

Original Article

Nest value mediates reproductive decision making within termite societies

Katharina Hoffmann,^a Kevin R. Foster,^{b,c} and Judith Korb^a

^aBehavioural Biology, University of Osnabrueck, Barbarastr. 11, 49076 Osnabrueck, Germany,

^bDepartment of Zoology, University of Oxford, Oxford, UK, and ^cOxford Centre for Integrative Systems Biology, University of Oxford, Oxford, UK

The influences of costs and benefits on social evolution remain poorly understood, despite their importance for explaining social behavior, and continue to fuel high-profile debates. Here, we investigate the effect of a major ecological factor, wood resource—that is, natal nest value—on reproductive decision making in the termite *Cryptotermes secundus*. Workers continually assess the available wood resources of the colony and adjust their developmental decisions, including investment into competition, accordingly. In particular, workers are more likely to stay and fight for inheritance within resource-rich nests. Comparable responses are seen in social wasps, which evolved sociality independently from the termites, demonstrating convergent evolution. Our results, therefore, indicate a general evolutionary link between resource wealth and societal conflict. **Key words:** competition, costs and benefits, decision making, evolutionary feedback, social evolution, termite. [*Behav Ecol*]

INTRODUCTION

A large body of evolutionary theory now exists to identify the factors that determine the path of social evolution (Wenseleers et al. 2010). These highlight the importance of genetic similarity (genetic relatedness) and phenotypic feedbacks for social evolution, which both affect whether the alleles that promote a social action are the ones that benefit from the action's effects. Although costs and benefits are present in all theories of social evolution, “empiricism” has tended to focus on the role of genetic and phenotypic correlations (Korb and Heinze 2008). The result is a discrepancy between 1) the predicted importance of costs and benefits in theories of social evolution and 2) the weight of evidence to support this prediction.

The roles of costs and benefits have been explored in some studies, mainly in cooperatively breeding birds and mammals (reviewed in Korb and Heinze 2008). There is less work on costs and benefits in the social insects but a number of important results come from work on small-colony social wasps (Field et al. 2006; Field 2008; Zanette and Field 2009) and social aphids (Abbot et al. 2001; Grogan et al. 2010). These studies show that factors including the availability of new nest sites, position in a social hierarchy, and worker number all affect social decision making in the nest. A key finding is that the investment into helping decreases, and the probability of escalated conflicts increases, for individuals that are likely to inherit a valuable nest (Abbot et al. 2001; Cant et al. 2006; Field and Cant 2009).

Here, we investigate the role of wood resource on reproductive decision making in wood-dwelling termites (see also Korb and Lenz 2004), which live in a single piece of wood that serves both as food and nest (Korb 2007a), “one-piece” nesting termites sensu Abe (1987). Only a few offspring of the royal pair become sterile soldiers that defend the colony, and most individuals are

what are typically called “workers” by analogy with more-derived termite species (Roisin and Korb 2011). These workers are totipotent and able to develop into all final castes.

In our study species *Cryptotermes secundus* (Kalotermitidae), the workers do not care for the brood (Korb 2007b) but rather stay in the nest as “hopeful reproductives” (Korb and Hartfelder 2008). In the presence of a reproductive pair, workers do not (or cannot, due to royal inhibition; Lüscher 1955) acquire direct fitness benefits. When a breeder's position becomes available, a subset of workers develops into neotenic replacement reproductives (hereafter called “neotenics”). Should more individuals develop than are needed to replace the queen or king, these neotenics will fight to the death in an attempt to inherit the natal nest. This suggests a “wait and see” strategy, balancing anticipated direct fitness benefits of dispersing to found a new colony against the possibility of someday inheriting the breeder's position within the natal nest (Korb 2007b, 2008; Korb and Hartfelder 2008, Figure 1A, B).

The potential fitness of colony members is largely linked to the wood volume of their home as this reflects a colony's longevity; the workers do not leave the nest to forage for new food sources, so the colony dies when it runs out of wood. Moreover, *C. secundus* has the impressive ability to measure the amount of wood in the nest using the vibrations generated during gnawing (Evans et al. 2005). The remaining value of the natal nest in the form of its wood reserves may be a critical factor in a worker's decision on whether to stay and fight with other colony members for the breeding position. We tested this by providing colonies with either a high- (more wood per termite) or a low-value (less wood per termite) nest and monitored worker behavior before and after removal of the royal pair.

MATERIALS AND METHODS

Colony collection and maintenance

Complete *C. secundus* colonies were collected in 2007 and 2008 from *Ceriops tagal* trees in the mangrove area near Palmerston-Channel Island in Darwin, NT, Australia (lat 12°30'S, long

Address correspondence to K. Hoffmann. E-mail: katharina.hoffmann.bio@gmx.de.

Received 31 January 2012; revised 17 May 2012; accepted 17 May 2012.

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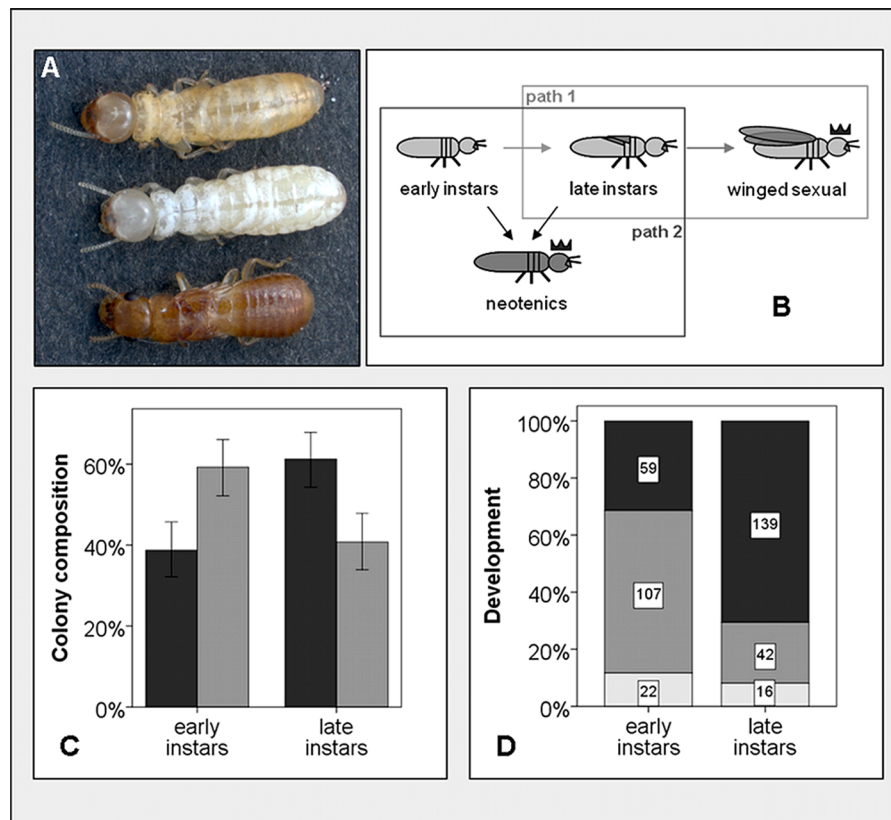


Figure 1

(A) Neotenic, worker, and a founding reproductive of *Cryptotermes secundus* (top to bottom). (B) Schema of developmental trajectories of workers. Path 1: early instars develop progressively via late-instar nymphs into dispersing winged sexuals that found new colonies. The number of winged sexuals (produced only once a year before the nuptial flight) can be reliably predicted from the number of late-instar nymphs (Korb and Katrantzis 2004). Path 2: early instars and late-instar nymphs can become neotenics via a single molt. This path is only available when a breeding position in the colony becomes vacant (i.e., when royals are removed). (C) Colony composition of LR and HR colonies ($N = 10$ colonies, dark and grey bars, respectively) 4 weeks after setting up of the colonies, before orphaning. Shown are mean proportions ($\pm 95\%$ correct) of early instars and late-instar nymphs. LR colonies had significantly higher proportions of late-instar nymphs than HR colonies (for detailed proportions of single instars, see Supplementary Figure S1B). (D) Development of early instars and late-instar nymphs in LR and HR colonies ($N = 197$ and 188 , respectively; no difference was found between resource conditions) before orphaning. Late-instar nymphs more often molted progressively toward winged sexuals, whereas early instars tended to show stationary development. Absolute numbers of molts are given in the diagram. Dark bars: progressive; grey bars: stationary; light bars: regressive molts.

131°00'E) as described elsewhere (Korb and Lenz 2004). Colonies were set up in standardized *Pinus radiata* wood blocks adjusted to colony size, providing abundant resource conditions (1 termite: about 10 cm³ wood; for details, see Korb and Lenz 2004). The use of *P. radiata* wood does not affect development of the colonies relative to *C. tagal* blocks (Korb and Katrantzis 2004). Colonies were transferred to the laboratory in Germany and kept in climate chambers at 28 °C and 70% relative humidity with 12-h day/night cycle. The development (including the timing of the nuptial flight) of relocated colonies kept in the laboratory is indistinguishable from relocated colonies kept in the field (Korb and Katrantzis 2004).

Setup of experiments

For the experiment, *C. secundus* colonies were extracted from their wood blocks in Germany (1–2 years after collection), and their colony composition and sizes were determined. Low- and high-resource colonies (hereafter referred to as LR and HR colonies, respectively) did not differ in their initial composition of instars (chi-square test: $\chi^2_7 = 0.02$, $P = 0.878$; Supplementary Figure S1A). Colony sizes ranged from 17 to 94 individuals. LR and HR treatments did not differ in their

mean colony sizes (LR: 57 ± 25.0 standard deviation [SD] vs. HR: 45 ± 19.9 SD; t -test: $t_{20} = 1.21$, $P = 0.244$). Only colonies with 1 pair of primary reproductives (hereafter referred to as “royals”) were used. Colonies were transferred into new *P. radiata* wood blocks with a predrilled observation chamber providing either LR (1 termite: about 2.5 cm³ wood) or HR (1 termite: about 10 cm³ wood) conditions when the experiment was started (Lenz 1994; for details, see Korb and Schmidinger 2004). For individual identification, up to 60 workers per colony were marked with an individual color code of enamel paint (Revell) on the abdomen and/or thorax. Individuals were checked throughout the duration of the experiment to ensure they retained their markings.

The development (see section Monitoring of development) of all workers was recorded for 4 weeks after setup and the behavior of the marked individuals was observed (see section Behavior assays) before removal of the royals. This provided the data set for the “with royals” treatments. Next, these colonies were orphaned for the “without royals” treatment, and 24 h later, the marked individuals were observed again. The loss of one or both reproductives happens in the field, for instance, during fusion of colonies founded in the same tree. Korb and Schneider (2007) found that about 25% of collected *C. secundus* colonies showed genetic hallmarks of having fused. The removal

of both royals increases the orphaning effect because now workers of both sexes develop into neotenics. The development of all workers was continuously monitored until a pair of neotenics had stably inherited the breeding positions (no further neotenics developed or were killed for 10 days). The number of neotenics developing, the time until the first neotenics developed, and the time until the neotenic pair was stable were measured for each colony. Experiments were set up in parallel for both resource conditions. In total, 281 individuals from 10 LR colonies and 268 individuals from 10 HR colonies were analyzed.

Monitoring of development

C. secundus workers can be any of 3 independent larval instars (without wing buds: 1st–3rd worker instar) and 5 nymphal instars (with wing buds: 1st–5th nymphal instar), reflecting the gradual development toward the winged sexual (Korb and Katrantzis 2004) (Figure 1B, path 1). With regard to their developmental trajectory, they can be classified into late-instar nymphs (2nd–5th nymphal instar), which will with high probability leave the colony as winged sexuals; and early instars (1st worker–1st nymphal instar), which will stay as workers in the colony for at least another year (Korb and Katrantzis 2004; see also RESULTS).

To determine the developmental trajectory of workers, we monitored their molting types. Besides the neotenic molt, when a worker develops via a single molt into a neotenic replacement reproductive after orphaning of the colony (Figure 1B, path 2), there are 3 other molting types: progressive, stationary, and regressive molts; the latter are unique to termites. They reflect, respectively, a molt into the next, the same, or the previous instar and are characterized by an increase, no change, or decrease in body size and morphological development (reviewed in Korb and Hartfelder 2008). Progressive molts reflect the developmental trajectory toward a winged sexual via several nymphal instars (Figure 1B, path 1), whereas stationary and regressive molts characterize workers that remain at the nest (Korb and Katrantzis 2004). Individuals that are about to molt have a whitish, opaque appearance (Korb and Schmidinger 2004). When this happened, they were separated, their developmental instar was identified before and after the molt, and the molting type was determined accordingly (for more details Korb and Katrantzis 2004).

Behavior assays

Behavioral observations were done as previously described (Korb and Schmidinger 2004). In brief, every marked individual was observed using focal sampling for 30 min each with royals present and then again for 30 min after orphaning; we recorded the following behaviors: (i) running, (ii) sitting, (iii) allogrooming, (iv) proctodeal trophallaxis (anal feeding), (v) butting, and (vi) antennation. The first 4 behaviors were recorded as the duration spent in the interaction and the last 3 as the total number of interactions between 2 individuals. We distinguished whether the interactions were carried out by the observed individual (active) or received from a nestmate (passive). The results for the passive behaviors are given in Supplementary Tables S1–S4.

Statistics

All data were checked for assumptions of parametrical testing and statistical tests were chosen accordingly. Additional analyses showed that both types of tests (parametric and nonparametric) assigned statistical significance identically. All tests were 2-tailed and analyzed with PASW 18.0 (SPSS Inc.). If not noted otherwise, mean values \pm standard errors are given.

Developmental data

We analyzed differences in colony composition (the frequencies of the different instars) and developmental trajectory (the frequencies of molting types) between HR and LR colonies using chi-square-contingency tables; and colony size using *t*-tests. We compared developmental differences between early instars and late-instar nymphs within and between resource conditions with chi-square-contingency tables. After removal of the royals, the “time until the first neotenic developed” and the “time until the neotenic pair was stable” were compared between resource conditions using *t*-tests. The percentage of developing neotenics per colony was analyzed between HR and LR colonies with Mann–Whitney *U* tests. The developmental trajectory of individuals (i.e., molting types) in colonies with and without royals was compared using chi-square-contingency tables and paired *t*-tests. Moreover, the proportions of late-instar nymphs and neotenics developing were correlated with the colony size using Pearson tests.

Behavioral data

The behavioral data did not fulfill the requirements for parametric testing. Therefore, nonparametric statistics were applied. To compare behaviors between resource conditions and between early instars and late-instar nymphs, Mann–Whitney *U* tests were used. These analyses were done separately before and after orphaning the colony. We also compared the behaviors before and after removal of the royals, separately for HR and LR colonies, using Wilcoxon paired-rank tests. As these comparisons did not reveal any fundamentally new results, they are given in the supplementary material. Difficulties with data collection mean that behavioral data were not available for one of the LR colonies.

RESULTS

Influence of wood resource when royals are present

In LR colonies, more individuals entered the developmental path toward becoming winged sexuals (Figure 1A, path 1) than in HR colonies. Development into a winged sexual that disperses from the colony can only be achieved after becoming a late-instar nymph (Figure 1A), and there was a significant increase in late-instar nymphs in LR colonies relative to HR colonies (chi-square test: $\chi^2_1 = 24.47$, $P = 0.001$; Figure 1C; for more details, see Supplementary Figure S1B). Late-instar nymphs were more likely to undergo progressive molts (chi-square test: $\chi^2_2 = 61.45$, $P < 0.0001$) compared with early instars, which more often showed evidence of arresting as workers (stationary molts; Figure 1D). This distinction in developmental trajectory between early instars and late-instar nymphs was seen under both resource conditions (no differences between HR and LR colonies: chi-square test: $\chi^2_2 = 1.33$, $P = 0.516$). The proportions of late-instar nymphs significantly correlated with colony size (Table 1, Figure 2): the larger the colony the more individuals chose to disperse.

Parallel to the changes in development, individuals in LR colonies altered their behavior relative to HR colonies (Supplementary Tables S2–S4, Figure S2). Individuals in LR colonies showed reduced behavioral interaction compared with their counterparts in HR colonies, with less butting (a dominance behavior; Korb et al. 2009) and (by trend) antennation (Table 2; for passive behaviors, see Supplementary Table S2, Figure S2). The late-instar nymphs in both resource conditions also showed a distinctive behavioral profile, showing more butting (Supplementary Tables S1 and

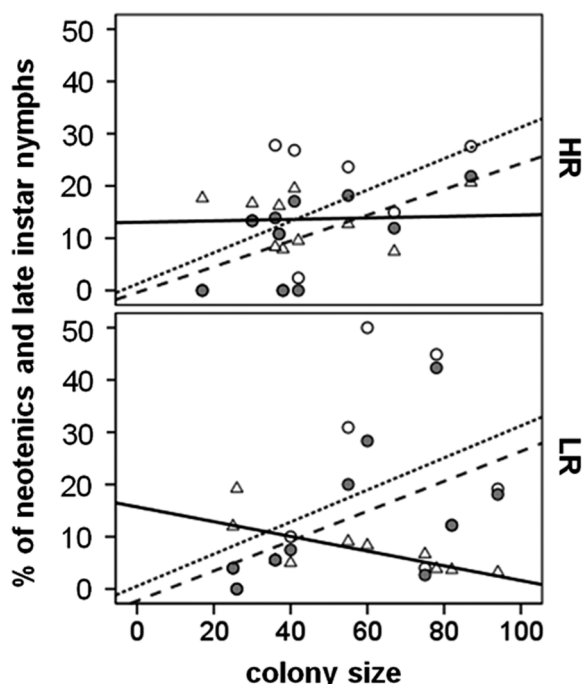


Figure 2
Percentage of workers developing into neotenics (Δ , straight line) and late-instar nymphs (with royals, \circ , dotted line; without royals, \bullet , broken line) depending on colony size. Trend lines were determined using Spearman rank tests (Table 1).

S3, Figures S3 and S4), which is consistent with development toward sexual maturity and, ultimately, winged dispersal in colonies that already have royals (Korb and Schmidinger 2004).

Influence of wood resource when royals are absent

The effect of colony resources was strongly altered when the existing queen and king had been removed. After removal of the royals, HR colonies showed an increase in sexual production in the form of worker development into neotenics that stay and attempt to take over the colony (Figure 1B, path 2; proportion of neotenics in HR vs. LR colonies: Mann-Whitney U test: $Z_{20} = -2.46$; $P = 0.014$). Under HR conditions, 13.7% (range: 7.5–20.7%) of workers developed into neotenics, whereas in LR colonies, only 7.7% (range: 3.2–12.0%; 1 outlier colony with 19.2%) of the workers became neotenics (Figure 3). In all cases, only 1 pair inherited the colony, with the remaining aspiring neotenics killed in the process. Development of neotenics was greatly affected by colony size, but only in LR colonies. The larger the colony, the fewer individuals tried to inherit the less-valuable nest (Table 1, Figure 2).

Setting the development of neotenics aside, the developmental trajectories of workers were not affected by the removal of the royals under both resource conditions. They showed the same preferences for certain developmental types as before orphaning; chi-square test yielded the following results: HR, with vs. without royals: $\chi^2_2 = 0.14$, $P = 0.933$; LR, with vs. without royals: $\chi^2_2 = 1.10$, $P = 0.578$. Both with and without royals, more individuals developed into dispersing winged sexuals when resources were low (chi-square test: with royals: $\chi^2_1 = 5.30$, $P = 0.027$, 42.1% late-instar nymphs in LR vs. 23.8% in HR colonies; without royals: $\chi^2_1 = 5.59$,

Table 1

Correlations between proportions of workers becoming neotenics or late-instar nymphs (with and without royals) and colony size (Spearman rank test, $N = 10$ colonies)

	HR		LR	
	r	P	r	P
Percentage of neotenics	-0.08	0.829	-0.81	0.005
Percentage of late-instar nymphs, with royals	0.64	0.045	0.75	0.013
Percentage of late-instar nymphs, without royals	0.46	0.181	0.56	0.090

$P = 0.023$, 69.1% late-instar nymphs in LR vs. 54.3% in HR colonies; see also Figure 2). In contrast to the “with royals” situation, the percentage of developing late-instar nymphs did not correlate significantly with colony size (Table 1, Figure 2).

One possible explanation for the low number of aspiring neotenics in LR colonies is that late-instar nymphs are developmentally committed to becoming dispersing sexuals before royal removal. Fewer workers would then be available to become neotenic in LR colonies, where the development toward dispersing sexuals is more progressed. In this experiment, neotenics developed from all instars except the 1st and 2nd larval instars in both treatments (see also Korb and Katrantzis 2004). However, in LR colonies, early instars developed more often into neotenics than expected based on their frequency (chi-square test: $\chi^2_1 = 11.65$, $P = 0.001$), something not seen in HR colonies (chi-square test: $\chi^2_1 = 1.00$, $P = 0.317$). This suggests that late-instar nymphs in LR colonies continue to display a preference toward dispersal after royals are removed, even though it appears developmentally feasible to switch to become neotenic.

Neither the time until the first neotenic developed (HR: 8.8 ± 0.65 days, LR: 9.2 ± 1.08 days; t -test: $t_{20} = 0.32$, $P = 0.755$) nor the time until a stable pair had established (HR: 21.1 ± 2.63 , LR: 20.6 ± 3.30 days; t -test: $t_{20} = 0.12$, $P = 0.907$) differed significantly between the 2 resource conditions. The response time of individuals to the vacant natal breeder's position was similar between HR and LR groups. When molting frequencies were compared between the 2 weeks before and after removal of the royals, we found that the total number of molts increased significantly after orphaning (paired t -test: HR: $t_{10} = -2.03$, $P = 0.073$; LR: $t_{10} = -3.91$, $P = 0.005$) but not when the molts into neotenics were omitted (paired t -test: HR: $t_{10} = -0.18$, $P = 0.858$; LR: $t_{10} = -1.59$, $P = 0.152$). This implies that molts into neotenics occur in addition to “normal” development.

The behavioral differences among workers of HR and LR colonies were similar before and after orphaning. Workers in HR colonies displayed more interactive behaviors than those in LR colonies, with more antennation, butting, and proctodeal trophallaxis (Table 2; see also Supplementary Table S2, Figure S2). This is consistent with workers increasing their investment in staying and fighting for reproductive status in resource-rich colonies.

DISCUSSION

We manipulated the wood resources of termite colonies and monitored worker response before and after removal of the royal pair. The data suggest that individuals continually evaluate societal conditions and change their development in

Table 2

Active behaviors of workers in LR ($N = 245$ in 9 colonies) vs. HR colonies ($N = 254$ in 10 colonies) with and without royals (Mann–Whitney U tests). Difficulties with data collection mean that behavioral data were not available for one of the LR colonies

LR versus HR		Sitting	Running	Allogrooming	Trophallaxis	Butting	Antennation
With royals	Z	−0.37	−0.33	−0.42	−0.90	−3.26	−1.92
	P	0.712	0.744	0.675	0.367	0.001	0.054
Without royals	Z	−0.22	−0.17	−1.94	−2.25	−2.28	−4.30
	P	0.829	0.869	0.052	0.025	0.023	<0.001

an attempt to maximize reproductive prospects. When royals are present, more individuals undergo progressive molts toward becoming a winged sexual in LR than in HR colonies. Consistent with earlier data from *C. secundus* and other species (Buchli 1958; Nutting 1969; Lenz 1994; Korb and Lenz 2004), the data suggest that more individuals try to leave the nest and found a colony elsewhere when future colony prospects decline.

Increasing colony size also increased the proportions of late-instar nymphs in both resource conditions. When royals are removed, more individuals vie to inherit HR nests and fight to the death to take over the breeding position in the colony (Hoffmann and Korb 2011). The percentages of workers developing into neotenic reproductives (LR 7.7%, HR 13.7%) are higher in both treatments in this study than those found in a previous study for *C. secundus* (Korb and Foster 2010), where the mean development was 2–5% (J.K., unpublished results). The earlier study did have some minor differences in experimental setup, but why more aspiring neotenic developed in the current study is unclear. However, both studies are internally controlled, so this does not affect our conclusions. We did not directly measure physical competition here, but the development of more neotenic certainly results in greater competition, both direct and indirect. In LR colonies, the development of neotenic is strongly negatively influenced by colony size, in contrast to the situation in HR colonies. In both treatments (with and without royals), the number of dispersing sexuals is higher under LR than HR conditions.

Nest value greatly determines an individual's potential fitness. A high-value nest provides more potential fitness benefits than a low-value nest. In the wood-dwelling termite *C. secundus*,

nest value may be thought of as the wood resource (food and nest space) relative to colony size, which determines the per capita resource availability. In our experiment, this effect of colony size was especially apparent in LR nests. The responses to the orphaning that we observe are consistent with previous studies on wood-dwelling termites, which suggest that the majority of “workers” are reproductives-in-waiting as opposed to helpers that invest in brood care (Myles 1988; Thorne et al. 2003; Korb and Schneider 2007; Korb 2008; Johns et al. 2009). For example, neotenic in the dampwood termite *Zootermopsis angusticollis* are especially likely to inherit the natal breeding position after intraspecific encounters (Thorne et al. 2003), which can result in an individual unrelated to the majority of the merged colony becoming one of the new reproductives (Johns et al. 2009). Phylogenies suggest that these patterns of nest inheritance are ancestral in termites, such that workers' nest inheritance probably played a general role in termite evolution (Myles 1988; Thorne et al. 2003; Korb and Schneider 2007; Korb 2008; Johns et al. 2009), even though workers' nest inheritance is no longer possible in some of the more socially derived species (Myles 1999; Hartke and Baer 2011).

Our finding of an association between societal resource wealth and competition is mirrored in work on small-colony vespid wasps. There, reducing the number of workers and brood leads to increased helping and a decreased propensity for escalating conflicts among dominants (Cant et al. 2006; Field et al. 2006; Field and Cant 2009). Wasps and termites are distantly related within the insects and have independently evolved sociality from very different ancestors (social wasps from a solitary wasp, termites from a cockroach). The link between societal resources and the potential for disruptive competition in both groups, therefore, implies convergent evolution.

CONCLUSION

Our data are suggestive of a general pattern: The greater benefit from taking over a resource-rich society reduces the threshold to stay and fight for dominance. This is only true when societal resources can be monopolized by one or a few individuals for reproduction (there is only 1 reproducing pair in *C. secundus*); otherwise, resource wealth can reduce the potential for competition because there is little to gain from attempting to take more than an equal share when shares are large anyway (Clutton-Brock et al. 1998, 1999; Brockhurst et al. 2008; Xavier et al. 2011). More generally, our data underline the ability of social organisms to assess changes in the costs and benefits of sociality and alter their behavior accordingly.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

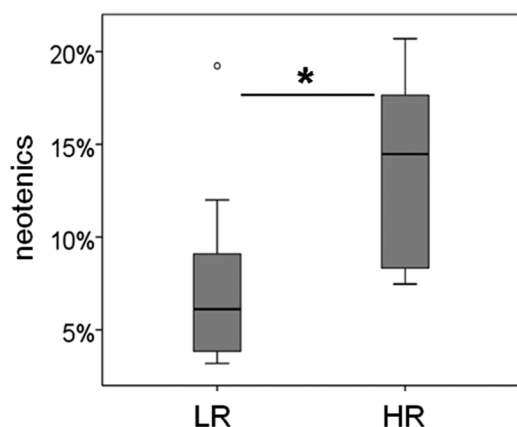


Figure 3

Percentage of workers becoming neotenic in LR and HR colonies after removal of the royals. Fewer neotenic developed in LR colonies than in HR colonies. Box plots show median, quartiles, and minimum and maximum values, (○) outlier, (*) significant difference. ($N = 10$ colonies, respectively).

FUNDING

This work was supported by a Volkswagen Foundation grant within the initiative "Evolutionary biology", file reference I83467.

We thank the Charles Darwin University, Darwin, Australia, for providing a place to split the termite wood; and 2 anonymous referees for helpful comments on the manuscript. Parks and Wildlife Commission and Environment Australia gave permission to collect (permits 26851 and 30073) and export (permits WT2007–4154 and WT2008–4184) the termites. The experiments comply with the current laws of the country in which they were performed.

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