Density dependence of passalid beetles in a high elevation oak forest

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Abstract: Two species of passalid beetles occur within oak logs of high elevation tropical forests. They form social colonies in which adults feed larvae. On Cerro de la Muerte, the two species tended to co-occur within logs more often than expected by chance, suggesting facilitation, mutualism, or parasitism. Local populations within logs did not appear to be influenced by either positive or negative density dependence, and many apparently suitable logs were unoccupied. It may be that immigration and emigration are the prevailing processes at the level of habitat patches (logs) and that density dependence and population regulation mainly arise at the level of metapopulation. We found no direct evidence of dispersal limitation, but did find that beetles were more likely to occupy relatively larger logs.

Key words: Coleoptera, colony, density dependence, dispersal, oak forest, resource limitation

Introduction

Passalid beetles (Coleoptera: Passalidae) are a unique family of beetles in that they exhibit social behavior. Colonies of mature adults and immature larvae occur in rotting oak logs where adults feed on decaying wood matter, which they partially digest and feed to larvae (White 1983). Two species of passalid beetles are present in the high elevation oak forests of Costa Rica: a smaller species of ~ 2.5 cm length (sp. A) and a larger species of ~ 4.6 cm (sp. B) (M. P. Ayres pers. comm.). Few previous studies have noted the presence of sp. B, and no studies have looked at the pattern of abundance of sp. A relative to sp. B. Because these two species appear to utilize the same resource, the two beetles may separate themselves spatially, either within a log or among different logs. Alternatively, there may be facilitation or even a mutualism, in which case the two species would be expected to co-occur more often than expected by chance. We evaluated the pattern of co-occurrence of these two species.

Passalid beetles lend themselves well to the study of population dynamics. Population fluctuations can be a function of exogenous effects, such as from generalist predators, and/or density dependent (endogenous) effects. Two forms of density dependence seem possible for passalids. Positive density dependence, also known as the Allee effect, is the tendency for per capita reproduction to increase as density increases. If positive density dependence is present, a population exhibits qualities of a positive feedback loop where greater and greater densities beget larger more fecund populations. Hence positive density dependence contributes to unstable population dynamics. Allee effects often occur in populations of social organisms, where larger groups of individuals facilitate reproduction (Begon et al. 1990). Thus, passalid beetles might be subject to Allee effects because of their sociality in feeding larvae.

In contrast, negative density dependence is the tendency for per capita reproduction to decrease as density increases. This can occur when a resource is limiting and conspecifics compete for this resource. It is unknown if passalid colonies within a log are commonly limited by resources (wood material). If negative density dependence does occur in passalid beetles, this would tend to stabilize population dynamics, possibly producing an equilibrium around which local abundance would tend to be regulated (Begon et al. 1990).

Alternatively, per capita reproduction may be largely independent of local density. It

is possible that a subpopulation of passalid beetles within a log is at too small a scale for density dependence to be important. In fact, Baptista et al. (1998) found that not all oak logs were inhabited by passalid colonies, and suggested that passalid distribution is a function of dispersal limitation. In this case, passalid populations would be more appropriately viewed as a metapopulation, in which colonization and extinction influence the occupancy of specific logs and density-dependent feedbacks mainly arise at the level of populations of logs. Baptista et al. predicted a relationship between presence of passalids and the local abundance of potential habitat (logs). We tested this prediction as a means of testing the hypothesis that passalid distribution is dispersal limited.

METHODS

We studied the passalid beetle populations of a *Quercus* dominated forest in Cuerici Biological Station at Cerro de la Muerte, Costa Rica. Colonies were sampled by haphazardly selecting fallen oak logs (maximum weight approximately 30 kg due to logistical constraints), located on or within 30 m of the trail. We overturned logs and counted adults and larvae of both passalid species. We searched for beetles by sifting through the soil under logs and breaking apart degraded parts of logs with an axe and trowel. We measured the height of each log and the area of ground it covered (shadowed area). We also estimated the percent of ground covered by woody debris (potential passalid habitat) within a 5 m radius of each log.

Sp. A, which was most abundant, was examined for evidence of resource limitation and density dependence. To evaluate density dependence, we calculated a per capita reproduction index (natural log (larvae/adult + 1)) in each log to compare to adult abundance. To evaluate resource limitation, we calculated a volume index for each log (shadowed area x log height) to compare to natural log transformed colony size. To examine the effects of dispersal from nearby logs on colonization, we used logistic regression to compare percent habitat cover and an index of log volume to the proportion of colonized logs.

RESULTS

Of the 48 logs we examined, we found 12 logs colonized only by sp. A, two logs colonized only by sp. B, four logs colonized by both species, and 30 logs uncolonized. Although sample sizes were limited, a G-test suggested that the two species tended to co-occur more than expected by chance ($G = 3.21$, $df = 1,46$, $P = 0.07$; Table 1). Colony size of sp. A ranged from one to seven adults and zero to ten larvae, and the volume of occupied logs varied by more than 51 times. However, colony size was unrelated to log volume ($r = 0.084$, $P = 0.31$).

Of the 16 logs colonized by sp. A, eight also contained larvae. In one colony, we found one callow adult and no other life stages. The highest ratios of larvae to adults (index of per capita reproduction) occurred in the smallest colonies, but there was no significant relationship between the reproduction index and adult abundance ($r = 0.00$, $P = 0.97$; Fig. 1); a second-order polynomial was also not significant ($p = 0.71$).

Table 1. Observed frequencies of large (sp. B) and small (sp. A) passalid species. Values in parentheses are expected frequencies under the null hypothesis of no association between species.

		Larger species	
		Present	Absent
Smaller species	Present	4 (2)	12 (14)
	Absent	2 (4)	30 (28)

Percent habitat cover within a 5 m radius did not differ between colonized logs and uncolonized logs (mean ± SE = 23.0 ± 2.4 vs. 22.5 ± 3.3 respectively; t = 0.13, df = 40, P = 0.89). The probability of a log being colonized did not vary with the ground coverage by logs within 5 m (percent habitat cover; $\chi^2 = 0.02$, df = 1, P = 0.89). The probability of a log being colonized did increase with increasing volume of the focal log ($\chi^2 = 4.65$, df = 1, P = 0.03; Fig. 2), but did not increase with increasing shadow area of the focal log ($\chi^2 = 1.11$, df = 1, P = 0.29).

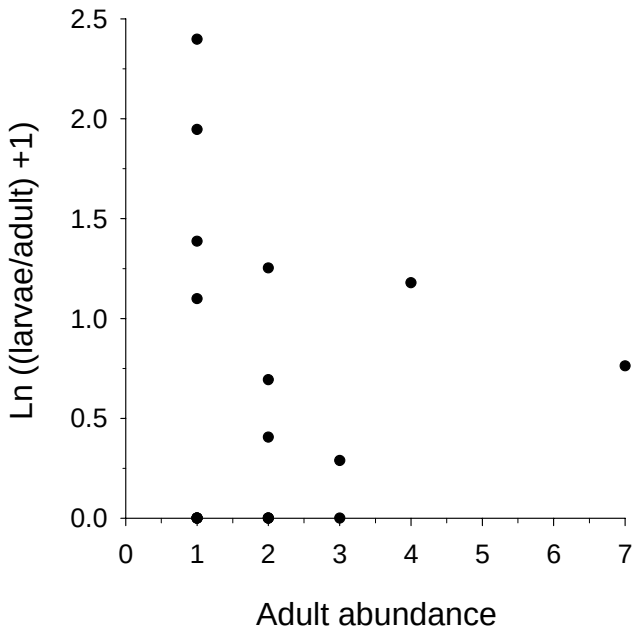

Figure 1. Index of per capita reproduction versus adult abundance in 13 colonies of passalid beetles.

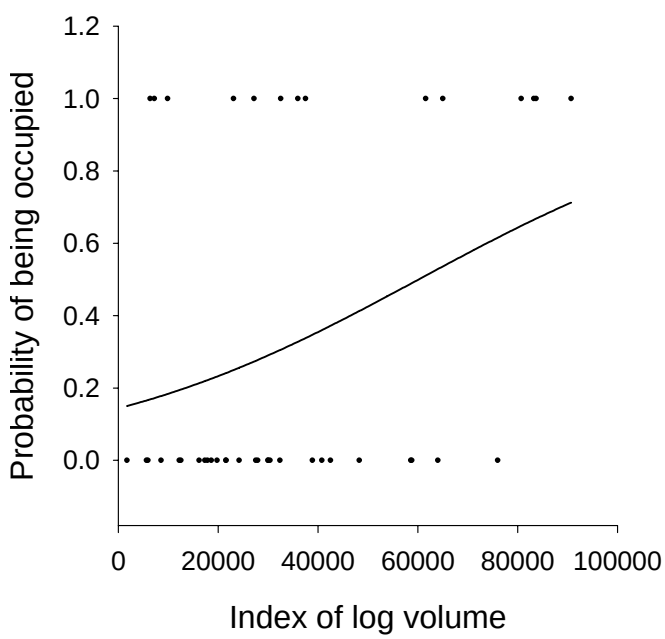

Figure 2. Index of log volume versus probability of being colonized by passalid beetles. Points show observations. Line shows best fit logisitic function.

Discussion

Because both species of passalids occupy the same environment, one might expect them to separate themselves in order to minimize competition. However, the tendency was for them to co-occur. This could be due to a feeding chain commensalism, in which sp. B breaks down wood to a finer particulate, which is then a better resource for sp. A. Alternatively, sp. B may benefit from sp. A. For example, sp. B might prefer logs that have already been colonized (and partly processed) by sp. A. In this case, sp. B might be functioning like a parasite.

Because our index of per capita reproduction did not vary with population density, populations of sp. A within logs appear to lack any density dependent feedbacks (positive or negative) to their population dynamics. The absence of resource limitations (negative feedback) was further supported by the lack of relationship between colony size and log size. One possible explanation is that natural enemies commonly limit populations of passalid beetles to such low abundances that resources are not limiting. The metapopulation structure of passalid beetles suggests an alternative explanation. It is possible that the prevailing processes of population dynamics of the passalids are different at the subpopulation and metapopulation levels. At the level of a log, it may be that local extinction probabilities are high relative to population growth rate, and that immigration and emigration are the prevailing processes. Presumably, negative density dependence and population regulation must arise at some spatial scale, but

maybe this is at the level of the entire metapopulation of passalid beetles on the mountainside, where birth and death rates must become the prevailing processes rather than immigration and emigration.

One limitation of this study was our inability to study large logs (i.e. fallen tree trunks) which may represent a significant portion of suitable habitat for passalid populations.

Contrary to predictions based upon dispersal limitations, the amount of surrounding habitat did not vary between colonized and uncolonized logs. This suggests that dispersal is not a limiting factor in beetle distribution at the scale of a 5 m radius. However, 65% of the logs that we judged to be suitable habitat were uncolonized. Because larger logs had higher probability of being occupied than smaller logs, it seems possible that dispersing beetles prefer larger logs, or that extinction rates are lower in larger logs. We also note that colonization probabilities were related to log volume (Fig. 2) but not to the shadow areas of logs. This suggests that all three dimensions of resource patch size play a role in the probability of colonization and/or local extinction rates.

Overall, our results suggest that examining the demographics of subpopulations may not give an accurate representation of the full population. While passalid reproduction seems to be independent of density within a log, studies of the metapopulation might still reveal density dependent feedbacks.

LITERATURE CITED

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