow development. Within this context, Nalepa postulates a behavioral shift within a young family: The older brood makes a transition from food recipients to food donors, thus shifting the responsibility for care of dependents from parents to older offspring. Because of the limiting nutrients that are directed toward neonates (and parents), individuals functioning as workers have depleted nutritional reserves and spend a prolonged period in the juvenile stages, although they may eventually become fertile, winged imagoes.

This scenario may reflect what occurred during the transition from a subsocial to a eusocial life history, but it does not address the selective dynamic favoring such a switch in responsibilities from parents to elder offspring. Why is it in the best interests of the “workers” to make this behavioral change, delaying or possibly foregoing their own reproductive potential to care for younger siblings and parents? Perhaps this is due to kin selection if a helper’s inclusive fitness is boosted by this behavioral transition, or the change might be postulated as a result of parental manipulation (still kin selection) (12). The shift of care from parents to older offspring is important because it allows the parents to invest more rapidly in their next clutch, but their production of first fertile offspring is apparently delayed in this scenario because the older offspring spend longer periods in the juvenile stages. Thus, the fundamental evolutionary question remains: What were the selective forces that favored this shift in dependent care and other features of the life histories of termite reproductives and helping offspring? What evolutionary forces resulted in termite eusociality, whereas *Cryptocercus* family groups, living with similar life histories in similar habitats, remain subsocial?

Intragroup Conflict and Selection for a Helper Phenotype Hypothesis

Roisin (106) proposes that intragroup competition among late instar larvae or nymphs to reach the alate stage would result in conflicts that could lead to a helper phenotype in prototermites. He suggests that some individuals are deflected from alate development because of wing pad injuries inflicted as bites due to competition among sibs vying to become alates. Individuals with damaged wing pads became “lower status” helpers with reduced chances of future dispersal. Roisin cites as evidence of such conflicts the wing bud damage (generally interpreted as mutilations by other colony members) on nymphs of kalotermitids, termopsids, and some rhinotermitids. Nymphs with damaged wing buds cannot molt directly into alates but instead undergo regressive or stationary molts (to become pseudergates). Subsequent wing bud regeneration and formation of a normal alate is possible, but it requires a delay and additional molts (105, 107, 115, 120, 142). Roisin suggests that the mutilated “losers” in

intracolony conflicts formed the original helpers in termites. At first only the losers would express the helper phenotype, but as helpers became increasingly efficient and effective in contributing to the colony, the phenotype was expressed by undamaged individuals because of indirect fitness benefits. This scenario would result in a caste of helpers that became fixed from a “condition sensitive” origin. This line of reasoning has been applied to the evolution of helpers in some bees (76) and wasps (137), and Roisin extended this theory to termites.

This is an intriguing hypothesis because it addresses some of the various interests among individuals within termite colonies, and how these may have contributed to the evolution of helpers. Three issues need to be considered in evaluating the likelihood of Roisin’s scenario. The first is that although the “losers” that become helpers have a reduced or delayed chance of future dispersal as alates, they are positioned to be reproductive winners if the opportunity arises to become a replacement reproductive within the colony. Roisin (106) recognizes that reproduction within the established natal nest is less risky than a dispersal flight and colony initiation, but in the model the “losers” are viewed as helpers, rather than as hopeful reproductives. A second consideration regarding Roisin’s theory pertains to developmental pathways. According to Roisin’s constructs, the original helper phenotypes derived from nymphs deflected from alate development that were forced to regress to pseudergates. This occurs relatively late in the ontogeny of an individual. In modern termites individuals from at least the 4th instar on function as workers, generally without first differentiating into a wingbud form. Thus Roisin’s earliest helpers develop indirectly and as older individuals. How the behavior would be expressed directly in young individuals is not explained. The third aspect of Roisin’s theory that is difficult to interpret is the fact, acknowledged by Roisin (106 p. 757), that wing bud scars in the Termopsidae appear to be due to self-induced abscission, not mutilation by colony members as apparently occurs in kalotermitids (29, 49, 51, 106, 142; Thorne et al, personal observation). Work in our lab on complete colonies suggests that wing bud abscission in *Zootermopsis* occurs in the context of opportunities to become a replacement reproductive (BL Thorne et al, unpublished data), as had been noticed by Lenz & Runko (67) in the rhinotermitid *Coptotermes lacteus*. Behaviors and dynamics in modern termites are difficult to interpret, but the case of the termopsids is of interest because they are socially, morphologically, and developmentally more primitive than the kalotermitids and rhinotermitids. The reproductive biology of termites, and the contexts under which primitive termites lose wing buds, need to be better understood before this hypothesis can be fully evaluated.

None of these five hypotheses can be summarily dismissed, but based on current knowledge, none is completely persuasive. It should also be noted that

the hypotheses are not mutually exclusive. The symbiont hypothesis is not overly compelling, although the symbiosis with protists enabled termites to specialize on a wood diet, a nutritionally weak food source that may have had its own implications, and the symbiosis required an overlap of generations for transfer of an inoculum of protozoa to juveniles. The chromosome linkage hypothesis was interesting when first proposed, but as data have accumulated on the phylogenetic distribution of the translocation complexes, and on lack of sex-biased behavior in termites, this hypothesis has been broadly discarded (23, 24).

It seems probable that eusociality in Isoptera evolved in response to a variety of contributing elements and the selective pressures that they generated. In addition to the hypotheses described above, a number of frequently overlooked factors warrant consideration as affecting the evolutionary dynamic of eusociality in termites. These pertain to the ecology and life history of termites and their ancestors, and these are particularly persuasive characteristics because many are present in a broad group of eusocial taxa, including Hymenoptera, beetles, aphids, thrips, naked mole rats, and shrimp (2, 19, 30, 42, 43, 57).

ECOLOGICAL AND LIFE HISTORY CORRELATES OF EUSOCIALITY

As eusociality is discovered in more and more animals and details of their life histories are unveiled, it is clear that a comparative approach may be productive in gaining insights into the evolution of highly social groups. Each evolutionary context was obviously unique, but there are enough characteristics shared among phylogenetically diverse eusocial animals to make a compelling case for the existence of suites of ecological and life-history characters that are correlates of eusociality, and in various clusters may serve as factors that foster the evolution of eusociality. A synopsis of some of these traits is presented in Table 1. The list of animal groups bearing each characteristic is likely incomplete; as more is learned about each eusocial species the table can be developed. Termites have each of the life-history components listed in Table 1 except for haplodiploidy. The following discussion expands upon each of those ecological characteristics as represented in primitive termites, along with a brief explanation about how these life-history features relate to eusocial evolution.

Primitive termites nest under the bark of large dead trees or logs. These environments provide a protected, food-rich habitat. The initial nest is a small, cloistered cavity, but is readily expanded into adjacent parts of the wood as a colony grows. In their confined nesting area, families live together for more than one generation, providing opportunities for kin-selected reproductive altruism and rendering it feasible for parents to capitalize on the food-gathering behaviors of their offspring (2, 3, 8, 16, 42, 43, 46, 102, 124). Parental care (sub-sociality) exists through the first several instars in young colonies, with brood

Table 1 Ecological and life history preconditions/correlates of eusociality

Precondition/correlate	Eusocial group	References
NESTING HABITAT		
<i>Claustral Familial Associations</i>		
<ul style="list-style-type: none"> • Safe, initially small, long-lasting (multigenerational), expandable, food-rich habitats; nesting in protected cavities keeps relatives together, thus providing opportunities for kin-selected reproductive altruism; Nesting aggregations make it easy for parents to parasitize the food-gathering behavior of their offspring 	Eusocial Hymenoptera, termites, naked mole rats, shrimp, ambrosia beetles, gall-dwelling aphids, thrips	(2, 3, 8, 16, 19, 42, 43, 46, 52, 57, 102, 114, 124)
PARENTAL CARE (SUBSOCIALITY)		
<ul style="list-style-type: none"> • Family (kin groups) 	Eusocial Hymenoptera, termites, aphids, ambrosia beetle, thrips, naked mole rat shrimp	(2, 4, 5, 17, 19, 30, 52, 57, 138)
DEVELOPMENT		
<i>Slow Development, Long Generation Time, Overlap of Generations</i>		
<ul style="list-style-type: none"> • Long life span, especially of reproductives (parents evolve to live longer than their helper offspring) 	Eusocial Hymenoptera, termites, naked mole rat	(2, 46, 62, 112)
<ul style="list-style-type: none"> • Gradual metamorphosis (individuals begin helping as immatures, and can improve in helping ability as they age) 	Termites, naked mole rat, shrimp	(2, 55, 98)
GENETICS		
<i>Haplodiploidy</i>		
<ul style="list-style-type: none"> • Genetic asymmetries increase the reproductive advantage of a female tending full siblings rather than producing offspring 	Hymenoptera, thrips	(3, 19, 42, 43)
<i>High Chromosome Numbers</i>		
<ul style="list-style-type: none"> • Relatively high chromosome numbers would reduce the ability of sibs to differentiate among each other based on relatedness, and would also reduce inclusive fitness variance among sibs, thus facilitating social evolution 	Most social Hymenoptera, termites	(112, 118, 125; but see 3, 12, 26)

(Continued)

Table 1 (Continued)

MATING SYSTEM: SINGLE FATHER		
(MONOGAMY)		
<ul style="list-style-type: none"> • In haploid-diploid groups monogamy assures that sisters share all the genes from their father and thus, on average, 3/4 of their genes are identical by immediate descent 	Primitive condition in social Hymenoptera	(42, 43)
<ul style="list-style-type: none"> • In diploid groups monogamy renders siblings genetically indifferent as to whether they rear fertile siblings or their own offspring 	Termites, naked mole rat?, possibly shrimp	(16, 45)
REPRODUCTIVE CYCLE:		
ITEROPAROUS		
<ul style="list-style-type: none"> • Older offspring care for younger siblings 	All eusocial animals	(2, 24, 112)
HIGH-RISK AND/OR TIME INVESTMENT IN DISPERSAL AND FOUNDING OF NEW NESTS		
<ul style="list-style-type: none"> • Remaining as a helper in the parental nest may be substantially safer and more efficient than attempting dispersal and successful development of a new nest 	Hymenoptera, termites, naked mole rat	(27, 51, 89, 103)
OPPORTUNITIES FOR SUBSTANTIAL INHERITANCE		
<i>Replacement Reproductive Opportunities</i>		
<ul style="list-style-type: none"> • Possibility of maturing and reproducing within the group, either as a replacement or supplementary reproductive, and thus inheriting group resources 	Termites, wasps (ants & bees produce male eggs, naked mole rat)	(2, 3, 79, 139)
DEFENSE		
<ul style="list-style-type: none"> • Need for group defense against predators 	Social insects	(12, 44, 70)
<ul style="list-style-type: none"> • Need for group defense against intra- and interspecific competitors 	Termites, shrimp	(30, 131)
<ul style="list-style-type: none"> • Specialized defense: sting (facilitated the evolution of eusociality among Hymenoptera in exposed locations); major or soldier caste (ants, termites, aphids, thrips); major claw (shrimp) 	Hymenoptera, aphids, thrips, shrimp	(2, 4, 6, 19, 30, 139)

care responsibilities largely transferred to older siblings as the colony grows (17, 31, 88, 109, 116, 138).

Termites have slow and gradual development, with relatively great longevity, especially of reproductives. The extended development time is thought to be due, at least in part, to the nutritionally impoverished diet of decayed wood (46, 62, 88, 117, 135). Life span of reproductives in the field is not known, and modern termites offer only inferences about ancestral characteristics, but a king of the primitive termite *Mastotermes darwiniensis* is known to have lived for 17 years in the laboratory (136). Termites have hemimetabolous development; thus, in contrast to Hymenoptera, they engage in social activities and assistance as soon as they pass the early instars (55, 98). A further consequence of gradual development in termites is that under certain circumstances larval and nymphal individuals can differentiate into neotenic reproductives, a widespread phenomenon in primitive termites (80, 82, 91, 98).

Termites generally have higher chromosome numbers than do related taxa, a characteristic that reduces the variance in the proportion of genes shared by siblings, thus making them less able to favor more closely related sibs and perhaps facilitating care and altruism among all siblings (112, 118, 125). The importance of high chromosome numbers is uncertain, however, because it is difficult to model how the trait would spread (3, 26). Also, it is dissuasive that a species in the primitive ant genus *Myrmecia* has a haploid chromosome number of one (21).

A monogamous reproductive pair normally cloisters to found a termite colony. Monogamy in a diploid organism results, on average, in both male and female siblings sharing one half of their genes. Because this degree of relatedness by descent is identical to the relatedness that termites share with their offspring, it is genetically (and fitness) neutral whether an individual termite produces fertile offspring or, by helping in its parents' colony, it boosts the production of fertile siblings by an equivalent number (16, 45). Alate dispersal and successful founding of new colonies are risky in termites (27, 51, 89, 102), thus there are clear safety advantages to remaining as a helper in the natal nest (79, 106). Temporal efficiency may also select for nondispersive helpers in termites because it takes time for queens to develop fully productive ovaries and a brood of helpers to support rearing her eggs. Individuals remaining in their parents' nest likely help their mother produce more offspring (including fertile progeny) than she would without their assistance, and workers partake of inclusive fitness benefits earlier, and with less risk, than if they sought direct fitness through independent colony development.

All eusocial insects are iteroparous. This leads to staggered age classes within colonies, enabling older offspring to rear younger siblings. It is notable that the woodroach *Cryptocercus* is semelparous (86), and not eusocial.

Termite societies offer several opportunities for substantial inheritance of resources to heirs within the colony. In the case of primitive termites, replacement reproductives differentiate among offspring following senescence or death of the original king and/or queen. In a decaying log, the presence of more than one colony will eventually result in intercolony interactions, which can lead to death of reproductives and opportunities for replacement (BL Thorne et al, unpublished data). Heirs also receive an established nest, food, a work- and defensive force of laborers and soldiers, and, possibly, close relatives that will differentiate into fertile alates. These possible inheritances constitute a potentially high payoff to some of the individuals that remain in the parent colony (79, 80). The fact that mechanisms exist for colony reproductive succession suggests that all individuals, both helpers and reproductives, are better assured persistence and thus an eventual pay-off of their investments.

A well-documented advantage to each individual living in a group is the benefit of cooperative defense against predators, parasites, and competitors (2, 32, 70, 139). In addition to the advantage of numbers, most eusocial groups have a specialized mode of defense. This may be weaponry present on all individuals, such as the sting in eusocial Hymenoptera (females) or the major chela (claw) in shrimp (2, 30). Alternatively, some eusocial taxa have a morphologically specialized defensive subgroup, or caste, such as major ants or soldier termites, aphids, and thrips (4, 6, 19, 139). The soldier caste in termites is considered to be monophyletic, and to have evolved early in the evolution of the order, but probably after or concurrently with the evolution of eusociality (90, 100). Although the Hymenoptera sting and the shrimp claw may have been preadaptations favoring social options, group defensive behaviors and specialized castes evolved along with social living. The risks of solitary living and the advantages of group defense may, however, have served as selective pressures for advanced social life in some or all of these organisms.

Thus a wide array of ecological characteristics of other eusocial animals, that are therefore viewed as potentially predisposing taxa toward eusociality, are also found in termites (Table 1). The fact that Isoptera have so many of these life-history characteristics lends credibility to the suggestion that some or all of these factors, probably acting in concert, served to channel prototermites toward evolution of eusociality.

TERMITE ANCESTORS AND THE TRANSITION TO EUSOCIALITY

There is a broadly accepted notion that termites are derived from a *Cryptocercus*-like ancestor (17, 85, 88, 121, 139), although the phylogenetic relationship between Cryptocercidae and Isoptera remains the subject of investigation (7, 35,

54, 130). Similarities in life histories between *Cryptocercus* and termites may have been due to convergence rather than common ancestry (46). Because discussions of social evolution so frequently link *Cryptocercus* and termites, insight can be gained by comparing and contrasting the biology of the two groups, at least based on modern representatives. Both *Cryptocercus* and termites nest in decaying wood, do not forage out of their nest galleries, live in families with overlapping generations, and rely on similar intestinal symbionts for digestion. However, it is not clear whether the symbionts were acquired in each taxon through inheritance or by transfer (36, 87, 127, 128).

Given the similarities in claustral habitat, diet, and family groupings, one can ask why one of these dictyopteran groups evolved eusociality whereas the other has not. In contrast to termites, *Cryptocercus* are semelparous, with high parental investment in small broods that average about 20 individuals in *C. punctulatus* (84–86, 111). Termites are iteroparous and have higher fecundity, although colony sizes of the primitive termite *Archotermopsis wroughtoni* are thought to be relatively small, typically consisting of 30–40 individuals (108). In termites offspring are cared for by other offspring whereas wood roaches rely on parental care. Another major difference is that *Cryptocercus* are apterous whereas termites have a winged, dispersive reproductive form. Termites also have non-winged reproductive forms (neotenics) that differentiate when the original founders die, thus enabling an established colony to persist for many generations.

Therefore, despite several similarities, the social systems and life histories of *Cryptocercus* and termites are significantly different, and the former does not necessarily represent an intermediate evolutionary transition to the latter. It is thus important to consider possible step-by-step scenarios for the evolution of eusociality in termites, beginning with a solitary ancestor and following the transition through to eusocial groups. Such a sequence is obviously impossible to reconstruct or to test, but plausible alternatives, with evolutionary justification for each step, may be constructed and evaluated. Below I describe one such scenario for the evolution of eusociality in termites, based in large part on the composite of life-history characteristics identified in Table 1.

There is a consensus that eusociality in termites evolved in dead trees rather than evolving elsewhere with a subsequent transition into decaying wood (46). Thus solitary ancestors of termites likely fed upon decayed vegetation. They began to consume decayed wood, first facultatively and then, with the symbiosis with cellulolytic protists firmly established, as specialists and permanent residents with occasional bouts of dispersal. They probably first inhabited the cambial layers (cambium plus phloem) of dead trees, a relatively rich and well-balanced food source in modern trees (40, 46, 117), and probably in Mesozoic gymnosperms as well (10). After reproductive pairs colonized the layers directly

under the bark, extended development times (that resulted from a wood diet) and the confined nest cavities of excavated wood favored sequestering of the monogamous family groups. Individuals did not leave the nest area to forage. All surviving offspring eventually matured into winged alates and dispersed. The claustral nests, relatively slow development, and need for reinfestation of symbionts selected for parental care and long-term associations of small family groups (subsocial “colonies”). Iteroparous parents produced a brood of staggered age classes all living together.

As prototermites became increasingly specialized in habitat and with symbiotic protists, and as the cambial tissues of a log became crowded with competitors, the insects may have fed upon adjacent decaying sapwood. Colonizing the sapwood and heartwood layers would have expanded resources and improved protection from predators, but the nutritional quality of those tissues is poorer than that of the cambial region (40, 46, 117, 135) and may have further slowed individual growth rates. Slow growth resulted in older sibs remaining in the nest for a relatively long time before maturing into alates. They would thus have been poised to assist as adolescent helpers feeding and grooming dependent instars, defending the group if necessary, and perhaps feeding and grooming parents. The costs of intermittent sharing of food in terms of delayed growth rates of the helpers might have been relatively low because no transit energy would have been required to acquire food. Feeding capabilities of juveniles are conceivable because both king and queen termites feed the earliest instars of their first brood; thus parenting behaviors could reasonably be expressed in male and female immatures (2, p. 20). Potential costs of nest defense by immatures would have been high (i.e. injury or death), but defense risks are high independent of group or solitary nesting, and the cost per individual might well be lower in a group (44). Thus circumstances that might have facilitated offspring remaining in the nest and assisting in sibling brood care were present as a result of the primitive termite habitat and diet.

A significant transition in this dynamic may have begun as a shift toward a larger and more consistent commitment toward brood care by older instar sibs (88). An extended maturation time for older offspring in the colony (due to energetic allocations to brood care) delayed the age of first reproduction of F1 (helper) individuals, the inclusive fitness that F1 individuals gained from reproduction by sibs, and production of fertile progeny by the parental generation. These costs were presumably balanced by higher fecundity of reproductives, made possible because the parents were relieved of some dependent care responsibilities, freeing time and energy for additional egg production. Parents also had assistants to support care of a larger brood. In competition with other colonies, increased colony size may have been a strong advantage. Thus in its earliest stages, with relatively small colonies, delay in reproductive output as a

result of sibling brood care was ultimately compensated by a higher probability of survival and production of a larger number of alates by the group as a whole.

The transition toward helping and delayed maturity would have required the evolution of a longer life span, but selection for longevity was already in progress as a result of slowed development due to the wood diet. The apparent altruism of older sibs delaying their own maturity to care for younger sibs can be explained by simple kin selection, plausible because in this monogamous, diploid system individuals share, on average, exactly as many genes by descent with their siblings as with their own offspring. Given the low probability that any individual termite alate would survive dispersal and successfully rear a brood to maturity, the fitness payoff may well have been higher and more assured to termites that remained to help boost sibling production in their already established parental nest.

In this evolutionary scenario thus far, the prototermite colonies have no morphological castes, and all surviving progeny eventually become dispersing alates. Two changes occurred in the next step of the social transition: the development of lifetime helpers and of neotenic reproductives within a colony. Because many offspring had delayed maturation and continued to assist within the natal nest, not all F1 individuals matured into alates, and a portion of the colony thus became lifetime helpers. It was at this point that the society could be considered fully eusocial (139), with overlapping generations, cooperative brood care, and a reproductive division of labor. The helpers were non-reproductive, but not sterile. All individuals could become neotenic reproductives even in relatively early instars, but inferences based on modern species suggest that neotenic differentiation probably occurred only after senescence or death of the primary reproductive of that sex. Sometime in this early evolution of termites, hormones became important in suppressing and releasing gonad development among individuals within the brood. The hormones were produced by functional reproductives and spread by trophallaxis (proctodeal trophallaxis had already evolved for transfer of hindgut symbiotic protists; oral trophallaxis was an established behavior for feeding dependent brood and, possibly, reproductives).

It need not have been altruism or parental manipulation that led to lifetime helpers in termite colonies. The evolutionary trade-off for F1 individuals was high-risk dispersal and improbable production of mature offspring versus the low risk of remaining in an established colony to rear siblings, coupled with a chance at the high pay-off of inheriting reproductive status as a neotenic should a parent senesce or die. Eusocial evolution occurred in small colonies. Primary reproductives may not have lived as long as they do in modern species, so opportunities for reproductive (and nest) inheritance may have been relatively high for individual helpers even in young colonies [a similar dynamic to “helpers

at the nest” in birds (14)]. Differentiation of neotenic replacement reproductives would be an advantage to the whole family in carrying on the colony. Each helper would “prefer” to become a reproductive, but at worst reproductive siblings would inherit the colony. Suppose, for example, that the original queen survived but that the king was replaced by one of his offspring. A helper in the colony would then be an offspring of the queen and a sibling of the neotenic replacement male. That helper would still share, on average, one half of its genes with progeny of that inbred union. Even if both primary reproductives died and were replaced by offspring, a helper sib of the new reproductives would rear inbred nieces and nephews, with potential rewards of substantial inclusive fitness.

Individuals that became extended helpers retained the option of eventual dispersal as alates. Primitive termites have remarkably flexible development, maintaining the ability to molt from apterous to brachypterous lines, and vice versa (99). In certain circumstances, such as depletion of host log resources or presence of numerous competitor colonies, a low probability of colony survivorship might induce a large percentage of individuals within the colony to become alates rather than to remain as helpers.

There is one exception to the options for flexible development, and another feature of termite evolution that must be addressed: the soldier caste. Soldiers apparently evolved early because they appear to be monophyletic among extant termites (48, 95, 99). The soldier caste is terminal; soldiers do not molt and therefore lack further developmental flexibility (92, 95, 99, 100). Their mandibles are clearly derived, extended versions of nymphal mandibles, with homologous dentition (48). In primitive living termites, soldiers differentiate from a variety of instars [normally beginning with the 4th (95)], and from both apterous and brachypterous individuals (126). All soldiers of *Archotermopsis wroughtoni* have fully developed gonads (51), and fertile reproductive soldiers (or “soldier neotenic”) differentiate in some Termopsidae (78). Reproductive soldiers are normally the first replacement reproductives to differentiate in young, orphaned colonies of the primitive dampwood termite *Zootermopsis nevadensis* (BL Thorne et al, unpublished data). The first termite soldiers may have retained reproductive capability, but it is unclear whether the soldier morph appeared and was selected for as a defensive caste or as replacement or supplementary reproductives. If the latter occurred, then subsequent evolution of gonad degeneration of most individuals differentiating along that soldier pathway would result in what is now a typically sterile defensive caste.

As termite species radiated, derived traits such as construction of nests, foraging away from the nest, and constrained developmental pathways (e.g. true workers) evolved. An overwhelming majority of the 2000+ extant species of termites have this highly derived colony structure, with discrete and canalized castes; a distinct division of labor; vestigial gonads and effective sterility of all

soldiers and, except under very unusual circumstances, all workers; a long-lived king and physogastric queen; large colony population size; and highly organized foraging behaviors. Many of these derived species build complex nest structures that provide a relatively homeostatic environment for reproductives and brood, and serve as a headquarters for foragers. Termites are ecologically important and conspicuous members of many temperate and tropical communities. Their success may be in large part due to the fact that they are eusocial, with the advantage of efficient allocation of tasks and resources among cooperating individuals within flexible and resilient societies (140).

CONCLUSIONS

It is unlikely that eusociality in termites arose as a result of evolutionary forces acting on any one dynamic or on any single life-history component. Circumstances such as cyclic inbreeding (8), confined, subsocial groups with a poor diet (2, 46, 88), or intragroup competition (106) may have all provided impetus toward eusociality in termites, but at this point no single condition can be identified as the dominant driving force. The additional ecological and life-history attributes that termites share with other eusocial animals as apparent correlates of eusociality (Table 1) are a particularly compelling ensemble because termites have all of these except haplodiploidy. Against this framework of favorable preconditions one must still define evolutionary dynamics that would have promoted the most extreme eusocial characteristic, highly skewed reproductive division of labor within a colony.

In termites, the "colonies" in which eusociality evolved were small families. Individual prototermites in a young family would have faced three options. First, they could spend no time or energy helping, and instead develop directly into a winged alate. Dispersal and colony initiation would have been risky, with no direct fitness pay-off until a successful colony produced fertile offspring. A second choice would be for offspring within a family to kill their parents and take over reproduction in the excavated nest galleries. Such behavior would not be favored by natural selection because it is in the interest of offspring to have their parents (the "king and queen") keep producing their siblings, especially given the neutrality of genetic relatedness between offspring and siblings (one half in a diploid system). Further, parents would likely evolve mechanisms to supplant mutinies among progeny.

A final choice for offspring developing slowly within a monogamous, iteroparous family living in a confined cavity within an expandable resource would be to remain in the nest, for at least a while, to help rear siblings. In animals like termites this might have been an especially productive strategy because fertile siblings provide an identical fitness pay-off (genetic relatedness = one

half) as offspring. Helping a colony to expand gives it a higher probability of survival, facilitating its persistence and continued production of fertile relatives. Further, the ability of termites to develop into neotenic reproductives offers the possibility that helper individuals may become replacement reproductives, which confers a fitness advantage augmented by inheritance of the nest, labor, and food resources. In primitive, developmentally flexible termites the helping alternative might have been relatively low risk because, except for soldiers and reproductives, all individuals retained the option of differentiating into an alate.

Thus the trade-off faced by individuals within small prototermite families was no helping, no boost in inclusive fitness, and early, high-risk dispersal as an alate versus temporary helping, potential replacement reproductive opportunities, and the cost of delayed high-risk dispersal as an alate. Ultimately, or perhaps immediately, some temporary helpers served their entire lifetime within the colony, thus becoming permanent helpers in a eusocial system.

Although we may never definitively identify and prove the driving forces behind the evolution of eusociality in termites, the probable life-history characteristics of their immediate ancestors suggest some compelling possible scenarios for eusocial evolution based on individual selection. Eusociality in Isoptera was probably fostered by a suite of contributing factors and the concurrent and cumulative selective pressures that they generated.

ACKNOWLEDGMENTS

I express sincere appreciation to NL Breisch, RF Denno, and ME Suárez for insightful and constructive comments on earlier versions of this manuscript. Discussions with many distinguished isopterists and social insect biologists during the course of my career have helped me to formulate and synthesize ideas presented in this paper. In the regard, I particularly acknowledge the mentoring and insights of Bert Hölldobler, Michael Lenz, Charles Noirot, Bill Nutting, Yves Roisin, and Ed Wilson.

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