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Presence of conspecific females motivates egg cannibalism owing to lower risk of filial cannibalism

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A cannibal has to weigh the benefits of the consumption and removal of competing conspecifics against the potential loss of fitness through filial cannibalism. We examined the role of the presence of conspecific females in informing adaptive cannibalism decisions. Females of the hemipteran bug *Geocoris pallens* express low egg cannibalism when alone but become much more cannibalistic in the presence of conspecific females and do not discriminate between their own eggs and those of other females. Experimentation showed that females that could not commit filial cannibalism exhibited strong egg cannibalism that was not reduced by the presence of conspecific females, whereas females that could commit filial cannibalism were very cannibalistic only in the presence of conspecifics. An experiment also showed that the presence of conspecific females triggered a stronger egg cannibalism response in *G. pallens* than did a heterospecific egg predator. These results suggest that *G. pallens* females become cannibalistic in the presence of conspecifics because they interpret conspecific presence primarily as an indication of decreased likelihood of committing filial cannibalism, and less so as an indication of lower expected survival of eggs or future resource competition. Our study highlights the importance of informational cues, in this case the presence of conspecifics, in modulating the expression of cannibalism.

Many animals face a key decision upon encountering a vulnerable conspecific individual: to cannibalize or not. Although the cannibal gains energy and reduces intraspecific competition through cannibalism, it will also lose direct fitness if it commits filial cannibalism (i.e. cannibalizing offspring; Polis 1981). Hence, cannibalism often increases when food resources are limiting (Mayntz & Toft 2006; Frank et al. 2010) or the likelihood of cannibalizing closely related kin is low (Schausberger & Croft 2001; Anthony 2003).

How might an animal that encounters a vulnerable conspecific that it can cannibalize evaluate its risk of committing filial cannibalism? There are two broad classes of possible mechanisms. First, offspring may be recognized directly using phenotypic cues that they express (e.g. males of the bluegill sunfish, *Lepomis macrochirus*, discriminate between their own fry and other fry using chemical cues and cannibalize more of the latter; Neff 2003; Neff & Sherman 2003). Second, offspring may be recognized indirectly using a reliable association between nonphenotypic cues and the likelihood of encountering offspring (Pfennig 1997; Schausberger 2003; Lissaker & Svensson 2008). For example, for species in which individuals may encounter offspring (e.g. if dispersal is limited), the individual may use the presence of reproductive conspecific adults in its vicinity as a cue to estimate the likelihood of encountering its own offspring (the presence of other reproductive conspecifics reduces the likelihood that any encountered conspecific juvenile is the individual's offspring; Manica 2004). Consequently, the likelihood of filial cannibalism decreases, and cannibalism may be more strongly favoured. This was demonstrated in the fish *Telmatherina sarasinorum*, in which spawning males increase egg cannibalism when they perceive the presence of other conspecific males (Gray et al. 2007).

The presence of conspecifics may, however, be important as a signal of two other important aspects of environmental conditions that could shape the optimal expression of cannibalism. First, the presence of conspecifics could indicate that the risk of cannibalism by other conspecifics in the vicinity is elevated, and consequently that offspring from the focal female are less likely to survive, even if they are not cannibalized by their parents. Offspring that are unlikely to survive have low fitness value for their parents. Regardless of whether or not a cannibal can reliably recognize kin, it may be adaptive for parents to cannibalize offspring that are unlikely to survive, as this allows the parent to reabsorb some of the

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energy invested in those offspring to be used in the future, when conditions may become more favourable, instead of losing it all to other predators. Predation risk posed by heterospecific predators has been shown to increase filial cannibalism in skinks, *Mabuya longicaudata*, and sand gobies, *Pomatoschistus minutus* (Huang 2008; Chin-Baarstad et al. 2009). Second, the presence of conspecifics may also indicate intensified intraspecific resource competition, for either the focal female or especially for her offspring, reducing the expected survival or fecundity of those offspring, and thus reducing their fitness value.

Thus, there are three possible hypotheses explaining why the presence of conspecifics might increase cannibalism: conspecifics may signal (1) a lower likelihood of filial cannibalism (the filial cannibalism hypothesis); (2) a greater risk of predation by conspecifics (the predation risk hypothesis); or (3) intensified intraspecific competition experienced by offspring in the future (the resource competition hypothesis). Here, we investigated the expression of cannibalistic behaviour in the omnivorous insect *Geocoris pallens* Stål (Hemiptera: Geocoridae), focusing on egg cannibalism by adult females. We first asked whether the presence of conspecific females increases egg cannibalism rates of *G. pallens* females (experiments 1 and 2). Then, having shown that it does, we asked which of the three hypotheses can best explain the higher egg cannibalism behaviour observed in the presence of conspecific females. The filial cannibalism hypothesis predicts that pre-reproductive females that cannot commit filial cannibalism should express cannibalism rates independent of the absence/presence of conspecific females. The predation risk hypothesis predicts that females should be cannibalistic on eggs whenever egg predation risks, from either conspecific or heterospecific predators, are high. The resource competition hypothesis predicts that females should be cannibalistic on eggs when perceived future resource competition is intense, irrespective of a female's current reproductive status, as long as reproductive activity is expected to commence soon. This study complements earlier studies (e.g. Gray et al. 2007) in disentangling and evaluating the three possible types of information contained in the presence of a conspecific individual (the likelihood of filial cannibalism, the intensity of predation risk for conspecific eggs and the intensity of competition for offspring) in motivating cannibalism decisions.

METHODS

Geocoris pallens, commonly found in agricultural fields, is native to California, U.S.A. Adults measure about 4 mm in length, forage actively and do not aggregate. Eggs are laid singly on the substrate and do not receive parental care. The generalist diet of *G. pallens* consists mainly of smaller arthropods as well as plant resources such as extrafloral nectar. *Geocoris* spp. are cannibalistic (Crocker & Whitcomb 1980; Takizawa & Snyder 2011), and egg cannibalism by *G. pallens* is easily observed in laboratory colonies (Y.-H. Law, personal observation). In choice tests, *G. pallens* females in the presence of conspecific females were presented with own eggs and unrelated eggs. They cannibalized both types of eggs indiscriminately, suggesting that they cannot distinguish between the two (Appendix Fig. A1).

For experiments 1, 2 and 5, *G. pallens* adults were collected from alfalfa or cotton fields in the San Joaquin Valley, California several days before the start of the experiment and maintained in laboratory colonies. *Geocoris pallens* focal females used in experiments 3 and 4 were reared from eggs in the laboratory. Laboratory colonies of *G. pallens* were maintained on frozen moth eggs (*Ephestia kuehniella* or *Spodoptera exigua*) and a combination of wet cotton, green beans or sugar snap peas. Moth eggs, a high-quality food for *G. pallens*, can sustain normal development and reproduction, whereas green beans or sugar snap peas alone cannot. Experiments 1 and 2 were conducted in growth chambers (30 °C, 14:10 h light:dark cycle), and experiments 3, 4 and 5 on laboratory counters (30 °C, ambient light cycle).

Presence of Conspecifics and Egg Cannibalism

Experiment 1, conducted on 15–18 August 2008, tested whether *G. pallens* females exhibit higher egg cannibalism when they perceive conspecific females in their vicinity. On Day 0 (15 August), individual *G. pallens* females were isolated in 25 ml vials with wet cotton and excess frozen moth eggs. This isolation served to standardize the females' pretreatment perception of local conspecific density. Females that oviposited during Day 0 were then allocated to the test arenas for the experiment. A test arena consisted of a closed petri dish (60×15 mm) divided in half by a mesh net (mesh size $= 1$ mm^2) along a diameter. The focal female was placed in one of these halves, while the other half was either left empty ($N = 10$) or received one conspecific adult female ($N = 6$). A slice of sugar snap pea (both ends wrapped with Parafilm to slow desiccation) was placed in both halves of the arena. Visual barriers were set up between the test arenas. Focal females laid eggs in their halves of the arena for 48 h, after which the number of cannibalized eggs was counted. The mesh net allowed the focal females to detect neighbouring conspecific females but prevented individuals from physically crossing over, although females could possibly touch each other across the net. This meant that eggs laid away from the net by the focal female could only be cannibalized by her. Although focal females did occasionally lay eggs on the mesh net, these eggs were not included in the measurement, as they might have been cannibalized by females on either side of the net. A cannibalized egg was identified by its empty, collapsed chorion. *Geocoris pallens* eggs hatch in about 6–7 days; thus no eggs could have hatched during the experiment.

Experiment 2, conducted on 5–8 August 2009, aimed to characterize the relationship between the number of neighbouring conspecific females and egg cannibalism expressed by focal females. Methods followed those described for experiment 1 with the following modifications. At the end of the 24 h isolation (Day 0), the pre-experiment cannibalism rate was measured by recording the numbers of eggs laid and cannibalized by each focal female. Numbers of neighbouring conspecific females were one of the following: zero, one, two, three or five adult females ($N = 9$, 8, 9, 9 and 10, respectively).

Test of Filial Cannibalism Hypothesis

Experiment 3, conducted in two blocks during 26–28 July 2010 and 3–5 August 2010, tested whether the likelihood of filial cannibalism modulates the expression of cannibalism. Egg cannibalism by virgin *G. pallens* females, which have no likelihood of filial cannibalism, was compared to that by mated *G. pallens* females, which have some likelihood of filial cannibalism. Females were reared from eggs in laboratory colonies and at eclosion to the adult stage were housed either individually (virgin females, $N = 18$) or with a male (mated females, $N = 15$) for 48 h (Day 0–2). Subsequently, females were transferred to petri dishes (60×15 mm) and provided with a green bean and frozen moth eggs ad libitum for another 48 h (Day 2–4). Females of different reproductive states (mated versus virgin) might have different nutritional needs, and this could confound any effect of varying likelihood of filial cannibalism on the expression of cannibalism. To assess the possibility that our manipulation changed the overall ingestion of prey, during Block 1, we recorded the total weight of moth eggs consumed by focal females between Days 2 and 4. Females were then held individually with five randomly selected *G. pallens* eggs on paper