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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 introduction

Overexploitation and prudent predation

The harvesting of a food source at a rate which the source cannot sustain itself, also known as overexploitation, is a phenomenon that attracts major interest nowadays from the scientific community due to its impact on biodiversity. Overexploitation occurs at all trophic levels and is called overharvesting, overhunting or overfishing when we refer to plants, terrestrial animals and fish respectively. It can lead to extinction either of a population or even of an entire species.

According to the International Union for Conservation of Nature (IUCN) Red List (2017) 24,431 species are threatened: 8,160 vertebrates, 4,553 invertebrates, 11,674 plants and 34 fungi and protists. These reports are of great concern to many people including the scientific community as well as for regulatory government agencies worldwide, and have led to adopting measures to reduce the current biodiversity loss (Pimm et al. 1995; Jones et al. 2011; Rodrigues et al. 2014). People nowadays are more informed and sensitive towards biodiversity loss because of overexploitation. An increasing percentage of the world population is adopting more prudent nutritional habits, such as becoming vegetarian or even vegan (avoid consumption of any animal product), which could lead to a reduction in overexploitation rates.

Overexploitation, however, is not a phenomenon limited to human activity, it also occurs in other herbivores and predators. A plant or prey population can be driven to extinction because of overexploitation by herbivores or predators. Prudent predators can manage prey population in a way that maximizes their density (Slobodkin 1968, 1974) by decreasing their predation rate (Gilpin 1975). In well-mixed populations, however, their exploitation strategy is not evolutionarily stable because they can be outcompeted by selfish predators (Maynard Smith 1964; Hardin 1968). The tragedy of commons describes a situation in which a selfish individual (so-called cheater) gains benefit of a shared source to maximize its individual fitness, at the expense of the productivity of the group (Hardin 1968; Rankin et al. 2007). The cheater exploits the source at its own interest leading eventually to overexploitation.

The role of dispersal in a patchy world

Food occurs in patches and overexploitation often takes place in spatially structured environments. In local predator-prey populations, selfish predators drive their prey to extinction but will eventually go extinct as a consequence. But how do such species then persist in nature? Even though local predator-prey populations go extinct, persistence is observed at a metapopulation level because of the asynchronies of the dynamics in local populations and the founding of new populations by dispersing individuals (Vandermeer 1973; Hilborn

1975; Crowley 1981; Jansen and Sabelis 1992; Janssen et al. 1997). Such dynamics occur, for example, when both predator and prey disperse at a sufficient rate to balance local extinction with recolonization (Huffaker 1958; Taylor 1990; Janssen et al. 1997; Ellner et al. 2001). Individuals dispersing from their patches at different time points create asynchronous fluctuations in local abundance, a prerequisite for the persistence of metapopulations (Holyoak and Lawler 1996).

Dispersal is a key process in population biology and ecology, not only influencing the persistence, distribution and abundance of local populations but also driving gene flow among populations (Dunley and Croft 1990; Dingle 1996; Quinn et al. 2011). The adaptive value of dispersal is determined by the balance between its costs and benefits, which are highly dependent on the life stage and condition of an individual, as well as on the contemporary local and environmental conditions (Bowler and Benton 2005, 2009; Bonte et al. 2012; Bonte and Doherty 2016).

From the perspective that dispersal is a life-history trait (Bonte and Doherty 2016) and that the decision to disperse from a patch is not only context-dependent but also heritable, we can consider predator dispersal as a prey exploitation strategy (van Baalen and Sabelis, 1995; Sabelis et al. 2002). In a local predator-prey population, early predator dispersal decreases predation and, as a consequence, predator offspring staying behind on the patch will have more food available, resulting in a longer interaction period between the predators and their prey. However, a longer interaction period can lead to higher risks of secondary predator invasions. These invaders can then exploit the prey population to their own interest by consuming the prey that prudent predators saved for their offspring (van Baalen and Sabelis 1995). Hence, prudent predation is not evolutionarily stable in well-connected metapopulations because prudent predators are outcompeted by invading cheaters (cf. Maynard Smith 1964; Pels et al. 2002).

The Milker-Killer dilemma

The consequences of predator dispersal for the population dynamics of predators and prey were modelled by van Baalen and Sabelis (1995), who defined the so-called Milker-Killer dilemma. They proposed two extreme types of dispersal strategies: the Killer strategy, in which the predators start dispersing only after prey depletion, and the Milker strategy, in which the predators disperse even though prey is abundantly available. According to this study, strategies can range from more Killer-like to more Milker-like, but overexploitation will take place in all cases. Prudent predators (i.e., Milkiers) will interact longer with the local prey population and will produce higher total numbers of dispersing offspring, but they will be exposed to invasions by selfish predators (i.e., Killers), whose populations will increase faster because they do not disperse early. Consequently, Milker-like strategies will be favoured only when local predator populations are sufficiently isolated from each other, thus reducing the risk of invasions by Killers (van Baalen and Sabelis 1995; Pels and Sabelis 1999; Pels et al. 2002).

The Killer and Milker exploitation strategies differ in dispersal rate in the presence of prey. Theoretically, the predator dispersal rate during the predator-prey interaction has three consequences for the population dynamics of prey and predator. First, prey populations

increase more when exploited by Milker predators than when exploited by Killer predators, because the predation rate by Killer populations is higher than that by Milker populations. Second, as a consequence, the local interaction period between a Milker population and its prey will be longer than that of a Killer population, because a prey population will increase more when attacked by Milkers than by Killers. Third, because of the increased growth of the prey populations and of the increased interaction time, local populations of Milker predators will produce more dispersing offspring over the entire local predator-prey interaction than Killer predators.

The formulation of the Milker-Killer dilemma was inspired by predator-prey interactions among plant-inhabiting mites (van Baalen and Sabelis 1995). The herbivorous mites occur in local populations, which can be locally driven to extinction by their predators (Janssen and Sabelis 1992). These local populations are connected by predator dispersal (Janssen et al. 1997; Ellner et al. 2001) and can only persist at a metapopulation level (Sabelis et al. 2005). In this context, it seems reasonable to use an acarine predator-prey system to test the Milker-Killer dilemma, provided that the predator is not a generalist or omnivore to ascertain a tight pairwise predator-prey interaction. Nevertheless, this theory can be applied to any system that is characterized by overexploitation, such as pathogen-host interactions.

Overexploitation, cannibalism and dispersal

When local populations are driven to extinction because of overexploitation in a spatially structured environment, an alternative way to obtain food is cannibalism. 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 predatory mites (review in Fox 1975; Polis 1981; Schausberger 2003). Animals prey on their conspecifics to obtain food, nutrients and remove source competitors in times of scarcity (Fox 1975). Cannibalism can act as a life boat mechanism and result in species persistence, when food is scarce (van den Bosch et al. 1988). 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).

Even though cannibalism and dispersal are important phenomena for the persistence of populations and can be driven by overexploitation, they hardly ever have been studied in relation to each other. So far, few theoretical studies are available (Pels 2001; Lion and van Baalen 2007; Rudolf et al. 2010), and only one experimental study (Pels 2001) addressed dispersal in relation to cannibalism. It is important to study these two phenomena together because they affect each other (e.g., cannibalism can delay dispersal of the cannibals but accelerate dispersal of individuals that stand to be cannibalized) and consequently can affect the genetic structure of a population.

There are two complementary theoretical approaches regarding the evolution of cannibalism and dispersal. The first approach treats cannibalism as a fixed trait that influences selection on dispersal, which can determine the spatial structure of natural populations (Lion and van Baalen 2007; Rudolf et al. 2010). The second approach treats cannibalism as the trait under selection due to different dispersal strategies (Pels 2001). Cannibalism can select

for dispersal when offspring try to escape from their cannibalistic parents or family members in general, thus avoiding loss of inclusive fitness (Rudolf et al. 2010). Dispersal after food depletion can select for high cannibalistic tendency (Pels 2001). Experimentally, there is lack of evidence for any of the two theoretical predictions. Using a Milker-like and a Killer-like line of a predatory mite, Pels (2001) explored whether high or low dispersal rate would result in low and high cannibalistic tendencies, respectively. His results, however, did not resolve this issue, as he did not detect differences between the two lines in either their dispersal or cannibalistic behavior. In this thesis, I investigate predator behavior in a situation, where the predators can either cannibalize or disperse or both and try to answer how dispersal affects cannibalism and vice versa.

A generalist herbivore and its predator

The most suitable prey-predator acarine system that we can use to study the Milker-Killer dilemma experimentally consists of the generalist phytophagous two-spotted spider mite (*Tetranychus urticae* Koch; FIGURE 1.1) and its predator *Phytoseiulus persimilis* Athias-Henriot (FIGURE 1.2). One may wonder why we chose this system besides being well-studied (Sabelis 1981; Helle and Sabelis 1985a,b), but there are other reasons why this system can be used to answer questions regarding the evolution of alternative exploitation strategies:

- (1) The predator is restricted to spider mites as food source. This limits the factors that can influence its exploitation and dispersal behavior in relation to prey availability.
- (2) In nature, *T. urticae* and *P. persimilis* live in spatially structured environments. The predatory mites drive local prey populations to extinction, after which they have to disperse in search of a new food source (Janssen and Sabelis 1992). This phenomenon makes this system the most suitable to experimentally study the Milker-Killer dilemma.



FIGURE 1.1 — Adult female (centre left) and a larva (bottom centre) of the spider mite *Tetranychus urticae*. Photo: Jan van Arkel.

- (3) The first experimental study on the Milker-Killer dilemma was conducted with this prey-predator system and thus I can relate my results to earlier studies.
- (4) Last but not least, both mite species play an important role in agriculture. The two-spotted spider mite is a generalist pest of many economically important plant species (Jepson et al. 1975), and the predatory mite *P. persimilis* is used as its biological control agent. The two-spotted spider mite feeds on the contents of leaf mesophyll cells, causing a characteristic symptom, consisting of small chlorotic spots. In cases where the infestation is large, the plant loses its ability to photosynthesize because of the lack of chlorophyll and the web that is produced by the mites. Consequently, the plant suffers from severe dehydration, leading to defoliation.



FIGURE 1.2 — A: An adult female and B: adult male of *Phytoseiulus persimilis*. In both pictures, some strands of web, produced by the prey, can be seen. Photos: Jan van Arkel.

Tetranychus urticae is an arrhenotokous haplodiploid species. Virgin females produce haploid males, whereas fertilized females produce diploid females and haploid males (Helle and Sabelis 1985a). Its life cycle consists of eight stages (with the three non-feeding molting stages given in brackets): the egg, larva (protochrysalis), protonymph (deutochrysalis), deutonymph (teleiochrysalis), and adult. Its development is rapid and at high temperatures (30-35 °C) its life cycle is completed in 8-12 days (Laing 1969).

Due to the continuous applications of acaricides and its short life cycle, this pest has developed resistance to most of the active ingredients of acaricides (Van Leeuwen et al. 2010). Hence, biocontrol is an efficient approach to control this mite. The predatory mite *P. persimilis* is used as a biological control agent against the two-spotted spider mites (Sabelis 1981). It was introduced into Germany from Chile in 1958 (Dosse 1958) and was proven very efficient in controlling two-spotted spider mites on many plant species, especially on greenhouse-grown vegetables, fruits and ornamentals (Huffaker et al. 1970; Sabelis 1981; Helle and Sabelis 1985b).

This predator is a pseudo-arrhenotokous haplodiploid species. Females require insemination in order to start oviposition and both females and males start as fertilized eggs (Huffaker et al. 1970; Schulten 1985). However, the males lose the paternal set of chromosomes shortly after syngamy (Helle et al. 1978; Sabelis and Nagelkerke 1988), so only females are diploid. Its life cycle has five stages: egg, larva, protonymph, deutonymph and adult, and lacks the three quiescent stages that *T. urticae* has (Laing 1968). The egg and the larva are non-feeding stages (Laing 1968; Sabelis 1981). Adult female predators can feed on all stages of *T. urticae* (Takafuji and Chant 1976). The life cycle of this predatory mite at 30 °C can last only 5 days (Sabelis 1981). Laing (1968) showed that when *P. persimilis* is offered *T. urticae* as prey, it can develop from egg to adult in 7.45 days under a diurnal temperature cycle of 14.4 to 28.3 °C. This is approximately half the time required for the development of the two-spotted spider mites under similar conditions (Laing 1969). This is one of the reasons for this predatory mite being so efficient at controlling *T. urticae*.

THESIS OUTLINE

The aim of this thesis is to experimentally test the occurrence of Milker-like and Killer-like strategies in *P. persimilis* and study the evolution of these alternative exploitation strategies. Predator dispersal influences predator-prey dynamics in local patches and is likely to determine persistence of the system at a metapopulation level. Decisions of predators to disperse typically depend on local conditions such as local density of conspecifics in the same patch (Otronen and Hanski 1983), food availability (Kuussaari et al. 1996), kin recognition and kin interaction (Hamilton and May 1977) and cannibalism (Pels 2001). In this thesis, I investigate how predator-prey interactions and interactions among conspecific predators can affect predator dispersal behavior.

In CHAPTER 2, I present a comprehensive survey of predator dispersal and exploitation strategies using strains of *P. persimilis* that I collected in Turkey and Sicily. My aim was to investigate whether there were differences in dispersal behavior among the collected strains and whether these differences would result in the effects on population dynamics predicted by the Milker-Killer theory (van Baalen and Sabelis 1995). I found significant variation in

the dispersal strategies among predator populations, and I therefore tested whether there was a genetic component for timing of aerial dispersal in the presence of prey, as was suggested earlier (Pels and Sabelis 1999). In CHAPTER 3, I therefore ask whether it is possible to select for Milker-like and Killer-like predatory mite lines. I aimed to explore whether this artificial selection resulted in differences between the two selected lines in the dispersal rate, the interaction period and the number of dispersers that were produced.

During daily observations in the experiments of both CHAPTERS 2 and 3, I noticed that many predators disappeared. Specifically, I often observed adult males cannibalizing larvae and this behavior had not been described before. Although it is known that cannibalism can affect dispersal behavior of individuals, there is a lack of experimental work linking these two phenomena. All these reasons led me to CHAPTERS 4 and 5, where I focused on the cannibalistic behavior of *P. persimilis* and how this behavior could affect its dispersal tendency. In CHAPTER 4, I ask to what extent prolonged culture of predators affects the cannibalistic behavior of adult females and males. I tested two contradictory hypotheses about adult cannibalism on juvenile. The first hypothesis predicts that strains that have been in culture for a long time have a higher tendency to cannibalize than strains in the field, because laboratory strains are unintentionally selected for higher tendency to cannibalize due to space limitation. This prediction will hold especially for females because they are the first to disperse from the patch when food is scarce. In the second hypothesis I took the increase in kin-relatedness among individuals when they are cultured for long time into account. I hypothesized that strains that have been in culture for long time have lower cannibalistic rates than strains that derived recently from the field. However, the experiments of CHAPTER 4 showed me only the potential occurrence of cannibalism, as I conducted my trials using a closed system, where the predators did not have the option to disperse. Thus, in CHAPTER 5 I aimed to investigate the interaction of cannibalism with dispersal using the selected lines of CHAPTER 3, which employ different dispersal strategies. In this chapter I ask (1) when food is limited and given the option to disperse, will predators choose to cannibalize or not and to disperse or not? And (2) if the predators cannibalize when they have the option to disperse, which line and gender of *P. persimilis* is more voracious towards its conspecifics?

The chapters of this thesis raise many questions about the evolution of prudent predation and cannibalism, as well as the applied aspect of the Milker-Killer dilemma to optimize biological control of spider mites. In the general discussion (CHAPTER 6) I address the following questions:

- (1) Eventually, which is the best strategy for a predator, to milk or to kill?
- (2) Despite the theoretical predictions about the evolution of prudent exploitation strategy, can we still find Milkers in nature?
- (3) Can we assume cannibalism as a form of prudent predation?
- (4) When we study cannibalism and dispersal together, which is the trait under selection? Does cannibalism drive the evolution of dispersal or does dispersal drive the evolution of cannibalism?

Despite the fact that *P. persimilis* is an efficient biocontrol agent of *T. urticae*, the growers face the problem of having to release it repeatedly: because of its high dependence on the

prey, *P. persimilis* goes extinct after the prey are overexploited. Therefore I also address the following questions:

- (5) Which exploitation and dispersal strategy is the best for efficient biological control, the Milker or the Killer? Is it better to release predators that allow the prey population to develop, but stay longer on the crop, i.e., Milkers, or is it better to use predators that exterminate the prey fast, but persist only for a short period on the plant, i.e., Killers?
- (6) How can cannibalism affect the ability of *P. persimilis* to control spider mite infestations?

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