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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 towel and green beans for 48 h (Days 4–6), after which the number of *G. pallens* eggs cannibalized by each female was counted. Both virgin and mated females began laying some eggs during Days 4–6, but these eggs were not included in the cannibalism counts. Virgin females apparently laid nonviable eggs, as none of the eggs developed into nymphs. Proportions of *G. pallens* eggs cannibalized were analysed with a generalized linear model (GLM; binomial distribution, logit link; R version 2.12, The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org) with reproductive states and block as the main factors.

Experiment 4, conducted on 27–31 July 2011, was a second test of the hypothesis that presence of conspecific females triggers egg cannibalism because it signals a lower likelihood of committing filial cannibalism. Our goal was to produce an independent test of the same hypothesis, using a different experimental manipulation. Egg cannibalism rates between mated but pre-ovipositing females (no likelihood of filial cannibalism) and mated, ovipositing females (with some likelihood of filial cannibalism) subjected to the absence/presence of conspecific females were compared. *Geocoris pallens* females can mate within 24 h of moulting to the adult stage but start ovipositing only 4 days later (Y.-H. Law, unpublished data). Under the hypothesis of decreasing likelihood of filial cannibalism, egg cannibalism by mated but pre-ovipositing females should be insensitive to the absence/presence of conspecific females, because they have no likelihood of committing filial cannibalism. However, ovipositing females should be sensitive to the absence/presence of conspecific females if it signals variation in the likelihood of committing filial cannibalism.

Two groups of *G. pallens* females reared from eggs were used: mated but pre-ovipositing females (1 day old, $N = 17$), and mated and ovipositing females (8–12 days old, $N = 24$). Focal females were placed in a covered petri dish arena that was divided by two parallel mesh nets (4 mm apart) placed along a diameter. One side of the arena housed an individual focal female, 10 *G. pallens* eggs unrelated to the focal female, and a slice of bean; the other side of the arena had a green bean with either two or no neighbouring females. Ten *G. pallens* eggs were provided instead of five as in experiment 3 to increase the resolution of recorded cannibalism rates. The double nets allowed visual and olfactory interaction between the focal females and the neighbours, but not physical contact, and hence prevented any possible tactile disturbance caused by neighbouring females. After 48 h, the number of *G. pallens* eggs cannibalized by the focal females was counted. Proportions of eggs cannibalized were analysed with a GLM (binomial distribution, logit link; R version 2.12) with presence of conspecifics and reproductive state as the main factors.

As in experiment 3, any changes in females' expression of egg cannibalism in this experiment could be a manifestation of different nutritional needs owing to the different ages or reproductive states of the females. To evaluate the possibility of such a confounding factor, moth egg consumption by focal females was measured. Following the 48 h cannibalism assay, focal females were placed individually in new petri dishes without any neighbours, and provided fresh green beans and a cup of preweighed moth eggs in excess. Forty-eight hours later, moth egg consumption by females was measured. The weights of consumed moth eggs were transformed with Box–Cox transformation before analysis. Moth egg consumption was compared between the groups of ovipositing and pre-ovipositing females, and also included as a covariate in an expanded GLM analysis of egg cannibalism.

Test of Predation Risk Hypothesis

Experiment 5, conducted on 1–3 August 2011, tested whether the presence of conspecific females triggers egg cannibalism because it signals lower expected survival of the eggs. *Geocoris pallens* focal females were exposed to the presence of either conspecific or heterospecific (green lacewing larvae, *Chrysoperla rufilabris*) egg predator neighbours, and the focal females' expression of egg cannibalism was compared. Green lacewing larvae are natural predators of *G. pallens* eggs (Rosenheim et al. 1999) and consume almost all *G. pallens* eggs offered in laboratory trials (personal observation). If lower expected survival of eggs triggers *G. pallens* females to cannibalize eggs, the presence of green lacewing larvae should elicit elevated egg cannibalism.

Before the experiment, field-collected focal female *G. pallens* were isolated for 24 h with excess moth eggs. They were then allocated to arenas set up like those in experiment 4; neighbours were absent ($N = 13$) or were two conspecific females ($N = 12$) or two third-instar green lacewing larvae ($N = 13$). After 48 h, the number of *G. pallens* eggs cannibalized by the focal females was counted. Because each egg is scored as either alive or cannibalized (binomial data), proportions of eggs cannibalized were compared between treatments with a GLM with binomial error distribution (R Development Core Team 2010).

RESULTS

In experiment 1, lone focal females expressed very low egg cannibalism. However, focal females in the presence of a neighbouring female expressed ca. 20-fold higher egg cannibalism (Fig. 1a; proportion of eggs cannibalized by lone females and females with a neighbour = 0.03 ± 0.02 and 0.54 ± 0.17, respectively; $\chi^2_1 = 6.9$, $P = 0.009$).

In experiment 2, during the 24 h of isolation before the cannibalism assay, all focal females expressed low egg cannibalism (proportion of eggs cannibalized = 0.04 ± 0.02). During the assay, focal females held alone continued to express low cannibalism (proportion of eggs cannibalized = 0.03 ± 0.03), but those held in the presence of conspecific females became 13-fold more cannibalistic (Fig. 1b; proportion of eggs cannibalized = 0.40 ± 0.07; $\chi^2_1 = 8.2$, $P = 0.004$). Egg cannibalism did not change significantly with increasing numbers of neighbouring females (Fig. 1b; $\chi^2_1 = 3.5$, $P = 0.32$).

Virgin females were more cannibalistic than mated females (Fig. 2; reproductive state: $\chi^2 = 4.42$, $P = 0.035$). Although cannibalism was higher in Block 1 than in Block 2, virgin females were more cannibalistic than mated females in both blocks (Fig. 2; block: $\chi^2_1 = 9.89$, $P = 0.002$; reproductive state*block: $\chi^2_1 = 1.08$, $P = 0.30$). Virgin and mated females consumed similar amounts of moth eggs ($t_{27} = -1.03$, $P = 0.32$), suggesting that the observed difference in cannibalism was not simply a result of greater overall food intake by mated females.

Pre-ovipositing females were twice as cannibalistic as ovipositing females (proportion of eggs cannibalized by pre-ovipositing and ovipositing females = 0.69 ± 0.09 and 0.28 ± 0.07, respectively; Fig. 3; effects of reproductive state: $\chi^2_1 = 71.04$, $P < 0.0001$). Consumption of moth eggs was similar between pre-ovipositing and ovipositing females ($t_{37} = -1.41$, $P = 0.16$). Furthermore, an expanded statistical model containing moth egg consumption as a covariate did not better explain cannibalism rates (Appendix Table A1). The presence of conspecific females triggered strong increases in cannibalism by ovipositing females but not in pre-ovipositing females, which expressed high cannibalism rates even when alone (Fig. 3; effects of neighbours: $\chi^2 = 6.9$, $P = 0.009$; neighbours*reproductive state: $\chi^2 = 14.5$, $P < 0.0001$; see also Appendix Table A1). These results are thus consistent with the hypothesis that the expression of cannibalism responds to the risk of filial cannibalism, and we found no evidence for a confounding effect of females' reproductive state on nutritional needs.

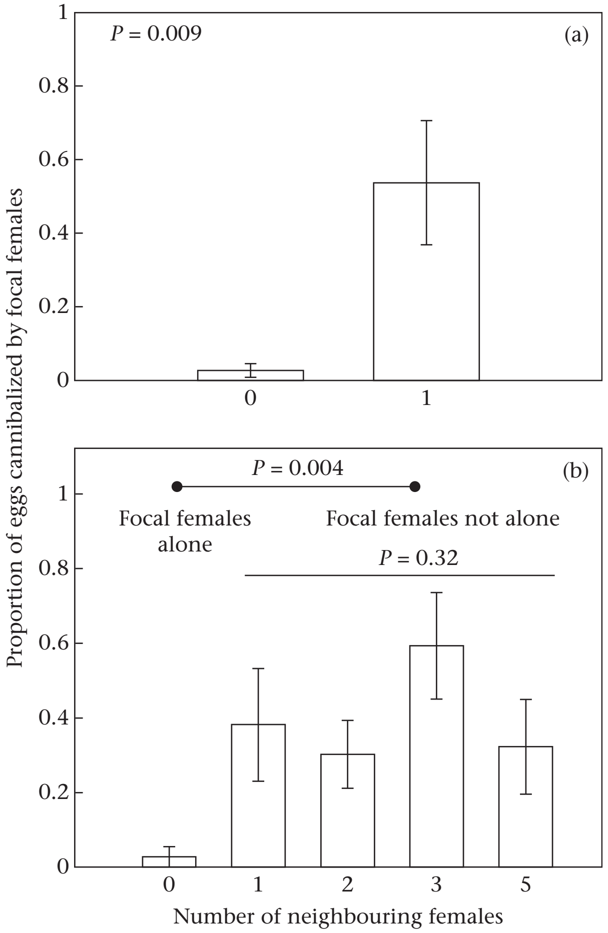

Figure 1. Proportion of own eggs (means ± SE) cannibalized by *G. pallens* focal females in (a) experiment 1 and (b) experiment 2. For experiment 2, the bar with circular ends indicates a comparison of egg cannibalism between focal females without versus with (i.e. one, two, three or five) neighbouring females.

The presence of green lacewing larvae, heterospecific predators of *G. pallens* eggs, elicited a small and marginally nonsignificant increase in egg cannibalism in *G. pallens* females (Fig. 4; proportion of eggs cannibalized by lone females and females with green lacewings = 0.22 ± 0.09 and 0.32 ± 0.08, $\chi^2_1 = 3.3$, $P = 0.07$). By contrast, the presence of conspecific females triggered a much stronger hike in egg cannibalism (Fig. 4; proportion of eggs cannibalized by lone females and females with conspecific neighbours = 0.22 ± 0.09 versus 0.55 ± 0.08, $\chi^2_1 = 28.9$, $P < 0.0001$).

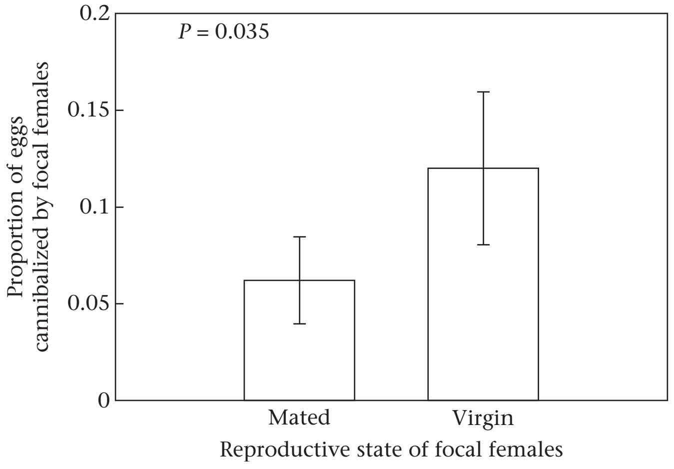

Figure 2. Proportion of provided *G. pallens* eggs cannibalized by focal females (mean ± SE) that were either virgin or mated.

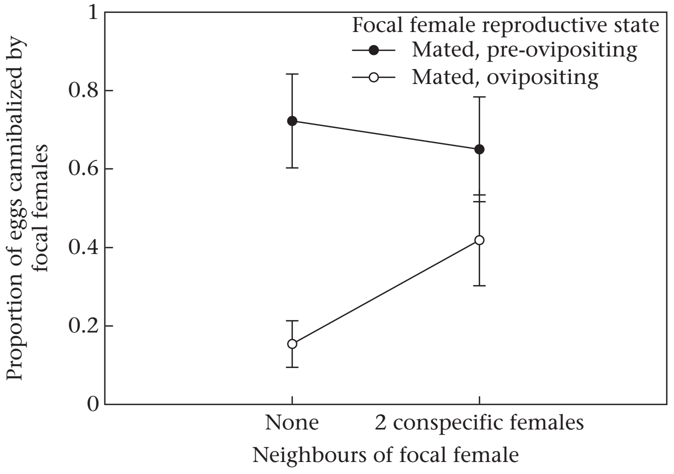

Figure 3. Proportion of provided *G. pallens* eggs cannibalized by focal females (mean ± SE). Focal females, all mated, were either ovipositing (8–12 days old) or pre-ovipositing (1 day old) and were held either alone or with two conspecific female neighbours.

DISCUSSION

Geocoris pallens females, which are rarely cannibalistic when alone, become highly cannibalistic in the presence of conspecific females (experiments 1 and 2). Expression of cannibalism is often attributed to increased aggression caused by resource limitation and high encounter rates between cannibals and conspecific prey when densities of the cannibalistic population are high (Polis 1981; Wise 2006). However, these two mechanisms cannot explain the cannibalism response in our study, because every focal female had similar access to resources (food and space) and encountered

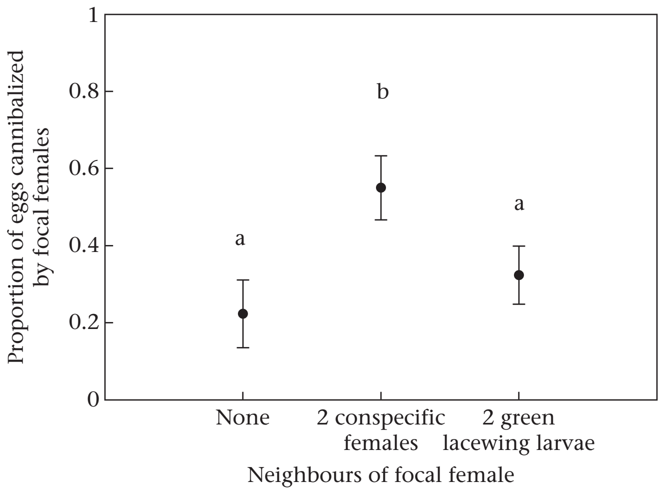

Figure 4. Proportion of provided *G. pallens* eggs cannibalized by focal females (mean ± SE). Females were either alone, had two conspecific females or two green lacewing larvae as neighbours. Treatments with different letter labels have significantly different means.

similar numbers of conspecific eggs (Y.-H. Law & J. A. Rosenheim, unpublished data). The focal females differed only in whether or not they had conspecific female neighbours.

It is possible that *G. pallens* females might use the absence/presence of conspecifics to estimate resource competition faced by their offspring in the future. If so, then it is expected that *G. pallens* females would be more likely to cannibalize eggs in the presence of conspecifics (a prediction that partially matches the results of this study), because any offspring produced under these conditions would have low chances of survival anyway. We suggest, however, that this hypothesis is inconsistent with the results of experiments 3 and 4. Unmated and prereproductive females were not laying eggs at the time cannibalism was assayed, but both would have a strong expectation of becoming reproductive in the near future (for prereproductive females, egg laying would predictably begin after 4 days, whereas for unmated females the duration of the delay would be less certain, but potentially very short). Thus, these females should also be expected to respond to the competitive environment likely to be experienced by their future offspring. However, results of experiment 4 clearly show that this is not the case: prereproductive females were highly cannibalistic even in the absence of conspecifics, and they did not further increase their egg cannibalism in the presence of conspecifics. Instead, the egg cannibalism rates of females were affected by an interaction of reproductive status and conspecific absence/presence, an observation that is best explained by the hypothesis of decreased likelihood of filial cannibalism. Hence, the resource competition hypothesis appears unlikely to explain the observed increase in egg cannibalism in response to the presence of conspecifics in *G. pallens* females.

What factors other than changing competition might explain why the presence of conspecific females triggers elevated egg cannibalism in *G. pallens* females? We tested two alternative explanations: the presence of conspecifics may increase cannibalism because (1) it signals a decreased likelihood that an encountered egg is the female's own offspring and thus that there is less likelihood of filial cannibalism or (2) it signals a high-predation environment in which the female's previously laid eggs have a low expectation of survival and thus a low fitness value. Either mechanism would decrease the potential fitness loss from cannibalism and hence increase females' egg cannibalism behaviour.

To evaluate these two potential explanations, we compared the cannibalism responses of females that could not commit filial cannibalism (virgin and pre-ovipositing females) with females that potentially could (mated and ovipositing females). If females use the presence of conspecific females to estimate their likelihood of cannibalizing offspring, then females that cannot commit filial cannibalism should be insensitive to the presence of conspecifics; we predicted that these females would be highly cannibalistic towards eggs regardless of the absence/presence of conspecific females. This prediction was met: in experiment 3, virgin females cannibalized more eggs than mated females did, and in experiment 4, mated but pre-ovipositing females expressed high egg cannibalism rates that were unaffected by the absence/presence of conspecific females. By contrast, mated and ovipositing females, which do incur a risk of committing filial cannibalism, restrained their egg cannibalism when alone but became cannibalistic in the presence of conspecific females (Fig. 3). This significant interaction is perhaps the strongest evidence that the increase in cannibalism expressed by females held with neighbours occurred in response to the perceived likelihood of filial cannibalism, and not other changes associated with the presence of neighbours. For example, it might have been hypothesized that neighbouring conspecifics could result in elevated stress levels that might lead to increased metabolic demands and thus greater cannibalism. But such an effect should have led to increased cannibalism for all females, regardless of their reproductive state, rather than just ovipositing females, as we have found here.

We know of no way to manipulate directly a female's perception of the likelihood of committing filial cannibalism; instead, we used manipulations of female reproductive state (virgin versus mated; pre-oviposition versus ovipositing) to create clear differences in the females' likelihood of filial cannibalism. This raises a potential difficulty: our manipulations might have influenced the expression of cannibalism in ways different from the causal pathway we intended. In particular, females of different reproductive state might also differ in their nutritional needs, with consequent effects on cannibalism (Anthony 2003; Green et al. 2008). To address this concern, we measured the consumption of moth eggs to quantify total food demand by females of different reproductive states and found no hint that nutritional needs were affected by our particular manipulations of reproductive state. Moth egg consumption was similar in virgin and mated females (experiment 3) and in pre-ovipositing and ovipositing females (experiment 4). Furthermore, moth egg consumption was not correlated with cannibalism rates nor did it improve our statistical model of cannibalism rates (Appendix Table A1). Thus, we found no evidence that differences in nutritional need explain the large differences in cannibalism responses observed in our study. This strongly suggests that the differences in cannibalism rate stemming from our experimental manipulations of female state probably reflected changing estimates of the costs associated with filial cannibalism.

Green lacewing larvae (sympatric, heterospecific predators of *G. pallens* eggs) appeared to elicit a small increase in egg cannibalism by *G. pallens* females (Fig. 4). Thus, it may be that female *G. pallens* respond to a decreased expectation of survival of their eggs by increasing their expression of egg cannibalism. Other studies have demonstrated that when offspring are exposed to elevated heterospecific predation risk, parents will abort parental care and cannibalize offspring (Huang 2008; Chin-Baarstad et al. 2009). Such filial cannibalism is adaptive, because cannibalizing offspring and regaining some of the energy invested is better than losing it all to heterospecific predators (Huang 2008; Chin-Baarstad et al. 2009). The presence of conspecific individuals, however, can signal both a lower expected survival of previously produced offspring and a lower expected likelihood of filial cannibalism, and these two signals may combine to augment the female's cannibalistic response (Johnstone 1996). Nevertheless, decreased survival of eggs appeared to be a relatively minor factor in our study, based on the much stronger cannibalism response elicited in *G. pallens* females by conspecific females than by green lacewing larvae.

Egg cannibalism by female *G. pallens* appears to be a flexible behaviour that allows the female to adapt to varying risks of filial cannibalism. The ability to discriminate kin and direct altruistic behaviour preferentially towards kin has evolved in many animal taxa (Hepper 1986; Pfennig 1997; Mateo 2004). Kin discrimination can be informed by direct cues, such as shared phenotypic traits, or by indirect cues that are contextual, such as spatial proximity (Mateo 2004; O'Connor & Shine 2006; Patterson et al. 2008). *Geocoris pallens* females did not demonstrate direct kin recognition using phenotypic cues (Appendix Fig. A1), but instead appeared to obtain information from a context-based cue, the presence of conspecific females, to estimate relatedness of encountered eggs, and hence the likelihood and risk of filial cannibalism (for an example of a similar behaviour in fishes, see Gray et al. 2007). Regardless of whether direct or indirect cues are used, the spatial structure of individual interactions is crucial for the evolution and maintenance of behaviours linked to kin discrimination (Lion & van Baalen 2007), including cannibalism (Rudolf et al. 2010). If females rarely encounter their offspring as a result of spatiotemporal segregation, then kin discrimination is unnecessary and is unlikely to evolve. We do not know the extent of *G. pallens* females' mobility after oviposition, but our results support context-based kin discrimination behaviour in *G. pallens* females, and hence we predict that *G. pallens* females should co-occur with their eggs spatiotemporally. This prediction remains to be tested.

Cannibalism that is modulated by the presence of conspecifics is a novel behavioural mechanism that may underlie strongly density-dependent cannibalism. This mechanism can complement and reinforce the other mechanisms for density-dependent cannibalism, such as density-dependent changes in resource competition and encounter rates. Although cannibalism is a ubiquitous process, it is most often associated with resource-limiting conditions. The behavioural mechanism reported here, which can greatly increase cannibalism even when resources are adequate, expands the conditions under which cannibalism may be influential (e.g. Law & Rosenheim 2011). Future work is needed to determine how widespread this behaviour is across other animal taxa, and its effects in the field.

Conclusions

We have demonstrated here that the mere presence of conspecific females triggers reproductive females to become highly cannibalistic towards eggs. Our experiments suggest that the presence of conspecific females functions primarily as a signal of decreased expected relatedness to encountered conspecific eggs, and thus a decreased cost associated with filial cannibalism. This effect may be reinforced by the presence of conspecifics also indicating a decreased expected survival of previously produced eggs. A strong response to the presence of conspecifics creates a novel behavioural mechanism underlying the density-dependent expression of cannibalism that is independent of resource availability.

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Appendix

Table A1
Statistical models explaining egg cannibalism rates by *G. pallens* females (experiment 4)

Source	*df*	χ^2	*P*
Basic model			
Neighbours	1	3.18	0.07
Reproductive state	1	71.04	<0.0001
Neighbours*Reproductive state	1	13.64	0.0002
Expanded model with moth egg consumption			
Neighbours	1	3.18	0.07
Reproductive state	1	71.04	<0.0001
Moth eggs consumed	1	0.14	0.71
Neighbours*Reproductive state	1	14.09	0.0002

The basic model includes effects of neighbours and focal female reproductive state, whereas the expanded model has moth egg consumption by focal females added as a covariate. Models are GLM with binomial distribution and logit link function (R Development Core Team 2010).

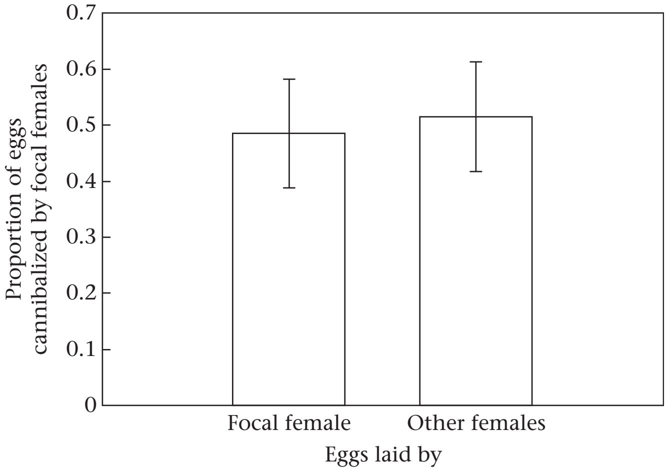

Figure A1. Proportion of own and unrelated eggs cannibalized by *Geocoris pallens* focal females. Females cannibalized their own eggs and those of other females without discrimination (paired *t* test: $P = 0.88$), indicating that females cannot recognize their own eggs phenotypically. This experiment, conducted on 19–21 June 2010, examined whether *G. pallens* females discriminate between their own eggs and those of other females. Focal females were held singly with excess frozen moth eggs (*Ephestia kuehniella*) and water for a day with strips of paper towel. Eggs laid during this isolation period were collected on the paper towel. Focal females were then placed in one half of a test arena (similar to arenas used in experiment 2; see text) for 2 days ($N = 11$), with one neighbouring female in the other half of the arena. Every focal female was also provided with six conspecific eggs on paper towel laid during the isolation period: three of her own and three laid by other females. Twenty-four hours later, the number of provided eggs, the focal female's own and those of other females, cannibalized by the focal female was recorded and compared.