

An evolutionary explanation of the aggregation model of species coexistence

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In ecology, the 'aggregation model of coexistence' provides a powerful concept to explain the unexpectedly high species richness of insects on ephemeral resources like dung pats, fruits, etc. It suggests that females aggregate their eggs across resource patches, which leads to an increased intraspecific competition within occupied patches and a relatively large number of patches that remain unoccupied. This provides competitor-free patches for heterospecifics, facilitating species coexistence. At first glance, deliberately causing competition among the females' own offspring and leaving resources to heterospecific competitors seems altruistic and incompatible with individual fitness maximization, raising the question of how natural selection operates in favour of egg aggregation on ephemeral resource patches. Allee effects that lead to fitness maxima at intermediate egg densities have been suggested, but not yet detected. Using drosophilid flies on decaying fruits as a study system, we demonstrate a hump-shaped relationship between egg density and individual survival probability, with maximum survivorship at intermediate densities. This pattern clearly selects for egg aggregation and resolves the possible conflict between the ecological concept of species coexistence on ephemeral resources and evolutionary theory.

Keywords: aggregation; Allee effect; competition; density dependence; *Drosophila*; egg-to-adult survival

1. INTRODUCTION

The spatial aggregation of competitors across food-limited resource patches has been shown to be a major determinant of local species coexistence (e.g. Atkinson & Shorrocks 1981; Ives 1988; Shorrocks & Sevenster 1995; Hartley & Shorrocks 2002). By aggregating with conspecifics in a few patches, superior competitors create partial refuges allowing inferior species to exist in patches with few or no heterospecific competitors. Consequently, an increase in intraspecific competition relative to interspecific competition is a fundamental feature of the 'aggregation model of species coexistence' (Shorrocks *et al.* 1984).

This ecological mechanism has been widely accepted as the underlying mechanism for the maintenance of local species diversity in insect communities exploiting ephemeral resource patches, e.g. decaying plant tissues, dung pads, mushrooms and carcasses (Atkinson & Shorrocks 1984; Kouki & Hanski 1995; Heard 1998; Woodcock *et*

al. 2002). In the light of maternal oviposition behaviour, however, the active aggregation of offspring seems to contradict the evolutionary thinking of individual fitness maximization (Tokeshi 1999). From a Darwinian point of view, it is unclear why dominant species accept the increased risk of intraspecific competition rather than competing against inferior species in less densely occupied substrate patches.

It has been suggested that insects on ephemeral resources have acquired the tendency to aggregate their eggs (with conspecifics) because offspring perform better when feeding in groups of larvae (Hoffmeister & Rohlf^s 2001; Wertheim *et al.* 2002b). This implies the existence of so-called Allee effects (Godfray *et al.* 1991; Stephens *et al.* 1999), which reduce fitness at low densities, thus resulting in a positive relationship between fitness and density. By contrast, competition usually increases with density and consequently leads to a negative relationship between fitness and density. Allee effects have the potential to outweigh the effects of competition (Stephens *et al.* 1999), and thus important larval fitness components may be maximal at intermediate densities. Hence, Allee effects can act as a selective force favouring aggregated egg distributions (Godfray *et al.* 1991).

Although evidence is accumulating for intraspecific aggregation as one important control of species coexistence in the vast group of insects that exploit ephemeral resources, the ultimate controls (e.g. Allee effects for larval development) that maintain these spatial patterns have not yet been detected in these ecological communities. With the following experiment on the density-dependent survival of *Drosophila*, we aimed to elucidate why insects show maternal behaviours that lead to offspring aggregation, when the negative effects of competition typically increase with density.

2. METHODS

We used the vinegar fly *Drosophila subobscura*, a dominant species in European fruit-breeding *Drosophila* communities, as a model species to investigate the density-dependent developmental success of fly larvae on decaying specimens of three fruit types (sloes (*Prunus spinosa*), Syrian plums (*P. domestica* ssp. *syriaca*) and common plums (*P. domestica*). All of these fruit types are known to constitute a suitable breeding site for *D. subobscura* under field conditions (M. Rohlf^s, personal observation). The fruits were directly collected from the trees or bushes and stored deep-frozen at -18°C . We used a *D. subobscura* strain that originated from a local fly population in Northern Germany (54°N , 10°E). Fly populations were reared on an artificial medium at $18-20^{\circ}\text{C}$, and at a 16 h photoperiod (see Hoffmeister & Rohlf^s 2001).

Approximately 5% of the skin of the experimental fruits was removed to provide an adequate site for egg laying. To obtain a huge range of different egg densities, the experimental fruits were exposed to populations of flies (100–150 specimens) over a period of 1–18 h under constant laboratory conditions ($18 \pm 1^{\circ}\text{C}$, 16 h photoperiod, ca. 70% humidity). The individuals in the populations were 10–15 days old (younger flies do not carry sufficient egg loads to oviposit) and had been supplied with water, sugar and dried brewer's yeast. After we had counted the eggs, each fruit was singly transferred to a translucent plastic tube (10 cm high, 4.5 cm diameter) containing an agar layer (ca. 2 cm) to prevent an early desiccation of the substrates. The tubes were sealed with foam rubber and incubated at $18 \pm 1^{\circ}\text{C}$ and a 16 h photoperiod. For at least three months, we recorded the number of emerging adults as a function of initial egg density for each singly incubated fruit.

We analysed the relationship between the individual survival probability and egg density with generalized linear models (GLM) (SAS v. 8.2, PROC GENMOD, with dscale option as the scaled deviance widely differed from unity). Because survival was measured as a binomial response (emerging versus non-emerging adults), model fitting was carried out with a binomial error distribution and a logit link function. Egg density was $\ln(\text{egg density} + 1)$ -transformed to buffer against strong statistical effects of few data points at very high egg

Table 1. The explanatory power of the first- and second-order term of initial egg density on egg-to-adult survival in *Drosophila subobscura* on three fruit species.

explanatory variable	<i>F</i> -value	<i>p</i>
sloes		
ln(egg density + 1)	$F_{1,119} = 14.63$	0.0002
(ln(egg density + 1)) ²	$F_{1,119} = 21.59$	< 0.0001
Syrian plums		
ln(egg density + 1)	$F_{1,103} = 13.52$	0.0004
(ln(egg density + 1)) ²	$F_{1,103} = 23.70$	< 0.0001
common plums		
ln(egg density + 1)	$F_{1,104} = 19.77$	< 0.0001
(ln(egg density + 1)) ²	$F_{1,104} = 30.83$	< 0.0001

densities (Wertheim *et al.* 2002b). The model-fitting procedure involved fitting a model of the form:

$$\text{survival} = \beta_0 + \beta_1 \ln(\text{egg density} + 1) + \beta_2 (\ln(\text{egg density} + 1))^2,$$

where β_0 is a constant, and β_1 and β_2 estimate the linear and the quadratic components of the survival function, respectively. The second-order term of egg density was included to capture curvilinear relationships between initial egg density and survival, such as hump-shaped relationships, i.e. an Allee effect for larval development. This procedure provides an analysis of the contribution of each explanatory variable to the total deviance of the model, which can be tested for significance because deviance has a *F*-distribution. The *F*-values indicate whether a removal of an explanatory term causes a significant increase in deviance of the model.

3. RESULTS

For all fruit types, the best fit to the data was obtained by nonlinear statistical models because the removal of the second-order terms significantly decreased the predictive value of the models (table 1). The models describe an initial increase in the egg-to-adult survival probability with increasing egg density and maximum survival probability at intermediate egg densities (figure 1). By setting the first derivative to zero, survival probabilities were found to be maximal for an egg density of 8.9 on sloes, 17.0 on Syrian plums and 19.0 on common plums. A further increase in egg density beyond these maxima leads to a decline in the egg-to-adult survival (figure 1). In a model including fruit type as well as first- and second-order terms for egg density, fruit type significantly influences the survival probability of fly larvae (GLM: $F_{2,330} = 50.68$, $p < 0.0001$), with plums increasing survival probability by a factor of 1.14 ($p < 0.0001$) and Syrian plums by a factor of 1.5 ($p < 0.0001$) compared with sloes. This influence indicates differences in the quality and quantity of the breeding substrate. Despite these different quantitative effects of fruit type on the developmental success of fly larvae, the hump-shaped relationship between egg density and survival probability is strikingly constant (figure 1). These results indicate the existence of Allee effects for larval development on each type of fruit substrate used in this study.

4. DISCUSSION

Mechanistic and functional explanations for the association of conspecifics in insects have repeatedly attracted the attention of entomologists (e.g. Courtney *et al.* 1990; Prokopy & Roitberg 2001) and the aggregation model of coexistence has provided a unifying framework for the effects of such intraspecific associations on the coexistence of

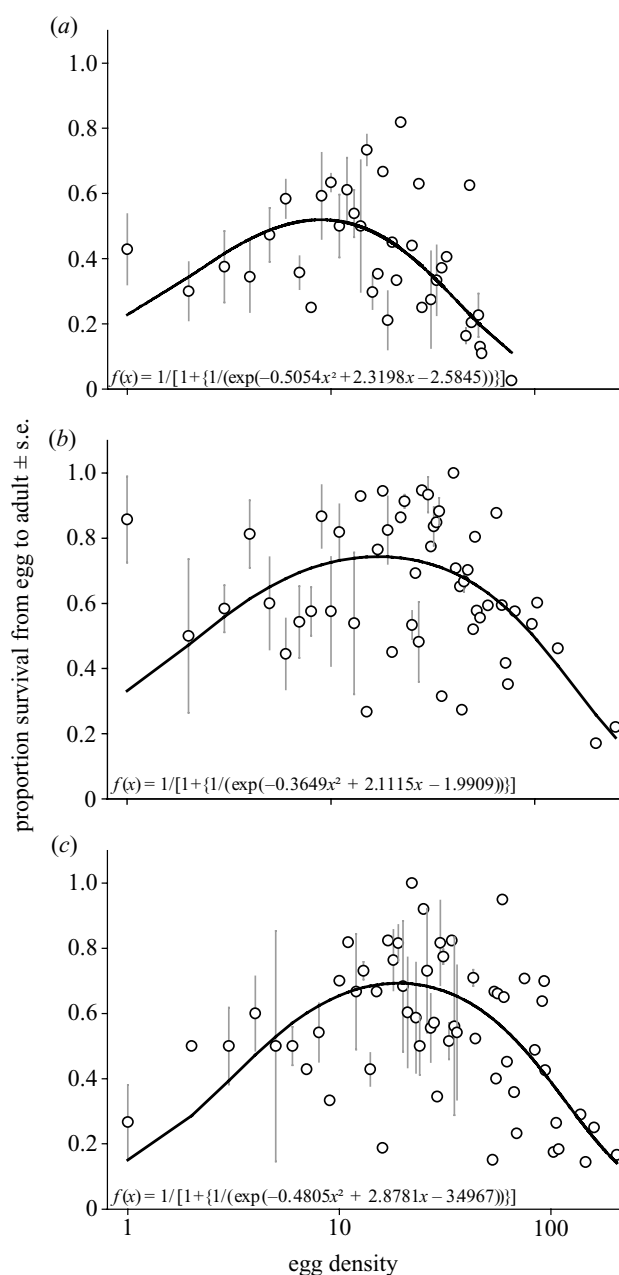


Figure 1. The proportional survival from egg to adult in *Drosophila subobscura* as a function of initial egg density (eggs per fruit), for decaying (a) sloes, (b) Syrian plums and (c) common plums. For better visibility, replicated egg densities are shown as means (\pm s.e.). To obtain the egg densities at which survival is maximized, the following first derivations were taken: sloes: $f'(x) = -1.0108x + 2.3198$; Syrian plums: $f'(x) = -0.7298x + 2.1115$; common plums: $f'(x) = -0.9610x + 2.8781$. x represents $\ln(\text{egg density} + 1)$ (see § 2). Note that the log-scale of the x -axis is only for better visibility, and that the statistical analysis was performed on $\ln(\text{egg density} + 1)$ -transformed data.

competing species (Atkinson & Shorrocks 1981; Shorrocks & Sevenster 1995). However, it has only recently been suggested that Allee effects for larval development may ultimately facilitate species coexistence in insect communities on ephemeral resources (Hoffmeister & Rohlf 2001; Wertheim *et al.* 2002b). Despite the fact that individual oviposition decisions of *D. subobscura* females lead to aggregated egg distributions, strong contest competition

was the only density-dependent effect on egg-to-adult survival on decaying rowan berries (Hoffmeister & Rohlfis 2001). Similarly, *D. melanogaster* larvae were found to suffer from directly density-dependent competition on pieces of apples (Wertheim *et al.* 2002b).

By contrast, the present study clearly demonstrates Allee effects on a demographic level, where larval survival reaches a maximum at intermediate competitor density (figure 1). Thus, the developmental success of *D. subobscura* larvae on various decaying fruits is not only determined by competition, because then the egg-to-adult survival would have shown a monotonic decline with increasing egg density. Density-dependent competition certainly does affect larval development on the substrates in this study, but the hump-shaped relationship between survivorship and egg density (figure 1) indicates that Allee effects can be more important than competition at lower larval densities. Because the survival functions around the maximum are not very steep, flies may produce egg densities that are four eggs smaller or eight eggs larger than optimal on sloes, 11 eggs smaller or 30 eggs larger than optimal on Syrian plums, and 11 eggs smaller or 24 eggs larger than optimal on common plums without losing more than 10% of the optimal survival probability (figure 1). Thus, within a relatively broad range of egg densities, egg aggregation can be regarded as a benefit to the larvae, whereas very high as well as very low densities reduce egg-to-adult survival.

The fact that demographic Allee effects have rarely been discovered in other studies (Hoffmeister & Rohlfis 2001; Wertheim *et al.* 2002b; but see Courtney *et al.* 1990) clearly demonstrates the problem that positive interactions through group living in *Drosophila* larvae depend on multiple features of the larval habitat and the maternal behaviour of flies. Wertheim *et al.* (2002b) have shown that the component Allee effect found in their study was caused by the presence of several females that visited a patch. Thus, the benefits that accrue from selecting resource patches that already contain conspecifics (Wertheim *et al.* 2002a) vary with the patch characteristics (substrate features) and the density of conspecifics.

Moreover, the degree of egg aggregation on ephemeral patches was found to depend on the spatial distribution of breeding sites in the habitat, with larval aggregation increasing strongly and consistently with declining patch density (Heard 1998). Because individual clutch-laying behaviour determines the spatial distribution of larvae (Heard & Remer 1997; Hoffmeister & Rohlfis 2001; Hartley & Shorrocks 2002), maternal decisions of what clutch size to lay on the currently visited patch are affected by the resource density in the habitat. Therefore, resource limitation leads to the production of larger clutches at low patch densities, whereas an increase in the encounter rate with breeding sites reduces clutch sizes at high patch densities (Godfray *et al.* 1991; Heard & Remer 1997). However, our study clearly shows that resource limitation *per se* is not the only adaptive explanation for individual egg aggregation, but that Allee effects can drive the production of large clutches, even if breeding site density is very high and resource limitation can no longer account for raising the number of eggs in a clutch.

In the search for a mechanism that leads to Allee effects, the involvement of micro-organisms, such as yeasts, in the

density-dependent success of *D. melanogaster* larvae has been suspected (Wertheim *et al.* 2002a,b). Yeasts constitute the major food source for the immature stages (Begon 1982); in addition, yeasts have the potential to hamper the growth of (toxic) moulds that might be harmful to the larvae (Wertheim *et al.* 2002b). To achieve conditions that provide a demographic Allee effect, the presence of several ovipositing flies on a patch might be required (Wertheim *et al.* 2002b). However, some substrates will lack the quantity or quality of nutrients for a sufficient extent of microbial growth to support larvae from multiple egg clutches, such that intense competition overrides the influence of Allee effects (Hoffmeister & Rohlfis 2001; Wertheim *et al.* 2002b). Accordingly, it is necessary to consider a wide range of relevant environmental conditions to grasp all possible facets of aggregation in opportunistic insect communities. Although our results provide evidence of the adaptive value of intraspecific aggregation across ephemeral resource patches for several breeding substrates, it remains to be seen whether *Drosophila* flies usually encounter substrates on which Allee effects override competition.

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