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Limited food induces nepotism in drywood termites

Judith Korb*

Biologie I, University of Regensburg, 93040 Regensburg, Germany
judith.korb@biologie.uni-regensburg.de

The evolution of cooperation and altruistic behaviour where individuals forego their own reproduction to help others reproduce can be explained by kin selection. Depending on the costs and benefits provided, altruism can be evolutionarily favoured if it is directed at close relatives. A considerable body of data supports the role of relatedness as a key determinant of cooperation and conflict within societies. However, the role of ecological factors and, in particular, how these costs and benefits interact with relatedness remains poorly understood. By studying 16 colonies, here I show that in a drywood termite ecological factors determine the importance of relatedness. In colonies with limited food supply, nestmates restrict cooperative interactions mainly to close relatives, while non-discriminative cooperation occurs when food is abundant. This shows for the first time directly the interaction between ecological conditions and relatedness in shaping cooperation.

Keywords: cooperation; ecological costs; kin selection; nepotism; relatedness; social insects

1. INTRODUCTION

Kin selection theory explains the evolution of cooperation and altruism where individuals forego their own reproduction to help others reproduce (Hamilton 1964). It predicts that the relatedness between the interacting individuals together with ecological conditions, expressed in the costs and benefits of the behaviour, determine whether altruism will be evolutionarily favoured. Research on social insects (ants, bees, wasps and termites) focused for a long time on relatedness and has variously demonstrated its influence in shaping cooperation and conflict among individuals in such societies (e.g. Bourke & Franks 1995; Crozier & Pamilo 1996; Ratnieks & Wenseleers 2005). By contrast, ecologically determined costs and benefits are less well studied (notable exceptions: Bourke 1997; Field *et al.* 1998; Langer *et al.* 2004) and a direct interaction of those with relatedness has never been shown in an experimental approach where both factors were changed concurrently, despite considerable awareness of its importance (Grafen 1991; Queller & Strassmann 1998). For cooperative breeding vertebrates, where a dominant breeding pair is assisted in offspring care by non-breeding helpers, ecological factors such as the vacancy of breeding sites have received more attention, and Griffin & West (2003) showed in a meta-analysis that with greater benefits of helping, the likelihood of helping relatives increases. In this study, I tested the influence of food availability and relatedness on behavioural interactions among nestmate termites.

The drywood termite *Cryptotermes secundus* lives inside a piece of wood that serves both as food and nest. As the termites never leave this nest log to exploit new food sources, its size is a key ecological parameter determining colony survival and reproduction, and hence the inclusive fitness of colony members (Korb & Katrantzis 2004; Korb & Lenz 2004). The offspring in the colony can be full-siblings ($r_{\text{fullsibs}}=0.5$), as the colonies are founded by a single king and queen, or the offspring can be a mixture of full-siblings and non-relatives ($r_{\text{fullsibs–non-relatives}}=0$). The latter happens in about 25% of all field colonies when two colonies that were independently founded in the same log fuse during colony expansion. When this happens one set of parents is often killed.

2. MATERIAL AND METHODS

I studied behavioural interactions among nestmates in 16 mixed colonies under different food regimes, eight each with abundant or limited wood. Field-collected colonies with their natural composition of individuals were set up in experimental cavities in wooden blocks of standardized dimensions (length : width : depth ratio of $4x:x:x$), but were provided either with abundant (about one termite: 10 cm^3 wood) or limited (about one termite: 2.5 cm^3 wood) food (Korb & Schmidinger 2004). *C. secundus* can assess its food availability via vibration signals produced during wood gnawing (Evans *et al.* 2005). Worker individuals (>4th instar) were marked with colour paint for observation (Korb & Schmidinger 2004). In a cross-fostering design, half of the marked workers of a colony were reciprocally transferred to another similar sized colony with the same food regime, so that the colonies were composed of about equal numbers of the mated pair's offspring and alien workers. After a resettlement phase of at least 3 days, the following interactive behaviours were recorded, using an established protocol of sampling focal individuals for 15 min (Korb & Schmidinger 2004): allogrooming (movement of mouthparts over another individual's body) and proctodeal trophallaxis (anal feeding). These cooperative behaviours are highly relevant as they influence the development of individuals from workers into reproductives (Korb & Schmidinger 2004). As focal individuals were followed, I noted whether the focal individual performed the behaviour (active) or whether it was involved as a partner (passive). In total, 254 individuals (14–20 individuals per colony, half offspring and half alien workers) were observed.

3. RESULTS

Behaviours did not differ between colonies under the same food regime (χ^2-contingency tables: all $p>0.100$), therefore they were pooled. Under abundant food conditions, the interaction frequency among nestmates did not differ from random. Offspring workers interacted with alien workers, and vice versa, as expected by chance (one-sample χ^2-test: offspring: $\chi_1^2=0.53$, $p=0.465$; alien: $\chi_1^2=0.27$, $p=0.602$; figure 1). However, under limited food conditions, offspring workers interacted significantly more often with related offspring workers, and alien workers with related alien workers, than would be expected by their occurrence (one-sample χ^2-test: offspring: $\chi_1^2=4.46$, $p=0.035$; alien: $\chi_1^2=5.45$, $p=0.020$; figure 1). Offspring workers increased their interactions from 30 to 44 and directed the extra interactions at related offspring workers (figure 1*a*). Alien workers showed about the same number of interactions under abundant and limited food conditions, but

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Figure 1. Interaction frequencies among (*a*) offspring workers and (*b*) alien workers under abundant and limited food conditions. Shown are the number of interactions in cooperative behaviours, allogrooming and proctodeal feeding, among nestmates; grey: interactions with non-relatives (offspring–alien interactions), white: interactions with relatives (offspring–offspring or alien–alien interactions). Under abundant food conditions, both offspring and alien workers interacted with each other according to their occurrence. Under limited food conditions, however, offspring workers interacted more frequently with offspring workers and alien workers interacted more frequently with alien workers than expected by chance.

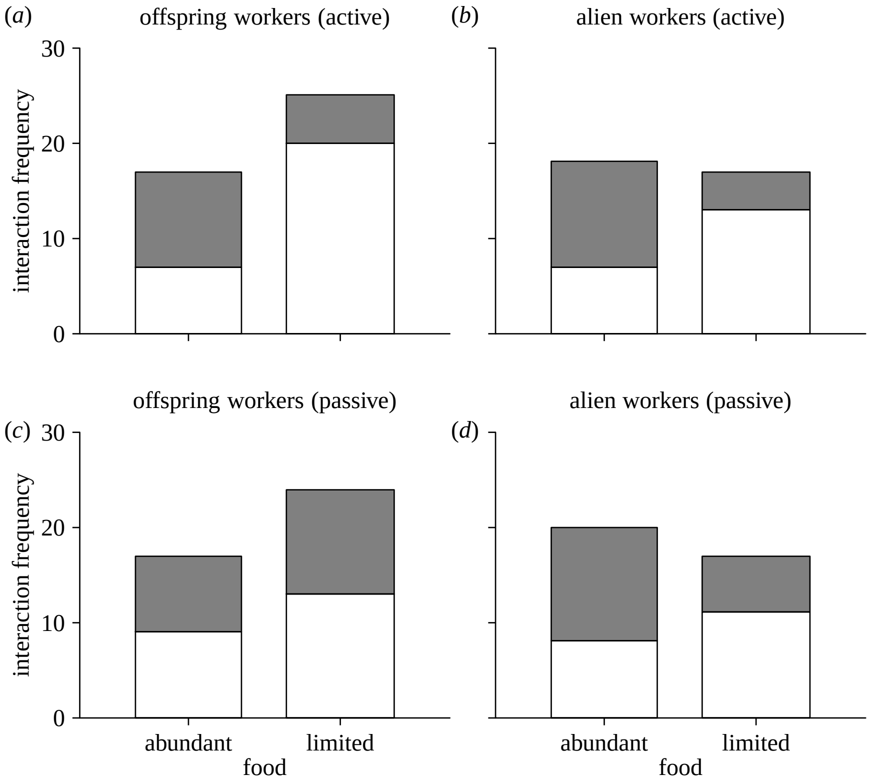

Figure 2. Active interaction frequencies among (*a*) offspring workers and (*b*) alien workers and passive interaction frequencies among (*c*) offspring workers and (*d*) alien workers under abundant and limited food conditions. Shown are the number of active and passive interactions in cooperative behaviours, allogrooming and proctodeal feeding, among nestmates; grey: interactions with non-relatives (offspring–alien interactions), white: interactions with relatives (offspring–offspring or alien–alien interactions). Under abundant food conditions, both offspring and alien workers actively interacted among each other according to their occurrence (one-sample χ^2-test: offspring: $\chi^2_1=0.53$, $p=0.467$; alien: $\chi^2_1=0.89$, $p=0.346$). Under limited food conditions, however, offspring workers actively interacted more frequently with offspring workers (one-sample χ^2-test: $\chi^2_1=9.00$, $p=0.003$) and alien workers interacted more frequently with alien workers (one-sample χ^2-test: $\chi^2_1=5.44$, $p=0.020$) than expected by chance. (*c*,*d*) For the passive interactions, under abundant as well as limited food conditions, both offspring and alien workers interacted with each other according to their occurrence (one-sample χ^2-test: abundant food: offspring: $\chi^2_1=0.06$, $p=0.808$; alien: $\chi^2_1=0.80$, $p=0.371$; limited food: offspring: $\chi^2_1=0.17$, $p=0.683$; alien: $\chi^2_1=1.47$, $p=0.225$).

redirected their interactions preferentially to related alien workers (figure 1*b*). Distinguishing between active and passive interactions, this discriminative pattern applied for active interactions only (figure 2*a*,*b*), while passive interactions were distributed as expected by chance (figure 2*c*,*d*). The results remained the same with and without sequential Bonferroni correction for multiple comparisons (i.e. adjusting the alpha-level to 0.025 for the active and passive interactions).

4. DISCUSSION

The results show that workers behaved cooperatively when food was abundant so that cooperation appeared to be low cost as the termites sit inside the food and no costly foraging is involved. However, when food was more limiting, they became more restrictive in their cooperation and directed it preferentially to relatives. By doing this, they probably increase the chance that related workers develop into dispersing sexuals, as allogrooming and proctodeal feeding are important regulators of sexual development (Korb & Schmidinger 2004). Colonies that switch to the production of dispersing sexuals are characterized by increased proctodeal feeding and allogrooming and the development of individuals towards winged sexuals is correlated with proctodeal feeding (Korb & Schmidinger 2004). In line with this, the interactions in this study were directed at nymphal instars (instars with wing buds; see below). These results show directly for the first time in an experimental approach the interaction between ecological factors and relatedness in shaping cooperation as predicted by kin selection theory (Hamilton 1964).

The failure to detect nepotistic passive interactions, while they were found in active interactions, can be explained as follows. Focal individuals comprised all worker instars (>4th instar). However, individuals involved in the active interactions were a partially different subset than those engaged in the passive interactions. There is no clear-cut characteristic trait that separates more active and more passive individuals, but available data suggest that active interactions of offspring workers were mainly directed at nymphal instars (individuals with wing buds). Thus, there might be a nepotistic treatment of nymphal instars, but not of other instars. Nevertheless, when pooling active and passive interactions, the differential treatment of relatives remained significant, showing that the passive data do not remove this trend, but actually go in the same direction (figure 2).

Why does this food-related switch from non-discriminative to nepotistic cooperation occur? Two potential explanations are that (i) the costs of the non-discriminative interactions (altruism) are no longer compensated by (indirect) benefits under limited food conditions, or (ii) direct benefits of these interactions (cooperation) disappear when food availability declines. For benefits of costly interactions to exist, the first scenario requires that fusion often occurs between related colonies, so that relatedness to alien workers is on average greater than zero and workers gain indirect fitness benefits. By contrast, the second scenario does not assume net costs of the interactions, but selfish direct benefits, for instance, as a result of increased colony size. These selfish benefits disappear when food availability, and thus the colonies' potential longevity, declines and individuals do best by developing into dispersing sexuals. Then workers will be selected that favour the sexual development of relatives only. Which scenario applies to *C. secundus* will be the question of future research.

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