LETTER

Ecological competition favours cooperation in termite societies

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Abstract

Conflict and competition lie at the heart of the theories of both ecology and sociobiology. Despite this, the interaction between societal conflicts on one hand and ecological competition on the other remains poorly understood. Here, we investigate this interaction in two ecologically similar sympatric termite species, *Cryptotermes secundus* Hill and *Cryptotermes domesticus* Haviland. We manipulated the incidence of king and queen loss (within-species conflict) and the incidence of cohabitation of the two species (between-species competition) in a series of 2 year experiments. Manipulation alone had no detectable effect and most colonies survived the 2-year period. In contrast, promoting both within- and between-species conflict caused the great majority of colonies to die. Moreover, the resulting colony loss was much more rapid in the conflict-ridden *C. domesticus* than in *C. secundus*. Our data suggest that ecological competition among species can greatly exacerbate the impact of internal conflicts, thereby promoting the evolution of within-species cooperation.

Keywords

Competition, conflict, cooperation, social evolution, termites.

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INTRODUCTION

The study of cooperation and altruism within species is a major focus in evolutionary biology (Frank 1998; Keller 1999; Sachs *et al.* 2004; Lehmann & Keller 2006; Wenseleers *et al.* 2010). The ecology of cooperation has received less attention and the interaction of ecology and evolution on cooperation even less (Korb & Heinze 2008). This leaves significant gaps in our understanding as evolutionary explanations for cooperation – defined here as an action that promotes the fitness of another individual – are implicitly ecological. Specifically, explanations for how natural selection favours one individual to help another centre upon the fitness costs and benefits of social actions. These costs and benefits are affected, if not determined, by species' interactions with their environment; their ecology (Lehmann & Keller 2006; Foster & Xavier 2007; Gardner & Foster 2008).

A growing number of studies highlight the importance of ecological costs and benefits for social traits (Hatchwell & Komdeur 2000; Korb & Heinze 2008). Meta-analyses suggest that helping behaviours are affected by both climate (Arnold & Owens 1999) and the benefits of helping (Griffin & West 2003; Cornwallis *et al.* 2009). In addition, manip-

ulative studies find that nutritional level affects the tendency to help in groups as diverse as social vertebrates (Clutton-Brock *et al.* 1999), insects (Korb 2006) and microbes (Brockhurst *et al.* 2008). Finally, work on microbes show that environmental disturbance (Brockhurst *et al.* 2007) and population density can be important for cooperation (Mehdiabadi *et al.* 2006; Rumbaugh *et al.* 2009).

The study of the ecology of social evolution, however, remains patchy. So much so that one of the principle factors in theoretical ecological remains largely unexplored: competition among species (Lotka 1925; Volterra 1928). General support for the importance of species interactions in cooperation comes from the long-time study of among-species mutualisms by ecologists (e.g., Gause & Witt 1935; Boucher *et al.* 1982; Okuyama & Holland 2008). Moreover, evolutionary models of mutualism show the potential for within-species evolution to affect among-species traits, e.g., cooperation within groups of one species can be required for mutualism with another species (Frank 1994; West *et al.* 2002; Foster & Wenseleers 2006). And while models of mutualism naturally focus upon positive interactions, recent theory suggests that competition among species can also be critical for social evolution (Rankin *et al.* 2007a,b). The idea is that within-species conflict may lead groups, or even

entire species, to be susceptible to between-species competition; a prediction that can also be phrased in terms of the two key works of ecologist Garrett Hardin. Mild disruption caused by societal conflicts (a nascent 'tragedy of the commons', Hardin 1968) can be rendered much more costly, if this renders the species prone to competitive exclusion by other species (Hardin 1960). As a result, competitive exclusion may promote more cooperative over less cooperative species that have been weakened by internal conflicts. We know of no direct tests of this potentially important interaction.

Here, we investigate the interaction between societal conflict and species competition in the termites *Cryptotermes secundus* and *Cryptotermes domesticus* (Fig. 1). These closely related species are sympatric and share a very similar ecology. Both species live communally inside logs – sometimes the same log – and share the same family structure. Workers are typically the offspring of a single reproductive king and queen with tens to hundreds of offspring. In addition, some colonies are fusions of two original colonies of the same species, where aggression after fusion will sometimes reduce the reproductives back down to one pair. In *C. secundus*, about 25% of all colonies in the field are fusions of two colonies (Korb & Schneider 2007). A few offspring are sterile soldiers that defend the colony but most are what are typically called 'workers' by analogy with more derived termite species. However, in *C. secundus* and *C. domesticus*, the workers do not care for the brood but rather just feed on wood and await the possibilities of either becoming winged sexuals that disperse to found a new colony, or inheriting the nest from one of the royals (Korb 2007, 2008; Korb & Hartfelder 2008). In *C. secundus* this reproductive replacement process is relatively 'peaceful', a single worker develops when a king or queen dies. In contrast in *C. domesticus* there is overt conflict over royal replacement and around 40% of the workers develop into
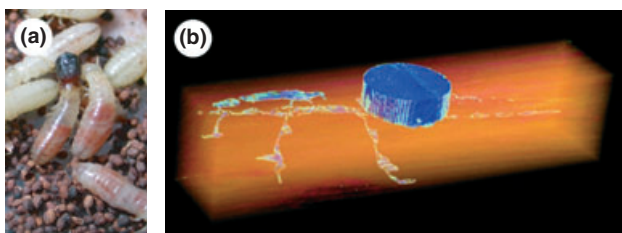
new reproductives (Lenz *et al.* 1985). These then fight to the death until a single pair of reproductives remains.

The combination of similar ecology but differing degrees of societal conflict makes *C. secundus* and *C. domesticus* a model system for the study of within-and between-species competition. Within-species conflict can be manipulated by removing the royals from colonies, or leaving them intact. Between-species conflict can be manipulated by allowing the species to directly interact within a single log or by keeping the species isolated. Here, we use these two manipulations to investigate the potential for interaction between ecological competition among-species and within-species conflict.

MATERIALS AND METHODS

Collection of colonies

Complete *C. domesticus* and *C. secundus* colonies were collected from *Ceriops tagal* trees in the mangrove area near Palmerston-Channel Island in Darwin Harbour, Northern Territory, Australia (12°30′ S 131°00′ E) as described elsewhere (Korb & Lenz 2004). Colonies were setup in standardized *Pinus radiata* wood blocks adjusted to colony size providing abundant food conditions (1 termite: about 10 cm^3 wood; for details see Korb & Lenz 2004). The colonies are robust to the relocation process and the great majority survive over a 2-year period (below) but some workers are lost as a result (Roux & Korb 2004). The use of *P. radiata* wood does not affect development of the colonies relative to setting them up in *C. tagal* blocks (Korb & Katrantzis 2004). Colonies were transferred to the laboratory in Germany and kept in climate chambers providing 28 °C and 70% relative humidity with a 12 h day/night cycle. The development of relocated colonies kept in the laboratory is indistinguishable from relocated colonies kept in the field (Korb & Katrantzis 2004).

Part I: Within-species conflict

Between 2002 and 2007, *C. domesticus* and *C. secundus* colonies were extracted from their wood blocks in Germany and their colony composition and sizes were determined. Only colonies with two reproductives were used for the experiments. Each colony was set up in new *P. radiata* wood blocks composed of one pre-drilled chambers (Fig. 1). Colonies were selected so that initial colony size did not differ between colonies, where we removed the reproductives and those where we did not, neither for *C. domesticus* (without replacement: 119 ± SE 22.2; with replacement: 116 ± 33.2; *t*-test for independent samples: $t_{23} = 0.07$, $P = 0.943$) nor for *C. secundus* colonies (without replacement: 94 ± 16.7; with replacement: 121 ± 38.47; *t*-test for independent samples: $t_{86} = -0.75$, $P = 0.456$).

Figure 1 Experimental setup. (a) A soldier and workers of *Cryptotermes domesticus* (*Cryptotermes secundus* morphology is nearly identical). (b) 3D computer tomography image of an experimental wood block in which the termites are housed. The blue shows both the circular chamber cut out of the block to form an initial chamber and the tunnels subsequently dug by the termites.

After 2 years in a wood block, all colonies were carefully dissected from their wood block to follow their tunnels and determine colony composition. In total, there were for *C. secundus* 62 colonies with low conflict over inheritance (reproductives present) and 26 with increased conflict over inheritance (reproductives removed). For *C. domesticus*, the corresponding values were 16 and 9, respectively. The uneven sample sizes reflect our inclusion of several years of early data here during which *C. secundus* was focussed upon as a laboratory model. *C. domesticus* was included in later years.

Part II: Within-species conflict and between-species competition

In 2007, *C. domesticus* and *C. secundus* colonies were extracted from their wood blocks in Germany and their colony composition and sizes were determined. Only colonies with two reproductives were used for the experiments. Colonies were sorted by colony size and 26 pairs were established that each consisted of one *C. domesticus* and one *C. secundus* colony with similar colony sizes. Pairs were matched in colony size to only differ by a maximum of 10 individuals or < 5% of the colony size. In total, colony size ranged from 10 to 210 individuals. Each pair was set up in new *P. radiata* wood blocks composed of two pre-drilled chambers, one for each colony providing abundant food conditions. The chambers were connected by a tunnel, which was loosely blocked with paper at the beginning. The colonies nibbled through the paper and contacted one another after 1–4 weeks.

Selecting pairs arbitrarily, in 16 of the colony pairs, the reproductives of both colonies were removed as in Part I to investigate competition when there is potential conflict over inheritance (raised conflict). In the remaining 10 pairs, the reproductives remained to determine the species' competitive abilities without turnover (low conflict). The larger sample size in the raised conflict case here allows for the predicted increase in mortality. Colony sizes were selected so that initial colony sizes did not differ between colonies without and with reproductive removal, neither for the *C. domesticus* (without conflict: $45 \pm$ SE 11.5; with conflict: 43 ± 13.0; *t*-test for independent samples: $t_{24} = -0.13$, $P = 0.901$) nor for the *C. secundus* colonies (without conflict: 45 ± 11.4; with conflict: 42 ± 12.6; *t*-test for independent samples: $t_{24} = -0.16$, $P = 0.872$). Colonies were left undisturbed in the climate chambers. Note that colonies were selected to be approximately half the size of the colonies in Part I so that, with two species in each log, the total number of individuals per log is constant in all experiments. However, the key results in Part I were also checked (and held) for the subset of smaller colonies that were in the same size range as for Part II.

The anticipated increase in mortality in these experiments relative to Part I meant that we checked the colonies after 1 year as well as after 2 years. At the year one mark, colonies were checked to see if they had survived and tunnelled into the wood by inspecting the pre-drilled chamber that is covered with a glass slide. We counted surviving colonies as those that have made tunnels and produce new frass (faecal pellets), after we had removed all old frass. Colony size was not counted at year one as this would require splitting of the wood block. After the second year, however, all colonies were carefully dissected from their wood block to follow their tunnels and determine colony composition.

Alates

No winged sexuals (alates) were produced during the experiment as these are only produced when colony sizes reach a certain size threshold or colonies become food limited (Korb & Schmidinger 2004) – both was not the case in our experiments.

Statistical analyses

We tested colony survival using both likelihood ratio tests in 2×2 contingency tables (hereafter: 'survival likelihood') and Fisher's exact tests. The two types of test assigned statistical significance identically and we present only the likelihood ratio here. For significant differences, we calculated the risk ratio (i.e. the statistical change in the probability that an event will happen) for survival with 95% confidence intervals (CI). Colony growth of surviving colony pairs was compared using *t*-tests for paired samples. All analyses are two-tailed and were performed with SPSS 15.0. Mean $\pm$ SE are presented.

RESULTS

Part I: Within-species conflict

Costs of reproductive removal
In the absence of ecological competition with another species, the majority of colonies survived the 2-year period in the wood block (Fig. 2a). In addition, there was no significant effect of removing the reproductives on colony survival likelihood (*C. secundus*: $\chi^2 = 0.57$, $N = 88$, $P = 0.449$; *C. domesticus*: $\chi^2 = 0.28$, $N = 25$, $P = 0.595$). For *C. secundus*, when reproductives were present 52 out of 62 colonies survived, while 20 of 26 colonies survived when the reproductives has been removed. For *C. domesticus*, 12 of 16 colonies survived with reproductives and 6 of 9 without reproductives. For all the experiments in which the reproductives were not removed – both in Part I and Part II – the surviving colonies also retained the original
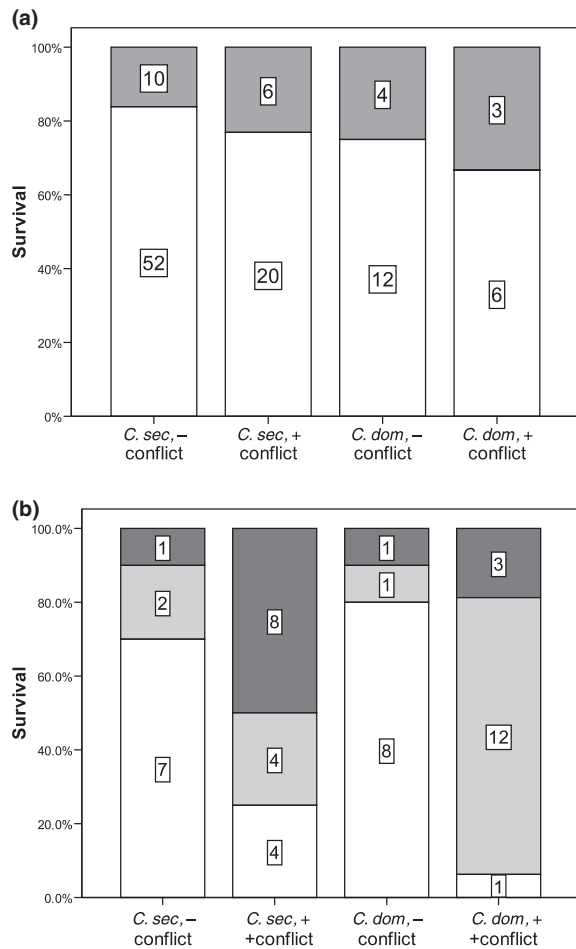
(a)

(b)

Figure 2 Colony survival in the termites *Cryptotermes secundus* and *Cryptotermes domesticus* as a function of reproductive turnover ('conflict') and direct between-species competition ('competition'). White bars: surviving colonies; light grey bars: dead after 1 year; dark grey: dead after 2 years. (a) Manipulation of reproductive turnover with no between-species competition. Treatments where reproductives were removed at the beginning of the experiment had slightly increased colony mortality over 2 years that was not significantly different from controls. (b) Manipulation of reproductive turnover with between-species competition. Colony survival over year 1 and year 2 is shown. Between-species competition alone resulted in little colony mortality but the combination of both turnover and competition resulted in catastrophic colony loss. This loss progressed much more rapidly in *C. domesticus* in which large numbers of individuals die during reproductive turnover, than in *C. secundus*.

reproductives, i.e. there was no reproductive turnover in cases where it was not caused experimentally. This is clear because primary reproductives are more sclerotized (darkly coloured) than replacement reproductives.

The mean size of the colonies in Part I were a little over twice the size of those in Part II to keep the total number of

termites in the wood blocks similar in both parts. To see if this design had an impact upon our findings, we also investigated the effects of reproductive removal on survival using a subset of the colonies in Part I that fell within the size range of the colonies in Part II (10–210 individuals: *C. secundus*: 54.26 ± 9.4, *t*-test compared to colony size in Part II, see above: $t = 1.17$, $P = 0.247$; *C. domesticus*: 58.02 ± 7.36; $t = 1.58$, $P = 0.119$). This confirmed that even for the smaller colonies, there was no significant effect of removing the reproductives on colony survival likelihood (*C. secundus*: $\chi^2 = 2.40$, $N = 62$, $P = 0.122$; *C. domesticus*: $\chi^2 = 0.07$, $N = 20$, $P = 0.788$). For *C. secundus*, when reproductives were present 40 out of 43 colonies survived, while 15 of 19 colonies survived when the reproductives has been removed. For *C. domesticus*, 10 of 13 colonies survived with reproductives and 5 of 7 without reproductives.

Competitive ability
Colony survival likelihood also did not differ between *C. secundus* and *C. domesticus* (without intraspecific conflict treatments: $\chi^2 = 0.48$, $N = 78$, $P = 0.491$; with intraspecific conflict treatments: $\chi^2 = 0.36$, $N = 35$, $P = 0.551$). Again, these results were the same for only the subset of smaller colonies that were in the same size range as those in Part II (without intraspecific conflict treatments: $\chi^2 = 2.33$, $N = 56$, $P = 0.127$; with intraspecific conflict treatments: $\chi^2 = 0.16$, $N = 26$, $P = 0.691$).

Part II: Within-species conflict and between-species competition

Costs of reproductive removal with ecological competition
The majority of colonies survived across 2 years when faced with between-species competition but low conflict over reproduction, i.e. the two species were in a single log but there was no reproductive turnover (Fig. 2b). After 1 year 9 out of 10 *C. domesticus* colonies and 8 out of 10 *C. secundus* colonies survived. In the second year, one additional colony from each species died.

In contrast to all other treatments, the combination of both ecological competition and reproductive turnover proved disastrous for colony survival. Over the 2 years, most colonies died. By the end of year one, 12 of 16 colonies *C. secundus* remained and only 4 of 16 *C. domesticus* colonies. By the end of year two, four *C. secundus* colonies and one *C. domesticus* colony remained. In no case did both species survive in a single log over the 2-year period, i.e. either both species died or there was competitive exclusion. These effects were significantly different to the parallel treatment that did not have colony turnover (but did have between species competition). For *C. domesticus*, colony survival likelihood was significantly lower when reproductives were removed rather than not, in both the first

($\chi^2_1 = 11.55$, $N = 16$, $P = 0.04$) and the second year ($\chi^2_1 = 5.27$, $N = 13$, $P = 0.022$). Specifically, the probability of a colony surviving was 3.6 times higher with reproductives than without across year one (CI: 1.50–8.62), and 3.5 times higher across year two (CI: 0.64–19.72). In *C. secundus*, survival likelihood was significantly lower with reproductives removed across the second year ($\chi^2_1 = 6.22$, $N = 20$, $P = 0.013$) but not across the first year ($\chi^2_1 = 0.09$, $N = 26$, $P < 0.767$). For year two data, the probability of survival was 2.6 times (CI: 1.13–6.09) higher with no reproductive turnover than with turnover.

Competitive ability
With no reproductive turnover, colony survival likelihood did not differ between *C. domesticus* and *C. secundus* (first year: $\chi^2_1 = 0.40$, $N = 20$, $P = 0.528$; second year: $\chi^2_1 = 0.01$, $N = 17$, $P = 0.929$) (Fig. 2b). However, comparison of the six colony pairs that survived for 2 years suggested that *C. domesticus* performed significantly better than *C. secundus* in terms of worker survival over 2 years (*C. domesticus*: -19 ± 3.2; *C. secundus*: -35 ± 8.5; *t*-test for paired samples: $t_5 = -2.58$, $P = 0.049$). For comparison, there was no difference in worker survival for similar-sized colonies from Part I that lacked both reproductive turnover and species competition but also survived the 2 years (*C. secundus*: -18 ± 11.5; *C. domesticus*: -19 ± 15.9; *t*-test for paired samples: $t_{48} = 1.56$, $P = 0.124$). The negative values here reflect the fact that colony relocation leads to a loss of some workers (Materials and Methods). As such, the colony size after 2 years is typically smaller than the initial size as the annual growth rates of these species are low. Colonies left for longer than 2 years (data not shown), however, do increase in size showing that the transfer protocol does not result in terminal decline.

The relative competitive ability of the two species reversed when reproductives were removed. Now, *C. secundus* – the species with less expressed conflict – fared better than *C. domesticus*. Specifically, colony survival likelihood through the first year was significantly higher in *C. secundus* than *C. domesticus* colonies ($\chi^2_1 = 8.37$, $N = 32$, $P = 0.004$), with the probability of survival 3 times higher (CI: 1.23–7.34) for *C. secundus* than *C. domesticus*. For the second year, the trend continued but survival likelihood did not differ significantly between both species ($\chi^2_1 = 0.1$, $N = 16$, $P = 0.752$); sample size was greatly reduced by mortality in the first year (Fig. 2b). Accordingly, with only one *C. domesticus* left after 2 years, and not a single matched colony pair, we did not compare colony size.

DISCUSSION

Our data suggest an important interaction between conflict within a species and competition between species. This interaction is evident at two levels. First, colony mortality is significantly raised, when experimental manipulations promote both forms of competition – within- and between-species – in both *C. secundus* and *C. domesticus*. In the three treatments with either no manipulation, only within-species conflict promoted, or only between-species competition promoted, the majority of colonies survived the 2-year period (Fig. 2). In contrast, in the treatment where both forms of competition – within- and between-species – were promoted, the great majority of colonies perished. This synergistic effect suggests that ecological competition can greatly increase the fitness costs of within-species conflicts.

The second manifestation of the interaction between our treatments is seen in the relative competitive ability of the two species. In the absence of royal replacement, *C. domesticus* performed significantly better in direct competition with *C. secundus* in terms of worker survival. However, when we removed the royals and increased within-species conflict, the competitive fates of the two species reversed. The species that now fares the worst is *C. domesticus*, which displays much stronger conflict over inheritance. This is consistent with the idea that conflict within a species can be decisive in the effect of among-species competition. One cannot be sure, of course, that the correlation between increased within-colony conflict in *C. domesticus* vs. *C. secundus* and decreased tolerance to ecological competition is in fact causal. However, as discussed above, the two species are otherwise extremely similar; both morphologically and ecologically. Moreover a lack of causality would require that: (1) another major difference exists between the two species that we have failed to identify and, more importantly, that (2) this factor is only expressed during colony turnover. Given this – and the fact that almost half of the workers die during turnover in *C. domesticus* (Lenz *et al.* 1985) but not in *C. secundus* – we conclude that our data are highly suggestive of a causal relationship between increased within-colony conflict and decreased tolerance to ecological competition.

Our ability to directly manipulate both within- and between-species conflict provides an unusual opportunity to experimentally investigate these conflicts and their interaction in a natural setting. However, one limitation of the system is that removing royals may cause fitness costs that are not due to reproductive conflict but rather due to the organizational cost of having to replace lost reproductives. In the absence of ecological competition, these latter costs, along with costs from conflict, are low (within the resolution of our study). However, it is possible that non-conflict costs contribute to the colony mortality seen when there is also ecological competition (Fig. 2b).

What are the possible non-conflict costs of reproductive turnover? One is if replacement reproductives have a lower fecundity than the original reproductives, although no significant difference was found in a previous study of

C. secundus in the absence of ecological competition (Korb & Schneider 2007). Another potential cost is the inevitable cessation of reproduction while new reproductives develop. This too may be minimal. The development and establishment of new reproductives occurs from 9 to 20 days in both *C. secundus* (J. Korb, unpublished data) and *C. domesticus* (Lenz *et al.* 1985), during which time only 2–5 workers would be produced at the estimated maximum colony growth rate (Roux & Korb 2004). These data suggest that organizational costs are unlikely to dominate the effects of reproductive removal. Moreover, whatever the relative importance of non-conflict costs, they seem unlikely to explain the shift in competitive fates of *C. domesticus* and *C. secundus* when one induces reproductive turnover (Fig. 2). If within-colony conflict is indeed critical for ecological success, however, one might ask how can *C. domesticus* survive at all? We do not yet understand these species well enough to answer this question but it is interesting that *C. domesticus* is the less abundant species in the study area (J. Korb, unpublished data), which is broadly consistent with it being the weaker competitor.

Our data suggest an important link between ecology and social evolution. Specifically, we find evidence that the extent of internal conflicts can be critical for a society's, and possibly species, survival in the face of competition with other species. We do not mean to imply here that ecological competition is the only important selective pressure on the termites and their conflict resolution. Species experience many selection pressures from a host of different factors in addition to ecological competition, including disease and famine, which were not considered in our study. Nevertheless, we hope that our study is a proof of principle that ecological competition among species has the potential to select against social groups suffering from internal strife. This suggests that competitive exclusion can effect the evolution of within-species cooperation in nature, and *vice versa*.

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