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Johanna Mappes

Maternal Care and
Reproductive Tactics
in Shield Bugs

UNIVERSITY OF JYVÄSKYLÄ

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To my family

ABSTRACT

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Yhteenvedo: Jälkeläishoito ja lisääntymistaktiikat *Elasmucha*-suvun luteilla.

Diss.

Parental care is an important life-history tactic in many species of Heteroptera. In Finland there are three *Elasmucha* (Heteroptera; Acanthosomatidae) species all of which show maternal care. These bugs lay different numbers of eggs in tight clusters and after egg laying females stay over their clutches and protect them against predators. Egg survival without maternal care is close to zero. Among *Elasmucha* species, females have different tactics in terms of egg size, egg number and duration of parental care. *E. ferrugata* laid few large eggs which developed rapidly and duration of maternal care was short. In addition, females allocated more resources to the offspring in the center of the clutch, where predation risk is lowest. *E. ferrugata* was the only species which could lay a second clutch after a successful first brood. *E. grisea* laid many small eggs with a long development time from egg to adult. Thus, *E. grisea* guarded their clutches relatively long and were not able to lay another clutch. Female ability to defend a clutch is limited by the clutch area she is able to cover. Small females guarding experimentally enlarged clutches lost significantly more eggs than large females guarding small clutches. Small females did not get any benefits from extra eggs they were guarding and thus, each female seemed to lay an optimal clutch size as determined by her defending ability. Parent bugs selected their host birch in relation to its safety from any predators, and thus they enhanced greatly survival of progeny. Parent bug females sometimes guard their clutches jointly on the same birch tree. Joint guarding was clearly advantageous in the experiment where it was compared to single guarding. Females that jointly guarded their clutches lost fewer eggs to predators than single females.

Key words: Egg size; *Elasmucha*; parental care; reproductive tactics.

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This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

- I Kaitala, A. & Mappes, J. 1994: Parental care and reproductive trade-offs in shield bugs. - (Manuscript).
- II Mappes, J. & Kaitala, A. 1994: Experiments with *Elasmucha grisea* (Heteroptera: Acanthosomatidae): does a female parent bug lay as many eggs as she can defend? - Behavioral Ecology 3: 314-317.
- III Mappes, J. & Mappes, T. 1994: Unequal maternal investment in offspring quality in relation to predation risk. - Evolutionary Ecology 1997, 11, 237-243.
- IV Mappes, J. & Kaitala, A. 1994: Host-plant selection and predation risk on offspring in the parent bug. - Ecology, Vol. 76, No 8 (Dec., 1995), 2668-2670.
- V Mappes, J., Kaitala, A. & Alatalo, R.V. 1994: Joint brood guarding in parent bugs - an experiment on defence against predation. - Behav. Ecol. Sociobiol. (1995) 36: 343-347.
- VI Mappes, J. 1994: Parasites and female ability to defend offspring in the parent bug *Elasmucha grisea*. - Ethology 97: 76-80.

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1 INTRODUCTION

Parental care is defined as "any form of parental behaviour that increases the fitness of a parent's offspring" (Clutton-Brock 1991). Thus, parental care in its broadest sense includes any form of parental behaviour from production of the sex cells to offspring feeding (see Trivers 1972). In its narrowest sense, parental care includes only the care of eggs or young after they have detached from the parent's body (Clutton-Brock 1991).

For parental care to evolve, the principal benefits of care must be higher than costs of parental care (Tallamy & Denno 1981, 1982, Tallamy & Wood 1986). The benefits of parental care to the care-givers arise from the better survival, growth and breeding success of the progeny. Measuring costs of parental care is more difficult, since offspring may not survive without care (Clutton-Brock 1991). Costs of parental care can be physiological or ecological (Sibly & Calow 1984). Ecological (direct) costs can be caused e.g. by parents increasing vulnerability to predation or parasitism during the different breeding actions (Lack 1966, 1968, Shine 1980, Tallamy 1984). Physiological costs (indirect or absorption costs) refer to the fact that time and energy which is invested to one offspring decreases investment in others, this means that there may be a trade-off between current and future reproduction (Williams 1966, Bell 1980, Tallamy & Denno 1982).

The benefits of parental care in improving offspring survival are frequently evident particularly among species in which offspring number is low and where offspring mortality without parental protection would be very high (Clutton-Brock 1991). How is the evolution of parental care understandable among insects in which selection seems to favour production of a large number of eggs and where parents seldom are able to protect their young effectively against predators (Zeh & Smith 1985,

Tallamy & Wood 1986, Clutton-Brock 1991)? Parental care has evolved repeatedly in 19 insect orders (Zeh & Smith 1985, Nafus & Schreiner 1988) and it is the most primitive form of sociality in insects (Bequaert 1935, Eickwort 1981, Tallamy 1984). Parental care is most common and most developed among Coleoptera (beetles), Embioptera (web spinners), Heteroptera (true bugs), Hymenoptera (ants, wasps and bees), Isoptera (termites) and Thysanoptera (thrips) (Wilson 1971, Eickwort 1981, Tallamy & Wood 1986). Several preadaptations are probably needed for the evolution of parental care. For example, adult mortality must be low, because caring parents have to survive over the whole caring period (Tallamy 1984). Furthermore, offspring must be group living (Wilson 1975, Tallamy 1984) and some kind of signalling between caring parent(s) and offspring is probably needed. These preadaptations are found in the maternal *Elasmucha* (Heteroptera: Acanthosomatidae) species (Table I). Several unfavourable abiotic factors, such as oxygen deprivation, seem to favour parental care. In such conditions offspring survival could not be possible without specialized parental behaviours to ensure the survival of offspring (Wyatt 1986). Insect parental care is also associated with rich but often patchy habitats where, however, presence of predators (Tallamy & Denno 1981, Hardin & Tallamy 1992, Melber & Schmidt 1975a, Kudó et al. 1989) or parasites (Odhiambo 1959, Eberhard 1975) increases juvenile mortality, or intense competition of conspecifics requires parental defence of resources (Milne & Milne 1976, Windsor 1982) (Table I).

TABLE 1 Life historical preadaptations for parental care in *Elasmucha* (Heteroptera; Acanthosomatidae) species.

Preadaptation	Reference
Sufficient adult longevity	(I), (VI)
Egg clustering in time and space	Melber & Schmidt 1975b, (I)
Group living	Melber & Schmidt 1975b, (I)
Specific parental behaviour	Melber & Schmidt 1975b, Melber et al. 1980, (VI)
Environmental characters	Reference
High juvenile mortality without parental care	Melber & Schmidt 1975a, Melber et al. 1980, (II), (IV)
Food resources locally abundant	(IV)

Predation (and parasitism) is perhaps the most important single force that has selected for parental care in insects. For example studies on lace bugs *Gargaphia solani* (Tallamy & Denno 1981) and *G. tiliae* (Hardin & Tallamy 1992), and shield bugs *Elasmucha grisea*, *E. fieberi* (Melber & Schmidt 1975a) and *E. dorsalis* (Kudó et al. 1989) have shown that offspring mortality is relatively low when caring parent(s) is present. Despite parental care, breeding may still be risky. Ability of parents to effectively defend their broods against predators may be limited. Insects are small in size and they are always in risk to meet superior predators. Moreover, many species (e.g. all *Elasmucha* species) guard their brood by "sitting" over it and, thus, physically protect offspring from predators (see also Odhiambo 1959, Eberhard 1975). Thus, type of parental care may cause constraints to the offspring number female is able to successfully guard, and the most productive clutch size (Lack's clutch size) (Lack 1947, 1954) in these species is probably the clutch female is able to defend against predators.

A clutch can consist of many small eggs or few large ones. This trade-off has been of central importance in the evolution of propagule size, and there is considerable evidence that large egg size incurs a selective advantage (Johnson 1982, Harvey 1985, Solbreck et al. 1989, Solbreck et al. 1990, Tauber & Tauber 1987, Tauber et al. 1990). Factors potentially affecting egg size in parental insects are female condition, amount of parental care and developmental time of the offspring. These factors are found to correlate with propagule size in many taxonomic groups (Roff 1992). Egg size may be under direct control of female or may be a consequence of competition between the propagules themselves for limited resources. Egg size may also vary within the brood. Such variation may be a consequence of position within the ovary (Telfer & Rutberg 1960, McKeown et al. 1976) but variation may also be adaptive. Variation in propagule size has been suggested to be a response to environmental heterogeneity (Janzen 1977, Capinera 1979, Kaplan 1980, Crump 1981, Nussbaum 1981, Westoby 1981, Stamp & Lucas 1983, Thompson 1984) or a consequence of unequal maternal investment to offspring of different quality (Temme 1986, Haig 1990). However, empirical support for these hypotheses is ambiguous, since in particular in animals experiments on these questions have been difficult to carry out.

The central theoretical framework for explaining the patterns in insect parental care is well documented (Wilson 1971, Tallamy 1984, Table I), but the knowledge about the importance of different mechanisms is still at its infancy and empirical tests are badly needed. To understand the diversity in insect subsocial behaviour we have to study variation in the type and amount of parental care and selective forces that

affect offspring number and quality. In this dissertation I studied maternal care and reproductive tactics in shield bugs (Heteroptera; Acanthosomatidae). I studied comparatively investment between size and number of offspring (trade-off between number and quality) and investment between current and future reproduction (I). I also applied Lack's (1947, 1954) hypothesis about optimal clutch size for birds by asking if shield bugs lay as many eggs as they can defend (II)? I studied causes and consequences of within brood variation in egg size (III). I experimentally studied host plant choice (IV) and female aggregations in terms of predation risk (V). Finally, I studied costs of parasitism to females during maternal care (VI).

2 MATERIAL AND METHODS

2.1 Shield bug species and the study areas

The shield bugs belong to family Acanthosomatidae which is a small family in Heteroptera. Sometimes it is regarded as a subfamily of Pentatomidae. Acanthosomatidae are called shield bugs, from their general shape or stink bugs because many species emit pungent fluids when alarmed (Chinery 1993). Parental care is known at least in two genus of Acanthosomatidae: In genus *Elasmucha* in Europe (Jordan 1958), Japan (Tachikawa 1971) and North America (Thomas 1991) and in genus *Meadorus* in North America (Frost & Haber 1944). In Finland three *Elasmucha* species show parental care of eggs and nymphs. These species of shield bugs were used in the experiments of this thesis:

1. The parent bug *Elasmucha grisea* is a common shield bug in Northern Europe (Jordan 1958). It is common in southern parts of Finland and its area of distribution reaches up to the latitude 62° (Linnavuori 1967). In Finland a female parent bug lays one clutch of 40 to 58 (mean 50) eggs usually on the lower surface of birch leaves (*Betula* sp.) in the beginning of June (I). After oviposition the female covers the clutch with her body and defends the eggs and developing nymphs by rotating and tilting her body, fanning wings and attacking invertebrate predators until nymphs hatch to fourth instar (Melber & Schmidt 1975b, Maschwitz & Gutmann 1979, Melber et al. 1980, I). Both adults and nymphs suck liquids of developing seeds of birch (Jordan 1958). Adult bugs probably overwinter in ground litter or under the bark of trees (I).

2. *E. fieberi* has a somewhat more northerly distribution, and it has type of maternal care than *E. grisea* (I). *E. fieberi* lays 30 to 50 (mean 40) eggs on the birch leaves but prefers *B. pubescens* as the host over *B. pendula* while *E. grisea* prefers *B. pendula* (I).

3. *Elasmucha ferrugata* Fabr. (Heteroptera; Acanthosomatidae) is a rare shield bug species in northern Europe (Strawinski 1951). In Finland it is found only in the southeastern parts in moist spruce forests. Females lay an average of 35 eggs in a compact clump on the lower surface of bilberry leaves. After oviposition females settle over the clutch and defend eggs and small nymphs until nymphs hatch to 2nd instar stage (Strawinski 1951, I). Both nymphs and adults suck liquids from berries. When disturbed, females press themselves tightly against the eggs and rotate their body against predators, but they may also fall down after heavy disturbance. This is a different to *E. grisea* and *E. fieberi* that do not leave their clutch even when meeting a superior predator (I).

These studies have been carried out at the Tovetorp Ethological Research Station, Central Sweden in 1992 (I, II, VI) and Tvärminne Zoological Research Station, Southern Finland in 1993 (I, III, IV, V) both in the field (II, IV, V) and in the laboratory (I, II, III, V, VI).

2.2 Laboratory studies

To obtain precise information about life-history traits such as development time from egg to adult and duration of maternal care in *Elasmucha* species we reared them in laboratory (I). The female-male pairs were kept in cages (20cm * 20cm * 30cm) in a laboratory under long day conditions (20h L 4h D and 22±1 °C). Each cage was provided with a fresh branch of birch or bilberry with many catkins or berries, respectively. These branches were changed approximately every third day. Matings, dates of egg laying, brood guarding and hatching to next instars were recorded without disturbing animals. Nymph survival in relation to their hatching size (III) was studied by rearing the nymphs individually to adulthood in petri dishes (10 cm diameter) covered by nets.

We measured size of females (breadth of the widest part of prothorax) under a Wild M3 stereo microscope by using 20x magnification to the accuracy of 0.1mm. Weight of females was measured by the analytical balance to the accuracy of 0.1mg. Individuals for experiments II, IV and V were also individually marked with spots on the thorax with a silver pen.

To be able to study how female body size affects clutch size and egg weight in *Elasmucha* species, we studied these relationships in

laboratory (I, II). All females were kept under conditions described above. Thus, possible variability in resources, predation and some abiotic factors such as temperature or day length could not affect the results. One day after the oviposition the number of eggs in the clutch was counted. The weight of eggs was estimated by the mean egg mass of five individually weighted eggs using a micro balance to the accuracy of 0.001mg. The mass of eggs and nymphs in relation to their site in the brood (III) was studied weighing each egg or nymph individually.

2.3 Experimental studies on predation risk

Very many birches which contain abundant numbers of catkins are not favoured for breeding by parent bugs. Therefore, we made an experiment on selection of oviposition site in relation to predation risk and breeding success of the parent bug. We collected female-male pairs; most of the bugs were copulating when they were collected. After marking we transplanted them back to the trees. "Control trees" were those trees which were naturally favoured by parent bugs. "Experimental trees" were those trees which did not have any bugs naturally, but where we transplanted bugs from control trees. We recorded the number of survivors from each tree. The number of ants which climbed upwards on the trunk were counted on each birch trunk to obtain precise information about predation risk in control and experimental birch trees (IV).

We manipulated clutch size by moving small and large females from their own eggs and gave them another clutch. In two control groups replacements were made within same sized groups. After the egg guarding period we counted survived eggs and number of females alive (II).

Parent bug females sometimes guard their clutches side by side on the same birch leaf. We hypothesized that females get some benefits for this joint guarding. In the field we compared clutch sizes in joint guarding versus single guarding females. In the laboratory, we studied the effectiveness of joint defence versus single defence against ant predators, *Formica uralensis*. We made female pairs from initially singly guarding females. In control groups, females singly guarded their eggs against same predator species. After the experiment we counted the number of survived eggs (V).

One cost for parental *Elasmucha* species may be an increased vulnerability to parasites. Brood guarding females may be easy targets for host seeking parasites. The specialist endoparasite *Subclytia rotundivertis* Fallén (Diptera; Tachinidae) uses the subsocial parent bug

Elasmucha grisea L. (Heteroptera; Acanthosomatidae). The parasite injects a single egg through the upper prothorax of female bugs and after hatching the larval parasites eat their host. We compared maternal responses and life span of parasitized and unparasitized females to disturbance in the laboratory. All the experimental females were guarding their second instar nymphs. Another set of experiments was made when nymphs were in the third instar stage (VI).

3 RESULTS AND DISCUSSION

3.1 Maternal care and reproductive trade-offs

Females of *Elasmucha* species differed from each other in how to share their time and energy between offspring number, quality and time of care. *E. ferrugata* laid a small number of large, fast developing eggs and guarded them only for a short time and *E. grisea* laid many, slowly developing, small eggs and guarded them longer. *E. fieberi* was intermediate in these life-history traits. Interestingly, time which nymphs had to spend alone did not differ among species (Figure 1). Accordance to hypotheses about life-history evolution (Tallamy & Denno 1982, Sibly & Monk 1987, Roff 1992) *E. ferrugata* that invested less to their brood in relation to total clutch mass and time of care was the only species that was able to lay another clutch after a successful first brood. Thus, there is a trade-off between offspring number, offspring size and duration of parental care. Evolutionary decisions to invest in a variable manner to parental care have produced equal tactics in relation to the productivity (the number of offspring) and costs (time of care) (I).

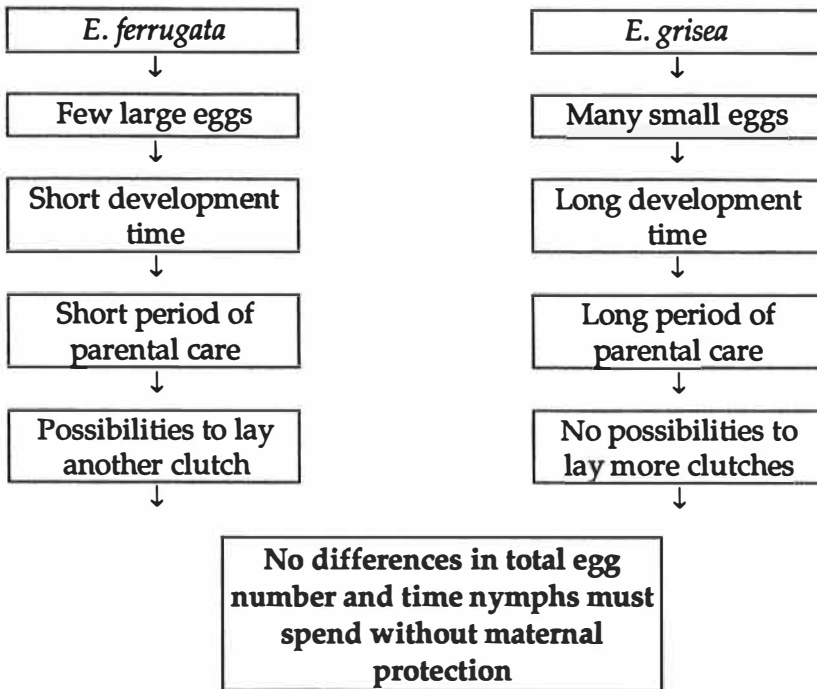


FIGURE 1. Reproductive tactics in *E. grisea* and *E. ferrugata*

Offspring of parent bugs cannot survive without maternal care (Melber & Schmidt 1975a, Melber et al. 1980, II), and females are constrained to successfully produce only one brood during their breeding season (I). Thus, females are forced to guard their unique broods and stay over them even against superior predators (II, IV). Type of maternal care of shield bugs (protection of young by sitting over them) limits the clutch size (II) and equal protection of all the young (III). Females are not able to successfully guard experimentally enlarged clutches and lost all of their "extra eggs" to predators. Thus, females successfully guarded only clutches of sizes their body could cover (II). The situation may be similar to that in precocial birds where clutch sizes are limited by incubation ability of females (Winkler & Walters 1983). The successful defence of brood become more difficult if female is parasitized. Parasitized females probably cannot defend their broods as effectively as unparasitized females (VI). Moreover parasites reduce female survival and significantly increase the probability of death before the end of maternal care (VI).

Type of maternal care in *E. ferrugata* is quite identical to maternal care of *E. grisea* (I). Like in *E. grisea* (II), predation seems to limit offspring

number (Mappes et al. unpubl.) and the innermost offspring survive better from predation (III). Females of *E. ferrugata* seemed to invest selectively in offspring of different value (in relation to survival) by sharing different quantities of resources to particular individuals. Eggs at the safe site (central) were clearly larger than eggs at the edge of the clutch. As in insects generally, egg size affects survival of nymphs (III). Thus, *E. ferrugata* nymphs at the centre had higher survival due to slighter predation pressure and the better physiological condition. In contrast to earlier studies, where parents make their decision to favour offspring of high quality (Drummond et al. 1986, Stephenson & Winsor 1986, Lyon et al. 1994), females of *E. ferrugata* make their decision "beforehand" in relation to the possibilities of the offspring to survive from predation.

3.2 Predation and behavioural adaptations

One of the most important results arising from the thesis is that maternal protection is not the only way to enhance offspring survival. The strongest single selection force seems to be predation by ants (II, IV, Mappes et al., unpubl. data) that affects host selection (IV), aggregation of females (V) and investment to offspring number and quality (II, III).

In contrast to nonparental species, mobility of parental insects is limited. Insects with prolonged parental care must make a choice of their place to live before egg laying. After oviposition they are constrained to live in same habitat whole the caring period. Exceptions are species that lay their eggs on the back of males where males guard them (e.g. the giant water bug *Abedus herberti*) (Smith 1976) and, thus, are also able to change their environment. For parent bug females it is beneficial to avoid host trees with high predator densities although they would offer resources for developing young. If females are forced to breed in trees with high ant density, most eggs are destroyed. In trees with low ant density of 70% eggs survived (IV). Thus, we suggest like Ohsaki & Sato (1994) that natural enemies may provide a major selection pressure for food plant preference in many herbivorous insects. Females may even avoid intrinsically superior food plants if they would attract a greater load of predators or parasites (Price et al. 1980, Bernays & Graham 1988). It would be also interesting to study whether the selection of suitable host trees varies in relation to other environmental characteristics such as density and type of host trees and predators.

Variation in risk of predation may also affect "joint brood guarding" that has been observed both in *E. grisea* (V) and also in *E. fieberi*

(unpubl. data). The frequency of joint guarding varies and in many study sites no females were aggregated while in other sites up to 50% of all females guarded their brood jointly (V). Aggregations of females cannot be forced by any lack of egg laying sites, because suitable places for oviposition are practically unlimited. Moreover, leaves of birch serve only as oviposition sites and do not offer resources for the offspring that move to forage on female catkins after hatching (Jordan 1958).

According to our hypothesis, joint guarding of parent bugs was clearly beneficial against strong ant predation. Experimentally formed female pairs defended their clutches significantly more successfully against ants losing fewer eggs than did the females that were singly on a leaf (V). The experiment supports the hypothesis that group living acts as a defence against predation (Kruuk 1964, Birkhead 1977). Our results may also support the idea that eusociality could evolve through parasociality (Michener 1958, Eickwort 1981, Brockmann 1984), in that two females guarding their broods together are more successful in brood guarding than singly breeding females. Parent bugs, however, are far from any real sociality. Moreover, selection that affects clumping in parent bugs is predation while for social and parasocial Hymenoptera it is probably the better ability of parents to build nests and feed the young together. In future, it is necessary to study costs and benefits of joint guarding in the field to find out the reasons for variation in frequency of joining. Probable costs and benefits of joint guarding are linked to types and densities of predators (Sillén-Tullberg & Leimar, 1988, V) and selection of safe host plants (IV).

4 CONCLUSIONS

The aim of this study was to empirically study reproductive tactics in parental insects. Insects that cover their egg clutch with their body and "incubate" give an excellent possibility to test central questions of life-history evolution. Determination of clutch size has traditionally been studied by manipulating clutch size in altricial birds (Roff 1992). Although the method has been critiqued (Reznick 1985, 1992), these manipulations have played a central role in forming the hypotheses of optimal clutch size (Godfrey et al. 1991, Stearns 1992). However, it is also necessary to test these hypotheses with other taxonomical groups. Clutch size manipulation in parent bugs showed that females adjusted their clutch size in terms of their own size and ability to defend the brood against predators (II). Thus, the experiment supports individual optimization also in parent bugs, although the mechanisms that limit clutch size in birds and parent bugs are different. Birds mainly adjust their clutch size with respect to their ability to incubate (Winkler & Walters 1983) or their ability to feed the young (Lack 1947, 1954), but in parent bugs clutch size is limited by predation. Further studies are, however, needed to understand the whole variation in clutch sizes in maternal shield bugs. For example, there may be temporal variation in the resources and density of predators that affect offspring fitness leading to variation in the clutch size. Moreover response to risk of predation seems to differ between environments as indicated by changes in the spatial distribution of females (IV, V). Finally, investment to each offspring is not independent from that to others. Offspring fitness may decline with clutch size if the resources used to provision eggs are limited (Smith & Fretwell 1974). Large nymphs are clearly better in quality in shield bugs (III) and, thus, the trade-off between egg size and clutch size occurs (I).

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Yhteenveto

Jälkeläishoito ja lisääntymistaktiikat *Elasmucha*-suvun luteilla

Jälkeläishoitoa pidetään alkeellisimpana sosiaalisen käyttäytymisen muotona ja sitä nimitetään esisosiaaliseksi käyttäytymiseksi. Jälkeläishoito hyönteisillä on kehittynyt suojaamaan jälkeläisiä erityisen ankarissa ympäristöoloissa (esimerkiksi vuorovesirannat) ja laikuttaisissa ympäristöissä (kuten raadot ja lantakasat) sekä suojaamaan jälkeläisiä lajitovereiden kilpailulta, pedoilta ja loisilta.

Suomessa tavataan kolmea jälkeläisiään hoitavaa *Elasmucha* -suvun (Heteroptera; Acanthosomatidae) luteita. Näiden lajien (koivulude *E. grisea*, suokkolude *E. fieberi* ja mustikkalude *E. ferrugata*) naaraat asettuvat muninnan jälkeen munaryhmän päälle vartioimaan munia ja jatkavat hoitoa vielä poikasten kuoriuduttua. On ilmeistä, että jälkeläishoito on näillä lajeilla kehittynyt nimenomaan suojaamaan poikasia pedoilta, sillä käytännössä kaikki munat tuhoutuvat ilman naaraan hoitoa. Tässä väitöskirjatyössäni tutkin edellämäinittuja lajeja esimerkkeinä käyttäen mm. naaraan allokontiratkaisua poikasten laadun ja määrän välillä, optimaalista pesyekokoa sekä allokontia säilyvyydeltään eriarvoisiin jälkeläisiin.

Jälkeläisiään hoitavilla luteilla munien määrän ja koon välisen allokontiongelman merkitys korostuu, koska munien puolustustehokkuuden kannalta on oleellista, että koko munaryhmä munitaan naaraan selkakilven peittämälle alalle. Pieniä munia mahtuisi paljon, mutta suuret munat ovat laadullisesti parempia ja sen lisäksi kehittyvät nopeammin kuin pienet. Toinen keskeinen kysymys on naaraan lisääntymispanostuksen eli jälkeläishoitoon käytetyn ajan ja energian jakaminen nykyisen pesyeen ja mahdollisten tulevien pesyeiden kesken. *Elasmucha*-suvun luteille ei ole kehittynyt yhtä tiettyä "optimaalista" ratkaisua siitä, kuinka jakaa aika ja energia jälkeläisten koon, määrän ja hoitoajan suhteen, vaan kaikki kolme lajia poikkeavat toisistaan näiden tekijöiden suhteen. Mustikkalude munii vähän suuria munia ja hoitaa poikasia toiseen toukkavaiheeseen saakka. Koivulude munii suuren ryhmän pieniä munia ja hoitaa poikasiaan keskimäärin neljänteen toukkavaiheeseen asti. Suokkoluteen allokontiratkaisut olivat koivuluteen ja mustikkaluteen väliltä. Kiinnostavaa on, että lajien välillä ei ollut eroja absoluuttisessa ajassa, jonka jälkeläiset viettivät ilman hoitoa, vaikka hoitoajat eri lajeilla ovatkin erilaiset. Mustikkaluteen vähäisempi

panostus poikasten hoitoon kompensoitui suurien munien nopeammalla kehitysajalla. Lisäksi se on vertailulajeista ainoa, joka tuotti myös toisen pesyeen. Yhteenlaskettu jälkeläistuotto ei siis *Elasmucha* lajeilla poikennut toisistaan.

Optimaalisen pesyekoon tutkimus alkoi ornitologi David Lack'in töistä (1947, 1954). Hän esitti hypoteesin, että luonnonvalinta suosii linnuilla sellaista pesyekokoa, joka käytännössä tuottaa suurimman määrän eloonjääviä jälkeläisiä eli on tuottavin. Optimaalista pesyekokoa on tähän asti tutkittu lähinnä linnuilla, mutta jälkeläisiään hoitavat hyönteiset, sopivat mainiosti kyseisen ongelman kokeelliseen testaamiseen. Kysymystä tutkittiin vertailemalla eri lajien naaraiden kokoa suhteessa munaryhmän kokoon. Lisäksi tehtiin koe, jossa pienet naaraat siirrettiin puolustamaan suurten naaraiden munaryhmiä ja päinvastoin. Kontrolliryhmissä naaraat vaihdettiin oman kokoluokkansa naaraiden munaryhmien päälle. Tutkimuksessa selvisi, että naaras muni optimaalisen pesyekoon suhteessa omiin kykyihinsä puolustaa sitä. Predaatio siis näyttäisi olevan pesyekokoa rajoittava tekijä koivuluteella.

Poikasten eloonjäämistodennäköisyyteen vaikuttaa luteilla selvästi munien ja siten poikasten sijainti munaryhmässä. Predaatoriski munaryhmän ulkoreunalla on yli kolminkertainen verrattuna munaryhmän sisäosiin. Munaryhmän sisäosissa munat olivat mustikkaluteella tilastollisesti merkitsevästi suurempia kuin ulko-osiin munitut munat. Sama kokoero näkyi myös ensimmäisen asteen toukissa. Naaras siis munii suuria, säilyvyydeltään parempilaatuisia munia munaryhmän sisäosiin, jossa predaatoriski on pienempi kuin munaryhmän ulko-osissa. Tulokset tukevat hypoteesia "ekonomisesta allokoinnista" siten, että naaraan kannattaisi jakaa rajalliset resurssinsa (ravinteet, ruokinta, puolustustehokkuus) siten, että lisääntymisarvoltaan parempiin poikasiin investoidaan suhteessa enemmän kuin lisääntymisarvoltaan vähempiarvoisiin poikasiin.

Koivulude, nimensä mukaisesti, lisääntyy koivuissa, joissa on runsaasti kehittyviä eminorkkoja. Poikasten kuoriuduttua ne siirtyvät norkoille, joista sekä poikaset että aikuiset imevät ravintoa. Kuitenkin vain osa "norkkokoivuista" kelpaa koivuluteen munintapaikoiksi. On siis ilmeistä, että ravinnon määrän lisäksi jokin muu tekijä vaikuttaa naaraan munintapaikan valintaan. Tätä koivuluteen valikoivaa munintakäyttäytymistä ja sen syitä tutkittiin siirtämällä osa naaraista munimaan koivuihin, joissa ei alunperin ollut koivuluteita (koekäsittely) ja vertaamalla näiden naaraiden lisääntymismenestystä naarasiin, jotka lisääntyivät puissa, joissa luonnostaan oli luteita (kontrolli). Kaikista puista tutkittiin myös muurahaisten määrä. Vaikka ravintoa oli riittävästi sekä koe- että kontrollipuissa, eloonjääneiden poikasten määrä oli huomattavasti alhaisempi koekäsittelyssä. Suurin osa jälkeläisistä tuhoutui jo munavai-

heessa. Muurahaisten puunkäyttöaktiivisuus korreloi positiivisesti poikaskuolleisuuden kanssa eli koivuluteet välttivät munimasta koivuihin, joissa muurahaiset liikkuvat. Valikoivalla munintakäyttämällä koivuluteet parantavat oleellisesti jälkeläistensä selviytymistodennäköisyyttä.

Kaksi koivuludenaarasta munivat usein munansa samalle lehdelle. Tämä "yhteenliittyminen" ei voi olla sattumaa eikä myöskään munintapaikkojen vähäisyydestä johtuvaa, koska tarjolla on tuhansia vapaita munintapaikkoja. Työhypoteesina oli, että naaraalle koituu jotain etua siitä, että se asettuu samalle lehdelle toisen naaraan viereen. Hyödyn tulee myös olla molempuolista. Yksi syy ryhmässä elämiseen voi olla predaation välttäminen. Ryhmässäeläminen voi "lieventää" yksilöön kohdistuvaa predaatiopainetta, koska kaikki ryhmän jäsenet "jakavat" ryhmän kimppuun hyökkäävät pedot. Aktiivisesti itseään puolustavilla lajeilla ryhmäpuolustus on myös todennäköisesti tehokkaampaa kuin itsenäinen puolustus. Yhteispuolustus olikin selkeästi tehokkaampaa verrattuna yksin puolustukseen. Kokeellisesti muodostetut naarasparit menettivät tilastollisesti merkitsevästi vähemmän munia muurahaisille verrattuna yksin jälkeläisiään puolustaviin naaraisiin.

Eräs jälkeläishoidon merkittävin riski voi olla naaraan lisääntynyt alttius loisille. Jälkeläisiään vartioiva naaras on helppo kohde isäntää etsivälle loiselle. *Elasmucha*-suvun luteilla tunnetaan specialisti endoparasiitti karpänen *Subclytia rotundiventris* Fallen (Diptera; Tachinidae), joka munii yhden munan naaraan sisälle selkäkilven läpi poraamastaan reiästä. Loisitulla koivuludenaarailla tehtiin koesarja kontrolliryhmänä loisimattomat naaraat, missä vertailtiin naaraiden kykyä puolustaa poikasiaan. Loinen rajoitti naaraan puolustuskykyä ja lyhensi sen elinikää. Merkittävin kustannus loisesta jälkeläisiään hoitavalle naaraalle on lyhentynyt hoitoaika, joka saattaa vaikuttaa poikasten mahdollisuuksiin selviytyä pedoilta.

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