Should I stay or should I go?
The role of dispersal and cannibalism in exploitation strategies of a predatory mite

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General discussion

This thesis extends our knowledge of exploitation and dispersal strategies in predator-prey interactions, using an acarine predator-prey system. The novelty of my study lies in three elements. First, I show that it is possible to select for differences in dispersal strategies, i.e., the Milker and Killer strategy, and this offers the opportunity to study the evolution of alternative exploitation strategies. Second, I found that prolonged culturing of predatory mites can affect their cannibalistic behavior especially in females. Third, I experimentally linked cannibalism and dispersal and investigated how these phenomena affect each other.

Prudent predation, exploitation and dispersal strategies

The exploitation of a growing food source by a consumer population at a rate that maximizes the long term yield is defined as prudent predation (Slobodkin 1968). A predator population can show prudent exploitative behavior either by decreased feeding on its prey or by part of the population dispersing away from it. Both strategies lead to a decrease in the predation rate and allow the local prey population to increase. However, prudent predation is evolutionary unstable (Maynard Smith 1964) because prudent predators are outcompeted by selfish predators. Therefore, prudent predation is only a viable strategy when the prudent predators are kin-related to the other individuals in the patch. Thus, although the fitness of the prudent individuals could be increased by being less prudent, their inclusive fitness increases by being prudent. In this thesis I focus on the second form of prudent predation, i.e., dispersal of part of the predator population before prey depletion. When a predator finds a prey patch, it is faced with a dilemma: which strategy is the best for the predator as well as the predator offspring? Is it better to adopt a selfish strategy by exploiting the prey population fast and disperse only after prey extermination, or is it more profitable to adopt a prudent strategy by dispersing before prey depletion, thereby decreasing the predation rate on the local prey population and allowing this population to grow? This dilemma is known as the Milker-Killer dilemma (van Baalen and Sabelis 1995a).

The predator's decision regarding which exploitation and dispersal strategy to adopt is affected by external factors such as prey density, the dynamics of the prey population, seasonality, connectivity of local populations, intraspecific interactions; as well as by group and kin selection. Here, I discuss how ephemeral factors, group and kin selection can affect predator exploitation and dispersal strategies. In doing so, I address the six questions that were presented in the general introduction (Chapter 1).

1. Which is the best exploitation strategy for a predator, to milk or to kill?

The short answer is that it depends on the probability of invasion by predators with a different exploitation strategy and on the initial predator-prey ratio in a prey patch. The Milker

strategy is a prudent exploitation strategy. Theoretical predictions show that this strategy cannot be evolutionary stable within a local population when the invasion probability by Killer predators is high (van Baalen and Sabelis 1995a). When Killer predators invade a patch inhabited by Milkers, they disperse only after they have consumed all the prey that the Milkers have set aside for future use by their kin. Hence, the Milker strategy can only be evolutionarily stable at a metapopulation level when local prey populations are sufficiently isolated from each other (van Baalen and Sabelis 1995a; Pels and Sabelis 1999; Pels et al. 2002).

Initial prey and predator densities in a local patch can also affect predator exploitation strategies. Van Baalen and Sabelis (1995a) calculated for which combinations of initial predator-prey ratios in the patch, predator and prey growth rate and predation rate the Milker strategy can evolve. Their simulations showed that the Killer strategy is generally favored by selection, but there is also space for the Milker strategy to evolve. The authors found that the Milker strategy can evolve when the probability of co-infestation of a prey patch by another female is low. When a predator population is founded by a single female, selection will favor prudent predation because the predator population will be only consisted of relatives. When the probability of subsequent invasions by other females is high, however, selection will favor predators that rapidly exploit the local prey patch, i.e., Killers.

Predator exploitation strategies can be affected by prey density, but prey density is, in turn, also affected by their own exploitation strategy. The Milker-Killer dilemma also occurs among prey exploiting a food source. Prey can exploit their food in a prudent (Milker) way, allowing the food to grow, resulting in a longer interaction – or in a selfish (Killer) way, causing fast overexploitation of the food. The best strategy for prey as well as for predators is a result of the interaction between the prey and predator strategies and it is not clear which of the two species gains the upper hand.

2. Can we find Milkers in nature?

Theory provides some evidence for the evolution of prudent exploitation strategies, such as the Milker strategy (van Baalen and Sabelis 1995a; Pels et al. 2002). But the question whether we can find this exploitation strategy in nature still remains. Pels and Sabelis (1999) collected nine populations of *P. persimilis* along the coast and one inland population on Sicily (Italy). They show that all predator strains exterminated local prey populations, and the timing of dispersal appeared to have a genetic basis: one isofemale line derived from a coastal strain consistently showed dispersal close to or after prey elimination, whereas individuals of an isofemale line derived from the inland strain consistently dispersed long before all prey were eliminated. Even though these two isofemale lines differed in their dispersal rate and their interaction period with the prey, they did not show the predicted differences in the cumulative number of dispersers: early dispersal did not result in higher overall numbers of dispersers. In CHAPTER 2, I presented a more thorough survey of predator dispersal behavior in natural populations and quantified the extent of variation in dispersal strategies from these populations. The collected strains differed in their dispersal rate, but the differences in the dispersal rate did not result in differences in the interaction period between the prey and the predators or in the cumulative number of dispersers, as predicted by van Baalen and Sabelis (1995). One may argue that the predictions of the Milker-Killer dilemma are not

accurate due to the simplifying assumptions of the model, such as a constant predator dispersal rate. The results of Chapter 3, however, revealed that selected lines for different timing of dispersal do show the population dynamical consequences predicted by theory. What then can we conclude about the existence of the Milker strategy in nature?

The experiments described in Chapters 2 and 3 were conducted in a climate room under stable environmental conditions and controlled interspecific interactions. In nature, however, abiotic and biotic conditions are involved. Seasonality can have a large impact on the abundance of predator-prey populations and as a result, also on the presence of Milkers and Killers. The Mediterranean region is characterized by wet mild winters and dry hot summers. Temperature and humidity are known to affect *P. persimilis* (Stenseth 1979), which requires high temperature and high relative humidity for its development. *Tetranychus urticae* is known to develop better at moderate temperatures, i.e., 25-30 °C (Jeppson et al. 1975; Sabelis 1981). Unfavorable environmental conditions due to seasonality may affect predator abundance and, as a consequence, also initial predator-prey ratios in a local patch and connectivity among local populations. During winter and summer, the environmental conditions are not favorable for the predators or prey. Thus, we can expect that during spring months there are higher chances to find Milkers in nature because prey densities are relatively higher than in winter and summer and connectivity among local populations is not yet strong. Pels and Sabelis (1999) collected predatory mites in Sicily during May, whereas in the current study the predators that derived from Sicily were collected early June. One month may not seem a large period, but for a predator that has a life cycle of 7 days at 25 °C (Laing 1968; Sabelis 1981) a month results in four generations. Based on the theoretical predictions we expect to find Killers at the center of the geographic distribution, where predator densities are high; and Milkers at the boarders, where predator densities are low (van Baalen and Sabelis 1995a; Pels and Sabelis 1999). In practice, for *P. persimilis* it is still unknown which is its geographic distribution, thus it is very difficult to accurately estimate where we can expect to find Milkers and Killers. Pels and Sabelis in 1995 managed to collect predators from an inland isolated site 50 km away from the coast in Enna. This collected strain was the one dispersing before prey elimination, supporting the theoretical predictions about the evolution of the Milker strategy in isolated sites. The authors, however, in their article stated that this finding may be 'sheerly coincidental' and pointed out the need for further studies. I visited this site in 2014 but I did not find predators. Hence one may speculate that the presence of Milker-like strains is ephemeral.

Seasonality also affects the occurrence of other species that can be food competitors or intraguild predators. *Phytoseiulus persimilis* is not the only predator feeding on *T. urticae* in the Mediterranean region. Other natural enemies that feed on spider mites are phytoseiid mites such as *Neoseiulus californicus* (Escudero and Ferragut 2005) and *Iphiseius degenerans* (McMurtry 1977), and mirid bugs, such as *Macrolophus pygmaeus* (Perdikis et al. 2011). In addition, several of these predators can prey on *P. persimilis* (Walzer and Schausberger 1999, 2011; X. Zhang, pers. obs.). How predator exploitation strategies are affected by intraguild predation, i.e., when predation also occurs among predators that share a food source (Polis et al. 1989), is an open question. Which exploitation strategy is the best under these conditions? The predators are faced with the exact same dilemma as the with-

in-species Milker-Killer dilemma, including attacking and consuming their competitors (cannibalism vs. intraguild predation), but then among species.

3. Can cannibalism be assumed as a form of prudent predation?

When an individual decides to prey on its conspecifics instead of its primary food source, it decreases predation on the prey in two ways, resulting in more prudent predation. First, the cannibal feeds less on the food source and second, the cannibal removes other consumers. So, can cannibalism really be seen as another form of prudent predation? No, it cannot. Because prudent predation is favored when a patch is exploited by kin-related individuals, cannibalism in these patches will occur among kin, resulting in loss of inclusive fitness for the cannibal. Hence, prudent predation is favored by selection exactly when cannibalism is not. Several studies have shown that phytoseiids can discriminate between kin and non-kin and prefer to feed on the latter (Faraji et al. 2000; Schausberger and Croft 2001).

Although cannibalism does not appear to be a form of prudent predation, it might be used to avoid secondary invasions. When a local predator-prey patch is being exploited by a Milker population and is invaded by a single Killer predator, the Milkers could easily control the invasion by cannibalizing the offspring of the invader. Due to the higher resident predator population, this strategy can control the invasion and maintain the high relatedness among the individuals, which is necessary for the evolution of the Milker strategy.

4. Cannibalism and dispersal: which drives which?

There are two perspectives of the same situation – cannibalism is the selective process and dispersal the trait under selection, or vice versa. In both cases, kin selection will affect the outcome. Kin selection theory predicts that individuals that disperse away from their relatives to avoid feeding on them or by them in times of food scarcity will be favored by natural selection; by dispersing, they will not suffer from (inclusive) fitness loss (Hamilton 1964a,b). They may, however, suffer from fitness loss because dispersal is risky. Dispersal only after the prey extermination, can select for increased cannibalism; the predators due to lack of food may engage in cannibalism to prolong their life or acquire energy to disperse. In this case, kin selection theory predicts that individuals that are able to discriminate between kin and non-kin and feed on the latter will be favored by natural selection (Hamilton 1964a,b).

Pels (2001) assumes that cannibalism is the trait under selection while keeping dispersal fixed, or conversely, assumed that dispersal evolved while cannibalism is fixed. Pels' model predictions show that predators that employ the Killer strategy are selected for a higher cannibalistic tendency (Pels 2001). The results of CHAPTER 5, however, do not support these predictions: the Milker and the Killer line that were used for these experiments did not differ in their cannibalistic behavior. The model of Pels (2001) wrongly assumes that only juveniles can cannibalize, whereas it is known that adult *P. persimilis* are the primary cannibals (Dosse 1958; Sabelis 1981). An extension of the model that includes the adult stage as cannibal might give more accurate predictions about the evolution of cannibalism in relation to different dispersal strategies. Furthermore, the differences between the two genders regarding their cannibalistic tendencies in CHAPTER 4 indicate that theoretical predictions should also account for different behavior depending on the sex. Reproduction in adult, mated females is through oviposition and requires food, whereas reproduction in adult males

is through mating, thus we should not expect that the genders behave in a similar way under the same conditions. Moreover, in haplodiploid species, there are asymmetries in the relatedness between individuals depending on the gender. Despite the results of CHAPTER 5, I cannot conclude that dispersal and cannibalism are genetically uncoupled, because they might be correlated but not always expressed to the same extend. Depending on the local patch conditions that the predators face, they can engage more or less in cannibalism. Studying cannibalism under different conditions, i.e., with heterospecific prey present, might have given me a clearer answer.

5. Milkers and Killers in biocontrol?

The Milker-Killer dilemma can be important for biological control. In the current thesis, I did not present experiments directly linked to biological control, nevertheless, I will discuss how we can use the current knowledge to optimize the use of *P. persimilis* in greenhouses. The first question that comes to mind when we link the Milker-Killer dilemma to biocontrol is which strategy is the most suitable for efficient biological control. The answer, however, is not straightforward; it depends on many factors, which I will discuss further.

At first, one may think that since the local predator-prey populations are unstable the desired strategy for efficient biological control of spider mites is that of the Killer, because these predators eradicate the local prey population rapidly and do not allow the prey population to increase in size. However, due to their low dispersal rate, they will not be efficient in providing control on other attacked plants that are further away from the point of release. In contrast, predators that employ the Milker strategy by dispersing more during the local interaction with the prey will find and colonize more prey patches, thus providing control that extends over a larger part of the greenhouse. Milker predators will not control locally the spider mite infestation as fast as Killer predators, but over time they will occupy more other infestations. Based on this, it becomes clear that the method of release and the extent of the infestation will affect the decision to use Milkers or Killers to achieve good control. If predators are released everywhere in the greenhouse, using Killers can result in efficient control. If, however, predators are released locally, where symptoms of the infestation are present, then it is better to use Milkers, because these predators can disperse further away from the point of release, persist longer in the greenhouse, and find other prey patches.

Phytoseiulus persimilis was adopted as a biocontrol agent by growers due to its ability to control small as well as large infestations within a reasonable time. Depending on the crop, but also the scale of the infestation, the growers decide when and how many predators they release to achieve the desirable results (Parrella et al. 1999). The pest density at which action should be taken to prevent reaching the economic injury level depends on the host plant. Vegetable crops have a higher economic threshold than ornamentals and can be sold even when they have been lightly infested (Parrella et al. 1999). Ornamentals, such as the roses used in the current study, cannot be sold if they show damage. Thus, a mass release of a Killer line of *P. persimilis* throughout the crop can be efficient for controlling the two-spotted spider mites in ornamentals, because it will eradicate the prey rapidly. In contrast, a spider mite infestation on a vegetable crop, such as cucumber, does not necessarily require the use of a Killer line. Because some increase in prey densities on cucumber plants can be tol-

erated, a Milker line may control local prey populations sufficiently and can persist longer in the crop, since the predators will start dispersing before prey elimination. There are examples where the release of *P. persimilis* takes place only after the prey are present (the so-called 'Pest-in-First' method) or even sometimes predators and prey are introduced simultaneously on the crop in order to enhance predator establishment (Parrella et al. 1999).

Although *P. persimilis* has covetable traits as biocontrol agent of *T. urticae,* such as its ability to cope with the spider mite web, the growers do face a problem. Because of its high dependence on the prey, *P. persimilis* goes extinct after the prey are overexploited. Thus, farmers need to repeatedly release the predators to prevent spider mite outbreaks. These releases increase costs and growers take this seriously into account before they decide to use this predator as a biological control agent. Predatory mites that employ the Milker strategy may offer a solution to this problem. Milker predators can persist longer than Killer predators and therefore have higher chances to be present when another spider-mite outbreak appears. Furthermore, due to their high dispersal tendency they can be released on a local infestation, but they will disperse to the surrounding plants as well. The growers may not notice prey patches in an initial phase, but dispersing predator females would find them and therefore provide better biological control. Of course, Milker predators can only be used when the host plant has a high economic threshold and the infestation is at an initial phase. In greenhouse experiments the Early-dispersal line, which behaves as a Milker line, controlled spider-mite infestations equally well as the Koppert line, which is a more Killer-like line (CHAPTER 2), but produced more dispersers (Revynthi et al. unpubl. data). Hence, a Milker line has the ability to control a mite infestation well at a local scale but provides protection of plants that are located further away from the point of release.

Other important parameters are prey dispersal and the cultivation system that the grower is using, which affects the plant distribution over the greenhouse. As was already discussed in a previous section of this thesis, the prey also have exploitation and dispersal strategies, and the ability of predators to control spider-mite infestations is affected by the behavior of the prey. The planting system that is used by the grower can also affect the efficiency of biocontrol. Highly dense plant systems provide good connection of the local prey population and accommodate predator dispersal (Takafuji 1977); hence Killer-like host exploitation strategies are favored. Plant systems that allow sufficient space among plants or rows can result in more Milker-like host exploitation strategies and reduced predator dispersal (Takafuji 1977).

6. Cannibalism in biocontrol: is it really a problem?

Overexploitation leads to food scarcity and an alternative way to obtain food and nutrients under these conditions is cannibalism (review in Fox 1975; Polis 1981; Schausberger 2003). It is known that *P. persimilis* starts feeding on conspecifics after exterminating its prey. Several studies have investigated the cannibalistic behavior of this mite species (Yao and Chant 1989; Walzer and Schausberger 1999; Schausberger and Croft 2001; Schausberger 2007; Schausberger and Hoffmann 2008), but none of them discussed the potential interference with biological control. The question that arises is whether and in which way cannibalism can affect biological control.

Cannibalism can affect biological control either negatively or positively. If the predators have high cannibalistic tendency and initiate cannibalism before prey depletion, then biocontrol is negatively affected. When predators cannibalize before prey are exterminated, they remove potential biological control agents that can contribute to the control of spider-mite infestation. When prey are exterminated, however, cannibalism may have a positive effect on biocontrol. This predatory species can persist for more than 2 weeks in the presence of water (15.7 days on average at 26 °C; Sabelis 1981) hence, when it feeds on its conspecifics it can persist even longer on the crop and be present if another spider-mite outbreak appears. The results of Chapters 4 and 5 show that predators that are deprived of food for at least 48 h engage in cannibalism, even when they have the option to disperse. Moreover, in Chapter 5 I showed that, predators will engage in cannibalism despite their dispersal behavior.

Phytoseiulus persimilis is massively cultured and sold by several biocontrol companies. The predators can be cultured in open or closed systems. Open systems allow the prey and predators to freely disperse from one plant to another and this may even result in selection for high dispersal tendency, since the prey are allowed to disperse and colonize new hosts. As a result, selection for cannibalism is not expected because when prey are locally exterminated, the predators can disperse and find a new patch. In closed mass cultures, barriers prevent the predators from dispersal. This method concomitantly selects artificially for predators with a low dispersal tendency that can deplete prey population fast, i.e., Killer predators (Elliot et al. 2002). As a consequence of the rearing method, these predators could also have increased their cannibalistic tendency. Because predator densities in this type of cultures eventually become high, prey becomes limited, thus there is high competition for food but also for mates. Therefore the predators are also selected for higher cannibalistic tendency, because via cannibalism they can obtain food and remove competitors. The results of Chapter 4 support this hypothesis and show that prolonged culture in closed systems increase the cannibalistic tendency of the predators. Nowadays, biological control companies are interested in lines of *P. persimilis* that are able to quickly control local spider mite infestations, have high dispersal tendency and low cannibalistic tendency. The findings of Chapter 3 can provide a basis for breeding programs to create Milker- or Killer-like strains that can be used depending on the specific situation, i.e., infestations in ornamental or vegetable crop.

The Milker-Killer dilemma in a broader context
The Milker-Killer dilemma is broadly applicable to predator-prey systems that are characterized by local overexploitation and metapopulation dynamics, typical for many arthropod predator-prey systems (Hassell 1978). Analogies may also be found in host-parasite interactions, extending to systems such as parasitoid-host and pathogens-host systems. In the same way as a predator can drive local prey to extinction rapidly or slowly, a parasite can reproduce fast in its host, thereby decreasing the host's longevity, or it can reproduce more slowly without affecting the longevity of its host much. This results in a continuum ranging from extreme virulence to extreme avirulence (van Baalen and Sabelis 1995a; Sabelis et al. 2002).

The trade-off hypothesis states that the parasites have to pay a cost when they increase the duration of infection by being avirulent (Anderson and May 1982). This hypothesis

describes the trade-off between parasite transmission and virulence – higher transmission increases parasite fitness, whereas higher virulence decreases parasite fitness, as the parasite overexploits its host quickly (Anderson and May 1982; Frank 1996; Alizon et al. 2009). When a parasite exploits its host alone, selection will favor the prudent exploitation strategy. However, in the case of multiple infections, the prudent exploitation strategy is not evolutionarily stable (Hamilton 1972). Less virulent parasites are outcompeted by more virulent parasites, hence in cases of coinfection, natural selection will favor increased virulence (Frank 1996; van Baalen and Sabelis 1995b). Regardless the exploitation strategy, the question is still the same: how can a parasite kill its host and yet not go extinct? Before the host dies or becomes resistant, the parasite should infect another host (primary or secondary) or a vector, otherwise it will go extinct.

The analogies among parasite-host interactions and local predator-prey interactions are quite obvious; however, they have different spatial structures. In predator-prey systems, the prey and predators often show a similar spatial structure, i.e., a prey patch can become a predator patch, and their metapopulations are of the same spatial scale. In contrast, in host-parasite and especially in host-pathogen systems, one host often contains a local population of the parasite or pathogen, so the spatial scales of their populations differ. For the host, a metapopulation consists of several host populations, but for the pathogen a metapopulation can consist of several individual hosts belonging to the same population. These differences may have consequences for the evolution of exploitation strategies, for example, because similar exploitation strategies as in the predators may occur within a prey population, which implies that the prey, rather than the predator, may determine the duration of the local interaction, offering less opportunities for the evolution of different predator exploitation strategies. Although there is much literature on the evolution of virulence in viruses and pathogens, we lack studies on the evolution of alternative exploitation strategies in arthropod systems.

Conclusions – Future perspectives

In this thesis I studied how exploitation strategies of predators can be affected by both timing of dispersal and their cannibalistic tendency. I showed that there are differences in dispersal and cannibalistic behavior between the two genders in haplodiploid systems, which should be taken into account. In this chapter I mentioned possible applications of the Milker-Killer dilemma to biological control and a generalization of the theory to other systems that are characterized by overexploitation. Nevertheless, many questions remain. An interesting question that asks for an answer is what happens when a Killer predator invades a patch of Milker predators. Theory predicts Milker predators will then be outcompeted by Killer predators (van Baalen and Sabelis 1995a); however, we lack experimental evidence. Furthermore, Pels et al. (2002) show that the Milker strategy can be evolutionarily stable in spatially structured environments and at a metapopulation level. Up to today, we lack genetic markers that we could use to discriminate between strains with different dispersal strategies. To the best of my knowledge, there are no genetic markers for dispersal behavior in *P. persimilis*. If these markers would exist, it would greatly help in designing experiments where Milker and Killer strains will be brought into competition to test the predictions of Milker-Killer theory.

The experiments presented in CHAPTER 4, give a different perspective to cannibalism in haplodiploid species. Male cannibalism was studied in *P. persimilis* for the first time. As was briefly mentioned in the section *Can cannibalism be assumed as a form of prudent predation?*, all the experiments so far, including CHAPTERS 4 and 5, show the propensity to cannibalize. We need more experiments that will offer the predators or their offspring the choice to escape cannibalism and then study whether they will engage in it. In CHAPTER 5, I quantified cannibalism in relation to dispersal, but in an artificial system without heterospecific prey. A good extension of this experiment would be the addition of *T. urticae*, which will give us the opportunity to study how the exploitation behavior can be affected by cannibalism. Moreover, the consequences of the differences in the behavior of males and females in addition to the asymmetries regarding inclusive fitness loss in haplodiploid species for population dynamics and evolution deserve further study.

Finally, greenhouse experiments can answer questions about the efficiency of Milkers and Killers in biocontrol. Variation of the initial predator-prey ratio, but also distribution and connectivity of the local patches can provide information on how to optimize the use of *P. persimilis* under greenhouse conditions but also to experimentally test the predictions of the Milker-Killer dilemma. Furthermore, we can use this knowledge to define a stable mixture of Milkers and Killers that can provide a better biological control. Application of the Milker-Killer dilemma to different biocontrol situations might allow for more efficient control in more crops. This action, however, would probably also require more information from the grower regarding the state of the infestation, the use of pesticides and other biological control agents before utilizing a Milker or a Killer strain. Direct application of the Milker-Killer dilemma as well as greenhouse experiments would give perspective for better biological control, but also would give ample opportunities to test theory.

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