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Distribution of Care-Giving Effort in a Communally Breeding Lace Bug: Fair Guarding Without Coercion

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*Cooperative care of offspring is a hallmark of animal sociality, but it is unclear how conflicts over care-giving effort are resolved in taxa that do not use dominance and physical force to induce cooperation in others. To ascertain if taxa without dominance-enforcing traits such as stings or biting mouthparts show conflicts over offspring care, we used a lace bug (Heteroptera: Tingidae) that has communal guarding of young but lacks morphologies for dominance or coercion. In *Leptobyrssa decora* females oviposit communally and then aggressively guard communal broods from arthropod predators. Since guarding has mortality risks, we tested if individuals lower their own risk by behaving less aggressively than the partner guard. We show that effort towards protecting brood, and thus guard risk of death, is strongly positively correlated between guarding partners. This finding suggests that mechanisms other than dominance or coercion are used by *L. decora* to establish an equitable and possibly conflict-minimizing distribution of care-giving effort.*

KEY WORDS: conflict; cooperation; lace bug; *Leptobyrssa decora*; Tingidae.

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INTRODUCTION

One of the primary hurdles to the evolution of cooperation is the potential for conflicts between individuals with different fitness interests (Frank, 1998; Maynard Smith and Szathmary, 1995). In animal societies conflicts may arise because of competition for benefits of cooperation such as increased reproduction, enhanced survival, or opportunities to inherit group resources (Bourke, 1997; Emlen, 1991; Heinsohn and Legge, 1999; Queller and Strassmann, 1998). Although less well understood theoretically, conflicts may also occur because group members compete to lower their own costs of behaving socially. For instance, many eusocial taxa show cooperative care of young and group defense, tasks which are energetically expensive (Russell *et al.*, 2003), may entail reproductive tradeoffs (Bourke, 1997) and increase individual exposure to predators (O'Donnell and Jeanne, 1992) and pathogens (Shykoff and Schmid-Hempel, 1991). In some taxa dominant individuals physically induce work in others (Herman *et al.*, 2000; Reeve, 1992; Reeve and Gamboa, 1983; Strassmann, 1981), a behavior which suggests that work avoidance threatens group productivity and, moreover, that morphologies and behaviors which promote dominance and social control may be crucial to maintenance of stable societies (Clutton-Brock and Parker, 1995; Crespi and Ragsdale, 2000).

It is not clear, however, how work-related conflicts are resolved in taxa that lack means of physically controlling other group members. In many eusocial arthropods threat of injury by stings or powerful mouthparts (Starr, 1985; Wilson, 1971) promotes dominance relationships. But since these morphological traits are pervasive within eusocial and related subsocial taxa (Alexander *et al.*, 1991), it is difficult to ascertain if evolutionarily stable social groups can evolve in their absence. Thus, taxa that lack dominance and morphologies for promoting social coercion are critical for testing the relative importance of social control mechanisms in the evolution of cooperation.

The lace bug *Leptobyrsa decora* (Heteroptera: Tingidae) is an excellent model for study of cooperation and conflict. *Leptobyrsa decora* lays eggs communally with conspecifics on leaves of its host plant (Melksham, 1984), and as we show here, some or all females that oviposit together also remain with eggs and nymphs and guard young against arthropod predators. Lace bugs do not possess stings or other weapons and instead use non-injurious interference against predators to effectively increase offspring survival (Hardin and Tallamy, 1992; Tallamy and Denno, 1981). However, guarding in lace bugs is costly in terms of total clutch production and individual survival (Loeb, 2003; Tallamy and Horton, 1990). Thus within communal associations of *L. decora*, selection may favor individuals that

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decrease their own guarding effort, leaving others to pay guarding costs. Such costs may explain the evolution of “egg dumping” behavior in lace bugs where some communally ovipositing females abandon their brood to the care of the lone individual that initiates the egg mass (Tallamy, 2005). Moreover, if the fitness benefits of communal guarding diminish with each additional guard, then individuals should be expected to reduce their own effort and risk with increasing number of guards.

To ascertain the nature of the relationship in guarding effort between communally guarding lace bugs, we quantified guard defensive response to staged predators attacks on *L. decora* broods of nymphs. To the extent that *L. decora* guarding associations are equitable with respect to effort and risk, coercive mechanisms are unlikely to account for fairness in distribution of labor. To our knowledge *L. decora* shows the first reported case of higher-order sociality in the Heteroptera and may thus serve as a new model to elucidate the factors favoring sociality in this species-rich order of insects.

METHODS

Leptobyrssa decora is native to Peru and Columbia, S. America, where it specializes on its host plant *Lantana camara* (Harley and Kassulke, 1971). As part of a biological control program to abate invasive spread of its host, *L. decora* has been deliberately released into habitats throughout the world where *Lantana* is abundant, including the Hawaiian islands (Davis *et al.*, 1992; Harley and Kassulke, 1971). We collected *L. decora* nymphs from a *Lantana* habitat on the island of Hawai'i and reared nymphs to adulthood on potted *Lantana* enclosed within fine mesh bags. We maintained potted *Lantana* under a covered, open-air structure that exposed plants to direct sun between 08:00 and 14:00. The remainder of the day plants were in full shade.

Leptobyrssa decora readily oviposits both communally or solitarily in the midrib of the abaxial surface of host leaves, with eggs of both brood types partially inserted along the length of the midrib (Melksham, 1984). After hatching, nymphs aggregate while foraging on the contents of leaf mesophyll. Guard females abandon the brood before most nymphs reach the end of the fourth instar of development (Melksham, 1984). After dispersal from the brood females then re-mate and search for fresh oviposition sites on the same or different host plant (Loeb, MLG unpublished observations). Thus, individuals potentially trade-off effort guarding current broods with survival to produce and guard future broods.

Guard lace bugs do not aid foraging of nymphs (Tallamy and Denno, 1981). Moreover, we observed in *L. decora* that over the course of several

hours of nymph foraging considerable shuffling of nymphs occurs within a foraging group. Thus, it would appear to be very difficult for guards to preferentially direct care towards their own young within communal, mixed-parentage broods. We confirmed prior to beginning experiments that *L. decora* guards show one or all of three discrete behaviors against predator attack: approach predator, fan wings towards predator, and body ram predator (sensu Tallamy and Denno, 1981). As shown previously with other lace bug species, guarding behavior can be easily induced through experimental exposure to simulated predator attack (Tallamy, 1982; Tallamy and Denno, 1981). We assume here that “approach” and “wing fan” are relatively less risky behaviors than “body ram” since the first two behaviors do not require physical contact with predators. Importantly, we did not observe aggression between guards in *L. decora*.

To test if jointly guarding females perform each of the three guarding behaviors with similar frequencies and thus assume similar levels of effort and risk, we first experimentally created guarded communal and guarded non-communal broods types. To create communal broods guarded by more than one female, we released onto potted, mesh-enclosed *Lantana* branches four same-aged, virgin females and four males that we randomly sampled from each of eight field-collected aggregations of nymphs. Given communal egg laying (Melksham, 1984) and multiple mating by females (Loeb, MLG unpublished observations), these field-collected aggregations represent at least eight, and probably more, families of nymphs. Thus randomly created groups of four females were on average non-kin as well as randomly assorted by phenotypic condition. To create non-communal broods guarded by a single female we released one male and one virgin female onto a single mesh-enclosed *Lantana* branch.

After release of lace bugs we observed plants daily for oviposition and noted the number of females on each egg mass. At present we cannot predict the number of females out of a group of four that will oviposit and guard communally; thus females were free to interact and form communal groups at will. We observed between two and four guards per communal brood, but for simplicity we only used guards from replicates where two different pairs of guarding females (i.e., two dyads) had formed out of the original group of four females. Our once-daily observations of oviposition may have failed to detect females that briefly oviposited within a neighbor's brood and then quickly dispersed; however, we assume that such incidents were infrequent and that each individual guard within a dyad simultaneously protected only their own young and the young of the partner guard. Guard behavior may vary with number of guards per brood and thus caution should be used when generalizing from the behavior of dyads to that of triads or quartets of guards, which were not tested in our study.

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We conducted predator-challenge tests with broods that were composed predominantly of first-instar nymphs. At the first-instar stage of development guards in our study had been present with the brood for approximately 12 days since beginning oviposition.

To prepare guards for predator-challenge tests, we clipped brood-bearing leaves from the host plant and pinned the leaf to a small sponge with the abaxial leaf surface facing away from the sponge. We then placed prepared broods close together on a laboratory bench top to acclimate within a common environment for 30 min. prior to beginning tests. To induce guard defensive behavior we gently provoked guards with a predator of *L. decora* nymphs, the coccinellid beetle *Curinus coeruleus*, which was dead and glued at the elytra to the end of a fine wire approximately 50 mm in total length. We arbitrarily decided at the beginning of the experiment that we would first challenge the guard of each dyad that was positioned furthest from the brood. In most cases the guard tested first was no more than a single body length (~4 mm) further from the brood than the guard tested second. Once tests of the first guard were completed the observer withdrew the beetle and let the first guard settle for 10 min before testing the second guard. In no case did the second-tested guard respond to staged attacks on the first female and vice versa.

We induced guard response to staged attacks by applying a standard test protocol to each guard individual. To provoke guard response the observer gently placed the tethered beetle about 5 mm in front of the focal guard and then made short, sideways movements with the beetle every 2 or 3 s. Each simulated attack lasted 30 s with a 10 s recovery time between attacks when the predator was withdrawn from the leaf surface. We repeated 30 s attacks a total of five successive times after the focal guard displayed at least one component of defensive behavior (i.e., approach, wing fan, body ram). We discontinued attacks on non-responsive guards after the tenth attempt to provoke a response. After completing each test of a dyad we then tested a singleton guard within the same half hour to serve as a temporally paired control guard. Controls were challenged in the same manner as their paired dyads; thus singletons allow us to test if behavioral correlation within a dyad is at least partially explained by common environmental factors such as temperature, humidity, etc. For instance, positive correlation of behavior between controls and paired dyads would suggest that shared sensitivity to environmental cues explains correlation within dyads.

To estimate individual guarding effort we summed across the five simulated attacks each guard's number of approaches, wing fans, and rams. Since frequencies of each guarding behavior are likely correlated within an individual, we used principle components analysis (PCA) to reduce the three observed behavioral responses to a single PCA score for each guard. We

also used tests of the raw behavioral observations when a more intuitive analysis was also informative, but the possibility of behavioral correlation within an individual suggests that caution be used when interpreting statistical significance of these tests.

RESULTS

We scored defensive reactions of each of eleven singletons, nine of which were each experimentally paired with one of nine dyads. We observed at least one approach, one wing fan, or one ram, respectively, from 67, 44, and 22% of singletons. By contrast, at least one guard within each dyad approached, wing fanned, or rammed the predator in 89, 67, and 44% of dyads, respectively. After correcting for the two-fold difference in guard number, however, guards in dyad and singleton treatments did not differ significantly in per capita number of observed defensive responses (paired *t*-tests for number of approaches: $|t| = 0.545$, $p > 0.6$; number of wing fans: $|t| = 0.385$, $p > 0.71$; number of rams: $|t| = 0.122$, $p > 0.9$; $n = 9$ for each test).

To ascertain if number of guards per brood affects total guarding effort, we tested if mean combined effort of guards within dyads was significantly different from a hypothetical two-fold increase in total effort of singleton guards. We calculated an expected mean for dyads by doubling the observed mean number of times each behavior was shown by singletons. We found that there was no significant difference between observed and expected values of dyad combined effort for each behavior (Wilcoxon signed-rank test: number of approaches: $|T_s| = 1.50$, $p > 0.85$; number of wing fans: $|T_s| = 4.50$, $p > 0.65$; number of rams: $|T_s| = 8.5$, $p > 0.25$, $n = 9$ for each test; Fig. 1). Thus, absolute magnitude of combined guard protection was two-fold greater on broods protected by two guards, but at the same time social context of guarding (i.e., guard number) does not affect average individual effort.

We used principle component (PC) scores of guards to test if within a dyad individuals showed quantitatively similar levels of guarding effort. Principle component 1 explained 88.9% of the total variation in behavior for 18 individuals within dyads and 11 singleton guards. By contrast, PC2 and PC3 explained 7.8% and 3.3% of the total variance, respectively, and we thus excluded these components from further analyses. Each of the three PC1 eigenvectors representing number of approaches, number of wing fans, and number of rams loaded positively and with quantitatively similar magnitudes of 0.591, 0.565, and 0.575, respectively. The first principle component therefore represents a major axis describing intensity of

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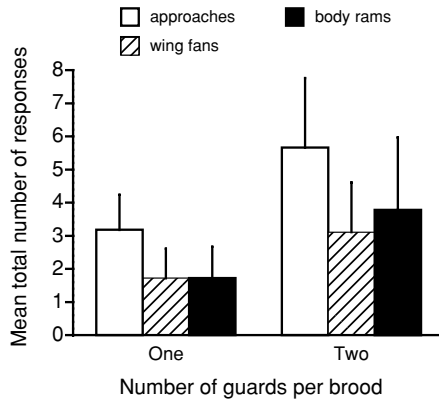


Fig. 1. Effect of guard number on total guarding effort. Two guards (i.e., dyads) showed a total guarding effort that was on average two-fold greater in magnitude than that shown by singleton guards. See text for statistical details. Error bars = 1 s.e.

guard defensive behavior, with higher PC scores indicating more effort exerted towards brood defense.

Order of guard testing may affect guarding intensity, but a paired *t*-test of PC1 scores showed that there was no significant difference between the first-tested and second-tested guards within each dyad ($|t| = 0.765$, $n = 9$, $p > 0.45$). To test the magnitude and direction of correlation in PC1 scores within dyads, we randomized the identity of the first-tested and second-tested guard 1000 times within each dyad, and after each iteration calculated the pair wise correlation coefficient for the entire sample of nine dyads. Resampled mean correlation coefficient of PC1 scores of dyad mates was $r = 0.84$ and significantly greater than zero (95% confidence interval upper limit = 0.968; lower limit = 0.757). More intuitively, estimates of paired correlation coefficients of number of approaches, number of wing fans, and number of rams each showed statistically significant and strongly positive correlation within a dyad (Fig. 2). Thus both analyses suggest that joint guards defend young with quantitatively similar, though not necessarily equivalent, levels of effort and risk.

There were no significant differences between guards in time to respond to predator attack, with the first-tested guard responding to attack on average within 8.98 s (1.42) and second-tested guard responding within 10.78 s (1.23; paired *t*-test: $|t| = 1.05$, $p > 0.30$; test of correlation between dyad mates: Spearman's rho = 0.133, $p > 0.70$).

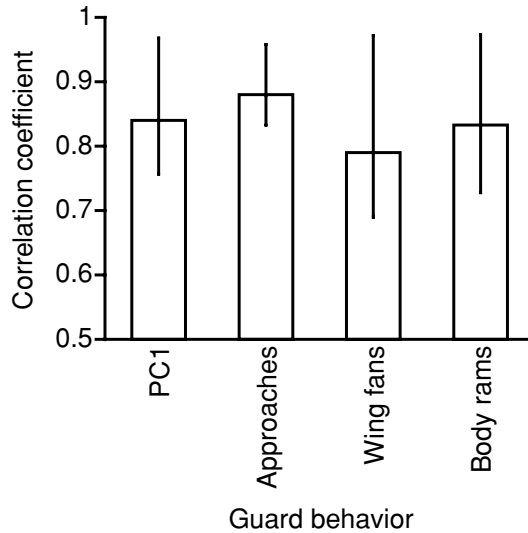


Fig. 2. Correlation of guarding effort within dyads. Each pair-wise correlation coefficient is estimated from a resampling procedure described in the text. PC: principle component. Error bars span the resampled 95% confidence interval.

Extrinsic environmental factors may explain correlation in guarding effort observed within dyads. We found, however, that PC1 scores of singleton guards that were each paired with a dyad and tested within the same half-hour time period and within the same test arena, were not significantly correlated with mean PC1 score of the paired dyad (pair-wise $r = -0.29$, $p > 0.50$, $n = 9$). Similarly, singleton PC1 score was not significantly correlated with either the highest PC1 score ($r = -0.23$, $p > 0.45$, $n = 9$) or the lowest PC1 score ($r = -0.27$, $p > 0.45$, $n = 9$) of the paired dyad. Absence of dyad behavioral correlation with temporally paired controls suggest that behavior of dyad mates is not correlated through extrinsic environmental cues, but more likely through cues associated with a partner guard's phenotype and behavior, or with the brood.

DISCUSSION

Theory posits that dominance, policing, and punishment are key conflict-minimizing mechanisms in cooperative animals. We show here, however, that such mechanisms may not be a necessary feature of stable

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social systems. In the lace bug *L. decora*, guarding females can withhold costly guarding effort apparently without obvious threat of physical coercion from partner guards. Nevertheless, we observed that dyad mates show strongly positively correlated responses towards staged predator attack, suggesting that the absence of coercion does not constrain ability of *L. decora* to maintain relatively equitable distribution of guarding costs. Correlated guarding effort arose despite the fact that individuals were experimentally paired at random with respect to phenotypic and genetic variation. To the extent that less complex social taxa such as *L. decora* approximate incipient stages of cooperative care giving, equitably divided care-giving costs may be an important feature of the origins of sociality.

Demonstration of correlated guarding effort raises the issue of how individuals proximally determine defensive responses to predators given a guarding partner's actions and innate abilities. Our design minimized the effects of behavioral correlation that may arise through preferential assortment of phenotypically similar individuals such as close kin. We also experimentally precluded lace bug assortment through host-plant preference, as well as behavioral correlation through extrinsic environmental cues. By elimination of these possibly confounding factors, our results suggest that guards determine their own actions through cues emanating from the partner guard or from the brood. For example, guards may be visually counting a partner's actions and responding with a similar number of approaches, wing fans, or body rams. However, a counting system would a priori seem to be an inefficient method of mustering simultaneous defense against fast-attacking predators. Moreover, counting a partner's anti-predator responses may not be evolutionarily stable because the individual that first responds to predator attack potentially incurs costs of abandonment by the partner who is able to assess risk and defect.

Biochemical compounds secreted by female *L. decora* are a more likely source of proximate information shared by guards. For example, in a related tingid species with communal oviposition and single-female care of young, egg masses are attractive to gravid conspecifics if a female-secreted compound is present on eggs (Monaco *et al.*, 1998). Volatile attractants may also facilitate kin discrimination in lace bugs (Loeb, 2003; Loeb *et al.*, 2000) and in principle such substances could communicate an individual's ability or intent to guard offspring, as well as convey a perceived level of predator threat. Future research into proximate factors driving coordination of guard effort must also consider the potential for asymmetric, and hence evolutionarily exploitable, use of information emanating from behavioral or chemical cues.

Interestingly, we observed correlated guarding effort within dyads even though we did not control female reproduction. Reproduction may

be proximately important if females facultatively adjust clutch size with changes in social environment, adjustment which may in turn affect guarding behavior. However, this scenario seems unlikely to explain our results because we found no difference in average guarding effort per individual shown in dyads and by singletons and thus variation in clutch size between dyads and singletons is uncorrelated with guarding behavior. Nevertheless, an important theoretical and empirical challenge is thus to understand the relationship between fecundity, offspring survival and the distribution of guarding effort within communal groups. Our results suggest that on average pairs of guards exert approximately twice the total guarding effort of singleton guards, but field experiments are needed to test if dyads have twice the reproductive success of singletons.

It is also of interest to determine if correlated effort within dyads is any more or less effective at protecting young than effort exerted at random with respect to a partner's effort. Offspring likely have high survival if each guard exerts maximal effort against predators, but it is not clear how correlation in guarding effort per se simultaneously affects guard fitness and offspring survival. Theoretical study of the relationship between the strength of correlation of care-giving effort and offspring survival could illuminate potential for conflicts of interest between partner guards and between guards and their young. For example, guard reproductive value may be maximized through positive correlation with partner guard effort, perhaps because by adjusting effort to match that of the partner neither individual assumes more than its fair share of the work. But such correlation may compromise offspring survival when total effort of guards is low but nevertheless positively correlated. A fruitful path of future research might consider how natural selection moulds fair systems of cooperative care when solutions to conflict between caregivers in turn create conflict between parents and their offspring. Such research effort could also benefit from considering pathways to stable cooperative groups which do not entail coercion and threats of punishment as solutions to conflict.

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