Evolution of animal dispersal:
Putting timing in perspective

Evolution von Ausbreitungsstrategien:
Die Fitnesskonsequenzen des Zeitpunkts von Emigration

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Milica Lakovic

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Gutachter: PD Dr. Thomas Hovestadt

Gutachter: Prof. Dr. Dries Bonte

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Doktorurkunde ausgehändigt am:

Name, Vorname: Milica Lakovic
Straße: Emil-Fischer Strasse 32
PLZ und Ort: 97074, Würzburg, Germany
Tel. 00499313188831
E-Mail: milica.lakovic@biozentrum.uni-wuerzburg.de

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Affidavit

I hereby declare that my thesis entitled: „**Evolution of dispersal:putting timing in perspective**” is the result of my own work.

I did not receive any help or support from commercial consultants. All sources and / or materials applied are listed and specified in the thesis.

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Hiermit erkläre ich an Eides statt, die Dissertation: „**Evolution von Ausbreitungsstrategien: Die Fitnesskonsequenzen des Zeitpunkts von Emigration**“, eigenständig, d. h. insbesondere selbständig und ohne Hilfe eines kommerziellen Promotionsberaters, angefertigt und keine anderen, als die von mir angegebenen Quellen und Hilfsmittel verwendet zu haben.

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Berlin, 24.07.2017

For my father

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Summary

Dispersal is an important life history trait with profound eco-evolutionary consequences. Ongoing global change has left many species confined to fragmented habitats, where dispersal has a key role in the persistence of populations. Insects are particularly vulnerable to such habitat fragmentation as many of them are specialists and therefore highly dependent on host presence and distribution. Hence, understanding causes and consequences of dispersal is crucial for conservation of these species. Moreover, species with different life-cycles can display distinct dispersal strategies, in particular in regard to the timing of mating and dispersal within the life-cycle: *Natal dispersal* is defined as moving away from the natal patch to a new patch for reproduction, while *breeding dispersal* means dispersing between two (or more) consecutive reproduction episodes. Natal dispersal can take place during the larval and (early) adult phase, whereas breeding dispersal can only occur during the adult (reproductive) phase. Furthermore, the timing of mating before or after dispersal is especially important for females that can potentially carry not just their own genes, but those of a mated male, into a new population. Clearly, the amount of gene flow and consequently eco-evolutionary dynamics will differ between strategies. In addition, information use by insects and its role in emigration related decisions has received much attention in the recent decades. Yet, the timing of information acquisition (i.e. in the larval or adult stage) and its relevance for the timing of dispersal has largely been overlooked by both theoreticians and empiricists. This thesis provides insights into evolution of dispersal and mating timing and the role of information acquisition in insect metapopulations.

In Chapter 2 of this thesis I investigate the evolution of emigration timing in patchy environments. Theoretical studies on dispersal typically assume 'natal dispersal', where individuals emigrate right after birth. But emigration may also occur during a later moment within a reproductive season ('breeding dispersal'). For example, some female butterflies first deposit eggs in their natal patch before migrating to other site(s) to continue egg-laying there. How breeding compared to natal dispersal influences the evolution of dispersal has not been explored. To close this gap we used an individual-based simulation approach to analyze (i) the evolution of timing of breeding dispersal in annual organisms, and (ii) its influence on emergent dispersal as compared to a model assuming natal dispersal. Furthermore, we tested (iii) its performance in direct evolutionary contest with individuals following a natal dispersal strategy. Our results show that evolution should typically result in lower dispersal under breeding dispersal, especially when costs of dispersal are low and population size is small. By distributing offspring evenly across two patches, breeding dispersal allows reducing direct sibling competition in the next generation whereas natal dispersal can only reduce trans-generational kin competition by producing highly dispersive offspring in each generation. This added benefit of breeding dispersal is most prominent in patches with small population sizes. Consequently, the evolutionary contests show that a breeding dispersal strategy would universally out-compete natal dispersal, in particular if local populations are small.

Chapter 3 deals with evolution of dispersal and mating timing in insect metapopulation. Dispersal can evolve under various known selective pressures as identified by a multitude of theoretical and empirical studies. Yet only few of them are considering the succession of mating and dispersal. The sequence of these events influences gene flow and consequently affects the dynamics and evolution of populations. We use individual-based simulations to investigate the evolution of the timing of dispersal and mating, i.e. mating before or after dispersal. We assume a discrete insect meta-population in a heterogeneous environment, where populations may adapt to local habitat conditions and only females are allowed to disperse. We run the model under different levels of species habitat tolerance, carrying capacity and environmental variability. Our results show that in species with narrow habitat tolerance, low to moderate dispersal evolves in combination with mating after dispersal (post-dispersal mating). With such strategy females benefit from mating with a resident male, as their offspring will be better adapted to local conditions. Contrary, in species with wide habitat tolerance higher dispersal rates and pre-dispersal mating evolves.

Consequently, individuals evolve an adaptation to the 'average' habitat where pre-dispersal mating conveys the benefit of carrying relatives' genes into a new population. With high dispersal rates and large population size, local adaptation and kin-structure both vanish and the temporal sequence of dispersal and mating may become a (nearly) neutral trait.

In Chapter 4 I investigated how time-investment into information collection and emigration affects evolution of dispersal. Theoretical studies on the evolution of density-dependent dispersal typically assume natal dispersal, and thus that emerging adults are already fully informed about local population density. This may be true for the species where already larvae compete for resources providing them with cues about the future population densities; an experience they could use to make density-related emigration decisions right after emergence. On the other hand, animals where competition occurs only between adults cannot make any density-related decision without collecting corresponding information. Such information may be acquired during habitat exploration in search for resources, mates or nesting sites. Here we assume that emigration decisions evolve in adaptive way and that individuals use the information they collected to make informed decisions. We tested this assumption with an individual-based model, where insect adults would learn, over the course of the season, about the density by encountering con-specific eggs on a critical host plant; individuals do not deposit eggs on plants that already carry an egg. Since the availability of 'free plants', where oviposition is possible, declines exponentially over the course of the season, our assumption is that the individual decision function (it’s expectation of the proportion of free plants) is also described by a negative exponential curve over the course of the season. Indeed, we found that animals evolve to make 'smart' decisions. That is, in very crowded patches individuals emigrate earlier in the season and more frequently, while in non-crowded patches they emigrate only later within the season resulting in a (partial) equilibration of population densities over the course of the season.

Chapter 5 of this thesis provides an overview of dispersal strategies across insect taxa. Dispersal can occur at different stages in individual's life-cycle (natal or breeding dispersal) that in turn has different effects on the amount of gene flow and individual survival. Additionally, information use and density-dependent dispersal has received a lot of attention in theoretical and empirical research. However, the underlying assumption that natal dispersal can be informed is misguiding for many species. We postulate that natal dispersal in larvae or (unmated) adults should occur in species that have access to the information during the larval stage or this information was transferred to them from their parents (i.e. maternal effects). On the other hand, informed dispersal in adults should rather be breeding dispersal, as most insects, due to their short adult lives, tend to mate soon after emergence before they can gather information about the habitat. Additionally, risk spreading and offspring distribution during breeding dispersal should be beneficial in insects living in variable environments. Finally, mating prior to dispersal may be important in species colonizing new (empty) habitats, while mating after dispersal should benefit those insects living in heterogeneous habitats where local adaptation in important. This chapter reviews such strategies in insects (mostly Pterygota) and some species of Arachnids (such as spiders and mites).

Overall, findings of this thesis provide new insights into evolution of dispersal with regard to timing of emigration, mating and information collection. This aspect of timing has largely been overlooked by both theoretical and empirical ecologist. Knowing the life cycle of a species and the timing of its most important life events (dispersal, mating and reproduction) is crucial for understanding its population dynamics and distribution in nature. This is an imperative if we aim to successfully implement conservation measures (i.e. reintroductions), or bio-control applications (i.e. introducing predators for pest species elimination).

Zusammenfassung

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Emigration und die daraus resultierende Ausbreitung („dispersal“) ist ein wichtiges Ereignis im Lebenszyklus, mit grundlegenden öko-evolutionären Folgen. Fortschreitender globaler Wandel hinterlässt viele Arten in stark fragmentierten Habitaten; der Verbreitungsstrategie kommt deshalb eine Schlüsselrolle im Fortbestehen von Populationen zu. Insekten sind besonders anfällig gegenüber Habitatzerstörungen, da viele von ihnen Spezialisten sind und daher z.B. stark von Präsenz bestimmter Wirtsarten und deren Verteilung abhängen.

Zum Schutz dieser Arten ist es folglich entscheidend, die Ursachen und Folgen von Ausbreitungsstrategie zu verstehen. Zudem können Arten mit unterschiedlichen Lebenszyklen spezifische Ausbreitungsstrategie aufweisen. Natale Emigration („natal dispersal“) ist definiert als das Verlassen des Ortes der Geburt, um an einem neuen Ort zu reproduzieren, während „breeding dispersal“[1] Ausbreitung zwischen zwei aufeinanderfolgenden Paarungen bedeutet. Natal dispersal kann während des Larval- und Adultstadiums stattfinden, breeding dispersal nur während des Adultstadiums. Weiterhin ist der Zeitpunkt der Verpaarung, entweder vor oder nach Ausbreitung, besonders wichtig für Weibchen, die nicht nur die eigenen Gene transportieren, sondern eventuell auch die eines verpaarten Männchens. Es ist eindeutig, dass sich Genfluss und öko-evolutionäre Dynamik zwischen diesen Ausbreitungsstrategien unterscheiden. Schließlich erhielt Informationsverarbeitung durch Insekten und dessen Rolle in emigrationsbezogenen Entscheidungen in jüngster Zeit viel Aufmerksamkeit. Dennoch wurde der Zeitraum der Informationsbeschaffung (z.B. während des Larven- oder Adultstadiums) und folglich die Verfügbarkeit von Information zum Zeitpunkt der Emigration von Theoretikern und Empirikern größtenteils nicht beachtet. Diese Doktorarbeit liefert theoretische Einsichten in den optimalen Zeitpunkt der Emigration, des Zeitpunktes der Paarung (in Relation zu

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[1] Keiner der in Frage kommenden Terme wie “Ausbreitung”, “Verbreitung” oder “Emigration” trifft, insbesondere in Kombination mit den Begriffen “natal” und “breeding”, die genaue Bedeutung der englischen Begriffe “natal dispersal” oder “breeding dispersal”. Ich verwende hier deshalb die englischen Begriffe.

Emigration) und die Rolle von Informationsbeschaffung in Insekten-Metapopulationen.

In Kapitel 2 dieser Arbeit untersuchte ich die Evolution des Emigrationszeitpunktes in Metapopulationen. Theoretische Studien zur Evolution von Emigrationsraten bzw. -wahrscheinlichkeiten nehmen typischerweise natal dispersal an, d.h. Individuen emigrieren direkt nach der Geburt. Emigration kann jedoch auch während eines späteren Zeitpunktes in der reproduktiven Phase stattfinden (breeding dispersal). Einige Schmetterlingsarten zum Beispiel, legen zuerst Eier in ihrem Geburtshabitat, bevor sie zu anderen Plätzen emigrieren, um die Eiablage fortzusetzen. Ob derartiges breeding dispersal grundsätzliche Vor- bzw. Nachteile gegenüber natal dispersal hat, wurde bisher nicht erkundet. Um diese Lücke zu füllen, nutzen wir einen individuen-basierten Simulationsansatz zur Analyse (i) der Evolution des Zeitpunktes von Fortpflanzungsverbreitung bei einjährigen Organismen und (ii) dessen Einfluss auf die sich etablierenden Emigrationswahrscheinlichkeiten verglichen mit einem Model, das natal dispersal voraussetzt. Weiterhin testeten wir (iii) den Erfolg von breeding dispersal in direkter evolutionärer Konkurrenz mit Individuen, die einer natal dispersal Strategie folgen. Unsere Ergebnisse zeigen, dass breeding dispersal typischerweise die Evolution von geringerer Emigrationswahrscheinlichkeiten zur Folge hat, besonders wenn die Kosten für Ausbreitung niedrig sind und die Population eine geringe Größe aufweisen. Durch die gleichmäßige Aufteilung der Nachkommen auf zwei Orte führt breeding dispersal zu einer reduzierten Geschwisterkonkurrenz in der folgenden Generation, wohingegen natal dispersal generationenübergreifende Konkurrenz der Nachkommen nur reduzieren kann, indem Nachkommen mit hoher Emigrationswahrscheinlichkeit gezeugt werden. Dieser Vorteil von breeding dispersal wird insbesondere in kleinen Populationen deutlich. Folglich zeigt sich in einem evolutionären Vergleich, dass breeding dispersal oft konkurrenzstärker wäre als natal dispersal.

Kapitel 3 behandelt die Evolution des (optimalen) Emigrations- und Paarungszeitpunkts in Metapopulationen von Insekten. Bislang erwägen nur wenige Studien die Bedeutung der Reihenfolge von Paarung und Emigration. Diese Abfolge beeinflusst Genfluss und die Dynamik und Evolution von Populationen. Um die Evolution des Timings und der Verbreitung zu analysieren, nutzen wir Individuen-basierte Simulationen, z.B. Paarung vor und nach Verbreitung. Wir setzen eine Insektenmetapopulation in einer heterogenen Landschaft voraus, in der sich Populationen an lokale Bedingungen anpassen können; nur Weibchen ist es erlaubt zu emigrieren. Wir lassen das Modell mit verschiedenen Graden an Habitattoleranz („Nischenbreite“) der Arten, ökologische Tragfähigkeit und Umweltvariabilität laufen. Unsere Ergebnisse zeigen, dass bei Arten mit geringer Habitattoleranz geringe bis moderate Emigrationswahrscheinlichkeiten evolviert, kombiniert mit Paarung *nach* Verbreitung. Mit solch einer Strategie profitieren Weibchen, die sich mit einem lokal beheimateten Männchen verpaaren, da ihre Nachkommen besser an die lokal vorherrschenden Umweltbedingungen angepasst sind. Im Gegensatz dazu entwickeln sich bei Arten mit einer großen Habitattoleranz größere Emigrationsraten und Verpaarung *vor* der Emigration. Folglich entwickeln Individuen eine Anpassung an das „Durchschnittshabitat“, in dem Paarung vor Verbreitung den Vorteil mit sich bringt, die Gene eigener Verwandten mit in neue Populationen zu bringen. Mit hohen Emigrationsraten und großen Populationen verschwinden lokale Anpassungen und Verwandtschaftsstrukturen und die zeitliche Abfolge von Verbreitung und Verpaarung kann (fast) fitness-neutral werden.

In Kapitel 4 untersuchte ich, wie die Investition von Zeit in das Sammeln von Information auf den Zeitpunkt und Häufigkeit von Emigration auswirkt. Theoretische Studien der Evolution von dichteabhängiger Verbreitung setzen typischerweise natal dispersal voraus. Dies mag auf Arten zutreffen, deren Larven um Ressourcen konkurrieren und dabei bereits einen Eindruck über künftige Populationsdichte bekommen können. Diese Erfahrung könnten sie nutzen, um dichte-bezogene Emigrationsentscheidungen direkt nach Schlupf der Adulten zu treffen. Andererseits können Tiere, bei denen Konkurrenz erst während des Adultstadiums auftritt, keine dichte-bezogenen Entscheidungen treffen bevor sie entsprechende Informationen gesammelt zu haben. Derartige Informationen können aber während der Erkundung des Habitats auf der Suche nach Ressourcen, Partnern oder Eiablageplätzen gesammelt werden. Wir nehmen an, dass Emigrationsentscheidungen adaptiv erfolgen und dass Individuen anhand der gesammelten Informationen Entscheidungen treffen. Wir überprüften diese Annahme mittels eines Individuen-basierten Models, in dem adulte Insekten während einer Saison – dadurch dass sie arteigenen Eiern auf kritischen Wirtspflanzen begegnen – (indirekt) Information über die Dichte konkurrierender Individuen sammeln können. Individuen legen in unserem Modell keine Eier auf Pflanzen ab, auf denen bereits Eier abgelegt wurden. Dadurch, dass „ei-freie“ Pflanzen, auf denen noch Eiablage möglich ist, über den Lauf einer Saison exponentiell abnehmen, nehmen wir an, dass auch die Entscheidungsfunktion, d.h. die Erwartung auf freie Pflanzen zu treffen, auch exponentiell über den Lauf der Saison sinkt. Wir nehmen an, dass, nach einer kritischen Zahl von Begegnungen, Tiere dann emigrieren, wenn die beobachtete Wahrscheinlichkeit unter die erwartete fällt. Tatsächlich fanden wir, dass mit einer derartigen Strategie Individuen früher und öfter in der Saison aus stark überfüllten Habitaten emigrieren, während sie aus wenig besetzten Habitaten später emigrieren.

Kapitel 5 dieser Arbeit zeigt einen Überblick über Verbreitungsstrategien verschiedener Insekten Taxa. Verbreitung kann während verschiedener Phasen im Lebenszyklus eines Individuums auftreten (natal oder breeding dispersal) und dadurch den Grad an Genfluss und das Überleben der Individuen beeinflussen. Weiterhin hat die informations- und dichteabhängige Verbreitung viel Aufmerksamkeit in theoretischer und empirischer Forschung erhalten. Die Annahme jedoch, dass natal dispersal informationsgesteuert sein kann, ist irreführend für viele Arten. Es ist anzunehmen, dass natal dispersal bei Larven oder unverpaarten Adulten auftritt, die Informationen während des Larvalstadiums

aufnehmen oder denen Informationen der Elterngeneration zur Verfügung steht (z.B. maternal effects). Da sich die meisten Insekten kurz nach der Entwicklung zum Adulten paaren, bevor ausreichen Information über das Habitat gesammelt wurde, ist breeding dispersal die bevorzugte Strategie der informationsgesteuerten Ausbreitung. „Risk spreading“ und die Verteilung der Nachkommen während breeding dispersal bieten Vorteile für Insekten in Habitaten mit wechselhaften Umweltbedingungen. Eine Verpaarung vor der Verbreitung ist besonders wichtig für Arten, die in ein neues (leeres) Habitat emigrieren, während die Verpaarung nach der Ausbreitung für Arten wichtig ist, die in heterogenen Habitaten leben, in denen lokale Anpassung eine entscheidende Rolle spielt. Dieses Kapitel beleuchtet oben genannte Strategien bei Insekten (hauptsächlich Pterygota) und einigen Arten von Arachniden (wie zum Beispiel Spinnen und Milben).

Ergebnisse dieser Thesis bieten neue Einsichten in die Evolution von Ausbreitung, insbesondere auf den richtigen Zeitpunkt und die Reihenfolge von Emigration, Verpaarung und dem Sammeln von Informationen. Dieser Aspekt des Timings wurde bisher von theoretischen und empirischen Ökologen größtenteils ignoriert. Um die Populationsdynamik und die Ausbreitung einer Art verstehen zu können, ist es essentiell den Lebenszyklus und die Zeitpunkte der wichtigsten Lebensereignisse (Verbreitung, Reproduktion) zu kennen. Dies ist zwingend nötig, wenn eine erfolgreiche Umsetzung von Naturschutzmaßnahmen (z.B. Wiedereinführung von Arten) oder biologischer Schädlingsbekämpfung (z.B. Einführung von Prädatoren zur Bekämpfung von Schädlingen) angestrebt wird.

Chapter 1

General introduction

1. Brief introduction to dispersal

Dispersal has a central role in ecology as it influences population dynamics and genetics of species and consequently shapes the whole communities. There are many definitions of dispersal, however, I will use the one given by Ronce (2007) where it is described as ‘any movement of individuals or propagules with potential consequences for gene flow across space’. Such and similar interpretations, consider natal and breeding dispersal, both being the focus of this thesis. Natal dispersal or pre-breeding dispersal is movement from place of birth to the place of reproduction, while breeding dispersal (post-breeding dispersal) describes movement between successive sites of reproduction (Basskett, 2012). Dispersal is a complex, multi-causal process (Clobert et al. 2012) and its consequences are manifold. It affects not only individual fitness but also the ecology and evolution of species (Hanski and Gaggiotti 2004) and communities as well (Chust et al. 2016). Trough immigration and emigration processes, dispersal affects population dynamics and it can rescue small populations from extinction (Amarasekare 1998?). It determines spatial distribution and abundance (Hanski et al. 1993), species coexistence (Holmes and Wilson 1997) and can e.g. help climate change mitigation via range expansion (Duckworth 2008). Furthermore, it has an effect on the local adaptation, speciation and life-history trait evolution. Moreover, dispersal is its self adaptive and there is a growing number of studies confirming the genetic basis and heritability of dispersal (Sinervo and Clobert 2003, Saastamoinen 2008, Doligez et al. 2009). It is now clear that, under certain conditions, dispersal can be selected for/or against, that has been confirmed by decades of research (see review Bowler and Benton 2005). Especially, theoretical models have proven to be a powerful tool when studying the evolution of dispersal, by providing insights in underlying mechanisms and the consequences.

2. Metapopulations

Studying dispersal becomes increasingly important in the face of ongoing global change, where habitat fragmentation and degradation leave species confined to patchy often isolated environments. Dispersal, or gene flow among such populations is often the key for their persistence. Spatially structured populations are usually referred to as metapopulations, although they often differ from the classical metapopulations. The original metapopulation concept was reported by Richard Levins (1969) to describe a ‘population of populations’ in his research of insect pests in agricultural fields. The persistence of Levins’ metapopulation is maintained by the balance of ‘births’ and ‘deaths’ (extinctions and colonizations) of discrete habitat patches, with asynchronous population dynamics. However, the term is often used broadly in academia and even applied research to describe any spatially structured population or patches that are connected trough dispersal processes. In general, metapopulation can be described as a system, consisting of local populations in discrete habitat patches that interact via dispersal of individuals moving through the matrix, buffered against extinction by gene flow among local populations (Baguette et al. 2013). True metapopulations are rather rare in nature with the most famous example being Glanville fritirally butterfly (Hanski 1995). However, the emergence of a classical metapopulation, where all the above assumptions are met, is possible only with certain life-history traits that are, indeed, most often found in arthropods (Fronhofer et al. 2012).

3. Drivers of the evolution of dispersal

The two main forces that act upon evolution of dispersal are those intrinsic (individual level, providing variation) and external (changing biotic and/or abiotic environment). The intrinsic forces for dispersal are numerous and include physical condition or body size, where individuals differ in their physical readiness and thus the tendency to emigrate. Additional, information-based- dispersal (i.e. density-dependent dispersal) that is conditional to external environment may also affect individual motivation to emigrate. There is great body of theoretical work established on the ultimate causes/drivers of dispersal, including: (i) risk of habitat extinction (Hanski 1999, Massot et al. 2007), (ii) kin competition (Hamilton and May 1997), (iii) inbreeding avoidance (Bengston 1978, Pussey 1987, Motro 1991, Pusey and Wolf 1996, Gandon 1999, Gros et al. 2003), (iv) temporal and spatial variability in habitat quality (McPeek and Holt 1992) and (v) dispersal costs (Bonte et al. 2012). All of these factors can independently select for or against dispersal and interact in their impact on dispersal evolution. The study of Hamilton and May (1977) highlights the competition among kin as one of the driving forces of dispersal evolution. Their simple model shows that dispersal is selected for even in stable and predictable environments and high dispersal mortality risk in order to reduce the competition among kin. However, many natural systems are not stable with some degree of spatio-temporal variation in these environments. In general, spatial variability selects against (Hastings 1983) while temporal variability selects for dispersal. If habitats fluctuate both spatially and temporally, the dispersal rate will depend on how these fluctuations are correlated (McPeek and Holt 1992). Naturally, dispersal will strongly be selected for if there is an inbreeding cost such as inviability or decreased offspring fitness as a result of mating with kin, (Bengston 1978, Pussey 1987, Motro 1991, Pusey and Wolf 1996, Gandon 1999, Gros et al. 2003). Inbreeding can select for dispersal independently of competition between related individuals. Increased dispersal costs tend to select against dispersal. These costs vary among different dispersal phases, namely, emigration, transition and settlement (Bonte et al. 2012). Firstly, there are energetic costs, metabolic or investment in dispersal morphology such as longer wing or limb size. Secondly, the time invested into dispersing could be used for mate finding, mating or resource acquisition. And finally, the risks during transfer (for instance predation) and settlement phase (e.g. potentially arriving in an empty patch with no mates or food) (Duputie & Massol 2013). Naturally, if these costs are high selection will act against dispersal. Nonetheless, under certain conditions, e.g. when extinctions and colonization occur in a metapopulation and local relatedness is high (strong kin structure) dispersal can be selected for. (Gandon and Michalakis 1999).

4. Information and dispersal

Information is important to all biological processes, from the information coded in our DNA o learning about our environment. Ecology of information studies how organisms use information in decision-making to manage their lives (Schmidt et al. 2010). It is now clear that information reduces uncertainty about the environment (Donaldson-Matasci et al., 2010) and it is considered to increase reproductive fitness (McNamara and Dall 2009). Higher animals with better neurone and brain development can exhibit learning and use information in their daily survival, however, there is now prevailing evidence that also insects rely on learning for their major life activities (Dukas 2008). For instance, selecting a high quality habitat is essential for successful reproduction (Boulinier and Danchin 2008). Therefore, individuals should be able to use information about their environment to assess quality of their patch, and consequently decide whether to reside there or to emigrate and reproduce somewhere else. It has been shown that that information-based habitat selection strategies are better than random as they could make populations less likely to go extinct (Schjørring 2002), especially in variable environments (Ponchon et al. 2015). Such information can be related to weather or resources, or it can be social, e.g. density of con-specifics (Clobert et al. 2009).

4.1. Density-dependent dispersal

In general competition (i.e. for space, mates, food) has been recognized as important driver of dispersal evolution. When animals explore their habitats in search for resources they may compete with other individuals, within their own species (intra-specific competition) or with other species (inter-specific competition) in order to obtain those resources. Clearly, resource depletion will occur quicker in an overcrowded habitat. Therefore, population density can often be an indicator of the strength of the local competition and thus reduced resource availability. Given this correlation, there are clear fitness benefits of leaving a crowded patch (or otherwise poor habitat) but staying in a low-density patch (Benton and Grant 2000), if an individual possesses corresponding information. There are indeed many empirical studies confirming density dependent dispersal across animal taxa, such as such as aphids (Mehrparvar 2013), butterflies (Baguette et al. 1996, Rhainds et al. 1997, Enfjäl and Leimar 2005, Nowicki and

Vrabec 2011), spiders (Duffey 1998, DeMeester and Bonte 2010), other insects (check first manuscript), lizards (Clobert et a. 2009) and finally birds and mammals (Greenwood 1980, Matthysen 2005). Consequently, density-dependent dispersal has received a lot of attention from theoreticians in the last decades (Travis et al. 1999, Poethke and Hovestadt 2002, Bach et al. 2006). Most of these studies assume that individuals perceive patch size and patch density with absolute accuracy and use different ‘decision functions’ for the density-dependent dispersal strategy (linear (Travis et. Al 1999), nonlinear (Poethke and Hovestadt 2002)). However, in order for animals to know con-specific densities, they first need to gather this information from the environment and clearly this is a process that requires time.

5. Timing of dispersal (natal and breeding dispersal)

Most of the theory developed around the evolution of informed dispersal consider natal dispersal, i.e. individuals that leave after emergence to a new patch to reproduce (Travis and Dytham1999, Poethke and Hovestadt 2002). That implies that these individuals have knowledge about the population density, for instance, right at birth or the moment of emergence. While this is true for species where larval stages experience competition giving them a clue of the future competition with adults or for those where dispersal is controlled maternally, it is not so for species that experience competition only during the adults stage. For instance, certain butterflies, tend to oviposit more on plants that already contains con-specific eggs (i.e. *Pieris napi*, Raitanen et al. 2014) that leads to larval competition for food. On the other hand, there are butterfly species that prefer empty plants and their oviposition is actually deterred by the presence of con-specific eggs (i.e. *Erynnis tagges,* Gutierrez et al. 1999). More extreme example is that of two closely related butterflies species from the genus *Pieris* where *P. brassicae* lays eggs in batches while *P. rapae* lays single eggs on the host plant. This oviposition behaviour is a consequence of host plant distribution and larval competition. The host of the *P. brassicae* has clumped distribution where hatched larvae can potentially move to other plants. On the other hand, the distribution of host plants for *P. rapae* is such that plants are growing isolated from each other thus disabling larval avoidance of local competition (Davis and Gilbert 1985). Importantly, a larva that grows up in isolation cannot perceive clues on the level of competition it has to expect after emergence. These examples show that competition can occur at different life stages, that might differently influence emigration decisions. While species experiencing competition during the larval stage may make density related emigration decisions right after emergence, this is certainly not the case for species with adult competition. This is especially important for insect species where adults live and reproduce during one short season. In such cases, females might mate right after emergence and immediately start ovipositing and/or searching for resources that will allow them to 'learn' about their natal habitat (e.g. host plant availability, con-specific densities, predation). Consequently, before (potential) emigration a female might already lay eggs in her natal patch and continue with egg laying in a new patch after a (potential) dispersal episode. This scenario conforms with the classical ‘breeding dispersal’ (Basskett 2012). It is important to note that with breeding dispersal females may have potentially different impact on the population dynamics then is the case with natal dispersal. That is, in natal dispersal, individual mates after dispersal in the new patch, in breeding dispersal individual dispersers between the two reproductions. Emigration right after birth leads to gene flow by individuals moving themselves. On the other hand when dispersing within the reproduction season, females can mate in one place (patch) however oviposit fertilized eggs in another patch. In this way, a female transfers not just her own genes but also the genes of a male form her natal patch to another patch. Mating before dispersal to the new patch has a benefit of securing reproduction in case of ending up in an empty patch with no males. However, in the light of adaptation, mating with a local male would increase offspring adaptation in the new patch. Clearly, many insects females do mate multiple times (Arnqvist and Nilsson 2000) however, mechanisms such as sperm competition, precedence sperm removal may contribute to the eggs being fertilized by one or fewer number of males.

Finally, the assumption that, true natal density-dispersal is limited to certain life-histories and that individuals need time to acquire information about these densities from the environment, is often disregarded in the the theoretical models.

6. Study system and methodology

Research conducted for this thesis is entirely theoretical, based on computer simulations. More specifically, we used individual based model simulations that are adapted for investigating the evolution of dispersal propensity in insect metapopulations. The basic model utilized is well established and has been used in many previous studies on insect dispersal (Travis and Dytham 1999, Poethke and Hovestadt 2002, Bach et al. 2006). The hypothetical species used for the purpose of this study is modeled to resemble life history of many insects species, such as butterflies, dragon flies grasshoppers and others that occupy patchy landscape in the form of a metapopulation.

Individual-based models (IBMs) represent simulations of local interactions of members of a population (individuals) with global consequences. There is decades long tradition of IBMs use in biological research, especially in the field of dispersal ecology and evolution. The notion is that all ecological systems consist of living organisms, e.g. individuals with certain characteristics (life-history traits). These individuals are building blocks of ecosystems and their behavior and properties determine the whole system. Furthermore, individuals differ from each other and therefore their interaction with the environment as well. Most importantly, individuals are adaptive and they use their environment in order to increase their fitness (Grimm and Railsback 2005). With that said, it is clear how simplified modeling of populations at the individual level can give us close approximations at ecological and evolutionary scales.

The control of dispersal (behavior) presumably is a very complex process. In this thesis, however, emigration propensity is described as a single gene that can be thought of as a whole morpho-physiological state of the individual that represents the tendency to disperse. This is indeed, common practice in theoretical studies of dispersal evolution, where evolution is quantified as a proportion of individuals dispersed (Duputie and Massol 2013). The environmental variability includes everything from biotic interactions, such as competition or predation, to habitat degradation or deterioration. Our model is a simplification of environmental variability where we manipulate (spatially and or/temporally) fecundity or carrying capacity.

7. Scope of the thesis

Studying metapopulations, in a broad sense, and their persistence is very important, especially in the light ongoing global changes. Climate change, habitat degradation and deterioration have left many species living in fragmented populations where dispersal is often crucial to their persistence. Therefore, we need a better understanding of dispersal strategies and their affects on the metapopulation dynamics in general, in order to provide adequate conservation measures (Driscoll et al. 2014). Furthermore, simulation models have proven to be a powerful tool in evolution, ecology and also conservation. The main goal of this PhD thesis is to investigate different effects of timing and information on the evolution of dispersal in fragmented environments, by means of individual-based model simulations.

In Chapter 2 of this thesis I study the evolution of emigration timing in patchy landscapes. In particular, I compare evolution of breeding and natal dispersal, something that has not been explored before. Chapter 3, expands the timing context, and explores mating timing in regard to dispersal in insect metapopulations. Insect adults are short often short lived, therefore, the the sequence of most important life events such as mating and dispersal influences gene flow and consequently affects the dynamics and evolution of populations. Therefore, I investigate the evolution of female dispersal and mating timing in heterogenous environemnst. Chapter 4, addresses evolution of informed dispersal. More specifically, how information collection affects emigration timing in insect metapopulations. Furthermore, Chapter 5, provides an overview of insect (and some Arachnidae) dispersal strategies in nature. It focuses on dispersal startegies in relation to mating startegy, sex and information collection. Finally, in Chapter 6 I dicuss theoretical and empirical methods in dispersal research and their limitations. And lastly the importance of dispersal research and its application in conservation, biocontrol and agriculture.

Chapter 2

Dispersal timing: Emigration of insects living in patchy environments

The major contents of this chapter have been published as: Lakovic, M., Poethke, H.-J., Hovestadt, T., 2015. Dispersal Timing: Emigration of Insects Living in Patchy Environments. PLOS ONE 10, e0128672.

1. Introduction

Dispersal is an important life history trait that can strongly affect population dynamics and has profound eco-evolutionary consequences (Dieckmann et al. 1999). This especially holds in changing environment where species are confined to increasingly fragmented landscapes and where movement between local populations can affect the persistence and the dynamics of whole meta-populations (Levins 1969). Hence, understanding dispersal has received much attention in experimental as well as theoretical research (Clobert et al. 2012).

The tendency to disperse evolves under the influence of various ultimate causes (Bowler and Benton 2005) including (avoidance of) kin competition (Hamilton and May 1977, Gandon and Michalakis 1999, Gandon 1999, Ronce et al. 2000, Bach et al. 2006, Poethke et al. 2007, Gyllenberg et al. 2008), inbreeding avoidance (Parker 1979, Waser 1986, Motro 1991, Perrin and Mazalov, 1999), and the spatial and/or temporal variability that affects attributes like demography (Travis and Dytham 1999, Metz and Gyllenberg 2001, Poethke and Hovestadt 2002, Cadet et al. 2003), habitat quality (Poethke and Hovestadt 2002, McPeek and Holt 1992) or habitat persistence (Topping and Sunderland, 1998).

Further, dispersal decisions are typically influenced by external factors (abiotic environment, biotic interactions) and the internal state of the organism, i.e. emigration decisions are, presumably, not just random (Clobert et al. 2009).

Particularly, population density can be an indicator of local competition and thus reduced resource availability. Hence, there are clear fitness benefits of leaving a crowded patch (or otherwise poor habitat) but staying in a low-density patch (Benton and Grant, 2000), if an individual possesses corresponding information: Migration from a high-density patch to another one increases (on average) fitness expectations of offspring. There is indeed much empirical research confirming density dependent dispersal in butterflies Baguette et al. 1996, Rhainds et al. 1997, Einfjäll and Leimar 2005, Nowicki and Vrabec 2011), spiders (Duffey 1998, De Meester and Bonte 2010) and other insects (Denno and Peterson 1995, Fonseca and hart 1996, Doak 2000, Rhainds et al. 2005).

Selective pressures outlined above could not only impact the individuals' propensity to emigrate as such but also the timing of emigration. The exact timing of dispersal is especially important, because whether an individual moves before, during, or after a reproductive episode impacts population dynamics (Hanson 1991). Regarding timing, two general types of dispersal have been distinguished in empirical as well as theoretical research, 'natal dispersal' and 'breeding dispersal' (also 'adult dispersal', (Basskett 2012)). Natal dispersal occurs if an individual permanently leaves its natal site before ever reproducing. It has been observed in a broad spectrum of animal groups like spiders (Powers and Aviles 2003), insects (Ruf 2011), reptiles reptiles (Clobert 2012), birds (Greenwood and Harvey 1982) and mammals (Bray et al. 2007, Zedrosser et al. 2007). Breeding dispersal, on the other hand, considers movement between successive sites of reproduction. Such repeated dispersal has the obvious consequence of distributing life-time reproduction over two or more sites. Usually such dispersal is assumed to occur between reproductive seasons, like in long-lived organisms such as birds or mammals (Greenwood and Harvey 1982, Greenwood 1980). Consequently, breeding dispersal is an aspect mostly ignored in the models for the evolution of dispersal in annual organisms where dispersal is typically implemented as natal dispersal (Travis and Dytham 1999. Metz and Gyllenberg 2001, Poethke and Hovestadt 2002, Einfjäll and Leimar 2009, Hovestadt 2010).

However, an effect comparable to breeding dispersal in perennial organisms would emerge in annual organisms that go through only one reproductive cycle but where individuals migrate within the reproductive phase. For example, a female butterfly can first deposit some eggs in the natal patch and then migrate to other site(s) to continue egg-laying there. How often such 'spatially distributed' allocation of reproductive effort within a season occurs in short-lived, seasonal animals is hard to evaluate. Indeed, it is not a trivial exercise to provide such evidence as it requires accurate assessment of the timing of emigration in the field (it is not sufficient to just prove that an individual moved from one site to another); typical mark-recapture studies, for example, do not provide such evidence.

The benefit of distributing offspring in space, either within or across reproductive seasons, has been explained as 'risk-spreading' (Gall 1984). Risk spreading may emerge as a response to environmental uncertainty because distributing offspring over several patches could reduce the variance in reproductive success and thus increase the geometric growth rate (Gillespie 1977, Hopper 1999). Such behaviour may especially be important for the persistence of species living in fragmented habitats where risk-spreading can save isolated populations form extinction and secure the persistence of the whole meta-population (Hopper 1999, Boer den 1990, Kuno 1981).

However, at the population level there is no fundamental difference between natal dispersal where e.g. 20% of the individuals disperse after birth and breeding dispersal where all individuals produce 80% of their offspring in the natal patch before emigrating and, provided they survive dispersal, producing another 20% of offspring somewhere else. It is thus an open question to what degree different net-emigration would evolve under the natal versus the breeding dispersal strategy and to what degree one of the strategies is superior (in terms of long-term fitness) to the other.

Therefore, the main goal of this paper is to model and quantitatively compare the evolution of natal and breeding dispersal in annual organisms. More specifically, we will evaluate evolution in four fundamentally different scenarios (all combinations of either density-dependent or independent and of either natal or breeding dispersal) and utilize evolutionary tournaments (Hovestadt et al. 2010) to identify whether and under which conditions one strategy would be able to outcompete the other.

2. The model

2.1. Population dynamics and life-cycle

Our individual-based simulation experiments are based on the model of insect dispersal in patchy landscapes originally published by Poethke and Hovestadt (2002). Landscapes are implemented as a predefined number of N habitat patches, each of them with the same mean carrying capacity (K).

We consider discrete non-overlapping generations of asexual organisms. In approximation of the life-cycle of insects like grasshoppers or butterflies, we assume that individuals emerge at the start of the season as adults. Adults may either disperse right after emergence ('natal dispersal') or during the reproductive season ('breeding dispersal'). Each individual is characterized by affiliation with a certain patch *i* (initially the natal patch), the dispersal strategy it follows (natal S_N or breeding S_N dispersal), and a parameter related to its dispersal strategy; more details on the dispersal process will be provided later.

For any individual, the number of offspring produced is drawn from a Poison distribution with mean Λ as will be explained in more detail below these offspring may, under breeding dispersal, be produced in different habitat patches. Adults die after completion of the reproductive phase. In agreement with the model of Poethke and Hovestadt (2002) survival to adulthood ($s_{i,t}$) in the next generation ($t+1$) of the $L_{i,t}\left(L_{i,t}=N_{i,t}\cdot\lambda\right)$ larvae produced in patch i and generation *t* is density dependent according to the Beverton-Holt model (Beverton and Holt 1957):

$$s_{i,t}=\frac{1}{1+\frac{a\cdot L_{i,t}}{\lambda}} \quad \text{with} \quad a=\frac{\lambda-1}{K_{i,t}} \tag{1}$$

$K_{i,t}$ is the carrying capacity of a patch *i* in generation *t*. To account for random influences like inter-annual fluctuations in patch quality, $K_{i,t}$ is a log-normal distributed random number with mean K and standard deviation σ_K .

In accordance with the model of Poethke and Hovestadt (2002) we also tested simulations with inter-annual fluctuations in fertility (λ), as might result from e.g. varying weather conditions during egg-laying. This alternative implementation of environmental stochasticity had no qualitative influence on our results.

2.2. Dispersal

The original model by Poethke and Hovestadt (2002) only allowed for natal dispersal (S_N) where an individual decides right after birth to emigrate or not.

To implement breeding dispersal we modified this model in a sense that individuals were allowed to disperse after spending a fraction t_N of their reproductive life in the natal patch, and then spend the remaining fraction $t_E=1-t_N$ in another patch. Consequently an individual produces a fraction $\lambda \cdot t_N$ of their offspring in the natal patch and $\lambda \cdot t_E$ in another patch. For example an individual spends 80 percent of life in its natal patch, thus leaves 80 % of its offspring in the natal patch ($\lambda \cdot 0.8$) and consequently leaves remaining 20 % of offspring in a new patch, given that it survives dispersal ($\lambda \cdot 0.2$). However, in both scenarios emigrants face a certain risk of mortality (μ) in which case individuals are immediately removed from the population (without reproducing in the target patch). For simplicity we allow for only one dispersal event during an individual's lifetime, i.e. it can maximally distribute its offspring over two different patches.

In case of density independent emigration both dispersal strategies can be characterized by (i) an individual's dispersal propensity p (emigration probability) and (ii) the fraction of time (t_E) spent in another patch after dispersal: Natal dispersal (S_N) is implemented by fixing $t_E=1$ but allowing emigration probability $d=p$ to evolve in the range $0 \leqslant p \leqslant 1$, whereas breeding dispersal (S_B) is implemented by fixing $p=1$ but allowing $d=t_E$ to evolve in the range $0 \leqslant t_E \leqslant 1$ (Figure 1).

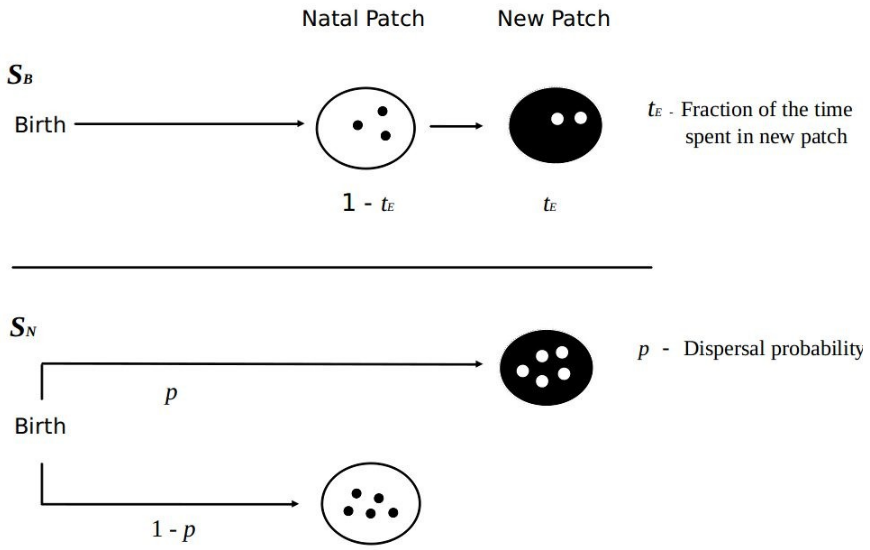

Figure 1. Schematic representation of the breeding S_B and natal dispersal strategy S_N. Under S_B reproduction takes place before and after dispersal with a fraction $1-t_E$ of offspring allocated to the natal patch and a fraction t_E to the target patch. In contrast, under S_N all reproduction always takes place either in the natal patch (with probability $1-p$) or in the target patch (with probability p). In both scenarios dispersing individuals carry a certain mortality risk μ during dispersal – in case of mortality individuals will not reproduce in the target patch.

For both scenarios we also performed simulation experiments with density-dependent emigration, as well: Density dependence was modelled according to Poethke and Hovestadt (2002) with

$$d=\begin{cases} 0 & if\, C_{i,t}<C_T \\ 1-\dfrac{C_T}{C_{i,t}} & if\, C_{i,t}\geq C_T \end{cases} \text{ with } C_{i,t}=\frac{N_{i,t}}{K} \text{ population density in } p_{i,t} \qquad (2)$$

Here the specific threshold density C_T defines either $d=p(S_N)$ or $d=t_E(S_B)$ according to equation (2). Below this threshold density individuals do not disperse.

Offspring inherit their dispersal trait from the parent. However, with a probability of $m_R=0.001$ the evolvable trait (either p or t_E in the case of density independent scenario or C_T in density dependent scenario) may mutate: In this case we add a random value drawn from the uniform distribution [-0.01 to 0.01] to the parent's trait value.

Dispersal is global; dispersing individuals randomly move to one of the N patches in the landscape, including its natal patch. As mentioned earlier, we impose a dispersal cost (μ) upon all emigrants regardless of the patch origin. This cost can be considered as a probability of mortality during the transitional phase of dispersal, e.g. death by predation or from exhaustion (Bonte et a. 2012).

2.3. Initialization and parameters tested

Simulations were initialized with K individuals in each patch. At initialization we assigned different values for the evolvable trait C_T (density dependent dispersal) or d (density independent natal or breeding dispersal) to each individual drawn from a uniform distribution $(C_T \in [0.6, 1.4]; d \in [0,1])$.

Our model includes three forces selecting for or against dispersal: (i) kin competition, (ii) spatio-temporal heterogeneity, (iii) cost of dispersal. To test for the influence of these forces on the evolution of dispersal we repeated simulations for different parameter settings (K, μ, σ): (1) To keep overall meta-population size comparable we ran simulations with either a large number $(N=1000)$ of low capacity $(K=10)$ patches or a small number $(N=100)$ of high capacity $(K=100)$ patches. (2) Previous studies have already confirmed that environmental variation selects for higher dispersal (Poethke et al. 2003, Bach et al. 2007). For simplicity and because this is not the major focus of this study we implement here only two extreme scenarios for environmental fluctuations: No fluctuations $(\sigma=0)$ or very high fluctuations $(\sigma=K)$. (3) We further ran simulations covering a broad range of dispersal mortalities $\mu \in [0.001; 0.01; 0.02; 0.05; 0.1; 0.2; 0.5]$. In all scenarios presented here we kept mean fecundity fixed at $\lambda=2$; we tested higher values that gave, qualitatively similar results. Mutation rate $(m_R=0.001)$ and size $m_S\in[-0.01, 0.01]$ were also kept constant across all simulations.

2.4. Simulations and data extraction

For each the 2x2x7 possible parameter combinations of K, σ, μ and any of the four different dispersal models we performed 15 replicate mono-culture simulation experiments, each running over 7000 generations. Only data from the last 2000 generations – after simulations had reached an evolutionary equilibrium – were utilized for data evaluation. For this period we calculated for every 10th generation the mean dispersal rate across the whole meta-population. The mean dispersal rate at the population level $\bar{d}$ is defined by the mean dispersal propensity ($\bar{d}=\bar{p}$) in the case of natal dispersal (see also Poethke and Hovestadt 2002), while it is equal to the average fraction of time spent away from the natal patch ($\bar{d}=\bar{t}_E$) in the case of breeding dispersal. For presentation in figures averages were taken over the last 2000 generations of all 15 replicate simulation runs.

We performed additional non-evolutionary simulations in order to compare how mode of dispersal affects the formation of the coefficient of relatedness (F). For this purpose we fixed the dispersal traits of all individuals to identical values ($d\in[0.5, 0.05]$) for both strategies, setting dispersal costs ($\mu=0$) in all simulations; After allowing for the population to reach ecological equilibrium (100 generations) we then marked all individuals from a single randomly selected patch with a neutral marker. We then calculated coefficient of relatedness F for the individuals carrying this neutral marker after 5 and 20 generations. Rousset (2002) defines F in structured populations as:

$$F=\frac{(Q_w-Q_b)}{1-Q_B} \qquad (3)$$

Here Q_w is the probability of identity within a ‘structural unit’ (patch in our case) and Q_b the probability of identity between two different patches. To link relatedness F to frequency p of a neutral marker within the entire meta-population we can follow the logic well known from the derivation of the Wahlund effect (Hendrick, 2009): The mean degree of homozygosity of sub-populations exceeds homozygosity in the entire population by twice between-patch variance in p_i ($V[p]$). From that it can easily be concluded that :

$$F=\frac{V[p]}{p\times(1-p)} \tag{4}$$

2.5. Evolutionary contest

To compare whether one of the dispersal strategies (S_N, S_B) would have an evolutionary benefit over the other in direct competition we performed 'evolutionary tournaments' between natal (S_N) and breeding dispersal (S_B) similar to those described by Hovestadt et al. (2010). For the tournament we initialized 'mixed meta-populations' by introducing 50% of individuals applying strategy S_N according to the distribution of parameter values that had established at the end of the previously introduced monoculture experiments and sampling the remaining 50% from the final parameter distribution as it emerged in the corresponding S_B monoculture experiments. For each contest and parameter combination the tournament was replicated 10 times and we recorded for each tournament whether and after which time one strategy completely outcompeted the other, meaning that one of the strategies went extinct.

3. Results

3.1. Natal vs. breeding dispersal

In general and expectedly (see discussion), increasing costs of dispersal tends to select against dispersal. Our results confirm previous findings (Bach et al. 2006, Poethke and Hovestadt 2002), regardless of whether dispersal is density-independent or -dependent and whether it is natal or breeding dispersal (Figure 2).

With high mortality risk during dispersal, dispersal is low and more or less equal rates evolve for natal and breeding dispersal. However, as dispersal mortality decreases ($\mu < 0.05$), an apparent difference between the two strategies arises: Populations following breeding dispersal S_B evolve substantially lower dispersal rates than those following natal dispersal (Figure. 2). More specifically, even at low dispersal costs, the proportion of offspring dispersed for S_B hardly increase above 0.5 – 0.6. At such value the offspring of a successfully dispersing parent are almost equally distributed between the natal and a new patch. It is indeed obvious (if costs of dispersal are low) that kin competition among siblings would be minimized if a parent would distribute its offspring evenly over two patches. However, under natal dispersal, when dispersal mortality is low, emigration probabilities evolve to values close to 1. This is because the kin competition reducing benefit of dispersal for the natal dispersal strategy only emerges in the generation of grandchildren (second generation) and beyond, while the breeding dispersal strategy can already reduce direct sibling competition in the first generation. This provides a strong incentive for the evolution of a residence time t_E near 0.5.

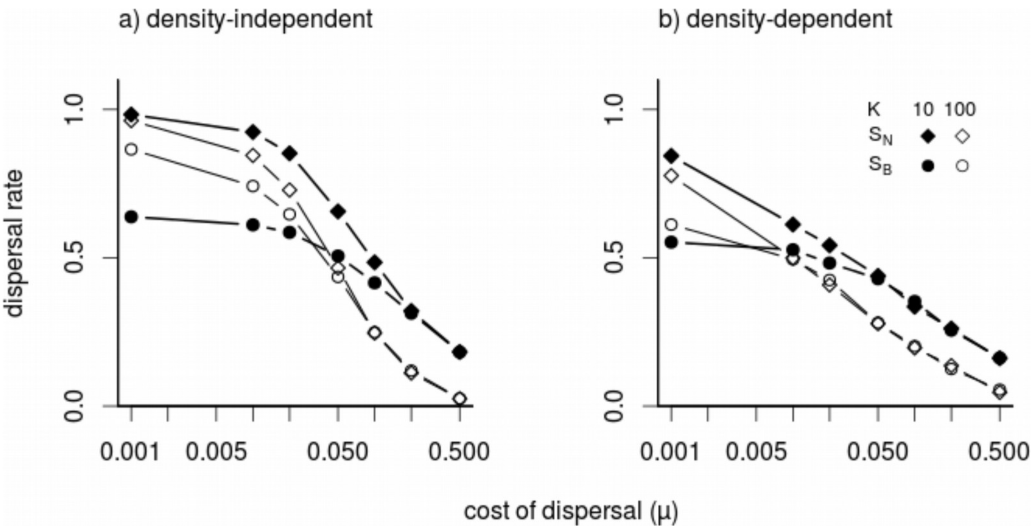

Figure 2. The effect of patch capacity K and dispersal strategy on evolved mean dispersal as a function of dispersal mortality, μ (log scale). (a) Density-independent (*DI*) scenario and

(b) density-dependent (*DD*) scenario. Filled circles and diamonds represent small patches ($K=10$) and empty circles and diamonds big patches ($K=100$). Diamonds indicate natal dispersal (S_N), circles breeding dispersal (S_B). Other parameter values: environmental variability ($\sigma=K$) and fecundity ($\Lambda=2$).

The coefficients of relatedness (F) calculated for the additional non-evolutionary simulations with fixed genetic traits of all individuals further confirm our speculations that breeding dispersal strategy is more advantageous avoiding kin competition. Thereby, we obtained significantly lower F after 20 generations values for breeding dispersal strategy when patches are small, while in big patches a difference is hardly noticeable (Figure 3). This corresponds with the stronger selection for S_B we observe in meta-populations with small patches, while in big patches the two strategies become more similar. Coefficients for relatedness calculated after 5 generations yield higher values, however qualitatively are the same as those after 20 generations.

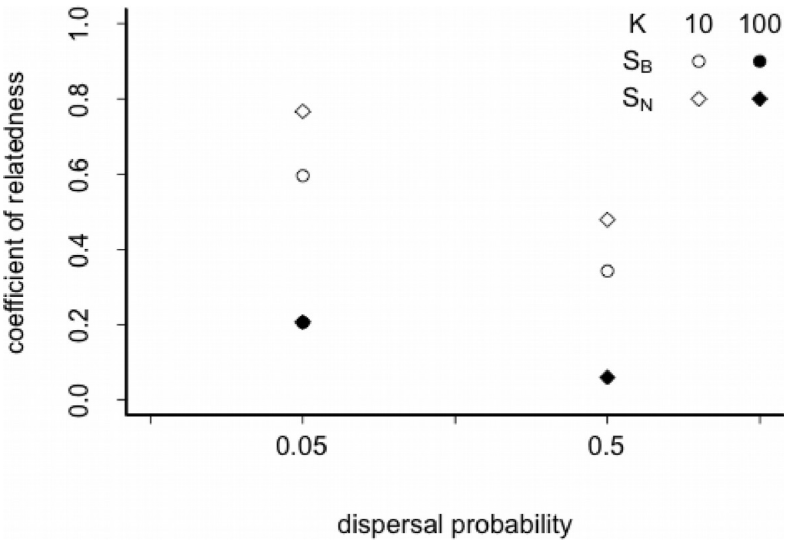

Figure 3. The effect of patch size (K), dispersal probability and dispersal strategy (S_B, S_N) on coefficient of relatedness after 20 generations. Different strategies S_B and S_N are represented by circles and diamond symbols, respectively. Small patch sizes ($K=10$) are depicted with open symbols and big patch sizes ($K=100$) with filled symbols

This effect is qualitatively similar, independent of whether we consider density-independent or density-dependent emigration (Figure 2). However, we observe the evolution of higher dispersal under density-independent compared to density-dependent scenario. This is not surprising because under density-independent scenario individuals disperse regardless of the patch density, thus risking to leave perfectly good habitat patch (patch of low density) while this is avoided under density-dependent emigration (Enfjäll and Leimar 2009, Hovestadt et al. 2010). Density dependence is thus more efficient in homogenizing fitness expectations between the patches. The discrepancy between DI and DD is especially large for low dispersal mortality and natal dispersal but it is considerably smaller under breeding dispersal.

3.2. Effect of carrying capacity and environmental variability

*I*n the natal dispersal scenario we observe an increase in dispersal rates when reducing patch size from $K=100$ to $K=10$ (Figure 2). Smaller carrying capacity selects for increased dispersal because small *K* speeds the establishment of kin-structure and consequently intensifies kin competition (Hamilton and May 1977, Ronce et al. 2000, Poethke et al 2007, Taylor 1988). On the other hand, in the breeding dispersal scenario increasing mean carrying capacity from $K=10$ to $K=100$ leads to a noticeable increase in dispersal, as long as costs of dispersal are low (Figure 2). In the case of small *K* our simulations suggest that the reduction of sibling competition is the dominant effect for the evolution of dispersal – the introduction of considerable environmental variability ($\sigma=10$ instead of $\sigma=0$) thus results only in a rather weak increase in dispersal for the breeding dispersal strategy as compared to its effect on natal dispersal. It is important to realize that with small patch capacities the offspring of a single parent have a noticeable effect on population density and thus competition in that patch in general (not just on that between siblings) because the total number of individuals in the patch is so small; for this reason it remains a good strategy to distribute offspring rather evenly over two patches even if environmental variability is small. However, with large *K* the offspring of a single individual contribute only marginally to the intensity of competition in a local population and consequently we see a much stronger increase in breeding dispersal in this scenario due to the effect of environmental variability.

However, for high dispersal costs the effect is reversed and we observe the evolution of more dispersal for $K=10$ compared to the scenario with $K=100$, i.e. there is a noticeable interaction between the effects of patch size and dispersal mortality on the evolution of dispersal. Such an interaction effect does not occur for natal dispersal as we witness a decline in dispersal as K is increased over the whole range of values for dispersal cost. Overall, evolved dispersal rates are thus more similar for natal and breeding dispersal for scenarios with $K = 100$ compared to the scenarios with $K=10$ (Figure 2a).

Making populations demographically more stable by reducing environmental variability σ to zero has no qualitative effect on the results mentioned above (Figure 4). Especially for $K=10$ we witness only a small to moderate reduction in evolving dispersal. For larger populations ($K=100$) the decline in dispersal is more dramatic, especially in the intermediate range of values for dispersal costs. Here dispersal is mainly driven by environmental variability where as with $K=10$ kin competition is a dominant factor (Poethke and Hovestadt 2002).

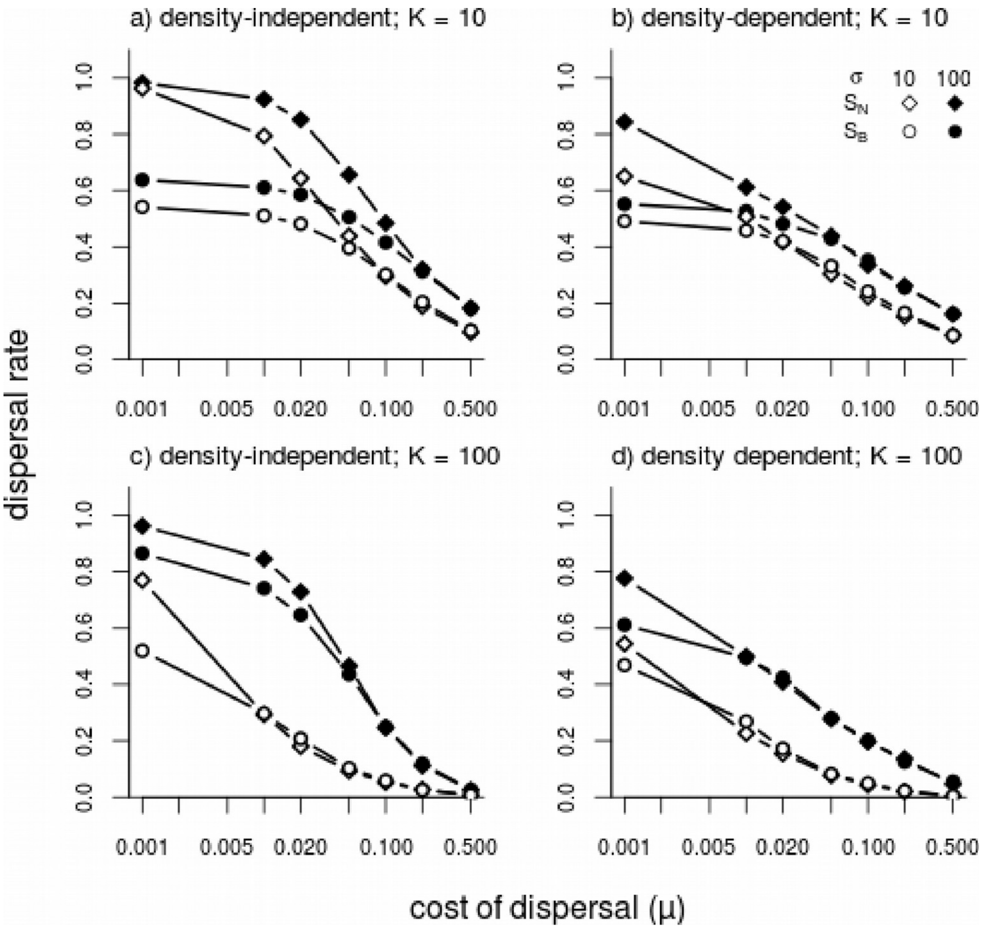

Figure 4. The effect of environmental variance (σ), patch capacity (K) and dispersal costs (μ) on evolved dispersal rates. Density-independent (DI) dispersal (graphs a,c) and density-dependent (DD) dispersal (graphs b,d). Small carrying capacity ($K=10$, graphs a,b) and big carrying capacity ($K=100$, graphs c,d). Empty symbols ($\sigma=0$) and filled symbols ($\sigma=K$). Diamonds and circles stand for S_N and S_B respectively.

3.3. Evolutionary tournament

Comparing the resulting dispersal rates for the natal and breeding dispersal scenario, as such, does not allow deciding whether one strategy would prevail over the other in direct evolutionary competition. The evolutionary tournament where both strategies compete directly with each other allows doing that - and the results of the experiments are unambiguous: In all contests breeding dispersal out-competes natal dispersal. This is even true in a parameter range where evolved dispersal is similar for both strategies, i.e. at high dispersal costs ($\mu=0.5$). However, in a scenario with large patch size (K) and high environmental variability (σ) where strategies tended to evolve very similar dispersal rates (cf. Figure 2), replacement of the natal dispersal strategy progressed much slower than in scenarios where evolved emigration rates were dissimilar (Figure 5).

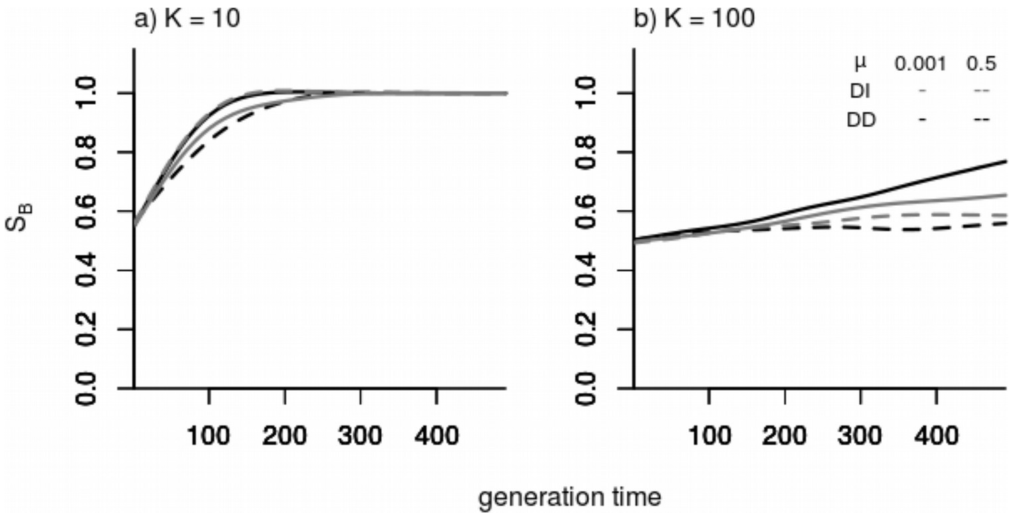

Figure 5. Exemplary change in the proportion ($S_B/(S_B+S_N)$) of individuals with the breeding dispersal strategy over time during evolutionary tournaments. (a) Scenario with small patch size ($K=10$) and (b) scenarios with large patch size ($K=100$); environmental variability $\sigma=K$ in all cases. Black and grey lines represent density-dependent (*DD*) and density-independent (*DI*) emigration scenarios, full and dashed lines represent mortalities $\mu=0.001\wedge 0.5$, respectively.

4. Discussion and Conclusions

Our simulations confirm previous studies with respect to the effect of changes in dispersal costs (Baguette and Van Dyck 2007) and environmental variability (Caset et al. 2003). The effects of these variables can be understood by their effect on the costs and benefits of dispersing: The dispersal reducing effect of increased dispersal costs is obvious (Bach et al. 2006, Poethke and Hovestadt 2002, Bonte et al. 2012). Environmental variability in turn enhances the formation of spatio-temporal variability in fitness expectations, which is known to promote dispersal (Levin et al. 1984). The principal effects of these parameters on dispersal hold whatever dispersal scenario we implement: Neither a change from density-dependent to density-independent nor from natal to breeding dispersal undermines these general conclusions.

As confirmed in the natal dispersal scenarios, dispersal increases with decreasing patch carrying capacity (Cadet et al. 2003). Accordingly, higher emigration from smaller patches has indeed been observed for many butterfly species in the field (Hill et al. 1996, Kuussaari et al. 1996, Bergman and Landin 2001, Hovestadt and Nieminen 2009, Duplouy et al. 2013). However, for breeding dispersal results are less clear in this respect: In the absence of environmental variability ($\sigma=0$) the decline in dispersal with increasing K is rather weak. And we even observe an increase in dispersal with increasing patch capacity (K) for low dispersal costs in the scenarios with environmental variability. This is clearly contradicting the theoretical findings mentioned above that were always based on the assumption of natal dispersal, however. We will return to this interesting effect further below.

We should first note, that we generally see an apparent difference between natal and breeding dispersal only when dispersal costs become small: In all these scenarios, breeding dispersal evolves towards lower dispersal rates than natal dispersal and the fraction of offspring dispersed does typically not raise much beyond 0.5 (except if $K=100$ and environment is variable). In contrast, under natal dispersal we see the evolution of emigration probabilities approaching one as dispersal costs approach zero; this is in good agreement with the predictions of Hamilton and May (1977).

To understand this discrepancy we have to consider the difference between the two strategies concerning their effect on kin and more specifically on direct sibling competition: Whatever the decision a 'natal disperser' takes – all of its offspring will always be born in a single patch. Under this strategy it is just impossible to reduce direct competition among siblings by dispersing. However by evolving a highly dispersive lineage, natal dispersal can reduce long-term 'trans-generational' kin competition, i.e. competition between grand-children and further descendants. In contrast, in the breeding dispersal strategy, dispersing parent can distribute offspring equally among two different patches and reduce kin competition among siblings already in the next generation.

Breeding dispersal out-competes natal dispersal under all conditions tested in our evolutionary tournaments, even where evolved dispersal rates are very similar and low. The previous argument concerning sibling competition is seemingly undermined at very low dispersal rates because in this case both strategies produce offspring more less in a same patch.. Reducing direct sibling competition is, however, not the only benefit of the breeding over natal dispersal. A further, non-exclusive argument in favour of this strategy is that of 'risk spreading' (Hirota 2005). In theory, distribution of offspring across different habitat patches with differing fitness expectations is thought to improve persistence in meta-populations (Boer den 1968). More precisely, by distributing offspring over several patches a parent may reduce the variance in the number of grandchildren produced as own offspring in different patches reproduce under different density conditions. Such a variance reducing effect should be beneficial as it increases the long-term geometric growth rate; and it is this rate that should ultimately be maximized by natural selection (Hopper 1999, Lewontin and Cohen 1969). Increasing the size of habitat patches (more precisely increasing the population size) shifts the balance from avoiding sibling competition in the next generation to the more long-term benefit of risk-spreading and promotes the evolution of more similar dispersal for the natal and breeding dispersal strategies. It is this shifting that is responsible for the increase in emigration rates in breeding dispersal above 0.5 whereas under natal dispersal it rather declines. Nonetheless, due to the benefits mentioned, breeding dispersal out-competes natal dispersal in all scenarios tested.

We as well as the other studies (Enfjäll and Leimar 2009, Hovestadt et al. 2010) observe lower emigration rates under informed dispersal (Figure 2). The effect and benefits of informed, i.e. density-dependent emigration has been discussed before (Nowicki and Vrabec 2011, De Meester and Bonte 2010, Hovestadt et al. 2010). Fitness expectations are more efficiently (that means with fewer dispersal events) homogenized (Enfjäll and Leimar 2005) across the landscape and overall lower net-dispersal evolves. This effect is especially valid in scenarios principally selecting for high dispersal, i.e. natal dispersal at low dispersal mortality. As a consequence we recognize that in the density-dependent scenarios dispersal becomes more similar between natal and breeding dispersal.

We should also note that the optimal residence time of $t_E = 0.5$ critically depends on the assumption that any individual is allowed to disperse at most once during its life-cycle. If we would allow for repeated dispersal during the reproductive season between several patches, leaving smaller fractions of offspring in each patch visited could clearly reduce sibling competition even further. We should consequently observe evolution of shorter patch residence times (smaller t_E values) in such a scenario.

Despite having clear theoretical benefits, mid-season breeding dispersal as we assume in this paper would not be an evolutionary option for organisms that care for their offspring, especially if that requires a stationary nest-site or territory. Yet for organisms like most insects or other annual organisms that typically do not show such behaviour and that live in populations distributed in fragmented landscapes and unstable environments (Frouz and Kindlmann 2001), breeding dispersal behaviour could also be favoured for additional reasons than those introduced here. Firstly, if an individual emerged in a certain patch, it might infer that it is a good quality patch. Thus, fitness-wise, the individual could benefit from staying some time and exploring the patch possibly leaving part of its offspring there. Secondly, it has been shown for some butterflies that older females tend to be more mobile than younger ones (Sei 2008). This is possibly due to the fact that older females already oviposited part of their egg-load and therefore become more agile in flight – increased mobility presumably increases the chance of successful dispersal. A study with spruce budworm moth species (Rhainds and Kettela 2013) shows that there is an oviposition threshold of around

50 % in the natal patch, before females emigrate. Finally, informed emigration strategies where emigration decisions depend on population density or other attributes of patch quality demand that individuals acquire information about such attributes. Information acquisition, however, is itself a time-consuming process and it may be a rational decision to already deposit eggs while collecting information (Nowicki and Vrabec 2011).

Empirical and theoretical work, especially that related to the investigation of insects or other annual organisms, has paid little attention to the subtle difference between natal and breeding dispersal; the typical assumption in fact is that dispersal is natal. Our study shows that natural selection may generally favour the evolution of breeding dispersal in patchy environments and that evolving dispersal rates may quantitatively differ depending on which strategy an organism applies. It may be worth in future field studies of insects or other, similar organisms, to pay more attention to this difference and more carefully define at what moment in their life-time an individual dispersed.

Chapter 3

Mating timing, dispersal, and local adaptation in patchy environments

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1. Introduction

Dispersal is an important life history trait that affects population dynamics and enables the persistence of spatially structured populations. It can evolve under various selective pressures that have been studied extensively in the past decades. There is ample theoretical work on the critical drivers of dispersal evolution, such as the role of kin competition (Hamilton and May 1977, Gandon 1999, Bach et al. 2006, Poethke and Hovestadt 2002, Gyllenberg et al. 2008), inbreeding avoidance (Bengtsson 1978, Motro 1991, Pusey and Wolf 1996, Perrin and Mazalov 1999), or spatial and temporal variability (McPeek and Holt, 1992, Topping and Sunderland, 1998, Metz and Gyllenberg 2001, Poethke and Hovestadt 2002, Cadet et al. 2003). In addition, the evolutionary drivers for dispersal may be different in females and males (Perrin and Mazalov 2000, Gros et al. 2008, Hovestadt et al. 2014). Female biased dispersal is common across animal groups, such as many birds (Greenwood and Harvey 1982), mammals (Nagy et al. 2007), reptiles (Olsson and Shine 2003), amphibians (Austin et al. 2003) and insect species (Ohsaki 1980, Albrectsen and Nachman 2001, Caudill 2003). Drivers of female dispersal can range from availability of resources and nesting sites to harassment by males. Contrary, for males the main drivers are availability of females (Hovestadt et al. 2014) or acquiring a territory (Dobson 1982).

Most evolutionary models assume natal dispersal (e.g. emigrating right after birth) but some consider also the timing of emigration within the life cycle (e.g. natal vs breeding dispersal (Johst and Brandl 1999, Hirota 2004, Lakovic et al. 2015)). However, only few of them (Taylor 1988, Hirota 2004, see also discussion) take into account the order in which mating and dispersal may occur. This issue is especially important with respect to insect females where emergence, mating and egg laying can occur in distinct habitat patches. In this case the critical aspect for a female may be to choose a mate either in the natal or the breeding habitat. For long lived species it is typically clear whether copulation takes place prior to or after dispersal but often enough this is less obvious in the case of insects, especially for species with a brief adult life-span. Furthermore, in the case of multiple mating (polyandry), sperm competition may determine which males ultimately father the females' offspring. In many butterfly species, last male sperm precedence is a general pattern (Boggs and Watt 1981 , Smith 2012). Therefore, if a female mates before and after dispersal, most of the eggs could be fertilized by the last reproduction partner. In other cases males have control by e.g. changing a female's physical appearance or pheromone composition thus making her unattractive for further mating (Thornhill and Alcock 1983, Tran and Wolfner 1998), or by damaging the females sexual organs and thus preventing her to copulate a second time (Stutt and Siva-Jothy 2001). Nonetheless, it has been shown in many species that fertilization is determined solely by the female, either by directly choosing which and how many males she mates with (Blum 2012), or by post-copulatory removal of spermatophores of some males before insemination so that her eggs are only inseminated by the most suitable mate(s) (Simmons 1986, LaMunyon and Eisner 1993, Simmons 2001).

Precise time of mating (pre/post-emigration) is especially important in the context of local adaptation. There is previous theoretical work on the topic of evolution of dispersal and local adaptation (Blanquart et al. 2012, Blanquart and Gandon 2014, Berdahl et al. 2015), but the question of how this would affect evolution of mating timing is largely overlooked. Whenever females have ultimate control over choosing their mating partner, it is interesting to understand under which conditions they should prefer to either mate in their natal habitat (patch) before emigration, or after immigration in a new habitat. Indeed, we speculate that the decision to choose a mate either before or after dispersal may have important fitness implications. More specifically, we hypothesize that (i) in species with wide habitat tolerance it is beneficial to mate in the natal patch with kin and therefore carry the genes of a related male into a novel population , whereas (ii) post-dispersal mating is advantageous in species with narrow habitat tolerance where mating with a locally adapted male increases offspring fitness. To investigate the principal validity and relative importance of theses arguments we used an individual-based model to explore how species habitat tolerance, environmental variability, and population size jointly affect the evolution of dispersal and mating timing (pre- or post-dispersal mating) in females, and how the sequence of these events interplays with the evolution of local habitat adaptation.

2. The model

Our study is based on the individual-based model of insect dispersal in patchy environments that was successfully implemented in many previous studies by ourselves (e.g. Poethke and Hovestadt 2002, Lakovic et al. 2015) and other groups (e.g. Bach et al. 2006, Travis and Dytham 1998). We model a time-discrete annual insect metapopulation in a landscape of habitat patches that may quantitatively differ in certain habitat attribute and where only females are allowed to disperse.

Landscape. We assume a landscape consisting of N habitat patches p, each with carrying capacity K. Habitats are heterogeneous with each patch having a unique habitat attribute H_p, e.g. a certain micro-climate drawn from a standard normal distribution $\phi(0,1)$. The fitness relevance of this variance is modulated by a scaling factor that accounts for the ability of the species to cope with such habitat heterogeneity – we call this factor habitat tolerance (see below).

2.1. Life history and cycle

We consider discrete, non-overlapping generations of sexual organisms. The life history implemented resembles those of many insects such as butterflies, moths, grasshoppers and others, as we consider an egg, larval and adult stage. Every individual is characterized by three traits, determined by two parent alleles (one inherited from the mother (index *f*) and one from the father (index *m*); see section mode of inheritance for more details. The first pair of genes (D_f, D_m) determines dispersal (= emigration) probability and the second (M_f, M_m) the probability to mate before dispersal: a value of M=0 would code for obligate post-dispersal mating and a value of M=1 for obligate pre-dispersal mating. It is important to note that although males also carry both genes, the phenotype is only expressed in females, e.g. only females are allowed to disperse and decide whether to mate prior or after dispersal. The third pair of genes (H_f, H_m) codes for the 'eco-type' that defines the individual's adaptation to the local environment (see below). In all cases an individual’s i phenotypes (d_i, m_i, h_i) are calculated as the arithmetic mean of the corresponding parent alleles, i.e. as $(Gene_f + Gene_m)/2$.

The life cycle (see Figure 1) starts in each patch with egg-laying by the resident female population. The number of eggs deposited by each female (fertility) is determined as a number drawn from a Poison distribution with mean $\lambda_{p,t}$; we thus account for demographic stochasticity in individual reproductive success. Females and males die after egg-laying. To account for spatially uncorrelated temporal variability in environmental conditions, we independently draw $\lambda_{p,t}$ for each patch p in each generation t from a log-normal distribution with mean Λ and standard deviation σ_λ . Such variation between habitat patches may occur due to e.g. climatic effects that affect density-independent egg or larval mortality or resource availability that in turn affects fertility.

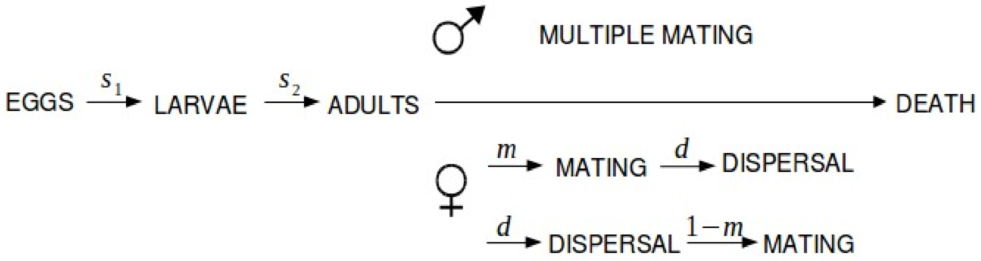

Figure 1. **Schematic representation of the simulated life cycle.** Eggs or young larvae first go through a phase of density-dependent survival (s_1) and then through survival that depends on local adaptation (s_2) before they emerge as adults. Females will first mate with probability m , and consequently emigrate (with probability d) or first emigrate with probability d and then mate (with probability $1-m$). Only females disperse. Females mate once with a randomly

selected male either from the natal or the patch they immigrated to. Males can mate as often as they get the chance to.

Eggs develop into larvae which first have to compete for space and resources within a patch (e.g. caterpillars on a plant). Consequently, we assume patch and time specific density-dependent survival of eggs, respectively young larvae (s_1), according to modified Beverton-Holt model (eq. 1) (Beverton and Holt 1957):

$$s_1 = \frac{1}{1 + a * L_{p,t}} \quad \text{with} \quad a = \frac{\Lambda - 1}{\lambda_{p,t} * K} \tag{1}$$

and $L_{p,t} \approx N_{t-1,p} \cdot \lambda_{p,t}$ the total number of eggs deposited in patch p during year t . Further survival s_2 of offspring then depends on their local adaption, i.e. the match between an individual’s phenotype h_i , and the patch's habitat attribute (H_P):

$$s_2 = e^{-\frac{(H_P - h_i)^2}{\sigma_H^2}} \tag{2}$$

In the case of exact habitat matching, i.e. $h_i = H_p$ the survival probability is $s_2 = 1$. The habitat tolerance parameter σ_H is a measure of the species' tolerance against habitat variation (Figure 2). Low tolerance values depict species with narrow habitat niches, whereas high tolerance defines species with wide habitat niches, i.e. species where survival is less affected by the (mis-) match between h_i and H_P . Surviving offspring emerge as reproductively mature adults, with equal chances of becoming a female or a male.

Females mate only once in their life-time, while males can mate an indefinite number of times. Right after emergence, all females have the opportunity to mate: The probability to do so is defined by a female's mating strategy phenotype m . Following eventual copulation, females disperse with probability d . We consider global dispersal but exclude the possibility that an individual disperses back into its natal patch. After the dispersal phase, all the virgin females (regardless of whether they dispersed or not) mate with a random male from the patch of residence. Our species is polygynous, where males can mate with multiple females. Note, however, that males are neither allowed to disperse nor to choose a mating strategy, but that the genes inherited from fathers affect the phenotypes of their daughters.

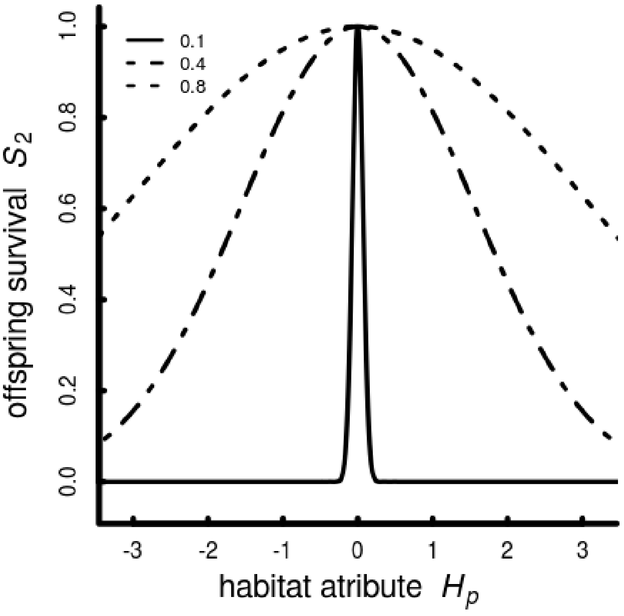

Figure 2. **Habitat-dependent survival probability s_2 depending on the match between an individual's habitat trait ($h_i=0$) and a patch habitat attribute H_P** . Curves are provided for three different tolerance values: continuous line $\sigma_H=0.1$, dashed line $\sigma_H=0.8$ and dotted line $\sigma_H=4.4$.

2.2. Mode of inheritance and mutation

Offspring inherit two alleles for each of the three loci defining the three phenotypes from their parents, one from the mother and one from the father. We assume simple Mendelian inheritance, where all of the genes are inherited independently . Following inheritance any gene may mutate with probability μ . In case of a mutation, the value of the gene inherited is modified by a small random value drawn from an uniform distribution $[-\delta,+\delta]$. In principle, we thus allow all genes to evolve to values in the range $[-\infty,+\infty]$. Note however, that the phenotypes for dispersal (d) and mating (m) are limited to the range $[0,1]$. Therefore, the genes can have values smaller than 0 or bigger than 1, yet their phenotypes are interpreted as 0 or 1 respectively.

2.3. Initialization parametrization and scenarios

In all simulation scenarios we initialized the model by creating a landscape with the same total carrying capacity (10000) and sex ration of 1:1. Therefore, simulations with N number of patches $N \in \{10, 20, 50, 100\}$ were run with the corresponding patch carrying capacity $K \in \{1000, 500, 200, 100\}$. At the start of the simulations all the individuals were locally adapted (i.e. $H_{f,m} = H_P$) to their natal patch. For the initialization of dispersal $D_{f,m}$ and mating strategy $M_{f,m}$ genes see below. The values of other model parameters are provided in Table 1.

We carried out three different simulation scenarios: (i) 'Full evolution' scenario where we allowed all three genes to evolve. The dispersal ($D_{f,m}$) and mating genes ($M_{f,m}$) were both initialized with random numbers drawn from the uniform distribution [0,1]; (ii) 'Fixed dispersal' scenario, where females' emigration probability was either fixed to $\bar{d}=1$ or $\bar{d}=0.15$, while the mating strategy (m) and the eco-type (h) were allowed to evolve; (iii) 'Fixed mating strategy' scenario, where we fixed mating either to pre- ($\bar{m}=1$) or post-dispersal mating ($\bar{m}=0$) but allowed for evolution of dispersal d and habitat adaptation h.

All three scenarios were tested with the same set of parameters (Table 1). For each parameter combination simulations ran for 20000 generations and with 20 independent replicates. For data presentation we calculated mean values (across the whole metapopulation) for the evolving attributes averaged over the final 200 generations of each simulation run.

The code was created with Free Pascal Lazarus Version 1.4.0, and the results were analyzed in the R software Version 3.2.1 (R Development Core Team 2008).

	Full evolution	Fixed dispersal	Fixed mating strategy
mating strategy (M)	evolving	evolving	$m \in \{0,1\}$
female dispersal (D)	evolving	$d \in \{0.15, 1\}$	evolving
eco-type (H)	evolving	evolving	evolving
habitat tolerance	$\sigma_H \left\{ \begin{matrix} 0.1, 0.4, 0.8, 1.2, 1.6, 2.0, 2.4 \\ 2.8, 3.2, 3.6, 4.0, 4.4 \end{matrix} \right\}$		
environmental var. in fertility	$\sigma_\lambda \in \{0,1\}$		
Patch size and number	$K=100, N=100$ $K=200, N=50$ $K=500, N=20$ $K=1000, N=10$		
mean fertility (per female)	$\Lambda = 6$		
mutation probability	$\mu = 0.001$		
mutation size	$\delta [-0.01 - 0.01]$		

Table 1. **Parameter settings and different scenarios tested.** Grey shading marks the traits that are allowed to evolve.

3. Results

3.1. Full evolution scenario

Our results show that the probability to disperse greatly increases with increasing habitat tolerance (Figure 3). Small tolerance increases the degree of ‘perceived’ habitat heterogeneity as the variance in patch attributes has substantial effect on survival. Results are thus consistent with previous findings stating that selection acts against dispersal in heterogeneous landscapes (Hastings 1983, Holt 1985). In contrast, cost of dispersal for a species with high tolerance is reduced since the fitness consequences of immigrating into a different habitat are small.

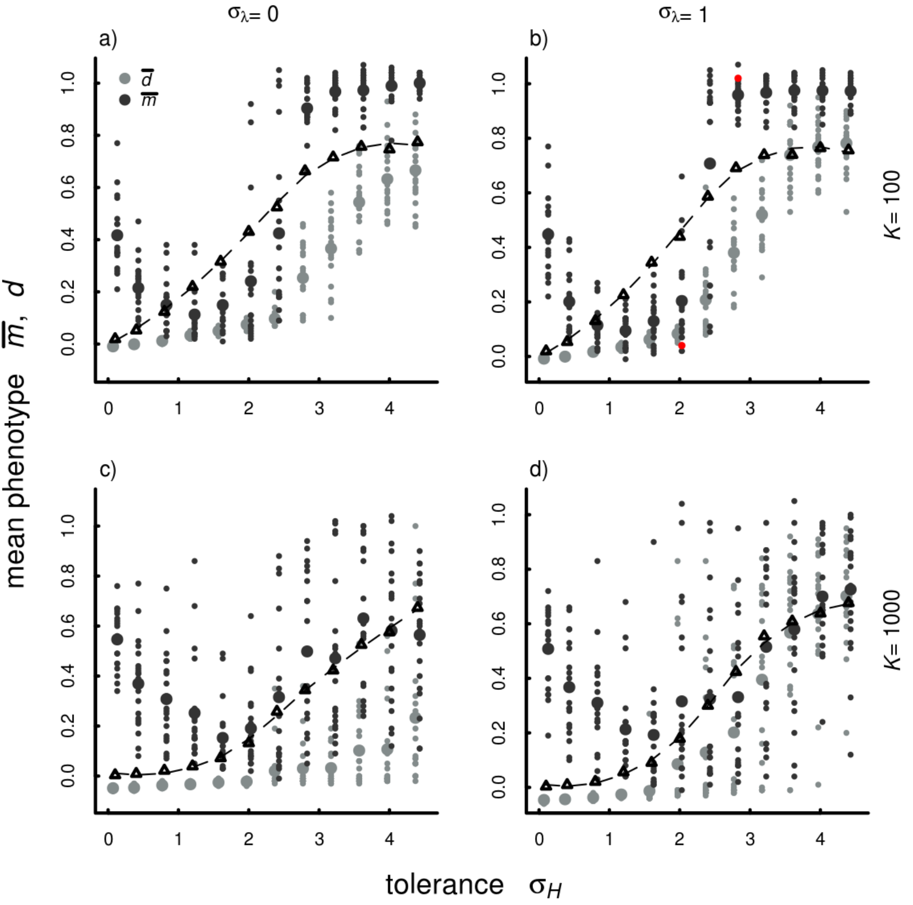

Figure 3. **Mean evolved dispersal probability $\bar{d}$ and mating strategy $\bar{m}$ plotted over different values of habitat tolerance.** Note that $\bar{m}$ is the probability to mate in the natal patch. Smaller symbols represent evolved mean values for individual simulation runs averaged over the last 200 generations (of 20.000 generations in total); larger symbols the mean of these averages over the 20 independent replicates. Dashed line with empty triangle symbols represents mean individual maladaptation $(H_{f,m} - H_P)$ averaged over the whole landscape. Red dots in panel b) indicate single simulations that are presented in Figure 4 in more detail.

Additionally, mean evolved mating strategy changes non monotonically with tolerance σ_H (Figure 3). When tolerance is very low ($\sigma_H = 0.1$) we observe the evolution of intermediate mating strategies $\bar{m} \sim 0.5$. At the same time, dispersal propensity evolves to values close to 0. Second, as tolerance is increased dispersal propensity evolves to higher levels whereas the mating strategy evolves to lower values, i.e. mating after dispersal as long as tolerance levels are low to intermediate ($\sigma_H \sim 2.0$). Finally, for very high tolerance levels we observe the evolution of high dispersal propensity in combination with high values of *m*, i.e. a high probability to mate at home. We assume that when dispersal is nearly absent ($\bar{d} \sim 0$) at the metapopulation level, the strategy becomes roughly neutral trait, since regardless of its value all females will mate at home anyways. This occurs at very low tolerances ($\sigma_H = 0.1$). However, as soon as dispersal propensity evolves to noticeable levels (from low to intermediate tolerance), we observe strong selection for post-dispersal mating. In other word, moderately tolerant species with emergent dispersal probabilities around 0.10-0.15 at the metapopulation level evolve post-dispersal mating strategy. On the contrary, high tolerance values coupled with high dispersal propensity lead to well mixed populations where the chances and consequently the benefits of mating with locally adapted male diminish, thus selecting for the pre-dispersal mating strategy.

The consequences and benefits of these evolved strategies are better understood if we consider their effect on the degree of local maladaptation, i.e. the deviation between an individual's genes coding for its eco-type (H_f, H_m) and the patch attribute H_P across the landscape (Figure 3, dashed line with triangles). With low tolerance and low dispersal evolving, we see weak local maladaptation , i.e. individuals are well adapted to the local conditions. This is shown by the dashed line with empty triangles that represents the mean genetic deviation from habitat type ($\left(H_{f,m} - H_P\right)$), where values close to 0 indicate weak local maladaptation.

To observe the shift between the two strategies in more detail, we show results of two exemplary simulations from scenarios marked by red dots in Figure 3. For a tolerance of $\sigma_H = 2.0$ (Figure 4 left panels) mean dispersal probability evolves to a value of about 0.15 (4a), and post-dispersal is strongly selected for (4c). Further, a diversity of eco-types is maintained across the metapopulation (4e) with a rather low level of maladaptation (cf. Figure 3) indicating that many individuals reside in habitats matching their eco-type (4e). On the contrary, for $\sigma_H = 2.8$ (Figure 4, right panels) dispersal evolves to much higher emigration probability $\bar{d} \sim 0.5$ (4b) and pre-dispersal mating is selected for (4d). At the same time we witness a collapse of eco-type diversity (4f): the values for the genes coding for individual eco-types h are closely centered around the average value for the landscape (i.e. $\bar{H} \approx 0.0$).Quantitatively this pattern is only weakly affected by a change in environmental variability σ_λ or patch capacity K . Larger K primarily selects for somewhat lower emigration probability (Figures 5a) and increased σ_λ for larger emigration probabilities (Figure 3). Both results are expected and correspond with previous findings (Poethke and Hovestadt 2002, Cadet 2003) and thus do not require further discussion here. However, in regard to evolution of the mating strategy, we observe larger variance between replicates as we increase population size (Figure 5b). Such variance is a result of the weak selection on the trait due to the diminished kin structure establishing in large populations . Large population sizes such as $K = 500$ and $K = 1000$, coupled with increased dispersal (at high tolerance values), lead to well mixed population where kin structure becomes nearly absent.

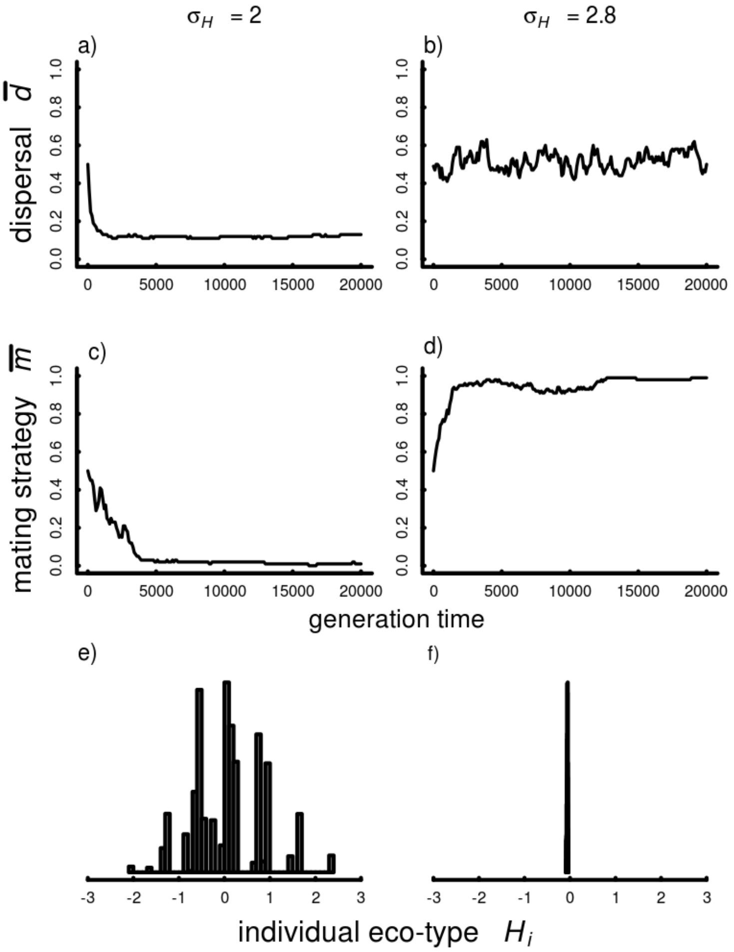

Figure 4. Mean evolved dispersal probability $\bar{d}$, mating strategy $\bar{m}$ and distribution of individual 'eco-types' h_i for two individual simulation runs. The panels in the first row (a, b) show the evolution of the mean dispersal phenotype ($\bar{d}$), the second row(c, d) mean of the mean mating strategy phenotype ($\bar{m}$); note that a value of $\bar{m}=0$ indicates obligate post-dispersal mating. The two histograms in the bottom row (e, f) show the corresponding distribution of values for individual eco-type (h_i) at the end of each simulation. All simulations were run with $K=100$ and $N=100$, environmental variability $\sigma_\lambda=1$ and a habitat tolerance of $\sigma_H=2.0$ for the figures in the left panel and $\sigma_H=2.8$ for the panels on the right.

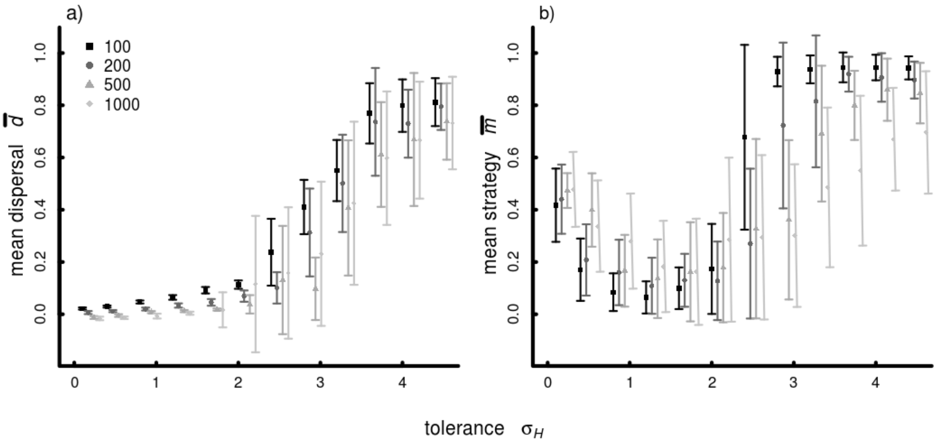

Figure 5. Mean evolved dispersal $\bar{d}$ and mating strategy $\bar{m}$ plotted over habitat tolerance, for different values of carrying capacity ($K \in (100, 200, 500, 1000)$. Means and standard deviations from 20 independent simulations. Note that $\bar{m}$ is the probability to mate in the natal patch.

3.2. Fixed dispersal scenario

To better understand results from the 'full-evolution' scenario and support the argumentation provided above we ran simulations with emigration probability fixed to constant values. We compared two different scenarios, one where dispersal was set to a moderate value of $\bar{d}=0.15$ and the other where dispersal was obligate $\bar{d}=1$. Again, the results demonstrate the benefit of post-dispersal mating in particular when habitat tolerance is low. However, similar to evolutionary scenario (Figure 3), we observe slightly higher $\bar{m}$ evolving for the lowest tolerance ($\sigma_H=0.1$) values. This arises from the fact that when tolerance is 0.1, the offspring survivorship range is very narrow (Figure 2), i.e. their phenotype needs to match the habitat's attribute nearly exactly. In particular for individuals adapted to very extreme habitats (e.g. $H_p>2$) even mating after dispersal is unlikely to generate such offspring. As a consequence, because post-dispersal mating does not generate any benefit, we observe that few genotypes adapted to extreme (and rare) habitats tend to evolve a pre-mating strategy thus pulling the overall mean value for $\bar{m}$ somewhat upwards. Without the added benefit of post-dispersal mating, the females evolve mating at home with kin.

The level of dispersal has a strong modulating effect on the evolution of the mating strategy (Figure 6 and Figure A1). Whereas the probability to mate at home increases with habitat tolerance in both scenarios, the evolutionary switch from post- to pre-dispersal mating occurs later (at larger tolerance values) when dispersal is moderate; this supports our notion that the more pronounced kin structure associated with lower dispersal promotes pre-dispersal mating. Correspondingly, local maladaptation is more pronounced (due to selection of a uniform eco-type of H=0.5) with $\bar{d}$ fixed to 1.0 compared to scenarios with $\bar{d}=0.15$, in particular as long as habitat tolerance is low. This is shown as mean individual deviation from the habitat adaptation value $(H_{f,m}-H_P)$ in each patch (Figure 6). Further, when dispersal is obligate, we observe global extinction for low tolerance values (Figure 6b and Figure A1b).

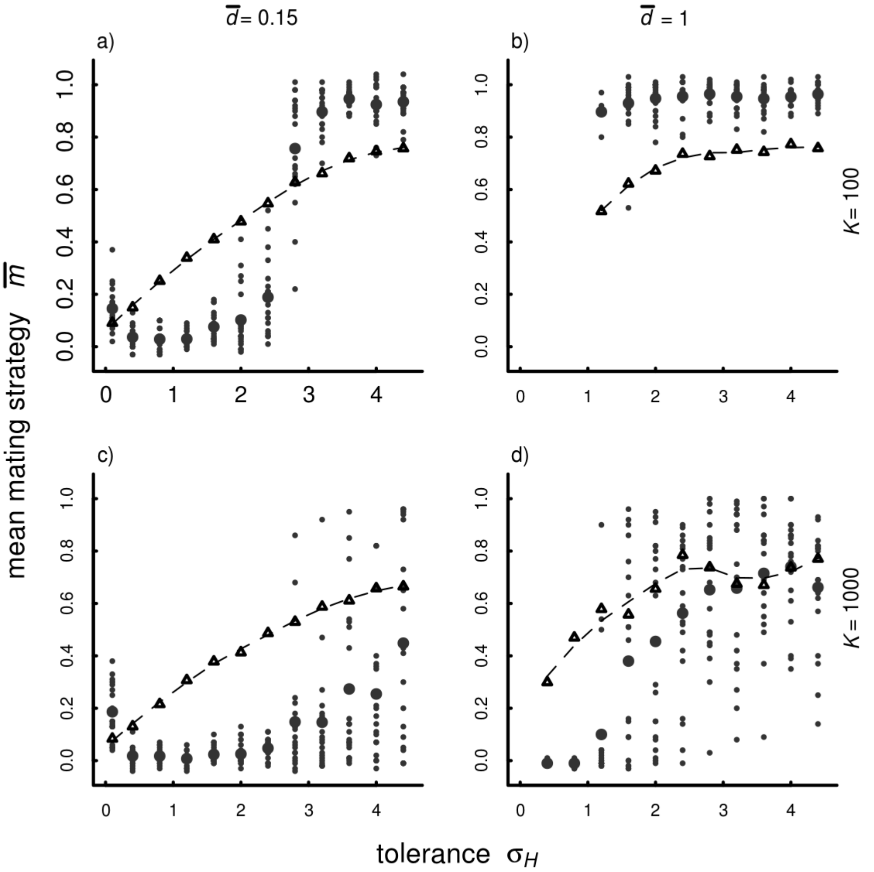

Figure 6. Mean evolved mating strategy $\bar{m}$ plotted against habitat tolerance in scenarios with fixed emigration probability. Note that $\bar{m}$ is the probability to mate in the natal patch. Smaller symbols represent evolved mean values for individual simulation runs averaged over the last 200 generations (of 20.000 generations in total); larger symbols the mean of these averages over the 20 independent replicates. Dashed line with empty triangle symbols represents mean individual deviation from the habitat adaptation value $(H_{f,m} - H_P)$ in each patch. Dispersal is fixed to $\bar{d} = 0.15$ in (a, c) and $\bar{d} = 1$ in (b, d) with patch capacity $K = 100$ in (a, b) and $K = 1000$ in (c, d). Environmental variability is $\sigma_\lambda = 1$ the same in all the panels.

3.3. Fixed mating strategy

Figure 7 and Figure A2 (in the appendix) show how dispersal evolves when strategy is fixed to obligate mating before ($\bar{m} = 1$) or after dispersal ($\bar{m} = 0$). If habitat tolerance is low we observe the evolution of higher values for dispersal probability when mating is fixed to obligate post-dispersal mating compared to pre-dispersal mating (Figure 7b compared to 7a).

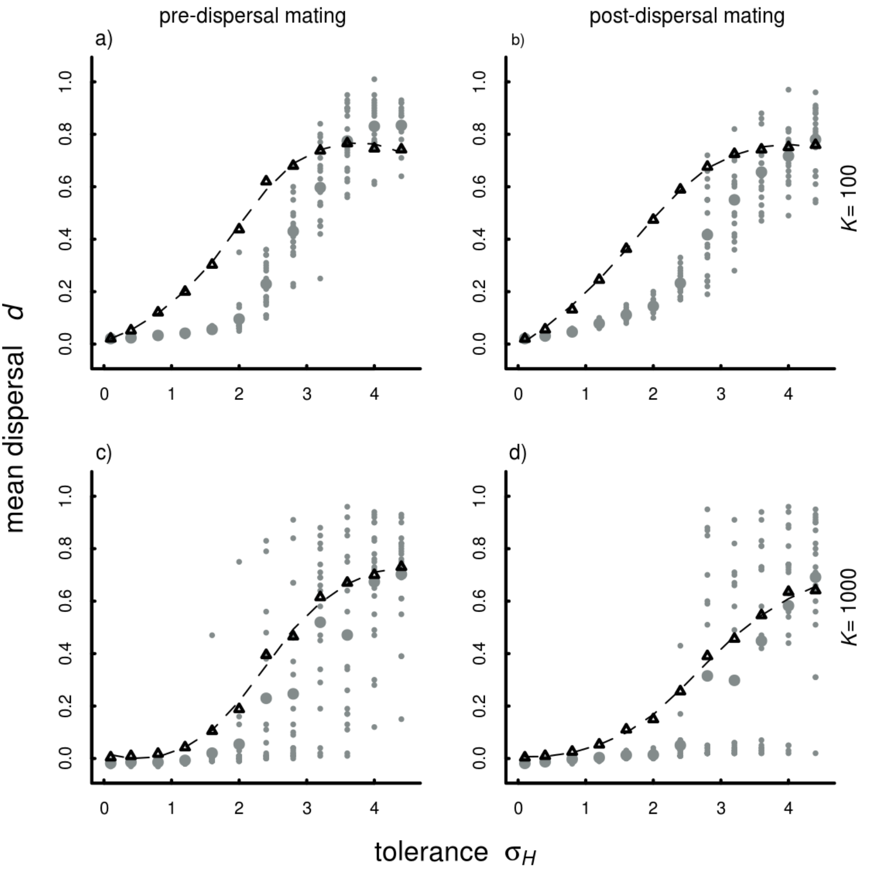

Figure 7. **Mean evolved dispersal $\bar{d}$ plotted against habitat tolerance in scenarios with fixed mating strategy**. Smaller symbols represent evolved mean values for individual simulation runs averaged over the last 200 generations (of 20.000 generations in total); larger symbols the mean of these averages over the 20 independent replicates. Dashed line with empty triangle symbols represents mean individual deviation from the habitat adaptation value $(H_{f,m}-H_P)$ in each patch. Mating strategy is fixed to pre-dispersal, $\bar{m}=1$ in (a,c) and post-dispersal mating, $\bar{m}=0$ in (b, d). Patch capacity $K=100$ in (a, b) and $K=1000$ in (c, d). Environmental variability is $\sigma_\lambda=1$ the same in all the panels.

If habitat tolerance is large, however, lower values of dispersal evolve in the post- compared to the pre-dispersal mating scenario. This latter effect is observed only for the smaller patch capacity simulated $(K=100)$. This is not surprising, as in the post-dispersal mating scenario higher dispersal is beneficial for low tolerant species where females can mate with locally adapted males. However, for high tolerance values this benefit vanishes and tighter kin structure arises in pre-dispersal mating (than in post-dispersal scenario) that promotes dispersal. Larger σ_λ selects for dispersal and reduces the variance between replicas. Results without environmental variability in λ for both 'fixed scenarios' can be found in the appendix (Figures A1 and A2).

4. Discussion and conclusions

Our results show that, given our principle model assumptions, habitat tolerance seems to be the main driver of the evolution of female dispersal and mating strategy. Indeed, we see a sigmoid behaviour in our results in regard to this factor. For low tolerance the potential fitness costs due to habitat maladaptation are large. As a result low emigration probabilities evolve in combination with post-dispersal mating. On the other hand, for habitat tolerance values that increase above a critical threshold, much larger emigration probabilities evolve and pre-dispersal mating is selected for.

This correlation between the level of female emigration and the mating strategy can readily be explained if we consider the level of local adaptation. If dispersal probabilities are large, local adaptation cannot emerge and a single 'eco-type', that is adapted to the 'average' habitat evolves ($\bar{h} \sim 0.0$); note that with the normal distribution assumed for the frequency of habitat types habitats close to the mean value for H_P will also be the most abundant. This preferentially occurs when tolerance is high. In such landscapes dispersal is less costly and gene flow is so high that local adaptation does not emerge. In this case, however, the benefit of post-dispersal mating vanishes as females cannot expect to mate with a locally adapted male any more. Consequently, the females' benefit of potentially carrying genes of a relative with them, takes precedence and, thus, pre-dispersal mating is selected for. Hirota (2004) has in fact shown that pre-dispersal mating also favours evolution of female-biased dispersal as females may then disperse their own genes and those of related males (something a male cannot do). The validity of our argumentation is supported by the results for the fixed dispersal scenarios (Figure 6 and Figure A1). With $\bar{d}=1$ the shift to pre-dispersal mating occurs at much lower tolerance values than if dispersal is fixed to $\bar{d}=0.15$. Moreover, we observe global extinction for low tolerance ranges (0.1, 0.4, 0.8) when female dispersal is obligatory (Figure 6b, left side). This implies that for less tolerant species dispersal coupled only with post-dispersal mating assures the survival of the metapopulation. Correspondingly, the results with fixed mating strategy (Figures 7 and A2) also indicate the benefit of post-dispersal mating with regard to local adaptation. We observe the evolution of higher emigration probabilities (at a low absolute level) in landscapes with low tolerance if mating is fixed to post-dispersal (left data points in Figures 7a, 7b and Figure A2a and A2b in appendix). This effect is readily explained by the reduced implicit cost of dispersal for females that mate with locally adapted males after they have emigrated. On the other hand, the kin-benefit associated with pre-mating dispersal is present only where a significant kin structure emerges. This is most likely the case where dispersal is low and local populations are small. It has already been demonstrated that smaller patch size and low dispersal promote establishment of higher within-patch relatedness (e.g. Parvinen and Egas 2004, Poethke et al. 2007, Kubisch et al. 2013). However, quantification of relatedness may be valuable when the reasoning developed in this manuscript shall be applied to empirical examples. Low dispersal is associated with lower habitat tolerance in the full evolutionary model where the benefit of post-dispersal mating would also be large. However, we need to notice that the question of mating before or after dispersal may become selectively irrelevant if neither a kin structure nor local adaption establishes. This is for example the case in simulations with large K and high tolerance where we notice a very wide scattering in the evolved mating strategy suggesting very weak selection on the attribute (especially visible in Figures 5b). Furthermore, selective neutrality may also explain the large scatter in the evolving mating strategy when tolerance is very low (Figure 3). Here dispersal evolves to such low levels that females typically remain in the natal patch and mate with resident males there regardless of whether their strategy is pre- or post-dispersal mating.

However, other mechanisms ignored in our model like avoidance of inbreeding may play a role in selecting for dispersal (Perrin and Mazalov 1999, Pusey 1987); at the same time, a risk of inbreeding depression should then also select for mating after dispersal.

In our model we consider species that utilize the same habitat but have different tolerance levels that affect offspring survival. Following this interpretation, less tolerant species should evolve lower female dispersal propensity coupled with post-dispersal mating strategy. Indeed, it is obvious that species with narrow habitat niches tend to disperse less as their fitness is strongly decreased in environments outside their tolerance range (and outside their natal patch). However, dispersing females could increase their offspring fitness by mating with a locally adapted male after dispersal. With this interpretation in mind a species tolerance level seems to be the most important factor for the evolution of mating strategy and dispersal. Further, as tolerance is an attribute of the species, it could itself become an evolving trait. Non-trivial evolution of tolerance (becoming a 'master of all trades') can only emerge if evolution of habitat tolerance is expected to come with a trade off, such as decreased fecundity or competitive ability (cf. Chaianunporn and Hovestadt 2012). In this context it would thus be interesting to study the interplay of selection on the mating strategy, dispersal, and habitat tolerance.

Overall, our model shows that an intricate interaction should exist between selection on dispersal and local adaptation, that strongly depends on the degree of a species' habitat tolerance. This in turn affects the balance between the benefit of mating with locally adapted males (post-dispersal mating) vs. that of mating with relatives (pre-dispersal mating). However, post-dispersal mating of females is more likely to maintain local adaptation when habitat tolerance is low and thus in turn affects selection on dispersal. Further, our simulation indicate, due to the rather narrow transition range with regard to tolerance, that we should often find characteristic and discrete suits of trait-combinations when comparing populations from different landscapes. With either highly dispersive females that are not adapted to local conditions and rather mate before dispersal (and are tolerant to habitat heterogeneity), or females that rarely disperse, are adapted to local conditions and mate after dispersal (and are rather specialized to certain habitat conditions).

The possible relevance of the timing of mating in relation to dispersal seems to be rather neglected issue. We could, in fact, not find a single other theoretical study that addresses this question, at least not in relation to its role for offspring fitness and local adaptation. Hirota's (2004) study rather addresses the question, how timing of mating would affect the sex-bias in dispersal. Some empirical observation may, however, be interpreted in light of our findings. For example, last male sperm precedence is reported for butterflies (Smith 1984), bush-crickets (Achmann et al. 1992) and presumably dominates in insects in general (Simmons 2001). In light of our study one possible benefit of this mechanism, that has mostly been discussed in the context of male-male competition, is that it allows female butterflies to first reproduce (lay eggs) in the natal patch following pre-dispersal mating, but then father eggs deposited in other patches by mating again (post-dispersal) with a resident male. Further, mating right after emergence in the natal patch may carry benefits if females take the risk of immigrating into (near) empty habitat patches where mate finding may be hard, but provides the chance to replace the first mate’s sperm in case they succeed in mating with a better (viz locally adapted) male later.

Our study assumes species where males are philopatric and only female disperse, such as in the case of the butterfly *Pieris rapae* (Ohsaki 1980). Clearly, there would be other selective forces acting on the evolution of female mating strategy if males were allowed to disperse too. For example, in such a scenario, females would benefit from the ability to identify the locally best adapted male using some adequate direct (e.g. match between the male's eco-type and habitat attribute) or indirect (e.g. male's general fitness) 'test criterion' when choosing a mating partner. Indeed, an interesting study was conducted by Veen and Otto (2015) on the evolution of female preference for locally adapted males. They found that female preference evolves only for intermediate levels of dispersal: When dispersal is rare there is no genetic variation within a patch and thus no benefit of mating preferences. In turn, for high levels of dispersal (~0.5) mating with locally adapted male has little impact on offspring fitness as the latter disperse with high probability and leave the patch anyway. In our model we do not foresee evolution of female preference but choosing to mate after immigration is an alternative way to increase the probability of mating with a locally adapted male. The congruence between our findings and those of Veen and Otto (2015) is thus not surprising and assuring. However, we should also notice that habitat heterogeneity would also affect the selection on male dispersal itself – from the males’ perspective it is most valuable if they leave their genes in a habitat patch they are well adapted too, typically the natal patch. As the drivers of dispersal evolution may generally be different for males and females (Hovestadt et al. 2014), in particular males often compete over mating opportunities whereas females compete over resources, it requires indeed further research how habitat heterogeneity would affect the evolution of dispersal and mating strategies in males. At the moment we can only speculate that habitat heterogeneity may be one factor promoting the evolution of sex-biased dispersal.

The relevance of the timing of mating has also been discussed in the context of evolution of resistance in heterogeneous landscapes, in particular of evolution of resistance to Bt toxins in pest species. Resistance genes are recessive (*rr*), thus mating with a male from a wild population would slow down the spread of the resistance gene (Dalecky et al. 2006 , Caprio 2001). Indeed, a high-dose refuge (HDR) is a popular strategy in Bt crop management. The basic principle is that in a heterogeneous landscape, i.e. a mixture of treated and non-treated crops, gene flow between different patches, will limit the spread of resistance to Bt toxins that emerges in Bt crop. This suggests that, albeit the simplified genetic assumption of ‘additive genetics’ in our model, the principle remains the same (mating after dispersal preserves local adaptation in heterogeneous environments) and we could indeed observe similar behaviour in the natural environment. It is clear however, that more complex genetic architectures could lead to different results. For example, if a habitat gene were dominant its bearer would actually not benefit from mating after dispersal with a locally adapted male as the female’s offspring would establish the mother’s phenotype nonetheless. In turn, bearers of recessive alleles would actually greatly benefit from the post-dispersal mating strategy so that in such a scenario the evolution of linkage between the mating and the habitat trait might establish. Equally, if heterozygotes were typically not well adapted to either habitat type, e.g. if habitat adaptation would be about adapting to the chemistry of particular host-plants, post-dispersal mating would presumably not be a good strategy; in this case females should mate before dispersal and then just hope to find another habitat with conditions similar to their natal patch.

In conclusion, this theoretical study highlights the importance mating timing and dispersal in heterogeneous environments in the context of local adaptation. We would suggest more research, as current literature on this topic is scarce with regard to both, theoretical and field studies.

Appendix

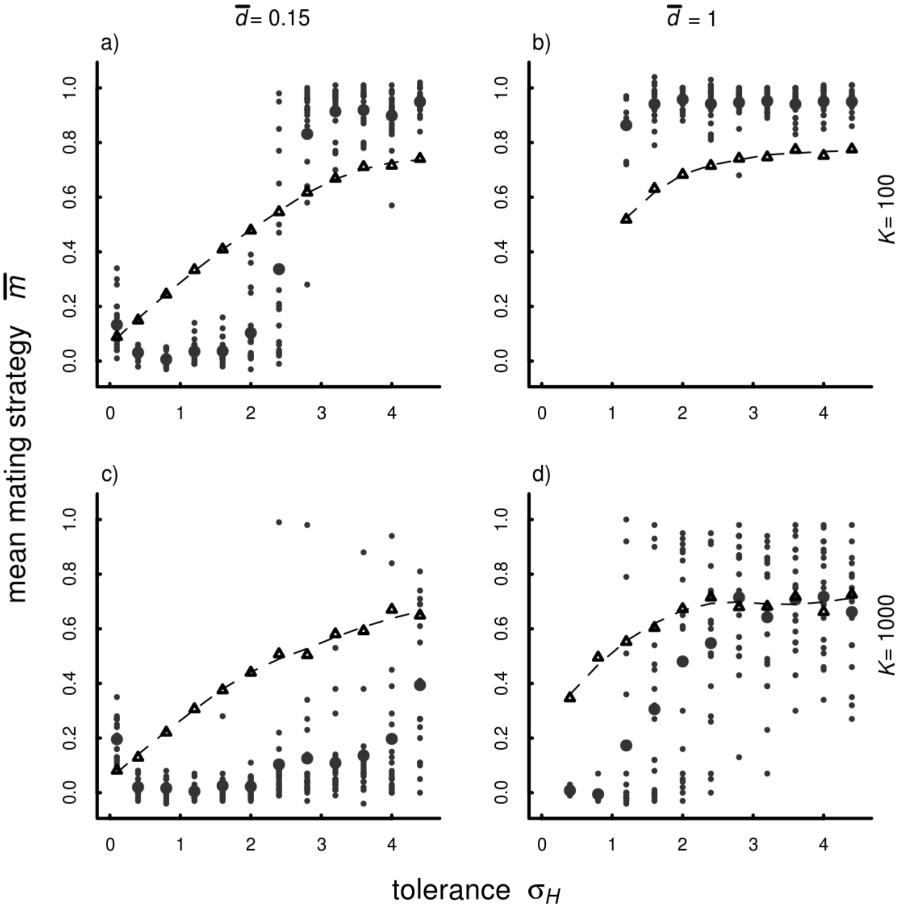

Figure A1. Mean evolved mating strategy $\bar{m}$ plotted against habitat tolerance in scenarios with fixed emigration probability. Note that $\bar{m}$ is the probability to mate in the natal patch. Smaller symbols represent evolved mean values for individual simulation runs averaged over the last 200 generations (of 20.000 generations in total); larger symbols the mean of these averages over the 20 independent replicates. Dashed line with empty triangle symbols represents mean individual deviation from the habitat adaptation value $(H_{f,m} - H_P)$ in each patch. Dispersal is fixed to $\bar{d} = 0.15$ in (a, c) and $\bar{d} = 1$ in (b, d) with patch capacity $K = 100$ in (a, b) and $K = 1000$ in (c, d). Environmental variability is $\sigma_\lambda = 0$ the same in all the panels.

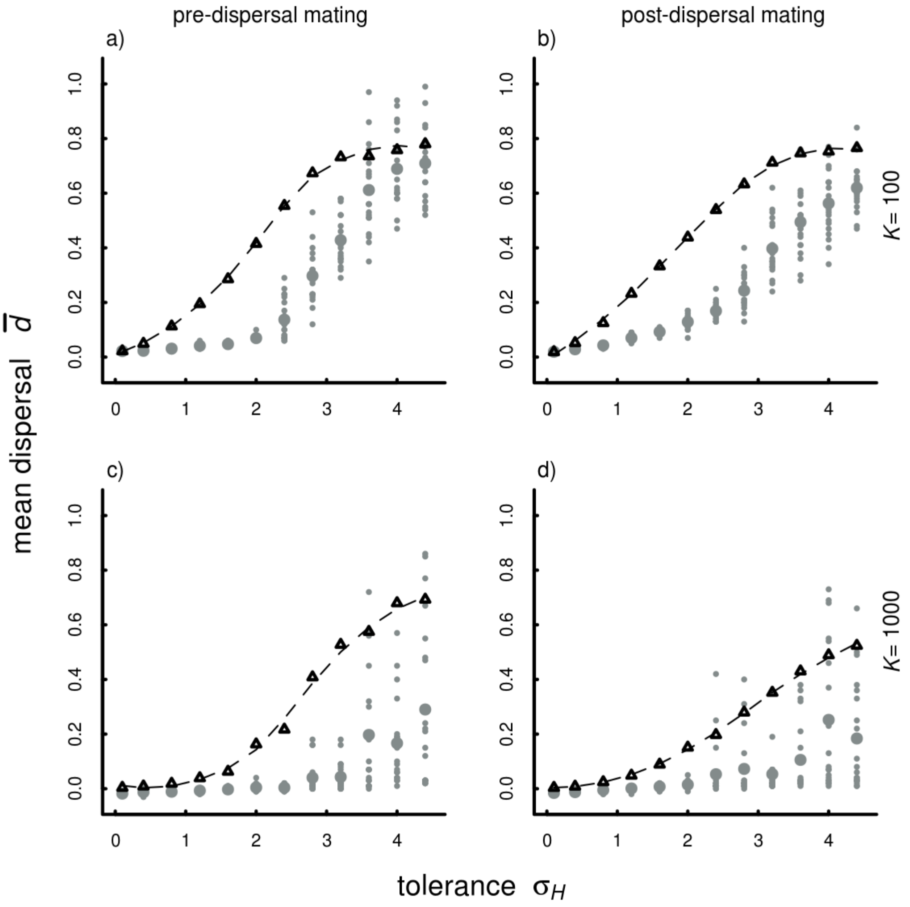

Figure A2. Mean evolved dispersal $\bar{d}$ plotted against habitat tolerance in scenarios with fixed mating strategy. Smaller symbols represent evolved mean values for individual simulation runs averaged over the last 200 generations (of 20.000 generations in total); larger symbols the mean of these averages over the 20 independent replicates. Dashed line with empty triangle symbols represents mean individual deviation from the habitat adaptation value $(H_{f,m} - H_P)$ in each patch. Mating strategy is fixed to pre-dispersal, $\bar{m} = 1$ in (a,c) and post-dispersal mating, $\bar{m} = 0$ in (b, d). Patch capacity $K = 100$ in (a, b) and $K = 1000$ in (c, d). Environmental variability is $\sigma_\lambda = 0$ the same in all the panels.

Chapter 4

Time investment into information acquisition and emigration

1. Introduction

In the past decades ecology of information or how organisms acquire and use information in decision-making to manage their lives (Schmidt et al. 2010), has received a lot of attention. Use of information can reduce the uncertainty about the environment (Donaldson-Matasci et al. 2010) and it is considered to increase reproductive fitness (McNamara and Dall 2009). There is prevailing evidence that insects rely on learning for their major life activities (Dukas 2008). For instance, selecting a high quality habitat is essential for successful reproduction (Boulinier and Danchin 2008). Therefore, individuals should be able to use information about their environment to assess quality of their patch, and consequently decide whether to remain there or to emigrate and try to reproduce somewhere else. It has been shown that information-based habitat selection strategies perform better than random strategies as they could make populations less likely to go extinct (Schjørring 2002), especially in variable environments (Ponchon et al. 2015). Such information can be related to weather or resources, or it can relate to social cues, e.g. the density of con-specifics (Clobert et al. 2009).

Con-specific densities, indeed play an important role in dispersal decisions as high densities may indicate high competition for resources, mates and nesting sites (Danchin et al. 1998, Clobert et al. 2009). There is ample empirical research providing evidence for density-dependent emigration in many animal taxa, such as aphids (Mehrparvar 2013), butterflies (Baguette 1996, Enfjäl and Leimar 2005, Nowicki and Vrabec 2011, Brunzel 2002), spiders (DeMeester and Bonte 2010), birds and mammals (Matthysen 2005). Hence, many theoretical studies have investigated mechanisms and consequences underlying density-dependent dispersal (Travis et al 1999, Metz and Gyllenberg 2001, Poethke and Hovestadt 2002, Bowler and Benton 2005). Since organisms explore patches in an adaptive way (Van Alphen et al 2003) they should evolve dispersal strategies that make them emigrate from patches where conditions are considered bad (Poethke and Hovestadt 2002) as compared to the fitness expectation in a new patch after emigration.

Most theoretical studies assume that information on density is available right at birth/emergence. However, this will only be possible under certain conditions, e.g. where insect larvae compete over resources (for instance, bark beetles Beaver 1974, leaf miner Quiring and McNeal 1984, mosquito Legros et al 2009, butterflies Gibbs et al. 2004). On the contrary, in species where only the adults experience competition (e.g. for resources, mates or oviposition sites), information about con-specific density and/or habitat quality must be acquired over time, through habitat exploration. Therefore, in species with such life-cycles, individuals need time to collect information to learn about their environment. Additionally, with increasing time spent in the natal patch the probability of mating and even ovipositing (in case of females) will increase as well. It is only logical to assume that short-lived adult insect would deny opportunity for mating or egg laying. Hence, when competition takes place at the adult stage, classical natal dispersal may not be the rule. However, majority of theoretical studies on density-dependent emigration (Travis et al 1999, Ruxton and Rohani 1999, Poethke and Hovestadt 2002, Enfjäl and Leimar 2009, Poethke et al. 2011) have ignored the fact that information acquisition may require time.

Information acquisition about the presence of con-specifics can occur by direct encounters with other individuals or indirectly via detecting some other population density indicator. For instance perceiving certain chemical cues, encountering the eggs of con-specifics, or just noting the temporal decline in resource availability (Bowler and Benton 2005). Female insects usually lack offspring care and larvae may be quite immobile; therefore selecting a good oviposition site is crucial for offspring survival. By selecting sites with fewer con-specific eggs, mothers can reduce competition in the next generation (Rausher 1979). Consequently, in many species, females avoid ovipostion sites that already contain eggs of other individuals (Chew and Robbins 1984, Peddle et al. 2002, Reiskind and Wilson 2004, Reiter 2007). For instance, females of the butterfly

Battus philenor can recognize plants that already have the eggs of con-specifics, which in turn inhibits oviposition on that site (Rausher 1979). Additionally, ovipositing single eggs, rather than a batch, can further reduce offspring competition. Such behaviour is observed in many insects, for instance seed beetles that lay only one egg per seed (Messina and Renwick 1985a), wevils (Messina and Renwick 1985b) parasitoids (Takasu and Hirose 1988), and butterflies (Williams and Gilbert 1981, Gutierrez et al. 1999).

Under conditions as outlined above sampling the environment for optimal breeding sites should thus be guided by similar mechanisms as in optimal foraging theory (Doligez et al. 1999). In birds individuals gather information about con-specific densities before taking a dispersal decision (Klopfer and Ganzhorn 1985). And some of them use the presence of eggs of con-specifics (Ward 2005) as a cue of future habitat quality rather than their density (Boulinier and Danchin 1997, Danchin 1998).

Competition for good oviposition sites will presumably be strong in high density patches or when resources (hosts) are scarce, which may in turn motivate individuals to emigrate into another patch(es). However, these individuals first have to explore the patch, in order to acquire such information. There are three different issues to be considered under such circumstance. Firstly, information acquisition may occur without any extra investment during the search for food resources, mates or oviposition sites. Encounters with other individuals or their eggs, provide insights about the density of con-specifics and/or more directly about the availability of critical resources. Secondly, such (new) information must continuously be used to update the estimate for the density of competitors (or the quality of a patch). Positive experience such as rare encounters with con-specifics or their eggs should indicate low density and possibly low competition for future generation. On the other hand, if encounters are frequent such negative experience should suggest bad patch quality. Finally, under such conditions individuals need to decide how long to accumulate information (and thus to wait with their decision) before taking an emigration decision. Obviously, consecutive positive or negative observations should lead to residency or sooner emigration, respectively. Marginal-value theorem and concept of optimal giving-up time (based on time-lags between positive encounters) in foraging theory has a long tradition for analyzing such problems (Charnov 1976). However, corresponding models are built on the assumption that a forager has a perfect knowledge of quality of all the patches in the landscape (McNair 1982); such assumptions, are unlikely to be realistic in unpredictable environments and individuals have to sample their environment and collect the information. Models typically assume that the ‘average’ of this information represents patch quality that in turn (de)motivates individuals to make patch leaving decisions. However, the environments are often stochastic, hence total average information may not be informative at the end of the season (McNamara and Houston 1987). One possible alternative is to consider ‘memory window’ where the average of only more recent information is used (Cowie and Krebs 1979). It would be interesting to see how such a ‘memory window’ evolves in different environments.

Here we use an individual based model of an insect metapopulation to investigate optimal duration of information sampling before taking a dispersal decision, where adults collect information about density of competitors by encounters with con-specific eggs deposited on critical host (plants). In particular, we simulate the evolution of a “competition-based” decision rule where the availability of resource of interest (host plant) declines everywhere over time because the resources only have a seasonal appearance and are everywhere exploited. A decision rule thus has to account for this effect and adjust fitness-expectation over the course of the season.

2. The model

We used individual based simulations to investigate how (indirect) evidence about the presence of competing con-specifics affects the timing of emigration itself. Model was created in Lazarus (1.6) programing language.

2.1. The landscape

Landscapes are implemented as N number of patches, each of them with P "unoccupied" host plants at the beginning of the season. Unoccupied plants are those on which no eggs have yet been deposited (see below). In each patch we initialize K number adults however, further numbers of insects are and emergent property.

2.2. Life history and population dynamics

We consider discrete non-overlapping generations of asexual organisms as an approximation of the life-cycle of many insect species such as butterflies, grasshoppers but also parasitoids, where adults emerge, start laying eggs on suitable hosts and potentially disperse over the course of the season (Figure 1). Egg-laying during the seasons is modeled in small time steps to approximate a continuous time model of a population where adults search for vacant oviposition sites. Parameters are set so that within a single time-step the probability that more than one individual detects a host plant is rather small after the first genration. In case of an encounter with an unoccupied plant, an individual deposits a single egg, marks the plant as "occupied", and continues the search. Encounter with a plant that already contains an egg leads to inhibition of oviposition and adult again continues the search (see section "Information acquisition" below). Such marking simulates the behaviour strategy of some species (Rausher 1979) where oviposition is inhibited by the presence of con-specific eggs.

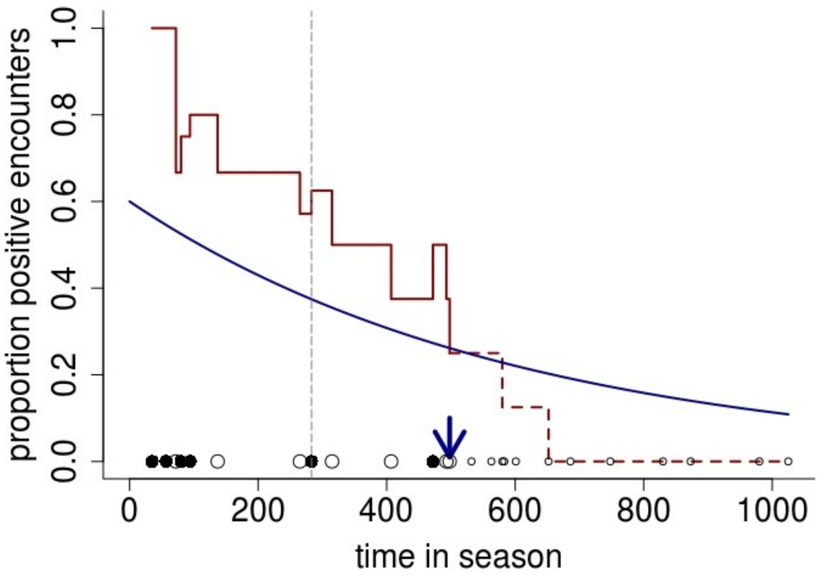

Figure 1. Exemplary representation of an individual female's searching history. The female emerges at time 0 and immediately starts searching for unoccupied host plants. Dots at bottom mark encounters with host plants (filled=positive, open=negative, i.e. already occupied) Red line is the individuals estimator of positive encounter probability based on last $i_S=8$ encounters (i_s itself is a heritable trait that may evolve; see text). The blue line is the individuals decision function defined by heritable parameters α and β . This individual emigrates at time c. 500 (blue arrow) after a negative encounter when the red line falls below the blue line. The small dots and hatched line further on are hypothetical encounters if the individual had not emigrated.

At end of the season adults die and a density-independent proportion (s) of eggs/larvae survive, opposite to our previous models (Poethke and Hovestadt 2002, Lakovic et al. 2015, Lakovic et al. 2017) where we implemented density dependent (DD) larval survivorship. Mean survival probability is fixed over the course of the simulations, however, we introduce variance in survival σ with s for each patch and year set set to $s+(-\sigma\cdot 100\ldots+\sigma\cdot 100)$. It is important to note, however, that in the current model the oviposition success itself is DD and thus leads to DD population growth.

2.3. Information acquisition and emigration decision

In this model we assume that individuals base their emigration decision on acquired estimators of local resource competition. We do not include any cost in information acquisition, but females are time limited by the overall length of the season and by the searching time invested to find unoccupied plants that will typically increase as more and more plants become occupied over the course of the season. We further assume that adults do not directly perceive the presence of other con-specifics in the patch that compete over egg deposition sites. However, they do so indirectly as they obtain information by encountering suitable host plants (with constant probability e_P) that already are or are not occupied by eggs laid by other individuals (or themselves).

The sequence of encounters with plants that are either occupied or not thus provides the basis for estimating the intensity of competition in patch and thus for the future perspective to find more unoccupied host plants. If many (other) competitors are present in the patch (we assume identical initial density of free host plants at the beginning of the season in all patches) the probability to encounter free plants will decline rapidly, but slowly if only few individuals search for host plants. However, the number of unoccupied plants will decline everywhere over time (except in a completely empty patches). Consequently, the individual's expectation for the probability of encountering unoccupied plants must also decline over the course of the season: At any moment, an individual should (ignoring the added costs of dispersal) only emigrate if its expects a larger chance of finding free plants elsewhere (this is the same argumentation as outlined in Metz and Gyllenberg 2001, Poethke and Hovestadt 2002). In fact, as long as the number of plants in a patch were constant, the probability of encountering unoccupied plants (the proportion of unoccupied hosts) must follow a geometric (negative exponential) function (Figure 1) over time. We thus assume that the individuals' decision criteria for emigration, an expected probability for encountering an unoccupied host, is also defined by a negative exponential function with two freely evolving parameters α (intercept) and β (decay parameter). We further assume that the individual's estimate of the encounter probability is based on observation window, i.e. the most recent i_s encounters with host plants, where i_s is the third, evolving gene that defines an individual's emigration (decision) strategy. A small value of i_s implies that the density estimate is only calculated over few encounters, that is a brief observation window.

The information collecting and dispersal strategy of all individuals is thus characterized by three genes. The first two, α and β impact the emigration decision, more specifically the intercept and the slope of the emigration decision function. The third gene i_S denotes the duration of observation window (see below). All genes are inherited from the parent but may mutate with a constant mutation probability (m_r) and mutation sizes ($m_{\alpha,\beta}$ for α and β and m_{is} for i_S). In case of a mutation the parentally inherited value of the affected gene is modified by adding a random value from the interval of mutation sizes [-m … +m], while in case of i_s the parental traits is modified by +/-1.

As our model is basically continuous in time and only one individual will be asked at any time step whether it emigrates, the reasoning of Metz & Gyllenberg (2001) applies: The emigration decision must be based on a time-dependent threshold, that is either the individual emigrates with certainty or it stays with certainty. Consequently, an individual will emigrate in our model following an encounter with an occupied host at time t_s (in the season) if it has encountered at least i_s hosts before (in the current patch of residence) and its empirical estimator for the probability of encountering an unoccupied host falls below the "expected probability" defined by the value of its inherited decision function (Figure 1); the empirical estimator is simply defined by dividing the number of positive encounters with hosts , among the last i_s , and dividing by i_s . It is important to note that the searching time for host plants itself is not informative in our simulations, as plant density is identical in all patches.

In case of emigration an individual will die with dispersal mortality μ . Otherwise, the individual is allocated to a new population (global dispersal) and the number of encounters with host plants is reset to zero. In principle, individuals are allowed to emigrate more than once during the season.

2.4. Initialization and parameterization of the model

Landscapes are initialized with $N=50$ habitat patches, each containing $P_E=1000$ empty plants and $K=200$ individuals and equal plant encounter probability $e_P=0.01$ for each patch. Mutation rate is fixed to $m_R=0.001$ for all three traits. In case of mutation the mutation sizes are as follows: $m_{\alpha}\in[-0.0001 \ldots 0.0001]$, $m_{\beta}\in[-0.001 \ldots 0.001]$, $m_{iS}\in(-1,1)$. We tested 3x3 scenarios in total, with differing dispersal mortalities ($\mu\in0.01, 0.05, 0.25$) and with different (year-to-year) variance in egg survival ($\sigma\in(0.02, 0.1, 0.5)$).Therefore, initialized egg survival probability $s=0.1$ will vary +/- 2 %, 10 % and 50 % according to different sigmas σ , respectively, We initialized the genetic traits of the genetically diverse population with random numbers drawn for each individual and for each gene from the following uniform distributions: $\alpha\in[0.0001, 0.001]$, $\beta\in[0,1]$ and $i_s\in[5,15]$ (for the latter, values were restricted to integer values). Finally, plant encounters were set to 0 for each individual at initialization. We ran 10000 generations/seasons, with each season lasting for 5000 time steps.

3. Results

Our results show that individuals evolve decision functions (parameters α and β) and observation time that allows them to make ‘smart decisions’. We observe that in patches with low initial population sizes, fewer (or non at all) emigrations occur over the course of the season and that emigrations only occur rather late in the season. On the contrary, in high density patches individuals start emigrating earlier in the season and more frequently. This is shown in Figure 3, where we see two exemplary patches from a single simulation with high environmental variability ($\sigma=0.5$) and high dispersal mortality ($\mu=0.25$). Figure 2a shows that with low populations size $N\sim20$ (dotted line) at the beginning of the season, first emigration occur rather late, toward the end of the season ($t\sim3000$), while with an initial population size of $N\sim60$ (2b) individuals start emigrating rather early in the season (~ 1000). This is the consequence of decreasing number of available plants over the course of the season. We further can see that at individual dispersal decision functions (solid black lines, Figure 2) do approach the real ‘free’ plant numbers toward the end of the season. These decision functions are not plotted from the beginning of the season but from the moment on when an individual has accumulated i_S number of observations and is allowed to disperse. For example, if an individual’s i_S is 10 then it can disperse only if once it collected at least 10 observations. Given that the plant encounter probability e_P is 0.01, this individual would need about 1000 time steps to have so many encounters with hosts. Furthermore, this plots represent individual decision functions and we can see the emergence of a single genotype within a patch.

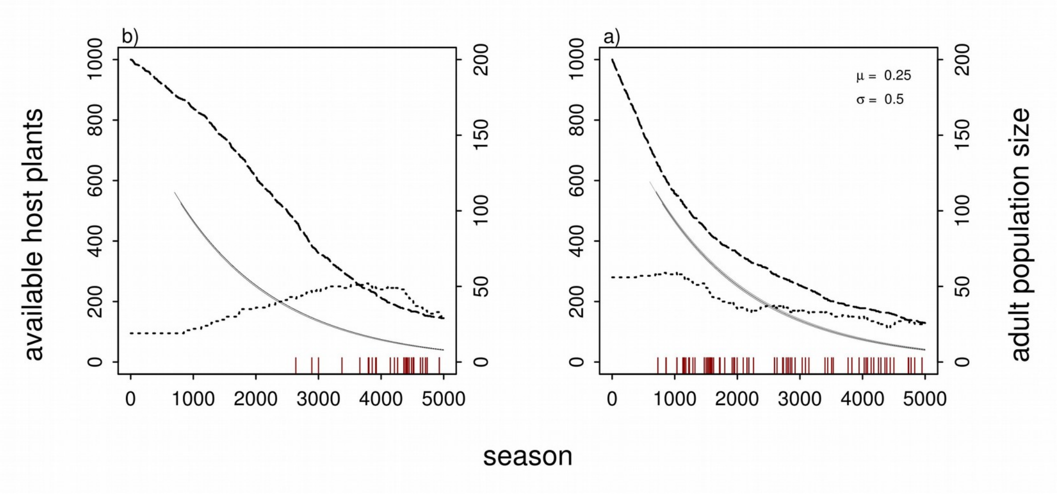

Figure 2. Patch characteristics plotted against the season time. Left y-axis represents the decreasing number of available plants (dashed line), while left y-axis denotes adult population size (dotted line). Thin black lines stand for individual dispersal decision functions in the patch. Red inner ticks (E_i) represent the timing of individual emigration events within the season. Each figure (a, b) represent one patch from a single simulation.

Furthermore, we find that the proportion of first emigrants (emigrants that leave their natal patch) in rather low (Figure 4a) in the beginning of the season (first 1000 season events, $t_s<1000$); fundamentally this must be so as individuals first need to accumulate the critical number of observations defined by trait i_S . However, the proportion of that eventually emigrate from their natal patch increases with larger initial population sizes in the patch. Interestingly the highest number of first emigrations occurs in the middle of the season (Figure 4c and 4b) but it decreases again towards the end of the season (Figure 4d). Note, however, that these figures are only accounting for the first emigration episode in the individuals' life. We further show that individuals take decisions to emigrate from initially low populated patches rather late in the season, while it is other way around for initially crowded patches. We observe the hump-shaped dispersal in the last two panels where the proportion of emigrated individuals is the highest for mid-size patches ($N_0=30-50$), while it is rather low for low and high density patches. The explanation for this patterns is that individuals will rarely emigrate from low density patches ($N_0 < 30$) at all, whereas most of them already emigrated from high density patches ($N_0 > 60$) at this time of the season.

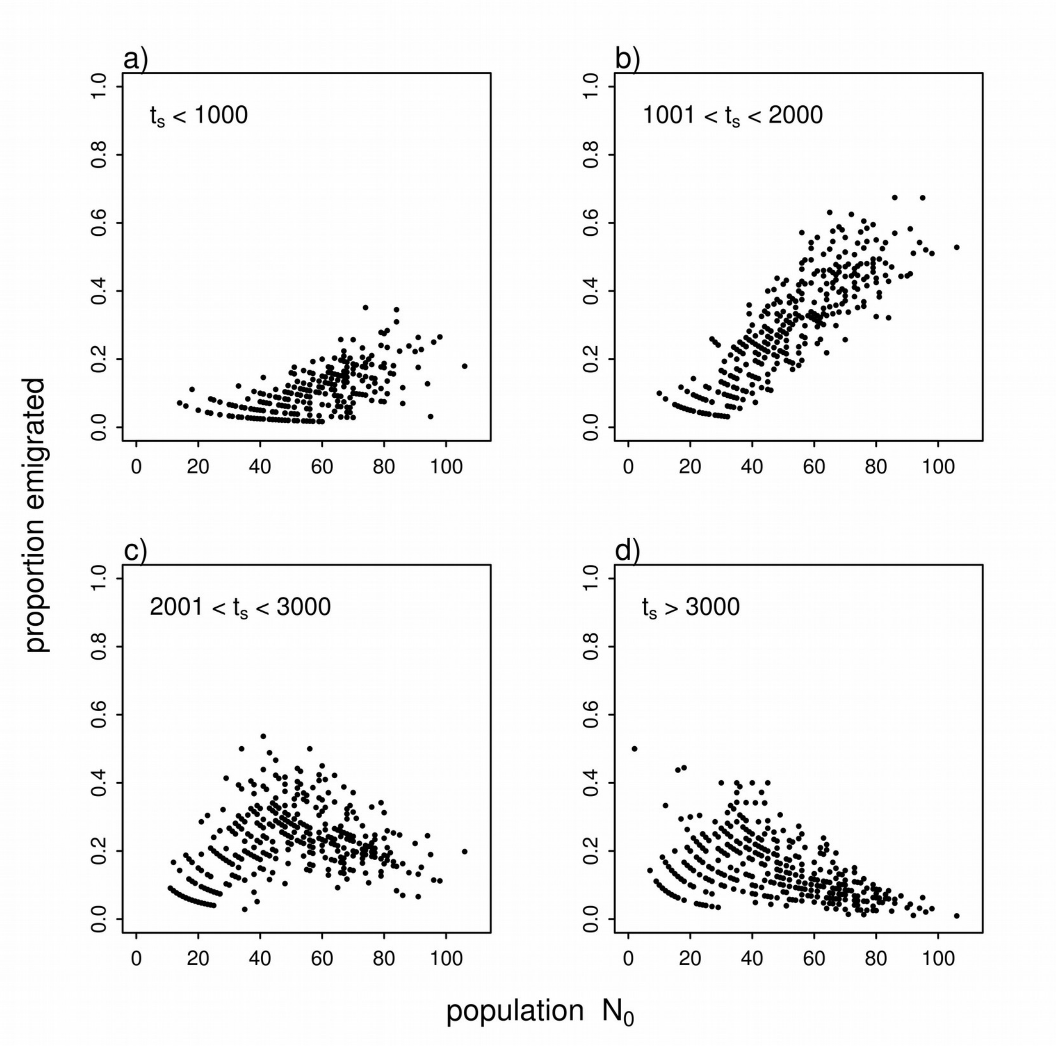

Figure 3. Proportion of first emigration plotted against initial density in that patch. Different panels, represent different times bins over the season. Scenario with high dispersal mortality $\mu = 0.25$ and environmental variability $\sigma = 0.5$.

Finally, we show that the first emigration timing is indeed later for low density patches and it decreases as initial population size increases (Figure 4). Additionally, in some patches where initial density is very low ($N_0 < 20$), individuals may never disperse.

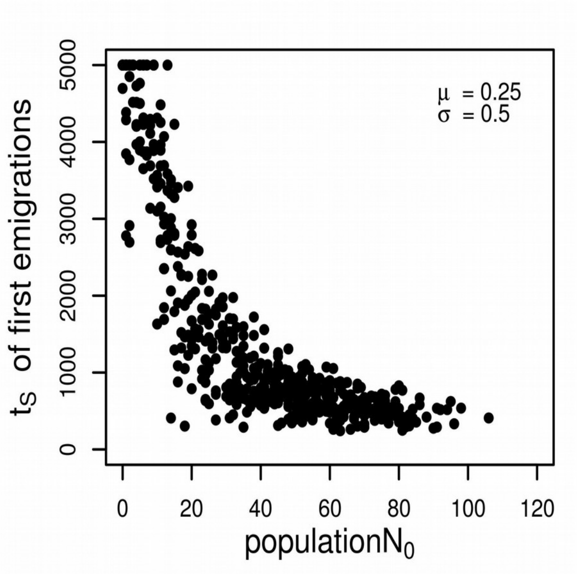

Figure 4. Mean time of first emigrations from each patch plotted against patches' initial population size, in scenario with high dispersal mortality and environmental variability ($\mu=0.25$ and $\sigma=0.5$). Values 5000 of t_S of first emigration indicated that dispersal never occurred in this patches.

3.1. Effect of environmental variability σ and dispersal mortality μ

It has already been shown in many previous studies that dispersal propensity increases with environmental variability, yet it decreases with dispersal mortality (McPeek and Holt 1992, Metz and Gyllemberg 2001, Poethke and Hovestadt 2002, Bach et al. 2006,). Our results show that when environmental variability is high, the genetic parameter i_S (observation window) decreases (Figure 5, black circles). Lower number of i_S means that individuals need less time for information collection and can consequently emigrate earlier. The opposite effect is observed for dispersal morality, where mean number of observations increases with increased μ (Figure 5). Accordingly, individuals accumulate more information about the habitat before emigration resulting in longer patch residence times. When we plot mean timing of emigration for these different scenarios, we see that when dispersal mortality is high, average emigration timing is actually later in the season (Figure 6). At the same time, when environmental variability is high, mean emigration timing is earlier in the season (Figure 6, black diamonds).

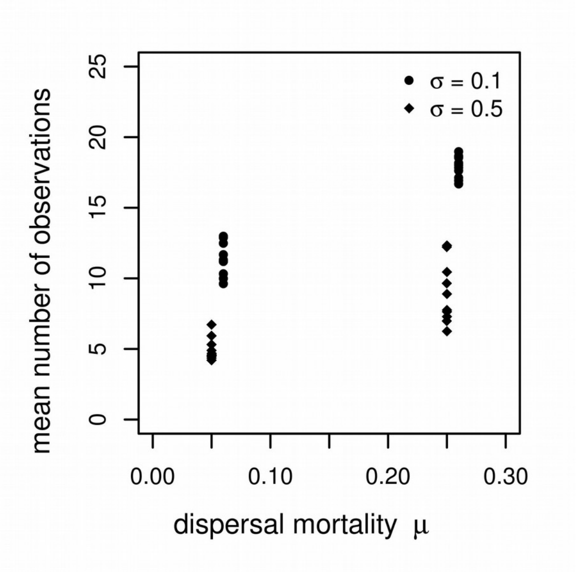

Figure 5. Mean evolved number of observations against the dispersal mortality for two environmental variability values ($\sigma \in (0.1, 0.5)$, circles and diamonds respectively).

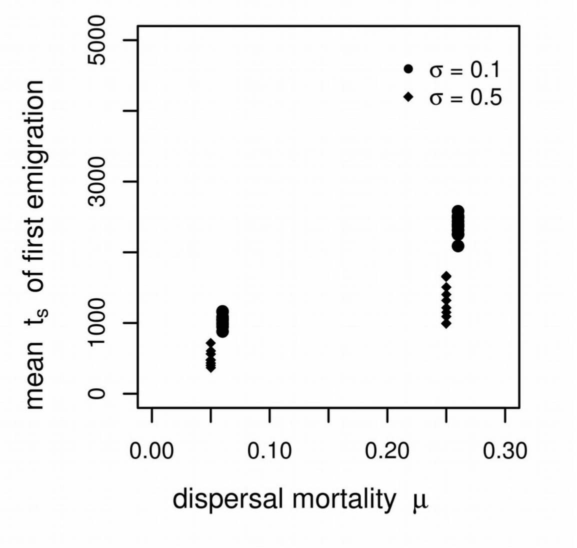

Figure 6. Mean timing of the first emigration plotted against dispersal mortality for two different sigma values $\sigma \in (0.1, 0.5)$, circles and diamonds respectively.

In more stable environments individuals take more time for information acquisition, while high variability makes them taking decisions earlier and disperse to different patches. In this way they spread their offspring and therefore the risk associated with offspring survival in unpredictable environments (Boer den 1990). Increase in dispersal mortality, on the other hand, selects against dispersal. Higher numbers for i_S that evolve indicate an increased tendency to disperse rather later in the season. Clearly, with lower dispersal mortality individuals spend less time assessing their environment as dispersal is less risky, therefore the number of observations individuals evolve is lower. With higher mortality 0.25, dispersal is more risky and individuals evolve spending more time to collect information and emigrate only when indeed necessary. Note in addition, that late in the season individuals will have deposited already most eggs so that they do not put much of their reproductive effort to risk when emigrating.

4. Discussion and conclusions

Biological information as a ‘factor that can affect the phenotype in ways that might influence fitness’ (Wagner and Danchin 2009) is essential to all biological and ecological processes in nature, from the information coded in DNA to learning by acquiring information from the environment. (Schmidt 2010, Smith 2000). Here we demonstrate by means of individual based modeling, that individuals may evolve to make ‘informed’ dispersal decisions based on the perceived intensity of competition over a limiting resource in their habitat patches, accumulated over time. We demonstrate that with such a simple rule , individuals emigrate earlier in the season from a crowded than from less populated natal patch.

Our results show that even for different scenarios of environmental variability and dispersal mortality, evolution always selects for some kind of informed dispersal, i.e. $i_s>0$ and non-trivial values for parameters α and β , and that individuals consequently collect and use the information about con-specific eggs in an adaptive way. Finding eggs on hosts is in this case considered as a proxy for con-specific density, since we do not include predation or egg mortality at this stage.

The decision rule we apply is such that ovipositing individuals that would continuously encounter ‘empty’ plants and lay eggs would never disperse; only in case of a negative encounter(s) (‘occupied’ plant) they may decide to emigrate. Therefore, in patches with low population size where the number of unoccupied plants is not quickly depleted , emigration occurs only later in the season (Figure 2a). A general tendency of ovipositing females to stay in a patch where there is a lot of available host plants should be typical for many species. For instance, such ‘incremental mechanism’ (each oviposition increases the tendency to stay in the patch, Waage 1979) is often related to parasitoids where any successful oviposition will halt dispersal in that moment (Van Alphen et al. 2003). Indeed, our results show that after emergence, when there is a lot of free plants and negative encounters are rare the proportion of emigrants is always low (Figure 3a), especially when population sizes are small. The highest emigration rates occur in the middle of the season (Figure 3b), when all individuals have investigated the patch sufficiently to take an informed decision. Toward the end of the season we observe hump-shaped distribution of emigration events over initial population size (Figures 3c and 3d) where individuals from patches with intermediate population size disperse more, on average, then those originating from patches with either low or high population density. This is non surprising, because many individuals occupying low density patch may never disperse, while those emerging in crowded patches will experience shortage of free host plants early in the season and thus emigrate; note that we only show the first (natal) emigration events in the figures. In contrast, individuals that reside in patches with intermediate initial population size experience such host plant shortage only lateer in the season. t

Emigration after partial oviposition (‘breeding dispersal’) seems indeed to be quite frequent in insect taxa (see Chapter 5). Additional argumentation for breeding dispersal in insects would be that adult stages are usually short-lived (couple of days or week), hence majority tends to mate soon after emergence. Therefore, truly natal density-dependent dispersal would be rather unlikely in adult insect, in particularly in those whose larvae are not exposed to any information regarding con-specific densities. However, this would be possible when there is density-dependent survival at larval stage (Beaver 1974, Quiring and McNeal 1984, Legros et al 2009, Gibbs et al. 2004). However, harsh competition at this stage can also have the opposite effect. For instance consequences of competition in high density patches can result in smaller body size or shorter life span (Atkinson 1979, Scott, 1994) that can potentially lead to less dispersive individuals.

In our simulations, the decision functions have evolved to approximate the mean (or expected) availability of unoccupied host plant density especially towards the end of the season. The resulting decision curves vary between replicates (especially for high mortality, Figure A1). The function allows for potential emigration early in the season with high values of β (the intercept). On the other hand, for a given beta, low α values increase the dispersal probability , in particular towards the end of the season. Note, however, that the observation window i_s can override the effect of high β (Figure A1). With increasing number of observations, individuals allocate more time to information collection, hence delaying dispersal. In turn, we observe that when environmental variability is high (an attribute strongly selecting for dispersal), i_s evolves in general to lower values (Figure 5 $i_S \sim 5$ for $\mu = 0.05$), but never approaches 0. This decline in i_s may also be due to a feedback effect. If few individuals disperse, the long accumulation of information provides an accurate estimator of current competition. However, if many individuals emigrate (and consequently also immigrate) this is not so anymore as local population size may rather rapidly change over time. By selecting low values for i_S evolution thus avoids the influence of experience too far in the past, as such information may not be very informative with regard to the current situation anymore. On the other hand observation window never evolves values close to 0, because such low nubler of observations would be uninformative.

Number of observations increases with dispersal mortality (Figure 5), because obvious risk associated with emigration. Therefore, individuals benefit from staying longer in the natal patch and leaving a substantial fraction of their offspring there prior to emigration, as they might not survive the dispersal phase. This would also be risk-spreading strategy associated with dispersal (Lakovic et al. 2015). Such ‘breeding dispersal’ is a good strategy for kin-competition avoidance and reduction of variance in offspring survival, and at the same time information collection is without cost.

Our model takes into account only the observations based on the ‘occupied’ oviposition sites as a proxy for con-specific densities. Clearly, for organisms like many butterflies that do not discriminate between plants with/without eggs (Robbins and Chew 1984), direct encounter with other individuals might be a more valuable indicator of con-specific competition and emigration decision would depend on the frequency of such encounters. However, in species where adult population density is generally low, e.g. because resources are rare, competition estimators that are cumulative like the proportion of resources exploited may be much more reliable than those based on rare direct encounters with con-specifics. Further, in some species con-specific attraction is a form of social information that might indicate high-quality habitats, which is the case with butterfly *P.napi* that prefers to lay eggs on plants already containing con-specific eggs (Ohsaki 1981). However, for many others crowding is an indication for intensified competition for resources and/or oviposition sites. In phytophagous insects, for example, larval fitness depends largely on female oviposition on a good host. (Janz 2003). For instance, female hover flies (aphid predators), refuse to oviposit on leaves where there are con-specific larvae or tracks of con-specific larvae (chemical volatiles). This shows that females can optimize oviposition and reduce competition in the future generation (Almohamad et al. 2010). Therefore, freshly emerged females learn about their environment while searching for good oviposition sites and consequently can make informed dispersal decision.

We assume in our simulations that there is no specific cost associated with information collection because females learn about the con-specific density while searching for oviposition sites. However, this would change if individuals could oviposit also on plants with eggs, and there was a density dependent survival of larvae. Then if they would invest more into finding an empty plant to reduce the competition in future generation, there may be a trade-off with realized fecundity (if choosy females are less fecund (Jaumann and Snell-Rood 2017)). If searching times are long females should eventually lay eggs on already occupied plants. However, the strategy may not be good where strong priority effects exists, e.g. where competition would be asymmetric much in favor of the first egg/larvae laid.

Furthermore, oviposition strategy can evolve as a consequence of spatial distribution and host abundance. Adult insects can reduce the competition in the future generation by depositing fewer or single eggs on a proper host. For instance two closely related butterfly species in genus Pieris rely on the same host but in different way. *Pieris rapae* lays single eggs, because it selects for isolated plants where competition would be harsh at high larval densities. On the other hand, *Pieris brasicca* lays egg clusters and selects for clumped hosts where larvae can migrate to neighboring plants (Davis and Gilbert, 1985). This is in agreement with preference-offspring performance hypothesis: Insects living in heterogeneous environments, whose larvae have limited dispersal should choose oviposition sites in a way to maximize offspring fitness (Rausher 1983).

Finding a suitable oviposition site, obviously takes time during which individuals learn about their environment. However, apart from optimal foraging and patch time allocation studies, mostly in parasitoids (Waage 1979, Van Alphen et al. 2003), there are few studies on information acquisition and oviposition behaviour in other insects. Fundamentally our model is analogue to optimal giving-up time models or ideal-free distribution models, yet it accounts for fact that attributes of the environment themselves always change over time. Our study shows that density-dependent dispersal requires time for information acquisition and that organisms can indeed evolve to make ‘smart’ emigration decisions. This should be taken into account when studying truly natal dispersal (emigration right after emergence) in species with similar life histories as our hypothetical organism.

Appendix

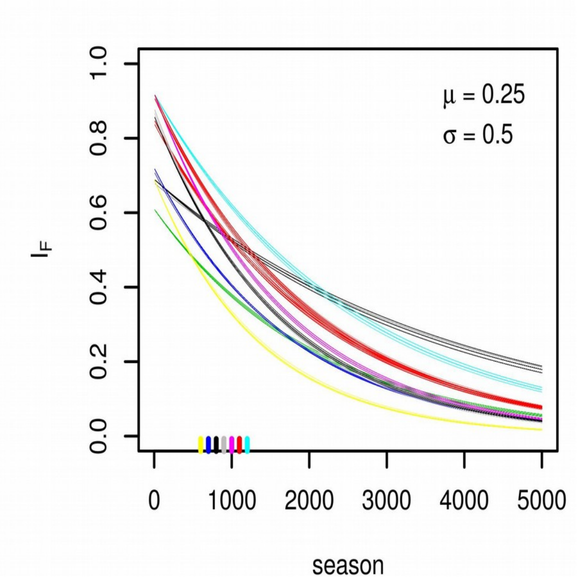

Figure A1. Individual decision functions (I_F) plotted against season time. Different colors represent 10 different replicates. The tick on season axis represent mean individual observation window (i_S). Therefore, if beta is ~ 0.9 in some replicates (i.e. red or blue lines), that may suggest increased probability of early dispersal, however corresponding thicks on the season axis show that due to larger information sample size, these individuals do not have the possibility to disperse before at least 1100 time steps

Chapter 5

A review: Dispersal timing across insect taxa

Studying insect dispersal in natural environment is often challenging, given their small size, great numbers and high mobility (Nathan 2001). Additionally, most of the mobile, adult, stages are short lived, completing their life cycle within a few days or weeks. Finally, insects frequently occupy ephemeral habitats that appear and disappear in short periods of time that can be difficult to track. The timing when dispersal takes place in the individuals life, i.e. as larvae or adult, prior to or post mating, remains poorly investigated by the empiricist and largely overlooked by the theoreticians. Previous chapters of this thesis show that the timing of dispersal within life-cycle has important implications for the population dynamics and evolution of dispersal. Hence, this chapter aims to review this in the light of different life-histories and environmental conditions. The following sub-chapters provide an overview of possible dispersal strategies with regard to life-stage, mating strategy and sex and their occurrence across insect and arachnid taxa.

1. Modes of dispersal: Importance of timing and information

Insect dispersal may occur, passively, or actively, at any life-stage. Dispersal right after emergence to another site for reproduction constitutes classical *'natal dispersal'*, while, dispersal between two consecutive reproduction events is typically denoted as *'breeding dispersal'* (Basskett 2012). Figure 1 provides a schematic overview of possible alternative female dispersal strategies in the context of emigration timing within a life cycle (males, however, will be discussed as well). It further denotes the possibility for information collection at different life stages and its role in the timing of emigration related decisions.

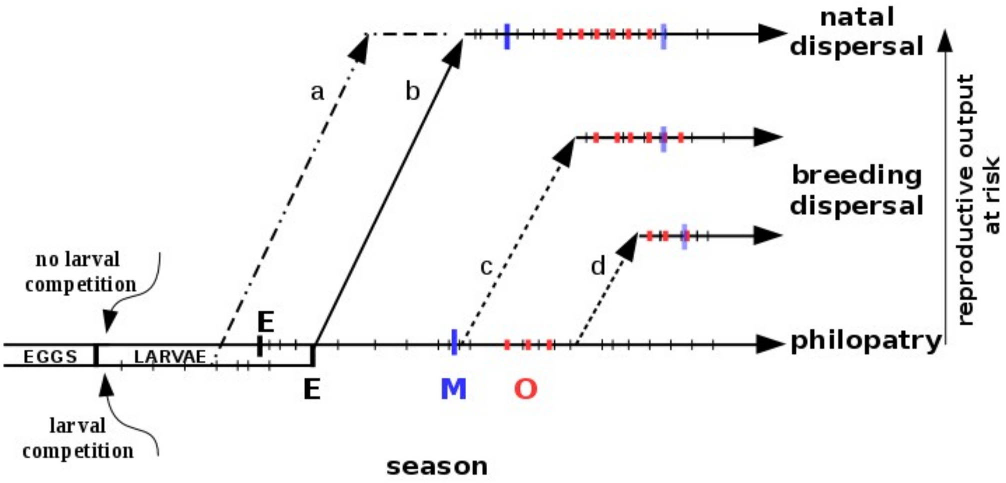

Figure 1. Schematic representation of a female's possible dispersal timing in relation to emergence, mating and reproduction. At the left hand side, the two lines for eggs and larvae represent different scenarios of larval development, that is, one where larvae experience (intra-specific) competition and the other where there is no such information. The short black ticks on the season axis stand for any information individual collects during its life time. The letters E (black ticks), M (blue ticks) and O (red ticks) stand for adult emergence, mating and oviposition events, respectively. Faded blue ticks denote possible secondary mating(s). The arrow at the right represents the increase in reproductive investment exposed to dispersal risk from philopatry to natal dispersal. Dot-dashed arrow represents dispersal during the larval phase, while the full and dotted arrows denote dispersal during the adult phase. Letters a, b, c, d denote different dispersal strategies.

Philopatric individuals are those that never disperse and consequently complete their entire life cycle in the natal habitat. As for dispersing individuals, there are three different strategies. First there is natal dispersal that may occur at any life stage (larval a or adult b dispersal), where both, mating and oviposition take place always away from the natal patch. Second, there are two different scenarios for breeding dispersal that can only be performed by reproductively mature adults. One is where a female disperses right after mating in the natal patch but lays eggs only in the new patch(es) (c), and the other where a female first oviposits (and thus obviously mates) at home and later on in a new patch(es), possibly after mating again (d). In this context males have only one breeding dispersal strategy where they can distribute their potential offspring by mating in two (or more) distinct patches.

Clearly, the different female strategies are associated with different proportion of the reproductive output exposed to dispersal risks, that actually increases from philopatry to classical natal dispersal. For instance, a female that emigrates right after emergence risks ending up in an empty habitat with no possibility to find a mate and ever have offspring. On the other hand, a female that mates before emigration does not bear this risk; however, both strategies risk mortality during transfer phase (i.e. predation) and consequently not producing any offspring. The third strategy that includes mating and leaving part of the eggs in the natal patch and then dispersing to oviposit the rest somewhere else secures at least part of the reproductive output (ignoring other possible ‘standard’ mortality risks). On the contrary, the dispersal mortality (i.e. predation) may be higher for gravid females (strategy c) that are possibly slower due to the egg load and easier target then natal dispersers (strategies a and b). Such risk is again reduced in individuals that oviposit part of their offspring in the natal patch (strategy d). Indeed, in Chapter 2 of this thesis I provide evidence that such risk spreading is generally a good strategy to reduce both kin competition and variance in offspring survival. Furthermore, evolutionary tournaments when populations are small and environmental variability is high, show that a risk-spreading strategy always out-competes natal dispersal strategy (Lakovic et al. 2015)

Another important aspect of dispersal, represented in the Figure 1, is gene flow. Namely, individuals, males or females, that emigrate right after emergence carry (potentially) their own genes into a new population. However, females that mate prior to dispersal also carry genes of the local mating partner into another gene pool. Results from Chapter 3 show that the habitat heterogeneity and species tolerance may modulate the shift from one strategy to another. More specifically, females of less tolerant species should mate after dispersal (natal dispersal) with locally adapted males in order to increase offspring fitness in the new environment/patch. Mating after dispersal is risky, especially if an individual arrives to an empty habitat whit no available mates. In addition, in many insects mating takes place soon after emergence and a female could choose to mate in the natal patch. However she re-mate in a new patch with a better adapted male if the opportunity arises, although such multiple matings were not explicitly included in this study. On the contrary, tolerant species that have more or less equal chances of survival across the landscape should mate prior to dispersal and take the genes of their own kin to another patch (Lakovic et al. 2017).

Finally, short black tick marks on the season axis in Figure 1, show that information relevant for informed dispersal decisions can be gathered at different moments in the life-cycle. The information cues that individual may gather, answer questions such as: ‘Did I find food, mates or nesting sites?’ or ‘How many competitors or predators have I encountered?’. Depending on the species life-history such information can be collected already during the larval stage or only later in the adult (and mobile) phase. Thus, if we are to consider informed natal dispersal, we have to account for the time necessary for information collection by an individual. For instance, informed natal dispersal is possible if information was collected during larval stage, which is not the case in species whose larvae grow up in isolation, as it is true for many solitary parasites/parasitoids but also for e.g. butterflies where females lay only single eggs (Gutierrez et al. 1999). In such species, information about the natal habitat can only be collected during the adult phase. This may be the reason why many individuals actually do not perform classical natal dispersal and mate and oviposit at least partly in the natal patch. In the Chapter 4, I studied how information use about con-specific density affects the evolution of dispersal. And found that individuals explore patches in adaptive way, and disperse more and earlier from crowded patches, and late or never from less populated patches.

There has been substantial research on the reproductive and breeding behaviour in context of dispersal in higher vertebrates (such as birds and mammals, Greenwood 1980, Greenwood and Harvey 1982, Matthysen 2005), as their longevity, size, limited numbers and offspring care allows better documentation of movement in the field. In contrast, it is not trivial to do so with small, short-lived, and numerous insects, that possibly mate many times and often have multiple oviposition sites within a rather short time period. An exception are the social insects that tend to live in colonies and provide brood care to some extent. However, due to their particular life-history such species are mostly excluded from the scope of this review. To my knowledge, only several reviews tried to describe general patterns of arthropod dispersal strategies and most of these focus on butterflies (Stevens et al. 2012, Stevens et al. 2013, Stevens et al. 2014), several suborders of Odonata (Conrad et al. 1999 and Conrad et al. 2002, Beirnickx et al. 2006), and passive dispersal in Arachnids (Szymkowiak et al. 2007). Additionally, only few theoretical studies (Johst and Brandl 1997, Hirota 2004, Hirota 2005, Massol and Debarre 2015, Lakovic et. al 2017) consider emigration and mating timing when studying evolution of dispersal. Therefore there is a great need for clarification of insect dispersal strategies because their consequences on population dynamics and evolution significantly differ when emigration timing is considered. Based on the findings of the Chapters 2, 3, and 4 of this thesis, I would in particular expect that:

(i) Natal dispersal of larvae (strategy a) or (pre-mated) adults (strategy b) should occur with higher probability in insects that experience competition or crowding already at the larval stage, or in those where mothers experience can be transferred to the next generation (maternal effects); It is important to note that natal dispersal of (pre-mated) adults may also occur towards the end of the season as a consequence of failure to find a mate.

(ii) Breeding dispersal (c and d) is more likely to occur when competition takes place at the adult stage. This is because information collection, about con-specific density for instance, is a timely process. Therefore, short lived females would presumably already mate and even deposit some of their eggs in the natal patch prior to emigration.

(iii) Additionally, offspring distribution or risk spreading strategy (strategy d), possibly even with multiple breeding dispersal, should occur in species that experience strong intra-specific competition or live in (very) variable environments (i.e. ephemeral habitats, variation in predation and/or abiotic conditions);

(iv) Mating, or more specifically egg fertilization, should take place before dispersal in species that frequently colonize new empty habitats (strategies c and d), otherwise they may risk not finding a mate if they end up in an empty habitat. In contrast, mating should occur after dispersal when local adaptation is important (strategy a), as is the case in heterogeneous landscapes for instance.

Given these general expectations, I would like to provide an overview of dispersal strategies (Figure 1) across different insect groups (and other arthropods where dispersal has been studied substantially, such as Arachnidae), in particular with regard to timing of mating and dispersal. More specifically, at what life stage and time within this stage dispersal takes place and how this (decision) correlates with sex, mating system and habitat type. Furthermore, I would like to highlight the role of information in the context of emigration and mating timing, that is largely overlooked when studying dispersal strategies.

2. Philopatry vs Dispersal

Many individuals spend their whole life in their natal patch; selection against dispersal is especially strong in big populations with low risks of inbreeding (Motro 1991, Perrin and Mazalov 1999) or kin-competition (Hamilton and May 1977, Gandon and Michalakis 1999, Gandon 1999, Ronce et al. 2000, Bach et al. 2006, Poethke et al. 2007, Gyllenberg et al. 2008), plenty resources, and stable environments (McPeek and Holt 1992, Metz and Gyllenberg 2001, Poethke and Hovestadt 2002, Cadet et al. 2003). However, man made changes to the environment often leave species in fragmented populations where dispersal is necessary for their long-term persistence. For instance, damselfly, *Coenagrion mercuriale*, that is endangered in Europe, is predominantly sedentary and shows negative density-dependent dispersal, especially in the isolated populations. The resulting low dispersal capability imposes difficulties for its conservation. This species is one of the poorest fliers among Odonata species, however seldom dispersal events have been shown between congruent populations. Hence, providing stepping stone habitats or dispersal corridors to reconnect isolated populations may prevent such species from extinction (Rouquette and Thompson 2007). Similarly, the endangered butterfly *Neonympha mitchellii francisci* metapopulation occupies wetland glade habitats where disturbances such as fires and beaver activity lead to local extinctions. This species is also very sedentary, yet rare dispersal events and colonizations of new habitats are observed (Kuefler et al. 2008). I would assume that for these rare emigrants classical natal dispersal (strategies a and b in Figure 1) would be very risky as they may end up in an empty patch with no potential mates. At least in such metapopulations that occupy unstable environments, pre-dispersal mating would be strongly selected for. Additionally, the selection should be on female dispersal as they, provided that they mated before, are the only ones that can colonize an empty patch.

There are potential costs for philopatric individuals, such as inbreeding, (kin-) competition for mates, resources and/or oviposition sites. However, these individuals take no risk of dispersal mortality and may, in particular in species with distinct dispersal morphs (Roff 1986), even avoid investing into dispersal attributes. It is often assumed that investing in dispersal (time and energy wise) might decrease female fecundity (Tsumuki et al. 1990). Such trade-offs are often reported and easier to quantify in truly wing dimorphic species. On the contrary, in wing monomorphic species, such as the Glanville fritillary butterfly (*Melitaea* *cinxia*), the opposite has been observed, where females from newly established populations are more mobile and have higher egg production compared to less dispersive females from older populations (Saastamoinen 2007). Such biology is similar to species that often colonize new habitats and produce more eggs, more specifically species that follow r-strategy (Hanski et al. 2006). Furthermore, a genetic basis for dispersal tested in Glanville fritillary butterfly seems to be an allele coding for enzyme that increases metabolic rate, and consequently dispersal and it is found more frequently in colonizer populations than sedentary (Haag et al 2005).

However, costs of dispersal are clearly higher in wing dimorphic species because they invest into wing production, in order to disperse, that often results in lower fecundity (Tsumuki et al. 1990). For instance, flightless females of *Gryllus rubens* (Orthoptera) cricket invest more in ovary development, while winged invest more in wing apparatus (Mole and Zera 1993), as a consequence of underlying genetic differences (Zera & Cisper 2001). Clearly, unfavorable patch conditions such as crowding (competition for resources) or predation can outweigh the costs (investment into dispersive morphs) and induce the production of winged/dispersive individuals when necessary.

3. Dispersal timing

While dispersal may occur at the larval or adults stage, emigration decision may be controlled either by the individual’s experience or even by the experience of its mother. In certain cases this is very obvious, for instance production of winged offspring by mothers that experienced ‘bad’ conditions in a patch (competition, predation etc.), however, often enough it is difficult to assess weather there is parental control behind motivation to disperse.

3.1. Maternal effects

Individuals that bare energetic and physiological costs of wing production may, however, disperse into a habitat with better conditions. In this case the information about the environment is collected already by the mother and 'transferred' to offspring. It is indeed, important to recognize that dispersal can be driven by the mother’s experience, i.e. by so called maternal effects. This is the case for many gregarious or semi-gregarious species such as aphids (Sutherland 1969b, Hatano et al. 2010) that perceive chemical cues of predator or con-specific (crowding) presence and will in turn produce greater numbers of winged offspring (Merhparvar et al. 2013). Ballooning dispersal length of survival until the feeding phase in gypsy moth (*Lymantria dispar*, Lepidoptera) larvae greatly depends of maternal investment into eggs (Diss et al. 1996). Dispersal (ballooning) propensity of dwarf spider *Erigone dentipalps* is higher in offspring whose mothers experienced starvation (Mestre & Bonte 2012). Therefore, mother’s experience within a patch may influence dispersal of her offspring.

When dispersal is controlled maternally, individuals have higher motivation to leave as soon as they emerge, for instance winged offspring comparing no non-winged. Therefore, I could assume that natal dispersal strategy such as larval natal dispersal (strategy a in Figure 1) is the most probable in insects species, where dispersal is controlled by the mothers experience.

3.2. Natal dispersal

However, natal dispersal of larvae and also eggs (strategy a in Figure 1) may, as well, occur passively. For instance, eggs and larvae may be displaced via certain vectors (water, wind or other animals). A particular case in question are freshwater taxa, where eggs or nymphs are carried by water current or some other vector (this dispersal is difficult to track and quantify, however). In mayflies significant larval/nymph dispersal occurs by water drift, while adults actively disperse in search for nesting sites (bellow Caudili 2003). In other species, such passive dispersal of larvae, may still be initiated actively by an individual. For instance, larvae of water mites (Hydracarina), disperse by attaching to adults of flying insects (Bohonak 1999b, Bilton et al. 2001) orwell known behaviour in many sub-adult arachnids, ballooning, as a means of dispersal by wind (Szymkowiak et al. 2007). Furthermore, adults of American and European Gypsy moth (Lepidoptera) are flightless and the most significant dispersal occurs during larval period on silk treads, carried by wind (Capinera and Barbosa 1976). In other cases where larvae are more-less immobile, active dispersal over longer distances and potentially to another habitat, is typically possible only during the adult stages.

3.2.1. Informed natal dispersal

Whenever larvae are able to disperse on their own, it is likely that emigration decisions will depend on their own experience. For instance, in addition to mothers' experience that may induce the production of winged morphs not all winged individuals will disperse (Shaw 1970). Similarly, in previously mentioned dwarf spider mother’s experience did affect propensity for ballooning dispersal, but, only starved juveniles ultimately emigrated into new habitat patches (via ambulatory movement), mostly toward the end of the juvenile stage (Mestre and Bonte 2012). Therefore, own experience during developmental phase, such as absence of food, is a more direct indication of habitat quality that may increase dispersal propensity. Similarly, little brown apple moths, that experience poor habitat conditions, are in general smaller but also better fliers compared to the bigger ones giving them a better chance to disperse into habitats of higher quality (Suckling and Brockerhoff 2010). In general, strong competition or other habitat properties (i.e. temperature), experienced as juvenile, are found to affect adult dispersal in spiders (Anelosimus cf. Jucundus, Powers and Aviles 2003, Szymkowiak et al. 2007, Bonte et al 2008b). Indeed many studies show that in some species net dispersal increases as a reaction to ‘bad’ patch conditions caused by different biotic and/or abiotic factors (Clobert et al. 2009). However, it depends on the species specific life-cycle and life history when (i.e. natal or breeding) and how an individual will disperse.

There is evidence that insects can estimate the quality of their environment via certain visual and/or chemical cues (Honda 1995, Wehner et al. 1996). Inbreeding avoidance, crowding, presence of predators or unfavorable environmental conditions can be indicators that dispersing, in search for better habitat may be a good decision (Perrin and Mazalov 1999, Metz and Gylleberg 2001, Poethke and Hovestadt 2002, Bach 2007, Enfjäl and Leimar 2009). For instance, in some moth species virgin adults are more dispersive than mated ones, possibly as a consequences of failure to find a mate in the natal patch (moth paper Collatz & Wilps, 1986, Schumacher 1997, Danthanarayana & Gu, 1992). Therefore, after unsuccessfully searching for mating partners, older virgin males and females will leave their natal habitat in search for mates elsewhere. This behaviour can be related to the classical foraging theory that suggests a certain 'giving-up time' before individuals continues search in another patch (Charnov 1976). Therefore, the information gathered passively during patch exploration (such as no available mates) will affect emigration decision. For example a female that emerges in a low density patch with plenty of resources, mates and nesting sites should, provided that is does mate successfully, has very low tendency to disperse.

Informed (natal) dispersal (right after emergence) is unlikely to occur when individuals are not exposed to any information. For instance, insect larvae that grow in isolation do not have opportunity to collect much information about their habitat during the development phase. Species as parasitoids within the hosts or beetles that develop singly within a tree trunk or a fruit seeds, cannot obtain the information about infra-specifc competition, predation or environmental conditions. For example, seed consuming beetles distribute eggs evenly across seeds (one egg per seed, to reduce kin competition), where a single larva has no information about the environment outside the seed (Wright 1983). Similarly, in other species that lay single eggs, such as certain butterflies (Gutierrez et al. 1999), larvae that develop and feed on a single leave/plant have at best the information about food quality at a very local scale. In such species natal dispersal immediately after emergence would undoubtedly be uninformed with regard to population density or habitat quality. On the other hand, some butterfly females will lay their eggs in aggregations, because the presence of con-specific eggs can be an indicator of good quality host plant (Raitanen et al. 2014, Chew and Robbins 1984). Hence, for numerous hatched larvae, on a single plant, this may be an indication of future competition. Therefore, information collected already at a larval stage can be used in freshly emerged adult as a motivation to emigrate or not.

3.3. Breeding dispersal

In contrast to natal dispersal that can occur in larval or adult phase, breeding dispersal can take place only within the adult reproductive phase (strategies c and d, Figure 1). In general, competition, predation or 'bad' abiotic conditions can increase individual emigration propensity, yet some drivers of dispersal may differ between adult and larval stage. Namely, larvae tend to be a feeding stage therefore sufficient food resources are important for their development into adults (i.e. metamorphosis). For adults, that are the reproductive stage, mates and oviposition sites (for females) are the critical resources for production of next generation whereas finding food may be an issue of lower importance. Indeed, in some species adults do not feed at all (Herbert 1983), while in others only females do not search for food as they may receive nuptial gifts from the males (Boggs 1995). Therefore, emigration decisions may, for such species, strongly depend on the mating and oviposition opportunities.,

3.3.1. Offspring care

A particular constraint with regard to the timing of dispersal may emerge in insects that provide some sort of brood care (apart from the specific case of social insects). In general, insects rarely invest into offspring care directly, unlike so many higher animal taxa. However, whenever they do, this has clear implications for the spectrum of dispersal. European earwig (Hymenoptera) females tend to care for their eggs after oviposition, and it has been shown that dispersiveness in negatively correlated with the degree of maternal care. That is, females with only one brood disperse four times further then females with two or more broods that care longer for their young (Moerkens et al 2010). Naturally, if a lot of offspring is produced at a single site (double brood), the added benefit of protecting it is higher. On the contrary, when broods are dispersed in space, the risk of all of them not surviving is lower (Rausher 1979, Gall 1984). Similarly, in cooperative breeder beetle (Ambrosia beetles, Coleoptera) females delay their dispersal or never disperse in order to help with the dependable juveniles, in order to raise colony fitness (Peer and Taborski2007). Therefore, unlike species that survive over multiple reproductive cycles and can thus disperse between reproductive episodes even when carrying for their young , in insects breeding dispersal (in this case, Figure 1 strategy d) is unlikely to co-occur with brood care.

3.3.2. Oviposition and risk-spreading

However, unlike earwigs, maternal care is lacking in the majority of insect species (with exception of social insects, of course). Consequently, females tend to invest in finding a good oviposition place rather than guarding the eggs. Insect populations are frequently spatially structured and search for a good site may involve dispersal to other patches. Patch quality is determined by resource abundance, density of con-specific, predators, and expected environmental variability in general. Therefore, dispersal within oviposition period (Figure 1 strategy d) may be favored. For instance, for female A. aegypty (Diptera), a mosquito of great epidemiological importance for human population, finding such good oviposition sites increases larval survival (Scheneket al. 2004, Santos De Abreu 2015). In both natural and urban environments, these females exhibit behaviour called ‘skip oviposition’, where they oviposit at different places during dispersal as a form of risk-spreading., In some cases less eggs are deposited in sites already containing con-specific eggs (Reiter 2007), thus avoiding resource competition. A female would lay about 40% of its eggs in the best suitable site (‘favorite site’), and distribute the rest over varying number of other sites (Santos De Abreu 2015). It is not clear weather this is a strategy to reduce offspring competition or to spread the risk of survival in often ephemeral oviposition sites. However, the dispersal and oviposition behaviour seem to be plastic in order to increase offspring fitness. Similar behaviour is reported for many beetles living in unstable environments (Wright 1983, Ferro 1991, Hanks 1998), moths (Ulagaray 1974, Andrews 1980, Rhainds and Kettela 2013), butterflies (Chew and Robbins 1984, Gilbert and Singer 1975, Bergman and Landin 2002, Sei 2008), damselflies (Purse et al. 2003) and others. Furthermore, such risk-spreading strategy via offspring distribution may be favored as long as benefits of doing so override the cost. For instance mayflies (Beatis, Ephemeroptera) have different oviposition strategies along the river, such as simply ovipositing on the water while others include dispersing to find suitable sites under rocks where egg survival depends on water level variations (flooding of the eggs). Despite having the highest mortality risk for the female (due to predation), the strategy of ovipositing single egg under different rocks at different locations, is the most favored one because the offspring survival is the highest with this strategy (Peckarsky et al. 2000, Encalada and Peckarsky 2007). In other cases it is not just the suitable oviposition site, but also the competition reduction among offspring that promotes egg distribution via dispersal. For instance, female *Epiphyas postvittana* moths do not have any specific oviposition host since neonate larvae are dispersive as well and can find suitable hosts on their own. Therefore, egg distribution by mated females is primarily means to reduce competition among kin and to spread the risk in offspring survival rather than to secure suitable host plant (Gu and Danthanarayana 1992, Suckling and Brockerhoff 2010). Similarly, mated females of spruce budworm moth (*Choristoneura fumiferana*) oviposit around 50% of their eggs in the natal patch and then do emigrate to deposit the rest of offspring elsewhere (Rhainds and Kettela 2013). Such strategy, is a perfect example of risk-spreading and it is likely that emigration of females is a function of local density, since emigration is not observed from less populated patches (Greenbank 1973).

Our individual-based model indeed shows (Lakovic et al. 2015) that offspring distribution across different patches is a superior strategy for kin competition reduction compared to natal dispersal. This risk-spreading strategy corresponds to the strategy (d) in Figure 1, where a female mates and leaves part of its offspring in the natal patch prior to emigration and the rest in another patch. This, strategy may have been adopted by insects that live in ephemeral or unstable habitats, such as mosquitoes and mayflies or those that experience high intra-specific competition at adult phase (i.e. for oviposition sites). Finally, such strategy may be more common in species where offspring care is lacking, since females abandon their eggs and continue oviposition elsewhere.

It is often very difficult to identify the exact moment of dispersal, and previous examples show that many species across different insect groups tend to oviposit while on the move. Therefore, current concepts and approaches that are much rooted in the metapopulation paradigm and the idea of discrete habitat patches may not always be the best concept.

4. Mating timing

Often enough adult stages are very short lived (few days to week), confiding mating, ovipostion and dispersal events to short time windows. However, the sequence of these events greatly affects the population dynamics. As females do not just disperse their own genes, but potentially those of a mating partner(s) via fertilized eggs, the timing of mating before or after dispersal has consequences on gene flow between populations and presumably local adaptation. Potential benefit of mating prior to dispersal (strategies c and d in Figure 1), is that a mated female can spread genes of a related male to a new gene pole and that it secures mating and thus reproduction when colonizing new (empty) habitats. For instance cabbage white butterfly *Pieris rapae crucivora*, occupies agricultural fields. Such environments are fluctuating and with frequent extinction and colonization events, due to farmer treatments. Mating in this species takes place before dispersal, while oviposition occurs in a new distant patch but also during dispersal phase (Ohsaki 1981, Hirota 2004). Such *r*-strategic species that colonize new habitats should rather mate in the natal patch in order to secure reproduction. Mating in the natal patch is characteristic for many insects species, such as sulfur butterfly (Watanabe & Nakanishi, 1996), mayfly (Caudill, 2003), spider mites (Li & Margolies, 1994) and others mentioned in the previous section. Additionally, in many moth species, such as European pine shoot moth and spruce budworm, virgin females rarely fly and rather wait to be mated in the natal patch (Green and Pointing 1962, Greenbank 1973, Rhainds and Kettela 2013).

Mating timing has received much attention especially when studying evolution of resistance genes in pest species (Mazzi and Dorn 2012). It seems that post-dispersal mating in bt-crop resistant insects can slow the spread of resistance genes if the gene is recessive and inheritance classical dominant-recessiveness (Reardon and Sappington 2007, Dalecky et al. 2006, Dunley and Croft 1992). For instance, resistant females that mate with a non resistant male will produce heterozygous (non-resistant) offspring that will later (given they survive due to lack of resistance) have to mate with either heterozygous or recessive individuals in order to produce some resistant phenotypes in the next generation. In contrast, from the pest species perspective, mating prior to emigration with resistant male is beneficial, because after successful dispersal they can produce homozygous resistant offspring that will survive on bt-crops and be able to spread the genes in the new population.

Mating after dispersal (Figure 1 strategies a and b) can improve offspring fitness if inbreeding risk is high (Pussey and Wolf 1996) or when local adaptation is important (Lakovic et al. 2017). Therefore, for some species mating after dispersal seems to be a rather obligatory strategy. For instance, common green lacewing *Chrysoperla carnea* (Neuroptera) individuals emigrate right after emergence, therefore females mate and reproduce after dispersal in the new patch. They can disperse multiple times and distribute their offspring over different patches. This ‘nomadic’ strategy seem to be means to secure survival in unpredictable, cultivated environments (Duelli 1984).

On the contrary to this rather obligatory lacewing behaviour, some species exhibit different mating and dispersal strategies (strategy b and c in Figure 1) at the population level. Such are, for instance, parasitoids from Trichogramma genus. These species are quasi-gregarious as their hosts occur in aggregations, however only one individual develops within a single host. Additionally, they are haplo-diploid, that is unfertilized eggs will produce males, while fertilized eggs will give rise to females. Females from *T. minutum* display certain fraction of virgin and mated females dispersal. Fraction of unmated females that disperse is lower than that in mated, and it may be a consequence of a failure to find a mate or it could be age related since peaks for dispersal of both mated and unmated females are at about same time. However, the study suggest that there might be a genetic predisposition for off-patch (post-dispersal) mating that would allow more gene exchange between different sub-populations (Martel & Boivin 2004). In general, for many parasitoids, low inbreeding risk and low possibility to find a mate after dispersal are the factors selecting for local mating prior to emigration. On the other hand, emergence in single-sex brood or when inbreeding risk is high will select for post-dispersal mating.

Many studies infer that mating after dispersal can arise as consequence of a failure to find a mate in the natal patch (Schumacher et a. 1997). On the other hand, harassment by males can lead to dispersal (of already mated) females. For instance, immature and unmated dragonflies that forage for food are often harassed by males, that frequently results in dispersal (Conrad et al. 1999). Similarly, the same can happen to mated females searching for oviposition sites (Brunzzel 2002). Harassment by males may also indicate high population density in a patch, and thus ultimate benefits of dispersal would be kin-competition avoidance in the current and future generation as well.

Finally, if a female emigrates because it does not find a mate then this is a signal for negative density-dependent emigration and possibly the explanation for observing such trends in some species. Yet this will only be a good strategy if in general females are likely to find other habitats where populations are denser. For mated females the expectation is clearly for positive-density dependent emigration as long as density indicates increased competition (and not e.g. high patch quality).

4.1. Mating status and age effect

In general, it is often difficult to disentangle effect of age and mating status on dispersal. For instance, female butterflies such as *Pieris rapae* enclose with few mature eggs and are more dispersive (Chew and Robbins 1984). On the contrary, in other species females emerge with high proportion of mature eggs and may not be able to disperse before mating and at least partial oviposition (i.e. *Euphydryas editha*). The questions is, whether individual readiness for dispersal is rather driven by the egg-load and mating status for instance, or by age per se (hormonal processes). Some studies report a negative correlation of dispersiveness with aging in female moths, where they experience reduction in certain enzyme activity as they get older (Collatz and Wilps 1986). However, others suggest that females are more mobile with age. For instance, Maritime ringlet butterfly females (*Coenonympha nipisiquit* McDunnough) lay most of the eggs in the natal patch however some eggs are laid in other patches, presumably because older females are more mobile and tend to disperse out of there natal patch (Sei 2008). Similarly, woodland brown butterfly, *Lopinga achine* females become more mobile with age, that is, on average females will disperse after laying 2/3 of their eggs in the natal patch (Bergman and Landin 2002).

Whether adult female's propensity to disperse increases with age or with decreasing egg-load remains poorly explained in insect dispersal research. Additionally, to gather information about habitat quality also takes time that may postpone dispersal at a later point during the season. However, regardless of the underlying mechanisms, it seems that dispersal in adult female stages tends to occur at a later time within their life cycle that corresponds to strategy (d) in Figure 1.

5. Male perspective

Selective forces for dispersal may differ for adult males and females as a consequence of different roles in the reproduction process. Male’s primary role is to find and mate with females. While females role is the same in that respect, she additionally has to invest resources into egg production and later energy and time into oviposition. However, the extent of these differences will depend on the species-specific reproductive strategy. Therefore, to further understand dispersal of a species, we need to know these reproductive strategies, that is whether a species is monogamous, monadrous, polyandrous, polygynous, semelparous or iteroparous (Deputi and Massol 2013). Unfortunately, details of these strategies are often not well known in insects. Additional difficulty in understanding reproductive biology of many insects is the existence of mechanisms, such as sperm competition, sperm precedence and displacement, that are reported for many Lepidoptera and Odonata species (Simons 1986). This is especially important in the context of dispersal and mating timing, where a female can mate multiple times in different patches but ultimately only few males will fertilize the eggs. Hence, a species may be polyandrous (females mate with multiple males) yet mechanisms such as sperm precedence can secure that the eggs are fertilized only by the first mated male. (Simons 1986 or some, check Chapter 3). Some studies report male’s role in securing his reproductive success, such as first sperm precedence, marking a female as ‘mated’ (Tram and Wolfner 1998), or harming a female in such a way that it cannot mate again (Stutt and Siva-Jothy 2001). Others, however, demonstrate females to be responsible for sperm removal after copulation, sperm storing or sperm randomization (LaMunyon and Eisner 1993, Simmons 2001). For example, polyandrous females can mate after emergence to secure the fertilization of their eggs, however, after dispersing in a new patch they might remove the sperm from previous male in order to mate with a (locally) better adapted one or to avoid inbreeding effects. These different mechanisms in securing reproductive success may result in different reproductive behaviours with potential consequences for dispersal. For instance, males may invest in sperm production (qualitatively or quantitatively) or in mating frequency. Both male strategies might select against male dispersal, where in the first one males should acquire more resources into sperm production, while in the second one they should invest into mating with as many females as possible. Interesting study of broad-horned flour beetle (*Gnatocerus cornutus*) has shown a trade-off between weapons (horns) on the one hand and dispersal and testis sizes, on the other. Males of this species are highly territorial and they fight with their mandibles (‘horns’) for the territory. However, sperm competition can often take place because females can mate with multiple males (polyandry). And indeed, Yemen et al. (2010) found that males either invest into horn development (long mandibles) or into wing and testis size that ultimately changes their mating strategy. More specifically, longer horns would allow them to out-compete other males and secure a territory, where they can mate with many females. These males have shorter wings because they do not need to fly in search for mates or resources, and also have smaller testis sizes because they mate with many females (sometimes multiple times with the same female) that secures them reproduction (in terms of sperm competition). On the other hand, males with short horns have bigger wings because they need to fly in search for females. Additionally, they have bigger testis size that increases their ejaculatory expenditure and secure their reproduction success when sperm competition is present. These differences may arise as a consequence of habitat conditions. For instance, high population density indicates strong competition for territory but also numerous females for mating, therefore a ‘winning’ strategy may be a dispersive male (avoiding competition) with big testis sizes (for sperm competition because in high densities females will have a lot of mates).

Many insect studies, show that male insects tend to be more phylopatric than females (Bergman and Landin 2002, Simoes & Quartau 2007, Greenbank 1973, Bohonak and Jenkins 2003, Caudilii 2003, Bierinckx et al. 2006) that may be the consequence of the mating system. Hirota (2004 and 2005) suggest that monandry and pre-dispersal mating should lead to female-biased dispersal because females mate at the natal patch and spread the offspring elsewhere – and thus the males' genes – while males stay at home and invest only in mating with as many females as possible. On the contrary, when females are polyandrous with last male sperm precedence, then there is no such bias in dispersal between the two sexes as females would typically not transfer the males' genes into a new gene pool.

Therefore, sex biased dispersal should occur when cost and benefits of dispersal differ between the two sexes and mating strategy can often be underlying cause. However, failure to find a mate is often enough driver of male dispersal (Gu and Danthanarayana 1992, Schumacher et al. 1997). Nonetheless, female-biased dispersal seems to be more frequent in insect taxa. For instance mayfly (Ephemeroptera) males swarm in order to attract mates, hence they have to invest all their energy into the mating process rather than into dispersal (Caudilii 2003). And indeed, female-biased dispersal, seems to be a general trend for mayflies, precisely due to the mating system (Flecker et al. 1988, Hershey et al. 1993 check , Caudilli 2003 for more). The same is observed for damselflies (see review in Bierinckx et al. (2006). Their meta-analysis shows that female biased dispersal predominates in damselflies as a consequence of behavioral differences between sexes during maturation and foraging. Territorial male Odonata are less dispersive compared to females; however, immature adults may emigrate prior to acquiring territory (Bohonak and Jenkins 2003). This is similar to behaviour of many birds, where males compete to secure a territory while females disperse (Greenwood 1980). In such mating system, males seem to be time minimizers and females energy maximizers. Therefore, for a male dragonfly frequent visits to a breeding site and frequent copulations will maximize reproductive success, while females will do so by investing in eggs/offspring via enhanced resource acquisition (Bierinckx et al. (2006). Higher resource acquisition may include increased foraging and mobility among females that potentially lead to emigration to another patch(es).

Dragonflies indeed provide a telling example of the effect that mating strategy has on dispersal and fitness. Namely, mate guarding is something characteristic for Odonata where, due to the potential sperm displacement, a males guards the female after copulation to secure its own reproductive success. Guarding can be tandem (male and female connected), non-contact (male follows a female) or no guarding at all. During tandem guarding, the risk from other male harassment or re-mating is the lowest (Fincke et al. 1997). The study of Schenk (2004) shows that tandem guarded females (*Pantala Flavescens* and *Sympetrum Fonscolombii*) spread their offspring over different habitat patches (risky behaviour but risk lowered by guarding) while non guarded females laid eggs locally. These species oviposits in all kind of aquatic habitats that are often ephemeral, hence spreading the offspring seems to reduce the risk on entirely unsuccessful reproduction.

6. Conclusions

This chapter provides a general overview of dispersal differences in insects regarding sex, mating strategy and environmental variability. The review indicates that dispersal is a complex process depending on wide array of additional life-history traits (morphology, habitat type, diet, seasonality and others). Indeed, dispersal syndromes that result from co-evolution of dispersal and other life history traits can be used as proxy to predict dispersal (distance, propensity and between patch gene flow): an excellent paper by Stevens et al. (2012) describes such syndromes for European butterflies, providing insights for future research and conservation. Butterflies have indeed received much attention in dispersal research (Hanski 2006, Baguette 1996, Stevens 2012, Legrand et al. 2014) and consequently there are many reviews about general patterns of butterfly dispersal.

Unfortunately, such comprehensive studies on other insect taxa are still lacking. In particular, informations are often enough too inaccurate to serve as tests cases for the general theoretical expectations I formulated at the beginning of the chapter.

Although dispersal research has received much attention in the past decades, improvement of the in-field methods for more precisely gathering relevant data, together with predictive models and computer simulations, should be used to provide more general understanding of insect dispersal in the context of life history traits.

Chapter 6

General Discussion and Conclusions

Previous chapters of this thesis evaluate the importance of mating and dispersal timing and information acquisition when studying the evolution of emigration decisions. The results indicate that insects can adapt the timing of their dispersal and mating strategies in order to increase their fitness. First we show that breeding dispersal (dispersal between two consequent reproductions) and offspring distribution across different habitat patches is a form of risk-spreading to reduce the variance in offspring survival and kin competition (Chapter 2). Our competition scenarios further show that such strategy indeed performs better and always out-competes natal dispersal, in unstable environments and when population sizes are small. Second, we show that in less tolerant species, living in heterogeneous environments, females may evolve a post-dispersal mating strategy, which in turn preserves local adaptation at the landscape level (Chapter 3). Chapter 4 further demonstrates that informed (adult) dispersal should occur later in the life-cycle as individuals need time to collect information about their habitat, given that they did not have the opportunity to collect the information at the larval stage. Given these interesting findings from our simulation experiments, it is astonishing how little literature there is on the topic of dispersal and mating timing, both in theoretical and empirical research. Therefore, Chapter 5 of this thesis provides an overview, that is based on the scarce (mostly empirical) literature. insect dispersal strategies in the context of emigration and mating timing and information acquisition.

1. The role of information and timing

Insects are a diverse group, however, most of them have larval stages that usually have quite different life styles than the adult stage (i.e. Holometabola, Hemimetabola), in regard to morpho-physiology, diet, and even habitat preferences. Therefore, informed dispersal can occur at larval or adult stage, given that the individual has the opportunity to collect relevant information about the habitat. Chapter 2 and 4 of this thesis, show that informed natal dispersal may not be the rule, in particularly in species where larvae have no access to the relevant information about their habitat.

Some studies show that maternal or juvenile/larval (in spiders Bonte et al. 2007, and lizards by Massot and Clobert 1995) experience has an effect on dispersal propensity, that can be seen as a form of informed dispersal. Low resource investment from mothers into eggs on the one hand, or lack of food or harsh competition and predation during the juvenile phase, on the other hand, may be good indicators of a 'bad' patch conditions and should provide sufficient motivation for informed emigration. On the contrary, in certain insect groups larval stages develop completely isolated from the external environment, or at least isolated from con-specifics. For instance, parasitic larvae of seeds or other animals feed and stay encapsulated until their emergence into adults. For these species information about habitat conditions and in particular about possible intra-specific competition is not available before emergence. Therefore if they are to make an informed dispersal decision they need time to collect such information. And this is a point often overlooked, especially by theoreticians that mostly assume informed natal dispersal right after emergence, which is clearly not possible for species with a life-cycle as just explained. Clearly, information collection by adults cannot be obtained instantaneously but occurs over the time during the patch exploration, via direct encounters with other individuals or with their reproductive output (i.e. eggs). Indeed Chapter 4 shows, that species with such life-cycles (uninformed larvae) should evolve strategies where emigration occurs sometimes in the mid-season after individuals have 'learned' about their habitat patch in parallel to ongoing reproductive activities (egg laying). Consequently, as insect adult stages tend to be rather short-lived (days or weeks) the timing of events, such as dispersal, can have profound effect on net gene flow and (meta-)population dynamics.

Particularly important aspect of dispersal timing is its occurrence in regard to mating and reproduction. Figure 1 from Chapter 5 outlines the plausible dispersal strategies of females in this context. If a female is making informed dispersal decision, then her emigration might happen only later in the season (Chapter 4), in particular if the emerging larvae is yet uninformed as explained above. However, the probability that such a female will mate and even oviposit in the natal patch increase with time; it would obviously not make much sense for a short-lived female to render reproductive opportunities, e.g. when finding a suitable mate or oviposition site. Indeed, reproductive stages of insects are usually short lived and tend to mate within hours after emergence. Therefore, mating and oviposition may occur across different patches, which is indeed true for many insects (see Chapter 5). Mating in the natal patch prior to emigration would be beneficial in species that are colonizing new habitats and therefore, risk ending up in an unsuitable habitat. However, in heterogeneous environments where populations are locally adapted it may be not the best strategy to mate in the natal patch prior to dispersal (Chapter 3). In particularly, in species with narrow habitat niches, females should mate after dispersal with locally adapted male in order to increase offspring fitness. On the contrary, in species with wide tolerance ranges we should observe rather opposite, where females mate prior to dispersal and then distribute genes of their kin. Nonetheless, many insect species are polyandrous where females mate with multiple males. However, if a female mates with multiple males, it is not obvious which one will father the eggs, especially when there are mechanisms of sperm manipulation involved. More specifically, a female can mate in the natal patch but use sperm removal mechanism to remove this sperm after it has found a better mate in the new patch. However, in other species first males' sperm is the one that fertilizes the eggs. Therefore, when we think about polyandry, that is indeed the most common strategy in insects (Arnqvist and Nilsson 2000), the question is whether some of the above mentioned mechanisms are involved. In this respect, mating timing (i.e. before or after dispersal) in insects has received very little attention and additionally it is quite difficult to study in the field especially for non monogamous species. Mating prior to emigration would benefit the most individuals that disperse into an empty habitat where there are no possible mates. These are possibly, species that occupy unpredictable and ephemeral habitats where extinction and colonizations are frequent. On the other hand, when local adaptation is important (i.e. in heterogeneous landscapes), mating should take place after dispersal with locally adapted individuals in order to increase offspring fitness.

In the light of the findings of this thesis, I would expect that natal dispersal should primarily occur in species that experience competition for space or resources during the larval phase compared to those where eggs are laid singly. On the contrary, density-dependent dispersal at the adult stage should typically occur later within the reproductive phase , indicating that this is rather breeding dispersal. As a risk spreading strategy (offspring distribution across several patches) that also most efficiently reduces kin-competition (Chapter 2) promotes breeding dispersal anyways, both arguments combine to predict (delayed), but favor informed dispersal later in the reproductive season for species that cannot collect information in the larval phase. Finally, mating before dispersal should be selected in species that colonize new habitats, while mating after dispersal should occur when local adaptation in important.

2. Dispersal research: Problems and perspectives in integration of empirical and theoretical approaches

2.1. Methods in dispersal research

Studying insect dispersal in natural environment is often challenging (Nathan 2001), given their small size, great numbers and high mobility. Additionally, most of the mobile stages are short lived, completing their life cycle within a few days or weeks. Finally, insects frequently occupy ephemeral habitats that appear and disappear in short periods of time that can be difficult to track. Nonetheless, scientists continue to perfect already established methods and invent new ones to track animal dispersal. These methods can be direct, such as describing the actual movement or individual mark-recapture experiments, or indirect methods, that include behavioral observations, mass mark-recapture, trapping, genetic markers, scanning and vertical radar (Turchin 1998, Osborne et al. 2002). However, a general consensus in dispersal research is missing, for instance the area covered in these, especially in mark-recapture studies, is often insufficient and therefor the interpretations must to be taken with caution. A study by Franzen & Nilsson (2007) suggests that a minimum area of 50 km^2 with large population of marked individuals and preferably 500 recaptures, is necessary when investigating dispersal of insects. Moreover, often enough researches interpret degree of mobility within a patch, as dispersal, although it does not necessary lead to inter-patch movement and gene flow. It may be intuitive to assume that more mobile individuals have higher chances of dispersal, that is often not shown explicitly and must be taken with care. Nonetheless, today we have artificial systems such as the Metatron in France, that are designed especially for studying dispersal in fragmented landscapes (Legrand et al. 2012). Such vast experimental enclosures in semi-controlled conditions, allow scientist a detailed examination of dispersal, something that may often be too complicated to achieve in the field.

Additionally, modeling dispersal allows extrapolation of small scale observation data to large scale patterns. On the other hand, computer simulations, such as individuals-based models used in this thesis, can further disentangle the influence of different factors on dispersal evolution over long periods of time (Grimm 2005). Additional problem is when studying evolution of this dispersal is the one regarding genes and heritability of genes behind it. It is not trivial to determine which genes are responsible for evolution of dispersal, how they correlate with other dispersal related traits, and finally what is the mode of inheritance. However, for behavioral ecologist it is often more important to understand what forces shape the evolution of a trait (the phenotype) regardless of the underlying genetic architecture however, it must be taken with caution, particularly in regard to epigenetics and behavioral inheritance systems. For instance, trans-generational epigenetic effects, seem to module fast range expansion in a mite (maternally induced dispersal, Van Petegen et al. 2015).

Finally, the choice of which method to apply largely depends on questions we want answer and on life-history of the organism that we study. In this particular case, the timing when dispersal takes place in the individuals life, i.e. as larvae or adult, prior to or post mating, remains poorly investigated by the empiricist and largely overlooked by the theoreticians.

2.2. Theoretical vs field studies

The discrepancy between theoretical advancement on understanding dispersal evolution and empirical research remains large as a result of, predominantly duration related, difficulties associated with studying evolution of dispersal experimentally (Duputie and Massol 2013). Nonetheless, at least in microcosm, a growing number of experimental studies provide further insights into evolution of dispersal and range expansions (Fronhofer et al. 2015). Additional issue may be the lacking consensus on how to investigate evolution of dispersal empirically. For instance, what are the main issues to focus on, what kind of data should be collected and over what period of time. Perhaps the most important is a general understanding of the life-cycle of species in question. In particularly, how to accurately estimate timing of (repeated) matings and/or (repeated) dispersal events. Additionally, we need to understand how information about patch quality and/or competition can be collected. Finally, documenting landscape heterogeneity in space and time at scales relevant to the organism in question.

Evolution of dispersal is often driven by multiple factors interacting in complex ways, that is impossible to study analytically. Hence, computer simulations, such as individual based model, used in this thesis, may be a valuable tool to disentangle such complexity. Growing number of such studies describe interesting phenomena that, unfortunately, are rarely tested by empiricists in the field. On the other hand, ample of ecological data collected over the decades, should be accounted for in theoretical studies. The joint work of theoretician and empiricist is the most efficient way of deepening our understanding of any ecological and evolutionary process.

3. Applied dispersal research

There are many important areas where theory and data must be united, such as conservation and biological control (for pest or invasive species). Man made changes to natural ecosystems drives some species towards extinction and leaves many confined to spatially fragmented, and often isolated, populations. Therefore, when planing reintroductions or dispersal corridors, we need data on biology and ecology of the species in question, that we can use to build predictive models and consequently develop efficient conservation strategies. For instance, when introducing aquatic insect taxa into streams where they were previously extinct, e.g. due to chemical pollution, it is important to know the mode of dispersal (and its timing) that will contribute to the recolonization. Many studies show that local oviposition and upstream larval dispersal to be successful in recolonization (Wiliams and Hyens 1976), whereas the process is slower when the recolonization requires movement of fecund females. (Petersen 1999). Therefore, in order to successfully reintroduce certain species, we have to acknowledge that dispersal might occur at different stages, and also timing during those stages that may greatly influence the outcome of our effort.

Agriculture and intensified land use that created fragmented landscape is largely responsible for leaving so many species endangered and in need for conservation. However, when it comes to pest species there is also an economic dimension that affects farmers directly. There is a growing number of both empirical and theoretical studies on the topic of evolution of resistance genes and dispersal timing (Caprio 2001, Dalecky et al. 2006). Clearly, intensified use of pesticides and later GMO crops against pest species has driven the evolution of resistance and its spread in these species. Many recent studies on how to impede the spread of these genes within agricultural landscapes point out the importance of dispersal timing (particularly post-dispersal mating) between resistant and wild populations.

4. Conclusions

In conclusion, this doctoral thesis provides evidence on the importance of timing and information acquisition when studying evolution of dispersal. In particularly, it highlights the relevance of understanding a species life-history, especially in terms of mating behaviour and biology when studying evolution of insect dispersal. More specifically, theoretical models about informed dispersal typically assume natal dispersal However we show that such strategy may not be the best strategy, in particular for insect species where the life-history excludes the ability to collect information during the larval phase. Additionally it is largely overlooked that breeding dispersal and offspring distribution, as form of a risk-spreading strategy, may arise in informed individuals. Furthermore, the timing of mating that has clear consequences for local adaptation in heterogeneous environments, has received little attention. Finally, this thesis will hopefully provide incentives for empirical studies of dispersal to address questions in a way that should contribute to general scientific advancement as well as to improving conservation efforts.

References

Abreu, F. V. S. de, Morais, M. M., Ribeiro, S. P., Eiras, A. E. 2015. Influence of breeding site availability on the oviposition behaviour of Aedes aegypti. Memórias do Instituto Oswaldo Cruz 110 (5), 669-676.

Achmann, R. et al. 1992. Last male sperm precedence in the bushcricket *Poecilimon veluchianus* (Orthoptera, Tettigonioidea) demonstrated by DNA fingerprinting. Molecular Ecology 1, 47-54.

Albrectsen, B. and Nachman, G. 2001. Female-biased density-dependent dispersal of a tephritid fly in a fragmented habitat and its implications for population regulation. -Oikos 94: 263–272.

Almohamad, R., Verheggen, F.J., Francis, F., Lognay, G., Haubruge, E., 2010. Assessment of oviposition site quality by aphidophagous hoverflies: reaction to conspecific larvae. Animal Behaviour 79, 589–594.

Amarasekare, P., 1998. Interactions between local dynamics and dispersal: insights from single species models. Theoretical Population Biology 53 (1), 44-59.

Andrews, K. L., Barnes, M. M., Josserand, S. A. (1980). Dispersal and oviposition by navel orangeworm moths. Environmental Entomology, 9 (5), 525-529.

Arnqvist, G., Nilsson, T., 2000. The evolution of polyandry: multiple mating and female fitness in insects. Animal Behaviour 60, 145–164.

Atkinson, W. D., 1979. A field investigation of larval competition in domestic Drosophila. The Journal of Animal Ecology, 91-102.

Austin, J. D. et al. 2003. Genetic evidence for female-biased dispersal in the bullfrog, *Rana catesbeiana* (Ranidae): Female-biased dispersal in bullfrogs. Molecular Ecology 12, 3165–3172.

Bach, L.A., Thomsen, R., Pertoldi, C., Loeschcke, V., 2006. Kin competition and the evolution of dispersal in an individual-based model. Ecological Modelling 192, 658–666.

Bach, L.A., Ripa, J., Lundberg, P., 2007. On the evolution of conditional dispersal under environmental and demographic stochasticity. Evolutionary Ecology Research 9, 663–673.

Baguette, M., Convié, I., Nève, G. (1996). Male density affects female spatial behaviour. Acta Oecologica, 17(3), 225-232.

Baguette M. and Van Dyck H., 2007. Landscape connectivity and animal behavior: Functional grain as a key determinant for dispersal. Landscape Ecology 22, 1117–1129.

Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M., Turlure, C., 2013. Individual dispersal, landscape connectivity and ecological networks. Biological Reviews, 88 (2), 310-326.

Basskett M.L. 2012. Dispersal, evolution of. In: Hastings A. and Gross L. J. (ed.), Encyclopedia of theoretical ecology. University of California Press, pp 192–198.

Beaver, R.A., 1974. Intraspecific competition among bark beetle larvae (Coleoptera: Scolytidae). The Journal of Animal Ecology, pp.455-467.

Beirinckx, K., Van Gossum, H., J Lajeunesse, M., R Forbes, M., 2006. Sex biases in dispersal and philopatry: insights from a meta-analysis based on capture–mark–recapture studies of damselflies. Oikos 113, 539–547.

Bengtsson, B. O. 1978. Avoiding inbreeding: at what cost? Journal of Theoretical Biology 73, 439-444.

Benton T. G. and Grant A. 2000. Evolutionary fitness in ecology: Comparing measures of fitness in stochastic, density-dependent environments. Evolutionary ecology research 2, 769–789.

Berdahl et al. 2015.On the evolutionary interplay between dispersal and local adaptation in heterogeneous environments. Evolution 69, 1390–1405

Bergman, K.-O., Landin, J., 2002. Population structure and movements of a threatened butterfly (*Lopinga achine*) in a fragmented landscape in Sweden. Biological Conservation 108, 361–369.

Beverton R.J. and Holt S.J. 1957. On the dynamics of exploited fish populations. Fishery Investigations 19, Ministry of Agriculture, Fisheries and Food.

Bilton, D.T., Freeland, J.R., Okamura, B., 2001. Dispersal in freshwater invertebrates. Annual review of ecology and systematics 32, 159–181.

Blanquart, F. et al. 2012. The effects of migration and drift on local adaptation to a heterogeneous environment. Journal of Evolutionary Biology 25, 1351–1363.

Blanquart, F. and Gandon, S. 2014. On the evolution of migration in heterogeneous environments. Evolution 68, 1617–1628.

Blum, M. 2012. Sexual selection and reproductive competition in insects. - Elsevier.

Boer den P. J., 1968. Spreading of risk and stabilization of animal numbers. Acta Biotheoretica 18: 165–194.

Boer den P. J., 1990. The survival value of dispersal in terrestrial arthropods. Biological Conservation 54, 175–192.

Boggs, C. L. 1986. Reproductive strategies of female butterflies: variation in and constraints on fecundity. Ecological Entomology 11, 7–15.

Boggs C. L. and Watt W. B. 1981. Population structure of pierid butterflies. IV. Genetic and physiological investment in offspring by male Colias. Oecologia 50, 320-324.

Boggs, C. L. (1995). Male nuptial gifts: phenotypic consequences and evolutionary implications. Insect reproduction, 215-242.

Bohonak, A. J., Jenkins, D. G., 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. Ecology Letters 6, 783–796.

Bonte, D., Van Belle, S., Maelfait, J.-P., 2007. Maternal care and reproductive state-dependent mobility determine natal dispersal in a wolf spider. Animal Behaviour 74, 63–69.

Bonte, D., Travis, J. M., De Clercq, N., Zwertvaegher, I., Lens, L. 2008. Thermal conditions during juvenile development affect adult dispersal in a spider. Proceedings of the National Academy of Sciences 105, 17000–17005.

Bonte D., Van Dyck H.,Bullock J., Coulon A., Delgado M., Gibbs M. et al. 2012. Costs of dispersal. Biological Reviews 87: 290–312.

Boulinier, T., Danchin, E., 1997. The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. Evolutionary Ecology 11, 505–517.

Bowler D. E. and Benton T. G., 2005. Causes and consequences of animal dispersal strategies: Relating individual behaviour to spatial dynamics. Biological Reviews 80: 205–225.

Bray, Y., Devillard S., Mauvy, B., Péroux, R., 2007. Natal dispersal of European hare in France. Journal of Zoology 273, 426–434.

Brunzel, S., 2002. Experimental density-related emigration in the cranberry fritillary Boloria aquilonaris. Journal of insect behavior 15, 739–750.

Cadet, C. et al. 2003. The evolution of dispersal under demographic stochasticity. The American Naturalist 162, 427–441.

Capinera, J.L., Barbosa, P., 1976. Dispersal of first-instar gypsy moth larvae in relation to population quality. Oecologia 26, 53–60.

Caprio, M. A. 2001. Source-sink dynamics between transgenic and non-transgenic habitats and their role in the evolution of resistance. Journal of Economic Entomology 94, 698–705.

Caudill, C. C., 2003. Measuring dispersal in a metapopulation using stable isotope enrichment: high rates of sex-biased dispersal between patches in a mayfly metapopulation. Oikos 101, 624–630.

Chaianunporn, T. and Hovestadt, T. 2012. Concurrent evolution of random dispersal and habitat niche width in host-parasitoid systems. Ecological Modelling 247, 241–250.

Charnov, E. L., 1976. Optimal foraging, the marginal value theorem. Theoretical population biology 9, 129–136.

Chew, F. S., Robbins, R. K., 1984. Egg-laying in butterflies. The biology of butterflies. Academic Press, London 65–79.

Chust, G., Villarino, E., Chenuil, A., Irigoien, X., Bizsel, N., Bode, A., ... Hoarau, G. 2016. Dispersal similarly shapes both population genetics and community patterns in the marine realm. Scientific reports, 6.

Clobert, J., Le Galliard, J. F., Cote, J., Meylan, S., Massot, M., 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12, 197–209.

Clobert J., Baguette M., Benton T. G., Bullock J. M., 2012. Dispersal ecology and evolution. Oxford University Press.

Conrad, K. F., Willson, K. H., Harvey, I. F., Thomas, C. J., Sherratt, T .N., 1999. Dispersal characteristics of seven odonate species in an agricultural landscape. Ecography 524–531.

Conrad, K. F., Willson, K. H., Whitfield, K., Harvey, I. F., Thomas, C.J., Sherratt, T.N., 2002. Characteristics of dispersing *Ischnura elegans* and *Coenagrion puella* (Odonata): age, sex, size, morph and parasitism. Ecography 25, 439–445.

Cowie, R. J. and Krebs, J. R., 1979. In: Population Dynamics (Anderson, R. M., Turner, B. D. & Taylor, L. R. eds). Oxford: Blackwell Scientific, 183-206.

L. R. eds). pp. 183-206, Oxford: Blackwell Scientific.

Collatz, K. G. and Wilps, H. 1986. Aging of flight mechanism. Insect Aging (ed. by K. G. Collatz and R. S. Sohal), pp. 55-72. Springer, Berlin

Dalecky, A., Ponsard, S., Bailey, R. I., Péllissier, C., Bourguet, D., 2006. Resistance Evolution to Bt Crops: Predispersal Mating of European Corn Borers. PLoS Biology 4, e181.

Danchin, E., Boulinier, T., Massot, M., 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79, 2415–2428.

Davies, C.R., Gilbert, N., 1985. A comparative study of the egg-laying behaviour and larval development of *Pieris rapae L.* and *P. brassicae L.* on the same host plants. Oecologia 67, 278–281.

DeMeester, N. and Bonte, D., 2010. Information use and density-dependent emigration in an agrobiont spider. Behavioral Ecology 21, 992–99.

Denno, R. F. and Peterson, M. A., 1995. Density-dependent dispersal and its consequences for population dynamics. In: Cappuccino N. and Price P.W.

(eds.), Population dynamics: New approaches and synthesis. San Diego (CA), Academic Press.pp, 113–130

Dieckmann U., O'Hara B., Weisser W., 1999. The evolutionary ecology of dispersal. Trends in Ecology and Evolution 14, 88–90.

Diss, A. L., Kunkel, J. G., Montgomery, M. E., Leonard, D. E., 1996. Effects of maternal nutrition and egg provisioning on parameters of larval hatch, survival and dispersal in the gypsy moth, Lymantria dispar L. Oecologia 106, 470–477.

Doak, P. 2000. Population consequences of restricted dispersal for an insect herbivore in a subdivided habitat. Ecology 81, 1828–1841.

Dobson, F. S. 1982 Competition for mates and predominant juvenile male dispersal in mammals. Animal Behavior 30, 1183–1192.

Doligez, B., Danchin, E., Clobert, J., Gustafsson, L., 1999. The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. Journal of Animal Ecology 68, 1193–1206.

Doligez, B., Gustafsson, L., Part, T., 2009. 'Heritability' of dispersal propensity in a patchy population. Proceedings of the Royal Society B: Biological Sciences 276, 2829–2836.

Donaldson-Matasci, M.C., Bergstrom, C.T., Lachmann, M., 2010. The fitness value of information. Oikos 119, 219–230.

Driscoll, D. A., Banks, S. C., Barton, P. S., Ikin, K., Lentini, P., Lindenmayer, D. B., Evans, M. J. (2014). The trajectory of dispersal research in conservation biology. Systematic review. PLoS ONE 9 (4), e95053.

Duckworth, R. A., 2008. Adaptive dispersal strategies and the dynamics of a range expansion. The American Naturalist, 172 (S1), S4-S17.

Duelli, P., 1984. Dispersal and opposition strategies in Chrysoperla carnea. Progress in world's neuropterology: proceedings of the 1st International Symposium on Neuropterology in Graz, Austria: (Insecta, Megaloptera, Raphidioptera, Planipennia).

Duffey, E. 1998. Aerial dispersal in spiders. Proceedings of the 17th European Colloquium of Arachnology, 1937: 187–191.

Dukas, R., 2008. Evolutionary Biology of Insect Learning. Annual Review of Entomology 53, 145–160.

Dunley, J. E., Croft, B. A., 1992. Dispersal and gene flow of pesticide resistance traits in phytoseiid and tetranychid mites. Experimental & applied acarology 14, 313–325.

Duplouy A., Ikonen S., Hanski I., 2013. Life history of the glanville fritillary butterfly in fragmented versus continuous landscapes. Ecology and Evolution 3, 5141–5156.

Duputie, A., Massol, F., 2013. An empiricist's guide to theoretical predictions on the evolution of dispersal. Interface Focus 3 (6), 20130028–20130028.

Encalada, A.C., Peckarsky, B.L., 2007. A comparative study of the costs of alternative mayfly oviposition behaviors. Behavioral Ecology and Sociobiology 61, 1437–1448.

Enfjäll K. and Leimar O. 2005. Density-dependent dispersal in the glanville fritillary, *MelitaeaCinxia*. Oikos 108: 465–472.

Enfjäll, K., Leimar, O., 2009. The evolution of dispersal - the importance of information about population density and habitat characteristics. Oikos 118, 291–299.

Ferro, D.N., Tuttle, A.F., Weber, D.C., 1991. Ovipositional and flight behavior of overwintered Colorado potato beetle (Coleoptera: Chrysomelidae). Environmental Entomology 20, 1309–1314.

Fincke, O.M., Waage, J.K., Koenig, W.D., Choe, J.C., Crespi, B., 1997. Natural and sexual selection components of odonate mating patterns. The evolution of mating systems in insects and arachnids 58, 74.

Flecker, A. S., Allan, J. D., McClintock, N. L. (1988). Male body size and mating success in swarms of the mayfly Epeorus longimanus. Ecography, 11(4), 280-285.

Fonseca, D.M. and Hart, D.D., 1996. Density-dependent dispersal of black fly neonates is mediated by flow. Oikos 75, 49–58.

Franzén, M., & Nilsson, S. G., 2007. What is the required minimum landscape size for dispersal studies?. Journal of Animal Ecology 76(6), 1224-1230.

Fronhofer, E. A., Kubisch, A., Hilker, F. M., Hovestadt, T., & Poethke, H. J., 2012. Why are metapopulations so rare?. Ecology *93* (8), 1967-1978.

Fronhofer, E. A., Klecka, J., Melián, C. J., Altermatt, F., 2015. Condition-dependent movement and dispersal in experimental metacommunities. Ecology letters, *18*(9), 954-963.

Frouz, J. and Kindlmann, P., 2001. The role of sink to source re-colonization in the population dynamics of insects living in unstable habitat: Example of terrestrial chirnomids. Oikos 93, 50–58.

Gall, L.F., 1984. Population structure and recommendations for conservation of the narrowly endemic alpine butterfly, Boloria acrocnema (Lepidoptera: Nymphalidae). Biological conservation 28, 111–138.

Gandon, S., Michalakis, Y., 1999. Evolutionarily stable dispersal rate in a metapopulation with extinctions and kin competition. Journal of Theoretical Biology 199, 275–290.

Gandon S. 1999. Kin competition, the cost of inbreeding and the evolution of dispersal. Journal of Theoretical Biology 200: 345–364.

Gibbs, M., Lace, L.A., Jones, M.J. and Moore, A.J., 2004. Intraspecific competition in the speckled wood butterfly *Pararge aegeria*: effect of rearing density and gender on larval life history. Journal of Insect Science, 4(1).

Gilbert, L.E., Singer, M.C., 1975. Butterfly ecology. Annual Review of Ecology and Systematics 6, 365–395.

Gillespie J. H., 1977. Natural selection for variances in offspring numbers: A new evolutionary principle. The American Naturalist 111, 1010–1014.

Green, G.W. and Pointing, P.J., 1962. Flight and Dispersal of the European Pine Shoot Moth, *Rhyacionia buoliana* (Schiff.) II. Natural Dispersal of Egg-laden Females1. The Canadian Entomologist, 94(3), pp.299-314.

Greenbank, D. O. (1973). The dispersal process of spruce budworm moths. Fredericton, NB. Information Report M-X-39. 24 p.

Greenwood P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28, 1140–1162.

Greenwood, P.J., Harvey, P.H., 1982. The natal and breeding dispersal of birds. Annual review of ecology and systematics 13, 1–21.

Grimm, V., and Railsback, S. F., 2005. Individual-based modeling and ecology. Princeton: Princeton university press.

Gros, A., Hovestadt T., Poethke, H. J., 2008. Evolution of sex-biased dispersal: The role of sex-specific dispersal costs, demographic stochasticity, and inbreeding. - Ecol Model 219: 226–233.

Gu, H., Danthanarayana, W., 1992. Quantitative genetic analysis of dispersal in Epiphyas postvittana. I. Genetic variation in flight capacity. Heredity 68, 53–60.

Gutiérrez, D., Thomas, C.D., León-Cortés, J.L., 1999. Dispersal, distribution, patch network and metapopulation dynamics of the dingy skipper butterfly (Erynnis tages). Oecologia 121, 506–517.

Gyllenberg, M., Kisdi, E, Utz, M., 2008. Evolution of condition-dependent dispersal under kin competition. Journal of Mathematical Biology 57, 285–307.

Haag, C.R., Saastamoinen, M., Marden, J.H., Hanski, I., 2005. A candidate locus for variation in dispersal rate in a butterfly metapopulation. Proceedings of the Royal Society B: Biological Sciences 272, 2449–2456.

Hamilton W.D. and May R.M. 1977. Dispersal in stable habitats. Nature 269, 578–581.

Hanks, L.M., Millar, J.G., Paine, T.D., 1998. Dispersal of the eucalyptus longhorned borer (Coleoptera: Cerambycidae) in urban landscapes. Environmental Entomology 27, 1418–1424.

Hanski, I., Kouki, J., & Halkka, A., 1993. Three explanations of the positive relationship between distribution and abundance of species. Species diversity in ecological communities: historical and geographical perspectives, 108-116.

Hanski, I., Pakkala, T., Kuussaari, M., & Lei, G., 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. Oikos, 21-28.

Hanski, I., 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos, 209-219.

Hanski, I., and Gaggiotti, O. E. (Eds.) 2004. Ecology, genetics, and evolution of metapopulations. Academic Press.

Hanski, I., Saastamoinen, M., Ovaskainen, O., 2006. Dispersal-related life-history trade-offs in a butterfly metapopulation. Journal of Animal Ecology, 75(1), 91-100.

Hansson L., 1991. Dispersal and connectivity in metapopulations. Biological Journal of the Linnean Society 42, 89–103.

Hastings, A., 1983. Can spatial variation alone lead to selection for dispersal? Theoretical Popululation Biology 24, 244-251.

Hatano, E., Kunert, G., Weisser, W. W., 2010. Aphid Wing Induction and Ecological Costs of Alarm Pheromone Emission under Field Conditions. PLoS ONE 5, e11188.

Hebert, P. D. (1983). Egg dispersal patterns and adult feeding behaviour in the Lepidoptera. The Canadian Entomologist, 115(11), 1477-1481.

Hendrick P. W. 2009. Genetics of populations, 4th Edition. Jones and Bartlett Publishers.

Hershey, A. E., Pastor, J., Peterson, B. J., & Kling, G. W. (1993). Stable isotopes resolve the drift paradox for Baetis mayflies in an arctic river. Ecology, 74(8), 2315-2325.

Hill J. K., Thomas C. D., Lewis O. T., 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: Implications for metapopulation structure. Journal of Animal Ecology 65, 725–735.

Hirota, T., 2005. The effect of female polyandry and sperm precedence on the evolution of sexual difference in dispersal timing: The evolution of sex-biased dispersal. Journal of Evolutionary Biology 18, 1395–1402.

Hirota, T., 2004. The evolution of sex-biased dispersal by pre-dispersal copulation and fluctuating environment. Journal of Animal Ecology 73, 1115–1120.

Holmes, E. E., and Wilson, H. B., 1998. Running from trouble: long-distance dispersal and the competitive coexistence of inferior species. The American Naturalist, 151 (6), 578-586.

Honda, K., 1995. Chemical basis of differential oviposition by lepidopterous insects. Archives of insect biochemistry and physiology 30, 1–23.

Hopper K. R., 1999. Risk-spreading and bet-hedging in insect population biology. Annual Review of Entomology 44: 535–560.

Hovestadt T. and Nieminen M., 2009. Costs and benefits of dispersal in butterflies. In: Settele J., Shreeve T., Konvicka M., Van Dyck H. (eds.), Ecology of butterflies in Europe. Cambridge University Press, Cambridge, pp 97–106.

Hovestadt T., Kubisch A., Poethke H. J., 2010. Information processing in models for density-dependent emigration: A comparison. Ecological Modelling 221, 405–410.

Hovestadt, T., Mitesser, O., Poethke, H. J., 2014. Gender-Specific Emigration Decisions Sensitive to Local Male and Female Density. The American Naturalist 184, 38–51.

Janz, N., 2003. Evolutionary Ecology of Oviposition Strategies, in Chemoecology of Insect Eggs and Egg Deposition (eds M. Hilker and T. Meiners), Blackwell Publishing Ltd, Oxford, UK.

Jaumann, S., Snell-Rood, E.C., 2017. Trade-offs between fecundity and choosiness in ovipositing butterflies. Animal Behaviour 123, 433–440.

Johst, K., Brandl, R., 1997. Evolution of dispersal: the importance of the temporal order of reproduction and dispersal. Proceedings of the Royal Society of London B: Biological Sciences 264, 23–30.

Klopfer, P. H., & Ganzhorn, J. U., 1985. Habitat selection: behavioral aspects, in: Habitat selection in birds (ed. M. L. Cody). Academic Press Orlando, Florida, 435-453.

Kubisch A., Fronhofer, E. A., Poethke, H. J., Hovestadt, T., 2013. Kin competition as a major driving force for invasions. - The Am. Nat. 181: 700-706.

Kuefler, D., Haddad, N.M., Hall, S., Hudgens, B., Bartel, B., Hoffman, E., 2008. Distribution, Population Structure and Habitat Use of the Endangered Saint Francis Satyr Butterfly, Neonympha Mitchellii Francisci. The American Midland Naturalist 159, 298–320.

Kuno, E., 1981. Dispersal and the persistence of populations in unstable habitats: A theoretical note. Oecologia 49, 123–126.

Kuussaari, M., Nieminen, M., Hanski, I., 1996. An experimental study of migration in the glanville fritillary butterfly *MelitaeaCinxia*. Journal of Animal Ecology, 791–801.

Lakovic, M., Poethke, H.-J., Hovestadt, T., 2015. Dispersal Timing: Emigration of Insects Living in Patchy Environments. PLOS ONE 10, e0128672.

Lakovic, M., Mitesser, O., Hovestadt T., 2017. Mating timing, dispersal and local adaptation in patchy environments. Oikos (in press)

LaMunyon, C. W. and Eisner, T., 1993. Post-copulatory sexual selection in an arctiid moth (*Utetheisa ornatrix*).Proceedings of the National Academy of Sciences 90, 4689-92.

Legrand, D., Guillaume, O., Baguette, M., Cote, J., Trochet, A., Calvez, O., Le Galliard, J. F., 2012. The Metatron: an experimental system to study dispersal and metaecosystems for terrestrial organisms. *Nature methods* 9(8), 828-833.

Legrand, D., Trochet, A., Moulherat, S., Calvez, O., Stevens, V.M., Ducatez, S., Clobert, J., Baguette, M., 2015. Ranking the ecological causes of dispersal in a butterfly. Ecography 38, 822–831.

Legros, M., Lloyd, A.L., Huang, Y. and Gould, F., 2009. Density-dependent intraspecific competition in the larval stage of *Aedes aegypti* (Diptera: Culicidae): revisiting the current paradigm. Journal of medical entomology, 46(3), pp.409-419.

Levin, S. A., Cohen, D., Hastings, A., 1984. Dispersal strategies in patchy environments. Theoretical Population Biology 26, 165–191.

Levins R., 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15, 237–240.

Lewontin, R.C. and Cohen, D., 1969. On population growth in a randomly varying environment. Proceedings of the National Academy of Sciences of the United States of America 62, 1056–1060.

Li, J., and Margolies, D. C. (1994). Responses to direct and indirect selection on aerial dispersal behaviour in T*etranychus urticae*. Heredity, 72(1), 10-22.

Martel, V., Boivin, G., 2004. Premating Dispersion in the Egg Parasitoid Trichogramma (Hymenoptera: Trichogrammatidae). Environmental Entomology 33, 855–859.

Massol, F., Debarre, F., 2015. Evolution of dispersal in spatially and temporally variable environments: The importance of life cycles: Dispersal evolution and life cycles. Evolution 69, 1925–1937.

Massot, M., and Clobert, J., 1995. Influence of maternal food avilability on offspring dispersal. Behavioral ecology and sociobiology 37 (6), 413-418.

Massot, M., Clobert, J., & Ferriere, R., 2008. Climate warming, dispersal inhibition and extinction risk. Global Change Biology, *14* (3), 461-469.

Mazzi, D. and Dorn, S., 2012. Movement of insect pests in agricultural landscapes. Annals of Applied Biology, 160 (2), pp.97-113.

McNair, J. N., 1982. Optimal giving-up times and the marginal value theorem. The American Naturalist, 119 (4), 511-529.

McNamara, J. M., & Houston, A. I., 1987. Memory and the efficient use of information. Journal of theoretical biology, 125 (4), 385-395.

McNamara, J.M., Dall, S.R.X., 2010. Information is a fitness enhancing resource. Oikos 119, 231–236.

McPeek, M. A. and Holt, R. D. 1992. The Evolution of Dispersal in Spatially and Temporally Varying Environments. The American Naturalist 140, 1010-1027.

Matthysen, E., 2005. Density-dependent dispersal in birds and mammals. Ecography 28, 403–416.

Mehrparvar, M., Zytynska, S.E., Weisser, W.W., 2013. Multiple Cues for Winged Morph Production in an Aphid Metacommunity. PLoS ONE 8, e58323.

Messina, F. J., & Renwick, J. A. A., 1985a. Ability of ovipositing seed beetles to discriminate between seeds with differing egg loads. Ecological Entomology, 10(2), 225-230.

Messina, Frank J., and J. A. A. Renwick, 1985b. "Mechanism of egg recognition by the cowpea weevil *Callosobruchus maculatus*. Entomologia experimentalis et applicata 37.(3),241-245.

Mestre, L. and Bonte, D., 2012. Food stress during juvenile and maternal development shapes natal and breeding dispersal in a spider. Behavioral Ecology 23, 759–764.

Metz, J.A. and Gyllenberg, M., 2001. How should we define fitness in structured metapopulation models? Including an application to the calculation of evolutionarily stable dispersal strategies. Proceedings of the Royal Society B: Biological Sciences 268, 499–508.

Moerkens, R., Leirs, H., Peusens, G., Gobin, B., 2010. Dispersal of single- and double-brood populations of the European earwig, Forficula auricularia: a mark-recapture experiment: Dispersal of Forficula auricularia in orchards. Entomologia Experimentalis et Applicata 137, 19–27.

Mole, S., Zera, A.J., 1993. Differential allocation of resources underlies the dispersal-reproduction trade-off in the wing-dimorphic cricket, Gryllus rubens. Oecologia 93, 121–127.

Motro U. 1991. Avoiding inbreeding and sibling competition—the evolution of sexual dimorphism for dispersal.—The American Naturalists 137: 108–115.

Nagy, M., Heckel, G., Voigt, C. C., Mayer, F., 2007. Female-biased dispersal and patrilocal kin groups in a mammal with resource-defense polygyny. - Proceedings of Royal Society of London: Biological Sciences 274, 3019–3025.

Nathan, R., 2001. The challenges of studying dispersal. Trends in Ecology & Evolution 16, 481–483.

Nowicki P. and Vrabec V. 2011. Evidence for positive density-dependent emigration in butterfly metapopulations. Oecologia 167, 657–665.

Ohsaki, N., 1980. Comparative population studies of three Pieris butterflies, *P. rapae*, *P. melete* and *P. napi*, living in the same area. Researches on Population Ecology 22, 163–183.

Olsson, M. and Shine, R., 2003. Female-biased natal and breeding dispersal in an alpine lizard, *Niveoscincus microlepidotus*. Biological Journal of Linnean Society 79, 277–283.

Osborne, J. L., Loxdale, H. D., Woiwod, I. P,. 2002. Monitoring insect dispersal: methods and approaches. Dispersal ecology 24-49.

Parker G., 1979. Sexual selection and sexual conflict. In: Sexual selection and reproductive competition in insects. Blum M. S. and Blum N. A. (ed.), New York: Academic Press, pp. 123–166.

Peckarsky, B.L., Taylor, B.W., Caudill, C.C., 2000. Hydrologic and behavioral constraints on oviposition of stream insects: implications for adult dispersal. Oecologia 125, 186–200.

Parvinen, K. and Egas, M. 2004. Dispersal and the evolution of specialisation in a two-habitat type metapopulation. Theoretical Population Biology 66, 233–248.

Peddle, S., De Groot, P., and Smith, S.,2002. Oviposition behaviour and response of *Monochamus scutellatus* (Coleoptera: Cerambycidae) to conspecific eggs and larvae. Agricultural and Forest Entomology, 4 (3), 217–222.

Peer, K., Taborsky, M., 2007. Delayed dispersal as a potential route to cooperative breeding in ambrosia beetles. Behavioral Ecology and Sociobiology 61, 729–739.

Perrin, N., Mazalov, V., 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. The American Naturalist 155, 116–127.

Perrin, N., Mazalov, V., 1999. Dispersal and Inbreeding Avoidance. The American Naturalist 154, 282–292.

Petersen, I., Winterbottom, J. H., Orton, S., Friberg, N., Hildrew, A. G., Spiers, D. C., 1999. Emergence and lateral dispersal of adult Plecoptera and

Trichoptera from Broadstone Stream, UK. Freshwater Biology *42* (3), 401-416.

Poethke, H.J. and Hovestadt, T., 2002. Evolution of density-and patch-size-dependent dispersal rates. Proceedings of the Royal Society B: Biological Sciences 269, 637–645.

Poethke, H.J., Hovestadt, T., Mitesser, O., 2003. Local extinction and the evolution of dispersal rates: causes and correlations. The American Naturalist 161, 631–640.

Poethke, H.J., Pfenning, B., Hovestadt, T., 2007. The relative contribution of individual and kin selection to the evolution of density-dependent dispersal rates. Evolutionary Ecology Research 9, 41–50.

Poethke, H. J., Gros, A., & Hovestadt, T., 2011. The ability of individuals to assess population density influences the evolution of emigration propensity and dispersal distance. Journal of Theoretical Biology, 282(1), 93-99.

Purse, B.V., Hopkins, G.W., Day, K.J., Thompson, D.J., 2003. Dispersal characteristics and management of a rare damselfly. Journal of Applied Ecology 40, 716–728.

Ponchon, A., Garnier, R., Grémillet, D., Boulinier, T., 2015. Predicting population responses to environmental change: the importance of considering informed dispersal strategies in spatially structured population models. Diversity and Distributions 21, 88–100.

Powers, K. S., & Aviles, L. (2003). Natal dispersal patterns of a subsocial spider *Anelosimus cf. jucundus* (Theridiidae). Ethology, 109(9), 725-737.

Pusey, A E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends in Ecology and Evolution 2, 295-299.

Pusey, A. E. and Wolf, M. (1996). Inbreeding avoidance in animals. Trends in Ecology and Evolution 11(5), 201-206.

Quiring, D.T. and McNeil, J.N., 1984. Exploitation and interference intraspecific larval competition in the dipteran leaf miner, Agromyza frontella (Rondani). Canadian Journal of Zoology, *62* (3), pp.421-427.

R Development Core Team (2008). 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.

Rausher, M. D. (1979). Larval habitat suitability and oviposition preference in three related butterflies. Ecology, 60(3), 503-511.

Rausher, M. D., 1983. Ecology of host-selection behavior in phytophagous insects. Vol. 223, Academic Press, New York.

Raitanen, J., Forsman, J.T., Kivelä, S.M., Mäenpää, M.I., Välimäki, P., 2014. Attraction to conspecific eggs may guide oviposition site selection in a solitary insect. Behavioral Ecology 25, 110–116.

Reardon, B.J., Sappington, T.W., 2007. Effect of Age and Mating Status on Adult European Corn Borer (Lepidoptera: Crambidae) Dispersal from Small-Grain Aggregation Plots. Journal of Economic Entomology 100, 1116–1123.

Reiskind, M.H., Wilson, M.L., 2004. *Culex restuans* (Diptera: Culicidae) oviposition behavior determined by larval habitat quality and quantity in southeastern Michigan. Journal of Medical Entomology 41, 179–186.

Reiter, P., 2007. Oviposition, Dispersal, and Survival in Aedes aegypti: Implications for the Efficacy of Control Strategies. Vector-Borne and Zoonotic Diseases 7, 261–273.

Renou M. Pheromones and General Odor Perception in Insects. In: Mucignat-Caretta C, editor. Neurobiology of Chemical Communication. Boca Raton

(FL): CRC Press/Taylor & Francis; 2014. Chapter 2. Available from: https://www.ncbi.nlm.nih.gov/books/NBK200986/

Rhainds M., Gries G., Chew P. S., 1997. Adaptive significance of density-dependent ballooning by bagworm larvae, *Metisaplana* (Walker) (Lepidoptera: Psychidae). The Canadian Entomologist 129, 927–931.

Rhainds M., Shipp L., Woodrow L., Anderson D., 2005. Density, dispersal, and feeding impact of western flower thrips (Thysanoptera: Thripidae) on flowering Chrysanthemum at different spatial scales. Ecological Entomology 30, 96–104.

Rhainds, M., Kettela, E.G., 2013. Oviposition Threshold for Flight in an Inter-Reproductive Migrant Moth. Journal of Insect Behavior 26, 850–859. doi:10.1007/s10905-013-9400-x

Roff, D.A., 1986. The evolution of wing dimorphism in insects. Evolution 1009–1020.

Ronce, O., Gandon, S., Rousset, F., 2000. Kin selection and natal dispersal in an age-structured population. Theoretical population biology 58, 143–159.

Ronce, O. (2007). How does it feel to be like a rolling stone? Ten questions about dispersal evolution. Annual Review of Ecology, Evolution and Systematics *38*, 231-253.

Rousset F. 2002. Inbreeding and relatedness coefficients: what do they measure? Heredity 88, 371–380.

Rouquette, J. R. and Thompson, D. J., 2007. Patterns of movement and dispersal in an endangered damselfly and the consequences for its management: Movement and dispersal in a damselfly. Journal of Applied Ecology 44, 692–701.

Ruf D., Dorn S., Mazzi D., 2011. Females leave home for sex: Natal dispersal in a parasitoid with complementary sex determination. Animal Behaviour 81, 1083–1089.

Ruxton, G. D., & Rohani, P., (1999). Fitness-dependent dispersal in metapopulations and its consequences for persistence and synchrony. Journal of Animal Ecology, 68(3), 530-539.

Saastamoinen, M., 2007. Mobility and lifetime fecundity in new versus old populations of the Glanville fritillary butterfly. Oecologia 153, 569–578.

Schenk, K., Suhling, F., Martens, A., 2004. Egg distribution, mate-guarding intensity and offspring characteristics in dragonflies (Odonata). Animal Behaviour 68, 599–606.

Schjørring, S., 2002. The evolution of informed natal dispersal: inherent versus acquired information. Evolutionary Ecology Research 4, 227–238.

Schmidt, K.A., Dall, S.R.X., van Gils, J.A., 2010. The ecology of information: an overview on the ecological significance of making informed decisions. Oikos 119, 304–316.

Schumacher, P., Weyeneth, A., Weber, D.C., Dorn, S., 1997. Long flights in *Cydia pomonella L.*(Lepidoptera: Tortricidae) measured by a flight mill: influence of sex, mated status and age. Physiological Entomology 22, 149–160.

Scott, D. E., 1994. The effect of larval density on adult demographic traits in *Ambystoma opacum*. Ecology, 75(5), 1383-1396.

Sei, M., 2009. Flight and Oviposition Behavior of the Adult Maritime Ringlet (*Coenonympha nipisiquit McDunnough*) Females in Response to Microhabitat. Journal of Insect Behavior 22, 87–100.

Shaw M. J. P. (1970). Effect of population density on alienocolae of Aphis fabae Scop. I. The effect of crowding on the production of alatae in the laboratory. Annals of Applied Biology 65, 191–196.

Simmons, L. W., 1986. Female choice in the field cricket *Gryllus bimaculatus* (De Geer). Animal Behaviour 34 (5), 1463-1470.

Simmons, L. W., 2001. Sperm competition and its evolutionary consequences in the insects. - Princeton University Press.

Sinervo, B., and Clobert, J. 2003. Morphs, dispersal behavior, genetic similarity, and the evolution of cooperation. Science, 300 (5627), 1949-1951.

Smith, D. A., 1984. Mate selection in butterflies. Competition, coyness, choice and chauvinism. - In Vane-Wright R. I. and Ackery P. R. (eds.), The biology of butterflies. Academic Press, London, pp. 225-244.

Smith, J. M., 2000. The concept of information in biology. Philosophy of science 67, 177–194.

Smith, R. L., 2012. Sperm competition and the evolution of animal mating systems. Elsevier.

Stutt, A. D. and Siva-Jothy, M. T. 2001. Traumatic insemination and sexual conflict in the bed bug *Cimex lectularius*. Proceedings of the National Academy of Sciences 98, 5683–5687.

Stevens, V.M., Trochet, A., Blanchet, S., Moulherat, S., Clobert, J., Baguette, M., 2013. Dispersal syndromes and the use of life-histories to predict dispersal. Evolutionary Applications 6, 630–642.

Stevens, V.M., Trochet, A., Van Dyck, H., Clobert, J., Baguette, M., 2012. How is dispersal integrated in life histories: a quantitative analysis using butterflies: Dispersal life-history correlates. Ecology Letters 15, 74–86.

Stevens, V.M., Whitmee, S., Le Galliard, J.-F., Clobert, J., B?hning-Gaese, K., Bonte, D., Brändle, M., Matthias Dehling, D., Hof, C., Trochet, A., Baguette, M., 2014. A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals. Ecology Letters 17, 1039–1052.

Suckling, D.M., Brockerhoff, E.G., 2010. Invasion Biology, Ecology, and Management of the Light Brown Apple Moth (Tortricidae). Annual Review of Entomology 55, 285–306.

Sutherland, O.R.W., 1969. The role of the host plant in the production of winged forms by two strains of the pea aphid, *Acyrthosiphon pisum*. Journal of Insect Physiology 15, 2179–2201.

Szymkowiak, P., Górski, G., Bajerlein, D., 2007. Passive dispersal in arachnids. Biological letters 44, 75–101.

Takasu, K., & Hirose, Y., 1988. Host discrimination in the parasitoid *Ooencyrtus nezarae*: the role of the egg stalk as an external marker. Entomologia experimentalis et applicata 47(1), 45-48.

Taylor, P. D., 1988. An inclusive fitness model for dispersal of offspring. Journal of Theoretical Biology 130, 363-378.

Thornhill, R. and Alcock, J., 1983. The Evolution of Insect Mating Systems. Harvard University Press, Cambridge, MA.

Topping, C. J. and Sunderland, K. D. 1998. Population dynamics and dispersal of *Lepthyphantes tenuis* in an ephemeral habitat. Entomologia Experimentalis et Applicata 87, 29–41.

Tram, U. and Wolfner, M. F. 1998. Seminal fluid regulation of female sexual attractiveness in *Drosophila melanogaster*. Proceedings of the National Academy of Sciences 95: 4051–4054.

Travis, J. M. and Dytham, C., 1998. The evolution of dispersal in a metapopulation: a spatially explicit, individual-based model. Proceedings of the Royal Society of London B: Biological Sciences 265, 17–23.

Travis M. J. and Dytham C., 1999. Habitat persistence, habitat availability and the evolution of dispersal. Proceedings Biological Sciences / The Royal Society 266, 723–728.

Travis, J. M., Murrell, D. J., & Dytham, C., 1999. The evolution of density–dependent dispersal. Proceedings of the Royal Society of London B: Biological Sciences *266* (1431), 1837-1842.

Turchin, P. 1998. Quantitative analysis of movement. Sinauer.

Tsumuki, H. Nagatsuka, H, Kawada, K. Kanehisa, K. 1990. Comparison of nutrient reservation in apterous and alate aphids, *Acyrthosiphon pisum* (Harris): 1. Developmental time and sugar content. Applied entolomogy and Zoology, 25 (2), 215-221

Ulagraj, S.M. 1975. Mole crickets ecology, behavior, and dispersal flight (Orthoptera: Gryllotalpidae: Scapteriscus). Environmental Entology 4, 265-273

Van Alphen, J.J., Bernstein, C., Driessen, G., 2003. Information acquisition and time allocation in insect parasitoids. Trends in Ecology & Evolution 18, 81–87.

Van Petegem, K. H., Pétillon, J., Renault, D., Wybouw, N., Van Leeuwen, T., et al., 2015. Empirically simulated spatial sorting points at fast epigenetic changes in dispersal behaviour. Evolutionary Ecology 29 (2), pp.299-310.

Veen, T. and Otto, S. P., 2015. Liking the good guys: amplifying local adaptation via the evolution of condition-dependent mate choice. Journal of Evolutionary Biology 28, 1804–1815.

Waage, J. K., 1979. Foraging for patchily-distributed hosts bye the parasitoid *Nemeritis canescens*. Journal of Animal. Ecology 48, 353 – 371

Wagner, R.H., Danchin, É., 2010. A taxonomy of biological information. Oikos 119, 203–209.

Waser P. M., Austad S. N., Keane B., 1986. When should animals tolerate inbreeding? The American Naturalist 128, 529.

Watanabe, M. & Nakanishi, Y., 1996. Population structure and dispersals of the sulfur butterfly *Colias erate* (Lepidoptera: Pieridae) in an isolated plain located in a cool temperate zone of Japan. Jpn. J. Syst. Entomol. 64, 17–29.

Wehner, R., Michel, B., Antonsen, P., 1996. Visual navigation in insects: coupling of egocentric and geocentric information. Journal of Experimental Biology 199, 129–140.

Williams D.D. and Hynes H.B.N., 1976. Stream habitat selection by aerially colonizing invertebrates. Canadian Journal of Zoology 54, 685-693.

Williams, K. S., & Gilbert, L. E., 1981). Insects as selective agents on plant vegetative morphology: egg mimicry reduces egg laying by butterflies. Science, 212 (4493), 467-469.

Wright, S.J., 1983. The Dispersion of Eggs by a Bruchid Beetle among Scheelea Palm Seeds and the Effect of Distance to the Parent Palm. Ecology 64, 1016–1021.

Yamane, T., Okada, K., Nakayama, S., Miyatake, T., 2010. Dispersal and ejaculatory strategies associated with exaggeration of weapon in an armed beetle. Proceedings of the Royal Society B: Biological Sciences 277, 1705–1710.

Zera, A., Cisper, G., 2001. Genetic and Diurnal Variation in the Juvenile Hormone Titer in a Wing? Polymorphic Cricket: Implications for the Evolution of

Life Histories and Dispersal. Physiological and Biochemical Zoology 74, 293–306.

Zedrosser A., Støen O., Sæebø S., Swenson J. E., 2007. Should I stay or should I go? Natal dispersal in the brown bear. Animal Behaviour 74, 369–376.

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Curriculum Vitae

Milica Lakovic
Department of Animal Ecology and Tropical Biology
Theoretical Evolutionary Ecology Unit
University of Würzburg
milica.lakovic@biozentrum.uni-wuerzburg.de

Education

University of Würzburg, Germany (2013-): PhD student

University of Ghent, Belgium (2011-2015): Master of Science in Biology

University of Novi Sad, Serbia (2006-2011): Bachelor with honours in Ecology

University of Aveiro, Portugal (2009-2010): Exchange student

University of Sophia Anipolis, Nice, France (2009): Practical placement for students

Extracuricular activities

'ICTP - SAIFR: School on Physics Applications in Biology' (2016, Sao Paulo, Brazil)

'ICTP - SAIFR: V summer school of mathematical biology' (2016, Sao Paulo, Brazil).

9th Workshop 'Ecological modelling across disciplines' (2014, Göttingen, Germany)

Workshop 'Dispersal evolution in a community context' (2014, field station Fabrickschleichach, University of Würzburg, Germany)