

Unequal maternal investment in offspring quality in relation to predation risk

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Summary

Equal investment within broods does not always maximize parental reproductive value if the reproductive value of some of the young is low. We examined maternal investment in terms of offspring size in relation to the prospects of survival from predation within broods of the shield bug *Elasmucha ferrugata* Fabr. (Heteroptera; Acanthosomatidae). Shield bug females guard eggs and first instar nymphs against invertebrate predators by covering the clutch with their body and by behaving aggressively towards their enemies. Survival of eggs was not possible without maternal care. When females were allowed to guard their brood, eggs at the periphery were more vulnerable to predators than eggs at the centre. We found that females laid significantly larger eggs in the safest, central part of the clutch. There seems to be an advantage of large nymph size, since when nymphs were reared separately with low food resources, the larger ones were more likely to survive. Larger nymphs were also more likely to push themselves to the safest, central part of the clutch. Females seem to allocate their resources more to the offspring with the highest probability of avoiding predation. Thus our study supports unequal maternal investment within broods of *E. ferrugata*.

Keywords: *Elasmucha ferrugata*; offspring quality; predation; unequal parental investment

Introduction

Parents are expected to allocate their investment in relation to its benefits to their offspring and its costs to themselves to maximize their reproductive value in each breeding attempt (Trivers, 1972; Winkler, 1987). The reproductive value of the offspring generally increases with increasing parental investment (Smith and Fretwell, 1974). However, if the reproductive value of some of the young is low, parents might decrease investment to them, and so either increase the investment given to survivors or enhance their capacity for future reproduction (O'Connor, 1978; Tait, 1980; Gosling, 1986; Wright *et al.*, 1988; Haig, 1990). Thus equal investment within broods will not always maximize parental reproductive value (Temme, 1986; Haig, 1990). Differences in offspring quality have been shown to cause parental discrimination within broods in many species. This unequal allocation has been related to sex of offspring (e.g. Gosling, 1986), size and/or age of offspring (e.g. Drummond *et al.*, 1986), different developmental abnormalities (Stephenson and Winsor, 1986) and different ornamentation of chicks (Lyon *et al.*, 1994). In many cases, however, any active parental manipulation is difficult to separate from sib competition.

Elasmucha ferrugata Fabr. (Heteroptera; Acanthosomatidae) is a quite rare shield bug species in Northern Europe (Strawinski, 1951). Females lay an average of 35 eggs in a compact clump on the lower surface of bilberry leaves. The number of eggs in a clutch varies little between females, but egg

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size varies widely between females and also within clutches (A. Kaitala and J. Mappes, unpublished data). After oviposition, females settle over the clutch and defend eggs and small nymphs until the nymphs hatch to second instar stage (Strawinski, 1951; A. Kaitala and J. Mappes, unpublished data). About 46% of females are able to lay another clutch in Central Sweden, though fewer do so in Finland (A. Kaitala and J. Mappes, unpublished data). Both nymphs and adults suck liquids from berries. When disturbed, females press themselves tightly against the eggs and rotate their body against predators (J. Mappes *et al.*, unpublished data). Survival of eggs and nymphs probably depends crucially on active female defence against predators. However, the efficiency of defence may not be equal in all parts of the clutch or aggregation, and offspring in the centre of a group are generally supposed to enjoy better security than individuals at the periphery, in accordance with the selfish-herd hypothesis of Hamilton (1971). Thus there is strong reason to expect maternal control of offspring production in this species in relation to egg quality and site in the clutch.

The questions posed in this study were as follows: (1) How much does a female benefit from guarding her brood? (2) Do offspring in the centre enjoy greater security? If yes, (3) does a female invest more to offspring in the centre than offspring at the periphery of the clutch?

Materials and methods

Benefit of maternal care

To establish the adaptive value of maternal care of *E. ferrugata*, we undertook the following experiment. We collected 24 females and their clutches of eggs by taking a whole bilberry branch from Miehikkälä, south-eastern Finland on 10 June 1993. Females were marked individually and randomly divided into control ($n = 14$) and experimental ($n = 14$) groups. The number of eggs in each clutch were counted. Females in the experimental group were taken away from their eggs, whereas the females in the control group were allowed to guard their clutches. Then the females with their clutches (control group) or eggs only (experimental group) were placed at random in a small forested area near the Tvärminne Zoological Research Station. In this area there is only a thinly settled natural *E. ferrugata* population. Bilberry twigs with the eggs and females were placed in plastic cups that were filled with water and litter. The cups were placed in the ground, thus allowing predators access to the bilberries. The experimental area was checked every day and the number of eggs in the experimental clutches counted. We also checked to see whether the females in the control group were still guarding their eggs. When the eggs began to hatch, they were moved to the laboratory to count how many nymphs were left in each group. We also noted the number and location of undeveloped eggs in each brood.

Predation risk at the centre and periphery of the clutch

We assessed whether predation risk varies among eggs within the clutches of *E. ferrugata*. We collected 11 females with their eggs. We removed the females and counted their eggs, marked on a 'map' the positions of individual eggs in each clutch, and then repositioned the females back over their eggs. To manipulate direct effects of predation, females with eggs were placed close to the laboratory nests of *Formica uralensis*. The ants, including several old queens, were housed in a laboratory nest made of ceramic flowerpots filled with material from the original nest (for further details, see Pamilo, 1982). During the predation trials, the ants were not provided with their standard diet. This led to slight protein starvation, which encouraged attacks against brood guarding females. The trial lasted 2 h, after which we counted how many eggs had been eaten at the centre and periphery of the clutch, where the periphery covered the outermost eggs and the centre the six innermost eggs.

Unequal maternal investment

We examined the investment of offspring size in relation to their location within the brood both at the egg and nymph stages. Females were collected close to Stockholm, Central Sweden before the breeding season at the beginning of June 1992. Females together with a male were kept in cages (20 × 15 × 30 cm) containing a fresh bilberry plant with plenty of berries in a light-to-dark ratio of 20:4 h. Six eggs from the centre and six eggs from the periphery of the clutches (as defined above) of eight females were carefully separated from each other with the help of a thin needle and paintbrush. The eggs were weighed using a microbalance to 0.001 mg accuracy 1 day after oviposition, thus ensuring that any micro-climatic differences between the eggs (e.g. humidity) did not affect their weight. The eggs at the periphery were chosen at random from the outermost eggs.

In 1993, another group of females ($n = 12$) and their eggs were collected from around Miehikkälä, south-eastern Finland. The eggs were reared and, immediately after hatching and before becoming nymphs, the 6 innermost and 12 outermost nymphs were weighed using a microbalance. We also noted the number and location of undeveloped eggs in each brood.

Sib competition

We examined the effect of body size on nymphs' ability to compete with their sibs. We used the later stages of first instar nymphs from the above experiment. Nine nymph groups were formed from five different broods. Each group contained 20 nymphs. Each group of nymphs was spread out and then allowed to aggregate again. After aggregation, 6 of the innermost and 14 of the outermost nymphs were weighted using a microbalance.

Egg size and survival

We also examined the effect of body size on nymphs' ability to survive with limited food resources. Females and males were collected around Stockholm in 1992 and pairs were kept in cages as above. After oviposition, the eggs were reared with the females still guarding them. All hatched nymphs ($n = 262$) of nine females were weighed. These nymphs were individually reared to adults in Petri dishes (10 cm diameter) covered with a net. The nymphs always had a fresh twig of bilberry to ensure humidity. Once a week, just one bilberry was provided for each Petri dish. Thus food was always available but not *ad libitum*.

Results

Benefits of maternal care

At the beginning of the experiment, the number of eggs in the clutches did not differ between the experimental (34.7 ± 2.0) and control (35.5 ± 1.3) groups (mean \pm s.d.). Two females in the control group deserted their clutches and thus were not included in the analyses. One female in the control group lost all of her eggs; at least 60% of the eggs hatched in the other 11 clutches. In the experimental group, 13 of 14 clutches were totally destroyed (Fig. 1). Thus survival of eggs without maternal care does not seem possible in this species. It is interesting to note that those eggs which did not hatch (injured or sterile eggs) seemed to come from the periphery of the clutch. This indicates that peripheral eggs were more vulnerable to predation.

Predation risk in the centre and at the periphery of the clutch

Eggs at the periphery were lost to predators significantly more often ($23.4 \pm 20.6\%$) than eggs from the centre of a clutch ($1.5 \pm 5.1\%$) (Wilcoxon's sign-test, $T = 0$, $n = 13$, two-tailed $P = 0.009$) (Fig. 2).

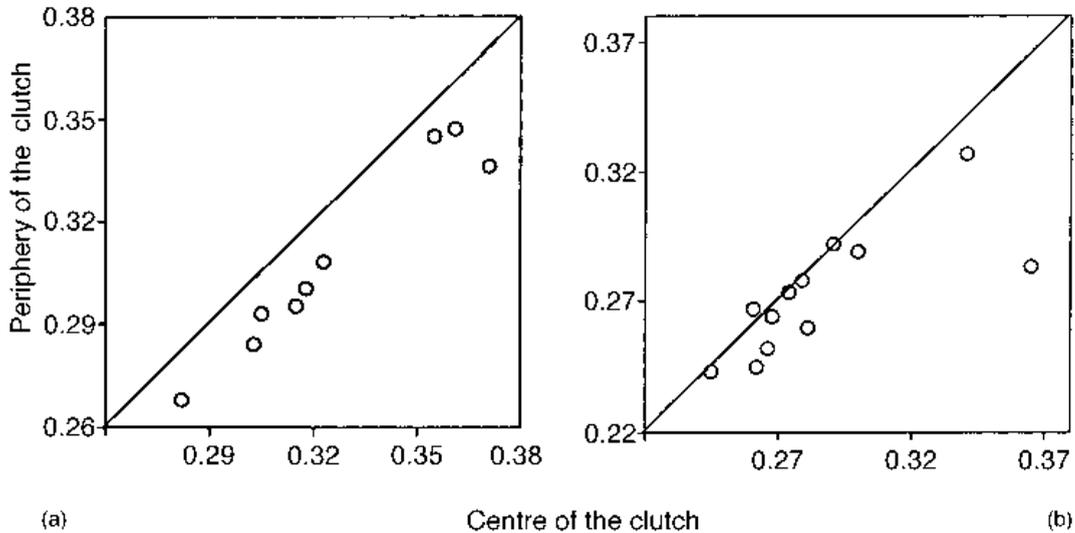


Figure 3. (a) Mean egg weight (mg) at the periphery and centre of the clutch. (b) Mean nymph weight (mg) (hatched first instar nymphs) at the centre and periphery of the clutch. Dots below the line show cases where mean egg or nymph weight at the centre was heavier than at the periphery of the clutch.

periphery (0.380 ± 0.017) (paired $t = 2.35$, two-tailed $P = 0.047$, d.f. = 8). Thus larger nymphs were found more often in the centre of the clutch and weaker individuals at the periphery.

Egg size and survival

Nymph survival at low food levels depended significantly on their size at hatching. Nymphs that survived were markedly heavier (mean weight of all survivors in brood) than nymphs that died (mean weight of all dead nymphs in brood) before reaching adulthood (paired $t = 3.85$, d.f. = 8, $P = 0.005$) (Fig. 4).

Discussion

Females of *Elasmucha ferrugata* seemed to invest selectively in offspring. Eggs in safe sites were larger than eggs at sites with a higher predation risk. Egg size and offspring size were shown to affect a number of fitness components, including hatching success, survival and growth of young (for a review, see Roff, 1992). In *E. ferrugata*, large nymphs seemed to be better able to compete for the best site in the aggregation than their smaller sisters. Larger nymphs may seek for themselves a central position in the aggregation by taking cover behind others. This may be important for nymph survival during the time when they aggregate under their mother's shield (Mappes and Kaitala, 1994). Large body size provided physiological benefit to the offspring also. The mortality of *E. ferrugata* nymphs decreased with increased hatching size. Thus individuals at the centre of a clutch experienced increased survival due to less predation pressure and better physiological conditions.

The pressure from predation appeared to be great and almost all females lost some eggs to predators. In addition, 93% of experimental broods without females were destroyed (Fig. 1). The type of maternal care in *E. ferrugata* makes equal safety for each offspring impossible. Females are forced to lay a number of eggs on the edge of the clutch where they are more vulnerable to

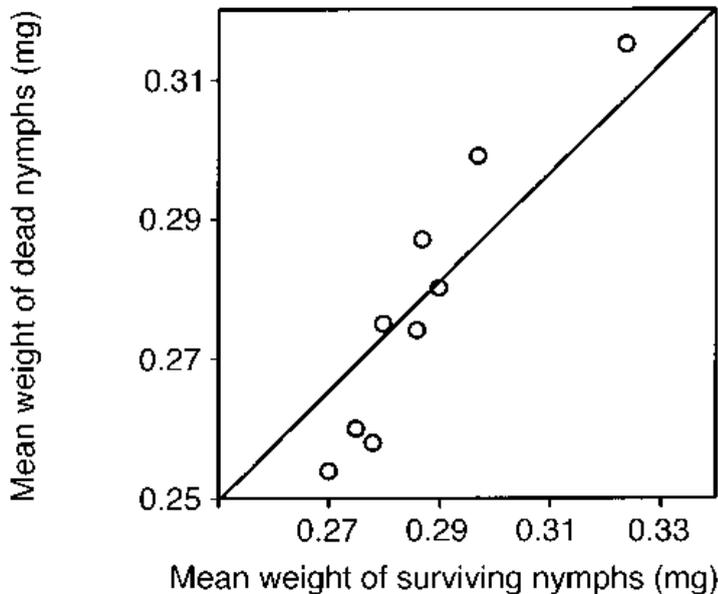


Figure 4. Mean weight (mg) of nymphs that survived and nymphs that died.

predation (see Odhiambo, 1959; Eberhard, 1975). If reproduction is costly for *E. ferrugata*, it might be beneficial for females to reserve resources for the guarding period and future reproduction. Thus the observed variation in size within broods might be adaptive. The maternal manipulation of *E. ferrugata* resembles the situation in the assassin bug *Rhinocoris tristis*, where males guard their brood against parasites. Males reduce their own energetic costs of care by selectively eating the eggs on the periphery of the brood (i.e. filial cannibalism). In this species, the eggs at the periphery are parasitized more often than the innermost eggs (L. Thomas, personal communication).

The present results support the idea that parents should allocate resources economically among offspring (O'Connor, 1978; Tait, 1980; Gosling, 1986; Wright *et al.*, 1988; Haig, 1990). In contrast to earlier studies, in which parents favoured offspring of high quality (Drummond *et al.*, 1986; Stephenson and Winsor, 1986; Lyon *et al.*, 1994), females of *E. ferrugata* decide before hatching which of their brood are most likely to survive predators. In *E. ferrugata*, risk of predation is more than ten times higher for offspring at the periphery of the clutch than for the offspring at the centre. Thus we suggest that predation selects for active maternal manipulation in favour of the offspring of the highest reproductive value.

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