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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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# Summary

Overexploitation is the harvesting of a resource at a rate which is higher than the resource renewal rate and is a phenomenon that occurs at various trophic levels. For example, a local plant population can be driven to extinction by a herbivore population and a local herbivore population can be overexploited by a predator population. In nature, however, species can persist despite local extinctions, because of dispersal among local patches, which together form a metapopulation. As long as the dynamics in the various local patches is asynchronous, there will always be patches with individuals. In predator-prey interactions, early dispersal of some predators after some reproduction decreases the predation rate and as a consequence the offspring of the dispersed predator will have more food available, resulting in a longer interaction period between the predators and their prey in the local patch. Conversely, late predator dispersal drives the local prey population to extinction faster, resulting in a shorter interaction period between the predator and its prey. The early dispersal strategy is called ‘Milker’, and the late dispersal strategy is called ‘Killer’, which are the extremes of a continuum of exploitation strategies. The Milker-Killer dilemma theory describes the effects of dispersal on local population dynamics. In this theory, the Milker strategy is presented as a form of prudent predation that can only be evolutionary stable when the probability of subsequent invasion of a patch by a Killer is low. This is because predators that employ the Killer strategy outcompete Milkers in local patches by exploiting the prey population faster. Nevertheless, predators of both strategies eventually will drive the local prey population to extinction.

When the local prey population is depleted, an alternative way for the predators to temporarily obtain food is through cannibalism. Such intraspecific predation is common in a wide range of animal taxa and may significantly affect population dynamics. 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 together, while they are likely to mutually affect each other. In this thesis, I used an acarine predator-prey system and I experimentally tested the Milker-Killer dilemma. In addition, I investigated predator behavior under conditions where the predators could cannibalize, disperse, or both and to study how dispersal and cannibalism interact.

In CHAPTER 2, I present a comprehensive survey of predator dispersal and exploitation strategies using strains of the predatory mite *Phytoseiulus persimilis* that I collected in Turkey and Sicily. My aim was to investigate whether there were differences among the collected strains in dispersal behavior and whether these differences would result in the local population dynamics predicted by the Milker-Killer theory. I found significant variation in the exploitation and dispersal strategies among predator populations. However, none of the collected strains showed the extreme Killer or Milker strategy. The results suggest that there is genetic variation for prey exploitation and dispersal strategies. Thus, different dispersal strategies in the Killer-Milker continuum may be selected for under natural conditions, which affects the predator-prey dynamics in local patches and is likely to determine persistence of the system at the metapopulation level.

In CHAPTER 3, I asked whether it is possible to select for Milker-like and Killer-like predatory mite lines. I aimed to explore whether artificial selection for early and late timing of dispersal results in differences in the dispersal rate between the two selected lines, and whether this affected the interaction period and the number of dispersers that are produced. I showed that 6 rounds of selection for early or late timing of dispersal resulted in predator lines displaying earlier or later dispersal. In a population dynamics experiment, I furthermore showed that selection for timing of dispersal also resulted in the predicted differences in the local interaction time with the prey and in the cumulative number of dispersers. I conclude that timing of dispersal is a heritable trait that can be selected for and results in lines with quantitative differences in local predator-prey dynamics.

In CHAPTERS 4 and 5, I focused on the cannibalistic behavior of *P. persimilis* and how this behavior could affect its dispersal tendency. Cannibalism can delay dispersal of the cannibals but accelerate dispersal of individuals that stand to be cannibalized. In CHAPTER 4 I asked to what extent prolonged culturing of predators affects the cannibalistic behavior of adult females and males. I tested two contradictory hypotheses about adult cannibalism on juveniles. The first hypothesis predicts that strains that have been in culture for a long time have higher tendency to cannibalize than strains in the field, because laboratory strains are unintentionally selected for higher tendency to cannibalize due to food limitation and lack of opportunities to disperse. This prediction will hold especially for females because they are the first to disperse from a patch when food is scarce. The second hypothesis is based on the increase in kin-relatedness among individuals of populations that were cultured for a long time. Owing to this increase in relatedness, I expected lower rates of cannibalism in strains that have been in culture for a long time than strains that were recently collected from the field. Using a laboratory and a field strain in a closed system, I observed the behavior of adult predators that were offered conspecific larvae as prey. The results show that males engaged more often in cannibalism than females, and females of the strain with a long culture history engaged more in cannibalism than those of the recently collected strain, both in agreement with the first hypothesis. To test the second hypothesis, I created an isofemale line from each strain and compared the cannibalistic behavior of adult male and female predators. The cannibalistic tendency of the strains and their isofemale lines was similar, suggesting that kin-relatedness did not affect their cannibalistic behavior. These results did not support the second hypothesis.

In CHAPTER 5 I investigated cannibalism in lines that were selected to employ different dispersal and exploitation strategies. In this chapter I asked (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? Using wind tunnels, I observed the behavior of adult predators with different dispersal strategies, when offered conspecific larvae as prey. The results show that both selection lines had similar dispersal and cannibalistic behavior, but differences occurred between males and females. Male predators stayed significantly longer in the patch and engaged more often in cannibalism, whereas females departed earlier and often did not cannibalize. I hypothesized that this result may be caused by differences in the biology of males and females. *Phytoseiulus persimilis* is a

pseudo-arrhenotokous species and therefore females require insemination and relatively large amounts of food to be able to oviposit. Adult males, in contrast, do not need much food, thus do not search for food but for mates. Hence, males search for females, which they can do on the local patch, and mated females search for food, which they could only find on other patches. While searching for mates, males also encounter more potential victims to cannibalize, whereas females disperse and thus encounter fewer potential victims. An alternative explanation for the observed differences in cannibalistic tendencies between males and females is based on the existing asymmetries in the relatedness of parents with their offspring. In haplodiploid species like *P. persimilis*, the cost of cannibalism regarding inclusive fitness loss is higher in females than in males. The diploid females have more offspring than the haploid males, because the latter only contribute genes to daughters. Thus, it is expected that females will suffer from greater inclusive fitness loss when engaging in cannibalism. Hence I hypothesize that under food limitation, adult females are less prone to cannibalize than adult males and will more often choose to disperse in order to refrain from cannibalism.

In this thesis, I tried to answer how exploitation strategies of predators are shaped by both timing of dispersal and cannibalistic tendency. In addition, I showed that there are differences in dispersal and cannibalistic behavior between the two genders in haplodiploid systems, which require further study.

In the general discussion (CHAPTER 6) I tried to address 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. The Milker-Killer dilemma is broadly applicable to systems that are characterized by local overexploitation and metapopulation dynamics and analogies may also be found in host-parasites interactions. I briefly discuss the evolution of virulence, similarities and differences between predator-prey and host-parasite interactions. Future experimental and theoretical studies may help to answer questions about the evolution of prudent predation and the role of genders in this process. In addition, greenhouse experiments can answer questions about the efficiency of predators with different exploitation strategies in biocontrol.

# Samenvatting

Overexploitatie is het oogsten van een voedselbron met zo'n intensiteit dat de bron zichzelf niet in stand kan houden, en dit is een fenomeen dat zich op verscheidene trofische niveaus voordoet. Ter illustratie, een lokale populatie planten kan tot uitsterven worden gebracht door een populatie herbivoren en een lokale populatie herbivoren kan overgeëxploiteerd worden door een populatie rovers. Soorten kunnen onder natuurlijke omstandigheden echter blijven voortbestaan ondanks dit proces van lokale extincties omdat individuen dispergeren tussen lokale leefgebieden die tezamen een metapopulatie vormen. Zo lang de dynamiek in de verschillende lokale leefgebieden uit fase verloopt, zullen er altijd leefgebieden bevolkt zijn met individuen. In het geval van rover-prooi interacties verlaagt vroege dispersie van sommige rovers de predatiedruk en als gevolg daarvan hebben de nakomelingen van de gedispergeerde rovers meer voedsel beschikbaar hetgeen resulteert in een langere interactieperiode tussen de rovers en hun prooi in het lokale leefgebied. Late dispersie van rovers daarentegen leidt sneller tot lokaal uitsterven van de prooipopulatie, resulterend in een kortere interactieperiode tussen de rovers en hun prooi. De vroege dispersie strategie wordt 'Melker' genoemd en de late dispersie strategie 'Moordenaar'; dit zijn de extremen in een continuüm aan exploitatie strategieën. De theorie van het Melker-Moordenaar dilemma beschrijft de effecten van dispersie op de lokale populatiedynamiek. De Melker strategie staat in deze theorie voor een vorm van prudente predatie die alleen evolutionair stabiel kan zijn wanneer de kans dat een Moordenaar een lokaal leefgebied met Melkers binnendringt klein is. De reden hiervoor is dat rovers met de Moordenaar strategie de Melkers wegconcurreren in lokale leefgebieden door de prooipopulatie sneller te exploiteren. Desalniettemin zullen rovers van beide strategieën de lokale prooipopulatie doen uitsterven.

Wanneer de lokale prooipopulatie uitgeput raakt, hebben de rovers een alternatieve manier om tijdelijk aan voedsel te komen door kannibalisme. Dergelijke intraspecifieke predatie komt algemeen voor bij een waaier aan diergroepen kan een bepalende invloed hebben op de populatiedynamiek. Hoewel kannibalisme en dispersie belangrijke factoren zijn voor het in stand houden van populaties en aangedreven kunnen worden door overexploitatie, zijn deze factoren vrijwel nooit in samenhang bestudeerd, ondanks het feit dat ze elkaar waarschijnlijk wederzijds beïnvloeden. In dit proefschrift gebruik ik een rover-prooi systeem van mijten om experimenteel het Melker-Moordenaar dilemma te toetsen. Ik heb rover-gedrag bestudeerd onder condities waar de rover kan kannibaliseren, dispergeren of beide, en de samenhang onderzocht tussen dispersie en kannibalisme.

In *Hoofdstuk 1* presenteer ik een uitgebreide inventarisatie van dispersie en exploitatie strategieën van stammen van de roofmijt *Phytoseiulus persimilis* die ik verzameld heb uit natuurlijke populaties in Turkije en Sicilië. Mijn doel was om te onderzoeken of er verschillen waren in dispersie gedrag tussen de verzamelde stammen en of deze verschillen zouden resulteren in de lokale populatiedynamica zoals voorspeld door de Melker-Moordenaar theorie. Ik vond significante variatie in de exploitatie en dispersie strategieën onder de rover stammen. Geen van de verzamelde stammen echter vertoonde de extreme Melker of Moordenaar strategie. De resultaten suggereren dat er genetische variatie is voor

prooi exploitatie en dispersie strategieën. Ergo, onder natuurlijke omstandigheden kunnen verschillende dispersie strategieën uit het Melker-Moordenaar continuüm geselecteerd worden, hetgeen de rover-prooi dynamiek in lokale leefgebieden beïnvloedt en waarschijnlijk het voortbestaan van dit rover-prooi systeem bepaalt op het metapopulatie-niveau.

In *Hoofdstuk 2* vraag ik of het mogelijk is om te selecteren voor Melker-achtige en Moordenaar-achtige lijnen van roofmijten. Mijn doel was om na te gaan of artificiële selectie voor vroege of late timing van dispersie leidt tot verschillen in de dispersiesnelheid tussen de twee geselecteerde lijnen, en of dit effect heeft op de interactieperiode en het aantal geproduceerde disperseerders. Ik laat zien dat 6 rondes van selectie voor vroege of late timing van dispersie resulteerde in lijnen van rovers die vroege of late dispersie vertonen. In een populatie-dynamisch experiment laat ik bovendien zien dat selectie voor timing van dispersie ook leidde tot de voorspelde verschillen in de lokale interactietijd met de prooi en in het cumulatieve aantal disperseerders. Ik concludeer dat timing van dispersie een erfelijke eigenschap is waarvoor geselecteerd kan worden en dat resulteert in lijnen met kwantitatieve verschillen in lokale rover-prooi dynamiek.

In *Hoofdstukken 3 en 4* heb ik me geconcentreerd op het kannibalistisch gedrag van *P. persimilis* en de manier waarop dit gedrag haar neiging tot dispersie kan beïnvloeden. Kannibalisme kan leiden tot uitstel van dispersie van de kannibalen maar ook tot versnelde dispersie van individuen die kans lopen gekannibaliseerd te worden. In *Hoofdstuk 3* vraag ik in welke mate het langdurig doorkweken van rovers het kannibalistische gedrag van volwassen mannetjes en wijfjes beïnvloedt. Ik testte twee tegenstrijdige hypothesen over kannibalisme door adulten op juvenielen. De eerste hypothese voorspelt dat lijnen die lang doorgekweekt zijn in het lab een hogere neiging vertonen tot kannibalisme dan lijnen uit het veld, omdat laboratorium lijnen ongewild worden geselecteerd voor een hogere mate van kannibalisme vanwege voedselgebrek in combinatie met gebrek aan mogelijkheden te dispergeren. Deze voorspelling is met name van toepassing op wijfjes omdat zij de eerste zijn om uit een voedselplek te dispergeren wanneer voedsel schaars wordt. De tweede hypothese is gebaseerd op de toename in verwantschap tussen individuen van populaties die langer doorgekweekt zijn. Vanwege deze toenemende verwantschap verwacht ik een lagere mate van kannibalisme in lijnen die lang doorgekweekt zijn dan in lijnen die recent uit het veld verzameld zijn. Ik heb het gedrag bestudeerd van adulte rovers van een lab en een veld lijn in een gesloten systeem waar ze larven van dezelfde soort als prooi aangeboden kregen. De resultaten tonen aan dat mannetjes vaker kannibaliseerden dan wijfjes, en wijfjes van de lijn met een lange historie van doorkweken vertoonden meer kannibalisme dan die van de recent verzamelde lijn. Beide bevindingen zijn in overeenstemming met de eerste hypothese. Om de tweede hypothese te toetsen, heb ik een isogene lijn gecreëerd van elke lijn en het kannibalistische gedrag vergeleken van adulte mannetjes en wijfjes van de rover. De neiging tot kannibalisme van de isogene lijnen was vergelijkbaar met de respectievelijke lijnen waaruit ze waren gecreëerd, hetgeen suggereert dat verwantschap geen effect had op het kannibalistische gedrag. Deze resultaten gaan in tegen de tweede hypothese.

In *Hoofdstuk 4* heb ik kannibalisme onderzocht in lijnen die waren geselecteerd op verschillende dispersie en exploitatie strategieën. In dit hoofdstuk vroeg ik: (1) als voedsel gelimiteerd is, en de mogelijkheid tot dispersie gegeven wordt, kiezen rovers dan om te kan-

nibaliseren of niet, en om te dispergeren of niet? En (2) als de rovers kannibaliseren wanneer ze de mogelijkheid hebben om te dispergeren, welke lijn en welk geslacht van *P. persimilis* is meer roofzuchtig jegens zijn soortgenoten? Met behulp van wind tunnels heb ik het gedrag van adulte rovers met verschillende dispersie strategieën geobserveerd, terwijl ze larven van dezelfde soort als prooi kregen aangeboden. De resultaten laten zien dat beide selectielijnen vergelijkbaar dispersie en kannibalisme gedrag vertoonden, maar verschillen traden op tussen mannetjes en wijfjes. Mannelijke rovers bleven significant langer in de voedselplek en begingen vaker kannibalisme, terwijl wijfjes eerder vertrokken en zich vaak onthielden van kannibalisme. Ik hypotheetiseer dat dit resultaat veroorzaakt kan worden door verschillen in de biologie van mannetjes en wijfjes. *Phytoseiulus persimilis* is een pseudo-arrhenotoke soort hetgeen betekent dat wijfjes bevrucht dienen te worden voor reproductie, en relatief veel voedsel nodig hebben om eieren te kunnen leggen. Adulte mannetjes, daarentegen, hebben niet veel voedsel nodig en zoeken dus niet zozeer naar voedsel als wel naar paringspartners. Dientengevolge zoeken mannetjes naar wijfjes, die ze kunnen vinden op de lokale voedselplek, en gepaarde wijfjes zoeken naar voedsel, hetgeen ze alleen kunnen vinden in andere voedselplekken zodra de lokale plek uitgeput raakt. Mannetjes komen dan meer potentiële slachtoffers tegen om te kannibaliseren tijdens hun zoektocht naar paringspartners, terwijl wijfjes dispergeren en dus minder potentiële slachtoffers tegenkomen. Een alternatieve verklaring voor de geobserveerde verschillen in kannibalistische neigingen tussen mannetjes en wijfjes is gebaseerd op de bestaande asymmetrieën in de verwantschap van ouders met hun nakomelingen. In haplodiploïde soorten als *P. persimilis* zijn de kosten voor kannibalisme, met betrekking tot verlies aan 'inclusive fitness', hoger voor de moeder dan voor de vader. De diploïde moeders hebben meer nakomelingen dan de haploïde vaders, omdat die laatste alleen genen bijdragen aan dochters. Daarom ligt het in de verwachting dat moeders meer inclusive fitness verliezen wanneer ze kannibaliseren. Ik stel dan ook de hypothese dat adulte wijfjes minder geneigd zijn tot kannibalisme bij gebrek aan voedsel dan adulte mannetjes en vaker zullen verkiezen te dispergeren om zich niet aan kannibalisme over te geven.

Dit proefschrift is gericht op het beantwoorden van de vraag hoe exploitatie strategieën van rovers worden gevormd door zowel timing van dispersie als kannibalistische neigingen. Daarnaast heb ik laten zien dat er verschillen bestaan in dispersie en kannibalistisch gedrag tussen de twee geslachten in haplodiploïde systemen, hetgeen nadere studie vereist.

In de *Algemene Discussie* behandel ik vragen over de evolutie van prudente predatie en kannibalisme, alsmede de toegepaste aspecten van het Melker-Moordenaar dilemma voor optimale biologische controle van spintmijten. Het Melker-Moordenaar dilemma is breed toepasbaar op systemen die gekenmerkt worden door lokale overexploitatie en metapopulatie dynamiek, en analogieën kunnen ook gevonden worden in gastheer-parasiet interacties. Ik bespreek kort de evolutie van virulentie, overeenkomsten en verschillen met roverprooi en gastheer-parasiet interacties. Nadere studies, zowel experimenteel als theoretisch, kunnen helpen om vragen te beantwoorden over de evolutie van prudente predatie en de rol van geslachten in dit proces. Bovendien kunnen experimenten in kassen vragen beantwoorden over de efficiëntie van rovers met verschillende exploitatie strategieën voor biologische bestrijding.

# Author contributions and project funding

1 – Prey exploitation and dispersal strategies vary among natural populations of a predatory mite

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

MWS – originally formulated the idea; MWS, AMR – designed the experiments; AMR – sampled the mites used for this study and performed the experiments; AMR, ME, AJ analyzed the data and wrote the manuscript.

2 – Timing of aerial dispersal is a heritable trait in the predatory mite *Phytoseiulus persimilis*

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

AMR, DV, ME – designed the experiments; AMR, DV – conducted the experiments; AMR, DV, AJ, ME – analyzed the data and wrote the manuscript

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

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

AMR – designed and conducted the experiments; AMR, AJ – analyzed the data; AMR, JA, ME wrote the manuscript

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

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

AMR, KvP – designed and conducted the experiments; AMR, KvP, AJ, ME – analyzed the data and wrote the manuscript

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# Curriculum vitae

Alexandra was born and raised in Athens, Greece, embraced with family and friends, many linked to the beautiful island of Serifos, in the western Cyclades, her preferred place on earth. She attended high school at Chosteas-Geitonas School, where very early, at the age of 11, she became interested in Horticulture. Upon graduation, she began bachelor studies in Plant Sciences, and very rapidly developed a strong interest for mites. In 2006, she enrolled in the Department of Crop Science, Agricultural University of Athens, where she specialized in Plant Protection and Environment and obtained a degree in Agricultural Engineering and Agricultural Sciences in 2011 (equivalent to an MSc.). During her program, she was granted four years of consecutive scholarships from the Union of Greeks who come from Egypt.

Before graduating, she conducted several internships that provided her with basic skills on acarology research and exposure to multiple aspects of commercial agriculture. Upon graduation Alexandra begins correspondence with Prof. Maurice Sabelis who eventually became her mentor and major graduate advisor. She then moved to the Netherlands and became a guest researcher at the Institute for Biodiversity and Ecosystems Dynamics, Group of Population Biology, University of Amsterdam. In her first year in Amsterdam, she conducted research on chemical communication and antipredator behavior of Thrips (*Frankliniella occidentalis*). In view of her capacities as a researcher, Prof. Sabelis then offers her to join the Research Group of Population Biology and start a Ph.D. program to study dispersal strategies and the evolution of prudent predation using the predatory mite *Phytoseiulus persimilis*. During her time as a Ph.D. student she gained knowledge in statistics, food web dynamics, life history theory and molecular techniques. Her contributions to the group include providing supervision to two masters and one bachelor students as well as teaching assistance in the course of Ecophysiology and Evolutionary Biology. She has also demonstrated the clarity of thought needed to clearly communicate scientific findings in thirteen international scientific meetings.

Alexandra is ready for the next step in her professional career, equipped with 5 languages (Greek, English, German, Dutch and Spanish) and a strong interest in acarology, entomology, nematology, behavioural ecology, population dynamics, evolutionary ecology, chemical communication, biological control and integrated pest management.