Should I stay or should I go?

The role of dispersal and cannibalism in exploitation strategies of a predatory mite

Revynthi, A.M.

Publication date
2017
Document Version
Other version
License
Other

4

Gender-specific differences in cannibalism between a laboratory strain and a field strain of a predator

A.M. Revynthi, A. Janssen & M. Egas

Abstract — Cannibalism – i.e., intraspecific predation – is a common phenomenon that often occurs when food is limited. Many phytoseiid species, including *Phytoseiulus persimilis*, are known to engage in cannibalism when food is scarce and when there is no possibility to disperse. Under natural conditions, however, especially the females of these predatory mites are known to disperse when food is scarce. Males, in contrast, are expected to stay and wait for potential mates to mature. While staying, they could then obtain food by cannibalizing. Because conditions under which these mites are usually cultured prevent dispersal, it has been suggested that prolonged culturing may affect cannibalistic behavior. We hypothesize that it should especially affect cannibalism by adult females, because they consume by far most food. We tested this by comparing two strains, one of which had been in culture for over 20 years, whereas the other was recently collected in the field. Because it is known that this predator can discriminate between kin and non-kin and prefers cannibalizing the latter, we also started isofemale lines of these two original strains, with the idea to construct lines with high kin-relatedness. We subsequently tested to what extent the adult females and males of the original strains and the isofemale lines fed on conspecifics from the same culture. In a closed system, we observed the behavior of adult predators that were offered conspecific larvae as prey. Males engaged more often in cannibalism than females, and females of the strain with the long culture history engaged more in cannibalism than those of the recently collected strain, both in agreement with our ideas. The original strains and the isofemale lines did not differ in cannibalistic behavior, suggesting that there was no large difference in kin-relatedness within the original strains and the isofemale lines.

INTRODUCTION

Cannibalism, the act of killing and consuming an individual of the same species, is a common phenomenon across the animal kingdom. It occurs in various species such as birds (Cain et al. 1984), fish (Okuda and Yanagisawa 1996), frogs (Ringler et al. 2017), salamanders (Takatsu and Kishida 2015), spiders (Bilde and Lubin 2001), insects (Tschinkel 1981) and mites (Yao and Chant 1989). Animals prey on their conspecifics mainly as a response to low food densities (Fox 1975). Cannibalism, however, can also be affected by stress, kin competition or mate competition and prey vulnerability (Fox 1975; Polis 1981; Pfennig 1997). In times of food scarcity, cannibalism can be very beneficial to the cannibal, because under certain circumstances it can be the only way of obtaining food and nutrients (Fox 1975; van den Bosch et al. 1988). Nevertheless, cannibalism can result in injuries, pathogen transmission and, in case the victim is a relative, in loss of inclusive fitness (Pfennig 1997).

Many mite species of the Phytoseiidae family are known for their cannibalistic behavior (Schausberger 2003), and the cannibalistic stage commonly used in experiments is the gravid adult female feeding on juveniles (Schausberger 2003). Many of the experiments on cannibalism in phytoseiids are done in closed arenas, where cannibal or victim cannot escape. Hence, these experiments test for the possibility for cannibalism to occur rather than assessing their importance under more natural conditions where individuals can disperse. For phytoseiids, this is essential because typical populations of predators and prey are short-lived, and end either by the host plant of the prey being overexploited or by the prey being exterminated by the predators (Janssen and Sabelis 1992; Pels and Sabelis 1999). At the end of this interaction period, the predators disperse in search of new prey patches. Adult females disperse earlier than adult males and juvenile stages (Pels 2001; Revynthi et al., CHAPTER 2); once inseminated, females need food to reproduce, and juveniles need to become mature and inseminated before they can successfully disperse. Consequently, males are better off not dispersing, but waiting for new mates to develop. In order to survive, males and juveniles can engage in cannibalism. In previous experiments with predatory mites, we indeed observed much cannibalism by adult males on larvae under conditions of low prey densities (Revynthi et al., CHAPTER 2). Hence, we suggest that males may have a higher tendency to cannibalize than females.

It is generally accepted that culturing organisms may result in changes in behavior, life history and genetic variation (Mackauer 1976; Hopper et al. 1993), and these changes may affect cannibalism (Dennehey et al. 2001). When rearing phytoseiids, dispersal is often prevented, for obvious reasons. However, this can result in strong selection against dispersal behavior because individuals that try to disperse either end up dead in some barrier, or loose time and possibly energy when attempting to escape. It has been suggested that under conditions of laboratory cultures, higher cannibalism tendency is unintentionally selected for: due to space limitation, predators cannot disperse in search of more food when the prey are temporarily eliminated (Elliot et al. 2002). This would mean that laboratory strains would have a higher tendency to cannibalize than strains in the field, and this would hold especially for females.

However, rearing for longer periods may also increase the kin-relatedness among individuals, and it is known that phytoseiids tend to avoid kin-cannibalism (Schausberger and Croft 2001). This would result in lower rates of cannibalism in strains that have been in cul-

ture for a longer period. In the present study we have tested whether a recently collected strain of the predatory mite *Phytoseiulus persimilis* is more or less cannibalistic than a strain that has been in culture for more than 20 years. Several studies investigated the cannibalistic behavior of adult females of this species (Yao and Chant 1989; Walzer and Schausberger 1999; Schausberger and Croft 2001; Schausberger 2007; Schausberger and Hoffmann 2008), but not cannibalism by adult males. We investigated cannibalism in both males and females and tested whether males and females of both strains differed in the tendency to cannibalize in relation to the time that had been in culture.

Material and methods

Plant and prey cultures

Lima beans (*Phaseolus lunatus*) were used as a host and were grown from seeds in a climate room (25 °C, 60% RH, 16L:8D) free of herbivores. The spider mites (*Tetranychus urticae*) that were used as food for *P. persimilis* were originally collected from cucumber plants in a commercial greenhouse in May 1994 (Pallini et al. 1997). They were reared on Lima bean plants in a walk-in climate room (26 °C, 60% RH, 16L:8D).

Predatory mites

Two strains of *P. persimilis* were used. One strain derived from Koppert Biological Systems (Berkel en Roderijs, the Netherlands) and one from Alcamo in Sicily (see Revynthi et al., Chapter 2). These two strains were chosen because we have information about their dispersal behavior (Pels and Sabelis 1999; Revynthi et al., Chapter 2) and because we were interested in observing whether there are differences in the cannibalistic behavior between a laboratory strain – i.e., Koppert – and a strain recently collected from the field – i.e., Alcamo. The predators were kept in closed rearing cages, which allowed the predators to leave and subsequently return to the prey patch (as described in Pels and Sabelis 1999) inside a climate room at 25 °C, 70% RH and 16L:8D. To test for an effect of kinship, an isofemale line of each strain was created by isolating a gravid female of *P. persimilis* from the culture and introducing it individually in a separate rearing unit with prey (*T. urticae*). The female was allowed to oviposit and create her own family. The strains and isofemale lines were fed 3× per week by introducing two bean (*P. lunatus*) leaves infested with spider mites (*T. urticae*).

To obtain sufficient numbers of gravid females and males of the same age (2-day-old adults), as well as larvae, cohorts were created as follows. Ten gravid female predatory mites from each of the two strains and 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 cultures.

Evaluation of cannibalistic behavior

To measure the cannibalistic tendency of the predatory mites in a closed system that did not allow for dispersal, small plastic cups (2.8 cm diameter, 2.2 cm height) were used. Each cup had a lid with a hole (12 mm diameter) covered with mite-proof gauze (80 μm diameter) for ventilation. Forty-eight h prior to the start of the experiment, males and gravid females from

the cohorts described above were individually isolated in a cup, which contained a bean leaf disc (24 mm diameter) on water-saturated cotton wool. The predators did not receive any food during this period (48 h in total).

At the start of the experiment, three young predator larvae from the same culture as the adult and from a cohort started three days earlier were transferred to a cup similar to those used for the starvation process. Subsequently, a starved adult predatory male or female was released in the same cup; hence, adults and larvae originated from the same culture, but were produced in separate cohorts. The predator was observed 5 min after its release and after that every 15 min for a total period of 1 h. Every time the number of alive and consumed larvae was recorded. Cannibalized larvae were recognized by the carcass from which the haemolymph was removed (Yao and Chant 1989). Replicates where a larva had molted to protonymph or died from natural causes were excluded. There were eight treatments, each with 30 replicates. In the 'non-kin' treatment, predators and larvae came from different cohorts of the same main culture; in the 'kin' treatment, predators and larvae were from different cohorts of the same isofemale line. The experiment was conducted in 12 blocks (days) and each block contained all the treatments.

Statistical analysis

To estimate which of the two genders and/or strains engaged more often in cannibalism and whether kinship affected their behavior a generalized linear mixed effect model with binomial distributions was 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, gender, strain and kinship were the fixed factors and block was used as a random factor. The analysis was performed using R v.3.0.1 (R Development Core Team 2015).

RESULTS

We only analyzed the data at the end of the observation period, i.e., after 1 h since the release of the adult predator in the cup, because we did not observe changes of cannibalism rate in the course of the experiment since within an hour on average one cannibalistic event occurred. Male predators engaged in cannibalism more often than females (GLMER: $\chi^2 = 25.5$, d.f. = 1, $P << 0.001$; FIGURE 4.1). The Koppert strain had significantly more cannibals than the Alcamo strain (GLMER: $\chi^2 = 8.93$, d.f. = 1, $P = 0.003$; FIGURE 4.1). This was because females of the Koppert strain cannibalized significantly more than females of the Alcamo strain (GLMER: $\chi^2 = 6.71$, d.f. = 1, $P = 0.0096$; FIGURE 4.1), but cannibalism by males was not significantly different ($\chi^2 = 2.24$, d.f. = 1, $P = 0.135$). Kinship did not affect cannibalistic behavior (GLMER: $\chi^2 = 0.032$, d.f. = 1, $P = 0.86$; FIGURE 4.1).

DISCUSSION

We used one laboratory strain and one that was recently collected in the field (Revynthi et al., CHAPTER 2) and found that the laboratory strain (Koppert) had a higher tendency to cannibalize than the field strain (Alcamo). It has been suggested that under conditions of laboratory cultures, higher cannibalism tendency is unintentionally selected for (Denehy et al. 2001; Elliot et al. 2002). Our results, however, show high levels of cannibalism in a field strain; the difference in cannibalistic tendency between the strains was small.

Earlier studies have focused on the voraciousness of cannibalistic females of *P. persimilis* (Walzer and Schausberger 1999) and their ability to discriminate between kin and non-kin (Schausberger and Croft 2001). To the best of our knowledge, this is the first time that the cannibalistic behavior of male predators of *P. persimilis* is investigated. Our experiments show that the males of two strains, one that has been in culture for a long time, and one that was recently collected, were more prone to cannibalize than gravid females, regardless of relatedness with the victims.

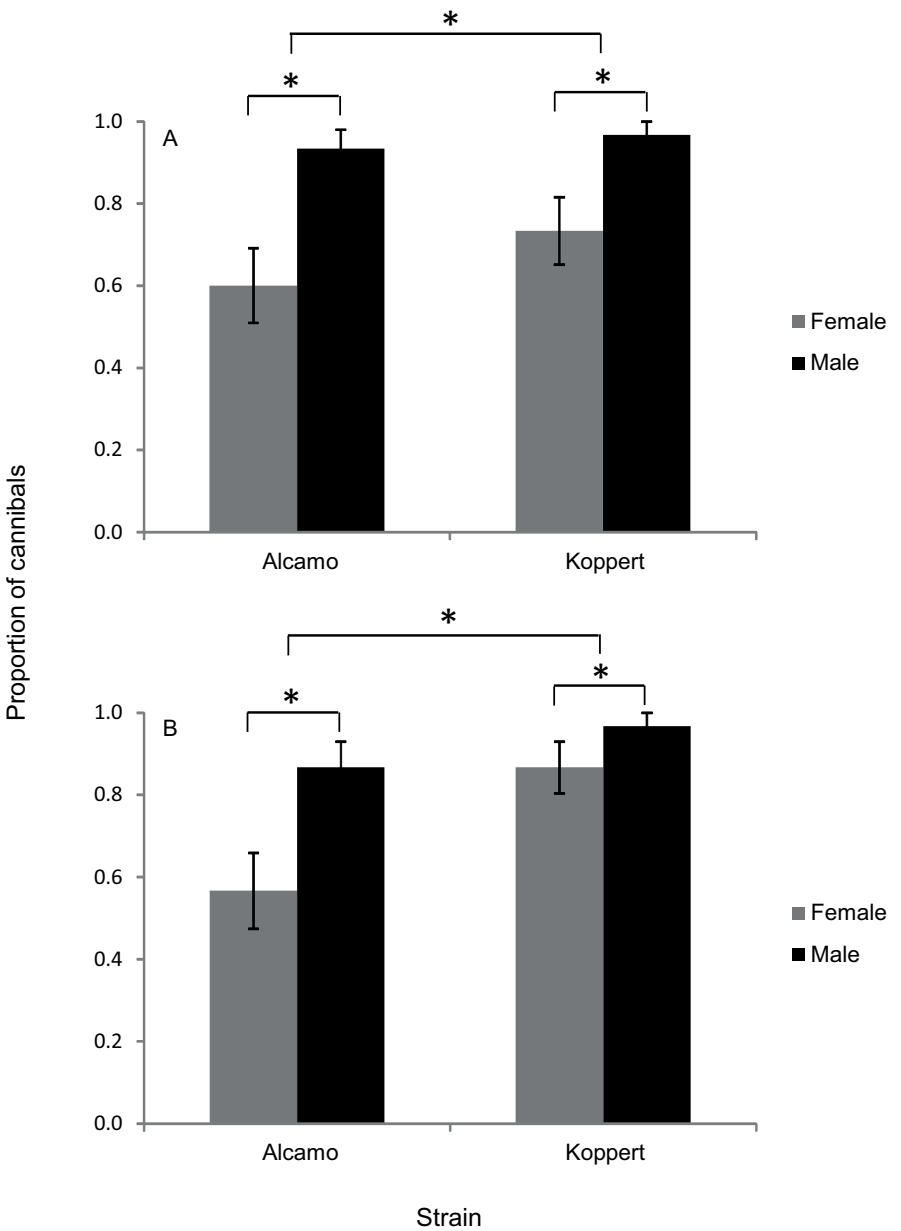

Figure 4.1 — The proportion of adult predators that cannibalized. Shown are proportions of males (black bars) and females (grey bars) of two strains (Alcamo and Koppert) that cannibalized on related larvae (kin, panel A) or unrelated larvae (non-kin, B). Asterisks indicate significant differences. N = 30 for each bar. Whiskers indicate the standard errors of the proportions.

Predatory mites that had been in culture for a long period had a significantly higher tendency to cannibalize than a recently collected strain of the same species. However, cannibalism rates were high for both strains. Interestingly, males cannibalized significantly more than females. This difference is probably caused by differences in the behavior of males and females: whereas females search for prey, males search for conspecifics to mate. However, there is an alternative explanation for the differences in the cannibalistic behavior of males and females, which is based on asymmetries in relatedness with offspring. Inclusive fitness theory (Hamilton 1964a,b; Gardner et al. 2011) suggests that evolution will favor the individuals that are able to recognize relatives and avoid feeding on them, regardless the gender (Pfennig 1997). In haplodiploid systems, however, differences are expected between the genders due to the difference in average degree of relatedness with the victim between male and female cannibals. Phytoseiid mites are pseudo-arrhenotokous (Schulten 1985): males and females both derive from fertilized eggs but only the females remain diploid and carry both maternal and paternal chromosomes (McMurtry et al. 1970). The males loose the paternal set of chromosomes shortly after syngamy (Helle et al. 1978; Sabelis and Nagelkerke 1988). Hence, in these predators, the adult females are expected to suffer from greater inclusive fitness loss than males, because they have more offspring than males, which only contribute genetically to daughters, and do not have sons. Thus it can be hypothesized that gravid adult females are less prone to cannibalism than males, despite higher energy requirements. We expect that males would specifically cannibalize other, immature males, because this reduces future competition for mates, and by letting female immatures live, they increase the chance on a future mate. This remains to be tested.

We found no effect of kinship on cannibalism, suggesting that under no-choice conditions, the decision to cannibalize is not affected by the degree of relatedness with the potential victims they encounter. Hence, this suggests that no inbreeding effects occurred in the strain that had a long history of being cultured or that inbreeding did not affect the tendency to cannibalize. To our best knowledge, inbreeding effects in *P. persimilis* are absent unless long periods of strong inbreeding are invoked (Poe and Enns 1970). This is common for haplodiploid species, where selection against recessive alleles always acts on the haploid males and the frequency of such alleles therefore remains low, except for genes that specifically code for female traits such as egg production (Tien et al. 2015). We also did not observe population declines or any other adverse effects of inbreeding in either of the two isofemale lines. The isofemale lines were started with one female of each strain. This female was therefore potentially not representative for the entire population. For example, it could have had a higher genetic tendency for cannibalism. This would then have resulted in less variation in the cannibalistic behavior in the isofemale lines than in the original lines, since those mites are genetically fixed whereas the original lines were genetically more diverse. However, we found no such difference in variation in the cannibalistic behavior between strains and lines.

Several studies have focused on kin recognition in phytoseiid mites (Faraji et al. 2000; Schausberger and Croft 2001), but also in other animal taxa (Pfennig 1997; Bilde and Lubin 2001; Parsons et al. 2013; Bayoumy and Michaud 2015; Ringler et al. 2017). Schausberger and Croft (2001) show that *P. persimilis* is able to discriminate between kin and non-kin and preferred to cannibalize the latter. Even though our study was not focused on kin discrimi-

nation of *P. persimilis*, we explored whether the level of relatedness with the prey could have affected cannibalistic behavior. The lack of variation between the kin and non-kin treatment does not contradict earlier reports of kin discrimination in this species (Schausberger and Croft 2001; Schausberger 2004) because we did not offer the cannibals a choice between kin and non-kin victims.

In natural settings, the predators can opt out of cannibalizing by dispersing away from the patch without prey and search for a new prey patch. For the two strains used here, we have information about their dispersal behavior (Pels and Sabelis 1999; Revynthi et al., CHAPTER 2). In wind tunnel experiments, both strains showed a tendency to disperse only after heterospecific prey were depleted, showing the so-called Killer strategy of prey exploitation (van Baalen and Sabelis 1995). Theoretical work on the evolution of cannibalism and predator dispersal predicts that predators with the Killer strategy are selected for higher cannibalistic tendency (Pels 2001). Given the variation for this prey exploitation behavior that was found in previous experimental work (Pels and Sabelis 1999; Revynthi et al., CHAPTER 2), we argue that there may also be variation among natural populations of *P. persimilis* in cannibalistic tendency. Future research should explore whether the two genders will show similar behavior as observed in this study when they have the option to disperse.

ACKNOWLEDGEMENTS — We want to thank Joren Bruggink for conducting pilot experiments in order to optimize the experimental procedure. This research was supported by the EFRO Green Innovation Cluster VP4.

REFERENCES

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting Linear Mixed-Effects Models Using **lme4**. *Journal of Statistical Software*, **67**, 1–48.

Bayoumy, M.H. & Michaud, J.P. (2015) Egg Cannibalism and its Life History Consequences Vary with Life Stage, Sex, and Reproductive Status in *Hippodamia convergens* (Coleoptera: Coccinellidae). *Journal of Economic Entomology*, **108**, 1665–1674.

Bilde, T. & Lubin, Y. (2001) Kin recognition and cannibalism in a subsocial spider. *Journal of Evolutionary Biology*, **14**, 959–966.

Cain, J.R., Weber, J.M., Lockamy, T.A. & Creger, C.R. (1984) Grower diets and bird density effects on growth and cannibalism in ring-necked pheasants. *Poultry science*, **63**, 450–7.

Dennehy, J.J., Robakiewicz, P. & Livdahl, T. Larval Rearing Conditions Affect Kin-Mediated Cannibalism in a Treehole Mosquito. *Oikos*, **95**, 335–339.

Elliot, S.L., Sabelis, M.W. & Adler, F.R. (2002) Virulence management in biocontrol agents. *In: Adaptive Dynamics of Infectious Diseases: In pursuit of virulence management. (Eds. Dieckmann U., Metz J.A.J., Sabelis M.W. & Sigmund K.).* Cambridge University Press. Cambridge. pp. 448-459.

Faraji, F., Janssen, A., Van Rijn, P.C.J. & Sabelis, M.W. (2000) Kin recognition by the predatory mite Iphiseius degenerans: discrimination among own, conspecific, and heterospecific eggs. *Ecological Entomology*, **25**, 147–155.

Fox, L.R. (1975) Cannibalism in Natural Populations. *Annual Review of Ecology and Systematics*, **6**, 87–106.

Gardner, A., West, S.A. & Wild, G. (2011) The genetical theory of kin selection. *Journal of Evolutionary Biology*, **24**, 1020–1043.

Hamilton, W.D. (1964a) The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, **7**, 1–16.

Hamilton, W.D. (1964b) The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, **7**, 17–52.

Harshman, L.G. & Zera, A.J. (2007) The cost of reproduction: the devil in the details. *Trends in Ecology & Evolution*, **22**, 80–86.

Hopper, K.R., Roush, R.T. & Powell, W. (1993) Management of Genetics of Biological-Control Introductions. *Annual Review of Entomology*, **38**, 27–51.

Lesne, P., Trabalon, M. & Jeanson, R. (2016) Cannibalism in spiderlings is not only about starvation. *Behavioral Ecology and Sociobiology*, **70**, 1669–1678.

Mackauer, M. (1976) Genetic Problems in the Production of Biological Control Agents. *Annual Review of Entomology*, **21**, 369–385.

McMurtry, J.A., Huffaker, C.B. & van de Vrie, M. (1970) Ecology of tetranychid mites and their natural enemies: A review: I. Tetranychid enemies: Their biological characters and the impact of spray practices. *Hilgardia*, **40**, 331–390.

Okuda, N. & Yanagisawa, Y. (1996) Filial cannibalism in a paternal mouthbrooding fish in relation to mate availability. *Animal Behaviour*, **52**, 307–314.

Pallini, A., Janssen, A., Sabelis, M.W., Pallini, A., Janssen, A. & Sabelis, M.W. (1997) Odour-mediated responses of phytophagous mites to conspecific and heterospecific competitors. *Oecologia*, **110**, 179–185.

Parsons, W., Zhong, W. & Rudolf, V.H.W. (2013) Mating status and kin recognition influence the strength of cannibalism. *Animal Behaviour*, **85**, 365–369.

Pels, B. and Sabelis, M.W. (1999) Local Dynamics, Overexploitation and Predator Dispersal in an Acarine Predator-Prey System. *Oikos*, **86**, 573–583.

Pels, B. (2001) Evolutionary Dynamics of Dispersal in Predatory Mites. ISBN: 9076894108. University of Amsterdam. pp. 147.

Pfennig, D.W. (1997) Kinship and Cannibalism. *BioScience*, **47**, 667–675.

Poe, S., & Enns, W. (1970). Effects of inbreeding on closed populations of predaceous mites (Acarina: Phytoseiidae). *The Canadian Entomologist,* **102**, 1222-1229.

Polis, G.A. (1981) The evolution and dynamics of intraspecific predation. *Ann. Rev. EeaL Syst*, **12**, 225–51.

R Development Core Team. (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Ringler, E., Barbara Beck, K., Weinlein, S., Huber, L. & Ringler, M. (2017) Adopt, ignore, or kill? Male poison frogs adjust parental decisions according to their territorial status. *Scientific Reports*, **7**, 43544.

Sabelis, M.W. & Nagelkerke, C.J. (1988) Evolution of pseudo-arrhenotoky. *Experimental & Applied Acarology*, **4**, 301–318.

Schausberger, P. (2003) Cannibalism among phytoseiid mites: a review. *Experimental & Applied Acarology*, **29**, 173–191.

Schausberger, P. (2004) Ontogenetic isolation favours sibling cannibalism in mites. *Animal Behaviour*, **67**, 1031–1035.

Schausberger, P. (2007) Kin recognition by juvenile predatory mites: prior association or phenotype matching? *Behavioral Ecology and Sociobiology*, **62**, 119–125.

Schausberger, P. & Croft, B.A. (2001) Kin recognition and larval cannibalism by adult females in specialist predaceous mites. *Animal Behaviour*, **61**, 459–464.

Schausberger, P. & Hoffmann, D. (2008) Maternal manipulation of hatching asynchrony limits sibling cannibalism in the predatory mite *Phytoseiulus persimilis*. *Journal of Animal Ecology*, **77**, 1109–14.

Schulten, G.G.M. (1985) Pseudo-arrhenotoky. In: Spider mites, Their biology, natural enemies and control 1B. (Eds. Helle W. & Sabelis M.W.). Elsevier. Amsterdam. pp. 67-71.

Takatsu, K. & Kishida, O. (2015) Predator cannibalism can intensify negative impacts on heterospecific prey. *Ecology*, **96**, 1887–1898.

Tien, N.S.H., Sabelis M.W. & Egas M. (2015). Inbreeding depression and purging in a haplodiploid: gender-related effects. *Heredity*, **114,**327-332.

Tschinkel, W.R. (1981) Larval dispersal and cannibalism in a natural population of Zophobas atratus (Coleoptera: Tenebrionidae). *Animal Behaviour*, **29**, 990–996.

van Baalen, M. & Sabelis, M.W. (1995) The Milker-Killer Dilemma in Spatially Structured Predator-Prey Interactions.*Oikos*, **74**, 391–400.

van den Bosch, F., de Roos, A.M. & Gabriel, W. (1988) Cannibalism as a life boat mechanism. *Journal of Mathematical Biology*, **26**, 619–633.

Walzer, A. & Schausberger, P. (1999) Cannibalism and interspecific predation in the phytoseiid mites *Phytoseiulus persimilis* and *Neoseiulus californicus*: predation rates and effects on reproduction and juvenile development. *BioControl*, **43**, 457–468.

Yao, D.S. & Chant, D.A. (1989) Population growth and predation interference between two species of predatory phytoseiid mites (Acarina: Phytoseiidae) in interactive systems. *Oecologia*, **80**, 443–455.