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Males cannibalise and females disperse in the predatory mite *Phytoseiulus persimilis*

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Abstract

Cannibalism is a widespread phenomenon in nature, often occurring when food is scarce, for example among predators that have overexploited a local prey population. Instead of cannibalising, predators can disperse, thereby avoiding being cannibalised or cannibalising related conspecifics, which results in inclusive fitness loss. Theory on prey exploitation in ephemeral predator-prey systems predicts that predators may be selected to display prudent predation 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 cannibalise or disperse after prey have been exterminated locally. We used two lines of the haplodiploid predatory mite *Phytoseiulus persimilis* that were selected for early and late dispersal, respectively. In wind tunnels, we observed the cannibalistic and dispersal behaviour of individual adult predators of these lines on a rose leaf with only conspecific larvae as food. Both selection lines behaved similarly, indicating that selection on dispersal behaviour did not result in correlated effects on cannibalism behaviour. Male predators stayed significantly longer on the leaf and engaged more often in cannibalism than females. The results suggest that there might be gender-specific differences in cannibalistic tendency in relation to dispersal. Future theoretical studies on the evolution of cannibalism and dispersal should take differences between the genders into account.

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Introduction

Cannibalism is a common phenomenon in nature and occurs in a wide range of animal taxa, such as birds, mammals, fish, insects, spiders and mites (reviews in Fox 1975; Polis 1981; Schausberger 2003). Animals prey on their conspecifics to obtain food, nutrients and remove 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 kin-related (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 cannibalise or not. Staying without cannibalising will result in starvation, and dispersing means losing the possibility to cannibalise, hence, different dispersal strategies can result in different levels of cannibalism. A similar choice between staying or dispersing and cannibalising or not is found in solitary predators that have a transient gregarious life stage, such as hatching spiderlings (Lesne et al. 2016), praying mantises (Fea et al. 2014), toads (Child et al. 2008) and coccinellids (Michaud and Grant 2004). Hence, dispersal and cannibalism are behaviours that often occur under the same circumstances, and selection on one type of behaviour 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, which also disperse earlier upon becoming adults, will have more food and, hence, they can interact with their prey for a longer, but finite, period of time. 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 through increased early dispersal (the so-called ‘Milker’ strategy; van Baalen and Sabelis 1995) results in higher overall fitness for the predators. Early dispersal will not only decrease predation of the prey, but also cannibalism, especially if this is driven by food shortage. In contrast, late predator dispersal drives the local prey population to extinction faster, resulting in a shorter interaction period between the predator and its prey and a lower fitness (the so-called ‘Killer’ strategy; van Baalen and Sabelis 1995). However, the early dispersal strategy can be invaded by the late dispersal strategy, because the latter consume the prey saved by the prudent predators faster than the prudent and early dispersing offspring. It also offers more opportunities for cannibalism once the local prey density is low (van Baalen and Sabelis 1995; Pels and Sabelis 1999; Pels 2001).

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, thus avoiding loss of inclusive fitness. Alternatively, Pels (2001) suggested that late dispersal can result in selection for high cannibalistic tendency among juveniles. We hypothesise that predators that disperse only after their local prey population is depleted are more prone to cannibalise than predators that disperse before prey depletion, 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. Spider mites avoid plants with predators to avoid predation (Pallini et al. 1999), and the chances that a patch with predators that have exterminated the local prey population will be recolonized by prey is therefore small. Therefore, dispersal or cannibalism are the only options open to predators after exterminating prey. In this study, we only consider the passive dispersal on air currents, and not ambulatory locomotion, which is used by the predators to reach other parts of the same prey patch on a plant or group of neighbouring plants (see Sabelis et al. 2002 for a definition of a patch of spider mite prey). The cannibalistic behaviour 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. 2018b). We are aware of only one study that measured dispersal behaviour of juvenile *P. persimilis* in the 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 from dispersal. In predatory mites, reproducing adult 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, both male and female juveniles 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 before these disperse 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 cannibalise more than adult females. Indeed, we recently found that adult male *P. persimilis* cannibalise more than adult females in a closed environment without the option to disperse (Revynthi et al. 2018b).

Here we aim to investigate whether late dispersers indeed cannibalise more than early dispersers, making use of selection lines of *P. persimilis* that show different dispersal and exploitation strategies (Revynthi 2017), i.e., predators that depart early and late from a patch with spider mite prey. Even though we have information about the dispersal and exploitation strategies of these two selected lines, little is known about their cannibalistic tendencies. Our experiments address the following questions: (1) When food is limited and given the option to disperse, will predators choose to disperse or stay and will they cannibalise or not? And (2) if predators cannibalise when they have the option to disperse, is there a difference in rate of cannibalism between early and late dispersers and between males and females?

Material and methods

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 twice per week and fertilized (20-10-20 N-P-K) once per week. Two-spotted spider mites (*Tetranychus 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*) in a climate room (26 °C, 60% RH and 16L:8D) and was used to maintain the predator cultures described below. We used two lines of *P. persimilis* that were selected for early and late dispersal (Revynthi 2017). Six rounds of selection were performed to create these lines. In each round, the first 20–25 female predators dispersing were selected to form the early-dispersal line, whereas the last 20–25 female predators dispersing within 24 h were selected to form the late-dispersal line. Selection was performed in the presence of adult female spider mites. The predators were kept on floating platforms in trays that contained water with dissolved soap inside a mite-proof cage (mesh 80 µm). Previous experiments showed no effect of kinship on the cannibalistic behaviour of females and males of this species (Revynthi et al. 2018b). We therefore conducted the experiments using only kin predators. Nine weeks prior to the start of the experiment, two isofemale lines were created, one from the early-dispersal and one from the late-dispersal line. A gravid female predator was isolated from each selection line and put in a separate cage with prey, where she could establish her own family. The generation time of this predatory mite is 7 days at 25 °C (Laing 1968; Sabelis 1981); thus 9 weeks resulted in nine generations of sib-mating. The isofemale lines were fed 3× per week by introducing two Lima bean leaves 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 larvae and gravid females and males of the same age (2 days into adulthood), 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 high). 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 under the same conditions as the isofemale lines.

Experimental procedure

To observe the cannibalistic behaviour of females and males when they had the option to disperse aerially, eight wind tunnels as described in Revynthi et al. (2018a) (Fig. 1) were used. In short, 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

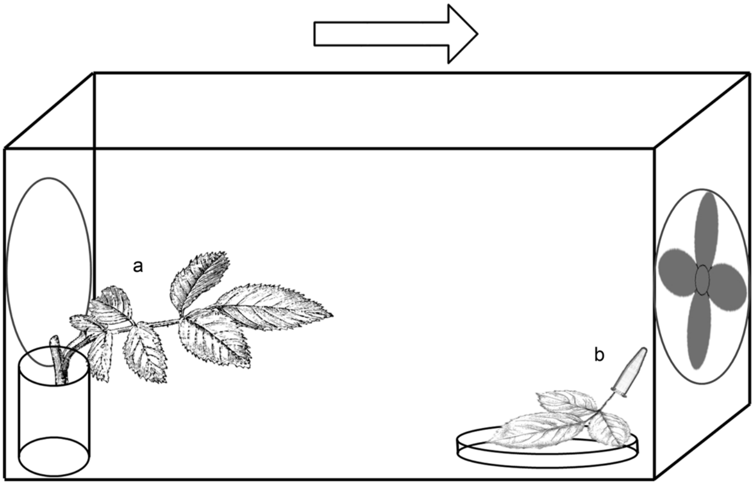

Fig. 1 Wind tunnel consisting of a plastic aquarium with two holes covered with mite-proof mesh and a fan attached to one of them. **a** Rose leaf where the adult predators and larvae were released and **b** trap with spider-mite infested rose leaf to attract the dispersing individuals. The arrow indicates the direction of the air current (after Revynthi et al. 2018a)

was kept at approximately 0.4 m/s during the experiments. This wind speed is known to be sufficient for aerial dispersal of *P. persimilis* (Sabelis and van der Weel 1993; Sabelis and Afman 1994; Pels and Sabelis 1999). The stem of a rose leaf with five leaflets was inserted in a plastic vial (24.5 mm diameter, 4 cm high) 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 by walking. 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. Notice that the predators could not perceive the (volatiles from) the trap leaf from the experimental leaf because the latter was positioned upwind (Fig. 1).

Forty-eight h prior to the start of the experiment, adult males and gravid females from the cohorts described above were individually isolated in a cup (2.8 cm diameter, 2.2 cm high). The cup contained a rose leaf disc (24 mm diameter) on water-saturated cotton wool and was sealed with a lid with a hole (12 mm diameter) covered with mite-proof gauze (80 µm). We thus starved the predators for 48 h before the experiment. *Phytoseiulus persimilis* predators can persist without food for more than 2 weeks in the presence of water (Sabelis 1981). Previous experiments (Revynthi et al. 2018b) showed that starvation for 48 h did not affect the cannibalistic behaviour of females more than that of males although the former have larger energy requirements. At the start of the experiment, seven young predatory mite larvae were transferred onto the first leaflet of the rose leaf at the upwind side of the wind tunnel. Larvae were chosen as prey, since they are the most vulnerable to cannibalism and do not feed (Amano and Chant 1977). Subsequently, a starved adult male or female predator from the same isofemale line as the larvae was released on the same leaflet. As a control, predators were individually put on the rose leaf without conspecific 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 leaf 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; the time of dispersal was recorded. The maximum of 6 h was chosen to prevent having larvae moulting to protonymphs, which can also cannibalise 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, thus also assessing the numbers of larvae that were missing. Only corpses from which the haemolymph was removed were counted as consumed larvae. We did not observe natural mortality in the larvae (dead larvae that were not eaten and their haemolymph had not been removed). For the control treatment without larvae, only the time of dispersal was recorded as 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 (N = 20 for each treatment).

Statistical analysis

During the experiments, one male and one female from the early-dispersal line died, resulting in the loss of one replicate of each. To determine whether there was a difference in the cannibalistic behaviour of the lines and genders, generalized linear mixed-effects models (GLMM) with a binomial error distribution were used (*glmer* of the lme4 package; Bates et al. 2015). The response variable was the occurrence of cannibalism (a binomial variable) during the entire observational period. Because the larvae are very small (ca. 230 µm long and 175 µm wide; Croft et al. 1999), the fate of missing larvae was unsure: they might have dispersed or their corpses might have dropped after having been cannibalised. We therefore performed two analyses. First, we assumed that missing larvae dispersed, and second, we assumed that they had been cannibalised and we assessed the occurrence of cannibalism under both scenarios. We furthermore analysed the proportions of cannibalised larvae, again considering both scenarios, with a similar model. Predator line, gender and their interaction were the fixed factors, whereas block was used as a random factor. Non-significant interactions and factors were removed to find the minimum adequate model (Crawley 2013). All models were checked for overdispersion and for normality of the error distribution.

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 (Therneau 2015). Censoring was applied to predators that did not disperse during the 6 h of the experiment. The fixed explanatory variables were line (early or late dispersers), treatment (cannibalism or control), 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 (Crawley 2013). All analyses were performed using R v.3.6.1 (R Core Team 2019).

To analyse differences in rates of cannibalism, we calculated cannibalism rate by dividing the numbers of larvae cannibalised and cannibalised + missing by the time until dispersal or until the end of the experiment, whichever came first. These rates were compared between lines and genders with a linear mixed effects model (*lme* of the package nlme, Pinheiro et al. 2017) with the $\sqrt{x}$-transformed rate of cannibalism as dependent variable and factors as above. To avoid problems with zero-inflated data, this was analysed only for those individuals that did cannibalise. Notice that the occurrence of cannibalism was analysed in the first analysis described, so this analysis can be seen as complementary to this first analysis.

Results

Assuming that the missing larvae dispersed, the tendency of the predators to cannibalise did not differ between the selection lines (GLMM: $\chi^2 = 0.033$, df = 1, P = 0.86), and males cannibalised more frequently than females but not significantly so (GLMM: $\chi^2 = 3.68$, df = 1, P = 0.055). In both lines, most males cannibalised, whereas ca. 50% of the females did not (Fig. 2a). Assuming that the missing larvae were cannibalised, predators

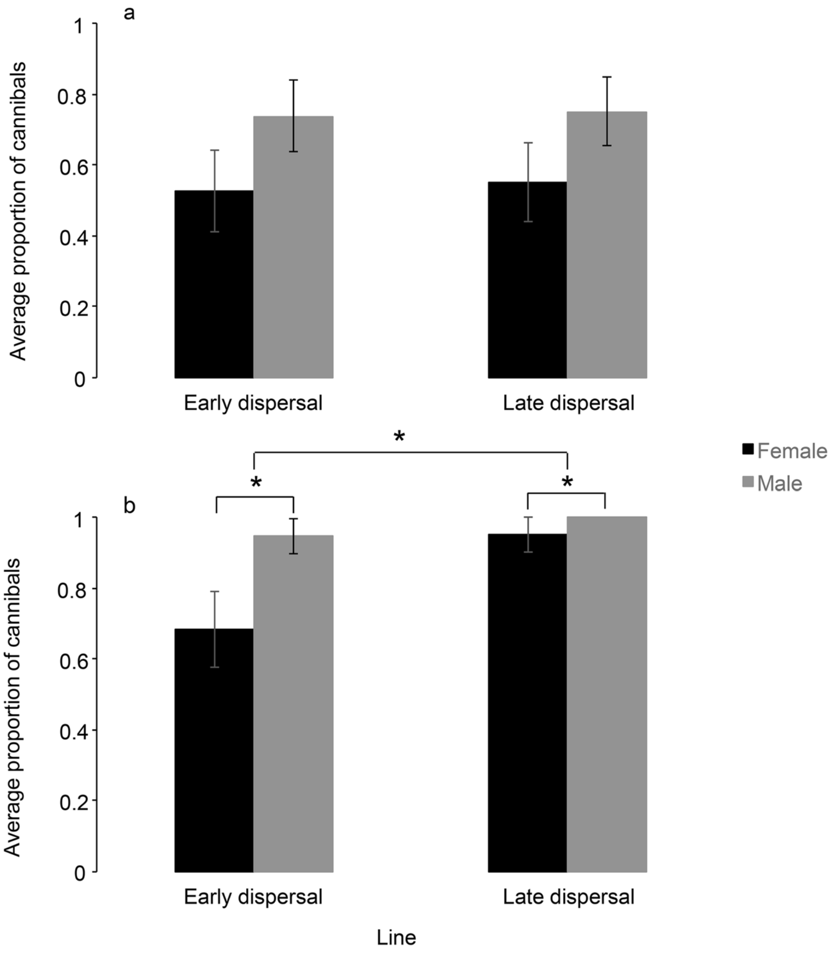

Fig. 2 Average proportion of adult predators that engaged in cannibalism, under the scenario that the missing larvae (**a**) had dispersed, or (**b**) were cannibalised by the female (black bars) and male (grey bars) predators of the early-dispersal line (both sexes, N = 19) and late-dispersal line (both sexes, N = 20). Whiskers indicate the standard error of the proportions. Asterisks indicate significant differences (GLMM, P < 0.05)

from the late-dispersal line had a higher cannibalistic tendency than predators from the early-dispersal line (GLMM: $\chi^2 = 13.79$, df = 1, P < 0.001). Under the same assumption, male predators engaged in cannibalism more often than female predators (Fig. 2b; GLMM: $\chi^2 = 13.54$, df = 1, P < 0.001).

Predators from both lines did not differ in timing of dispersal (Cox proportional hazards: $\chi^2 = 1.07$, df = 1, P = 0.30; Fig. 3) and there was no difference in dispersal with or without the presence of conspecific larvae (Cox proportional hazards: $\chi^2 = 0.029$, df = 1, P = 0.87; Fig. 3). Females, however, dispersed earlier than males (Cox proportional hazard: $\chi^2 = 4.56$, df = 1, P = 0.033).

Under the scenario that the missing larvae had dispersed, the proportion of cannibalised larvae did not vary with either the predator line (GLMM: $\chi^2 = 0.09$, df = 1, P = 0.77) or with gender (Fig. 4a; GLMM: $\chi^2 = 3.09$, df = 1, P = 0.08). Assuming that the missing larvae were cannibalised, predators from the early- and late-dispersal line did not differ in the amount of larvae that they consumed (GLMM: $\chi^2 = 0.44$, df = 1, P

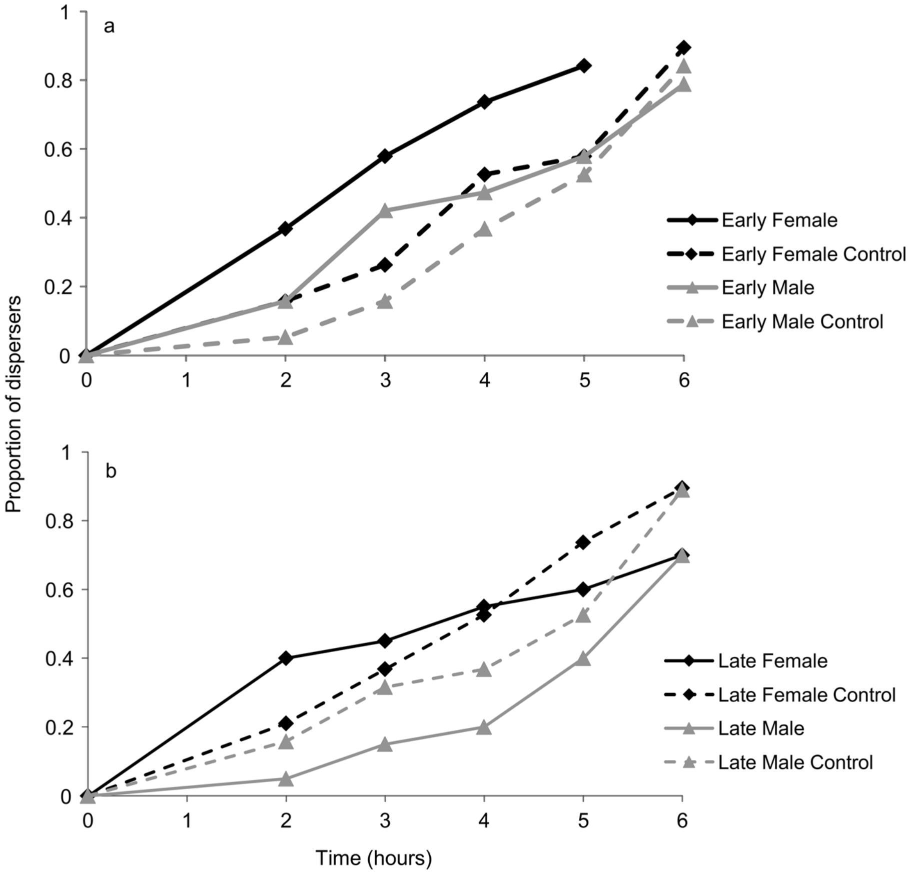

Fig. 3 Timing of male and female predatory mite dispersal with or without (control) the presence of conspecific prey. Curves show cumulative proportions of dispersers over time. **a** Early-dispersal isofemale line; **b** Late-dispersal isofemale line. Black lines (diamonds) are females, grey lines (triangles) are males, solid lines are treatments with conspecifics (cannibalism), dashed lines are control (no cannibalism)

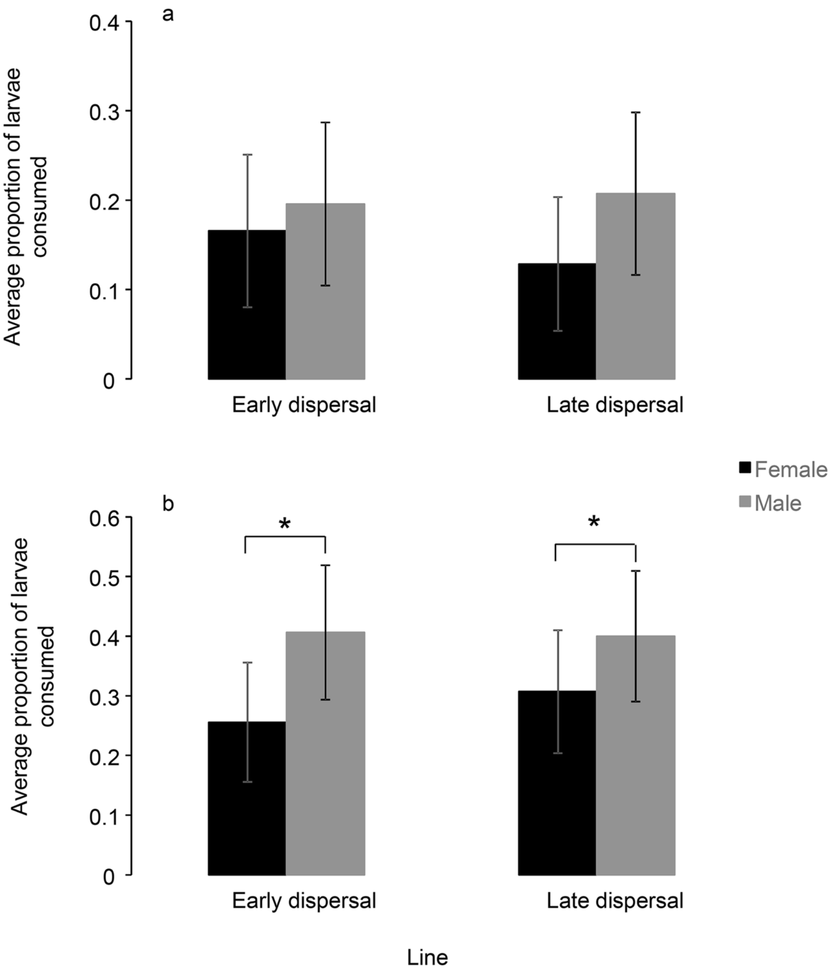

Fig. 4 Average proportion of consumed larvae, under the assumption that the missing larvae (**a**) dispersed, or (**b**) were consumed by the female (black bars) and male (grey bars) predators of early-dispersal line (both sexes, N = 19) and late-dispersal line (both sexes, N = 20). Whiskers indicate the standard error of the proportions. Asterisks indicate significant differences (GLMM, $P < 0.05$)

= 0.51), but male predators consumed more larvae than females (Fig. 4b; GLMM: $\chi^2 = 9.25$, df = 1, P = 0.002).

Although it is clear that males dispersed later than females and cannibalised more, it is not clear what is cause and what is effect: males could cannibalise more because they disperse later, and thus will have more time to encounter and attack larvae, or males could engage in cannibalism and as a result disperse later. Under the first scenario, we would expect that the numbers of larvae cannibalised by males and females per unit of time would be equal, whereas if males would have a higher tendency to cannibalise, they would attack more larvae per unit of time. An analysis of the rate of cannibalism of males and females of both lines showed no difference in these rates, neither when missing larvae were included as being cannibalized ($\chi^2 = 1.49$, d.f. = 1, P = 0.22) nor when excluded ($\chi^2 = 1.85$, d.f. = 1, P = 0.17; Fig. 5). The cannibalism rates also did not differ between lines ($\chi^2 = 1.34$, d.f. = 1, P = 0.25 and $\chi^2 = 1.93$, d.f. = 1, P = 0.16, respectively).

Discussion

Cannibalism and dispersal are two important phenomena that affect population 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; van den Beuken et al. 2019). Although many studies focus on how kin recognition can affect decisions of individuals to cannibalise (Pfennig 1997; Faraji et al. 2000; Schausberger and Croft 2001; van den Beuken et al. 2019) 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 behaviours are studied together. Due to the lack of an additional control for larval mortality and/or dispersal, it was not possible to know whether the missing larvae were eaten or dispersed, therefore we

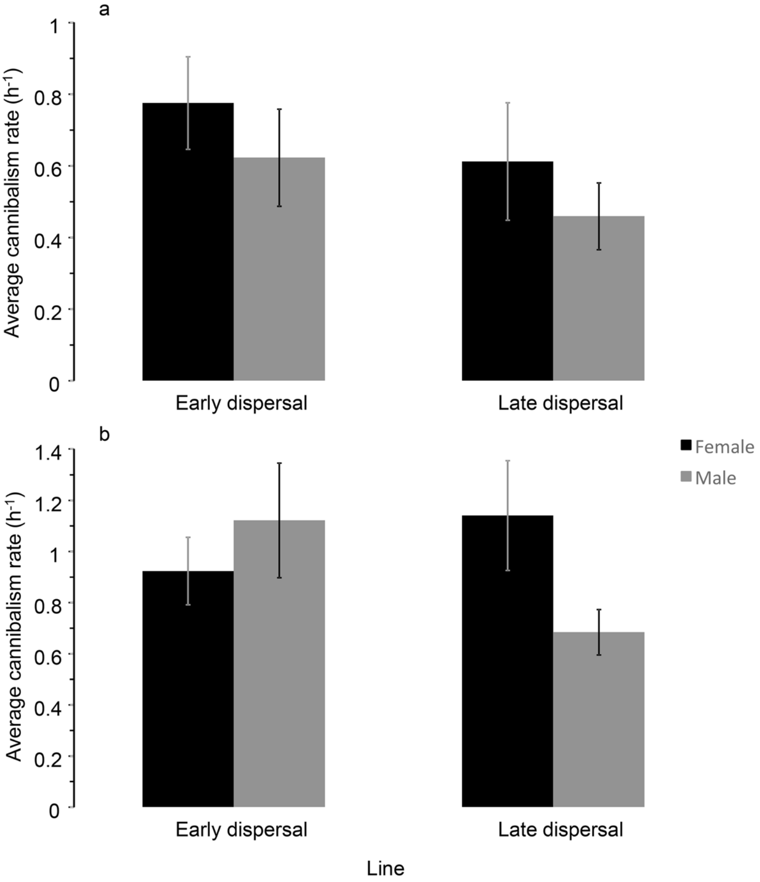

Fig. 5 Average (± SE) rates of cannibalism for individuals that did cannibalise (see Fig. 1 for proportions) under the scenario that the missing larvae (**a**) had dispersed, or (**b**) were cannibalised by the female (black bars) and male (grey bars) predators of the early- and late-dispersal line

assumed two scenarios. In the first scenario we assumed that the missing larvae dispersed but we could not detect them in the wind tunnel, whereas in the second we assumed that the missing larvae were cannibalised by their conspecifics but we could not detect the carcasses. Under the first scenario and contrary to expectations, our results did not show any statistically significant differences in cannibalism or dispersal behaviour between the two lines; hence, predators from the late-dispersal line were not more prone to cannibalise than those from the early-dispersal line. There was a trend towards male predators being more cannibalistic than females. Under the second scenario, however, predators from the late-dispersal line appeared to be more prone to cannibalise than those from the early-dispersal line and male predators engaged more often in cannibalism than female predators. Under both scenarios, the proportion of adults cannibalizing and the proportion of larvae consumed showed the same trend (Figs. 2 and 4), and we therefore tentatively conclude that predators from the late-dispersal line have a somewhat higher tendency to cannibalize than those of the early-dispersal line, and that males have a somewhat higher tendency to cannibalize than females.

Male predators were more prone to cannibalise and stay, whereas females engaged less in cannibalism and dispersed earlier from the leaf (Figs. 2 and 3). One explanation for the observed differences between the genders might be differences in the biology of males and females. Gravid females of *P. persimilis* need a lot of food to produce eggs (approx. seven *T. urticae* eggs to produce one *P. persimilis* egg; Laing 1968; Sabelis 1981) and females do not oviposit when cannibalising (Yao and Chant 1989). Adult males, in contrast, do not need much food (Sabelis, 1981), and instead spend most time searching for mates. 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 before these females disperse to find other prey patches. While waiting, males can cannibalise to survive. Cannibalising on immature males would then be the best option because it does not result in fewer future mates but does remove potential mate competitors.

An alternative explanation for the observed differences in the cannibalistic behaviour of males and females is based on 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 females are diploid and males haploid (only carrying genetic material from their mothers), there are asymmetries in relatedness with juveniles (Hamilton 1964a,b). When a female mates with a male, the female will have more offspring than the male, because the male only contribute genes to daughters. Thus, females will suffer from greater inclusive fitness loss if they engage in cannibalism than do males because of a higher chance that the cannibalised juvenile was related to the female cannibal. Hence, we hypothesize that under food limitation, adult females are less prone to cannibalise than adult males and will more often choose to disperse in order to refrain from cannibalism. We expect that males would specifically cannibalise other, immature males, to which they are less kin-related. This hypothesis, however, remains to be tested.

When cannibalising, males appeared to be more voracious (Fig. 4b), but fewer females than males engaged in cannibalism (Fig. 2a and b) because they dispersed earlier (Fig. 3). In other words, males dispersed later than females and thus had more time to cannibalise. To assess whether males and females were equally voracious, we analysed the rate of cannibalism by dividing the numbers of larvae eaten by the time until dispersal or, in case of no dispersal, until the end of the experiment. There was no significant difference in cannibalism rates between males and females (Fig. 5), suggesting that males and females were equally voracious when cannibalising, and that differences in the numbers of larvae cannibalised were caused by differences in the amount of time spent on the patch. Likewise, the differences in cannibalism between the two selection lines is not reflected in differences in the rate with which they cannibalize (Fig. 5).

The current experiments showed no significant differences in dispersal behaviour between the two selection lines. At first sight, this is strange because the lines were selected for different dispersal tendencies and have different prey exploitation strategies (Revynthi 2017). However, this selection took place in the presence of spider-mite prey, and dispersal in the experiments here was measured without spider mites. Even when the prey population has been exterminated by the predators, chemical cues associated with earlier presence of prey on the patch, may alter predator dispersal behaviour (Sabelis and Afman 1994). 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 behaviour between a Milker-like and a Killer-like line in the absence of prey. The current experiments simulated extreme conditions where spider mite prey and cues related to them were completely absent, and it was therefore expected that the predators would disperse from the arena in search for prey, regardless their dispersal strategy.

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 support this prediction only under the scenario that the missing larvae were cannibalised; the late-dispersal line engaged more in cannibalism than the early-dispersal line (Fig. 2b). The current experimental study on dispersal and cannibalism gives new insight into the cannibalistic behaviour of the two genders based on differences in their behaviour and we therefore propose that future theoretical studies should take these differences into account.

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Compliance with ethical standards

Conflicts of interest The authors declare no conflict of interest

Ethics approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Consent to participate Informed consent was obtained from all individual participants included in the study.

Consent for publication All individual participants consent to the publication of this study.

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