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ORIGINAL ARTICLE

Judith Korb · Sandra Schmidinger

Help or disperse? Cooperation in termites influenced by food conditions

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Abstract Ecological factors have been claimed paramount for the evolution and maintenance of cooperative group living in eusocial termites, as well as in cooperatively breeding birds and mammals. However, a clear demonstration of the role of any specific ecological factor in termites has been lacking. In the termite *Cryptotermes secundus*, individuals have two options, staying as helpers at the natal nest or developing into winged sexuals that disperse to found new colonies. An important ecological factor expected to influence the course of termite development is food availability; *C. secundus* nests inside a single piece of wood that serves as the sole source of food for the duration of the colony. As wood is consumed, the longevity of the colony is reduced, thus diminishing the potential fitness gains of staying at the nest. We experimentally investigated the occurrence of cooperative behavior and development under abundant- and limited-food conditions. Workers exposed to food-limited conditions were more likely to develop into dispersing sexuals and increased "selfishly" their food-acquisition behaviors. Proximately, a reduced frequency of proctodeal trophallaxis may have interfered with the distribution of pheromones that inhibit sexual development. Ultimately, decreased inclusive fitness benefits in food-limited, and thus short-lived nests, appear to explain the development of dispersing sexuals, supporting (1) the benefits-of-philopatry hypothesis as developed for the occurrence of cooperative breeding in vertebrates, and (2) predictions of reproductive skew theories.

Keywords Cooperation · Dispersal · Termite · *Cryptotermes secundus* · Food availability

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J. Korb (✉) · S. Schmidinger
Universität Regensburg,
Biologie I, 93040 Regensburg, Germany
e-mail: Judith.Korb@biologie.uni-regensburg.de
Tel.: +49-941-9432461
Fax: +49-941-9433304

Introduction

Termites are the oldest social organisms and, as in ants, all species are eusocial. However, in contrast to Hymenoptera, few studies have been performed on Isoptera addressing the evolution of altruism, where individuals forego their own reproduction to help enhance the fitness of close relatives. Kin selection theory (Hamilton 1964; Maynard Smith 1964) provides the generally accepted framework for addressing the evolution of altruism. In the diplodiploid termites, most studies have concentrated on identifying mechanisms that could create a genetic situation similar to that of the haplodiploid Hymenoptera (i.e. Bartz 1979; Lacy 1980). However, these models have been largely discredited (Leinaas1983; Crozier and Luykx 1985; Myles and Nutting 1988; Husseneder et al. 1999), and ecological factors are claimed to be paramount in favoring and maintaining altruism in termites. However, studies that quantitatively test these factors are scarce (Myles and Nutting 1988; Shellman-Reeve 1997; Thorne 1997). We manipulated the relative ecological constraints on dispersal by experimentally changing the benefits of staying in a nest to investigate its influence on the cooperation and development of individuals in a lower termite.

Recently, an experimental study with the drywood termite *Cryptotermes secundus* (Hill) indicated that abundant food seems to be of prime importance for workers to stay at their natal nest. Colonies with limited food produced more dispersing sexual offspring than comparable colonies with abundant food (Korb and Lenz 2004). *C. secundus* belongs to the so-called "one-piece" termites (hereafter "OP-termite") that spend their entire colony life in a single piece of wood that serves both as shelter and food (Abe 1987). As these termites do not forage for new resources, the availability of wood in the nest is of prime importance for the maximal longevity and the stability of the colony. This seems to have considerable evolutionary implications (Higashi et al. 1991). In contrast to most other termite species, OP-termites have no true worker caste and the "helper" individuals that perform most colony tasks are totipotent, late instar larvae and young nymphs, which retain the potential to develop into reproductives (Sewell and Watson 1981; Watson and Sewell 1985; Roisin 2000). They have the option to stay as "workers" in the nest or develop into dispersing sexuals that found their own colony. Thus, they are equivalent to the helpers found in cooperatively breeding vertebrate species (e.g. Emlen 1997) and are called "helpers" hereafter (see also Roisin 2000). Despite differences between both groups, for example in their life history (Pen and Weissing 2000), similar factors may shape their social life. Both groups lack the specific genetic predisposition of haplodiploidy of social Hymenoptera. Thus ecological costs and benefits, like high mortality rates during dispersal, nest inheritance and "a safe haven" at the parental nest (Kokko and Ekman 2002) may have favored altruism in both groups. Furthermore, an application of reproductive skew models (Vehrencamp 1983; Reeve and Ratnieks 1993; Keller and Reeve 1994; Johnstone 2000) may offer some important insights on the factors favoring cooperative staying at home versus dispersing in animals in general. These models are an extension of Hamilton's rule that include ecological, genetic, and social factors in a single explanatory framework, and aim to determine how these factors jointly influence the apportionment of reproduction (reproductive skew) among colony members. They define the conditions under which the best option for a focal individual is to cooperate and stay in the nest, sacrificing part or all of its direct offspring production (Keller and Reeve 1999).

We experimentally studied the importance of food availability in the nest, which is linked with staying benefits, on the occurrence of cooperation and dispersal in *C. secundus*. First, we tested whether food influenced the development of helpers, with limited food resulting in progressive molts towards dispersing sexuals. Second, we examined the potential proximate mechanisms of how these developmental changes might be achieved. Therefore, the development and behavior of individuals was studied under abundant and limited food regimes, trying to link behavior and development. Finally, we discuss our results in comparison to available hypotheses for the evolution of cooperatively breeding vertebrates and reproductive skew theory to show similarities and differences between termites, cooperative vertebrates and social Hymenoptera.

Methods

Experimental set-up

All colonies were collected from dead *Ceriops tagal* trees near Darwin (Northern Territory, Australia). They were kept in *Pinus radiata* wood blocks stored at 28°C and 70% relative humidity with a 12 h day/night cycle (Lenz 1994). We established 14 colonies, 7 each with either abundant or limited food. They were complete, monogamous colonies with a natural composition of instars and castes. Colony sizes ranged from 23 to 350 individuals reflecting the natural size range. To assess food abundance, *Cryptotermes* species use ultrasonic acoustic emissions generated by wood gnawing, as suggested by Lenz (1994) and confirmed in recent experiments (M. Lenz and T.A. Evans, unpublished data). Therefore, for the set-up of the experiment, abundant food colonies were transferred to *P. radiata* wood blocks that were appropriate for their size (1 termite:10 cm^3 wood; Table 1; see Lenz 1994), while limited food colonies were set up in wood blocks that measured only one-quarter that size (1 termite:2.5 cm^3 wood; Table 1). The use of *P. radiata* wood does not affect the growth and development of the termites (Korb and Lenz 2004). To control for the interaction and encounter frequency between both food conditions, we housed the termites in chambers in these blocks which were adjusted to colony size with no difference between abundant and limited food colonies (Table 1). The chamber size remained constant during the whole experiment by blocking all new tunnels immediately with paper. Thus, termites were also prevented from disappearing and could be continuously monitored during the whole study period. Under both food conditions, similar-sized pieces of *P. radiata* wood were constantly provided as food in these chambers so that neither abundant nor limited food colonies experienced an actual shortage of food. As these wood pieces were small (<0.25 cm^3; *Cryptotermes secundus* has a low rate of wood consumption), the influence on chamber size and total food supply was rather negligible.

Table 1 Wood-block volume (in cm^3) and chamber sizes (in cm^2) in abundant- and limited-food colonies. All wood blocks had a length:width:depth ratio of 4x:x:x.; for the chambers it was not possible to use constant ratios because of block-dimension constraints

Colony size	Block volume		Chamber size	
	Abundant	Limited	Abundant	Limited
≤50	500	125	14	14
51–100	1000	256	28	28
101–200	1985	500	54	54
201–300	3006	750	82	82
301–400	4000	1000	108	108

From each colony, we used at least 15 medium and large helpers as focal individuals because they had the potential to develop into dispersing sexuals in time for the next nuptial flight (J. Korb, unpublished data). Therefore, at the start of the experiment, each individual was classified under a dissecting microscope according to wing-bud development and thorax shape, using the schemata provided by Sewell (1978). Other standard morphometric measurements for classification of individuals and their developmental stage (Sewell 1978; Sewell and Watson 1981) were also used, but they did not provide unambiguous results. All individuals were marked with a unique color code, consisting of two small dots of email paint (Revell, Germany), one placed on the head and the other on the thorax.

Development

Individuals were checked at least six times a week throughout the duration of the experiment to ensure they retained their identifying markings and to assess their state of molting readiness. Termites that are about to molt have a whitish, opaque appearance. We reapplied vanishing markings and separated whitish termites into individual 2.0-ml vials. These termites were provided a piece of moistened wood for food and water, and were kept isolated until they molted, for a maximum of 5 days. Earlier experiments had shown that such a short separation from the colony had no influence on the development of individuals (J. Korb, unpublished data). After the molt, wing-bud development and thorax shape were redetermined and the molts were classified as progressive, stationary or regressive according to an increase, no change or decrease of wing-bud development. Newly molted termites were remarked with their previous color code and repatriated into their colony.

Behavioral observations

The marked individuals were observed during two 15-min periods conducted 2 months apart to observe whether behavioral changes occur during the course of the experiment. Two months were chosen because this period roughly corresponds to the mean interval between two consecutive molts (results from previous experiments: 64.5±3.2 days, *N*=134). Observations were initiated 2 months after the annual nuptial flights, and the total observation time for the experiment covered 6.5 months. During each observation, we used focal sampling to record all behaviors performed by an individual (active) and those in which it was involved as a partner (passive). In total, we observed 398 and 332 different individuals during the first and second observation, respectively. Differences in sample sizes for different behaviors are caused by missing values. The following behaviors were recorded:

1. Non-interactive behaviors (durations were recorded and classified into three categories: I: 0–5 min; II: 5–10 min; III: 10–15 min):
   - resting/feeding: individual does not move; this also includes feeding from the wood as it was not always possible to identify feeding (movement of mouth parts) unambiguously.
   - moving: individual moves.
2. Interactive behaviors between individuals (the total number of interactions were recorded, separately for actors and recipients of the behavior):
   - antennation: contact between individuals with the antennae.
   - allogrooming: one individual grooms another by moving the mouth parts over the others body.
   - proctodeal trophallaxis: exchange of substances between individuals via the anus; anus-mouth contact.
   - body shaking: back- and forward movement of an individual; thereby either butting into another individual or without contact with another individual.

Additional behaviors observed but too rare for analysis were: feeding on corpses, self-grooming, self- and stomodeal trophallaxis (exchange via the mouth).

Statistics

We compared the development (molting types) and behavior of individuals between the different food regimes with χ^2-contingency tables (non-interactive behaviors) and Mann-Whitney *U*-tests (interactive behaviors), separately for both observation periods. To investigate whether there was a link between the behavior of an individual and its development, we analyzed by means of Kruskal-Wallis tests whether individuals with different molting types behaved differently before the molt. This was done separately for abundant- and limited-food colonies and for both observation periods. All data were Bonferroni-corrected and analyzed with SPSS 10.0. All tests were two-tailed. The means and standard errors of the results are provided.

Results

Development

The frequency of the different molting types differed significantly between limited- and abundant-food colonies [abundant food: regressive: 22 (23.1%; range across colonies: 12.5–46.2%), stationary: 41 (43.2%; range: 11.1–55.6%), progressive: 32 (33.7%, range: 11.1–66.7%); limited food: regressive: 54 (23.2%; range: 8.0–40.7%), stationary: 44 (18.9%; range: 12.5–25.0%), progressive: 135 (57.9%; range: 40.7–76.0%); χ_2^2=23.14, *P*<0.001]. Limited-food colonies had significantly more progressive molts (χ_1^2=15.89, *P*<0.001) and fewer stationary molts (χ_1^2=20.71, *P*<0.001) than abundant-food colonies, while the frequency of regressive molts did not differ (χ_1^2=0.00, *P*=1.00).

The molting interval (i.e. the period between 2 molts) did not differ among molting types (regressive: 65.0±2.53 days, stationary: 69.6±3.71 days, progressive: 65.1±2.74 days; χ_2^2=2.89, *P*=0.472) or between the different food conditions (Mann-Whitney *U*-test, abundant food: 65.1±2.22 days, limited food: 68.3±2.82 days; *U*=260.5, $N_1=N_2=26$, *P*=0.312).

Behavioral observations

During the first and second observation, the time spent moving was significantly higher in abundant-food colonies than in limited-food colonies (Fig. 1; first observation: χ_2^2=25.8, *P*<0.001; second observation: χ_2^2=8.23, *P*=0.032), while it was the opposite for the time of resting/feeding during the first observation (Fig. 1; first observation: χ_2^2=22.1, *P*<0.001; second observation: χ_2^2=0.73, *P*=0.999). The frequency of proctodeal trophallaxis was significantly higher in abundant-food colonies than in limited-food colonies, during the first observation for both active and passive proctodeal trophallaxis and also during the second observation, but only for passive proctodeal trophallaxis (Tables 2, 3). In contrast, the following behaviors were more common in limited-food colonies (Tables 2, 3): body shaking (active and passive) during both observations, allogrooming (passive) and antennation (active and passive) during the first observa-

Table 2 Comparison of interactive behaviors in abundant- and limited-food colonies during the first observation. Shown are the mean (±SEM) frequencies and results of Mann-Whitney *U*-tests comparing different behaviors between abundant- and limited-food colonies during the first observation (*ac.* active, behavior performed by the observed individuals; *pa.* passive, observed individual was involved in behavior as a partner; *proc trophalla.* proctodeal trophallaxis)

	Abundant	Limited	*U*	N_1	N_2	*P*
Antennation ac.	0.81±0.045	1.02±0.036	13554	145	250	<0.001
pa.	0.66±0.028	0.95±0.026	10225	147	251	<0.001
Body shaking ac.	45.8±3.81	67.9±4.43	15212	143	251	0.024
pa.	41.7±2.47	52.7±2.50	14724	143	251	0.006
Proc trophalla ac.	0.07±0.008	0.04±0.003	7335	98	187	0.010
pa.	0.07±0.007	0.05±0.003	9150	124	188	0.002
Allogrooming ac.	0.03±0.007	0.02±0.003	10031	119	180	0.568
pa.	0.03±0.006	0.04±0.005	11568	126	217	0.018

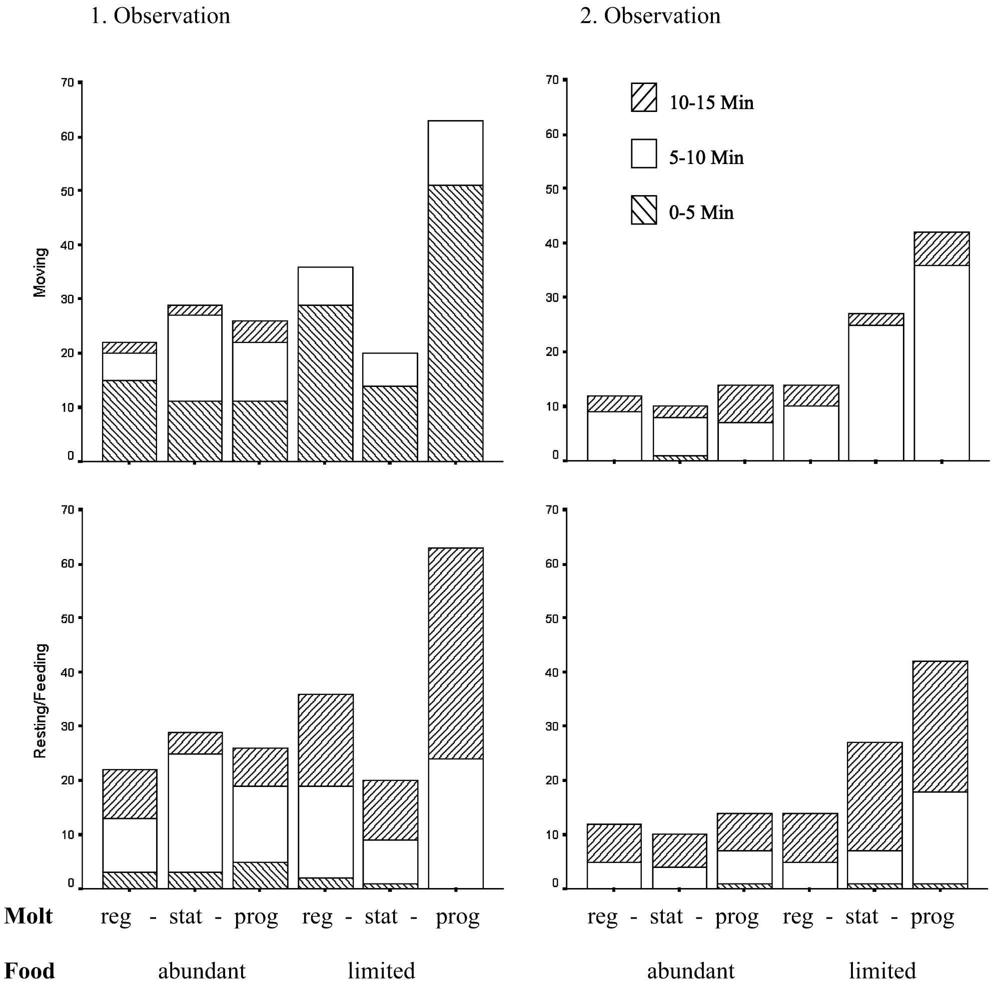

Fig. 1 The frequency of time (in categories) spent moving and resting/feeding in abundant- and limited-food colonies for different molting types during the first and second observation (*Molt reg* regressive, *stat* stationary, *prog* progressive). Because not all observed individuals could be followed until they molted, the sample size is smaller than for the behavioral observations

Table 3 Comparison of interactive behaviors in abundant- and limited-food colonies during the second observation. Shown are the mean (±SEM) frequencies and results of Mann-Whitney *U*-tests comparing different behaviors between abundant- and limited-food colonies during the second observation (*ac.* active; *pa.* passive; *proc trophalla.* proctodeal trophallaxis)

	Abundant	Limited	U	N_1	N_2	P
Antennation ac.	1.99±0.190	1.13±0.038	5398	64	265	<0.001
pa.	1.81±0.144	1.11±0.025	5205	66	266	<0.001
Body shaking ac.	17.6±3.47	43.9±3.38	5077	61	265	<0.001
pa.	14.8±5.48	37.9±1.89	2646	61	265	<0.001
Proc trophalla ac.	0.10±0.026	0.04±0.003	4844	47	207	0.999
pa.	0.13±0.025	0.04±0.003	4636	57	203	0.042
Allogrooming ac.	0.19±0.060	0.06±0.011	4776	52	188	0.999
pa.	0.10±0.023	0.06±0.008	6068	55	221	0.999

tion. However, during the second observation, antennations (active and passive) were more common in abundant-food colonies.

Link between behavior and development

Individuals with different molting types did not differ in their behavioral repertoire before the molt ($P>0.100$) with the following exceptions. During the first observation in abundant-food colonies, individuals that went through progressive molts actively allogroomed at significantly higher rates ($\chi_2^2=8.94$, $P=0.022$). During the second observation in limited-food colonies, individuals that developed progressively actively engaged in proctodeal trophallaxis at significantly higher rates ($\chi_2^2=9.61$, $P=0.016$).

Discussion

Influence of food availability

The results of this study indicate that food availability has a strong influence on cooperation and dispersal in *Cryptotermes secundus*. Limited food led immediately to both an increase in the frequency of “selfish” behaviors and an increase in progressive molts, away from being helpers towards dispersing sexuals. Individuals did less proctodeal feeding, spent less time moving and more time resting/feeding. These changes would allow individuals to conserve and accumulate the resources necessary for progressive development (Nalepa 1994). Also, the level of inspection behavior (antennation and being allogroomed) and aggression, indicated by body shaking, was higher in limited-food colonies. These differences occurred mostly during the first observation. During the second observation, when individuals had already changed their tactic towards development into dispersing sexuals, only body shaking remained higher in limited-food colonies and the frequency of antennation became higher in abundant-food colonies. The immediate behavioral response indicates that the termites are able to quickly assess food availability. This is in line with using ultrasonic acoustic emissions generated by wood gnawing as a fast and reliable method to measure food abundance (Lenz 1994; M. Lenz and T.A. Evans, unpublished data).

Regulation of development

Compared to many of the eusocial Hymenoptera, in which caste development is determined early in life and is under exogenous control (Bourke and Ratnieks 1999; Ratnieks 2001; but see also *Melipona* stingless bees: Ratnieks 2001), termites, especially those that live in one-piece nests, tend to have a very flexible development that is more autonomously regulated. However, experiments with OP termites (*Kalotermes flavicollis*, *Zootermopsis*) have shown that functional reproductives inhibit reproductive development of nest-mates (Springhetti 1969; Lüscher 1974). Although the proposed pheromones have not been identified (Stuart 1979), it is believed that they are transmitted through the colony via proctodeal trophallaxis (e.g. Springhetti 1969; Lüscher 1974; but see also Pasteels and Roisin 2001). Our results, at least at the colony level, are consistent with such a mode of transmission; the proportion of progressive molts increased as the frequency of proctodeal exchange decreased immediately after reduction in food availability. This increase was caused by a shift from stationary to progressive molts, while the proportion of regressive molts did not change. However, on an individual level, no such correlation was found between trophallactic behavior and type of molt directly after changing food conditions, while there was a positive correlation between progressive development and feeding others later during the experiment. Together these results suggest the following mechanism of caste regulation: as individuals in food-limited colonies try to accumulate resources, the overall rate of proctodeal exchange decreases, resulting in a reduction of circulating inhibitory pheromones that allows all competent individuals to switch to progressive development, independent of their individual behavior. After this switch, progressive-developing individuals did most proctodeal feeding which may inhibit other nest-mates from sexual development. According to this, proctodeal trophallaxis would be a costly behavior and its reduction at the start of the manipulation is selfish only in the sense that it reduces these costs. The incompetence of individuals that molted regressively when food conditions deteriorated appears to be a matter of physiological competence rather than a result of aggressive manipulation by nest-mates (Roisin 1994; J. Korb, unpublished data). If this model is correct, then the reproductive inhibition of sexual development resulting from exposure to trophallactically transmitted pheromones would be a costly, self-regulated signal rather than direct manipulation by the reproductives (sensu Keller and Nonacs 1993). A direct link between food availability and the circulation of inhibitory substances results in a presumably adaptive regulation of the number of helpers versus dispersing sexuals. However, there may still be conflict between the reproductives and the helpers over the ratio of dispersing sexuals. Reproductives maximize their fitness by maximizing the reproductive success of the current colony, whereas helpers maximize their fitness by a combination of the reproductive success of the current parental and their future colony (see parent-offspring conflict; Trivers 1974). When food conditions deteriorate, the helpers benefit from dispersing because their inclusive fitness benefits in the natal-nest decline (J. Korb, unpublished data; see below). The reproductives would also benefit by the reduced competition for food between current and future offspring, but the food threshold for leaving the nest might differ between both castes.

Comparison with cooperatively breeding vertebrates and social Hymenoptera

In accordance with studies on cooperatively breeding vertebrates, our results showed the importance of ecological factors for cooperative helping and philopatry in termites. However, there are some differences that can be distinguished between the groups. For vertebrates, the three most widely accepted hypotheses for the evolution of sociality are: (a) the ecological constraints hypothesis, which states that opportunities for independent breeding are limited or risky because of ecological factors such as low availability of nesting sites or a high risk of mortality during dispersal (Emlen 1997); (b) the life-history hypothesis, which emphasizes that certain life-history characteristics of a species limit the opportunity for independent breeding (Arnold and Owens 1998); (c) the benefits-of-philopatry hypothesis, which stresses the long-term direct benefits of staying at the natal nest, such as inheritance of the natal territory (Stacey and Ligon 1991). In vertebrates, the ecological constraints hypothesis is strongly supported by intraspecific studies, while the life-history hypothesis seems to be the most suitable for explaining interspecific variation in the occurrence of cooperative breeding (Hatchwell and Komdeur 2000). Thus, the latter hypothesis is unlikely to apply to our intraspecific study which investigates variation of helping behavior within a species. Rather, our results support the benefits-of-philopatry hypothesis. Helpers seem to gain considerable long-term direct benefits through nest inheritance as long as food availability—and thus the potential longevity of the nest—is high (J. Korb, unpublished data). Additionally, helpers may also derive immediate indirect benefits from raising siblings (J. Korb, unpublished data). However, with decreasing food availability both benefits of philopatry decline, thus favoring dispersal and independent nest founding.

In our study system, the ecological constraints hypothesis may also apply, albeit with restrictions. In *Cryptotermes secundus*, appropriate nest sites do not appear to be limiting, as the stochasticity of the habitat—e.g. caused by thunderstorms that suddenly create new patches of dead trees—seems to prevent habitat saturation (J. Korb, unpublished data). Furthermore, OP termites do not have the opportunity to check the availability of nesting/breeding vacancies as they never leave the nest before the nuptial flight (Roisin 1994, 1999). Thus, the ecological constraints cannot be assessed by the termites, and so can be considered constant. However, in spite of this restriction, ecological constraints are still important as they determine the costs of philopatry. Other factors being equal, if ecological constraints on founding a new colony are not very restrictive, then the benefits of philopatry need to be high to favor staying and helping (see Hamilton's rule; Koenig et al. 1992; Kokko and Lundberg 2001). In termites, the greatest ecological constraint is probably the high mortality risk associated with dispersal (Nutting 1969; J. Korb, unpublished data).

As is the case for vertebrates, it is unlikely that a single hypothesis can explain cooperative helping in the Isoptera. While ecological constraints (representing the costs in this system) and philopatric benefits appear to dictate intraspecific behavior, interspecific differences in life histories can then profoundly influence these costs and benefits (Hatchwell and Komdeur 2000). Hence, a combined approach that considers all factors is necessary to understand the evolution and maintenance of helper behavior in termites (see Hatchwell and Komdeur 2000; Pen and Weissing 2000; Kokko and Ekman 2002). Such a unifying approach may be provided by reproductive skew theory, which aims to explain the extent to which reproduction is biased within animal societies by identifying the role of ecological, genetic, and social factors (Vehrencamp 1983; Reeve and Ratnieks 1993; Keller and Reeve 1994; Johnstone 2000). In high skew societies, one or a few individuals monopolize reproduction; in low skew societies, reproduction is distributed more equitably. One kind of these models is referred to as "transactional" because groups' members are envisioned as trading parcels of reproduction for peaceful cooperation. A recent model for arbitrary-sized (*N*-person) groups predicted a generally high skew in parent-offspring groups (with asymmetrical relatedness), as offspring will never receive staying incentives regardless of relatedness (Reeve and Emlen 2000). The decision of subordinate offspring to leave the group is voluntary, as dominants are not predicted to evict subordinate offspring under conditions when it is favorable for offspring to stay in the group. Offspring are predicted to stay in the nest when the increase in group productivity by staying exceeds the expected reproductive output of a solitary breeder. Thus, with decreasing ecological constraints, more individuals are expected to stay in the nest, and group size should increase. Our results for *Cryptotermes secundus* are in good agreement with these predictions. First, reproductive skew is always high because only one pair reproduces and no staying incentives are offered by the reproductives to the helpers, regardless of relatedness (J. Korb, unpublished data). Second, there are no indications that reproductives force helpers to leave the colony. Third, as the ecological constraints for founding an own colony are constantly high, the decision to leave the colony should solely depend on the increase in group productivity achieved by staying. For a given colony size, this is predicted to decrease when the food availability, and thus the nest's longevity, declines. Under these circumstances, helpers are predicted to leave the colony, which indeed they did.

For social Hymenoptera, there are as yet few reports of parent-offspring associations in which helping individuals can facultatively leave the nest (J. Heinze, personal communication), although studies have now shown the importance of ecological factors for the occurrence of workers (e.g. Gadagkar 1991; Field et al. 1998). The scarcity of examples in which hymenopteran workers can leave the nest may reflect a problem of power (sensu Beekman et al. 2003). In termites, juveniles can forage independently, and their development is more autonomously regulated. However, in Hymenoptera, the larvae are generally entirely dependent on tending adults, which may manipulate their nutrition to ensure that nearly all of the larvae are forced to become workers during the colony-growth phase (Keller and Reeve 1994). Thus, the larvae may lose the option to develop into dispersal sexuals and leave the nest when it would be advantageous for them to do so. This contrasts with our study species, in which helping individuals are totipotent to become dispersing sexuals, and which provides therefore an excellent system to investigate factors favoring cooperation.

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