TOSSING PASSALIDS: EFFECTS OF SUBGROUP TRANSPLANTATION AND DISTURBANCE ON SOCIAL INTERACTIONS

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Abstract: Social behavior is uncommon in Coleoptera. A notable exception is the Passalidae, which live in social colonies, stridulate (potentially to communicate), and are reported to have parental care. We tested if parental care extends to protecting brood from disturbance. We collected groups (putative family groups beneath logs) of two passalid species in the high altitude forests of Costa Rica and studied their responses to laboratory simulations of disturbance. The coordinated defense hypothesis predicted that members of the same social group in both species would aggregate, and members from different groups would move away from each other in response to disturbance over time. We found no difference in the distance between members of the same or different social group or any signs of social interaction, suggesting that passalid social behavior degrades in the face of disturbance.

Key Words: Aggregation, coleoptera, colony, communication, sociality

INTRODUCTION

A subset of insect species, chiefly Hymenoptera and Isoptera, show social behavior such as parental care and coordinated movement. Additionally, Coleopterans are known to exhibit primitive eusocial behaviors (Brandmayr 1992). Passalid beetles (Scarabaeoidea) live in colonies in which adults and teneral (immature) adults cooperate in brood care of larvae, pupae, and eggs in rotting logs (Borror et al. 1963). However, little is understood concerning whether social group behaviors such as aggregation and parental care hold up under severe disturbances such as predators overturning their logs. Previous observations suggest that adults have the capacity to defend their larvae, but this behavior may dissolve under direct threats to the colony.

Two species of passalid beetles inhabit the high elevation forests of Costa Rica, a larger species approximately 4.5 cm in length (species A) and a smaller 2.5 cm long (species B) (Whited et al. 2004). We assessed movement of passalid beetles from the same and mixed social groups using laboratory bioassays. This experimental setup made possible the manipulation of social groups and more standardized results than would have been possible in the field.

Adult passalids are reported aid immatures by repairing pupal cases, feeding larvae with macerated

wood pulp, and defending colonized logs from other passalid intruders (Schuster 1975b). Reciprocal stridulation occurs between adults and larvae, presumably for communication, but its function is not well understood. A large investment in larval care may extend to protection of larvae in the event of disturbance.

Given their apparent capacities for communication, we hypothesized that disturbance would invoke a strong social interaction among family members. From this we expected to see a coordinated escape response and/or reciprocal stridulation. We compared the social responses to disturbance of putative family groups with unrelated adults and larvae. This provided a test of whether social behavior is upheld in a mixed social group setting. If social behavior persists in these conditions, adults would move closer to larvae and adults of the same group over time, and away from members of another group.

METHODS

On the morning of 1 Feb 2008 we systematically searched for beetle-inhabited logs along the Mirador Trail in high elevation secondary forest of Cuerici, Costa Rica. We found eight discrete groups of passalids that contained at least one adult and one larva (4 groups each of the large species and the small species). In the colonized logs, we noted the number of adults and larvae of either species. We then collected all adults and larvae for laboratory experiments, keeping each discrete social group (defined as all the individuals found on a single log) in its own bag.

We monitored each group's response to disturbance by creating a 1 x 1 m arena, with a thin soil layer and two oak logs (formerly inhabited by passalids) on either side. We "disturbed" each social group of each species by carefully handling them and gently placing ("tossing") groups into the center of the arena. We then tested each group after disturbance, measuring (every 1 min up to 5 min) the distance (in cm) among all individuals, and noting whether distances were adult to adult, adult to larva, or larva to larva. At every 1 minute interval we also recorded whether any individuals were engaged in any other escape behaviors such as digging or burrowing under a log.

We conducted a second experiment to test whether beetles of mixed social groups responded to disturbance in a similar manner as they did in their own social group. We conducted intraspecific trials to control for potential variation between species A and B. From each social group, we randomly paired one adult and one larva for study (referred to as 'pairs'). We then

tested for variations in aggregative behavior by measured mean adult-adult and adult-larvae distances in pairs from different social groups.

RESULTS

We searched 53 oak logs and found beetles within or beneath 15 of them. Seven were inhabited by the large species (11 adults and 15 larvae) and 8 by the small species (14 adults and 15 larvae). The two species did not co-occur in any logs.

When placed in the center of an experimental arena (simulated forest floor), the adults appeared to move away haphazardly, while the larvae barely moved, remaining within 5 cm of where they were placed in all trials. Adults from the same social group never relocated to opposite sides of the grid after five minutes (adults recruited to same side in 2 of 7 trials; in the other 5 trials, one stayed in center while the second hid under a log), whereas adults from different social groups relocated to opposite sides in 5 of 7 trials. However, there were not enough data to test whether this pattern was nonrandom. Some adults hid beneath one of the logs, while others burrowed in the soil in the middle or edge of the arena. We did not observe any stridulations or direct interactions between beetles.

There was no evidence that movements within an unfamiliar arena were coordinated within social groups. Coordinated movements could have been evident as a tendency for individuals of the same social group to be closer to each other than to members of another social group. However, this was not true for either adult-larva distances (Fig. 1; $t = 0.19$, $df = 4$, $P = 0.43$, for paired t-test) or adult-adult distances (Fig. 2; $t = 0.89$, $df = 6$, $P = 0.21$).

Distances between conspecific individuals did not differ between species A and B (distance between adults from the same group: $t = -0.80$, $df = 6$, $P = 0.45$; adults from different groups: $t = 0.87$, $df = 5$, $P = 0.42$); adults and larvae from the same group: $t = 0.61$, $df = 12$, $P = 0.55$; and adults and larvae from different groups: $t = 0.41$, $df = 7.35$, $P = 0.69$].

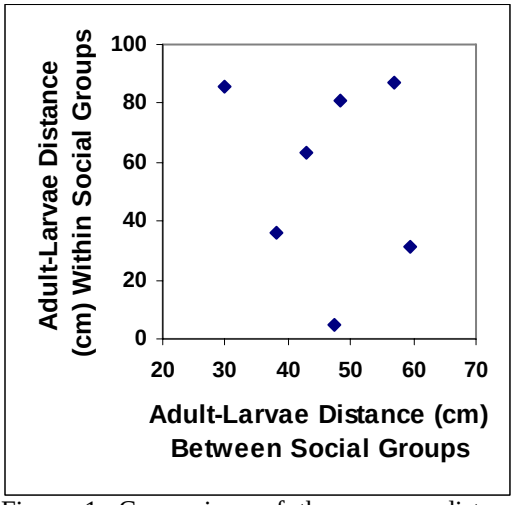

Figure 1. Comparison of the average distance between adults and larvae depending upon whether or not they were members of the same social group. Figure shows measurements five minutes after animals were placed together in the center of an unfamiliar arena. Seven individuals were tested (black = large species, grey = small species). Social groups of beetles were collected along the Mirador Trail behind the Estación Biologica, Cuerici, Costa Rica.

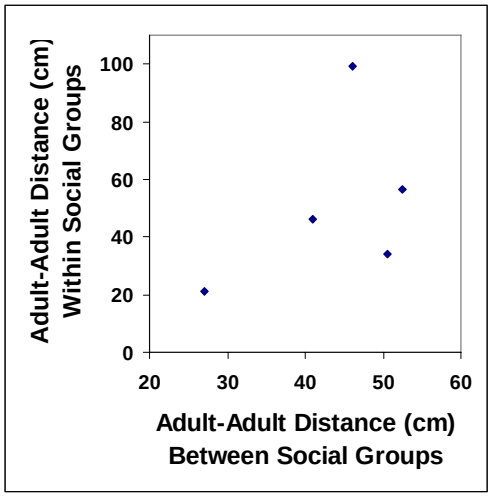

Figure 2. Mean distance between adults from the same social group (y-axis)) and adults from different social groups (x-axis) five minutes after disturbance in two species of passalid beetles. Five individuals were tested (black = large species, grey = small species). Social groups were collected along the Mirador Trail behind the Estación Biologica, Cuerici, Costa Rica.

DISCUSSION

We found no indication that passalids influenced larval or other adults' behavior, irrespective of social group identity.

Beetles stridulated readily when we picked them up or poked them, but they never stridulated during our trials. If stridulating is a mode of communication among passalids, we would have expected to observe some degree of reciprocal stridulation, either between adults, as demonstrated in previous experiments (Close et al. 2002), or between adults and larvae.

The simple interpretation of our results is that passalids simply lack the social skills for a coordinated escape response. However, another possibility is that it is adaptive for adults to abandon their young when the social group is disturbed. The life history of passalids at Cuerici is not known, but passalids in general are reported to produce brood at least annually, and to live as long as 14-16 months as adults. Therefore, they may have future reproductive opportunities even if they lose one brood, and the value of preserving future reproduction might exceed the benefits of trying to protect or shepherd their current brood. Also, it may be adaptive to disperse after a disturbance rather than aggregating into a larger prey target.

In contrast to some previous studies at Cuerici, we found passalid social interactions to be limited at best. Stork et al. (2006) suggested that disturbance may invoke a coordinated escape response in which adults aid larvae. In their studies, larvae that were discovered beneath logs in the morning had all disappeared by the afternoon, leading them to hypothesize that adults assisted in moving the relatively immobile larvae to another location. Our studies seemed to validate that the larvae have limited mobility, but we found no evidence of parent-assisted movements of larvae.

Passalids inhabit moist, dark logs, and it is possible that our experimental arena was too artificial

to reveal the natural tendencies of our study species to aggregate as social units. Alternatively, passalid aggregations might be better understood as the coincidental clumping of individuals within isolated habitat patches (oak logs) rather than socially structured family groups.

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