SOCIAL STRUCTURE AND REPRODUCTIVE SUCCESS IN PASSALID BEETLE COLONIES

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Abstract: Aggregative behavior can evolve when individuals in aggregations of animals tend to have higher per capita fitness than solitary animals or smaller groups. Passalid beetles near Cuerici, Costa Rica, appear to be social, but it is not known what, if any, are the benefits to individuals within colonies. We hypothesized that passalid beetles have increased fitness from raising larvae in colonies (perhaps due to cooperation among adults). However, larvae-per-adult (a putative proxy for fitness) was unrelated to colony size. Analysis of the spatial configuration of larvae and adults revealed no spatial structure in colonies. However, one of the treatments appeared to evoke a coordinated escape response in which adults may have aided larvae. If so, this indicates some level of social integration in passalids.

Key Words: Passalidae, sociality, colony, reproductive success

INTRODUCTION

Aggregative behavior can be selected for if individual fitness is enhanced by joining a group or staying in a group. Individuals within groups might experience benefits in foraging efficiency, defense, and/or reproductive activities. The social structure within aggregations of animals can range from loose to highly complex. Many species of ants and bees provide examples of complex social structure with strict castes. Passalid beetles (Coleoptera: Passalidae) seem to exhibit a looser form of sociality in small colonies beneath rotting logs, where adults provide food for larvae (White, 1983). However, it is unclear what fitness benefits (if any) arise from living in passalid groups.

If passalids are aggregated because of the benefits for individuals, then, other things being equal, individuals within medium to large colonies should have higher fitness than individuals within small colonies. If individual fitness increases with colony size, and if the ratio of larvae to adults is a reasonable proxy for individual fitness, then the total number of larvae per colony should increase more than linearly with colony size (Fig. 1, Model I). However, if colony size is unrelated to per capita reproduction, total larvae per colony should increase linearly with colony size (Fig. 1, Model II). Finally, if larger colonies tend to experience intra-colony competition for resources, per capita reproductive success might decrease with increasing colony size, in which, case, total larvae as a function of total colony size could be a decelerating function (Fig. 1, Model III). We tested these alternatives using a survey of passalid colonies.

Sociality implies that there is some structure to the interactions of individuals within a group. We tested for nonrandom spatial configurations of larvae and adults within passalid colonies by comparing the actual configuration of larvae and adults in a colony with the random distribution predicted by a null model. Social structure

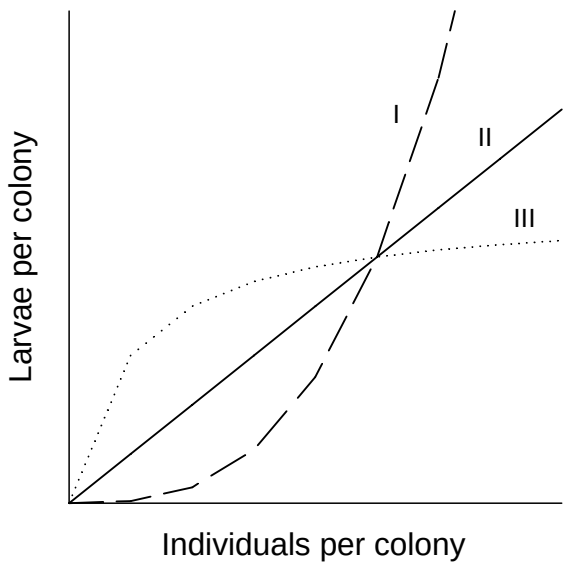

Figure 1. Three theoretical alternatives for the relationship between reproductive success and colony size. The number of larvae per total individuals in a colony might increase (I), remain the same (II), or decrease as colony size increases (III). The slope of these functions is a putative proxy for average fitness of adults within the colony.

could also be apparent temporally (individuals exhibiting a coherent schedule over time). We attempted to observe this by tracking the movements of individual passalids over time.

METHODS

We sampled logs located in the oak-dominated canopy areas along trails at Cuerici Biological Station, Costa Rica, and found 12 colonies of passalid beetles (the smaller of two species; 2.3 – 2.9 cm in length). In each colony, we counted the number of adults and larvae and sketched a map of the colony, determining the x-y coordinates of each individual. We gave each adult a unique mark using a colored oil marker. We repeated this process three times (morning and afternoon on 27 January 2006, and morning on 28 January), noting changes in spatial distribution on each occasion.

We estimated the ratio of number of larvae to total colony size with a linear regression, forced through the origin (using JMP 5.0.1). We evaluated lack of fit from this linear model to determine which of the three theoretical models in Figure 1 matched the data most closely.

For the five colonies containing at least two adults and two larvae, we used the x-y coordinates of each individual to quantify the spatial configuration. We calculated (1) mean larva-larva distance, (2) mean larva-nearest adult distance, and (3) mean adult-adult distance. We generated a null model of spatial configuration for each colony by randomly assigning stage identity to individuals 999 times (with the provision that adult and larvae number were constant and equal to that actually observed). For each simulated configuration of larvae and adults, we calculated the same three metrics (using the original distance matrix), and generated a frequency distribution of possible distances for each metric under the null hypothesis. For each log, for each of the three metrics, we calculated the distance between the observed distance and the median from the randomization results. Then we used a t-test (n = 5 logs) to test whether the observed distances tended to be larger or smaller than expected by chance.

RESULTS

Larvae constituted 75 ± 4% (mean ± SE) of each colony across colonies. A simple linear model of number of larvae vs. colony size provided good fit (r^2 = 0.80; Fig. 3). A

lack of fit test for this model was non-significant ($F_{4,7}$ = 2.29, P = 0.22), and a second order polynomial provided no improvement to fit (r^2 = 0.80). Thus, there was no evidence for any relationship between fitness and colony size.

We were unable to track marked adult beetles because most marked beetles could not be found. Between the first and second observations, 8 of the 12 beetle colonies decreased in apparent colony size, and 0 individuals were visible in 3 of those colonies (larvae disappeared from sight along with adults). Between the second and the third observations, 6 colonies decreased, and 0 individuals were visible in a total of 8 colonies. Only 2 colonies retained a constant visible population throughout all 3 observations. Therefore, we based the analyses of spatial structure on data from the first observation of each colony.

We found no evidence of spatial structure (Table 1). There was no aggregation in either larvae (t_4 = 0.38, P = 0.72) or adults (t_4 = 0.97, P = 0.39). The position of adults relative to larvae did not suggest care of larvae: the mean larva-nearest adult distance (3.58 cm) was 1.77 cm greater than the randomly predicted distribution (marginally significant, t_4 = 2.61, P = 0.06)

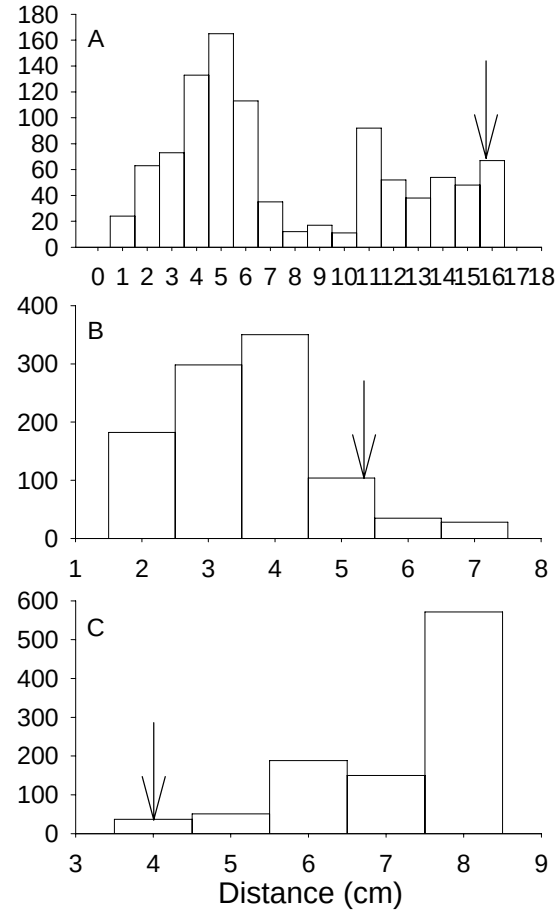

Figure 2.Random distributions of distances of (A) adult to adult, (B) larva to nearest adult, and (C) larva to larva, calculated for one passalid beetle colony (Colony 9) at Cuerici Biological Station, Costa Rica. Arrows indicate actual distances for the three distance categories. In Colony 9, the actual values for adult-adult and larva-larva distance were 96.2% and 99.9% more extreme than the randomized estimates (Panels A and C). However, these values were not typical of other logs and the overall tests for nonrandom aggregations of adults and larvae were not significant. The actual value for larva-nearest adult was 85.4% more extreme than randomized estimates in this colony, and among the five colonies, that value was significantly farther than the nonrandom estimates (Table 1).

Table 1. Actual mean adult-adult distance, larva-larva distance, and minimum adult-larva distance (average distance from a larva to the nearest adult) compared to the median value for the same metric from randomization tests. Studies involved five passalid colonies found under logs at Cuerici Biological Station, Costa Rica. All colonies that had at least 2 adults and 1 larva were analyzed. Units are cm.

			Adult-adult distance		Larva-larva distance		Larva-nearest adult distance	
Log #	Adults	Larvae	Actual	Random	Actual	Random	Actual	Random
2	3	11	16.20	7.95	4.50	7.77	5.80	4.13
6	2	3	4.00	2.48	2.00	2.33	1.30	1.63
9	3	12	12.30	6.57	3.40	6.60	4.80	3.03
10	4	4	3.60	11.21	17.40	11.00	10.00	6.06
11	2	3	12.30	6.57	3.40	6.60	4.80	3.03
Median	2.80	6.6	9.68	6.96	6.14	6.86	5.34	3.57

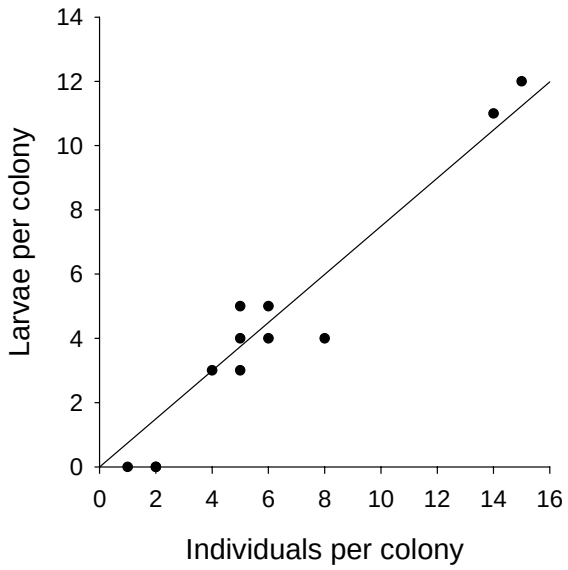

Figure 3. Relationship between reproductive success and colony size in 12 colonies of passalid beetles at Cuerici Biological Station, Costa Rica. Data match Model II in Fig. 1 (r^2 = 0.80), suggesting that colony size does not affect proportion of larvae in each colony.

DISCUSSION

We found no evidence that group size (a measure of sociality) influenced fitness (Figs. 1, 3) and no evidence for spatial structure of individuals within colonies (Fig. 2, Table 1). However, the benefits that colonies confer to individuals and the social mechanisms driving those benefits may be functioning in a different way. For example, although increased colony size does not seem to increase per capita larval abundance, it is possible that larval survival and/or the number of reproductive bouts per breeding season could increase with colony size. If colonies do confer such benefits to individuals, it is possible that the driving mechanism is something we were unable to observe, such as temporal social structure. Alternatively, because beetle larvae are known to make noise by stridulating (White 1983), it is possible that direct adult-larvae communication drives parental care in beetle colonies, rather than spatial or temporal structure.

We were surprised that apparent colony size decreased so much, and so fast, after our first visit to the logs. Some of the passalids were probably foraging inside the log, coincidentally out of view, but it appears that many colonies reacted to the handling disturbance by burrowing to hide themselves or abandoning the log collectively. Because we did not handle the larvae, and because larvae are not highly mobile, we did not expect them to move away from disturbance independently as an escape response. The disappearance of larvae following disturbance probably involved some form of assistance of larvae by adults. If so, this would represent a form of sociality.

LITERATURE CITED

White, R.E. 1983. Passalid Beetles. Pp. 137 in Peterson Field Guide to Beetles. Houghton Mifflin: New York.