

The consequences of spatial environmental variability on dispersal and on the spatial distribution of species



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Academic dissertation

**The consequences of spatial environmental variability on
dispersal and on the spatial distribution of species**

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Contents

Abstract	5
Introduction and summary	6
Dispersal: definition and causes	6
Complexity of dispersal	8
Consequences of dispersal on species distribution	9
The aim of this thesis	11
When is information on availability of nesting sites important for dispersal? Chapter I	12
Study species and system	14
Does the availability of mates influence the evolution of sex-specific dispersal? Chapter II	16
Influences spatio-temporal variability in host density the spread rate of an ectoparasite? Chapter III	18
Spatial modelling	19
Concluding remarks	20
References	22
Acknowledgements	31
Chapter I: Birds search for nesting opportunities whenever time allows: on the use of personal information in Collared Flycatchers	35
Chapter II: Mate limitation causes sexes to coevolve towards more similar dispersal kernels	61
Chapter III: The invasion speed of the ectoparasite deer ked is modified by spatio temporally varying host density	73

Abstract

A central goal in ecology is to identify and understand causal factors that lead to the expansion or contraction of species' ranges. Spatio - temporal population dynamics depend on biotic and abiotic environmental conditions, local demography, dispersal behaviour, and phenotypic variation. In particular understanding dispersal behaviour turns out to be a tough problem, because complex feedback loops between dispersal, local demography, and individual variations can arise. Furthermore, previous attempts to understand dispersal by reducing the complexity either in space or time have often resulted in a disregard of these feedbacks. The aim of this thesis was to investigate the influence of dispersal on spatio-temporal population dynamics with models and experiments that explicitly consider the multi causality of dispersal. The thesis is composed of three different studies: Firstly, for an active dispersing species, a plausible factor affecting dispersal behaviour could be personal information. Birds, for example, might gather information on future nest sites and, as a result, individuals differ in the amount and quality of information they possess for use in reaching a dispersal decision. We manipulated the information available to flycatchers (*Ficedula hypoleuca*) in a field experiment and we

found that individuals which were longer exposed to the information altered dispersal behaviour to a greater extent, but only at a local spatial extent. Secondly, models of sex-biased dispersal rarely take space into account. With a computer simulation model, we showed that acknowledging the spatial distribution of the sexes has consequences for the evolutionary outcome of the model leading to selection of more similar dispersal behaviour among the two sexes. Thirdly, models of invasion spread rate often ignore the dependency of dispersal on environmental heterogeneity. We expanded on a reaction-diffusion model to improve this deficit and show that the invasion dynamics of an ecto-parasite (deer ked, *Lipoptena cervi*) is dependent on the local density of its main host, moose (*Alces alces*), across its Finnish range. In conclusion, these studies point at the necessity to consider interactions between dispersal and environmental variability, feedbacks between causal factor of dispersal, and realistic assumptions about space and time in order to solve the conundrum of factors determining the spatio-temporal distribution of species.

Introduction and summary

Understanding the factors that determine the expansion or contraction of a given species' spatial distribution is a central question in ecology. Intuitively, species occurrence should first of all be determined by variation in the abiotic and biotic environment, i.e. a species' niche. Niche-based species distribution modelling approaches indeed appear to be successful in predicting stationary species' ranges (e.g. Guisan and Zimmermann 2000, Thuiller et al. 2005), however these models typically fail to account for any dynamics in the species distribution (Phillips et al. 2008b, Gallien et al. 2010). The reason is that the distribution of a species also depends on ecological and evolutionary constraints. The actual distribution therefore fails to correspond, or does so only with a delay, to the spatiotemporal variation in the environment due to factors intrinsic to the species biology (Gaston 2003). Thus it is crucial to establish a mechanistic understanding of a species' ability to reach a location and to establish as a vital population there (Kokko and Lopez-Sepulcre 2006, Gallien et al. 2010). This requires understanding the dynamics of spatially structured populations (Hanski and Gaggiotti 2004), together with the fundamental eco-evolutionary components like local population dynamics and individual variation. Foremost, it requires us to understand

dispersal, since this is the behaviour which leads to the spatial dynamic in a species' distribution (Holt 2003, Kinlan and Hastings 2005).

With this summary, I will briefly introduce dispersal and highlight some of the challenges for studying dispersal. I will then explain how dispersal has direct consequences on the distribution of a species, before I will move on to the question of my own work. And finally I will present my findings and discuss the implication.

Dispersal: definition and causes

Traditionally, dispersal has been defined as movement from the natal patch to the breeding patch (natal dispersal) and in animals (birds in particular) also as relocation between consecutive breeding patches (breeding dispersal) (Greenwood and Harvey 1982). Thus, for example, annual migration of birds is not considered dispersal because it does not involve reproduction and hence does not make a lasting contribution to the species distribution. In that sense Greenwood's definition is very useful because it clearly separates dispersal from other movement without the direct purpose of reproduction (thus I used it in Chapter I). However, dispersal is often risky and individuals might fail to survive or reproduce after dispersal (Bonte et al. 2011). This has important consequences for the fitness of a dispersal strategy and a better definition is therefore "dispersal is movement that

potentially leads to gene flow" because, defined this way, it also includes failed breeders and attempts to disperse (Ronce 2007).

Ronce (2007) also highlights that dispersal is a very complex trait that can have multiple simultaneously acting causes. To disentangle the relevance of different causal factors the literature has often argued about the costs and benefits of a sedentary versus a dispersal strategy (Clobert et al. 2001). This has led to the broad recognition of ultimate causal factors behind dispersal evolution (Bowler and Benton 2005, Ronce 2007): spatiotemporal variability in the abiotic and biotic conditions leads to variation in local fitness and, as a consequence, evolving dispersal allows individuals to reach sites with higher fitness rewards (McPeck and Holt 1992). Likewise, demographic stochasticity introduces variation in densities between different populations and promotes the evolution of dispersal (Travis and Dytham 1998, Cadet et al. 2003). In ephemeral environments dispersal is vital to avoid confinement to a patch which eventually goes extinct (Comins et al. 1980, Olivieri et al. 1995). In addition, the evolution of dispersal is affected by the spatial clumping of parents and their offspring as well as siblings. This clumping results in stronger local competition among kin compared to non-kin for space and resources. Hamilton and May 1977 showed that this is, in itself, sufficient to promote dispersal even under

the absence of external environmental fluctuation. Likewise, the spatial concentration of kin increases the probability of inbreeding, thereby favouring sex-biased dispersal strategies (e.g. only one sex emigrates) to assure outbreeding (Gandon 1999, Perrin and Mazalov 2000).

Typically, there is high between-individual variation in dispersal probability, and philopatry is not uncommon (Greenwood 1980). This can often be explained by proximate factors (Clobert et al. 2001, Bowler and Benton 2005), which can be extrinsic abiotic and biotic environmental factors, for example barriers between habitats (Hanski et al. 2002, Schneider et al. 2003) and vegetation cover at the habitat (Orians and Wittenberger 1991, Nocera et al. 2006, Arlt and Part 2008), or factors intrinsic to populations, including the availability of mates (Greenwood 1980, Lawrence 1987, 1988), breeding failure (Greenwood and Harvey 1982, Switzer 1997) and density of conspecifics (Matthysen 2005).

The direction of the effect these factors have on dispersal is not predetermined, for three reasons. First, dispersal is a process that consists of different phases: departure, transience and settlement (Stamps 2001). Proximate factors might have different effects dependent on the phase during which they prevail (Bonte et al. 2012). Second, each factor's influence on dispersal can interact with the state of the individual (Dufty et al. 2001). For

example, dispersal rate is often different between the sexes and age classes (Greenwood and Harvey 1982) and chapter II). And third, the reaction norm for each factor does not have to be constant, which can result in condition dependent dispersal (Ims and Hjermann 2001). In particular, population density often has a positive effect on emigration probability (Matthysen 2005), but this effect can reverse at low densities to avoid Allee effects. Especially in birds this can often be observed in combination with conspecific attraction (Stamps 2001, Nocera et al. 2006).

Dispersal can be state dependent or condition dependent which makes it a plastic trait, allowing quick and opportunistic adoption of behavioural tactics in fast-changing environments (Stamps 2001). Condition dependent dispersal can outperform a random dispersal strategy, provided there is a cue that provides reliable information about the pay-off of philopatry or dispersal (Travis et al. 1999, Doligez et al. 2003). Clobert et al. (2009) has suggested that to understand this plasticity we need to study how the organism perceives information related to the environment and how it then uses the information for dispersal decision making. He suggests two mechanisms by which an individual can perceive this information: either during development, such that an internal state or special morphological features develops to affect the individual's probability to

disperse, or as a cognitive process which includes active information gathering to allow decision making in each phase of dispersal. The latter behaviour, best studied in birds, is called prospecting (Reed et al. 1999). It is, for instance, known that birds collect information on the breeding success of conspecifics and use this to direct their dispersal towards successful breeding sites (Boulinier et al. 2002, Doligez et al. 2004b). Nevertheless, relatively little is known about prospecting, because credible test of how birds collect information have to rely on elaborate manipulative experiments (Doligez et al. 2002). Therefore it is, for example, still unclear when the relevant information is gathered. The timing of prospecting could enlighten how far ahead dispersal decisions are made and could help us understand the types of information involved in decision making. I will return to these questions later in the introduction of chapter I.

Complexity of dispersal

Finding a coherent framework for dispersal has been difficult beyond detecting the causes. Dispersal is a life history trait that contributes substantially to an individual's fitness and is thus itself under selection (Clobert et al. 2004). Since dispersal is a process with several phases, different fitness costs levied by different causal factors of dispersal can act in series at different phases. As we pointed out last year, this can create feedbacks between

different dispersal phases and other life history traits, and consequently constrains dispersal evolution (Bonte et al. 2011). Thus, understanding dispersal essentially requires manipulative experiments which can separate the influence of each factor individually.

A second problem is that explicit spatial consequences of dispersal are rarely considered, even though dispersal is obviously a spatial trait (Ronce 2007). Theory often only attempts to explain whether it is adaptive to stay or to disperse, whereas in reality dispersal can lead to an organism moving any distance, on a continuum scale, from its place of birth, and the fitness consequences can accordingly vary. For addressing this problem our focus should be directed towards explaining the evolution of dispersal distance, rather than dispersal probabilities (Travis and French 2000, Murrell et al. 2002, Ronce 2007). This is important because different causal factors of dispersal might not operate at the same spatial scale (Ronce et al. 2001), and trade-offs between factors can only be fully understood when the spatial aspect of dispersal is explicitly acknowledged. For example, when dispersal costs increase with distance, these costs trade off with the ability of an organism to avoid competition among kin and with its ability to colonize new suitable habitat in a highly patchy environment. How the trade-off is solved only becomes apparent when the spatial scale is explicitly accounted for. To

avoid kin competition, moving out of the parent's territory might be sufficient, while to find suitable habitats in a patchy environment, longer distance dispersal might be required and selected for. Similarly, parent-offspring conflict over the optimal dispersal strategy only becomes apparent when explicitly considering space (Starrfelt and Kokko 2010), and the same is necessary to study differences in dispersal behaviour between males and females (see chapter II).

Finally, eco-evolutionary feedback loops are formed when a trait has consequences for the variance in population demography, in turn determining, via frequency dependence, the selection pressure for this trait (Kokko and Lopez-Sepulcre 2007). Dispersal is a trait that introduces spatial variance in population demography, thus the eco-evolutionary feedback needs to be considered for the evolution of dispersal. However, the feedback loop only becomes apparent when the effect of dispersal on the local population demography is realistically described, which is only the case when actual dispersal distances are captured. This point I will consider further in chapter II.

Consequences of dispersal on species distribution

Simulation models show that dispersal can be the most important aspect of the spatial distribution of a species (Coutts et al. 2011). However, the complexity of

dispersal has hindered full integration of this mechanism in models of dynamic species' ranges (Gallien et al. 2010). The current state of art of modelling the distribution of a non-static species distribution uses reaction-diffusion models, metapopulation models, or integrodifference models (Kinlan and Hastings 2005, Jongejans et al. 2008). Reaction-diffusion models assume that an individual's movement resembles the random movement of molecules (Okubo 1980, Turchin 1998, Okubo and Levin 2002). Metapopulation models assume a network of discrete habitat sites exchanging individuals among sites, usually dependent on the size of sites and the distance between them (Hanski 1994, Hanski and Gaggiotti 2004). Finally, integro-differential models predict a stage-structured population at a discrete number of sites (Neubert and Caswell 2000). These models make few restrictive assumptions about dispersal, though they can only model discrete time steps (Van den Bosch et al. 1990, Van den Bosch et al. 1992, Kot et al. 1996). All models resemble each other in how the spatial population dynamic is implemented: it comprises the growth rate of each local population and dispersal. For this purpose, dispersal is subsumed to a dispersal kernel, which is a continuous function describing the probabilistic distribution of propagules in relation to the distance of the source (Cousens et al. 2008). The kernel is simply a statistical summary of the pattern how

propagules of the entire population spread in space from their place of birth. In plants this is often referred to as "seed shadow".

The motivation to summarize dispersal in the form of a kernel is necessary for an analytical mathematical solution for the propagule density in space (I spare the mathematical details here, and refer to a good introduction in Cousens et al. 2008 or Turchin 1998). The conclusion is: the kernel is a function that should contain all information about dispersal. Therefore great attention has been paid to the shape skewness and the variance of the kernel (Bullock et al. 2002, Cousens et al. 2008, Jongejans et al. 2008). In particular, the tail of the kernel has important implications since it describes the proportion of long-distance dispersal moves, which is known to have a significant influence on the invasion speed of a species (Clark 1998, Clark et al. 2001). This finding sparked criticism of the reaction-diffusion model, which offers no flexibility to assume a long tailed kernel (Kot et al. 1996). Furthermore, a kernel does not have to be constant over time. The evolution of the kernel is indeed relevant for predicting species' distributions, since evolution can happen while an invasion is ongoing, i.e. within a short time of only few decades (Phillips et al. 2008a). Simulation models have examined selection on the kernel in response to frequency and aggregation of suitable habitat (Murrell et al. 2002, Cousens et al. 2008, Lindstrom et al.

2011), and in the presence of kin selection (Hovestadt et al. 2001, Rousset and Gandon 2002, Starrfelt and Kokko 2010). Despite these growing insights about the kernel's shape, there is still a wide gap before other aspects of dispersal can be incorporated in species' distribution models. Generally the kernel is expected to be invariant both spatially and between individuals (With 2002, Hastings et al. 2005, but see e.g. Petrovskii et al. 2011). This expectation contrasts with numerous studies that report spatial variation in spread rate correlating with environmental heterogeneity (e.g. Sharov et al. 1999, Urban et al. 2007, LeBrun et al. 2008). This has led to a growing body of literature studying how environmental variability could be integrated with more realism (Gilbert et al. 2004, Muirhead et al. 2006) or even in mechanistically derived dispersal kernels (Jongejans et al. 2008, Travis et al. 2011). Especially mechanistic models hold the promise that ultimately they potentially yield more robust results which are more confident when making projections into novel parameter space, because they capture more of the biological relevance in the system (Travis et al. 2012). Kernels, for example, were developed for wind dispersed seed, to model the influence of seed release height and wind velocity on the trajectory of seeds (Katul et al. 2005, Skarpaas and Shea 2007), and in seeds with zoochory the behaviour of the vector and retention time of the seed on the

vector have been investigated to improve prediction for dispersal (Wichmann et al. 2009, Bullock et al. 2011). As a result adopting a combination between spatially realistic and mechanistic models is increasingly becoming popular in models for the spread of species, in particular for scenarios with future climate expectations (Bullock et al. 2012), or different land management strategies (Travis et al. 2011).

An interesting alternative could be the inverse modelling approach: inferring the shape of the kernel from the pattern we observe when a species invades (Wiegand et al. 2003, Grimm et al. 2005). A model using this approach has the advantage that it can infer the shape of the dispersal kernel which captures information that is indeed relevant for the dynamic process of the species distribution (in particular the spread of the species). The challenge, however, is to explain both spatial and temporal variability in the environment (Cook et al. 2007, Hooten and Wikle 2008, Stanaway et al. 2011). Chapter III presents a possibility how such a model can be constructed.

The aim of this thesis

The aim of this thesis was to focus on particular gaps in our knowledge of how spatial variability in the environment affects the dispersal and the dynamics of species' ranges. I had the aspiration to investigate the question both by theoretical approaches and by

experimental work. I chose to focus on three different research questions on the complex interaction between the spatial variability and the way it affects the spatial distribution of individuals. In chapter I, I investigated if birds use information on availability of nesting sites for their dispersal decision. Specifically I was interested in when exactly birds gather this information, because this could shed light on how much information is available at the moment of making the dispersal decision. In chapter II, I study how alternative selective pressures on the evolution of sex-specific dispersal arise when dispersal is modelled in a spatially explicit way. Such a model includes the link between dispersal and the distribution of individuals in space, which is necessary to account for spatial variation in local sex ratio and acknowledging the eco-evolutionary feedback at work. Finally, in chapter III, I tested whether spatio-temporal variability in host density has an influence on the spread rate of an ectoparasite when the ectoparasite is expanding its range.

When is information on availability of nesting sites important for dispersal? Chapter I

For active dispersal it can be of great advantage to perceive variation in environmental suitability and use this information for dispersal decisions (Danchin et al. 2001). Gathering information for this purpose, termed

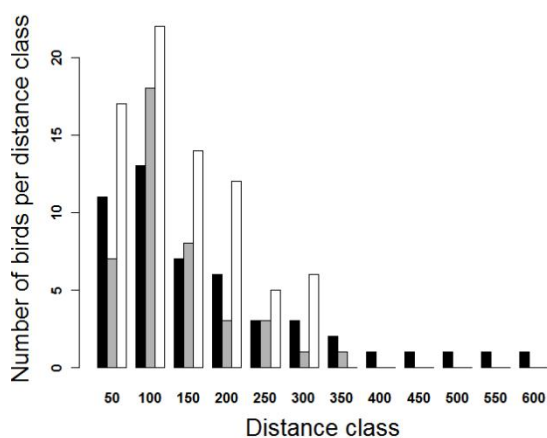
prospecting, is very widely observed in birds (Reed et al. 1999). Examples include birds other than the parents entering foreign nest box to retrieve information on the status of the brood of conspecifics (Doligez et al. 1999). There is clear evidence that birds actually use such information when making dispersal decisions (Reed et al. 1999). Birds are often attracted to settle in the vicinity of conspecifics (Valone and Templeton 2002, Fletcher 2006) and experiments have shown that they preferably settle near locations where conspecifics had high reproductive success in the previous year (Doligez et al. 2002, Boulinier et al. 2008).

Open question about prospecting remain: an interesting and potentially important one is when exactly do birds collect the relevant information (Reed et al. 1999)? One could expect that the decision of where to settle requires systematic consideration of different locations, and this might take time. This time might be lacking at the peak of breeding activity, requiring birds to spend considerable time for brood care (Danchin et al. 2001, Danchin and Cam 2002). Migratory birds might be even more time constrained, since they attend breeding grounds for only a short period of the year. These birds might only have a short time span after the breeding season to prospect the environment. Furthermore, some cues might be harder to sample than others. Checking whether the neighbour was

successful in fledging some chicks might take less time than estimating food availability or precise locations of nests in a certain area (Boulinier et al. 1996, Danchin et al. 2001).

For chapter I, I performed a field experiment to test when collared flycatcher gather information on the availability of nesting sites (see section 'study system'). This is a system where time constraints for prospecting are likely: Collared flycatchers are migratory and obligate secondary cavity-breeders that have to invest searching time in finding available nesting sites. We manipulated the density of available nesting sites in different forest plots and studied the dispersal decisions that birds made in the successive year. This was compared to *control* forest plots where the density of breeding sites remained unchanged. To determine when the birds use the information, we manipulated density of breeding sites with two treatments (i)

a)



during the nestling period only (*half-time* treatment) and (ii) during both the nestling period and the pre-migration period (*full-time* treatment).

In contrast to expectations, time did not seem to constrain the birds when gathering information on availability of breeding sites, because both treatments were found to have an effect on the birds' dispersal behaviour. The longer we had manipulated available breeding sites, the further birds tended to dispersal in the next year (Fig 1). This treatment had no effect on the proportion of birds dispersing among forest plots, but it affected how far birds dispersed within each forest and thus it had consequences on the small scale distribution of individuals. Interestingly, the birds' activity of singing and alarming also decreased in manipulated forests plots the year after the treatment (Fig 2). This decline was strongest immediately after the birds returned from migration. It

b)

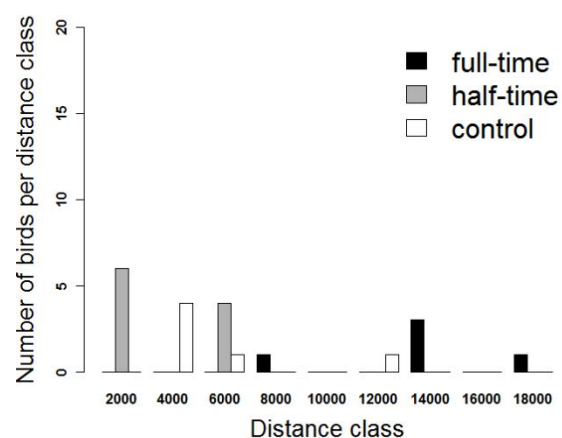


Figure 1. Distribution of observed (a) within and (b) between plots dispersal distances in collared flycatcher. Dispersal distances increased when nest boxes were available for prospecting for a shorter time. The label on the x-axes shows the maximal distance for each distance classes.

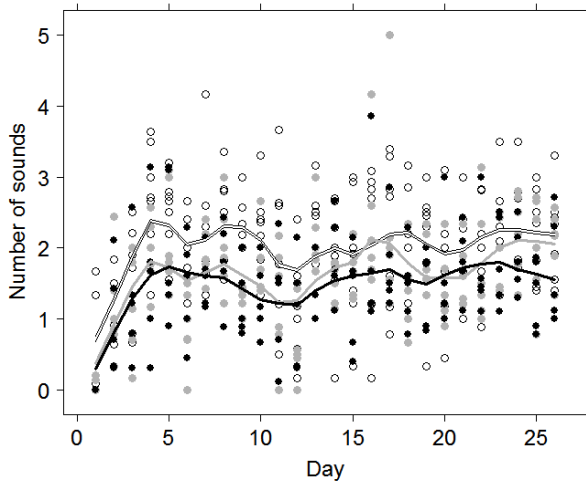


Figure 2. Temporal change in acoustic activity (alarm calls and songs) in each forest plot over the season for the different treatments: *full-time* (black), *half-time* (gray), and *control* (white with double line), starting on April 24th 2009 (which corresponds to day 1). Flycatchers in plots with nest boxes removed, and thus with less opportunity for prospecting, showed a lower acoustic activity compared to the *control* forest plots at the beginning of the season following the manipulation, and this difference remained longer in the *full-time* treatment.

bounced back as the season progressed and the birds had time to update their information on the restored breeding site's density.

My experiment therefore showed that birds indeed collect information on availability of nesting sites in advance of making their dispersal decision. However, there seems to be no time constraints for prospecting on a cue which is permanently available. This conclusion only held true within a forest, and beyond this spatial scale birds do not appear to rely on information on the availability of nesting sites.

Study species and system

The collared flycatchers (*Ficedula albicollis*) (Fig. 3) of Gotland offer an excellent system to study the dispersal of birds. The landscape in the south of Gotland, a Swedish island in the Baltic Sea (57°6'N, 18°19'E), is composed of agricultural land with fragments of pine and deciduous forests in between (Fig. 4). Especially the deciduous forests are

habitat for the northernmost breeding populations of collared flycatcher (Svensson 1992). In these forest fragments nest boxes have been provided for the birds since the early 80s (Gustafsson 1986, 1987). By now, the entire project comprises over 2800 boxes in 41 forest fragments. Collared flycatchers readily accept artificial nest boxes: Pärt and Gustafsson (1989) estimated that when boxes are available fewer than 5% of the birds breed in natural holes (Pärt and Gustafsson 1989). This allows trapping, banding, and monitoring breeding success of a substantial part of the entire island's flycatcher breeding population, offering a unique opportunity to track the birds' natal and breeding dispersal.

The collared flycatcher is a long-distance migrant that overwinters in central Africa. The birds arrive on Gotland in late April until late May, yearlings arriving on average a few days later than adults. About one week after arrival birds start building nests. From mid-May until the beginning of June, females lay 5-7 eggs (rarely 4 or

8), incubate alone for about 13 days, after which both parents provision the brood between 16 to 19 days (Cramp and Simmons 1988). This was the time when we caught birds: females during incubation, males between day 6 and day 14 of brood provisioning, and chicks were banded when they were 8 days old. Afterwards, from mid-June until early July, juveniles fledge and parents, which undergo their molt at the same time (Jenni and Winkler 1994), still provide for them another two to three weeks. Departure for migration starts in August, adults usually departing before juveniles. Regarding dispersal behavior in collared flycatcher, it is known that most birds return faithfully to the same forest plot every year, but within the forest, shifting between breeding sites is more likely than in other comparable birds (Gustafsson 1989, Pärt and Gustafsson 1989). As is generally found for birds (Greenwood 1980), collared flycatchers disperse longer distances in natal than breeding dispersal (Pärt 1990), females disperse generally further than males (Pärt and Gustafsson 1989, Pärt 1990) and low reproductive success in one year increases dispersal distance (Doligez et al. 1999). The propensity to disperse in the species is heritable to some degree (Doligez et al. 2009). The propensity to leave a forest can be density dependent, although the effect depends on the individual's state: Density affects breeding dispersal positively in adult males, but the effect on the dispersal



Figure 3. Male (left) and female (right) of collared flycatcher. The female has built its nest in a artificial box belonging to the study area of Gotland. Pictures kindly provided by Heikki Eriksson.

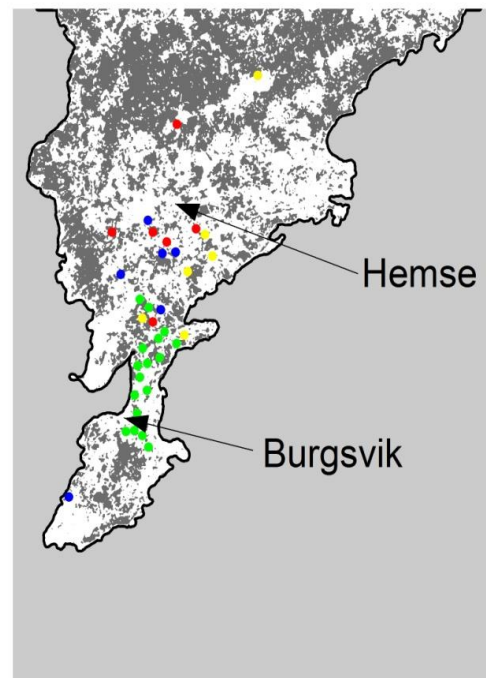


Figure 4 Location of flycatcher study plots within the forest (grey) fragmented landscape in the southern part of Gotland. The colours of the plot refer to *full-time* treatment (blue), *half-time* treatment (red), *control* plots (yellow), and forest plots not included in the experiment set up of chapter I, but where birds were also recaptured (green). Map reconstructed from Google map.

of females and yearling males is negative (Doligez et al. 1999). Previous studies already confirmed that information

gathering exists in collared flycatchers: Birds are attracted by high breeding activities of conspecifics (Doligez et al. 2004a). They use this information, in that local high reproductive success of conspecifics (both chick condition and quantity) impacts settlement decisions in the next year (Doligez et al. 2002, Doligez et al. 2004b).

An important reason why birds may have to shift their breeding site within the forest is competition for nest holes with great tits (*Parus major*), and to a lesser extent also with blue tits (*Cyanistes caeruleus*), Eurasian nuthatches (*Sitta europea*), coal tits (*Parus ater*) and pied flycatchers (*Ficedula hypoleuca*) (Gustafsson 1987). As the flycatcher species is the only migratory species on this list, they have the opportunity to choose nest-holes approximately only 2 weeks after the resident species. Nevertheless, flycatchers have been found to be attracted by high tit density, which could be another type of information use. Presumably because tits stay at the breeding site overwinter, flycatchers might usefully copy their habitat choice after they return from Africa (Forsman et al. 2008).

Finally, this system is attractive for the several advantages it offers for studying dispersal. By now, up to 30 people are monitoring the flycatchers on Gotland every year. This guarantees high recapture rates, including birds which disperse further. In addition, the size of the project

facilitates collaboration in the field which was important to conduct my experiment in chapter I.

Does the availability of mates influence the evolution of sex-specific dispersal? Chapter II

Sex-specific dispersal behaviour has been documented in a wide range of different species (Greenwood 1980). Avoidance of inbreeding (Lehmann and Perrin 2003), sex-specific competition between kin (Motro 1991), sex-specific costs of dispersal (Bonte et al. 2009), mating success, and benefits of philopatry (Handley and Perrin 2007) have all been invoked as explanations for these patterns. All of these factors have, however, focused on explaining why dispersal behaviour differs between the sexes. Only rarely has it been pointed out that there is also a risk for males and females to remain unmated, if the different dispersal distances lead to strong reductions in the local availability of mates (Gros et al. 2008, Gros et al. 2009). The fitness of both sexes is therefore strongly dependent on densities of both sexes (Hirota 2007), which is sufficient to create an evolutionary feedback (Kokko and Lopez-Sepulcre 2007). Densities of both sexes have been overlooked as selective force in the evolution of sex-biased dispersal. It appears important to fill in this gap, not least because, in contrast to all the other forces this should lead to more, rather than less, similar dispersal behaviour in

the sexes. First we illustrated with a conceptual model how dispersal and demographic stochasticity can create variance in the density of one sexes, and how increased variance indeed results in a higher selective pressure for the opposite sex to disperse, balancing some of this variance in density.

Then we investigated how this can influence the evolutionary dynamic of sex-specific dispersal with an individual based model (see section on spatial modelling). With the individual based model we were able to account for dispersal distances explicitly, which was necessary for realistically accounting for the effect that dispersal has on the densities. To demonstrate that the evolution of the two sexes indeed depend on each other we

examined three scenarios: First, females were forced to disperse according to a fixed mean dispersal distance and males could adapt to the emerging female densities, second, the opposite situation where males were forced to disperse and females could evolve, and third, both sex could evolve in accordance to the other's sex density.

The result was clear: after evolution for approximately 1000 generations, dispersal distances of males and females across all 500 replicates per scenario were positively correlated (Fig 5). Both males and females adapted to the dispersal distance of the opposite sex, and when both sexes could evolve, we observed co-evolution towards more similar dispersal behaviour.

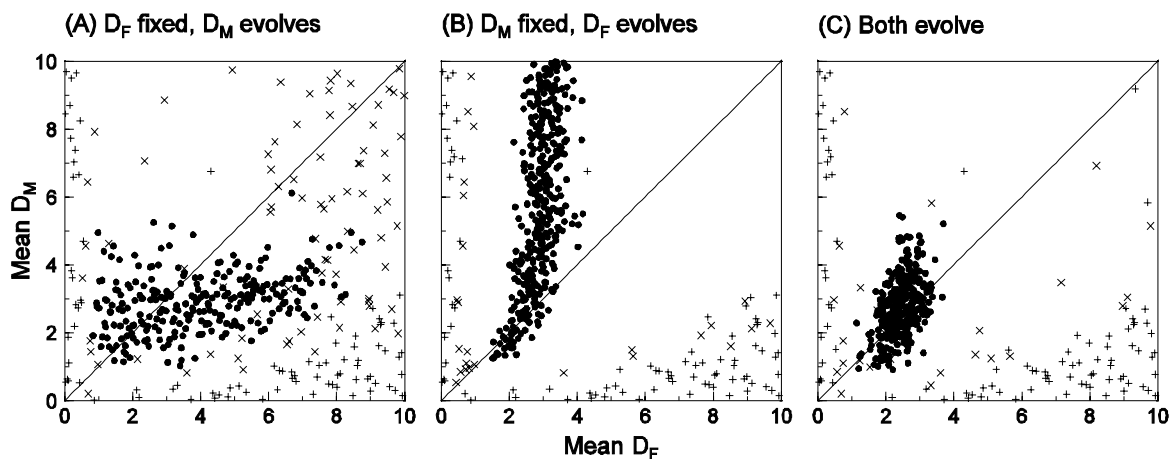


Figure 5. Results of 500 simulations for each of three scenarios: males could adapt to the fixed dispersal kernel of females (A), females could adapt to the fixed dispersal kernel of males (B), and both sexes were free to evolve (C). Simulations differed only in the combination of initial mean of the dispersal kernels of males and females. Symbols indicate the initial mean of the dispersal kernels of populations that went extinct during the settlement period (+), during the time we simulated evolution (x), and the evolved means of the population that persisted (•). The smaller the bias in sex-specific dispersal in a population the closer the symbols are to the diagonal (solid line). The white areas (where + and x are missing) show the parameter space where populations were viable.

Thus, because our model accounted for the possibility of an eco-evolutionary feedback, we could highlight the role of a factor (mate limitation) which leads to coevolution between the sexes in dispersal distance, reduces the sex bias in dispersal and, thus, potentially mitigates sex-bias promoting factors.

Influences spatio - temporal variability in host density the spread rate of an ectoparasite? Chapter III

Environmental suitability evidently changes over time and affects also the distribution of invasive species (Domenech et al. 2005, Ficetola et al. 2010). Insects, for example, often take advantage of incidentally occurring favourable conditions when invading new habitat (Loxdale and Lushai 1999). Also, in host-parasite systems, spatio-temporal variation is recognised as one of the most important factors driving epidemics (e.g. Keeling et al. 2001). It is therefore highly likely that the spread of an invading parasite is influenced by the spatio-temporal variability of its host. Thus, a model which can account for host variability may be needed to explain the pattern of the species' spread.

To test this prediction we used the invasion of deer ked (*Lipoptena cervi*), a common ungulate ectoparasite, which has spread across Finland within the last 50 years (Välimäki et al. 2010). The adult deer ked is permanently attached to its host. Females constantly produce pupae,

which drop off the host and develop on the ground before searching for a new host at the end of summer (Haarlov 1964). The deer ked disperses either by flying short distances during this search period, or by hitchhiking on the host. The history of the invasion had been documented by eight published surveys (Hackman 1972, Von Brander 1976, Hackman 1977, 1979, Hackman et al. 1983, Zoological Museum Finland 1988, unpublished data A. Kaitala 2008). As an additional dataset we used annual moose densities for every Finnish hunting district provided by the Finnish Game and Fisheries Research Institute.

We used Skellam's reaction diffusion model (Skellam 1951) to describe the spread of the parasite in continuous two-dimensional space. To account for spatio-temporal variability we allowed each parameter (i.e., local population growth rate r and diffusion coefficient D) of the model to depend on local host density. The result was a series of four models, which included movement rate, the population growth rate, both variables, or no parameter dependent on host densities. Then we fitted the model with Bayesian parameter estimation and applied model selection techniques to quantify the strength of the parasite-host interaction and its impact on invasion speeds (see section on spatial modelling).

We found that, in the best model, both movement rate and the population growth rate were dependent on local moose density. Higher local moose densities

imply higher host abundance for the deer ked, thus increasing the spread rate. Furthermore this model predicts a minimal density of 0.08 moose per km² below which the growth rate becomes negative and the deer ked should not be able to spread (Fig. 6). This value coincides with the moose densities in 1960 when the deer ked invasion started. Moose densities have been increasing in Finland, being generally lower than the threshold density before 1960, and almost always higher after 1960 (Luoma 2002). This adds confidence to the model we selected.

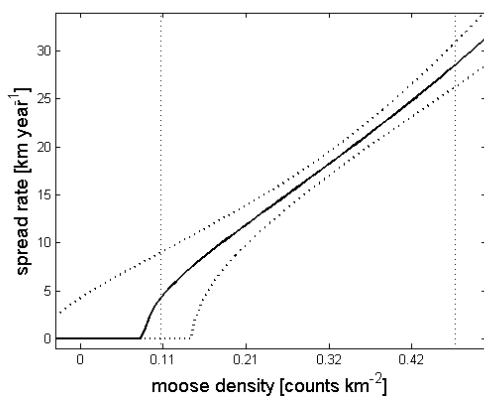


Figure 6. Spread rate of the deer ked invasion predicted by the Model 3. The bold solid line shows the posterior median and the dotted lines the 95% credible interval. The vertical dotted lines indicate the lower and the upper range of the annual mean of observed moose densities between 1960 and 2008.

Spatial modelling

Models accounting for explicit spatial variability are often too complex to be solved analytically. Therefore I had to rely on numerical solutions in my thesis. In chapter II, I have used an individual based model, because these offer great flexibility for defining the relevant properties of the

system: individual dispersal behaviour, population dynamics and even the spatial variation in the environment and simple rules which specify the interaction in this virtual world (Travis and Dytham 1998, 2002, Grimm et al. 2006, Kokko 2007). For example, I had to implement how individuals disperse, reproduce, die, and how each of these processes depends on density. In addition, it was essential to define the dimensions of the system in both space and time. High flexibility comes at the cost that most spatial explicit individual based models provide a highly stochastic outcome (Grimm et al. 2006). Therefore, a single run of the simulation model provides little information about the system properties. The greatest strength of individual based models is that it can provide a proof of principle. The general direction of evolution emerges from the model, which has implemented a broad range of the principles of the system under investigation, after the model has been run sufficiently often (Grimm et al. 2005). The same logic was utilized in chapter II to demonstrate that a co-evolutionary feedback can emerge in the evolution of sex-specific dispersal if the model accounts for spatial heterogeneity in sex-ratio. Because the principle emerged from the system we implemented in the model, the precise choice of parameter values was of minor importance. For example, the magnitude of the dispersal distance was not crucially important; the important finding is that

the other sex adapted towards the same (as such relatively arbitrary) distance.

The second model in chapter III is a reaction-diffusion model which is a partial differential equation with two parameters: r for local population growth and D for the diffusion-like movement of individuals. This model predicts the density of the spreading species in space and time, which we interpreted as probability of the population being detected. This allowed us to calculate the likelihood of the model fitting the spatial pattern of the observed invasion. Finally we could estimate the parameters r and D using Bayesian parameter estimation through an adaptive Metropolis-Hastings MCMC algorithm (Ovaskainen et al. 2008). Consequently, we found parameter values which provide model results that fit best to describe pattern of the invasion.

Both models are extremely flexible in considering realistic spatial assumptions, though they come at the cost of calculation power, excessive for a single desktop workstation. In our case, this made the use of cluster computer necessary.

Concluding remarks

Human influence, especially on land use and climate, has initiated a fast change in the environment rapidly leading to changing living conditions on this planet. To predict the consequences of this change on the ecosystem, and to prepare for responsive measures, it is necessary to understand how changes in the

environmental conditions will alter species' distributions. The three chapters I present all highlight some of the complexities we are facing when trying to understand how spatial variability in the environment effects on the dispersal and on the dynamic of distribution of species.

Firstly, dispersal behaviour can interact with the state of an individual; here, collected information can be one aspect of the individual's state. Being able to pinpoint which information is relevant for dispersal decisions and when this information is collected by individuals brings us therefore a step closer towards better understanding of dispersal behaviour. Furthermore, my experiment also shows that the effect of some information is limited to a local scale. In the future, research should therefore concentrate on identifying cues that individuals use when deciding to disperse long distances and/or to settle in a new habitat. Since abiotic and biotic environmental conditions generally affect species' distribution patterns at a large scale, it is advisable to focus on such factors first. A long tradition of research on habitat selection has identified numerous factors correlating with nest site selection (e.g. Clark and Shutler 1999, Stamps 2001, Pärt et al. 2011). It appears that now would be the time to conduct more experiments which can unravel whether these factors are also involved with active decision-making in informed dispersal behaviour.

Secondly, dispersal interacts not only with the individual's state, but also with the population dynamic. The latter interaction can result in an evolutionary feedback, which has consequences for the evolution of dispersal (chapter II). This finding results from modelling dispersal in a spatially explicit manner. In the future, models on the evolution of dispersal should pay greater attention to assumptions concerning space, and the implications this has for the evolving dispersal rules. This message is strengthened by the fact that other models found similar surprising effects when accounting for space more explicitly. For example the spatial configuration of metapopulations can have an influence on the connectivity between subpopulations (Vuilleumier and Possingham 2006), and the propagation of deleterious genes can become possible in a population spreading in space (Travis et al. 2010).

Thirdly, we know that dispersal greatly depends on variation in environmental conditions, but models for species' distribution that incorporate the dynamics of spread rarely account for this fact. This is very unfortunate, because it is possible to incorporate spatio-temporal variation in the environment to the spread rate, as we show in chapter III. And even though we use the reaction-diffusion model with its very restrictive assumptions about the tail of the dispersal kernel, we found an improvement of the model when we accounted for variation in the

environment. Furthermore, by fitting the model to the pattern of a historic invasion, we also received a goodness of fit measure which can be employed for pitting different models against each other using model selection (Burnham and Anderson 2002, Cabral and Schurr 2010). In fact, both Bayesian parameter estimations and model selection are techniques, which increasingly find application in the analysis of invasion dynamics and which hold great promises for further insight. The Bayesian framework allows linking mechanistic models of spread to complex spatial pattern of the invasion (Cook et al. 2007, Phillips et al. 2008, Pagel and Schurr 2012), and Hierarchical Bayesian models allow the consideration of several different underlying processes in combination (Wikle 2003, Bled et al. 2011). This is important because dispersal itself is a combination of different processes, which all contribute simultaneously to the spatial distribution of individuals (Carrasco et al. 2010). Schurr et al. (2008), for example, suggests the differentiation between source and path effects, which either comprehend factors of the local environment or of the environment along the whole dispersal trajectory of an individual. Models in the future will have to explore which of these processes are most relevant for predicting the pattern of species distribution at the large scale. Model selection will therefore be an important tool to identify kernels

(e.g. Wang et al. 2011) and mechanistic models (e.g. Drury and Candelaria 2008)

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