Beyond metapopulation theory: Determinants of the dispersal capacity of bush crickets and grasshoppers

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Zusammenfassung

Zahlreiche Tierarten sind mehr und mehr vom Aussterben bedroht. Hauptursachen dafür sind die Zerstörung und Fragmentierung von Lebensraum durch den Menschen. Mit der anthropogenen Landnutzung sind vielfältige, negative Auswirkungen auf die betroffenen Tierpopulationen verbunden. Das langfristige Überleben und die Stabilität von räumlich strukturierten Populationen in fragmentierten Landschaften hängen dabei wesentlich von der Besiedlung von Habitatflächen, sowie dem Individuenaustausch und dem damit verbundenen genetischen Austausch zwischen einzelnen Populationen ab. Das Ausmaß der Ausbreitung von Individuen zwischen einzelnen Habitatflächen wird dabei (i) durch die Ausbreitungsfähigkeit der betreffenden Tierart, als die Kombination physiologischer und morphologischer Faktoren, welche die Ausbreitung eines Individuums begünstigen, und (ii) von der Struktur der Landschaft, wie z.B. dem Matrix-Typ oder die räumliche Anordnung von Habitatflächen, bestimmt. Da die Fragmentierung von Lebensräumen und die Anzahl bedrohter Tierarten stetig zunehmen, ist ein umfassendes Verständnis der Ursachen und Konsequenzen der Ausbreitung essenziel für das Management natürlicher Populationen sowie für die Entwicklung effektiver Schutzmaßnahmen.

Eine gängige und sehr häufig angewandte Methode, Ausbreitung zu untersuchen, sind Fang-Wiederfang-Studien zum Laufverhalten einzelner Individuen. Dabei wird grundsätzlich davon ausgegangen, dass das Markieren und das Versetzen der Tiere keinerlei Einfluss auf deren Verhalten haben. Für die Analyse und Interpretation solcher Experimente ist es entscheidend, diesen Einfluss ausschließen zu können, da er die Effekte, die eigentlich untersucht werden sollen, überlagern kann. Kapitel 2 der vorliegenden Arbeit ist eine Fang-Wiederfang-Studie, die diese Annahme und damit den Einfluss des Versetzens auf das Laufverhalten der Blauflügelige Ödlandschrecke (*Oedipoda caerulescens*) untersucht. Wie sich zeigte, hat das Versetzen von Individuen auf eine geeignete, jedoch fremde Habitatfläche einen signifikanten Einfluss auf das Laufverhalten der versetzten Tiere. Versetzte Individuen legten größere Strecken zurück und zeigten ein geradlinigeres Bewegungsmuster als die Tiere, die genau an ihrem Fundort im „Heimathabitat“ wieder freigelassen wurden. Dieser Effekt war am ersten Tag nach der Freilassung der Versuchstiere am deutlichsten ausgeprägt, kann jedoch auch noch darüber hinaus anhalten. Die zurückgelegten Tagesstrecken der versetzten Individuen, die in eine ihnen unbekannte

Habitatfläche verbracht wurden, waren im Durchschnitt 50 % länger, als die der nichtversetzten Tiere. In Abhängigkeit von der Dauer eines Experiments führt dies zu erheblichen Unterschieden hinsichtlich der Nettostrecken, die insgesamt von versetzten und nicht versetzten Tieren zurückgelegt werden. Zusammenfassend lässt sich sagen, dass die in Kapitel 2 präsentierten Ergebnisse deutlich zeigen, dass in zukünftigen Untersuchungen des Laufverhaltens von Arthropoden bzw. deren Ausbreitung, der Effekt des Versetzens berücksichtigt werden muss. Studien, die diesen Einfluss ignorieren, können zu falschen Vorhersagen bezüglich des Ausbreitungsverhaltens, der Fähigkeit geeignetes Habitat zu detektieren oder der Habitatpräferenzen einer Art führen.

Neben direkter Beobachtung mittels Fang-Wiederfang-Methoden kommen auch genetische Methoden zur Anwendung, um das Ausbreitungsverhalten von Tieren zu untersuchen. Kapitel 3 beinhaltet Daten zur genetischen Struktur von Populationen der Zweifarbigen Beißschrecke (*Metrioptera bicolor*), einer Heuschreckenart mit ausgeprägtem Flügeldimorphismus. Die Untersuchung fand in einer räumlich strukturierten Landschaft statt, in der geeignete Habitatflächen verteilt in einer diversen Matrix von unterschiedlichen nicht-geeigneten Habitattypen vorliegen. Mit Hilfe von Mikrosatellitenmarkern wurde der Einfluss der geographischen Distanz und unterschiedlicher Matrixtypen auf die genetische Differenzierung von 24 lokalen Populationen von *M. bicolor* untersucht. Die Ergebnisse dieser Studie zeigen deutlich, dass der Isolationsgrad lokaler Populationen dieser Heuschreckenart wesentlich von der umgebenden Matrix abhängt. Wie sich zeigte, werden der Individuenaustausch und der damit verbundenen Genfluss zwischen den untersuchten Populationen wesentlich durch Wald und einen Fluss eingeschränkt, da das Vorhandensein dieser beiden Matrixtypen positiv mit dem Grad der genetischen Differenzierung zwischen den Populationen korrelierte. Zudem zeigte sich für eine Teilauswahl von Populationen, welche nur durch landwirtschaftlich genutzte Flächen und Siedlungen voneinander getrennt sind, eine signifikant positive Korrelation zwischen der paarweise berechneten genetischen und der geographischen Distanz zwischen zwei Populationen. Dies bedeutet eine größere Differenzierung der Populationen je weiter sie voneinander entfernt sind. Für den vollständigen Datensatz mit allen untersuchten Populationen, konnte dieser Zusammenhang nicht nachgewiesen werden. Am wahrscheinlichsten ist dies darauf zurück zu führen, dass der nachteilige Effekt von Wald und Fluss auf den Genfluss den Effekt der geographischen Distanz überlagert. Die Analysen in Kapitel 3 machen deutlich, dass sich verschiedene Matrixtypen unterschiedlich auf die Ausbreitung einer Art auswirken, und unterstreichen wie wichtig eine eingehende

Betrachtung der Matrixqualität für Metapopulationsstudien ist. Studien mit Fokus auf den unterschiedlichen Einfluss verschiedener Matrixtypen können wesentlich genauere Informationen zur Ausbreitungsfähigkeit einer Art liefern, als eine alleinige Analyse des isolierenden Effekts der räumlichen Trennung von Populationen. Gerade solche Informationen sind essentiell und nötig, um landschaftsorientierte Modelle für den Artenschutz verbessern zu können.

Zusätzlich zu dem unmittelbaren Einfluss der Struktur der Landschaft auf die realisierte Ausbreitung von Individuen (siehe Kapitel 3), kann Landschaft auch als evolutionärer Selektionsfaktor agieren, da sie Kosten und Nutzen der Ausbreitung bestimmt. Ein entsprechender Selektionsdruck sollte sich sowohl auf morphologische Merkmale und Verhaltensmerkmale eines Individuums als auch auf das Ausmaß, mit dem ein bestimmter Genotyp auf Variationen der Umwelt reagiert, auswirken. Kapitel 4 untersucht den Einfluss der Größe und der Isolation einer Habitatfläche, sowie der Habitatstabilität (in Form der Sanddynamik) auf die Thorax- und Flügellänge, als Maße für die Ausbreitungsfähigkeit, der Blauflügeligen Ödlandschrecke in einem Küstengebiet. Die vorliegende Studie zeigte deutliche, geschlechtsspezifische Effekte der Sanddynamik und der räumlichen Anordnung der Habitatflächen zueinander auf die untersuchten morphologischen Merkmalen. Mit zunehmender Flächengröße und abnehmender Habitatkonnektivität, waren die Männchen von *O. caerulescens* kleiner und hatten zudem kürzere Flügel. Männchen und Weibchen von instabilen Habitatflächen (gekennzeichnet durch eine hohe Sanddynamik) waren größer als die Individuen von stabileren Habitatflächen (geringerer Sanddynamik). Insgesamt machen die vorliegenden Ergebnisse deutlich, dass sowohl landschaftsbezogene als auch habitatflächenbezogene Umweltfaktoren für die individuelle Investition in ausreitungsrelevante, morphologische Merkmale von Bedeutung sind. Diese Ergebnisse stimmen mit den Vorhersagen theoretischer Modelle zur Evolution der Ausbreitung in Metapopulationen überein und liefern einen weiteren Nachweis dafür, dass ausbreitungsrelevante, morphologische Merkmale variieren und in kürzlich strukturierten Populationen einer Selektion unterliegen.

Die Ausbreitung eines Individuums ist mit unterschiedlichen Fitnesskosten verbunden. Dazu zählen zum Beispiel: Ein erhöhtes Predationsrisiko, energetische Kosten, das Risiko kein geeignetes Habitat zu finden, Kosten die mit der Ausbildung von ausbreitungsrelevanten Merkmalen verbunden sind, sowie Reproduktionskosten. Die Entscheidung, ob sich ein Individuum ausbreitet, sollte daher nicht zufällig erfolgen, sondern von dessen Entwicklungsstadium oder dessen physiologischer Konstitution, sowie von aktuellen Umweltbedingungen abhängen. Man spricht von einer kontextbezogene Ausbreitung, die zum Beispiel vom Geschlecht oder der Flügelmorphe eines Individuums abhängt. Ein Ungleichgewicht in der Ausbreitung verschiedener Geschlechter oder Morphen wird als *biased dispersal* bezeichnet. Für die Untersuchung von *biased dispersal* werden häufig Weibchen und Männchen oder sesshafte und sich ausbreitende Individuen einer Art morphologisch, physiologisch oder hinsichtlich ihres Verhaltens miteinander verglichen. Für einige Taxa, insbesondere Heuschrecken, liegen bislang nur wenige Studien zum *biased dispersal* in Form von Fang-Wiederfang-Experimenten (die auch wirklich Ausbreitung und keine Routinebewegungen einzelner Individuen untersuchen) oder genetischen Analysen vor. Allerdings sind gerade Informationen hierzu von großer Bedeutung, da zum Beispiel ein unentdecktes *biased dispersal* dazu führen kann, dass falsche Schlüsse aus den Ergebnissen genetischer Untersuchungen gezogen werden. Kapitel 5 der vorliegenden Dissertation untersucht das Auftreten von *biased dispersal* der Zweifarbigen Beißschrecke unter Verwendung eines kombinierten Ansatzes morphologischer und genetischer Analysen. Die hier präsentierten Ergebnisse zeigen nicht nur, dass makroptere Individuen aufgrund ihrer Morphologie prädestiniert für die Ausbreitung sind. Auch die genetischen Daten deuten an, dass sich makroptere Tiere stärker ausbreiten als mikroptere Tiere. Darüber hinaus besitzen innerhalb der Gruppe der makropteren Individuen Männchen eine bessere Ausbreitungsfähigkeit als Weibchen. Um die Flugfähigkeit von *M. bicolor* beurteilen zu können, wurden die morphologischen Daten der vorliegenden Untersuchung mit den Ergebnissen von Studien über *Locusta migratoria* and *Schistocerca gregaria* verglichen. Beide Arten sind für ihr sehr gutes Flugvermögen bekannt. Darauf basierend ist für maktoptere Individuen von *M. bicolor* eine gute Flugfähigkeit anzunehmen, wenn auch in natürlichen Populationen fliegende Tiere dieser Art nur selten beobachtet werden.

Summary

Habitat fragmentation and destruction due to anthropogenic land use are the major causes of the increasing extinction risk of many species and have a detrimental impact on animal populations in numerous ways. The long-term survival and stability of spatially structured populations in fragmented landscapes largely depends on the colonisation of habitat patches and the exchange of individuals and genes between patches. The degree of inter-patch dispersal, in turn, depends on the dispersal ability of a species (i.e. the combination of physiological and morphological factors that facilitate dispersal) and the landscape structure (i.e. the nature of the landscape matrix or the spatial configuration of habitat patches). As fragmentation of landscapes is increasing and the number of species is continuously declining, a thorough understanding of the causes and consequences of dispersal is essential for managing natural populations and developing effective conservation strategies.

In the context of animal dispersal, movement behaviour is intensively investigated with capture-mark-recapture studies. For the analysis of such experiments, the influence of marking technique, handling and translocation of marked animals on movement pattern is of crucial importance since it may mask the effects of the main research question. Chapter 2 of this thesis presents a capture-mark-recapture study investigating the effect of translocation on the movement behaviour of the blue-winged grasshopper *Oedipoda caerulescens*. Transferring individuals of this grasshopper species to suitable but unfamilliar sites has a significant influence on their movement behaviour. Translocated individuals moved longer distances, showed smaller daily turning angles, and thus their movements were more directed than those of resident individuals. The effect of translocation was most pronounced on the first day of the experiment, but may persist for longer. On average, daily moved distances of translocated individuals were about 50 % longer than that of resident individuals because they have been transferred to an unfamiliar habitat patch. Depending on experiment duration, this leads to considerable differences in net displacement between translocated and resident individuals. In summary, the results presented in chapter 2 clearly point out that translocation effects should not be disregarded in future studies on arthropod movement, respectively dispersal. Studies not controlling for possible translocation effects may result in false predictions of dispersal behaviour, habitat detection capability or habitat preferences.

Beside direct field observations via capture-mark-recapture methods, genetic markers can be used to investigate animal dispersal. Chapter 3 presents data on the genetic structure of populations of *Metrioptera bicolor*, a wing-dimorphic bush cricket, in a spatially structured landscape with patches of suitable habitat distributed within a diverse matrix of different habitat types. Using microsatellite markers, the effects of geographic distance and different matrix types on the genetic differentiation among 24 local populations was assessed. The results of this study clearly indicate that for *M. bicolor* the isolation of local populations severely depends on the type of surrounding matrix. The presence of forest and a river running through the study area was positively correlated with the extent of genetic differentiation between populations. This indicates that both matrix types severely impede gene flow and the exchange of individuals between local populations of this bush cricket. In addition, for a subsample of populations which were separated only by arable land or settlements, a significant positive correlation between pairwise genetic and geographic distances exists. For the complete data set, this correlation could not be found. This is most probably due to the adverse effect of forest and river on gene flow which dominates the effect of geographic distance in the limited set of patches investigated in this study. The analyses in chapter 3 clearly emphasize the differential resistance of different habitat types on dispersal and the importance of a more detailed view on matrix 'quality' in metapopulation studies. Studies that focus on the specific dispersal resistance of different matrix types may provide much more detailed information on the dispersal capacity of species than a mere analysis of isolation by distance. Such information is needed to improve landscape oriented models for species conservation.

In addition to direct effects on realised dispersal (see chapter 3), landscape structure on its own is known to act as an evolutionary selection agent because it determines the costs and benefits of dispersal. Both morphological and behavioural traits of individuals and the degree to which a certain genotype responds to environmental variation have heritable components, and are therefore expected to be able to respond to selection pressures. Chapter 4 analyses the influence of patch size, patch connectivity (isolation of populations) and sand dynamics (stability of habitat) on thorax- and wing length as proxies for dispersal ability of *O. caerulescens* in coastal grey dunes. This study revealed clear and sex-specific effects of landscape dynamics and patch configuration on dispersal-related morphology. Males of this grasshopper species were smaller and had shorter wings if patches were larger and less connected. In addition, both sexes were larger in habitat patches with high sand dynamics compared to those

in patches with lower dynamics. The investments in wing length were only larger in connected populations when sand dynamics were low, indicating that both landscape and patch-related environmental factors are of importance. These results are congruent with theoretical predictions on the evolution of dispersal in metapopulations. They add to the evidence that dispersal-related morphology varies and is selected upon in recently structured populations even at small spatial scales.

Dispersal involves different individual fitness costs like increased predation risk, energy expenditure, costs of developing dispersal-related traits, failure to find new suitable habitat as well as reproductive costs. Therefore, the decision to disperse should not be random but depend on the developmental stage or the physiological condition of an individual just as on actual environmental conditions (context-dependent dispersal, e.g. sex- and wing morph-biased dispersal). Biased dispersal is often investigated by comparing the morphology, physiology and behaviour of females and males or sedentary and dispersive individuals. Studies of biased dispersal in terms of capture-mark-recapture experiments, investigating real dispersal and not routine movements, and genetic proofs of biased dispersal are still rare for certain taxa, especially for orthopterans. However, information on biased dispersal is of great importance as for example, undetected biased dispersal may lead to false conclusions from genetic data. In chapter 5 of this thesis, a combined approach of morphological and genetic analyses was used to investigate biased dispersal of *M. bicolor*. The presented results not only show that macropterous individuals are predestined for dispersal due to their morphology, the genetic data also indicate that macropters are more dispersive than micropters. Furthermore, even within the group of macropterous individuals, males are supposed to be more dispersive than females. To get an idea of the flight ability of *M. bicolor*, the morphological data were compared with that of *Locusta migratoria* and *Schistocerca gregaria*, which are proved to be very good flyers. Based on the morphological data presented here, one can assume a good flight ability for macropters of *M. bicolor*, although flying individuals of this species are seldom observed in natural populations.

1

General introduction

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1.1 Dispersal – an introduction

Fragmentation and destruction of natural habitats are the major causes for the increasing extinction risk of many species and have a detrimental impact on animal populations in numerous ways (Saunders and Hobbs 1991, Abbitt et al. 2000, Vandermeer and Carvajal 2001, Fahrig 2002, 2003, Henle et al. 2004, Marchettia et al. 2006). In fragmented landscapes, dispersal (associated with the exchange of individuals and genetic material between habitat patches) is a key process of particular importance that influences the dynamics and evolution of spatially structured populations and hence determines their long term survival (Andrén 1994, Hanski and Thomas 1994, Thomas 2000, Ronce 2007). It not only secures the re-colonisation of patches where populations went extinct (Fahrig and Merriam 1994), it may also rescue small populations and thus prevent local extinction events (Brown and Kodric-Brown 1977). Dispersal is also of significant influence to the genetic diversity of local populations and thus controls their adaptation to local conditions in general, and more specifically their potential to adapt to changing environmental conditions under global climate change (Kawecki and Ebert 2004). Due to global climate change, ranges of many species are under pressure, and range shifts with subsequent shifts in population dynamics are more and more documented (Altermatt et al. 2008, Thomas 2010). In contrast to less or even non-mobile individuals or species, good dispersers are able to track suitable climatic conditions and therefore are able to cope with the consequences of global climate change (Kubisch et al. 2013). Last not least, dispersal affects the distribution and abundance of species and plays a pivotal role in community dynamics, speciation and species diversity (Clobert et al. 2001, Bullock et al. 2002, Clobert et al. 2004, Ronce 2007, Biswas and Wagner 2012). As fragmentation of landscapes is increasing and the number of species is continuously declining, a thorough understanding of the causes and consequences of dispersal (especially in the context of ongoing global climate change) is essential for managing natural populations and developing effective conservation strategies (Caughley 1994, Baguette et al. 2000, Kokko and López Sepulcre 2006).

Definitions of dispersal

One of the earliest definitions of dispersal was given by Howard (1960). He defined dispersal as the permanent movement of individuals from their place of birth to the place where they reproduce or would have reproduced if they had survived and found a mate. This corresponds to Bullock *et al.* (2002) who use a common definition of dispersal as ‘intergenerational movement’ and thereby exclude dispersal in time (e.g. seed banks) as well as routine movements of animals such as foraging. Lidicker (1975) defined dispersal as any movement of individual organisms leaving their home area and sometimes establishing a new home area, and excluded short term exploratory movements or changes of home range boundaries, such that the new range includes at least part of the former one. However, dispersal is not always a on-off process in the life of an individual; it can take place at any time in the life-cycle and may happen on several occasions (Boyd 2002). Especially for birds, the situation is more complicated as individuals were repeatedly recaptured at different breeding sites. Thus, Greenwood (1980) distinguished natal dispersal (the movement between the natal site and the site where reproduction first takes place) and breeding dispersal (the movement between two successive breeding sites). Natal dispersal refers to events that occur within a distinct ontogenetic stage of the development of an individual and that, once completed, do not occur again (Clobert et al. 2001). In contrast, breeding dispersal can take place several times during the life span of an individual. However, movements between successive sites often do not fit into the simple framework of natal and breeding dispersal (Kenward et al. 2001). Therefore, Kenward *et al.* (2001) modified the terminology of Greenwood (1980). According to them, the transition out of the natal area to the new home area in which an individual first settles is an exnatal movement, and subsequent transitions between home areas outside the natal area are extranatal movements. Movements resulting in pairing or nesting are labelled as prenuptial, and movements between nuptial sites (the breeding dispersal of Greenwood 1980) are postnuptial (Kenward et al. 2001). A few authors (Johnson and Gaines 1990) distinguish between ecological dispersal (the movement of an individual from one place to another) and genetic dispersal (the movement of an individual from one breeding population to another and successfully breeding there). But according to Clobert *et al.* (2012), dispersal, defined as any movement of an individual leading to spatial gene flow (Kokko and López Sepulcre 2006, Ronce 2007, Clobert et al. 2012), does not require movement followed by reproduction (as gene flow occurs by an individual moving its own genes across space).

Phases of dispersal

Dispersal is a three-step process including three consecutive phases: the departure from the local environment (emigration), the movement across a more or less hostile matrix (transfer), and the settlement in a new habitat (immigration) (Clobert et al. 2012). Due to emigration populations may go extinct, while immigration is responsible for recolonization events and may prevent a population from going extinct through rescue effects (Brown and

Kodric-Brown 1977). Often, the movement phase is the only phase observed under natural conditions. During this phase, the transition of an individual out of the natal area to the new home area can be accomplished actively or passively. In the case of active dispersal, the dispersing individuals control the direction and the distance of their movement and thus the place where they end up. Of course they also control when and how often they disperse during their lifespan. The movement of passive dispersers largely depends on external dispersal vectors such as wind or water currents and other animals including humans. Thus, passive dispersing individuals have limited immediate control on where they end up. However, they can exert some influence on the dispersal process by choosing the time of dispersal and the dispersal vector or by deciding how many times they disperse. For example, the neotropical flower mite *Spadiseius calyptrogynae* can cover long or short distances by actively choosing between different dispersal vectors (Fronhofer 2013). Moreover, some spider species display two different dispersal behaviours; ballooning (using a silk thread as a sail) for long-distance dispersal and rappelling (using a silk thread as a bridge) for short-distance dispersal (Bonte et al. 2008, Bonte et al. 2009). Ballooning species can also vary the length of the silk thread und thus the potential covered distance and possibly also the duration of the ballooning event (Bell et al. 2005, Bonte et al. 2008). In addition, different mechanisms of dispersal can co-occur in the same population; the combination of short-distance colony budding and long-distance jump dispersal in ants (Drescher 2011), the dispersal of plants by wind and animal vectors (Bullock et al. 2002); and the combination of active movement and passive ballooning in spiders, mites and moth larvae (Bell et al. 2005, Bonte 2009).

Benefits and costs of dispersal

The dispersal of an individual has far reaching consequences not only for population dynamics, population genetics or the distribution and abundance of species (Hanski and Gilpin 1997, Hanski 1999, Clobert et al. 2001), but also for the fitness of an individual (for review see Bowler and Benton 2005, and Ronce 2007). In general, individuals should disperse when their expected inclusive fitness in their natal area is less than it is elsewhere and of course when benefits exceed dispersal costs. Several factors are assumed to promote the dispersal of an individual into a new area. Kin competition and inbreeding avoidance are two important drivers of dispersal. Because they are both expected in situations where kin interact frequently and dispersal would reduce both pressures, it is difficult to decide whether dispersal is motivated by one or the other (Perrin and Goudet 2001). Undirected, random fluctuations as well as directed changes in habitat quality due to natural succession or anthropogenically induced habitat degeneration also force individuals to disperse. Generally, individuals should leave poor quality habitats where critical resources are rare or absent and prefer good quality habitats. Thus, habitat quality not only affects emigration but also immigration (Kuussaari et al. 1996, Haddad 1999). However, habitat quality cannot be considered independently from population density, when high density leads to frequent intraspecific interactions and consequently to competition between individuals for resources (e.g. food, mates or nesting sites). For many taxa it has been shown that emigration propensity increases with increasing population density (positive density-dependent emigration; Doak 2000, Albrectsen and Nachman 2001, Enfjall and Leimar 2005). But also the opposite (higher emigration rates at lower population densities) can be found (Kuussaari et al. 1996, Roland et al. 2000), if for example the benefits of living in a group (e.g. diluted predation risk, increased probability to find mates or foraging facilitation) exceed the costs of competition between group members. Sex ratio can also force individuals to leave if competition is asymmetric between both sexes and if the mating success varies due to special differences in the number of available mates. In addition, some studies provide evidence that the emigration of females can be induced by the harassment of males (Odendaal et al. 1989, Petit et al. 2001). Not only intraspecific interactions with kin and unrelated individuals of the same species, but also interspecific interactions with competitors of a different species, predators (Weisser et al. 1999, Weisser 2001, Sloggett and Weisser 2002), parasites (Brown and Ehrlich 1980, Petit et al. 2001) or diseases can lead to the dispersal of individuals. Last but not least, patch size has also been shown to influence emigration rates with individuals emigrating in higher proportions from small habitat patches (Kuussaari et al. 1996, Kindvall 1999, Baguette et al. 2000). This effect is often explained by a greater edge to size ratio of smaller patches, where individuals are more likely to encounter the edge and thus are more likely to finally leave the patch (Stamps et al. 1987, Thomas and Hanski 1997, Kindvall and Petersson 2000). However, as other factors like relatedness among individuals, population size and density may vary with the size of a habitat patch, it may be not the patch size per se provoking this effect. Considering all these potential benefits of dispersal, the question arises why do only a small fraction of individuals really emigrate from their natal site, while the majority of individuals stay at home?

To leave the natal habitat and disperse can be risky and involve different individual fitness costs which can be classified into four types of costs (for review see Ronce 2007, and Bonte et al. 2012). Energetic costs are defined as costs due to the development of dispersal-related morphological or physiological traits (e.g. large wings or flight muscles) and due to movement itself. Dispersing individuals also spend time to disperse (time costs) which they cannot invest in other activities (e.g. reproduction). Costs related to increased predation or failure to find suitable habitat (mortality risks) and delayed attrition costs by accumulated damage or physiological changes of an individual are labelled as risk costs. The fourth type are opportunity costs and originate from choosing one out of several exclusive options. These costs are indirect costs (in contrast to the other types of costs) and can be directly related to time or energetic costs. All costs, irrespective of their type, can be incurred immediately or in the future during every phase of dispersal (emigration, transfer and immigration). Some costs are even paid by the next generation, so called transgenerational fitness costs. For example macropterous (long winged) individuals of *Lygaeus equestris* (milkweed bug) produce relatively smaller eggs than micropterous (short winged) individuals, leading to offspring which are not resistant to starvation (Solbreck and Sillentullberg 1990). Both, costs and benefits of dispersal can vary in time and space, and among individuals for most animal species. Depending on the developmental stage or age of an individual, its sex, mating status, genotype, and morphological or physiological condition, the payoff of leaving the natal habitat and disperse can differ between individuals (Bowler and Benton 2005 and references therein, Stevens et al. 2010). In addition, landscape structure (e.g. habitat isolation and fragmentation or type of surrounding matrix), as well as changes in land use and climate are supposed to alter the benefits and costs of dispersal (Hovestadt and Nieminen 2009 and references therein, Bonte et al. 2012 and references therein).

Dispersal polymorphism and trade-offs

Dispersal polymorphism is a widespread phenomenon in many insect groups, where two distinct morphs can be distinguished (Harrison 1980, Zera and Denno 1997, Ingrisch and Köhler 1998). The sedentary morph of dispersal polymorphic insects is flightless with reduced (micropter) or no wings (apter) and reduced flight muscles. In contrast, the dispersal morph is much more mobile (Higaki and Ando 2003) and exhibits fully developed wings (macropter) and well developed flight muscles, which facilitates the movement over long distances by flight (Harrison 1980, Zera and Denno 1997). Beside these obvious morphological differences, both morphs can also differ in physiological and behavioural traits, which are linked to dispersal ability, i.e. flight fuel storage, enzyme activities, number of mitochondria in the flight muscles or movement behaviour (Zera et al.

1994, Zera et al. 1999, Crnokrak and Roff 2000, Gäde 2002, Socha and Zemek 2003, Gu et al. 2006, Hanski et al. 2006).

The development of dispersal-related traits, especially flight capability, is energetically expensive (Rankin and Burchsted 1992, Nespolo et al. 2008). As the energy resources of an individual are limited and cannot be simultaneously invested in different life-history traits, an increase in one trait is supposed to be counter-balanced by a decrease in another (for review see Rankin and Burchsted 1992, and Zera and Denno 1997). Many studies on insects have shown such trade-offs where the ability to disperse is accompanied by for example increased developmental time (Zera 1984, Goodwyn and Fujisaki 2007), decreased longevity (Denno et al. 1989, Gu et al. 2006, Hanski et al. 2006), delayed onset of reproduction (Tanaka 1976, Roff 1984, Denno et al. 1989), decreased fecundity (Roff and Fairbairn 1991, Gu et al. 2006, Lorenz 2007) or decreased mating success (Crnokrak and Roff 1995, Crnokrak and Roff 2000, Langellotto et al. 2000). Especially trade-offs between dispersal ability or mobility and reproduction (oogenesis-flight syndrome) are proposed as a general relationship (Johnson 1969). However, there are also various studies failing to show such trade-offs (for review see Rankin and Burchsted 1992, Holtmeier and Zera 1993, and Zera and Denno 1997, Jiang et al. 2010). Even positive correlations can be found where dispersive individuals exhibit shorter developmental time, lay more eggs and mate earlier than sedentary individuals (Lavie and Ritte 1978, Aukema 1991, Hanski et al. 2006). Such correlations are an example of the coloniser syndrome in which colonisers should not only be highly mobile and dispersive, but also mature quickly and show early reproduction and high fecundity in order to rapidly exploit the new habitat (Baker and Stebbins 1965, Simberloff 1981, Palmer 1985).

Dispersal of pests and invasive species

Pest species, irrespective whether they are indigenous or non-indigenous and invasive species, which are often but not always pests, cause serious ecological and economic damages all over the world, resulting in enormous financial costs (Pimentel et al. 2001 and references therein, Reinhardt et al. 2003, Gong et al. 2009, Vilà et al. 2010 and references therein). First and foremost, these costs are direct economic losses such as crop, pasture, forest, livestock, and commercial fishery losses, induced by plants, animals and pathogens (Pimentel et al. 2001, Pimentel et al. 2005, Vilà et al. 2010). In addition, invasive species are supposed to be a serious threat especially for endangered, but also for other indigenous species due to competition or predation (Pimentel et al. 2001, Pimentel et al.

2005). Also hybridization with non-indigenous species and ecosystem changes caused by them can be a risk for indigenous species (Pimentel et al. 2001). Last but not least, the management of pest- and invasive species provokes enormous economic costs. The control, eradication, and monitoring of these species is expensive and not always successful (Pimentel et al. 2001 and references therein, Vilà et al. 2010 and references therein). Aside from the fact, that the intensive usage of pesticides and herbicides requires an enormous amount of money, it also kills indigenous species and causes environmental pollution and thus the damage to ecosystems. Therefore, a thorough understanding of the causes and consequences of dispersal is not only essential for managing threatened, natural populations and developing effective conservation strategies for endangered species (Caughley 1994, Baguette et al. 2000, Kokko and López Sepulcre 2006). It is also substantial for the development of pest management strategies and the prevention or the deceleration of the spread of invasive species. This especially holds as human activities (e.g. travelling, trade and transport of goods and materials or recreation activities) accelerate the spread of plants, animals, and pathogens locally and worldwide (Johnson et al. 2001, Pimentel et al. 2001, Hulme 2009, Mazzi and Dorn 2012).

1.2 Scope and outline of this thesis

The scope of this thesis is to contribute to a better understanding of insect dispersal using a combined approach of (i) testing assumptions of classical capture-mark-recapture studies, (ii) investigating morphological characteristics as well as (iii) investigating the result of dispersal via genetic analyses. I have chosen grasshoppers and bush crickets as study species as their habitat requirements are well known (Cherrill and Brown 1992, Kindvall 1995, Gardiner et al. 2002, Gröning et al. 2007). Thus, suitable habitats are readily identified in a given landscape. Furthermore, their movement behaviour has been intensively investigated in recent years leading to extensive information on the utilization of different landscape structures (With et al. 1999, Berggren et al. 2002, Hein et al. 2003, Diekoetter et al. 2007). And most notably, many orthoptera species display a distinct wing dimorphism with short winged (micropterous) and long winged (macropterous) individuals of both sexes. These macropters are generally supposed to serve as dispersal unit (Vickery 1965, Simmons and Thomas 2004).

In the context of animal dispersal, movement behaviour has been frequently investigated with capture-mark-recapture studies where animals are captured at one site (their familiar 'home' site), marked, and transferred to other unfamiliar sites (Kindvall 1999, Hein et al. 2003, Berggren 2004, 2005a, Moerkens et al.

2010). The conclusions drawn from these studies crucially depend on the assumption that the marking technique and the translocation of animals from their familiar habitat patch to unfamiliar sites itself have no (or at most a negligible) influence on the behaviour of these individuals. The impact of different marking methods on the physiology and behaviour of marked animals has been intensively investigated (Ambrose 1972, Fairley 1982, Gall 1984, Pavone and Boonstra 1985, Korn 1987, Wood and Slade 1990, Cooley et al. 1998, Evans and Gleeson 1998, Baminger 2000, Lindner and Fuelling 2002, Bates and Sadler 2004, Kobayashi and Kikuchi 2004, Henry and Jarne 2007). However, although there was some evidence that transferring animals to suitable but unfamiliar sites has an impact on the movement behaviour of translocated individuals (Tomiyama 1992, Armstrong and Herbert 1997, Clarke and Schedvin 1997, Jacquot and Solomon 1997, Armstrong et al. 1999, Belanger and Rodriguez 2001), the effect of translocation itself was not explicitly investigated so far. To fill this gap, I investigated the effect of translocation on the movement behaviour of the blue-winged grasshopper *Oedipoda caerulescens* in a capture-mark-recapture study. The results of this study are presented in chapter 2.

Beside direct field observations via capture-mark-recapture methods, also methods using genetic markers can be used to investigate animal dispersal. Conclusions drawn from direct field observations may be misleading as the probability of detecting dispersal events declines with dispersal distance, while death and emigration events cannot always be clearly distinguished (Koenig et al. 1996, Prugnolle and De Meeus 2002). Often, it is also unknown whether the individuals under investigation even have a propensity to disperse or just display routine movements such as foraging (Van Dyck and Baguette 2005). In addition, direct field observations measure the mobility (ability to move in space) of organisms, which is not necessarily equivalent to effective dispersal (migration followed by successful reproduction; Prugnolle and De Meeus 2002). Hence, frequently applied alternatives are methods investigating the gene flow between populations as a result of dispersal rather than observing dispersing individuals directly (Keyghobadi et al. 2005, Bailey et al. 2007, Ortego et al. 2011). In the study presented in chapter 3, I investigated the population genetic structure of the two-coloured bush cricket *Metrioptera bicolor* in a spatially structured landscape. Using microsatellite markers, I assessed the effects of geographic distance and different matrix types on the genetic differentiation among 24 local populations in order to identify potential dispersal barriers for this species.

In addition to direct effects on realised dispersal (see chapter 3), landscape structure (i.e. the spatial configuration of habitat patches or the nature of the landscape matrix) on its own is known to act as an evolutionary selection agent because it determines the costs and benefits of dispersal (Olivieri et al. 1995, Olivieri and Gouyon 1997, Merckx et al. 2003, Merckx and Van Dyck 2006, Bonte et al. 2012). Both morphological and behavioural traits of individuals and the degree to which a certain genotype responds to environmental variation have heritable components, and are therefore expected to be able to respond to landscape changes (Thomas et al. 1998, Hill et al. 1999a, Roff and Fairbairn 2001, Price et al. 2003, Bonte and Lens 2007). Chapter 4 is an example for how landscape characteristics affect morphological traits of individuals in recently structured populations. This study was conducted in a landscape with habitat patches varying in patch size, patch connectivity (isolation of populations) and sand dynamics (stability of habitat) to investigate the influence of habitat fragmentation on the dispersal-related morphology of *O. caerulescens*.

To leave the natal habitat and disperse can be risky and involve different individual fitness costs (Tanaka 1976, Rankin and Burchsted 1992, Roff and Fairbairn 2007, Hovestadt and Nieminen 2009, Bonte et al. 2012). Therefore, the decision to disperse should not be random but depend on the developmental stage or the physiological condition of an individual just as on actual environmental conditions (context-dependent dispersal; Ims and Hjermann 2001, Bowler and Benton 2005, Matthysen 2005). Sex-biased dispersal, where the propensity to disperse is linked to the gender of an individual (e.g. Markow and Castrezana 2000, Sundström et al. 2003, Beirinckx et al. 2006, Lagisz et al. 2010), and wing morph-biased dispersal, where macropterous (long-winged and supposed to be dispersive) and micropterous (short-winged and supposed to be sedentary) individuals can be distinguished (Harrison 1980, Zera and Denno 1997, Ingrisch and Köhler 1998, Simmons and Thomas 2004), are two examples for context-dependent dispersal and the topic of chapter 5. In the study presented in this chapter, I used a combined approach of morphological and genetic analyses, to investigate sex- and wing morph-biased dispersal of *M. bicolor*.

2

The effect of translocation on movement behaviour ─ A test of the assumptions of behavioural studies [1]

Contents

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[1] This chapter has been published as:

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Abstract

Animal movement behaviour is intensively investigated with capture-mark-recapture studies. For the analysis of such experiments, the influence of marking technique, handling and translocation of marked animals on movement pattern is of crucial importance since it may mask or overrule the effects of the main research question. Here we present a capture-mark-recapture experiment on the movement behaviour of the blue-winged grasshopper *Oedipoda caerulescens*. We analysed the influence of translocation of individuals from familiar to unfamiliar sites. Our study clearly demonstrates a significant influence of translocation to unfamiliar sites on the movement behaviour of *O. caerulescens*. Translocated individuals moved longer distances, showed smaller daily turning angles, and thus movements were more directed than those of resident individuals. The effect of translocation on daily moved distances was most pronounced on the first day of the experiment. We thus conclude that at least for the first day after translocation, movement behaviour is significantly influenced by translocation itself. Data ignoring this influence will be unsuitable for the prediction of dispersal behaviour, habitat detection capability or habitat preference.

2.1 Introduction

Dispersal plays a crucial role in the ecology and evolution of species and the persistence of metapopulations (Dieckmann et al. 1999, Wu et al. 2000, Poethke et al. 2003, Hovestadt and Poethke 2006, Rouquette and Thompson 2007, Schtickzelle et al. 2007). It influences the dynamics and persistence of populations, the distribution and abundance of species, community structure, the level of gene flow between populations, local adaptation, speciation and determines how organisms respond to fragmentation of landscape and climate change (Dieckmann et al. 1999, Hanski 1999, Bullock et al. 2002, Clobert et al. 2004). As fragmentation of landscapes is increasing and the number of species is continuously declining, a thorough understanding of the processes governing dispersal is becoming more and more important and may be essential in developing effective conservation strategies (Caughley 1994, Baguette et al. 2000, Diekoetter et al. 2007).

In the context of animal dispersal, movement behaviour has been frequently investigated with capture-mark-recapture studies (Baguette and Neve 1994, Hill et al. 1996, Kindvall 1999, Ricketts 2001, Hein et al. 2003, Berggren 2004). Conclusions drawn from these studies crucially depend on the assumption that the marking technique and the translocation of animals from their familiar habitat patch to unfamiliar sites has no (or at most a negligible) influence on the behaviour of these individuals.

The impact of different marking methods on the physiology and behaviour of marked animals has been investigated in many studies. Most of them showed no significant effect on behaviour, body weight and growth, flight ability, mating propensity and fecundity, mortality or predation risk due to markings (Ambrose 1972, Cooley et al. 1998, Evans and Gleeson 1998, Baminger 2000, Lindner and Fuelling 2002, Bates and Sadler 2004, Kobayashi and Kikuchi 2004, Henry and Jarne 2007). In contrast, some studies revealed a negative influence of the marking on the activity, body weight, survival and recapture rates of marked animals (Fairley 1982, Gall 1984, Pavone and Boonstra 1985, Korn 1987, Wood and Slade 1990).

In many capture-mark-recapture studies, animals are captured at one site, their familiar 'home' site, and transferred to other unfamiliar sites to investigate their behaviour. Unfamiliar sites may comprise suitable habitat (Kindvall 1999, Berggren 2004, 2005a) or different types of unsuitable sites (matrix) (Kindvall 1999, Hein et al. 2003), where animal behaviour is studied e.g. to predict how fast or well this area can be crossed to reach suitable habitat. In such a case, it is very important that translocation itself does not influence movement behaviour since it is impossible to separate other effects, for example type of matrix, from the effect of translocation. Nevertheless, to our knowledge, there is no study focusing on the impact of translocation itself although there is some evidence that transferring animals to suitable but unfamiliar sites has an effect on the movement behaviour of translocated individuals. Jacquot and Solomon (1997) investigated the effect of site familiarity on movement pattern of male voles. In this experiment, individuals released in unfamiliar outdoor enclosures moved farther than their conspecifics released in familiar enclosures. However, not only translocation but also social interactions between translocated and resident males could have influenced the movement behaviour of translocated individuals. In addition, bird reintroduction studies of endangered species for conservation purpose revealed that for birds extensive and rapid movement seems to be typical after their release in unfamiliar habitat, even in normally sedentary species (Clarke and Schedvin 1997, Armstrong et al. 1999). There are also experiments on homing behaviour after artificial translocation to unfamiliar sites with birds, fishes and snails which show that animals react on translocation (Tomiyama 1992, Armstrong and Herbert 1997, Belanger and Rodriguez 2001). However, since translocation was not the main focus of these studies, the effects on individual behaviour could not be verified. With no control group the impact of translocation cannot be distinguished from other potentially confounding factors that could have influenced behaviour.

Here we present a capture-mark-recapture study on the effect of translocation on movement behaviour of the blue-winged grasshopper *Oedipoda caerulescens* in coastal grey dunes. We chose a grasshoppers species because grasshoppers are often used as bioindicators and capture-mark-recapture experiments are easily conducted with grasshoppers (Andersen et al. 2001). In our study, we investigated individuals of *O. caerulescens* on two sites simultaneously to exclude an influence of the study site, where individuals were released or the population where individuals originated from.

2.2 Material and methods

Study species

The blue-winged grasshopper *O. caerulescens* (LINNAEUS 1758; Orthoptera: Acrididae) is a thermo- and xerophilic grasshopper species of medium to large size (body length: 15-30 mm) (Detzel 1998). *O. caerulescens* inhabits stony calcareous meadows with sparse vegetation, quarries and sand pits and can also be found in dry heathlands, spoil heaps and railroad yards (Schlumprecht and Waeber 2003). This species is described as moderately sedentary although some individuals can move over long distances up to 800 m (Hein et al. 2005, Maes et al. 2006). Individuals usually move on the ground but fly a few meters (3 to 6 m) if disturbed. Long distance flights are seldom observed (Detzel 1998).

Field work

The study was carried out in the Westhoek Nature Reserve (De Panne, Belgium; 51°03’ N-51°05’ N, 2°34’ E). For our experiments, we chose two study sites of typical grey dunes, characterised by open sand, moss and herbaceous plants. Distance between both sites was about 825 m. On each site, we caught 14 females and 14 males of *O. caerulescens* and marked their exact position where an individual was found with a numbered stick. This position is assumed to represent the preferred microhabitat of each individual. Grasshoppers were individually marked with numbered reflective tape, fixed on the femur of one hind leg (Heller and von Helversen 1990). Until all insects were released in the late evening next to a numbered stick, we kept them in numbered plastic vials in a cooling box to reduce potential handling trauma (Stettmer 1996).

To investigate movement behaviour in the familiar habitat patch half of the individuals (7 females, 7 males) captured on one site were randomly chosen and released exactly at the position where they were found (resident individuals). The second half of grasshoppers were transferred to the respective other site and released to test their movement behaviour in unfamiliar suitable habitat (translocated individuals). Thus, half of the caught individuals from one patch were replaced by individuals of same sex from the other patch thereby keeping density constant in both patches. As a control for a potentially different microhabitat choice of females and males, we released females only at positions where females were caught and males only at positions where males were caught.

We determined the position of each (re-sighted) individual in the following four nights. Thereby daily moved distances, turning angles and net displacement after each day were recorded. The first recapture of individuals was 24 hours after release. We chose an observation interval of 24 hours.

Re-sight rates

Re-sight rates allow an estimation of mortality (or emigration) rates, detection error and the quality of the marking method. We used re-sight rates of individuals as well as findings of lost reflective tape to compare our two study sites with respect to these factors. Tape could either be lost accidentally or be left by predators feeding on grasshoppers. Individuals that we could not find on one day, but that were re-sighted on one of the following days were probably overlooked and allow an estimation of the detection error during the experiment. Individuals that we never re-sighted until the end of the observation period were assumed either to be dead or to have emigrated.

Statistical analyses

Analysis of data was complicated by the fact that not all individuals were found continuously in the four observation nights resulting in incomplete data sets on movement distances and turning angles. For statistical analysis we chose only data resulting from measurements during two consecutive nights, even if the record was previously interrupted (see also Hein et al. 2003). Linear mixed-effects models were applied to analyse the effect of sex, translocation, release site and capture site on movement behaviour of *O. caerulescens*. As we caught individuals at several consecutive days, 'individual' and 'day' were used as random effects in all models. Starting from a full model (all main factors and all interaction terms), model selection was conducted by stepwise backward elimination of not significant interaction terms with p-values above 0.15. We did not remove main factors, even if they were non-significant. Sequential type III sums of squares were used in all F-tests to analyse whether a significant proportion of variance in movement parameters could be explained by sex, translocation, release site or capture site. Parameter estimates were obtained using the restricted maximum log-likelihood (REML) method. We used log-likelihood (ML) fits for model comparison with Akaike's Information Criterion as model selection criteria. For statistical analyses, distance data were box-cox transformed and angle data were johnson transformed. To compare daily moved distances and turning angles between resident and translocated individuals for each recapture day, we used Mann-Whitney U tests for two independent samples. All analyses were conducted with the statistics software packages R 2.6.2 (r-project.org) and SAS 9.1.

2.3 Results

Re-sight rates

The loss of individuals (mortality and/or emigration) was highest for translocated animals on site one (> 60 % at last recapture day). In general, the proportion of lost individuals was higher for animals released on site one than for those released on site two, irrespective of whether they were translocated or not.

Corresponding to this finding, the proportion of not continuously re-sighted animals was higher for study site one than for site two. Re-sight rates were highest for the resident individuals on study site two where day-to-day re-sight rates were > 80 % during the whole experiment. For both study sites, proportion of not continuously re-sighted animals was higher for translocated individuals than for resident ones.

Movement behaviour

Our results clearly show that translocation had an impact on the behaviour of individuals. Compared to animals which were released in their familiar habitat patch, translocated individuals moved longer distances per day (Figure 2.3.1, Table 2.3.1) and showed greater net displacement (Figure 2.31, Table 2.3.2). Besides translocation, the sex of an individual significantly influenced daily moved distances and net displacement with males moving longer distances than females (Table 2.3.1 and 2.3.2). In addition, interaction between sex and release site had a significant influence on daily distances (Table 2.3.1) and net displacement (Table 2.3.2) too.

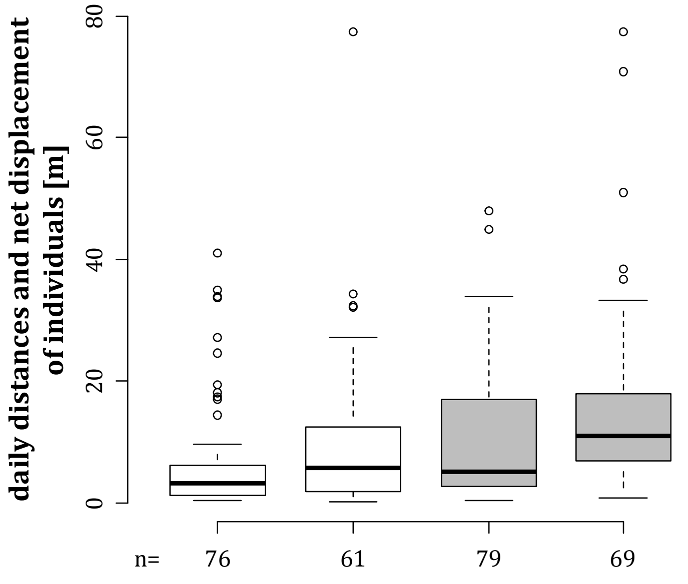

Figure 2.3.1: Comparison of daily moved distances (white) and net displacement (grey) between all resident and translocated individuals of *O. caerulescens*. The boxes represent the median, and 25 % and 75 % percentiles. The whiskers extend to the minimum and maximum values, the circles denote outliers.

Table 2.3.1: Effects of sex, translocation and release site on box-cox transformed daily moved distances of all individuals and males of *O. caerulescens*. Estimates, standard errors of estimates (SE), denominator degrees of freedom (Den. d.f.), F and P- values of mean effects as derived from a linear mixed-effects model after model selection are given.

Factor	Estimate (b)	SE	Den. d.f.	F-value	p-value
Daily moved distances of all individuals on both sites					
Sex	0.16	0.05	37.8	47.33	<0.01
Translocation	-0.08	0.04	34.5	4.96	0.03
Release site	-0.09	0.05	38.3	0.21	0.65
Sex* Release site	0.22	0.08	37.5	7.94	<0.01
Daily moved distances of males on both sites					
Translocation	-0.17	0.10	16.9	2.74	0.12
Release site	0.22	0.11	18.8	4.22	0.04

Table 2.3.2: Effects of sex, translocation and release site on box-cox transformed net displacement of all individuals and males of *O. caerulescens*. Estimates, standard errors of estimates (SE), denominator degrees of freedom (Den. d.f.), F and P- values of mean effects as derived from a linear mixed-effects model after model selection are given.

Factor	Estimate (b)	SE	Den. d.f.	F-value	p-value
Net displacement of all individuals on both sites					
Sex	0.10	0.06	41.1	25.66	<0.01
Translocation	-0.14	0.04	40.8	10.69	<0.01
Release site	-0.07	0.06	41.3	1.45	0.24
Sex* Release site	0.24	0.09	41.1	7.45	<0.01
Net displacement of males on both sites					
Translocation	-0.34	0.21	19.6	2.55	0.13
Release site	0.57	0.22	20.0	6.96	0.02

The effect of translocation on daily moved distances was most pronounced at day one and was not significant on the following days (Mann-Whitney U test, $p<0.05$; Figure 2.3.2). For daily turning angles, translocation had a tendentious effect (Table 2.3.3), with translocated animals showing smaller turning angles than resident ones. The sex of an individual had no effect but interaction between translocation and release site significantly influenced daily turning angles (Table 2.3.3). However, no significant differences of daily turning angles between translocated and resident individuals on single days could be found.

Separate analyses for each sex revealed that the site where an individual was released had an influence on daily moved distances (Table 2.3.1, Figure 2.3.3) and net displacement (Table 2.3.2, Figure 2.3.3) for males but not for females. Males moved significantly longer distances on study site one than on study site two, irrespective of their origin. Furthermore, the interaction effect of translocation and release site on daily turning angles (see above) was significant for males (Table 2.3.3). In contrast to males, this effect was not significant for females.

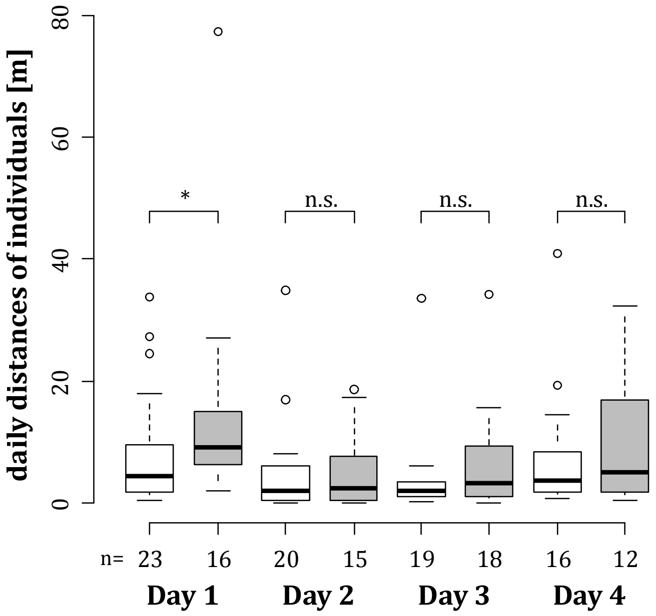

Figure 2.3.2: Comparison of daily moved distances between all resident (white) and translocated (grey) individuals of *O. caerulescens* as a function of time after translocation. Asterisks indicate significant differences between resident and translocated individuals (Mann-Whitney U-test, p<0.05).

Table 2.3.3: Effects of sex, translocation, release site and capture site (population of origin) on johnson transformed daily turning angles of all individuals and males of *O. caerulescens*. Estimates, standard errors of estimates (SE), denominator degrees of freedom (Den. d.f.), F and P- values of mean effects as derived from a linear mixed-effects model after model selection are given.

Factor	Estimate (b)	SE	Den. d.f.	F-value	p-value
Daily turning angles of all individuals on both sites					
Sex	0.15	0.21	86	0.48	0.49
Translocation	-0.18	0.26	86	2.83	0.09
Release site	-0.72	0.34	86	0.44	0.51
Translocation * Release site	1.13	0.46	86	6.12	0.02
Daily turning angles of males on both sites					
Translocation	-0.28	0.37	42	2.45	0.12
Release site	-0.72	0.54	42	0.09	0.77
Translocation * Release site	1.64	0.69	42	5.58	0.02
Daily turning angles of all individuals released on site one					
Sex	0.60	0.39	10.8	2.44	0.15
Translocation	0.83	0.38	10.9	4.69	0.04
Daily turning angles of males released on site one					
Translocation	1.36	0.46	11	8.65	0.01
Daily turning angles of resident males on site one and two					
Capture site	0.92	0.41	26	4.97	0.04

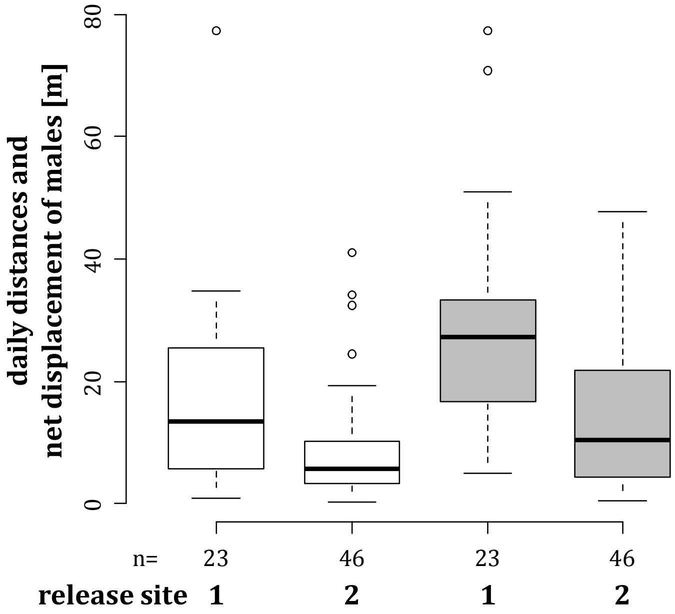

Figure 2.3.3: Comparison of daily moved distances (white) and net displacement (grey) between males of *O. caerulescens* released on study site one and two.

Separate analyses for each release site showed that for study site one translocated individuals showed smaller daily turning angles and thus moved more directed than resident ones (Table 2.3.3). This effect was significant only for males released on experimental area one (Table 2.3.3, Figure 2.3.4). In addition to this finding, resident males captured and released on study site one showed larger turning angles than resident males on site two (Table 2.3.3, Figure 2.3.5). For females, such an effect could not be detected.

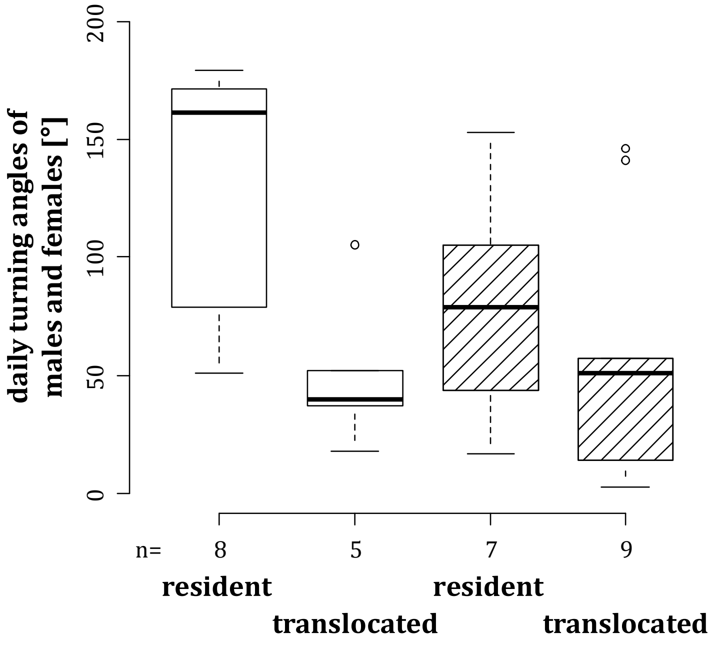

Figure 2.3.4: Comparison of daily turning angles between resident and translocated males (white) and females (shaded) of *O. caerulescens* released on study site one.

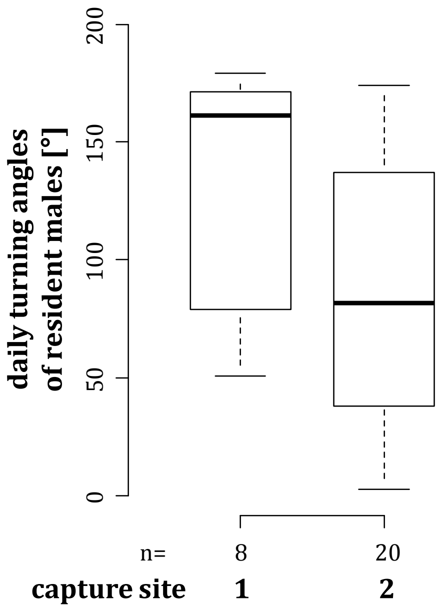

Figure 2.3.5: Comparison of daily turning angles between resident males of *O. caerulescens* captured on study site one and two.

2.4 Discussion

Movement behaviour

Our experiment clearly demonstrates an influence of translocation on movement behaviour of individuals in capture-mark-recapture studies. Translocated individuals of *O. caerulescens* moved longer distances irrespective of site, showed smaller daily turning angles on site one and thus moved more directed than resident individuals. The latter showed rather routine movements, which are characterized by short distances and large turning angles and which animals usually show when they are moving in their familiar habitat (Van Dyck and Baguette 2005).

Effect of translocation on daily moved distances was only significant on the first day after translocation. The most likely explanation might be that translocated individuals showed a change in movement behaviour after translocation and then switched to routine movements after habituating to the unfamiliar surroundings. The effect of translocation is limited to a certain time period after release. Such a temporal effect has also been shown for the influence of marking on butterflies in a capture-mark-recapture experiment, where the handling of animals disrupted flight activity solely at the day when individuals were captured for the first time and marked (Gall 1984). In addition, bad weather conditions after the first recapture could have led to a reduced activity of test individuals as *O. caerulescens* is a thermophilic species with low activity at low temperatures (Detzel 1998, Walters et al. 2006). However, daily maximum temperature was highest at the last day of experiment and nonetheless translocated animals moved shorter distances compared to the first day of experiment. This indicates that weather conditions alone cannot explain the attenuation of translocation effect after the first day.

Daily distances and net displacement for males released on study site one were longer than for those on site two. This finding could be explained by the fact, that site one is twice as large as site two and males do not encounter boundaries that often. In small habitat patches, individuals encounter patch boundaries more frequently than in large ones while avoiding to cross them and moving back to the inner part of the habitat patch (Ries and Debinski 2001, Schtickzelle and Baguette 2003, Ross et al. 2005). On large sites, individuals can move longer distances without reaching the boundary. Thus, our finding is in good accordance with previous studies which have shown, that movement or dispersal distances of insects and vertebrates increases with study area size (Koenig et al. 1996, Schneider 2003, Franzén and Nilson 2007). In our experiment, the effect of study site size was not significant for females presumably because they are in general less active than males (Maes et al. 2006).

On study site one, translocated males moved more directed than resident ones whereas on site two this effect was not significant. In addition, resident males captured and released on study site one showed larger turning angles than resident males on site two. Thus, local conditions of sites where individuals were released or originated from also influence individual behaviour and may enhance or attenuate the effect of translocation. According to local conditions, reaction of individuals on translocation can vary and therefore the impact of translocation is difficult to predict.

Effect of translocation was most pronounced on the first day of the experiment, but may persist for longer. The exact duration of this translocation effect is difficult to determine and may depend on species and weather conditions. Although our results are restricted to *O. caerulescens*, we expect that similar effects of translocation could also occur in other arthropods. On average, daily moved distances of translocated individuals were about 50 % longer (9.14 m +- 12.25 m) than of resident individuals (6.17 m +- 8.87 m) because they have been transferred to an unfamiliar habitat patch. Depending on experiment duration, this leads to considerable differences in net displacement between translocated and resident individuals. Therefore, extrapolation on dispersal behaviour based on movement data derived from capture-mark-recapture experiments is, strictly speaking, only valid if individuals are released at the same position (at least on the same site) where they have been caught. In addition, for the comparison of movement patterns in different habitat types, a control experiment observing translocated individuals in a new suitable habitat is required. In summary, our results clearly point out that translocation effects should not be disregarded in future studies on arthropod movement, respectively dispersal.

Re-sight rates

The analysis of re-sight data shows that loss of individuals was higher for study site one than for site two. This is probably not due to differences in predation risk or food availability. In our experimental design we tried to choose areas of similar vegetation composition, vegetation structure and amount of open soil thus we assume no differences in food availability and predation risk between the two study sites. For both sites, proportion of not continuously re-sighted animals was higher for translocated individuals than for resident ones. Translocation may lead to a higher propensity of the translocated animals to leave an unfamiliar habitat patch or to move further away from the release point at least. In contrast, resident individuals may tend to stay where they are in their familiar habitat patch and thus are easier to find which leads to higher re-sight rates. Translocated individuals may also experience an increased predation risk because they are released in an unknown surrounding in which they take longer to reach cover and may show atypical behaviour (Metzgar 1967, Ambrose 1972, Jacquot and Solomon 1997). In addition, increased movement, maybe due to an orientation behaviour in the new surroundings, of translocated individuals may lead to an increased predation risk compared to resident individuals (Yoder et al. 2004).

3

The genetic structure of populations of *Metrioptera bicolor* in a spatially structured landscape: effects of dispersal barriers and geographic distance [1]

Contents

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Abstract

The stability and long-term survival of animal populations in fragmented landscapes largely depends on the colonisation of habitat patches and the exchange of individuals between patches. The degree of inter-patch dispersal, in turn, depends on the dispersal abilities of species and the landscape structure (i.e. the nature of the landscape matrix and habitat distribution). Here, we investigated the genetic structure of populations of *Metrioptera bicolor*, a wing-dimorphic bush cricket, in a spatially structured landscape with patches of suitable habitat distributed within a diverse matrix of different habitat types. Using six microsatellite markers, we assessed the effects of geographic distance and different matrix types on the extent of genetic differentiation among 24 sampling sites. We found that forest and a river running through the study area both impede inter-patch dispersal. The presence of these two matrix types was positively correlated with the extent of genetic differentiation between sites. In addition, we found a significant positive correlation between pairwise genetic and geographic distances for a subsample of sites which were separated only by arable land or settlements. For the complete data set, this correlation could not be found. This is most probably because the adverse effect of forest and river on gene flow dominates the effect of geographic distance in our limited set of patches. Our analyses clearly emphasize the differential resistance of different habitat types on dispersal and the importance of a more detailed view on matrix 'quality' in metapopulation studies.

3.1 Introduction

Dispersal is a key process of particular importance in the highly fragmented landscape of central Europe that determines the long term survival of populations (Andrén 1994, Hanski and Thomas 1994, Thomas 2000, Ronce 2007). In a network of well-connected habitat patches, dispersal not only secures the re-colonisation of patches where populations went extinct (Fahrig and Merriam 1994), it may also rescue small populations and thus prevent local extinction events (Brown and Kodric-Brown 1977). Dispersal is of significant influence to the genetic diversity of local populations and, thus, controls their adaptation to local conditions in general, and more specifically their potential to adapt to changing environmental conditions under global climatic change (Kawecki and Ebert 2004). Last not least, dispersal plays a pivotal role in community dynamics and species diversity (Biswas and Wagner 2012). Reliable information about dispersal propensity and dispersal distances of species is thus of outstanding value for species conservation.

The investigation of dispersal in natural populations via direct field observations (i.e. mark-recapture or radio-tracking) is challenging. Conclusions drawn from such studies may be misleading because the probability of detecting dispersal events declines with dispersal distance, while death and emigration cannot always be distinguished (Koenig et al. 1996, Prugnolle and De Meeus 2002). Often, it is also unknown whether the individuals under investigation even have a propensity to disperse or just display routine movements such as foraging (Van Dyck and Baguette 2005). Furthermore, direct field observations measure the mobility (ability to move in space) of organisms, which is not necessarily equivalent to effective dispersal (migration followed by successful reproduction) (Prugnolle and De Meeus 2002). Hence, methods using genetic markers to infer dispersal rather than observing dispersing individuals directly are a frequently applied alternative. Such methods can be used to investigate gene flow between populations as a result of dispersal and the effects of geographic distance (isolation by distance) or landscape matrix on realised dispersal (Wright 1943, Slatkin 1985, Cockerham and Weir 1993, Slatkin 1993, Roderick 1996, Neigel 1997, Bohonak 1999, Whitlock and McCauley 1999, Storfer et al. 2007).

Isolation by distance analyses, where the genetic distance is plotted against the geographic distance to assess whether more distant population pairs are more genetically distinct, allow testing for the effects of geographic features on population differentiation (Slatkin 1994, Bohonak 2002). In addition, potential barriers to gene flow such as agricultural fields, roads, waterways, or mountain ridges can be identified (Mader 1984, Bohonak 2002, Keller et al. 2004, Funk et al. 2005, Antolin et al. 2006, Ridley et al. 2006, Storfer et al. 2007).

In our study, we investigated the population genetic structure of *Metrioptera bicolor* in a spatially structured landscape with suitable habitat patches scattered throughout a diverse matrix of less suitable or completely unsuitable habitat. *M. bicolor* is a wing-dimorphic bush cricket which prefers open habitats such as semiarid or sandy grassland (Detzel 1998). Based on capture-mark-recapture studies concerning the movement behaviour of individuals of *M. bicolor*, this species is described as very sedentary (Kindvall and Ahlén 1992, Kindvall 1999). Using microsatellite markers, we assessed the effects of geographic distance and different matrix types (arable land, settlements, forest, and a river) on the genetic differentiation between sampling sites in order to identify potential dispersal barriers for this species.

3.2 Materials and methods

Study species

The two-coloured bush cricket *M. bicolor* (PHILIPPI 1830; Orthoptera: Tettigoniidae) is a medium-sized (body length: 15-18 mm), thermo- and xerophilic bush-cricket (Detzel 1998, Ingrisch and Köhler 1998). It is orientated towards vertical structures and thus prefers tall-grass biotopes. *M. bicolor* mainly inhabits semiarid grassland, but can also be found on juniper heath or poor and sandy grasslands, whereas arable land (arable crops, fertile meadows, marsh areas and other meadows regularly mowed for hay production) and forest represent unsuitable habitats for this species (Detzel 1998, Ingrisch and Köhler 1998). Individuals of this species are usually short-winged (micropterous) and flightless. Only long-winged (macropterous) animals are able to fly (Voisin 1982, Nadig 1988), but this morph is typically rare (mean: 1.1 %; max.: 5.3 %; a total of 992 individuals sampled at 8 sites; Heidinger unpublished data), and their flight capability has been little investigated. As *M. bicolor* adults do rarely leave their native habitat patch (less than 3 % according to Kindvall and Ahlén 1992, Kindvall 1993), this species is described as very sedentary with a critical inter-patch distance for colonisation of about 100 m and a maximum observed dispersal distance of about 300 m (Kindvall and Ahlén 1992).

Sampling and sampling sites

A total of 957 adult individuals of *M. bicolor* were sampled from 24 different grassland sites in the rural district 'Hassberge' in Northern-Bavaria, Germany (latitude 50° 03′, longitude 10° 36′, Table 3.2.1, Figure. 3.2.1). Suitable habitat patches in the study area are relatively small (0.47 ± 0.32 ha) and the mean nearest neighbour distance between sampling sites is 2.08 ± 1.02 km. Pairwise distances between sites range from 1.08 km to 18.43 km (6.93 ± 3.73 km).

Table 3.2.1: The number, the geographic coordinates, the size, the total number of individuals sampled, as well as the number of sampled females and males are shown for each sampling site. Numbers in parentheses refer to macropterous females and males, respectively.

Site	Latitude (N)	Longitude (E)	Altitude [m]	Area [ha]	Individuals	Females	Males
1	50°01`59``	10°34`31``	335	0.35	44	22 (3)	22 (2)
2	49°57`60``	10°34`08``	340	0.14	40	20 (0)	20 (1)
3	50°03`34``	10°33`18``	290	0.32	40	20 (3)	20 (2)
4	50°00`15``	10°37`32``	360	0.52	40	20 (1)	20 (0)
5	50°03`10``	10°34`46``	325	0.24	40	20 (1)	20 (0)
6	50°02`50``	10°33`37``	265	0.24	40	20 (0)	20 (0)
7	50°00`30``	10°36`07``	305	1.02	40	20 (0)	20 (1)
8	50°03`08``	10°35`40``	315	0.31	38	18 (0)	20 (0)
9	50°02`46``	10°38`19``	348	0.36	38	19 (0)	19 (1)
10	49°58`34``	10°42`32``	250	0.26	40	20 (1)	20 (0)
11	50°01`05``	10°35`48``	270	0.50	40	20 (2)	20 (3)
12	50°02`11``	10°35`31``	302	0.14	40	23 (4)	17 (1)
13	50°02`01``	10°38`34``	350	0.53	40	20 (0)	20 (1)
14	50°01`10``	10°34`38``	258	0.29	40	20 (1)	20 (1)
15	49°59`47``	10°38`51``	290	0.21	40	20 (0)	20 (0)
16	50°00`47``	10°41`44``	280	0.61	39	18 (0)	21 (0)
17	50°02`41``	10°41`35``	370	0.35	41	20 (0)	21 (0)
18	50°04`03``	10°38`13``	390	0.33	39	19 (1)	20 (1)
19	50°03`58``	10°35`43``	340	1.09	40	20 (1)	20 (0)
20	50°04`17``	10°34`14``	340	1.31	40	20 (1)	20 (0)
21	49°59`25``	10°39`34``	275	0.95	40	20 (0)	20 (0)
22	49°58`58``	10°36`39``	290	0.27	40	20 (1)	20 (0)
23	49°58`33``	10°46`39``	285	0.21	40	20 (0)	20 (0)
24	50°00`23``	10°44`41``	330	0.63	38	18 (1)	20 (0)

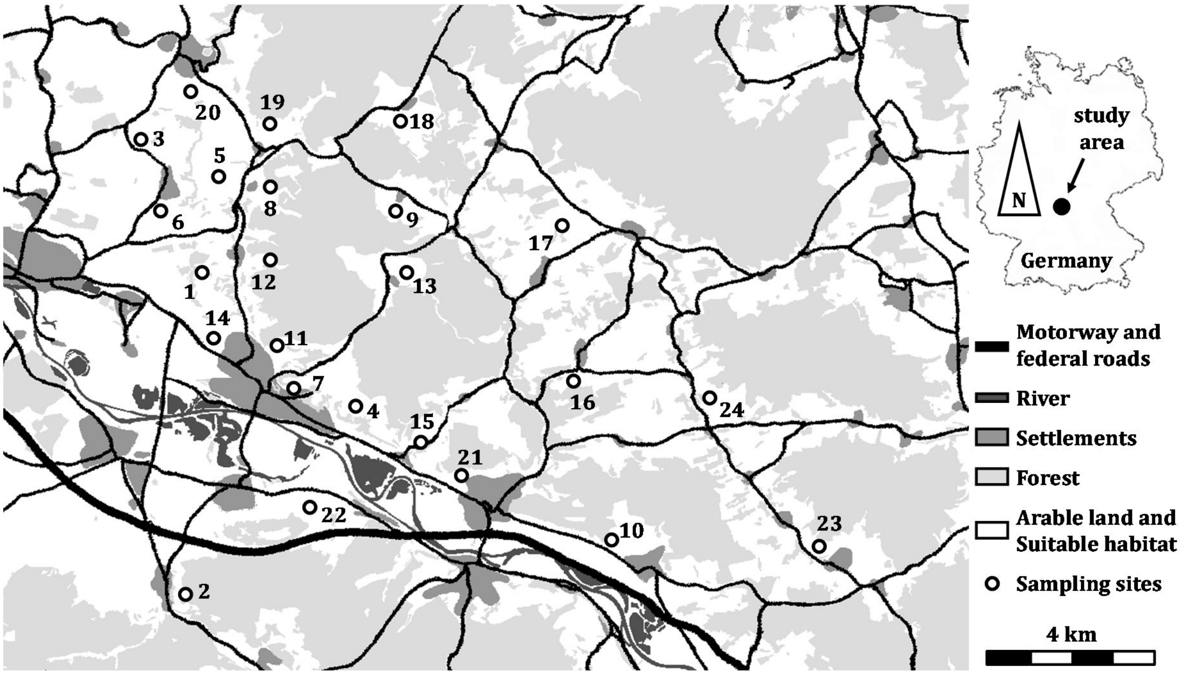

Figure 3.2.1: Location of the 24 sampling sites in the rural district 'Hassberge' in Northern-Bavaria, Germany. White areas consist of arable land and small patches of suitable habitat embedded in a mosaic of fields of different arable crops and agriculturally used meadows. For a definition of the different matrix types considered in this study see table 2.

For our sampling scheme, we selected sites separated by different types of matrix, such as arable land, forest, and settlements (Table 3.2.2). Sampling sites in the northwest of the study area (sites 1, 3, 5, 6, 8, 11, 12, 14, 19, and 20) are situated in the nature reserve 'Hohe Wann', which is characterised by a patchwork of vegetation traceable to the underlying geological and geomorphological heterogeneity of this area. The most obvious characteristic of the 'Hohe Wann' is an abundance of mesoxerophytic grassland, formerly used as vine yards or pastures (Elsner 1994). These patches are separated by small agricultural fields of different usage, resulting in a patchy mosaic of different habitat types. Sampling sites to the east and southeast of the nature reserve 'Hohe Wann' are separated from the sites in the northwest by a large forest. These sites are embedded in a mosaic of arable land, mesoxerophytic grassland and small fragments of forest. Assuming a strong disjunctive effect of rivers for this species, we also sampled two sites (site 2 and site 22) in the southwest of the study area that are separated from the remaining sites by a river (50-140 m width). Genetic material was acquired by sampling one hind leg from each individual directly in the field. All animals were released afterwards and legs were stored in 100 % ethanol p.a. for further analysis.

Table 3.2.2: Description of the different matrix types considered in this study.

Matrix type	Description
Arable land	Fields of different arable crops and agriculturally used meadows like fertile meadows, marsh areas and other meadows regularly mowed for hay production
Settlements	Small villages and towns with 69 to 5574 inhabitants, predominantly single houses with gardens, some larger apartment buildings and industrial buildings
Forest	Predominantly broadleaf trees
River	River with watergates, dead stream branches and small lakes

Microsatellite analysis

DNA was extracted from the femur muscle using the Puregene DNA Purification Kit by Gentra Systems according to the manufacturer's recommendation and stored in 50 µl low TE-buffer at -20°C. An amplification reaction was performed in a Biometra or an Eppendorf thermocycler in a total reaction volume of 12.5 µl. Each reaction contained approximately 40 ng of template DNA, 10 x PCR-Puffer, 2 mM MgCl2 and 0.5 U of Taq DNA polymerase (MolTaq basic by Molzym GmbH), 0.2 mM dNTPs (PureExtremeTM dNTPs by Fermentas Life Sciences) and 0.2 µM of each Primer (forward primer labelled with fluorescent IR-700 or IR-800 dye by Licor). The thermal cycling protocol consisted of an initial denaturation at 95 °C for 3 min followed by 30 cycles of 30 sec denaturation at 95 °C, with 30 sec annealing at 55.5 °C, and 30 sec elongation at 72 °C. A final elongation step was performed at 72 °C for 3 min. PCR products were diluted 1:15 and analysed on a LI-COR Biosciences 4300 DNA Analyser. All samples were analysed at six polymorphic microsatellite loci developed for *Metrioptera roeselii*: MR3-12, MR2-16, MR3-24, MR3-34, MR2-42 and MR3-44 (Holzhauer and Wolff 2005).

Data analysis

In the following, we use 'sampling site' for all individuals sampled at the same site and 'population' for all sampling sites grouped together according to our analysis with Geneland 3.1.5 (see below).

Genetic diversity and linkage

Using Micro-Checker 2.2.3 (Van Oosterhout et al. 2004), we checked data for the presence of large allele dropout and scoring errors due to stuttering. Null allele frequencies were calculated with FreeNa (Chapuis and Estoup 2007). This software uses the expectation maximization algorithm of Dempster et al. (1977) and was chosen because this estimator shows better performance than others (Chapuis and Estoup 2007). We also calculated null allele frequencies according to the population inbreeding model with INEst 1.0 (Chybicki and Burczyk 2009). In contrast to other estimators, this method takes the possibility of inbreeding into account, as both null alleles and inbreeding can cause an excess of homozygotes within a population. Frequencies of null alleles were calculated for each locus and sampling site and then arithmetically averaged over all sampling sites. To test for significant genotypic linkage disequilibrium at pairs of loci for each sampling site we used Genepop 4.0.10 (Raymond and Rousset 1995, Rousset 2008). P values were obtained after a sequential Bonferroni adjustment for multiple tests (Rice 1989). Neutrality of the microsatellite loci used in this study was verified using BayeScan 2.0 (Foll and Gaggiotti 2008, Foll et al. 2010).

The genetic diversity of each sampling site was estimated by the arithmetic mean number of alleles per locus (AP) and the mean number of alleles corrected for sampling effort AW (weighted allelic richness) calculated with Fstat 2.9.3.2 (Goudet 2001). Using Arlequin 3.5.1.2 (Excoffier et al. 2005), we also assessed the unbiased (sample size-corrected) observed (HO) and expected (HE) heterozygosity according to Nei (1978). All diversity measures were computed per locus and arithmetically averaged for each sampling site. In addition, we calculated the inbreeding coefficient FIS (Weir and Cockerham 1984) for each sampling site using Genepop 4.0.10 (Raymond and Rousset 1995, Rousset 2008) and we tested for significant deviation of the sampling sites from Hardy-Weinberg Equilibrium across all loci (Guo and Thompson 1992).

Null allele frequencies per locus calculated with INEst ranged from 0.018 to 0.298, with a mean of 0.111 ± 0.128. The values obtained via FreeNA ranged from 0.093 to 0.280, with a mean of 0.170 ± 0.096. Such values are not unusual for orthopterans (Chapuis et al. 2008, Lange et al. 2010) and are very common in studies dealing with microsatellite data (Dakin and Avise 2004). We detected high proportions of null alleles (estimator of Dempster) in MR3-34, MR2-42 and MR3-44 (see also Holzhauer et al. 2009, Lange et al. 2010). Null alleles lead to incorrect estimates of allele frequencies and overestimation of inbreeding as they decrease the estimated frequency of heterozygotes (Pemberton et al. 1995). Null alleles can also affect the estimation of population differentiation by reducing the genetic diversity within populations, which results in increased FST and genetic distances values (Paetkau and Strobeck 1995, Slatkin 1995, Paetkau et al. 1997). Therefore, we adjusted our data for the presence of null alleles using Micro-Checker 2.2.3 (Van Oosterhout et al. 2004) and repeated all of our calculations apart from those concerning observed heterozygosity and FIS values because this would have been inappropriate (Van Oosterhout et al. 2006). However, as we got qualitatively similar results (not shown), we present results for the original data set only.

Metapopulation structure

Genetic differentiation between pairs of sampling sites were derived via the fixation index FST (Weir and Cockerham 1984), its standardized measure F'ST (Meirmans and Hedrick 2011), and Jost's differentiation measure D (Jost 2008). To calculate FST and D values we used Arlequin 3.5.1.2 (Excoffier et al. 2005) and SPADE (Chao and Shen 2003), respectively. As SPADE gives D values for each locus separately, the arithmetic average was used to obtain pairwise D values across all loci (Jost and Chao 2010). Values for F'ST were obtained as described in Meirmans and Hedrick (2011). Traditional measures like FST (Weir and Cockerham 1984) or GST (Nei 1973) usually underestimate the true level of genetic differentiation (Heller and Siegismund 2009). As newly developed and traditional measures have their advantages and drawbacks (Jost 2008, 2009, Ryman and Leimar 2009, Meirmans and Hedrick 2011), we followed the recommendations of Meirmans and Hedrick (2011) in using both, and found no qualitative difference in results for the different measures used.

Population structure was inferred via Geneland 3.1.5 (Guillot et al. 2005a, Guillot et al. 2005b, Guillot 2008, Guillot et al. 2008). For verification of the consistency of our results, we ran the MCMC simulation 15 times independently, allowing K to vary from 1 to 30. For each run, we used 100,000 iterations and a thinning of 100 iterations. The model with the highest mean logarithm of posterior probability was post-processed to provide a graphical output of the spatial distribution of the populations. Using Geneland 3.1.5 (Guillot et al. 2005a, Guillot et al. 2005b, Guillot 2008, Guillot et al. 2008), we also calculated the inbreeding coefficient (FIS) within and the pairwise FST values between inferred populations.

Dispersal barriers and isolation by distance

Using the 'Mantelise it!' option of Fstat 2.9.3.2 (Goudet 2001), we performed Mantel tests (10,000 randomizations) to assess the effects of arable land, settlements, forest or the river on the extent of genetic differentiation between sampling sites. For this purpose, four matrices coding for the absence (coded as 0) or presence (coded as 1) of these respective landscape elements or habitat types between two sampling sites were correlated with genetic distance matrices of FST, F'ST and D values. To construct these (0,1)-matrices, we drew a direct line between the centres of any two sampling sites using the online source for spatial data BayernViewer (Bavarian State Office for Survey and Geoinformation, Munich). We assigned a value of 0 to sites separated by less than 300 m and a value of 1 to sites separated by more than 300 m of continuous arable land, settlements or forest. We chose this range because *M. bicolor* is described as a sedentary species able to cover a distance of about 300 m at the maximum (Kindvall and Ahlén 1992, Kindvall 1993). The absence or presence of the river was coded as 0 or 1 independently of the river's width.

We also conducted an isolation by distance (Wright 1943) analysis by comparing pairwise estimates of FST, F'ST, as well as D, and the logarithms of geographic distances (as the crow flies) between sampling sites with IBD 3.1.5 (Bohonak 2002) (10,000 randomizations). The latter we did for the dataset of all sampling sites and for the subset of sites situated in the nature reserve 'Hohe Wann' (sites 1, 3, 5, 6, 8, 11, 12, 14, 19 and 20), which are not separated from each other by large forest, settlements or a river, to exclude potential barrier effects of these habitat types. Unfortunately, it was not possible to exclude a potential barrier effect of arable land, because this matrix type is very common in the study area.

3.3 Results

Genetic diversity and linkage

All sampling sites displayed high levels of allelic variability (Table 3.3.1). Significant linkage disequilibrium was present in 19 out of 360 pairs of loci, but this was unlikely due to true physical linkage as significant linkage was not restricted to specific pairs of loci throughout. Furthermore, all p values obtained after a sequential Bonferroni adjustment for multiple tests were nonsignificant. For all sampling sites we found significant multi-locus deviation from Hardy-Weinberg equilibrium ($p < 0.0001$), associated with positive FIS values (Table 3.3.1), i.e. heterozygote deficiencies. This is most probably due to the presence of null alleles (see above).

Table 3.3.1: The number of genotyped individuals (N), the arithmetic mean number of alleles per locus (AP), the mean number of alleles corrected for sampling effort AW (weighted allelic richness), the observed (HO) and expected (HE) heterozygosity (Nei 1978) and the inbreeding coefficient FIS (Weir & Cockerham 1984) are shown for each sampling site. For values of AP, AW, HO and HE, both the mean and the standard deviation (SD) at six loci are given.

Site	**N**	**Arithmetic mean number of alleles per locus**	**Mean number of alleles corrected for sampling effort**	**Observed heterozygosity**	**Expected heterozygosity**	**FIS**
		Mean (SD)	**Mean (SD)**	**Mean (SD)**	**Mean (SD)**	
1	44	12.33 (5.43)	11.40 (4.82)	0.50 (0.20)	0.84 (0.09)	0.40
2	40	10.17 (4.75)	9.72 (4.34)	0.61 (0.21)	0.80 (0.10)	0.23
3	40	13.50 (5.65)	12.49 (4.58)	0.62 (0.14)	0.84 (0.06)	0.26
4	40	15.17 (6.08)	13.96 (5.29)	0.48 (0.20)	0.88 (0.08)	0.46
5	40	13.83 (5.67)	12.33 (4.92)	0.57 (0.16)	0.83 (0.10)	0.30
6	40	12.33 (5.47)	11.48 (4.98)	0.54 (0.19)	0.83 (0.11)	0.35
7	40	10.67 (4.32)	10.06 (3.97)	0.57 (0.19)	0.82 (0.09)	0.31
8	38	12.67 (5.20)	12.01 (4.77)	0.61 (0.16)	0.84 (0.12)	0.28
9	38	12.33 (6.35)	11.34 (5.38)	0.55 (0.28)	0.77 (0.17)	0.27
10	40	12.67 (5.32)	11.81 (4.88)	0.42 (0.15)	0.81 (0.12)	0.48
11	40	10.67 (4.32)	9.85 (3.87)	0.50 (0.25)	0.78 (0.11)	0.34
12	40	13.17 (4.71)	12.27 (4.04)	0.55 (0.14)	0.85 (0.08)	0.35
13	40	12.83 (5.42)	11.88 (4.77)	0.49 (0.21)	0.82 (0.10)	0.40
14	40	11.67 (4.76)	11.01 (4.24)	0.48 (0.08)	0.84 (0.08)	0.43
15	40	9.17 (3.13)	8.66 (2.69)	0.37 (0.14)	0.75 (0.17)	0.51
16	39	10.50 (4.46)	9.84 (3.70)	0.42 (0.10)	0.82 (0.06)	0.50
17	41	12.50 (5.75)	11.41 (4.82)	0.43 (0.21)	0.82 (0.10)	0.47
18	39	13.67 (6.47)	12.47 (5.40)	0.56 (0.17)	0.84 (0.11)	0.33
19	40	11.83 (5.35)	11.05 (4.53)	0.48 (0.21)	0.85 (0.08)	0.42
20	40	12.50 (4.14)	11.43 (3.81)	0.57 (0.18)	0.84 (0.08)	0.32
21	40	11.83 (4.75)	10.93 (4.22)	0.44 (0.16)	0.80 (0.13)	0.45
22	40	13.83 (7.36)	12.59 (6.16)	0.52 (0.20)	0.79 (0.14)	0.35
23	40	12.83 (5.53)	11.93 (4.87)	0.42 (0.18)	0.84 (0.08)	0.50
24	38	12.50 (5.32)	11.73 (4.73)	0.48 (0.26)	0.83 (0.14)	0.42

Metapopulation structure

Pairwise FST values ranged from 0.016 to 0.135 with a mean of 0.047 ± 0.021 (Table 3.6.1, supplemental material) indicating little to moderate differentiation between pairs of sampling sites. Values of F’ST and Jost's D were substantially higher than the corresponding FST values and ranged from 0.074 to 0.541 with a mean of 0.242 ± 0.092, and 0.130 to 0.502 with a mean of 0.287 ± 0.071, respectively (Table 3.6.2 and 3.6.3, supplemental material). The number of populations inferred via Geneland was K = 5 in 13 out of 15 independent runs (Figure 3.3.2, Table 3.3.2). Sampling sites 2 (population E) and 15 (population B) formed clusters by themselves, whereas sites 9 and 18 were grouped together (population D), as were sites 17 and 24 (population C). All samples collected at the remaining sites belong to population A (sites 1, 3, 4, 5, 6, 7, 8, 10, 11, 12, 13, 14, 16, 19, 20, 21, 22, 23). FIS values were overall moderate to high (Table 3.3.2), whereas FST values for pairs of populations were comparatively low, except for population B (site 15; Table 3.3.3).

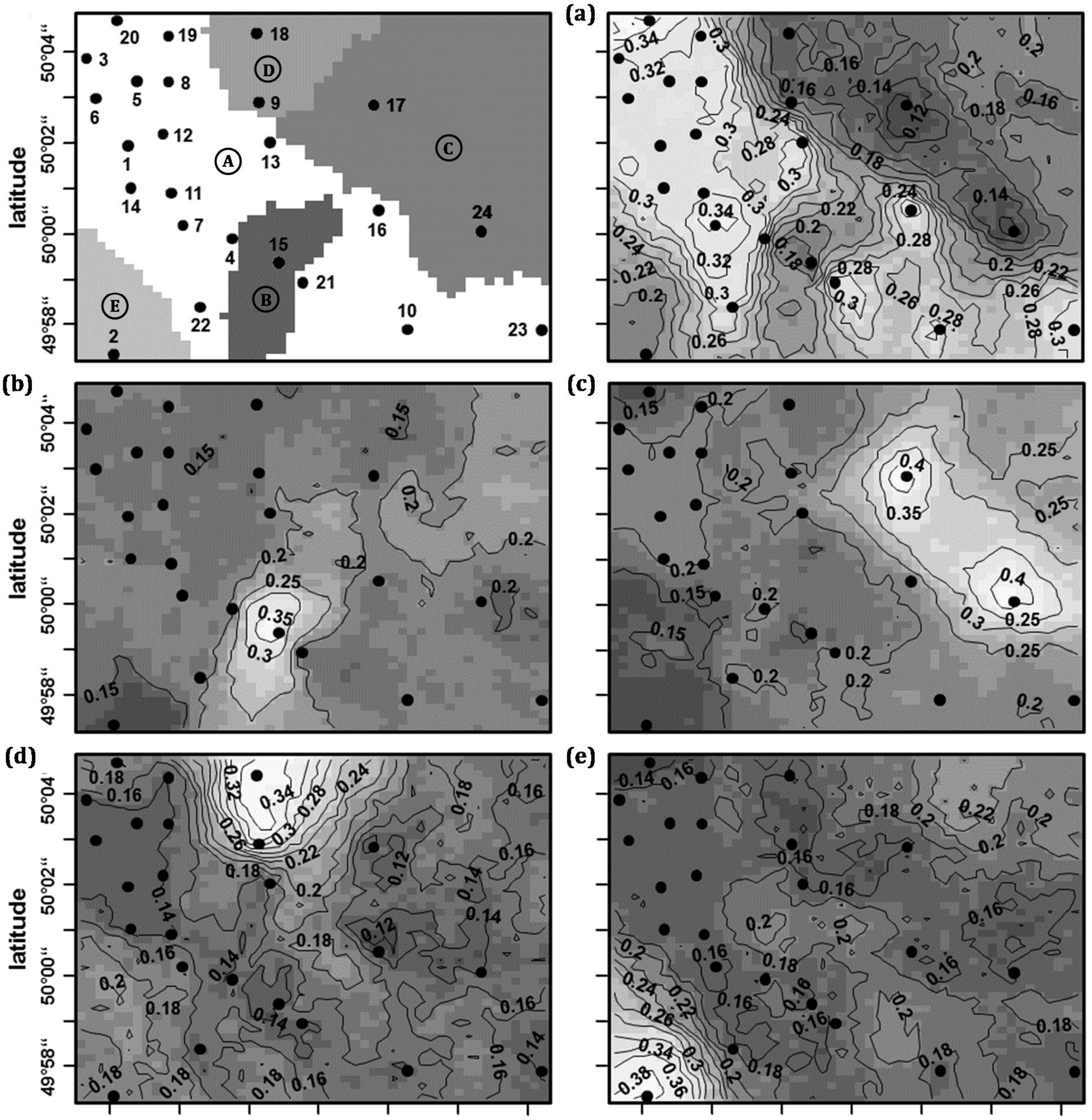

Figure 3.3.2: Map of the spatial distribution of the populations (upper left corner) and map of the probability of population membership for (A) population A, (B) population B, (C) population C, (D) population D and (E) population E. Light colours indicate high probability whereas dark colours indicate low probability.

Table 3.3.2: Population membership of the 24 sampling sites and values of the inbreeding coefficient FIS (Weir & Cockerham 1984) calculated within inferred populations.

Population	Sampling sites	FIS
A	1,3,4,5,6,7,8,10,11,12,13,14,16,19,20,21,22,23	0.41
B	15	0.51
C	17 and 24	0.46
D	9 and 18	0.33
E	2	0.25

Table 3.3.3: Values of the fixation index FST (Weir & Cockerham 1984) calculated between inferred populations (sampling sites grouped together according to our analysis with Geneland 3.1.5).

	Population A	Population B	Population C	Population D
Population B	0.072	-		
Population C	0.016	0.094	-	
Population D	0.017	0.099	0.034	-
Population E	0.031	0.109	0.045	0.040

Dispersal barriers and isolation by distance

We found no effect of arable land or settlements on the extent of genetic differentiation between sampling sites. However, pairwise FST-, F'ST- and D values were positively correlated with the presence of forest and the river (Table 3.3.4). Investigation of all 24 sampling sites revealed no evidence for isolation by distance as genetic distances between sites did not significantly depend on their geographic distances (FST: $r = 0.001$, $p > 0.05$; F'ST: $r = 0.011$, $p > 0.05$; D: $r = 0.121$, $p > 0.05$). Restricting the analysis to those sampling sites in the nature reserve 'Hohe Wann' that are not separated from each other by large forest, settlements, or the river (sites 1, 3, 5, 6, 8, 11, 12, 14, 19 and 20), we found a positive correlation between pairwise genetic and geographic distances (Figure 3.3.3).

Table 3.3.4: Results of the Mantel tests conducted to assess the effects of arable land, settlements, forest or a river on the extent of the genetic differentiation between sampling sites. For each test, the correlation (r) between the explanatory variable and dependant variables (FST, F'ST and Jost's D) and the significance level (p) are given.

Explanatory variable	Fixation index FST		Standardized fixation index F'ST		Jost's differentiation measure D	
	r	p	r	p	r	p
Arable land	-0.003	>0.05	0.028	>0.05	0.064	>0.05
Settlements	-0.039	>0.05	-0.061	>0.05	-0.056	>0.05
Forest	0.131	<0.05	0.115	<0.05	0.169	<0.01
River	0.132	<0.05	0.120	<0.05	0.151	<0.05

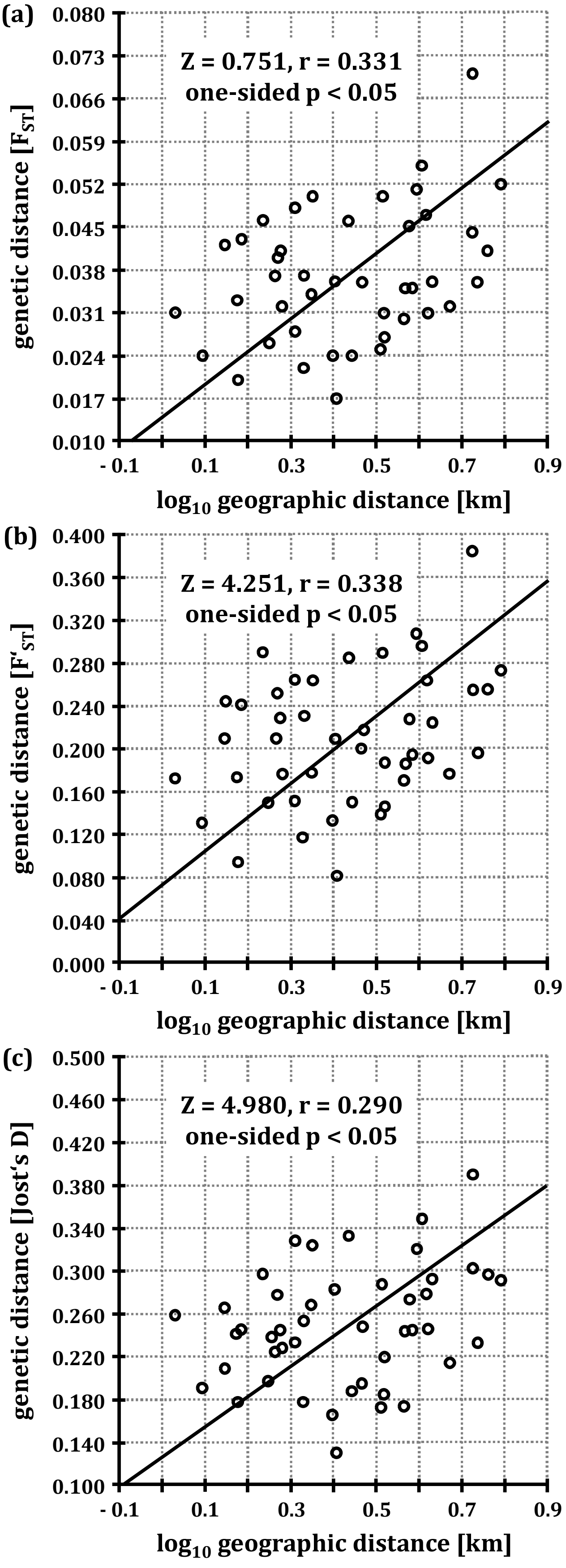

Figure 3.3.3: Relationship between pairwise genetic distances derived via (a) the fixation index FST (Weir & Cockerham 1984), (b) its standardized measure F'ST (Meirmans & Hedrick 2011) and (c) Jost's D (Jost 2008) and the logarithm of geographic distances between populations of *M. bicolor*.

3.4 Discussion

Using microsatellite markers, we investigated the population genetic structure of *M. bicolor*, a wing-dimorphic bush cricket, in a spatially structured landscape. Suitable habitat patches were of relatively small size, and embedded in a diverse matrix of different habitat types. Although all 24 sampling sites were clearly separated (inter-patch distances range from 1.08 km to 18.43 km), our analysis of the population structure revealed only five distinct populations (populations A-E, Fig. 2).

Most sites of population A are rather well connected to each other as more suitable, but unsampled habitats exist in the area. They are situated in the nature reserve 'Hohe Wann', which is characterised by an abundance of mesoxerophytic grassland, formerly used as vine yards or pastures (Elsner 1994). Such grassland represents suitable habitat for *M. bicolor* and its general abundance, even if individual patches are typically small, may facilitate inter-patch dispersal between different sites (Wood and Pullin 2002). Additional sites (4, 7, 10 and 21) belonging to population A are situated in the vicinity of a federal road following the course of a river from the northwest to the southeast. The edges of this road provide suitable conditions and may be used as dispersal corridors (Kindvall and Ahlén 1992, Sutcliffe and Thomas 1996, Berggren et al. 2002). Further, two nature reserves ('Pfaffenberg' and 'Ebelsberg') along this road provide suitable habitat for dispersing individuals of *M. bicolor*. In addition, wind could also play a role in the genetic exchange between these sampling sites, due to the prevailing western wind direction.

Sampling site 15 (population B) is a small unmanaged meadow (about 0.21 ha) with tall grass and scattered fruit trees along a road surrounded by a 70 to 300 m broad strip of forest in the northwest. Although geographically placed almost in the centre of population A, site 15 seems to be particularly isolated. The values of any differentiation measure we used to estimate the isolation of this site were up to two times higher than that of any other site. This population also displayed the lowest number of alleles and the lowest observed heterozygosity compared to all other sites, indicating severe genetic drift or a reduction of population size (a bottleneck; Nei et al. 1975, Leberg 1992). As three years before our sampling a golf course had been created in the vicinity of this site (200 m), site 15 may be a relic of a population currently passing through a bottleneck event. However, a test of this hypothesis via bottleneck 1.2.02 (Cornuet and Luikart 1996) and the average (over all loci) ratio M (Garza and Williamson 2001) provided no evidence for such a bottleneck (results not shown).

The results obtained for populations C and D support the hypothesis, that forest is a particularly strong dispersal barrier for *M. bicolor* (Kindvall and Ahlén 1992, Berggren et al. 2001). Both sites belonging to population D (sites 9 and 18) are surrounded by forest (except to the east of site 9). Sampling sites 17 and 24 (population C) are situated in a mosaic of arable fields of different land use, mesoxerophytic grassland and small fragments of forest. They are also separated by forest from most of the other sampling sites, whereas it is not obvious what separates them from sites 9, 16 and 23.

Sampling site 2 (population E) is a small abandoned area (about 0.14 ha) formerly used as a vineyard. This population is surrounded by forest, mesoxerophytic grassland, and vineyards. A motorway (23 m width) and a river (50-140 m width) separate this site from all other sampling sites (except site 22, which is also situated at the same riverside but not at the same side of the motorway). Although the number of alleles was almost as low as for site 15, sampling site 2 had a comparatively high observed heterozygosity compared to all other sites or populations. Therefore, this site may be a comparatively young population founded by individuals of genetically distinct neighbouring sites during one or several immigration events, allowing for the mixing of different genotypes.

Our analysis of the combined effect of geographic distance and different matrix types on the extent of genetic differentiation between sampling sites confirms the strong negative influence of forest on inter-patch dispersal of *M. bicolor*. Arable land and settlements seem to have no effect, whereas the presence of forest and a river was positively correlated with pairwise FST-, F'ST- and D values (Table S1-S3, Online Resource 1). For our analysis, we could not distinguish different types of arable land (e.g. cultivation of grain or vegetables and agriculturally used meadows) due to the lack of detailed information on land use. However, arable land in our study area is not a uniform matrix, but rather a mixture of varying habitat types, which are supposed to be differently permeable for *M. bicolor* due to differences in land use (Ricketts 2001, Hein et al. 2003, Castellón and Sieving 2006). To detect an effect of arable land on the gene flow between sites and the population genetic structure of *M. bicolor*, it may be necessary to execute a more detailed analysis, requiring additional information on the type of land use and the area covered by a defined habitat type (Berggren et al. 2001, Berggren et al. 2002, Keyghobadi et al. 2005). Moreover, information not only about the current, but also about the former land use may be necessary, as land use can change dramatically over time (Holzhauer et al. 2006, Orsini et al. 2008, Holzhauer et al. 2009).

The genetic structure of *M. bicolor* seems to be unaffected by the presence of settlements. As the sampling sites are situated in a patchy mosaic of different habitat types in a rural landscape, settlements in the study area may be too small to form strong barriers for dispersing individuals of this bush cricket. In addition, settlements may not be as inhospitable as supposed because of the presence of undeveloped building lots and gardens within settlement zones (Leidner and Haddad 2010). Last not least, edges of roads and grassy margins along fields may act as dispersal corridors facilitating the exchange of individuals between sites separated by arable land or settlements (Kindvall and Ahlén 1992, Sutcliffe and Thomas 1996, Berggren et al. 2002).

In accordance with the general assumption that forest impedes the dispersal of species inhabiting open habitats (Gerber and Templeton 1996, Haddad 1999, Keyghobadi et al. 1999, Ries and Debinski 2001, Leidner and Haddad 2010), we found forest to be a dispersal barrier for *M. bicolor*, although values for the coefficient of correlation were low. *M. bicolor* prefers high temperatures and predominantly inhabits sites exposed to the sun (Holst 1986). Therefore, extended areas of forest may impede the dispersal of this species, although road banks and ditches could be used as corridors through forest. Kindvall (1995) reported that during an exceptional drought in 1992 *M. bicolor* used otherwise unsuitable habitats including pine forest – normally a severe barrier for the dispersal of this bush cricket (Kindvall and Ahlén 1992, Berggren et al. 2001).

The disjunctive effect of the river passing through our study area indicated by our analyses could (at least partly) also be caused by the presence of a motorway (23 m width), running more or less in parallel to the river and separating site 2 from the remaining sites, including site 22. This interpretation may explain the result of the Geneland analysis, where site 2 clustered alone, while site 22 belonged to population A despite being separated by the river from all other sites of this population. Several studies have shown the negative effect of roads on gene flow (Mader 1984, Keller et al. 2004, Ridley et al. 2006, Marsh et al. 2008). We did not investigate this aspect further, because almost all sites are separated by several roads or farm tracks from the other sites, and thus we did not expect to detect such an effect.

We also executed a more detailed analysis of our data using not only the presence and absence of a specific matrix type, but also taking into account the amount (distance between the sites covered by habitat X) and the frequency (number of times habitat X occurs between the sites) of a specific habitat type. Using the distance covered by a specific matrix slightly improved our results. However, this analysis did not yield new insights as settlements and arable land still had no significant influence on isolation. In addition, we know little about the mechanism underlying the effects of different matrix types on dispersal (amount or frequency of a specific habitat, or a combination of both). Therefore, we decided to keep our analysis simple.

Investigating all 24 sampling sites we found no pattern of isolation by distance, most probably because forest and rivers have a dominant restricting effect on the gene flow between sites compared to the range of geographic distances as they occur in our study area. However, restricting our analysis to the sites situated in the nature reserve 'Hohe Wann', we detected a significant positive correlation between pairwise genetic and geographic distances, independent of the differentiation measure used. Sampling sites in the nature reserve 'Hohe Wann' are not separated from each other by large areas of forest or rivers. Therefore, in the absence of such strong separators, geographic distance appears to be the main disjunctive factor acting on inter-patch dispersal, and clear isolation by distance can be found.

Inter-patch dispersal of *M. bicolor* presumably depends on two main factors: the presence of macropterous individuals, and the use of dispersal corridors. Several studies highlight the importance of macropters for species range expansion and the genetic exchange between sites (Peterson and Denno 1997, Thomas et al. 2001a, Simmons and Thomas 2004, Hochkirch and Damerau 2009). However, macropterous individuals of *M. bicolor* are rare in natural populations, and no detailed analysis of their flight ability in terms of flight duration, flight speed or flight distances exists (as far as we know). Nonetheless, macropterous *M. bicolor* are supposed to play a major role in dispersal and gene flow. The flight speed of orthopterans ranges from 3.3 to 6.1 m/s for Locusta migratoria (Baker et al. 1981) and 1.9 to 3.1 m/s for *Scapteriscus acletus* (Ulagaraj 1975). Assuming a flight speed of 2 m/s, a macropterous individual of *M. bicolor* could cover a distance of 7 km (mean distance between any two sites in our study) within an hour. Continuous flights of several minutes have already been reported for other orthopterans (3 to 45 minutes for *S. acletus*, Ulagaraj 1975, 0.5 to 17 minutes for *Platycleis albopunctata*, Gottschalk 1997). In addition, *M. bicolor* is regularly found on road edges and grassy margins along fields (Schlumprecht and Waeber 2003). Both are common features in most agricultural landscapes (Berggren et al. 2001) and may act as dispersal corridors (Kindvall and Ahlén 1992, Berggren et al. 2002). Using such linear structures, flightless micropterous individuals may also contribute to the genetic exchange between different sites. Even in intensively used agricultural landscapes, where patches of grassland seem to be highly isolated, a dense network of linear grassland structures may thus facilitate inter-patch dispersal of individuals and hence enable gene flow between sites, thereby preventing the extinction of local populations (Lange et al. 2010).

3.5 Conclusions

The results of our study clearly indicate that for *M. bicolor* the isolation of local populations severely depends on the type of surrounding matrix. Thus, a mere analysis of isolation by distance may not yield essential information on the dispersal capacity of the species. Moreover, population viability studies that use inter-patch distance as the main determinant of habitat isolation may lead to wrong or inaccurate predictions.

Although the connectance of local habitat patches in our study area is rather high, larger forest areas may severely reduce the gene flow between populations. The same holds for rivers (or motorways). We could clearly show that both habitat types severely impede gene flow and the exchange of individuals between local populations, while our results concerning the permeability of arable land should be taken with care as we could not discriminate different types of land use.

As modern GIS-based landscape analysis delivers detailed information on habitat types, population genetic analyses that focus on the specific dispersal resistance of different matrix types may provide much more detailed information on the dispersal capacity of species. Such information is needed to improve landscape oriented models for species conservation. It would allow to focus conservation measures on specific dispersal barriers and to optimize investment into landscape management.

3.6 Supplemental material

Table 3.6.1: Pairwise calculated values of the fixation indices FST (Weir & Cockerham 1984; below diagonal) and the significance level of each comparison after sequential Bonferroni adjustment (**: $p<0.01$; n.s.: not significant; above diagonal).

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
1	-	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
2	0.046	-	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
3	0.050	0.041	-	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
4	0.030	0.045	0.030	-	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
5	0.034	0.042	0.041	0.024	-	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
6	0.032	0.053	0.042	0.025	0.020	-	**	n.s	**	n.s	**	n.s	**	**	**	**	**	**	**	**	**	**	n.s	**
7	0.038	0.065	0.042	0.026	0.028	0.028	-	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
8	0.036	0.046	0.036	0.021	0.031	0.024	0.041	-	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
9	0.060	0.062	0.069	0.048	0.058	0.054	0.068	0.044	-	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
10	0.032	0.052	0.040	0.025	0.032	0.021	0.030	0.031	0.046	-	**	n.s	n.s	n.s	**	**	**	**	**	**	n.s	**	n.s	n.s
11	0.050	0.064	0.036	0.047	0.055	0.047	0.044	0.045	0.063	0.028	-	**	**	**	**	**	**	**	**	**	**	**	**	**
12	0.024	0.039	0.030	0.022	0.028	0.017	0.027	0.026	0.041	0.019	0.048	-	**	n.s	**	**	**	**	**	**	**	**	n.s	**
13	0.034	0.037	0.039	0.029	0.037	0.035	0.039	0.035	0.044	0.019	0.031	0.032	-	n.s	**	**	**	**	**	**	**	**	**	**
14	0.033	0.052	0.032	0.022	0.035	0.027	0.035	0.035	0.048	0.019	0.042	0.022	0.021	-	**	**	**	**	**	**	**	**	**	**
15	0.107	0.113	0.081	0.079	0.102	0.094	0.106	0.111	0.135	0.091	0.098	0.090	0.117	0.094	-	**	**	**	**	**	**	**	**	**
16	0.038	0.070	0.063	0.034	0.051	0.036	0.051	0.036	0.063	0.044	0.058	0.040	0.043	0.046	0.122	-	**	**	**	**	**	**	**	**
17	0.040	0.056	0.050	0.046	0.044	0.038	0.062	0.033	0.060	0.044	0.052	0.036	0.048	0.054	0.105	0.061	-	**	**	**	**	**	**	**
18	0.042	0.053	0.045	0.030	0.052	0.052	0.045	0.048	0.056	0.039	0.055	0.043	0.038	0.037	0.105	0.046	0.062	-	**	**	**	**	**	**
19	0.051	0.067	0.036	0.027	0.037	0.025	0.043	0.043	0.080	0.049	0.070	0.031	0.059	0.044	0.087	0.059	0.060	0.049	-	**	**	**	**	**
20	0.036	0.056	0.046	0.026	0.037	0.024	0.032	0.046	0.070	0.039	0.052	0.031	0.040	0.041	0.098	0.058	0.050	0.057	0.040	-	**	**	**	**
21	0.040	0.050	0.062	0.031	0.044	0.039	0.048	0.036	0.043	0.026	0.045	0.031	0.032	0.041	0.102	0.060	0.038	0.055	0.061	0.053	-	**	**	**
22	0.046	0.064	0.079	0.045	0.043	0.025	0.052	0.053	0.050	0.036	0.072	0.032	0.039	0.036	0.127	0.057	0.058	0.057	0.048	0.045	0.047	-	**	**
23	0.031	0.034	0.023	0.021	0.028	0.018	0.026	0.037	0.055	0.020	0.039	0.016	0.026	0.024	0.077	0.044	0.041	0.035	0.039	0.030	0.032	0.049	-	**
24	0.031	0.056	0.059	0.041	0.033	0.029	0.044	0.037	0.057	0.024	0.056	0.027	0.045	0.045	0.120	0.053	0.037	0.060	0.045	0.046	0.047	0.042	0.033	-

Table 3.6.2: Pairwise calculated values of the standardized measure F'ST (Meirmans & Hedrick 2011).

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**
2	0.255																						
3	0.289	0.228																					
4	0.190	0.288	0.192																				
5	0.178	0.227	0.229	0.133																			
6	0.177	0.307	0.245	0.145	0.094																		
7	0.208	0.355	0.240	0.156	0.147	0.146																	
8	0.209	0.248	0.200	0.128	0.173	0.133	0.233																
9	0.295	0.265	0.336	0.267	0.282	0.271	0.333	0.216															
10	0.146	0.255	0.214	0.149	0.162	0.109	0.157	0.162	0.200														
11	0.264	0.284	0.196	0.289	0.296	0.264	0.243	0.228	0.261	0.127													
12	0.131	0.227	0.171	0.128	0.152	0.082	0.152	0.150	0.200	0.097	0.264												
13	0.173	0.179	0.208	0.166	0.193	0.183	0.210	0.185	0.190	0.077	0.132	0.167											
14	0.174	0.272	0.177	0.129	0.187	0.146	0.192	0.194	0.220	0.074	0.210	0.118	0.094										
15	0.476	0.487	0.376	0.393	0.453	0.426	0.463	0.507	0.541	0.378	0.411	0.418	0.515	0.420									
16	0.196	0.359	0.351	0.208	0.268	0.195	0.275	0.190	0.284	0.201	0.286	0.220	0.218	0.236	0.533								
17	0.211	0.287	0.269	0.278	0.231	0.194	0.337	0.166	0.275	0.220	0.249	0.193	0.234	0.289	0.461	0.321							
18	0.235	0.286	0.256	0.176	0.285	0.291	0.256	0.273	0.269	0.202	0.274	0.245	0.191	0.205	0.481	0.247	0.336						
19	0.307	0.377	0.218	0.179	0.210	0.139	0.256	0.241	0.405	0.260	0.385	0.187	0.341	0.255	0.406	0.329	0.335	0.297					
20	0.225	0.326	0.290	0.180	0.231	0.151	0.212	0.285	0.352	0.223	0.273	0.191	0.225	0.256	0.465	0.343	0.271	0.353	0.252				
21	0.203	0.239	0.328	0.165	0.220	0.196	0.241	0.185	0.182	0.116	0.201	0.151	0.139	0.207	0.425	0.302	0.176	0.278	0.337	0.287			
22	0.231	0.311	0.417	0.250	0.209	0.114	0.259	0.275	0.214	0.162	0.328	0.154	0.179	0.169	0.531	0.282	0.279	0.286	0.245	0.237	0.208		
23	0.192	0.172	0.136	0.157	0.175	0.130	0.181	0.214	0.253	0.096	0.179	0.097	0.129	0.132	0.362	0.229	0.234	0.195	0.245	0.190	0.161	0.254	
24	0.155	0.292	0.328	0.242	0.161	0.141	0.223	0.197	0.268	0.107	0.286	0.140	0.225	0.236	0.520	0.278	0.179	0.326	0.240	0.274	0.227	0.193	0.196

Table 3.6.3: Pairwise calculated values of Jost's differentiation measure D (Jost 2008; below diagonal) and the 95 % confidence interval of each comparison (above diagonal).

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
1	-	0.093 0.510	0.179 0.396	0.141 0.386	0.068 0.469	0.093 0.363	0.079 0.490	0.123 0.443	0.188 0.554	0.056 0.395	0.114 0.533	0.032 0.350	0.081 0.398	0.083 0.401	0.130 0.609	0.066 0.465	0.135 0.406	0.134 0.487	0.201 0.440	0.091 0.495	0.096 0.460	0.142 0.412	0.115 0.428	0.079 0.385
2	0.302	-	0.111 0.329	0.199 0.485	0.140 0.408	0.176 0.544	0.207 0.616	0.144 0.490	0.116 0.644	0.094 0.629	0.100 0.650	0.121 0.467	0.072 0.378	0.088 0.615	0.254 0.664	0.176 0.628	0.117 0.579	0.160 0.551	0.241 0.547	0.142 0.585	0.112 0.553	0.162 0.580	0.096 0.374	0.150 0.618
3	0.288	0.220	-	0.099 0.304	0.096 0.394	0.076 0.342	0.151 0.358	0.104 0.286	0.158 0.567	0.086 0.411	0.089 0.377	0.048 0.300	0.079 0.276	0.105 0.323	0.153 0.643	0.196 0.522	0.122 0.465	0.144 0.459	0.121 0.375	0.163 0.432	0.218 0.494	0.226 0.530	0.037 0.340	0.100 0.567
4	0.264	0.342	0.201	-	0.112 0.249	0.103 0.254	0.100 0.323	0.087 0.297	0.177 0.437	0.124 0.268	0.217 0.406	0.040 0.377	0.096 0.255	0.055 0.302	0.247 0.476	0.129 0.422	0.180 0.496	0.069 0.357	0.097 0.385	0.130 0.301	0.125 0.309	0.095 0.382	0.104 0.343	0.134 0.498
5	0.269	0.274	0.245	0.181	-	-0.002 0.357	0.036 0.388	0.088 0.429	0.160 0.580	0.051 0.483	0.132 0.567	0.007 0.459	0.097 0.355	0.048 0.439	0.194 0.556	0.112 0.600	0.085 0.521	0.153 0.567	0.102 0.348	0.117 0.390	0.133 0.476	0.119 0.424	0.041 0.492	-0.017 0.550
6	0.228	0.360	0.209	0.179	0.177	-	0.051 0.329	0.012 0.320	0.180 0.517	0.069 0.282	0.115 0.442	0.043 0.218	0.100 0.326	0.073 0.296	0.201 0.490	0.092 0.437	0.091 0.417	0.196 0.471	0.022 0.323	0.092 0.283	0.122 0.420	0.055 0.293	0.052 0.348	-0.022 0.504
7	0.285	0.412	0.254	0.211	0.212	0.190	-	0.173 0.388	0.171 0.627	0.040 0.424	0.138 0.354	0.030 0.378	0.124 0.357	0.065 0.405	0.221 0.603	0.117 0.548	0.163 0.592	0.111 0.560	0.155 0.407	0.081 0.333	0.077 0.510	0.139 0.465	0.046 0.443	0.043 0.577
8	0.283	0.317	0.195	0.192	0.259	0.166	0.281	-	0.124 0.459	0.094 0.390	0.139 0.408	0.113 0.280	0.084 0.386	0.097 0.392	0.270 0.624	0.090 0.394	0.055 0.428	0.186 0.465	0.101 0.389	0.191 0.475	0.112 0.439	0.133 0.487	0.144 0.456	0.049 0.549
9	0.371	0.380	0.363	0.307	0.370	0.349	0.399	0.292	-	0.115 0.471	0.096 0.598	0.109 0.426	0.076 0.465	0.105 0.432	0.322 0.682	0.137 0.585	0.096 0.631	0.144 0.483	0.263 0.556	0.259 0.545	0.042 0.516	0.042 0.533	0.159 0.525	0.178 0.573
10	0.226	0.361	0.248	0.196	0.267	0.175	0.232	0.242	0.293	-	0.039 0.365	0.042 0.293	0.029 0.241	0.038 0.239	0.155 0.552	0.103 0.411	0.089 0.501	0.102 0.478	0.150 0.486	0.115 0.460	0.016 0.383	0.069 0.289	0.009 0.378	0.048 0.330
11	0.324	0.375	0.233	0.312	0.349	0.279	0.246	0.274	0.347	0.202	-	0.099 0.557	0.061 0.311	0.045 0.486	0.194 0.584	0.136 0.484	0.079 0.573	0.145 0.543	0.235 0.545	0.137 0.446	0.078 0.466	0.169 0.537	0.051 0.462	0.130 0.565
12	0.191	0.294	0.174	0.208	0.233	0.130	0.204	0.197	0.268	0.168	0.328	-	0.005 0.423	0.020 0.335	0.110 0.600	0.054 0.546	0.027 0.443	0.107 0.483	0.099 0.340	0.077 0.416	0.027 0.420	0.067 0.356	0.039 0.304	0.006 0.443
13	0.239	0.225	0.178	0.175	0.226	0.213	0.241	0.235	0.270	0.135	0.186	0.214	-	0.038 0.248	0.235 0.602	0.095 0.443	0.113 0.513	0.098 0.397	0.138 0.493	0.118 0.397	0.030 0.400	0.077 0.361	0.096 0.263	0.105 0.501
14	0.242	0.352	0.214	0.179	0.244	0.185	0.235	0.245	0.268	0.139	0.266	0.178	0.143	-	0.202 0.586	0.087 0.521	0.138 0.537	0.070 0.545	0.100 0.506	0.104 0.489	0.046 0.490	0.089 0.341	0.009 0.422	0.090 0.516
15	0.370	0.459	0.398	0.361	0.375	0.345	0.412	0.447	0.502	0.354	0.389	0.355	0.419	0.394	-	0.231 0.699	0.178 0.600	0.300 0.656	0.220 0.628	0.208 0.526	0.224 0.498	0.248 0.621	0.177 0.496	0.187 0.626
16	0.265	0.402	0.359	0.276	0.356	0.264	0.332	0.242	0.361	0.257	0.310	0.300	0.269	0.304	0.465	-	0.180 0.552	0.123 0.475	0.232 0.481	0.190 0.640	0.115 0.632	0.143 0.528	0.089 0.533	0.156 0.546
17	0.271	0.348	0.293	0.338	0.303	0.254	0.378	0.242	0.364	0.295	0.326	0.235	0.313	0.338	0.389	0.366	-	0.213 0.506	0.181 0.529	0.120 0.561	0.102 0.389	0.152 0.455	0.118 0.470	0.115 0.375
18	0.310	0.356	0.302	0.213	0.360	0.334	0.335	0.326	0.314	0.290	0.344	0.295	0.248	0.308	0.478	0.299	0.360	-	0.127 0.527	0.190 0.585	0.135 0.596	0.162 0.461	0.101 0.471	0.193 0.527
19	0.321	0.394	0.248	0.241	0.225	0.173	0.281	0.245	0.409	0.318	0.390	0.220	0.316	0.303	0.424	0.356	0.355	0.327	-	0.113 0.443	0.207 0.505	0.124 0.368	0.132 0.476	0.097 0.413
20	0.293	0.363	0.298	0.215	0.253	0.188	0.207	0.333	0.402	0.288	0.292	0.246	0.258	0.297	0.367	0.415	0.341	0.387	0.278	-	0.206 0.452	0.171 0.393	0.105 0.339	0.074 0.627
21	0.278	0.332	0.356	0.217	0.305	0.271	0.294	0.275	0.279	0.200	0.272	0.224	0.215	0.268	0.361	0.374	0.246	0.366	0.356	0.329	-	0.066 0.456	0.077 0.405	0.137 0.534
22	0.277	0.371	0.378	0.238	0.272	0.174	0.302	0.310	0.288	0.179	0.353	0.212	0.219	0.215	0.434	0.336	0.304	0.312	0.246	0.282	0.261	-	0.130 0.448	0.125 0.436
23	0.272	0.235	0.189	0.224	0.267	0.200	0.244	0.300	0.342	0.193	0.257	0.172	0.179	0.216	0.337	0.311	0.294	0.286	0.304	0.222	0.241	0.289	-	0.071 0.502
24	0.232	0.384	0.334	0.316	0.267	0.241	0.310	0.299	0.375	0.189	0.348	0.224	0.303	0.303	0.406	0.351	0.245	0.360	0.255	0.351	0.336	0.281	0.287	-

4

Patch connectivity and sand dynamics affect dispersal-related morphology of the blue-winged grasshopper *Oedipoda caerulescens* in coastal grey dunes [1]

Contents

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[1] This chapter has been published as:

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Abstract

Anthropogenic land use leads to increasing habitat fragmentation and habitat loss for many species. Exchange of individuals between and recolonisation of habitat patches is essential for the stability and long-term survival of populations in fragmented landscapes. Interpatch dispersal depends on the dispersal ability of species and on landscape structure. In this study, we analyzed the influence of patch size, patch connectivity and sand dynamics on thorax- and wing length as proxies for dispersal ability of the blue-winged grasshopper *Oedipoda caerulescens* in coastal grey dunes. Our study revealed that sand dynamics and patch configuration had clear though sex-specific effects on dispersal-related morphology. Males were smaller and had shorter wings if patches became larger and less connected. In addition, both sexes were larger in habitat patches with high sand dynamics compared to those in patches with lower dynamics. Investments in wing length were only larger in connected populations when sand dynamics were low, indicating that both landscape and patch-related environmental factors are of importance. The observed effect of landscape characteristics on morphology agrees with predictions from theoretical models on the evolution of dispersal in metapopulations. However, as effects appear to be less pronounced in females, it is possible that selection pressures act differently on both sexes. An alternative explanation, however, would be that the observed patterns could be due to sex-specific phenotypic plasticity. The presented results add to the evidence that dispersal-related morphology varies according to expectations on dispersal evolution in recently structured populations at small spatial scales.

4.1 Introduction

Habitat fragmentation and loss are the main factors for the increasing extinction risk of populations in landscapes shaped by anthropogenic land use. For the survival of animal populations in fragmented landscapes, the rate of exchange of individuals between habitat patches is crucial and considered a key process for the persistence of metapopulations and spatially structured populations (Hanski 1994, Gustafson and Gardner 1996, Hill et al. 1996, Moilanen and Hanski 1998, Moilanen and Nieminen 2002, Baguette et al. 2003). Interpatch dispersal depends on (i) the dispersal ability of species, i.e. the combination of genetic, physiological and morphological factors that facilitate dispersal, and (ii) landscape structure. Besides the spatial configuration of habitat patches (Gustafson and Gardner 1996, Zollner and Lima 1999, King and With 2002, Hein et al. 2004, Pfenning et al. 2004), the nature (i.e. permeability) of the landscape matrix, in which dispersal takes place, also greatly affects realised dispersal (Gustafson and Gardner 1996, Moilanen and Hanski 1998, Thomas et al. 2001b, Wiens 2001, Hein et al. 2003).

In addition to these direct effects on dispersal, landscape structure on its own is known to act as an evolutionary selection agent because it determines the costs and benefits of dispersal (Olivieri et al. 1995, Olivieri and Gouyon 1997, Merckx et al. 2003, Merckx and Van Dyck 2006). Both morphological and behavioural traits of individuals and the degree to which a certain genotype responds to environmental variation have heritable components, and are therefore expected to be able to respond to selection pressures (Thomas et al. 1998, Hill et al. 1999a, Roff and Fairbairn 2001, Price et al. 2003, Bonte and Lens 2007).

Several studies on butterflies and damselflies revealed differences in dispersal-related traits depending on landscape structure (Dempster 1991, Taylor and Merriam 1995, Thomas et al. 1998, Hill et al. 1999b, Norberg and Leimar 2002, Merckx et al. 2006). Traits, which are important for successful dispersal, such as body size, thorax mass, wing development or habitat-finding ability can vary depending on patch connectivity (isolation of populations) or the degree of landscape fragmentation (Wagner and Liebherr 1992, Wootton 1992, Taylor and Merriam 1995, Norberg and Leimar 2002, Berggren 2005b, Merckx and Van Dyck 2006, 2007).

In the current study, we investigated the influence of habitat fragmentation on dispersal-related morphology (body size and wing length) of the blue-winged grasshopper *Oedipoda caerulescens* (LINNAEUS 1758; Orthoptera: Acrididae) at a small spatial scale. Within one landscape, we chose habitat patches varying in patch size, patch connectivity and sand dynamics. For biochemical and energetic reasons, migrating individuals should be large to maximize the distance they can travel without refuelling (Roff 1991, Roff 2002). In addition, several studies have shown that migrants are larger than none-migrants, and that flight- and acceleration capacity, for example, is positively correlated with body size (Davis 1984, 1986, Denno 1994, Kuussaari et al. 1996, Berwaerts et al. 2002). With regard to flight morphology of dispersing individuals, relatively longer wings (higher aspect ratio) may be more advantageous for forward flight, improve the efficiency of prolonged flights and increase acceleration capacity or flight speed (Marden 1987, Dudley 1990, Wootton 1992, Berwaerts et al. 2002). This has also been recorded in an experiment to investigate flight responses after disturbance by humans (Bonte unpublished data). Here, larger females made significantly longer flight distances compared to males (mean flight distance females: 24.3 ± 4.6se meters (n=45), mean flight distance males: 7.6 ±2.0 se meters (n=86)). Within sexes, this flight distance depended on the subpopulation in question (those from open landscapes had higher tendencies to cross shrubs, and subsequently larger flight distances) and on the size (with smaller females making shorter distances; for males the same tendency was observed). However, within a certain landscape entity (a set of connected grey dunes; see Maes et al. 2006), seasonal displacements were not related to body size in both males and females. But of course, given the difficulty to track dispersal events in CMR (capture-mark-recapture) methods (Van Dyck and Baguette 2005), this is likely due to the fact that observed displacements represent sequences of daily routine movements rather than dispersal as such. Therefore, based on our observations of special movements after disturbance, we expect dispersive individuals of *O. caerulescens* to be large with long wings.

According to metapopulation theory, dispersal rates increase in patches with high probability of extinction. However, if the quality of the matrix habitat also deteriorates, leading to increased mortality during migration, the evolutionary response is more complex with evolution tending to increase dispersal rates when patches remain largely empty (Heino and Hanski 2001). As such, opposing forces of selection for and against dispersal change with the relative size and the environmental qualities of the source and sink habitats (Mathias et al. 2001) or the resource grain (Baguette and Van Dyck 2007). Based on predictions from above mentioned theory, we expect that large habitat patches will deter individuals from emigrating because of their good quality (i.e. high resource abundance) (e.g., Kuussaari et al. 1996, Schtickzelle and Baguette 2003). Therefore we expected that individuals from large and continuous sites show a lower investment in dispersal-related morphology (Bonte et al. 2003, Fred and

Brommer 2003). Low patch connectivity is also expected to select against dispersal of individuals because low connectivity increases dispersal costs (Bonte et al. 2006). High connectivity, on the other hand, is expected to lead to an increase in mobility facilitated by individual size and wing length (Hanski et al. 2004). Patches with high sand dynamics represent habitat of low stability, where local populations may frequently become extinct. Such patches may be recolonized by dispersive individuals, which are more likely to establish new populations than sedentary ones (Hanski et al. 2002, Hanski et al. 2004). This should lead to increased dispersal ability (e. g. large size and long wings) of individuals in patches with high sand dynamics.

4.2 Material and methods

Study species

The blue-winged grasshopper *O. caerulescens* (LINNAEUS 1758; Orthoptera: Acrididae) is a thermo- and xerophilic grasshopper species of medium to large size (body length: 15-30 mm) (Detzel 1998). This species is discontinuously distributed in Flanders (North Belgium). *O. caerulescens* inhabits stony calcareous meadows with sparse vegetation, quarries and sand pits and can also be found in dry heathlands, spoil heaps and railroad yards (Schlumprecht and Waeber 2003). In coastal areas this species is restricted to dynamic grey dunes (Provoost and Bonte 2004). *O. caerulescens* is described as moderately sedentary although some individuals moved over long distances of up to 833 m between different habitat patches in a mark-recapture study (Maes et al. 2006). Mean daily moved distances of this species is 5.7 m (0.1-77 m) and 4.5 m (0.5-23 m) for daily movements in habitat and 9.5 m (0.5-39 m) for non-habitat (Hein et al. 2005, Heidinger et al. 2009). Direct observations of spontaneous flights over 100 m are occasionally reported (Detzel 1998). Due to the rarity of grey dune habitats *O. caerulescens* is listed as Vulnerable in Flanders (Decleer et al. 2000).

Methods

The study was carried out in the Westhoek Nature Reserve (De Panne, Belgium; 51°03’ N-51°05’ N, 2°34’ E). Within an area of 6.94 km2 we chose 21 study sites, which all represented typical grey dunes characterised by open sand, moss and herbaceous plants but varying in terms of size, connectivity and the degree of sand dynamics. Mean patch size of these 21 sites was 9.19 ha (7.19 ha-10.69 ha). Using Hanski’s connectivity measure (Hanski 1994), mean patch connectivity was calculated using the following equation: $Si = \sum j{\neq}i \exp(-\alpha dij)Nj$ where α is a constant describing the strength of the inverse relationship between numbers of migrants from patch j and distance between patches, and Nj is the size of patch j multiplied by the population size at patch j. Parameter value α was set to 25 (Appelt and Poethke 1997, Maes et al. 2006). The mean value of patch connectivity was 0.24 (0.00-1.18). We measured levels of sand dynamics by digging jars with diameter 9 cm and depth 20 cm into the soil. Sand accumulation from August 29th till September 20th was used as a proxy of sand displacement. A total of five sand traps, randomly located in each patch were used. The mean sand deposition was 8.26 cm (1.0-17.5 cm).

To assess morphometrics of individual blue-winged grasshoppers, we caught 177 females and 366 males, originating from these 21 different habitat patches. The sampling took place from 21/7/2005 till 10/10/2005 by hand net (0.4 m diameter). All patches were frequently and randomly visited during the season. Each individual was morphologically characterised in terms of thorax length (total length of dorsal pronotum) and wing length (total length of forewing) as a measure of body size and flight ability, respectively. All measurements were taken directly in the field with a digital measuring calliper with a precision of 0.03 mm (TCM).

Statistical analyses

Linear mixed-effects models were applied to analyse the effects of patch characteristics on morphometric parameters. As individuals caught on the same patch are non-independent replicates, we used 'patch' as a random effect in all models. Patch size, patch connectivity and sand dynamics were chosen as explanatory variables. In order to test for differences in individual investment in wing length, body size (thorax length) was retained as a covariate, hence allowing the analysis of residual values. Starting from a full model (all main factors and all two-way interaction terms), model selection was conducted by stepwise backward elimination of non-significant interaction terms with p-values above 0.15. We did not remove main factors, even if they were non-significant. Sequential type III sums of squares were used in all F-tests to analyze whether a significant proportion of variance in morphometric parameters could be explained by the patch characteristics. Parameter estimates were obtained using the restricted maximum log-likelihood (REML) method. We used log-likelihood (ML) fits for model comparison with Akaike's Information Criterion as model selection criteria. As females and males of *O. caerulescens* differ in morphology and mobility (Detzel 1998, Maes et al. 2006), we run the analyses on the influence of patch characteristics separately for each sex. Differences in morphological traits between females and males were tested with t-tests for independent samples. All analyses were conducted with the statistics software package R 2.6.2 (r-project.org).

4.3 Results

Morphometrics differed significantly between sexes. Compared to females, males were smaller (unpaired t-test: t311.68 = -49.60; $p < 0.001$) and had shorter wings in absolute terms (unpaired t-test t291.11 = -51.60; $p < 0.001$), but longer wings relative to their thorax length (unpaired t-test t538.00 = 7.71; $p < 0.001$).

The analyses separated by sex revealed that males were smaller and had shorter wings if patches became larger and less connected. Males in habitat patches with high sand dynamics were larger compared to males in patches with lower dynamics (Table 4.3.1). Residual wing length, i.e. wing length corrected for body size decreased with patch size (Table 4.3.1), but increased when highly connective patches showed low sand dynamics (interaction sand dynamics x Connectivity: Table 4.3.1, Figure 4.3.1a).

In contrast, females' thorax length showed no relation to patch size and patch connectivity, although directions of the responses were similar in both sexes. But as for males, females were larger in habitat patches with high sand dynamics compared to those in patches with lower dynamics (Table 4.3.2). Female residual wing length showed similar patterns as for males (Table 4.3.2, Figure 4.3.1b). Overall levels of significance were tendentious at the 0.05-level and in accordance with our expectations based from metapopulation theory.

Table 4.3.1: Effect of patch characteristics on morphometrics of males. Estimates, standard errors of estimates (SE), denominator degrees of freedom (Den. d.f.), F and p- values of mean effects as derived from a linear mixed-effects model after model selection are given.

Factor	Estimate (b)	SE	Den. d.f.	F-value	p-value
Thorax length					
Intercept	4.25	0.17	343	601.34	<0.001
Patch size	-0.04	0.02	16	6.46	0.022
Connectivity	0.27	0.09	16	8.94	0.009
Sand dynamics	0.02	0.01	16	14.14	0.002
Wing length					
Intercept	10.31	0.68	342	232.09	<0.001
Thorax length	2.06	0.14	342	232.35	<0.001
Patch size	-0.15	0.04	15	17.68	<0.001
Connectivity	1.00	0.42	15	5.74	0.030
Sand dynamics	0.03	0.01	15	3.97	0.065
Connectivity*Sand dynamics	-0.11	0.05	15	4.78	0.045

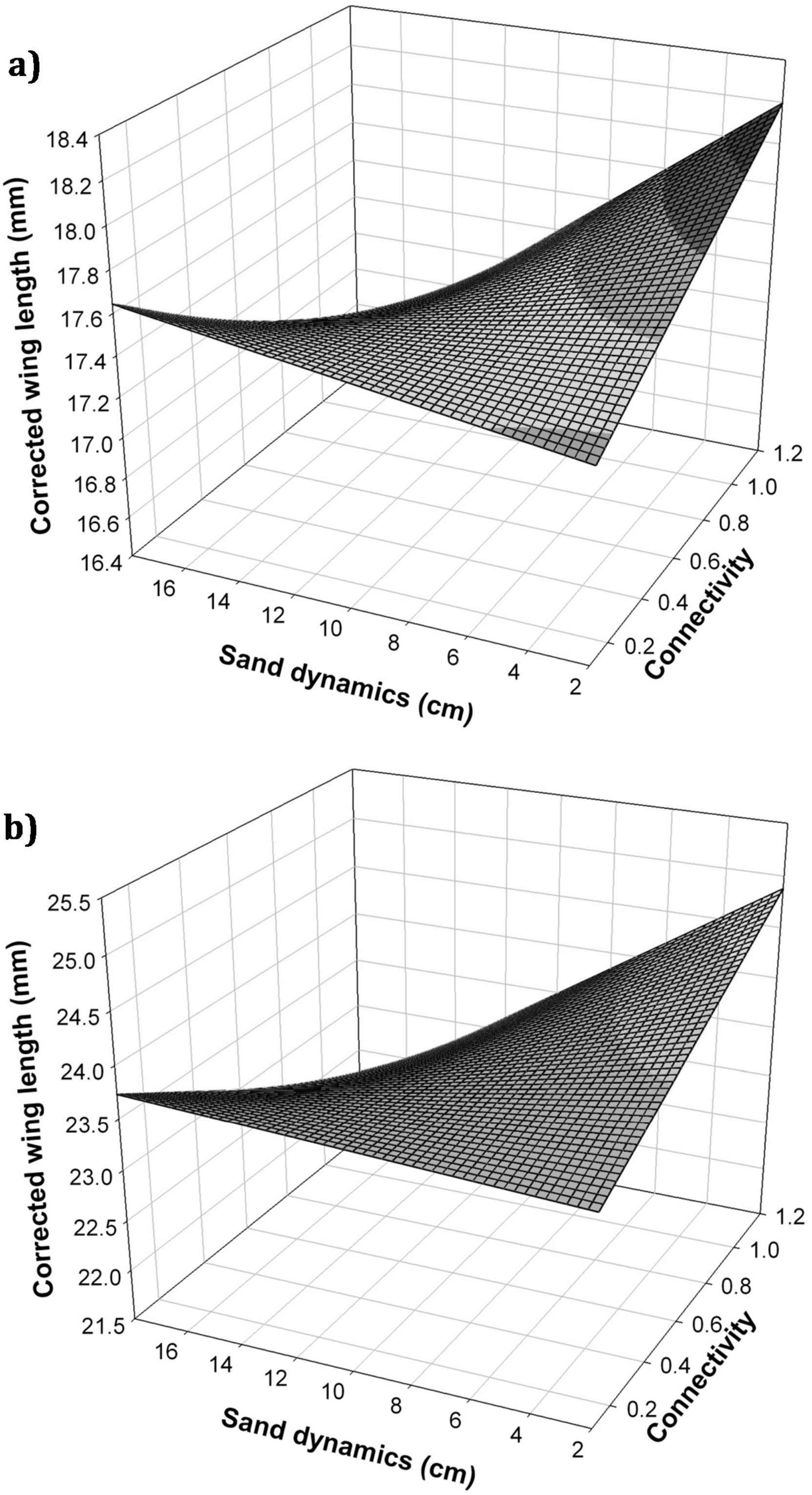

Figure 4.3.1: Modelled wing length of both males (1a) and females (1b) in relation to patch connectivity and sand dynamics. Estimated wing length is estimated with model parameters given in Table 1 and Table 2 for average sized grasshoppers inhabiting patches of average size (i.e., estimates are corrected for variation in body size and patch area).

Table 4.3.2: Effect of patch characteristics on morphometrics of females. Estimates, standard errors of estimates (SE), denominator degrees of freedom (Den. d.f.), F and p- values of mean effects as derived from a linear mixed-effects model after model selection are given.

Factor	Estimate (b)	SE	Den. d.f.	F-value	p-value
Thorax length					
Intercept	5.58	0.22	163	643.52	<0.001
Patch size	-0.04	0.02	10	2.79	0.126
Connectivity	0.21	0.14	10	2.43	0.150
Sand dynamics	0.02	0.01	10	6.64	0.028
Wing length					
Intercept	11.52	1.33	162	74.89	<0.001
Thorax length	2.24	0.21	162	110.47	<0.001
Patch size	-0.13	0.06	9	5.04	0.052
Connectivity	1.57	0.73	9	4.60	0.061
Sand dynamics	0.03	0.03	9	1.05	0.332
Connectivity*Sand dynamics	-0.17	0.09	9	3.85	0.081

4.4 Discussion

Our results clearly demonstrate that patch characteristics such as patch size, patch connectivity and sand dynamics have clear effects on thorax length and wing length as proxies for dispersal ability. Males of *O. caerulescens* were smaller and had shorter wings if patches became larger and less connected. Furthermore, both sexes of this species were larger in habitat patches with high sand dynamics compared to males and females in patches with lower dynamics. This field study also confirmed differences in size and wing length between the sexes (Detzel 1998, Picaud and Petit 2008).

Patch area is often related to good habitat quality and therefore deters individuals from emigrating (Kuussaari et al. 1996, Bonte et al. 2003, Schtickzelle and Baguette 2003). This results in decreased emigration rates out of large habitat patches in fragmented landscapes (Hill et al. 1996, Thomas and Hanski 1997, Kindvall 1999, Baguette et al. 2000, Hanski et al. 2000, Petit et al. 2001, Wahlberg et al. 2002, Baguette et al. 2003). Hence, selection pressure on dispersal is assumed to be low in large patches, and individuals are believed to invest rather in reproduction than in dispersal-related traits (Zera and Denno 1997, Hughes et al. 2003, Gu et al. 2006). In the current study, males from large habitat patches showed lower investment in dispersal-related morphology as they were smaller and had shorter wings. We did, however, not collect reproduction-related traits like investments in egg production, spermatophores or song frequency.

Alternatively, because patch area and habitat quality, are positively linked to population size and population viability (Bonte et al. 2003, Fred and Brommer 2003), individuals inhabiting small patches experience high probabilities of extinction due to demographic or environmental stochasticity, recently documented for specialised dune arthropods in general and leading to recurrent colonisation processes (Hanski 1999, Bonte and Maes 2008). In our study system an increased investment in dispersal-related traits of males from small habitat patches could arise if populations in small patches frequently become extinct and if these patches get recolonized by dispersive individuals which are more likely to establish new populations than sedentary ones (Thomas et al. 1998, Thomas et al. 2001a, Hanski et al. 2002, Hanski et al. 2004).

Low patch connectivity increases the costs of dispersal and thus will select against dispersal and related morphological traits of individuals (Dempster et al. 1976, Dempster 1991, Baguette et al. 2000, Baguette et al. 2003, Bonte et al. 2006). In contrast, high patch connectivity facilitates interpatch dispersal leading to an increase in large and more dispersive individuals (Hanski et al. 2004). This is mirrored in our experiment, as higher investment in dispersal ability of males (and females – despite lower levels of significance) in patches with high connectivity, appears to be reflected in both body size and wing length.

As in temporary habitats, where dispersal-related traits like wing length are favoured for reasons of habitat escape (Denno et al. 1991, Denno 1994), males of habitat patches with high sand dynamics were larger and had longer wings compared to those inhabiting patches with low dynamics. Habitat patches with high sand dynamics may represent temporary habitats in which populations frequently become extinct and abandoned patches are recurrently colonized by dispersive individuals (Thomas et al. 1998, Hill et al. 1999b, Thomas et al. 2001a, Hanski et al. 2002, Hanski et al. 2004). In addition, dynamic dunes consist of open landscapes with low and less dense vegetation (Provoost 2004) in which exchange between habitat patches may be less restricted for this species and costs of dispersal can be expected to be low.

When edges between habitat and matrix are soft, and as such not function as barriers for regular movements, interpatch dispersal can be achieved by routine movements instead of directed dispersal by special, long, continuous flights (Bonte et al. 2004, Van Dyck and Baguette 2005). And although patch connectivity can act as a selection agent on dispersal-related morphological traits, this factor may be of less importance in dynamic dunes. This may lead to the finding that males and to a lesser extend also females from patches with high connectivity but low sand dynamics had longer wings compared to males in patches with high connectivity and high dynamics. As the investigated patch characteristics can be positively linked to habitat quality (Kuussaari et al. 1996, Bonte et al. 2003, Schtickzelle and Baguette 2003, Maes and Bonte 2006), not solely landscape structure, but also landscape quality could influence species' morphology. Apart from that, interpretation of morphological differences among populations is difficult, as morphological traits (especially body size) are multifunctional (Hill et al. 1999b, Van Dyck and Matthysen 1999, Norberg and Leimar 2002) and can be related to thermoregulation (Prange and Pinshow 1994, Kemp and Krockenberger 2004, Verdu et al. 2006), predator avoidance and escape (Rydell and Lancaster 2000) or mate location and foraging (Denno and Roderick 1990, Denno 1994).

Both local adaptation and phenotypic plasticity can generate these patterns of variation in dispersal-related traits. Our correlative study, however, does not allow the delineation of the underlying mechanisms. Rather, we show that both remain plausible. In case of ultimate mechanisms related to local adaptation, however, similar effects on females' dispersal-related morphology would be expected unless selection pressures act differently on both sexes (Srygley and Chai 1990, Hanski et al. 2002, Hanski et al. 2004). Although morphology of both sexes responded in the same direction to habitat fragmentation, in females, only thorax length was significantly linked to sand dynamics. This might indicate sex-specific costs and benefits of investment in dispersal-related morphology. As fecundity of insect females is generally positively correlated with body size and negatively associated with flight capability, females' morphology may be shaped rather by factors concerning reproduction than by patch characteristics facilitating or impeding dispersal (Denno et al. 1989, Roff and Fairbairn 1991, Zera and Denno 1997, Nylin and Gotthard 1998, Zera and Zhao 2003, Hanski et al. 2004). Such a trade-off (oogenesis-flight syndrome) is proposed as a general relationship (Johnson 1969) and trade-offs between dispersal ability or mobility and reproduction are very common (Dingle 1996, Zera and Denno 1997, Zera and Harshman 2001, Turlure et al. 2009). Nevertheless, there are many exceptions and its validity is still debated (Dempster et al. 1976, Hill et al. 1999b, Hanski et al. 2006).

In conclusion, dispersal-related morphology of male blue-winged grasshoppers is significantly linked to the fragmentation of grey dune habitat in coastal areas. The observed changes are in agreement with predictions from models of the evolution of dispersal in metapopulations (Clobert et al. 2004). However, because effects appear to be less pronounced in females (especially with respect to body size), different selection pressures may act differently on both sexes.

Alternatively, observed patterns can be due to sex-specific phenotypic plasticity. Irrespectively of the underlying mechanisms, our results add to the evidence that dispersal-related morphology varies and is selected upon in recently structured populations at small spatial scales.

5

Biased dispersal of *Metrioptera bicolor*, a wing dimorphic bush cricket [1]

Contents

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[1] This chapter has been submitted for publication as:
Heidinger IMM, Hein S, Feldhaar H and Poethke H-J (submitted) Biased dispersal of *Metrioptera bicolor*, a wing dimorphic bush cricket.

Abstract

In the highly fragmented landscape of central Europe, dispersal is a key process of particular importance as it determines the long-term survival of animal populations. Dispersal not only secures the re-colonisation of patches where populations went extinct, it may also rescue small populations and thus prevent local extinction events. As dispersal involves different individual fitness costs, the decision to disperse should not be random but context-dependent (e.g. sex- and wing morph-biased dispersal). Although biased dispersal has far-reaching consequences for animal populations, immediate studies of sex- and wing morph-biased dispersal in orthopterans are very rare. Here, we used a combined approach of morphological and genetic analyses to investigate biased dispersal of *Metrioptera bicolor*, a wing dimorphic bush cricket. Our results clearly show wing morph-biased dispersal for both sexes of *M. bicolor*. In addition, we found sex-biased dispersal for macropterous individuals, but not for micropters. Both, morphological and genetic data, favour macropterous males as dispersal unit of this bush cricket species. To get an idea of the flight ability of *M. bicolor*, we compared our morphological data with that of *Locusta migratoria* and *Schistocerca gregaria*, which are proved to be very good flyers. Based on our morphological data, we suggest a good flight ability for macropters of *M. bicolor*, although flying individuals of this species are seldom observed.

5.1 Introduction

Habitat fragmentation and destruction due to anthropogenic land use are the major causes of the increasing extinction risk of many species and have a detrimental impact on animal populations in numerous ways (Saunders and Hobbs 1991, Abbitt et al. 2000, Fahrig 2002, 2003). The long-term survival of spatially structured populations in fragmented landscapes largely depends on dispersal and the associated exchange of individuals and genetic material between habitat patches (Andrén 1994, Hanski and Thomas 1994, Thomas 2000, Ronce 2007). Dispersal not only secures the re-colonisation of patches where populations went extinct (Fahrig and Merriam 1994), it may also rescue small populations and thus prevent local extinction events (Brown and Kodric-Brown 1977).

However, to leave the natal habitat and disperse can be risky and involve different individual fitness costs like increased predation risk, energy expenditure, costs of developing dispersal-related traits, failure to find new suitable habitat as well as reproductive costs (Tanaka 1976, Rankin and Burchsted 1992, Roff and Fairbairn 2007, Hovestadt and Nieminen 2009, Bonte et al. 2012). Therefore, the decision to disperse should not be random but depend on the developmental stage or the physiological condition of an individual just as on actual environmental conditions (context-dependent dispersal; Ims and Hjermann 2001, Bowler and Benton 2005, Matthysen 2005).

Sex-biased dispersal, where the propensity to disperse is linked to the gender of an individual, is one example for context-dependent dispersal which can be found in different animal classes including insects (e.g. Markow and Castrezana 2000, Sundström et al. 2003, Beirinckx et al. 2006, Lagisz et al. 2010). Four main hypotheses have been established to explain sex-biased dispersal: local mate competition (Greenwood 1980, Dobson 1982), local resource competition (Clarke 1978, Greenwood 1980), inbreeding avoidance (Dobson 1982, Wolff 1994) and cooperative behaviour among kin (Perrin and Goudet 2001, Le Gaillard et al. 2006). No bias in dispersal is expected when local competition equally affects both sexes, as it is the case in monogamous breeding systems and also in polygynous or promiscuous ones as long as female fitness is limited by extrinsic factors (e.g. food or nesting sites; Perrin and Mazalov 2000). For polygynous or promiscuous systems, male-biased dispersal is predicted when local mate competition exceeds local resource competition and when female fitness is limited by intrinsic factors (maximal rate of processing resources) rather than by resources themselves (Perrin and Mazalov 2000). Female-biased dispersal is predicted in monogamous systems under intense local resource competition among females (Greenwood 1980). Although sex-biased dispersal is well documented for some taxa (e.g. Clarke et al. 1997, Hutchings and Gerber 2002, Lawson Handley and Perrin 2007), studies of sex-biased dispersal in orthopterans are very rare.

Furthermore, to disperse or not can also be a matter of the morphology or physiology of an individual. Dispersal polymorphism is a widespread phenomenon in Orthoptera and many other insect groups, where two distinct morphs (sedentary and dispersal) can be distinguished (Harrison 1980, Zera and Denno 1997, Ingrisch and Köhler 1998). The macropterous (long-winged) morph of insect species is generally assumed to serve as dispersal unit, which maintains the gene flow between populations (Vickery 1965, Peterson and Denno 1997, Simmons and Thomas 2004). However, having long wings does not necessarily imply that such individuals do disperse or are good flyers (Roff 1986, Ritchie et al. 1987, Roff and Fairbairn 1991, Gäde 2002, Kutsch et al. 2002, Socha and Zemek 2003).

In this study, we used a combined approach of morphological and genetic analyses, to investigate sex- and wing morph-biased dispersal of *Metrioptera bicolor*, a wing dimorphic bush cricket. Most individuals of this species are short-winged (micropterous) and flightless. In contrast, long-winged (macropterous) animals are able to fly (Voisin 1982, Nadig 1988) but are rare in natural populations (mean: 1.1 %; max.: 5.3 %; total of 661 individuals sampled at 8 sites; Heidinger unpublished data). The mean proportion of macropterous females and males is approximately equal (mean females: 0.6 %; max females: 2.6 %; mean males: 0.4; max males: 2.6; total of 661 individuals sampled at 8 sites; Heidinger unpublished data).

5.2 Material and methods

Study species

The two-coloured bush cricket *M. bicolor* (PHILIPPI 1830; Orthoptera: Tettigoniidae) is a medium-sized (body length: 15-18 mm), thermo- and xerophilic bush-cricket (Detzel 1998, Ingrisch and Köhler 1998). It is orientated towards vertical structures and thus prefers long lawn biotopes. *M. bicolor* mainly inhabits semiarid grassland but can also be found on juniper heath or poor and sandy grassland (Detzel 1998, Ingrisch and Köhler 1998). Individuals of this species are usually short-winged (micropterous). The fore wings (elytra) of micropterous males cover at least half of their abdomen but never exceed the abdomen. Micropterous females have even shorter elytra (usually shorter than the half of their abdomen) and the hind wings (alae) of both sexes are tiny rudiments. The elytra and alae of long-winged (macropterous) females and males are considerably longer than their abdomen with rounded wing tips. Occasionally, brachypterous individuals with intermediate wing forms can be found in natural populations. Their elytra and alae are shorter with pointed tips compared to macropters and only slightly longer than their abdomen (Heidinger unpublished data).

Sampling

All sampling sites are situated in the rural district 'Hassberge' in Northern-Bavaria, Germany (50° 02′ 13.84″ N, 10° 30′ 57.69″ E). For the morphological analysis, 22 macropterous females and 18 macropterous males of *M. bicolor* were caught together with one micropterous individual of the corresponding sex at 19 different grassland sites (17 sites were also sampled for the genetic analysis see below). All individuals were stored at -20 °C until further analysis. For the genetic analysis, 957 adult individuals (456 micropterous females, 21 macropterous females, 466 micropterous males and 14 macropterous males) were caught at 24 different grassland sites. Genetic material was obtained by sampling one hind leg from each individual directly in the field. All animals, except the individuals for the morphological analysis, were released directly afterwards at the sites where they have been caught. The legs were stored in 100 % ethanol p.a. for further analysis.

Morphological analyses

Initially whole animals were weighted to the nearest 0.1 mg with a Mettler AE 163 analytical balance and their head width was determined as a measure of body size, because head width (in contrast to total body length which includes the soft abdomen) does not depend on the nutritional condition or the reproductive status of an individual. The head width was measured using a stereomicroscope with a micrometre ocular at 16-fold magnification. Scale units of the ocular were converted into millimetres by a microscope slide with millimetre scaling (Eschenbach, scale accuracy 0.01 mm). Afterwards head, wings, legs, thorax, and abdomen were dissected and stored separately until further analysis at -20 °C.

To determine the flight muscle mass, dissected thoraces without legs, wings, and oesophagus were weighed to the nearest 0.001 mg using a Mettler MT5 analytical balance, dried for three days to a constant weight at 60 °C in a drying oven, and weighed again to the nearest 0.001 mg. After 3 days soaking in 1 ml NaOH (0.35 mol/l), thoraces were rinsed two times with distilled water to remove all muscle tissue and dried again for two days at 60 °C to a constant weight. Subtraction of exoskeleton mass from original thorax mass yields the weight of flight muscle mass (Marden 1987), which divided by the body weight provides the relative flight muscle mass (flight muscle ratio), a size-independent measurement of flight performance of animals (Marden 1989, 2000). The maximum force generated by a flying animal is almost entirely determined by its flight muscle mass (Marden 1987). Therefore, the ratio of force to mass, and thereby acceleration, should be proportional to the ratio of flight muscle mass to total body mass (Marden 1989), and individuals with high values for the flight muscle ratio should have a great aerial acceleration.

Bush crickets and grasshoppers exhibit two pairs of wings. However, the fore wings are almost meaningless for the flight ability of orthopterans, which primarily depends on their hind wings (Detzel 1998). Hence, only the latter were spread on a microscope slide with millimetre scaling (Eschenbach, scale accuracy 0.01 mm) to take a picture with a Nikon Coolpix 4500. Using ImageJ 1.36b (Abramoff et al. 2004), the wing length and wing area were determined, and the aspect ratio was calculated as wing length squared, divided by the wing area (Marden 1987, Kutsch et al. 2002). High aspect ratio values indicate narrow wings, whereas low values indicate short, stubby wings. Relatively longer wings (higher aspect ratio) may be more advantageous for forward flight, improve the efficiency of prolonged flights, and increase acceleration capacity or flight speed (Marden 1987, Dudley 1990, Wootton 1992, Berwaerts et al. 2002). All three measures were obtained for both hind wings separately and arithmetically averaged for each individual. In addition, wing load, also a size-independent measurement of flight performance, was calculated as body weight, divided by the arithmetic mean of the area of both hind wings (Marden and Waage 1990, Marden and Rollins 1994). Individuals with a low wing load carry less body weight per unit wing area and individuals with relatively longer wings require less induced power to counteract their weight (Ellington 1984). Thus, low wing load and high aspect ratio should enhance lift production and takeoff ability of animals (Savile 1957). In addition, individuals with low wing load could also benefit from low energetic costs of flight (Angelo and Slansky 1984). For this analysis, only macropterous individuals were used, because micropterous individuals have very tiny hind wings (2-3mm; Heidinger unpublished data).

Microsatellite analysis

DNA was extracted from the femur muscle using the Puregene DNA Purification Kit by Gentra Systems according to the manufacturer's recommendation and stored in 50 µl low TE-buffer at -20 °C. An amplification reaction was performed in a Biometra or an Eppendorf thermocycler in a total reaction volume of 12.5 µl. Each reaction contained approximately 40 ng of template DNA, 10x PCR-Puffer, 2 mM $MgCl_2$ and 0.5 U of Taq DNA polymerase (*MolTaq* basic by Molzym GmbH), 0.2 mM dNTPs (PureExtreme™ dNTPs by Fermentas Life Sciences) and 0.2 µM of each primer (forward primer labelled with fluorescent IR-700 or IR-800 dye by Licor). The thermal cycling protocol consisted of an initial denaturation at 95 °C for 3 min followed by 30 cycles of 30 sec denaturation at 95 °C, with 30 sec annealing at 55.5°C, and 30 sec elongation at 72 °C. A final elongation step was performed at 72 °C for 3 min. PCR products were diluted 1:15 and analysed on a LI-COR Biosciences 4300 DNA Analyser. All samples were analysed at six polymorphic microsatellite loci developed for *Metrioptera roeselii*: MR3-12, MR2-16, MR3-24, MR3-34, MR2-42 and MR3-44 (Holzhauer and Wolff 2005).

Using Micro-Checker 2.2.3 (Van Oosterhout et al. 2004), we checked data for the presence of large allele dropout and scoring errors due to stuttering. Null allele frequencies per locus calculated with INEst ranged from 0.018 to 0.298, with a mean of 0.111 ± 0.128. The values obtained via FreeNA ranged from 0.093 to 0.280, with a mean of 0.170 ± 0.096. Such values are not unusual for orthopterans (Chapuis et al. 2008, Lange et al. 2010) and are very common in studies dealing with microsatellite data (Dakin and Avise 2004). We detected high proportions of null alleles (estimator of Dempster) in MR3-34, MR2-42 and MR3-44 (see also Holzhauer et al. 2009, Lange et al. 2010, Heidinger et al. 2013). All sampling sites displayed high levels of allelic variability (see table 3.3.1). Significant linkage disequilibrium was present in 19 out of 360 pairs of loci, but this was unlikely due to true physical linkage as significant linkage was not restricted to specific pairs of loci throughout. Furthermore, all p values obtained after a sequential Bonferroni adjustment for multiple tests were nonsignificant. For all sampling sites we found significant multi-locus deviation from Hardy-Weinberg equilibrium ($p < 0.0001$), associated with positive F_{IS} values (see table 3.3.1), i.e. heterozygote deficiencies. This is most probably due to the presence of null alleles (see above).

Data analysis

Differences in morphological traits between females and males of *M. bicolor* were tested with Mann-Whitney U tests for independent samples. To compare the morphology of micropterous and macropterous individuals, we used Wilcoxon tests for two dependent samples (matching micropterous and macropterous individuals of the same sex from the same site). All analyses were conducted with the statistics software package R 2.10.1 (r-project.org). Using Fstat 2.9.3.2 (Goudet 2001), we analysed the genetic data for evidence of sex-biased and wing morph-biased dispersal. We conducted the analysis for females and males as well as for micropterous and macropterous individuals separately.

To detect biased dispersal, Fstat uses several statistical descriptors of an individual's genotype. For example, the inbreeding coefficient FIS (Weir and Cockerham 1984) describes how well the genotype frequencies within a population fit with Hardy Weinberg expectation (Hartl and Clark 1997). Individuals of the dispersing sex or wing morph sampled from a single sampling site should be a mixture of at least two populations (residents and immigrants). Due to the Wahlund effect, this sample should show a heterozygote deficit accompanied by positive FIS values. Therefore, individuals of the dispersing sex or wing morph should exhibit higher FIS values compared to the members of the more philopatric group. The fixation index FST (Weir and Cockerham 1984), as another descriptor, displays the proportion of the total genetic variance that resides among populations (Hartl and Clark 1997). For the dispersing sex or wing morph, allele frequencies should be more homogeneous and therefore, FST values should be lower than those for the philopatric individuals. Values for the relatedness calculated as relatedness = 2 FST / (FIT) should also be lower for dispersing individuals than for residents. As the immigrants of one sampling site presumably originate from several populations with different allele frequencies, the within group gene diversity Hs should be largest for the dispersing individuals. The assignment index (AI; Paetkau et al. 1995) of an individual is the probability that its genotype occurres by chance in the population where it was sampled. Assuming that the loci segregate independently, the probability of the occurrence of a multi-locus genotype is the product of the probabilities of the individual loci. The multi-locus probabilities of individuals of different populations are not directly comparable because different populations can contain very different levels of gene diversity. Therefore, the corrected assignment index (AIc; Favre et al. 1997) of an individual is calculates by subtracting the average probability of the sampled population from the individual multi-locus probability. Positive values of AIc indicate genotypes more likely than average to occur in their sample (likely residents), while negative values indicate genotypes less likely than average (potentially dispersers). As immigrants should have lower AIc values than residents, the mean corrected assignment index (mAIc) for the sex or wing morph that disperses most is expected to be lower than that for the more philopatric animals. The variance of the corrected assignment index (vAIc) should be largest for the dispersing sex or wing morph, because the dispersing group is likely to consist of residents with common genotypes and immigrants with rare genotypes. To test whether these statistics differ significantly between the two sexes or wing morphs, a randomisation approach was used (10000 permutations, one-sided test). For more details see Goudet (2001) and Goudet et al. (2002).

5.3 Results

The morphological analysis revealed that micropterous individuals had a significantly lower flight muscle mass and significantly lower values of flight muscle ratio compared to macropters (Table 5.3.1; Figure 5.3.1). In addition, micropters were significantly larger than macropterous individuals regardless of their sex (Table 5.3.1). However, we found no significant difference concerning the body weight of both wing morphs (Table 5.3.1).

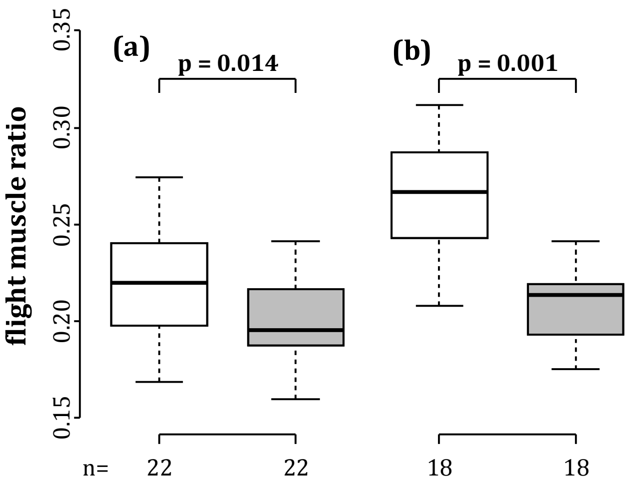

Figure 5.3.1: Comparison of the flight muscle ratio between both wing morphs for (a) females and (b) males. White boxes represent macropters and grey boxes represent micropters.

Comparing individuals of both sexes, we found females having a greater flight muscle mass, but lower values of flight muscle ratio compared to males (significant only for macropters, Table 5.3.2, Figure 5.3.2b). Furthermore, macropterous females had significantly longer wings and a significant larger wing area (Table 5.3.2), but also a slightly lower aspect ratio (Figure 5.3.2c) and a significantly higher wing load (Figure 5.3.2d) than macropterous males. We also found a general sexual dimorphism for *M. bicolor* with females being significantly larger and heavier than males (Table 5.3.2).

Table 5.3.1: Comparison of the morphology and physiology of micropters (mic) and macropters (mac) of *M. bicolor*. For each comparison, the median with the 25th and 75th percentiles as well as the results of the Wilcoxon tests for dependent samples (Z- and two sided p-values) are shown.

Trait	Wing	Median	25th	75th	Z-value	p-value
Comparison of female micropters and macropters						
Head width [mm]	mic (N=22)	4.38	4.31	4.50	-2.72	0.007
	mac (N=22)	4.19	4.13	4.38		
Body weight [mg]	mic (N=22)	201.00	192.05	227.93	-1.73	0.084
	mac (N=22)	240.65	203.48	252.00		
Flight muscle mass [mg]	mic (N=22)	41.34	33.62	46.79	-3.72	0.001
	mac (N=22)	47.53	44.46	55.69		
Comparison of male micropters and macropters						
Head width [mm]	mic (N=18)	4.06	4.06	4.15	-3.41	0.001
	mac (N=18)	3.88	3.88	4.02		
Body weight [mg]	mic (N=18)	186.25	179.95	198.95	-1.68	0.093
	mac (N=18)	168.00	157.80	186.08		
Flight muscle mass [mg]	mic (N=18)	38.29	34.96	42.43	-3.03	0.002
	mac (N=18)	43.22	38.42	48.43		

Table 5.3.2: Comparison of the morphology and physiology of females (f) and males (m) of *M. bicolor*. For each comparison, the median with the 25th and 75th percentiles as well as the results of the Mann-Whitney U tests for independent samples (U values and two sided p-values) are shown.

Trait	Sex	Median	25th	75th	U-value	p-value
Comparison of macropterous females and males						
Head width [mm]	f (N=22)	4.19	4.13	4.38	19.50	0.001
	m (N=18)	3.88	3.88	4.02		
Body weight [mg]	f (N=22)	240.65	203.48	252.00	15.50	0.001
	m (N=18)	168.00	157.80	186.08		
Flight muscle mass [mg]	f (N=22)	47.53	44.46	55.69	111.00	0.045
	m (N=18)	43.22	38.42	48.43		
Wing length [mm]	f (N=15)	19.77	19.06	20.38	45.00	0.009
	m (N=14)	19.03	18.29	19.42		
Wing area [mm2]	f (N=15)	137.02	134.56	146.39	53.00	0.023
	m (N=14)	126.98	115.01	135.84		
Comparison of micropterous females and males						
Head width [mm]	f (N=22)	4.38	4.31	4.50	6.00	0.001
	m (N=18)	4.06	4.06	4.15		
Body weight [mg]	f (N=22)	201.00	192.05	227.93	50.50	0.037
	m (N=18)	186.25	179.95	198.95		
Flight muscle mass [mg]	f (N=22)	41.34	33.62	46.79	160.00	0.302
	m (N=18)	38.29	34.96	42.43		

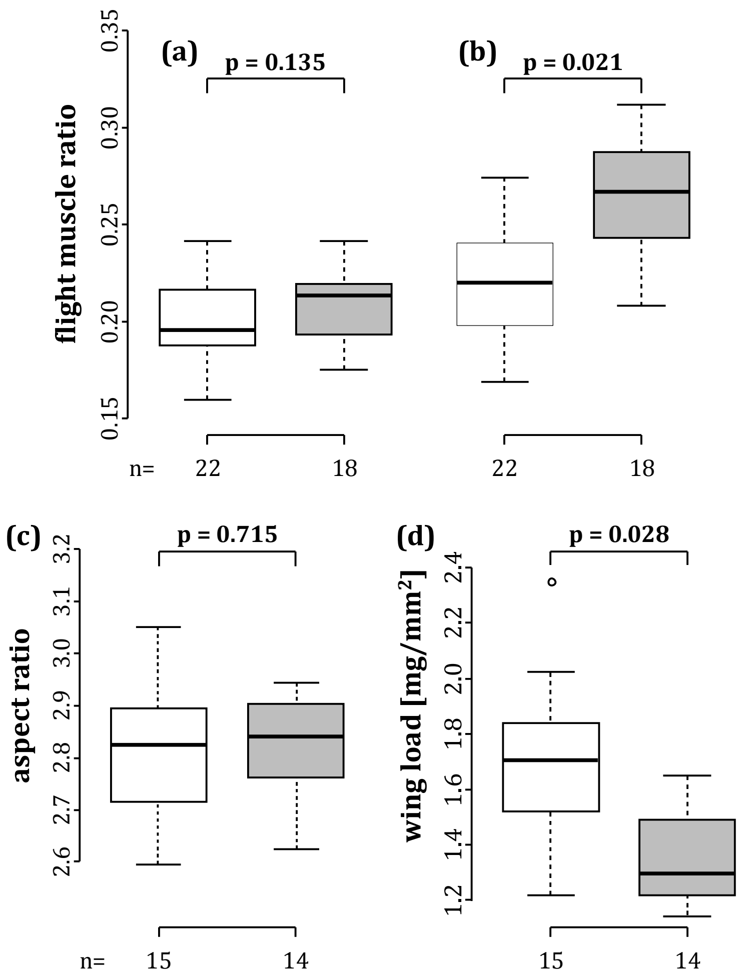

Figure 5.3.2: Comparison of the flight muscle ratio between (a) micropterous and (b) macropterous individuals of both sexes, and comparison of (c) the aspect ratio and (d) the wing load between macropterous females and males. White boxes represent females and grey boxes represent males.

The analysis of the genetic data revealed a significant difference between micropterous and macropterous individuals concerning the mean corrected assignment index (mAIc, also significant difference in FIS values for males, Table 5.3.3). The values of the other estimators for biased dispersal were not significantly different between both wing morphs. However, the direction of the differences favours macropters as dispersal unit (Table 5.3.3, except vAIc for females). We also found a significant difference between macropterous females and males concerning the variance of the corrected assignment index (vAIc) indicating that males are the more dispersive sex (Table 5.3.3). In contrast, we found no evidence for sex-biased dispersal for micropterous individuals (Table 5.3.3).

Table 5.3.3: The number of individuals (N), values for FIS, FST (Weir and Cockerham 1984) and relatedness (Relat), the within group gene diversity (HS), as well as the mean and the variance of the corrected assignment index (mAIc and vAIc) are shown for females and males as well as for micropterous and macropterous individuals of *M. bicolor*. The first line indicates the expected direction of the difference between dispersing (d) and not dispersing (nd) individuals. In addition, one sided p-values for each comparison are given.

Expected difference		d>nd	d<nd	d<nd	d>nd	d<nd	d>nd
	N	**FIS**	**FST**	**Relat**	**HS**	**mAIc**	**vAIc**
Micropterous females	241	0.368	0.038	0.054	0.835	0.101	6.869
Macropterous females	21	0.386	0.020	0.028	0.845	-1.156	2.348
p-value		0.487	0.278	0.278	0.336	0.001	0.998
Micropterous males	184	0.328	0.043	0.064	0.815	0.139	6.257
Macropterous males	14	0.464	0.035	0.048	0.845	-1.825	8.644
p-value		0.043	0.484	0.474	0.344	0.014	0.144
Females macropterous	14	0.323	-0.012	-0.018	0.873	0.004	0.774
Males macropterous	10	0.432	0.015	0.021	0.863	-0.005	2.178
p-value		0.094	0.438	0.438	0.347	0.496	0.028
Females micropterous	456	0.386	0.046	0.065	0.824	-0.037	9.261
Males micropterous	466	0.383	0.045	0.064	0.823	0.036	9.438
p-value		0.621	0.398	0.408	0.660	0.619	0.405

5.4 Discussion

Using a combined approach of morphological and genetic analyses, we found wing morph-biased dispersal for both sexes and sex- biased dispersal for macropters of *M. bicolor*. Both, morphological and genetic data, favour macropterous males as dispersal unit of this bush cricket species. In addition, like many other orthopterans, *M. bicolor* exhibits a general sexual dimorphism with females being larger and heavier than males independent of their wing morph (Berggren 2005b, Picaud and Petit 2008, Heidinger et al. 2010).

Based on our data, macropters are favoured as dispersal unit over micropters, independent of their sex. Despite the obvious reduction in wing length, micropterous females and males also exhibit a significant reduction in flight muscle mass resulting in lower values for the flight muscle ratio, compared to macropterous individuals. Whether these differences are persistent throughout their whole lifecycle (see Fischer and Kutsch 2000), because micropters generally develop less muscle mass, remains unknown. It is also possible that micropterous individuals histolyse their flight muscles with the onset of reproduction, but this could also be the case for macropters. Compared to micropterous males, macropterous males are smaller and lighter, which may facilitate wind mediated passive dispersal (Ortego et al. 2011). An opposite tendency is observed in females, where macropters are also smaller but tend to be heavier (n.s.) than micropters. This finding is in contrast to Roff (1991, 2002) who holds that migrating individuals should be larger, which has been confirmed by several studies (e.g. Davis 1986, Kuussaari et al. 1996, Hill et al. 1999a).

Although not all tests of the genetic analyses were statistically significant, probably due to the low number of sampled macropterous individuals, calculated values that reflect wing morph-biased dispersal support a pattern that suggests a higher migration rate for macropterous individuals. Possibly, flightless micropters of *M. bicolor* may also contribute to the genetic exchange between neighbouring populations to a certain extent by using linear structures along roads as dispersal (walking) corridors (Kindvall and Ahlén 1992, Sutcliffe and Thomas 1996, Berggren et al. 2002). Nonetheless, micropters are very likely of less importance for the long distance dispersal of this bush cricket species compared to macropterous individuals. In contrast, macropters are generally supposed to serve as dispersal unit which maintains the gene flow between different populations (Vickery 1965, Peterson and Denno 1997, Simmons and Thomas 2004) and serve for the recolonisation of empty patches. For the two wing dimorphic bush crickets *Conocephalus discolour* and *M. roeselii*, recently founded populations at the range margin showed increased frequencies of dispersive, macropterous individuals, compared to longer-established populations in the range core (Thomas et al. 2001a, Simmons and Thomas 2004). Furthermore, macropterous bush crickets also account for the range expansion of their species (Thomas et al. 2001a, Simmons and Thomas 2004, Hochkirch and Damerau 2009). Peterson and Denno (1997) showed for plant hoppers that in regions with a high level of macroptery, the genetic subdivision is weaker than in regions with a low level of macroptery.

For biochemical and energetic reasons, migrating individuals should be large to maximize the distance they can travel without refuelling (Roff 1991, Roff 2002). Furthermore, several studies have shown that migrants are larger than none-migrants, and that flight- and acceleration capacity, for example, is positively correlated with body size and body mass (Davis 1986, Denno 1994, Kuussaari et al. 1996, Berwaerts et al. 2002). Under this point of view, females seem to be more qualified for dispersal than males. The more so as macropterous females have a greater flight muscle mass, longer wings and a larger wing area than macropterous males. However, females are also much heavier than males and the values for the size-independent measurements of flight performance we used (flight muscle ratio, wing load) indicate that macropterous males are favoured as dispersal unit over macropterous females. As fecundity of insect females is positively correlated with body size (Nylin and Gotthard 1998) and negatively associated with flight capability (Denno et al. 1989, Zera and Zhao 2003), female's morphology may be shaped rather by factors concerning reproduction than by dispersal. In addition, males could benefit from their smaller size with regard to wind mediated passive dispersal (Ortego et al. 2011).

Individuals of both sexes were dissected and most females had developed eggs whereas none of the males had a spermatophore (independent of their wing morph; data not shown), although it is assumable that both sexes were reproductively active when individuals were sampled. Subtracting the eggs' weight from females' body weight, macropterous females still had a lower flight muscle ratio and a higher wing load (both significant, data not shown). A higher wing load could be compensated by increasing the beating frequency or the amplitude of the wing stroke (Gäde 2002). Furthermore, macropterous females could have begun to histolyse their flight muscles with the onset of reproductive activity to gain energy-rich substrates for egg production, resulting in lower values of flight muscle ratio. Various insect species including crickets are able to histolyse their flight muscles (Tanaka 1976, 1993, Lorenz 2007). Of cause, this could also be valid for macropterous males (Chapman 1956, Andersen 1973, Crnokrak and Roff 2000) and the production of spermatophores. However, in some species, histolysis of flight muscles is restricted to females (Edwards 1969, Kaitala 1988).

Not only our morphological but also our genetic data indicate that macropterous males are more dispersive than macropterous females. Male-biased dispersal is common in polygynous or promiscuous mating systems (Greenwood 1980) and predicted when local mate competition exceeds local resource competition and when female fitness is limited by intrinsic factors (Perrin and Mazalov 2000). This could be the case for *M. bicolor*, which has a wide diet breadth (Ingrisch and Köhler 1998) and for which we assume a promiscuous mating system because for the two closely related species, *Metrioptera brachyptera* and *M. roeselii*, polyandry has already been reported (Vahed 2006). Ortego et al. (2011) and Bailey et al. (2007) have shown male-biased dispersal for Mioscirtus wagneri, a long-winged grasshopper, and the gregarious morph of the flightless Mormon cricket (Anabrus simple), respectively. The authors hold that females might have less time to disperse after mating because they eat the spermatophore and oviposit, while males move onwards searching for food and other females. It could also be that both sexes have similar dispersal capabilities, but a shorter life span of females or female-biased predation lead to male-biased dispersal in our study (Bailey et al. 2007, Ortego et al. 2011). However, this does not mean that macropterous females do not disperse at all, as for example sex-biased dispersal patterns of a species can vary according to the spatial scale investigated (Fraser et al. 2004, Gauffre et al. 2009).

As expected, we found no significant differences between micropterous females and males (which are both flightless) concerning the flight muscle mass or the flight muscle ratio. Moreover, the values of the statistical descriptors of an individual’s genotype, we used to detect biased dispersal, were almost identical for both micropterous sexes (except for mAIc, n.s.). This confirms the assumption that micropters do not disperse at all. On the other hand, it could also indicate that micropterous females and males contribute in a similar way to population spread, as it is suggested for *Pholidoptera griseoaptera*, a flightless bush cricket with greatly reduced wings and no macropterous individuals (Diekoetter et al. 2005).

Macropterous individuals of *M. bicolor* are rare in natural populations and their dispersal potential is hardly investigated. However, based on our data, it is reasonable to assume that macropters play a major role for the long distance dispersal of *M. bicolor*. As observations of flying individuals of this bush cricket are rare (Heidinger unpublished data), we compared our morphological data with that of two typical migratory grasshopper species to get an idea of the flight ability of *M. bicolor*. *L. migratoria* (Gewecke 1975, Worm and Beenakkers 1980, Baker et al. 1981, Kutsch et al. 2002), and *S. gregaria* (Weis-Fogh 1956, Mayer and Candy 1969, Waloff 1972, Brown and Southwood 1983, Fischer and Kutsch 2000, Kutsch et al. 2002) are proven to be very good flyers. Surprisingly, individuals of both species have a lower flight muscle ratio compared to macropterous *M. bicolor* (Table 4). On the other hand, *L. migratoria* and *S. gregaria* have a higher aspect ratio and a lower wing load than *M. bicolor* (Table 4) which may compensate for the lower flight muscle ratio. Altogether, our morphological data suggest a good flight ability for macropterous individuals of *M. bicolor*, particularly as they could compensate their higher wing load by increasing the beating frequency or the amplitude of the wing stroke (Gäde 2002). Assuming a flight speed of 3 m/s and a flight duration of at least 30 minutes (minimum values for *L. migratoria* and *S. gregaria*, see Table 4), macropters of *M. bicolor* could cover a distance of 5.4 km at once. Even much greater distances could be possible, if they use wind (e.g. updrafts before thunderstorms) for passive dispersal (Webster 1902, Johnson 1969, Tomlinson 1973).

Table 5.4.1: Comparison of the flight muscle ratio (fmr), wing load (wl), aspect ratio (ar), flight speed (fs), and flight duration (fd) of *M. bicolor* (only macropters), *L. migratoria* (Gewecke 1975, Worm and Beenakkers 1980, Baker et al. 1981, Kutsch et al. 2002), and *S. gregaria* (Weis-Fogh 1956, Mayer and Candy 1969, Waloff 1972, Brown and Southwood 1983, Fischer and Kutsch 2000, Kutsch et al. 2002). For fmr, wl, and ar, mean and standard deviation are given. For fs and fd, the range of values is given. Note that the wing load is given as N/m2 to make the different data sets comparable.

Species	**Sex**	**fmr**	**wl [N/m2]**	**ar [1/mm]**	**fs [m/s]**	**fd [h]**
M. bicolor	females	0.20 ± 0.03	16.64 ± 2.77	2.81 ± 0.13	unknown	
	males	0.27 ± 0.03	13.29 ± 1.57	2.82 ± 0.10		
L. migratoria	females	0.11 ± 0.01	12.39 ± 1.22	3.25 ± 0.16	3.3-6.1	0.3–2.0
	males	0.16 ± 0.02	11.52 ± 1.08	3.71 ± 0.18		
S. gregaria	females	0.13 ± 0.02	10.05 ± 0.90	3.93 ± 0.19	2.8-8.0	0.5–2.0
	males	0.20 ± 0.01	7.86 ± 0.20	3.91 ± 0.21		

Biased dispersal is often investigated by comparing the morphology, physiology and behaviour of females and males or sedentary and dispersive individuals. Studies of biased dispersal in terms of capture-mark-recapture experiments, investigating real dispersal and not routine movements, and genetic proofs of biased dispersal are still rare for certain taxa, especially for orthopterans. However, information on biased dispersal is of great importance as for example, undetected biased dispersal may lead to false conclusions from genetic data (Vandergast et al. 2009, Kindler et al. 2012). The results of our study not only show that macropterous individuals of *M. bicolor* are predestined for dispersal due to their morphology, our genetic data also indicate that macropters are more dispersive than micropters. Furthermore, we could show that even within the group of macropterous individuals, males are supposed to be more dispersive than females.

6

Discussion

Contents

6.1 Levins' metapopulation concept and its practical application in conservation biology

Richard Levins was the one who coined the term metapopulation to describe a population of local populations connected to each other by occasional migration. In a simple model, he encapsulated the fundamental idea of metapopulation persistence in a stochastic balance between local extinction and recolonization (Levins 1969, 1970). Focusing on this interplay between extinctions and recolonizations, Levins' metapopulation concept provides a framework for the study of spatially structured populations and is therefore of major relevance for conservation biology. Especially in the context of population viability analyses (PVA; for review see Hanski 2002), modified and expanded models based on Levins' concept have been frequently applied in conservation biology (Hanski 1994, Hanski and Thomas 1994, Gilpin 1996, Bulman et al. 2007, Dolrenry et al. 2014, Eaton et al. 2014). PVA is a tool widely used to identify the threats and viability requirements of endangered species or populations based on species-specific data and models (Boyce 1992, Norton 1995, Beissinger and Westphal 1998, Beissinger 2002). It can be used to evaluate the likelihood that the populations under study will persist for a given time into the future and allows the evaluation and comparison of alternative management strategies (Akçakaya et al. 1995, Cancino et al. 2010, Peng et al. 2010, McElderry et al. 2015, Rømer et al. 2015). Various types of models are used for PVAs, ranging from simple (e.g. occupancy models) to complex (e.g. individual-based models) with spatially structured metapopulation models in between (Akçakaya 2000a, Akçakaya and Sjögren-Gulve 2000, Lacy 2000, Sjögren-Gulve and Hanski 2000). These models differ in their assumptions, the factors they incorporate, and the amount as well as the type of data they require (Akçakaya 2000b, Akçakaya and Sjögren-Gulve 2000 and references therein, Keedwell 2004). Depending on the model used in a PVA, data on demography (e.g. birth and death rates, sex ratio, and population size), landscape (e.g. amount and quality of habitat types, distance between habitat patches, and location of patches), and dispersal (e.g. emigration rates, dispersal mortality, and movement rules) are needed, which are usually obtained via empirical studies (ideally long-term).

6.2 Testing experimental assumptions

The reliability of the results of PVAs crucially depends on the quality of empirical data provided to the respective model (Beissinger and Westphal 1998, Reed et al. 2002, Keedwell 2004). The validity of these –predominantly field – data depends on several factors, starting with an appropriate experimental design and ending with the thorough interpretation of statistical results. One factor often neglected is the experimenter himself/herself. To be more exact, the experimenters‘ assumptions about methods and experimental designs, as the results presented in chapter 2 clearly demonstrate.

In the context of animal dispersal, movement behaviour has been frequently investigated with capture-mark-recapture studies where animals are captured at one site (their familiar ‘home’ site), marked, and transferred to other unfamiliar sites (Kindvall 1999, Hein et al. 2003, Berggren 2004, 2005a, Moerkens et al. 2010, Ibarra-Macias et al. 2011, Villard and Haché 2012). Conclusions drawn from these studies crucially depend on the assumptions that the marking technique, handling, and the translocation of animals from their familiar habitat patch to unfamiliar sites itself have no (or at most a negligible) influence on the behaviour of these individuals. If such elementary assumptions are not met, it is impossible to separate the effect of the main research question from other confounding factors, provoking biased or misleading results.

Chapter 2 of this thesis presents a capture-mark-recapture study investigating the effect of translocation on the movement behaviour of the blue-winged grasshopper *Oedipoda caerulescens*. As the results of this study show, transferring individuals of this grasshopper species to suitable but unfamiliar sites has a significant influence on their movement behaviour. Studies ignoring this effect may lead to false conclusions. Therefore, the prediction of dispersal behaviour based on movement data derived from capture-mark-recapture studies is, strictly speaking, only valid if individuals are released at the same position (at least on the same site) where they have been caught. In addition, for the comparison of movement patterns in different habitat types, a control experiment observing translocated individuals in a suitable but unfamiliar habitat patch is inevitable. In summary, the results presented in chapter 2 clearly point out that translocation effects should not be disregarded in future studies on arthropod movement, respectively dispersal. Data ignoring this influence may lead to false predictions of dispersal behaviour, habitat detection capability or habitat preferences, and may result in misleading conclusions if used for PVAs and the conservation and management of endangered species.

6.3 Matrix matters

Beside data quality, the applicability of PVA results for conservation purposes depends on the validity of model assumptions. Many models assume dispersal to be solely distance-dependent (Euclidean distance) and thus that metapopulations exist within a homogeneous and ecologically unimportant matrix (Hanski 1994, Hanski and Thomas 1994, Hill et al. 1996, Moilanen et al. 1998, Hanski et al. 2000, Hokit et al. 2001). In these models, the matrix is featureless except the fact that it is uninhabitable for the species of interest. This assumption is certainly appropriate for terrestrial organisms on oceanic islands but usually not the case in natural landscapes. Both, empirical and theoretical studies, as well as chapter 3 of this thesis, show that matrix matters (Roland et al. 2000, Jonsen et al. 2001, Ricketts 2001, Vandermeer and Carvajal 2001, Hein et al. 2003, Walker et al. 2003).

The study presented in chapter 3 focuses on the effects of different matrix types and geographic distance on the genetic structure of populations of the two-coloured bush cricket *Metrioptera bicolor* in a spatially structured landscape with patches of suitable habitat distributed within a diverse matrix of different habitat types. For this bush cricket the isolation of local populations severely depends on the type of surrounding matrix. The analyses of this study clearly emphasize the differential resistance of different habitat types on dispersal and the importance of a more detailed view on matrix 'quality' in metapopulation studies. A mere analysis of isolation by distance may not yield essential information on the dispersal capacity of a species. Moreover, population viability studies that use inter-patch distance as the main determinant of habitat isolation may lead to wrong or inaccurate predictions. Instead of the Euclidean distance as a determinant of habitat isolation, least-cost-path analysis or resistance surfaces can be used (LaRue and Nielsen 2008, Wang et al. 2009, Hokit et al. 2010, Spear et al. 2010). As modern GIS-based landscape analysis delivers detailed information on habitat types, analyses that focus on the specific dispersal resistance of different matrix types may provide much more detailed information on the dispersal capacity of species. Such information is needed to improve landscape oriented models for the conservation of endangered species. It would allow to focus conservation measures on specific dispersal barriers and to optimize investment into landscape management.

6.4 Nothing stays the same except change

Species-specific data and models are the basis of PVAs (Akçakaya 2000a, Akçakaya and Sjögren-Gulve 2000, Keedwell 2004). Thereby, morphological, physiological as well as behavioural traits of a species are assumed to be static and unchanged over the time horizon of the PVAs. However, these traits can vary (in time and space) due to phenotypic plasticity and evolutionary adaptation

(Krebs 2008, Freeman and Herron 2013). As morphological or behavioural traits of individuals and the degree to which a certain genotype responds to environmental variation have heritable components, they are expected to be able to respond to selection pressures (Thomas et al. 1998, Hill et al. 1999a, Roff and Fairbairn 2001, Price et al. 2003, Bonte and Lens 2007, Roff and Fairbairn 2007). This evolutionary response does not necessarily take several centuries. Instead it can be surprisingly fast (within a few decades and even less than 10 years), not only due to artificial selection as shown in in vitro evolution experiments (for review see Roff and Fairbairn 2001, Friedenberg 2003, Scoville and Pfrender 2010), but also in natural populations (Hanski et al. 2004, Simmons and Thomas 2004, Phillips et al. 2006, Huntley 2007, Swain et al. 2007, Hill et al. 2011, Renaud et al. 2015).

In addition to direct effects on realised dispersal (see chapter 3), landscape structure (i.e. the spatial configuration of habitat patches or the nature of the landscape matrix) on its own is known to act as an evolutionary selection agent because it determines the costs and benefits of dispersal (Olivieri et al. 1995, Olivieri and Gouyon 1997, Merckx et al. 2003, Merckx and Van Dyck 2006, Bonte et al. 2012). Traits, which are important for successful dispersal, such as body size, thorax mass, wing development or habitat-finding ability can vary depending on patch connectivity (isolation of populations) or the degree of landscape fragmentation (Wagner and Liebherr 1992, Wootton 1992, Taylor and Merriam 1995, Norberg and Leimar 2002, Berggren 2005b, Merckx and Van Dyck 2006, 2007). Chapter 4 investigates the influence of habitat fragmentation on the dispersal-related morphology of *O. caerulescens* in a coastal landscape with habitat patches varying in patch size, patch connectivity (isolation of populations) and sand dynamics (stability of habitat). The correlative study revealed that these landscape characteristics had clear though sex-specific effects on the morphology of this grasshopper. These effects agree with predictions from theoretical models on the evolution of dispersal in metapopulations (Clobert et al. 2004). However, as effects appear to be less pronounced in females, different selection pressures may act differently on both sexes. Alternatively, observed patterns can be due to sex-specific phenotypic plasticity. Irrespective of the underlying mechanism (evolutionary adaptation or phenotypic plasticity), the presented results add to the evidence that dispersal-related morphology varies and is selected upon in recently structured populations at small spatial scales. Such responses to varying environmental conditions are generally ignored by metapopulation models used in PVAs. However, species adapt to environmental changes due to phenotypic plasticity or evolutionary adaptation. This has a profound impact on the prognoses of PVAs under changing environmental conditions (e.g. changes in land use or global climate change). For reliable predictions from PVAs it is inevitable to account for the fact that dispersal-related traits and other life-history attributes may vary in time and space for certain species. This is particularly important, as dispersal is a critical component of metapopulation survival (Johst et al. 2002, Bohrer et al. 2005, Hovestadt and Poethke 2006, Best et al. 2007)

6.5 Sex and wing-morph make a difference

Modelling of population viability and most studies on extinction risk of populations rely on the simplifying assumption that populations can be represented by adult females only and neglect the presence of males (Caswell 2001). Single-sex models assume even sex-ratio, same life history for both sexes, and that females and males do not interact (Caswell and Weeks 1986, Lindström and Kokko 1998, Engen et al. 2003). These assumptions keep models simple, and simple models not requiring extensive parameterization are handy for conservation practitioners (Ludwig and Walters 1985, Beissinger and Westphal 1998) but presumably not applicable to natural populations. In most animal species, both sexes differ in regard to intrinsic (morphology, physiology or behaviour; Wehrhahn 1979, King 1989, Härkönen et al. 1999, Lewis et al. 2002, Catchpole et al. 2004, El Wakil et al. 2013, Stevens et al. 2013, Aggarwal 2014) and extrinsic (e.g. sex-specific predation, parasitism or mortality; for review see Møller 2003) factors. Hence it is not surprising that sex-specific demographic and other variables can play an important role for the determination of extinction risks and the extinction probability (Härkönen et al. 1999, for review see Møller 2003, and Rankin and Kokko 2007, Gerber and White 2014). Especially when sexes differ in their dispersal ability and propensity, which are critical components for the survival of populations, considering only one sex in a PVA can seriously bias estimates.

In chapter 5 of this thesis, a combined approach of morphological and genetic analyses was used to investigate sex- and wing morph-biased dispersal of *M. bicolor*. The presented results not only show that macropterous individuals are predestined for dispersal due to their morphology, the genetic data also indicate that macropters are more dispersive than micropters. Moreover, within the group of macropterous individuals, males are supposed to be more dispersive than females. Both, morphological and genetic data, favour macropterous males as dispersal unit of this bush cricket species. Such sex-biased dispersal can be found in many insect species (Markow and Castrezana 2000, Caudill 2003, Sundström et al. 2003, Beirinckx et al. 2006, Lawson Handley and Perrin 2007, Sallé et al. 2007, Lagisz et al. 2010, López-Uribe et al. 2014) and other animal classes including mammals (Kerth et al. 2002, Möller and Beheregaray 2004, Douadi et al. 2007, Lawson Handley and Perrin 2007), birds (Greenwood and Harvey 1982, Clarke et al. 1997), fishes (Pardini et al. 2001, Hutchings and Gerber 2002, Fraser et al. 2004), reptiles (Tucker et al. 1998, Dubey et al. 2008, Pernetta et al. 2011, Hofmann et al. 2012), amphibians (Austin et al. 2003, Liebgold et al. 2011, Helfer et al. 2012, Wang et al. 2012), and insects (Markow and Castrezana 2000, Caudill 2003, Sundström et al. 2003, Beirinckx et al. 2006, Lawson Handley and Perrin 2007, Sallé et al. 2007, Lagisz et al. 2010, López-Uribe et al. 2014). Dispersal polymorphism, where two distinct morphs (sedentary and dispersal) can be distinguished (Harrison 1980, Zera and Denno 1997, Ingrisch and Köhler 1998), is also a widespread phenomenon in many insect groups. As dispersal is a critical component for metapopulation survival (Johst et al. 2002, Bohrer et al. 2005, Hovestadt and Poethke 2006, Best et al. 2007), neglecting sex-or wingmorph-specific differences in dispersal behaviour in PVA models would have a serious impact on the PVA results and lead to wrong predictions.

6.6 PVA revisited

Although PVAs have certain limitations, as any other assessment method used for conservation (e.g. habitat suitability models, landscape indices and Gap analysis), they are a central tool for conservation planning and the evaluation of management options (for review see Akçakaya and Sjögren-Gulve 2000). Provided that adequate data exist and the models and assumptions are carefully assessed, PVA is a valid and sufficiently accurate tool for managing endangered species and quantitative predictions (e.g. risk of population extinction or projected population size over time) are precise where extensive long-term datasets exist (Brook et al. 2000). However, several authors recommend to rather use PVAs for qualitative predictions and to focus on relative (e.g. comparing the outcome of different management or conservation strategies) rather than absolute results, because relative results are supposed to be less sensitive to uncertainties in the data (Beissinger and Westphal 1998, Akçakaya and Sjögren-Gulve 2000, Coulson et al. 2001, Keedwell 2004). In addition, PVAs should be continuously updated and models should be tested and refined if new data are available (Brook et al. 2000, Keedwell 2004). Since the first PVA by Mark Shaffer (1978), new types of PVA models using Bayesian theory (Marcot et al. 2001, Goodman 2002, Maunder 2004, Heard et al. 2013) and decision theory (Harwood 2000, Possingham et al. 2002, Drechsler and Burgman 2004, Converse et al. 2013) have emerged and they are becoming more widespread. Even multi-species PVA models exist (Witting et al. 1994, Colding 1998, Blackwell et al. 2001, for review see Sabo 2008, Prowse et al. 2013). These may be more realistic for natural populations where different species interact, and where one species can have a considerable impact on the survival of another species. In addition, also methods to incorporate parametric uncertainty into PVA models have been developed (McGowan et al. 2011, Nadeem and Lele 2012). To ensure that management decisions based on PVA results are the most appropriate, choosing the best approach for modelling is fundamental (Keedwell 2004). However, as essential data are often lacking (about e.g. dispersal behaviour, dispersal barriers or adaptation of species on local environmental conditions) and interactions between the focus species and landscape or other species can be very complex, the outcome of PVAs remain an estimation of risks and the benefits of different management strategies rather than an exact prediction of the future of threatened species or populations.

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Authors' contributions

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Erklärungen

nach §4 Abs. 3 Satz 3, 5, 8 der Promotionsordnung der Fakultät für Biologie

Affidavit

I hereby declare that my thesis entitled: „Beyond metapopulation theory: Determinants of the dispersal capacity of bush crickets and grasshoppers" 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. Furthermore I verify that the thesis has not been submitted as part of another examination process neither in identical nor in similar form.

Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, die Dissertation: „Beyond metapopulation theory: Determinants of the dispersal capacity of bush crickets and grasshoppers", 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. Ich erkläre außerdem, dass die Dissertation weder in gleicher noch in ähnlicher Form bereits in einem anderen Prüfungsverfahren vorgelegen hat.

Würzburg, den 13.11.2015

Ina Heidinger