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To cannibalize or disperse? Males cannibalize and females disperse in the predatory mite *Phytoseiulus persimilis*

A.M. Revynthi, K. van Pol, A. Janssen & M. Egas

ABSTRACT — Cannibalism is a widespread phenomenon in nature, often occurring when food is scarce, for example among predators that have over-exploited a local prey population. Instead of cannibalizing, predators can disperse, thereby avoiding being cannibalized or cannibalizing kin-related conspecifics, resulting in inclusive fitness loss. Theory on prey exploitation in ephemeral predator-prey systems predicts that predators may be selected to display prudent predation ('Milker' predators) by dispersing early, thus saving food for their remaining offspring. This is especially advantageous when average relatedness in the local population is high. Less prudent predators refrain from dispersing until all prey are exterminated. These prey exploitation strategies may also have repercussions for cannibalism, especially when it is driven by food shortage. We therefore investigated to what extent adult females and males of lines with different dispersal strategies cannibalize or disperse when prey are exterminated. We used two lines of the haplodiploid predatory mite *Phytoseiulus persimilis* that were selected for early and late dispersal. Using wind tunnels, we observed the behavior of adult predators of these lines, offering conspecific larvae as victims. Our results show that both selection lines behaved similarly but that male predators stayed significantly longer in the patch and engaged more often in cannibalism than females. This is in agreement with differences in their behavior and in their kin-relatedness to the other individuals on the patch. We therefore propose that males and females of haplodiploid species may have different tendencies to cannibalize.

INTRODUCTION

Cannibalism (i.e., intraspecific predation) is a common phenomenon in nature and occurs in a wide range of animal taxa, such as birds, mammals, fish, insects, spiders and mites (review in Fox 1975; Polis 1981; Schausberger 2003). Animals prey on their conspecifics to obtain food, nutrients and remove resource competitors in times of scarcity (Fox 1975). Killing and consuming a conspecific, however, may result in injuries, pathogen transmission and loss of inclusive fitness if the victim is a relative (Pfennig 1997). Nevertheless, cannibalism occurs often when food is scarce.

When a local prey population is overexploited by a local predator population, the predators eventually need to disperse to find a new prey patch. Such dispersal promotes persistence at a metapopulation level due to the foundation of new local populations by dispersing individuals (Huffaker 1958; Taylor 1990; Janssen et al. 1997; Ellner et al. 2001). After exterminating the prey, predators have the option to stay or disperse and to cannibalize or not. Staying without cannibalizing will result in starvation, and dispersing means losing the possibility to cannibalize, hence, different dispersal strategies can result in different levels of cannibalism. A similar choice between staying or dispersing and cannibalizing or not is found in solitary predators that have a transient gregarious life stage, such as hatching spiderlings (Lesne et al. 2016), preying mantids (Fea et al. 2014), toads (Child et al. 2008) and coccinellids (Michaud and Grant 2004). Hence, dispersal and cannibalism are behaviors that can often occur under the same circumstances, and selection on one type of behavior can therefore affect the other (Rudolf et al. 2010).

There is a continuum of strategies for the exploitation of ephemeral prey patches by predators. Early dispersal of adult predators, before the prey are exterminated, reduces predation and the prey population can therefore persist longer. As a result, the offspring of the dispersed predators will have more food and, hence, they can interact with their prey for a longer, but finite, period of time, and this will result in a higher total number of dispersing predators over the entire local predator-prey interaction period (van Baalen and Sabelis 1995). Because the number of dispersers is an appropriate stand-in measure for fitness in metapopulations (Gyllenberg and Metz 2001), such prudent predation (the so-called ‘Milker strategy; van Baalen and Sabelis 1995) through increased early dispersal results in higher overall fitness for the predators. Early dispersal will not only decrease predation of the prey, but also cannibalism for the same reason. Late predator dispersal in contrast, drives the local prey population to extinction faster, resulting in a shorter interaction period between the predator and its prey and a lower fitness. It also offers more opportunities for cannibalism once the local prey density is low. However, the early dispersal strategy can be invaded by the late dispersal strategy (the so-called ‘Killer’ strategy; van Baalen and Sabelis 1995), because the latter consume the prey saved by the prudent predators faster than the prudent offspring.

In theoretical studies, cannibalism has been treated either as a selective process in the evolution of dispersal, which can determine the spatial structure of natural populations (Lion and van Baalen 2007; Rudolf et al. 2010), or as the trait under selection due to different dispersal strategies (Pels 2001). In both cases the evolution of cannibalism is affected by kin selection (Hamilton 1964a,b). Rudolf et al. (2010) showed that cannibalism selects for dispersal because offspring try to escape from their cannibalistic parents, avoiding this way loss

of inclusive fitness. Alternatively, Pels (2001) suggested that late dispersal can select for high cannibalistic tendency among juveniles. We hypothesize that predators that disperse only after their local prey population is depleted (Killers) are more prone to cannibalize than predators that disperse before prey depletion (Milkers), but run a higher risk of substantial loss in inclusive fitness because they might consume relatives.

A model organism to study cannibalism in relation to dispersal and to test the above hypothesis is the haplodiploid predatory mite *Phytoseiulus persimilis*. It is a specialist predator that feeds on tetranychid mites and lives in spatially structured environments (Nachman 1981; Ellner et al. 2001), where it drives local prey populations to extinction (Janssen and Sabelis 1992; Janssen et al. 1997; Pels and Sabelis 1999). Subsequently, the predators may disperse in search of food or remain in the patch and obtain food via cannibalism. The cannibalistic behavior of females of this predator has been repeatedly studied in closed environments without the option to disperse (Yao and Chant 1989; Walzer and Schausberger 1999; Schausberger and Croft 2001; Schausberger 2007; Schausberger and Hoffmann 2008; Revynthi et al., CHAPTER 4). We are aware of only one study that measured dispersal behavior of juvenile *P. persimilis* in absence of prey (Pels 2001), however, the author focused on quantifying the number of dispersed individuals and did not quantify cannibalism.

It is important to distinguish among the different life-history stages of the predators because they face different consequences of dispersal. In predatory mites, adult reproducing females consume by far the most prey, and convert a large part of the ingested food into eggs (Sabelis 1981). Females that stop feeding can survive for long periods without food as long as there is water available (Sabelis 1981). Because the predatory mites disperse passively on air currents (Sabelis and Dicke 1985), the possibility that they will find a new prey patch is low, and the possibility to find a prey patch with conspecifics is consequently even lower. This means that the best stage for dispersal is the adult, mated female, which is the only stage that can start reproducing when arriving on a new prey patch without conspecifics. To mature, juveniles, either male or female, need much less food than reproducing adult females (Sabelis 1981), and they may therefore develop into adult by consuming the odd prey left at the end of the local interaction between predators and prey. Adult males also need little food, and for them it is actually better to stay on the patch and mate with newly developed adult females rather than dispersing to find mates. We therefore expect that mated adult females will disperse more readily than adult males, and that adult males may consequently cannibalize more than adult females. Indeed, we recently found that adult male *P. persimilis* cannibalize more than adult females (Revynthi et al., CHAPTER 4).

In a recent study, Revynthi et al. (CHAPTER 3) selected for predators that depart early (i.e., ‘Milker’-like) and late (‘Killer’-like) from a patch with spider mite prey. Although we have information about the dispersal and exploitation strategies of these two selected lines, little is known about their cannibalistic tendencies. Here we aim to investigate to what extent these selected lines that employ different dispersal and exploitation strategies cannibalize and we ask:

- (1) When food is limited and given the option to disperse, will predators choose to cannibalize or to disperse?
- (2) If predators cannibalize when they have the option to disperse, which line and/or gender of *P. persimilis* is more voracious towards its conspecifics?

MATERIAL AND METHODS

Roses

Young rose plants (*Rosa* sp. var *Avalanche*) were obtained from Dummen Orange (De Lier, the Netherlands) and transferred to a climate room, where they were hydroponically grown on rock wool. Conditions in the climate room were 25 °C, 70% RH and 16L:8D. The rose plants were watered 2× per week and fertilized (20-10-20 N-P-K) once per week.

Spider mites

Two-spotted spider mites (*T. urticae*) were originally collected from cucumber plants in a commercial greenhouse in May 1994 (Pallini et al. 1997). The spider mite culture was kept on Lima bean plants (*Phaseolus lunatus* L.) in a climate room (26 °C, 60% RH and 16L:8D) and was used to maintain the predator cultures described below.

Predatory mites

In the present study, we used two lines of *P. persimilis* that were selected for early and late dispersal (the so-called Early- and Late-dispersal line; Revynthi et al., CHAPTER 3). The predators were kept on floating platforms in trays that contained water with dissolved soap inside a mite-proof cage (80 µm diameter). Previous experiments showed no effect of kinship on the cannibalistic behavior of females and males of this species (Revynthi et al., CHAPTER 4). Hence, based on this finding we conducted the experiments using only kin predators. Therefore, isofemale lines were created by isolating a gravid female predator from each selection line and individually putting it in a separate cage with prey, where it could establish its own family. The isofemale lines were fed 3× per week by introducing two Lima bean leaves (*P. lunatus*) infested with spider mites (*T. urticae*), and were kept in a climate room at 25 °C, 70% RH and 16L:8D.

To obtain sufficient numbers of gravid females and males of the same age (2 days into adulthood), as well as larvae, cohorts were created as follows. Ten gravid female predatory mites from each of the two isofemale lines were placed on a spider mite-infested bean leaf on a bed of water-saturated cotton wool in a Petri dish (14 cm diameter, 2 cm height). In this way, the leaves remained turgid for at least 10 days. The gravid females were allowed to oviposit for 48 h, after which they were removed and only their eggs and prey were left on the leaves. The cohorts were kept in the same climate room as the lines.

Experimental procedure

To observe the cannibalistic behavior of females and males when they had the option to disperse aurally, eight wind tunnels were used as described in Revynthi et al. (CHAPTER 2). Each wind tunnel consisted of a plastic aquarium (25.3 × 15.8 × 15.5 cm) with holes (11.5 cm diameter) on both sides, covered with a fine mesh (80 µm). The aquarium was closed with a glass lid and sealed with Parafilm. The combination of a fan on one side and gauze on the other created a constant air flow inside the wind tunnel, which was kept at approximately 0.4 m/s during the experiments. The stem of a rose leaf, with five leaflets, was inserted in a plastic vial (24.5 mm diameter, 40 mm height) filled with water-saturated Oasis floral foam and a thick layer of lanolin was applied to the base of the petiole to prevent mites

from escaping. Then the vial was placed at the upwind end of the wind tunnel. At the downwind side, a trap was placed in order to capture the aerially dispersing predatory mites. The trap consisted of a Petri dish containing the three top leaflets of a rose leaf infested with spider mites, with the stem (ca. 3 cm) inserted through a hole in the lid of an Eppendorf tube (1.5 ml) filled with wet Oasis floral foam.

Adult males and gravid females from the cohorts were individually isolated in a cup (2.8 cm diameter, 2.2 cm height), 48 h prior to the start of the experiment. The cup contained a rose leaf disc (24 mm diameter) on water-saturated cotton wool and was sealed by a lid with a hole (12 mm diameter) covered with mite proof gauze (80 μm diameter). We starved the predators until the start of the experiment, i.e., in the 48 h they did not receive any prey.

At the start of the experiment, seven young predatory mite larvae were transferred onto the first leaflet of a rose leaf. Larvae were chosen as prey, since this stage is the most vulnerable to cannibalism and does not feed (Amano and Chant 1977). After the introduction of the larvae, a starved adult male or female predator from the same isofemale line as the larvae was released next to the larvae. Observations started 2 h after the initiation of the experiment, as pilot experiments revealed that no predators dispersed within an hour. Every hour, the trap was replaced with a new one and the old one was checked for dispersers. The experiment stopped as soon as the adult had dispersed or after 6 h and the time of dispersal was recorded. The experiment ran for a maximum of 6 h to prevent having larvae molting to protonymphs. The protonymph stage is the first feeding stage and they cannibalize when there is lack of heterospecific prey, thus they could feed on the remaining larvae. At the end of the experiment, each rose leaf was inspected to determine whether the adult predatory mite had engaged in cannibalism by counting the consumed and alive larvae. Only corpses from which the hemolymph was removed were counted as consumed larvae. We did not observe natural mortality in the larvae (dead larvae that were not eaten and their hemolymph had not been removed). If the number of consumed and alive larvae did not add up to seven, the remaining larvae were recorded as missing. In this way, we quantified cannibalism and dispersal tendencies of both genders from both selection lines (Early- and Late-dispersal). As a control for each treatment, predators were individually put on the rose leaf without conspecific larvae and only the time of dispersal was recorded by making the same hourly observations as described above. The experiment was performed in 20 blocks in a climate room (25 °C, 70% RH and 16L:8D), each block consisting of one replicate of all treatments.

Statistical analysis

To determine whether there was a difference in the cannibalistic behavior of the lines and genders, a χ^2 test was used on the numbers of cannibalistic males and females, crossed with the numbers of males and females that dispersed.

In order to detect possible differences in the timing of dispersal between the treatments, a time-to-event analysis with a Cox proportional hazard model was used. Censoring was applied to predators that did not disperse during the 6 h of the experiment. The fixed explanatory variables were the line (Early or Late), treatment (cannibalism or control) and the gender (male or female) and their interactions. Block was included as a random factor. Non-significant interactions and factors were removed to find the minimum adequate model.

To determine which of the two genders was more voracious towards its conspecifics and to detect possible differences between the two lines, two generalized linear mixed effect models with a binomial error distribution were used (glmer of the lme4 package; Bates et al. 2015). In the first model, we used all predators, because we were interested in the effect of gender and line on the average predator voraciousness. In the second model, we analyzed differences in voraciousness among cannibals. In both models the number of alive and consumed larvae combined in a vector was used as a response variable, predator line and the gender were the fixed factors, and block was a random factor. During the experiments, one male and one female from the Early-dispersal line died. Hence, for those two treatments, $N = 19$ instead of $N = 20$. All analyses were performed using R v.3.0.1 (R Development Core Team 2015).

RESULTS

The choice of the predators, to either cannibalize or not, did not differ between the selection lines ($\chi^2 = 0.46$, d.f. = 1, $P = 0.50$), but males cannibalized significantly more frequently than females ($\chi^2 = 4.06$, d.f. = 1, $P = 0.04$). Most males cannibalized, whereas ca. 50% of the females did not (FIGURE 5.1).

Predators from both lines did not differ statistically significant in timing of dispersal (Cox proportional hazard: $\chi^2 = 1.07$, d.f. = 1, $P = 0.30$; FIGURE 5.2) and there was no statistically significant difference in dispersal with or without the presence of conspecific larvae (Cox proportional hazard: $\chi^2 = 0.029$, d.f. = 1, $P = 0.87$; FIGURE 5.2). Females, however, dispersed significantly earlier than males (Cox proportional hazard: $\chi^2 = 4.56$, d.f. = 1, $P = 0.033$).

The number of larvae that the predators consumed did not vary statistically significant with line either for overall consumption (GLMER: $\chi^2 = 0.02$, d.f. = 1, $P = 0.88$; FIGURE 5.3a) or for consumption per cannibal (GLMER: $\chi^2 = 0.58$, d.f. = 1, $P = 0.45$; FIGURE 5.3b). Males of both lines consumed significantly more larvae than the females (GLMER: $\chi^2 = 3.9$, d.f. = 1, $P = 0.048$; FIGURE 5.3a). There was no statistically significant difference between

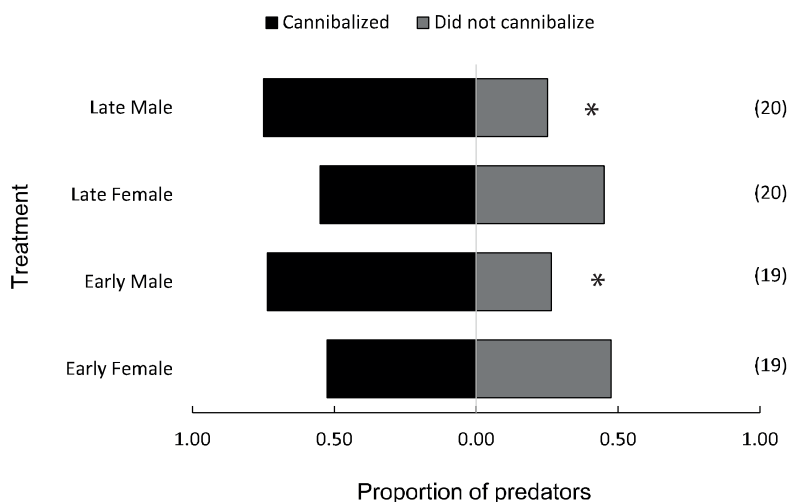


FIGURE 5.1 — Proportions of adult males and females from the Early and Late-dispersal line that cannibalized (black bars) or not (grey bars). Numbers in the parentheses indicate the sample size. Asterisks show significant differences between the proportions of cannibals and non-cannibals (χ^2 test, $P < 0.05$).

the genders, however, in the number of larvae consumed per cannibal (GLMER: $\chi^2 = 0.003$, d.f. = 1, $P = 0.96$; FIGURE 5.3b), hence, the differences in overall cannibalism between genders (FIGURE 5.3a) were caused by a higher proportion of males cannibalizing (FIGURE 5.1). On average 1.18 larvae out of seven were missing.

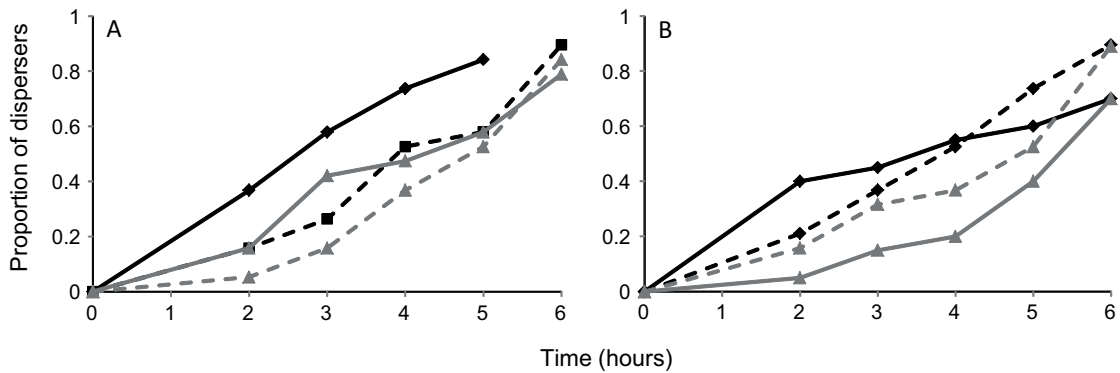


FIGURE 5.2 — Timing of male and female predatory mite dispersal with or without (control) the presence of conspecific prey. Panels show cumulative proportions of dispersers over time. A: Early-dispersal isofemale line; B: Late-dispersal isofemale line. Black lines with rhombus are females, grey lines with triangles are males, solid lines are treatments with conspecifics (cannibalism), interrupted lines are control (no cannibalism).

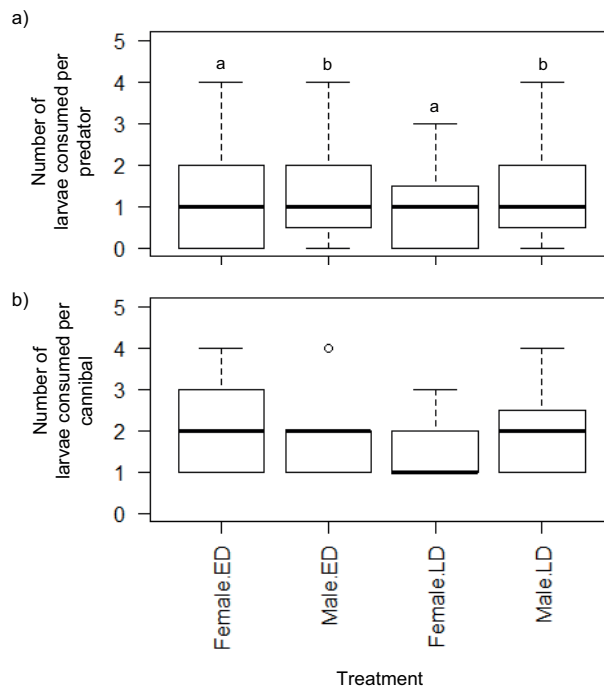


FIGURE 5.3 — Numbers of larvae consumed a): per female or male predator and b): per female or male cannibal of Early (ED) and Late (LD) dispersal line. Boxes indicate the second and the third quartile, horizontal lines separating the boxes indicate the medians, whiskers above and below the box indicate the 90th and 10th percentiles. Different letters indicate significant differences (GLMER, $P < 0.05$).

DISCUSSION

Cannibalism and dispersal are two important phenomena that affect the population-genetic structure and are dependent on densities of the cannibals and victims, but also of their food (Fox 1975; Polis 1981; Otronen and Hanski 1983; Ellner et al. 2001). Although many studies focus on how kin recognition and kin interaction can affect decisions of individuals to cannibalize (Pfennig 1997; Faraji et al. 2000; Schausberger and Croft 2001) or to disperse (Hamilton and May 1977; Lambin et al. 2001), to the best of our knowledge, this is the first experiment in which these two behaviors are studied together. Contrary to expectations, our results did not show any statistically significant differences in cannibalism or dispersal behavior between the Early-dispersal and the Late-dispersal line, therefore do not support our hypothesis that a Killer line would be more prone to cannibalize than a Milker line.

Male predators were more prone to cannibalize (FIGURE 5.1), whereas females engaged less in cannibalism by dispersing earlier from the leaf (FIGURE 5.2). One explanation for the observed differences between the genders might be differences in the behavior of males and females. *Phytoseiulus persimilis* reproduces by pseudo-arrhenotoky, which means that females need to be inseminated before they can produce eggs (Helle et al. 1978; Sabelis and Nagelkerke 1988). Furthermore, gravid female predators cannot oviposit when cannibalizing (Yao and Chant 1989). Adult males, in contrast, do not need much food (Sabelis 1981), and do not search for food but for mates. Thus, males search for conspecifics; and mated females search for food, i.e., heterospecific prey, which they must find in other patches. When the local prey population is depleted, males can wait for immature females to mature and subsequently mate with them. While waiting, males can cannibalize to survive, preferably on immature males.

An alternative explanation for the observed differences in the cannibalistic behavior of males and females is based on the existing asymmetries in the relatedness of male and female parents with juveniles. In haplodiploid species such as *P. persimilis*, the cost of cannibalism regarding inclusive fitness loss is not balanced between the two genders. Because the females are diploid and the males haploid (only carrying genetic material from their mothers), there are asymmetries in relatedness with juveniles (Hamilton 1964a,b). Given that a local population consists of the offspring of one female and one male, the females will have more offspring than males, because the latter only contribute genes to daughters. Thus, females will suffer from greater inclusive fitness loss if they engage in cannibalism than do males. Hence we hypothesize that under food limitation, adult females are less prone to cannibalize than adult males and will more often choose to disperse in order to refrain from cannibalism. We expect that males would specifically cannibalize other, immature males, because this reduces future mate competition, and by letting female immatures live, they increase the chance on a future mate. This hypothesis, however, remains to be tested.

When cannibalizing, both genders appeared to be equally voracious (FIGURE 5.3b), but fewer females than males engaged in cannibalism (FIGURE 5.2) because they dispersed earlier. Hence, males dispersed later than females thus had more time to cannibalize. To assess whether males and females were equally voracious, we analyzed the proportion of larvae eaten, correcting for the time that the individuals remained on the patch, where they could cannibalize. This was done by including time until dispersal and gender as fixed factors and

their interaction into a mixed effects model. This analysis showed that gender had no significant effect (GLMER: $\chi^2 = 0.65$, d.f. = 1, $P = 0.42$), but that the proportion of larvae cannibalized increased significantly with the time that individuals spend on the patch before dispersing. This suggests that males and females were equally voracious when cannibalizing, and that differences in the numbers of larvae cannibalized were caused by differences in the amount of time spent on the patch. An interesting hypothesis that can be tested in haplodiploid species is that, given the asymmetries between the two genders in the relatedness with their potential victims, whether males cannibalize more often after having encountered a victim.

Besides finding no difference in cannibalism between the two lines, we also did not find statistically significant differences in dispersal behavior. At first sight, this is strange because the lines were selected for different dispersal tendencies and had different prey exploitation strategies (Revynti et al., CHAPTER 3). However, this selection took place in the presence of heterospecific prey, and dispersal in the current experiments was measured without prey. In fact, both Milkers and Killers are expected to disperse when the prey population is depleted (Pels and Sabelis 1999), and Pels (2001) also found no differences in dispersal behavior between a Milker-like and a Killer-like line in the absence of prey.

Theoretical studies that focus on the evolution of dispersal and cannibalism (Pels 2001; Lion and van Baalen 2007; Rudolf et al. 2010) predict that selection on dispersal results in a genetically correlated effect on cannibalism. Our results, however, do not support this prediction at least with respect to our selected lines. The current experimental study on dispersal and cannibalism gives new insight into the cannibalistic behavior of the two genders and we therefore propose that future theoretical studies should take these differences into account.

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