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correlation or causality ? : exploring mechanisms using
correlative and experimental approaches in a passerine
bird species, the collared flycatcher**

Marion Germain

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par **Marion GERMAIN**

**THE LINKS BETWEEN DISPERSAL AND INDIVIDUAL
FITNESS: CORRELATION OR CAUSALITY?**

Exploring mechanisms using correlative and experimental approaches
in a passerine bird species, the collared flycatcher

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ASBTRACT

Dispersal is commonly defined as the movement of an individual from its natal or previous breeding site to a new breeding site. Because dispersal involves movements of individuals and genes among populations, it is widely recognized as a key life history trait with strong effects on many ecological and evolutionary processes, such as population dynamics and genetics but also species spatial distribution or response to brutal environmental variations induced by human activities. Yet, the consequences of dispersal in terms of individual fitness remain poorly understood despite their crucial importance in the understanding of the evolution of dispersal. The aim of this PhD is to get better insights in the fitness consequences of dispersal using both correlative and experimental approaches at different scales, *i.e.* annual and lifetime scales, in a wild patchy population of migratory passerine bird, the collared flycatcher (*Ficedula albicollis*). Using a long-term data set encompasses more than 20 years of data, differences between dispersing and philopatric individuals were showed both at a lifetime and annual scale. The results highlighted strong phenotypic- and condition-dependent effects of dispersal and underline that the balance between the costs and benefits of dispersal is likely to be the result of subtle interactions between environmental factors and individuals' phenotype. Moreover, the experiment of forced dispersal demonstrated that dispersal might entail costs linked with settlement in a new habitat, which only some individuals may overcome. Nevertheless, the absence of difference in major fitness related decisions after settlement suggests that dispersal is mostly adaptive for individuals overcome such costs.

Key words: dispersal, fitness, collared flycatcher, dispersal costs and benefits, experimental approach, correlative approach, passerine.

RÉSUMÉ

La dispersion est définie comme le mouvement d'un individu entre le site de naissance et le premier site de reproduction ou entre deux sites de reproduction. La dispersion se traduit par des échanges d'individus et des flux de gènes entre les populations et est donc reconnue comme un trait d'histoire de vie clé de part son rôle déterminant sur de nombreux processus écologiques et évolutifs comme la dynamique ou la génétique des populations, la répartition spatiale des espèces ou encore la capacité des espèces à faire face aux changements brutaux induits par les activités humaines. Pourtant les conséquences de la dispersion en terme de valeur sélective individuelle restent mal connues malgré leur importance dans l'évolution de la dispersion. Le but de cette thèse est d'identifier plus précisément les conséquences de la dispersion en terme de valeur sélective individuelle en utilisant à la fois des approches corrélative et expérimentale dans une population sauvage de passereaux migrateurs, le gobe mouche à collier (*Ficedula albicollis*). Grâce à des données à long terme comprenant plus de 20 ans de suivi, des différences entre les individus dispersants et philopatrics ont pu être mises en évidence à la fois à l'échelle de la vie des individus et à l'échelle annuelle, celle de l'événement de reproduction. Les résultats mettent en évidence des effets de la dispersion dépendant à la fois des conditions et du phénotype des individus et soulignent donc le fait que la balance entre les coûts et les bénéfices est le résultat d'interactions subtiles entre l'environnement et les caractéristiques de l'individu. D'autre part, l'expérience de dispersion forcée a permis de démontrer clairement l'existence de coûts liés à l'établissement dans un environnement non familier que seuls certains individus sont capables de surmonter. Enfin, l'absence de différence dans les décisions majeures de reproduction une fois les individus établis, suggère que la dispersion doit majoritairement être adaptative, une fois les coûts de l'installation surmontés.

Mot clés: dispersion, valeur sélective individuelle, gobe mouche à collier, coûts et bénéfices de la dispersion, approche corrélative, approche expérimentale, passereaux.

« You can't even begin to understand biology, you can't understand life, unless you understand what it's all there for, how it arose - and that means evolution. »

Richard Dawkins



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Chapter 1

General introduction

WHAT DO WE MEAN BY DISPERSAL?

Dispersal is a really widespread life history trait affecting most species as soon as they are mobile at least once during their lifetime. It therefore concerns organisms as diverse as mammals, birds, insects and invertebrates or vegetal and any discussion about dispersal begins with questions about its definition. In ecology and evolution, authors vary in their use of terms depending on the topic or on the specie(s) of their research. For some organisms, movements only happen once in the individual's life while others continually move throughout their lives, some organisms migrate between two centres of activity, others move most of the time around relatively small localities (Stenseth & Lidicker 1992). Given this variety and continuum of movements, it is easy to catch that there is no simple definition of dispersal universally applicable. Here, I choose to focus on the definition adopted by many ecologists studying dispersal among vertebrates.

In that context, one of the first synthetic definition of dispersal comes from Howard (1960) who described dispersal as “the movement the animal makes from its point of origin to the place where it reproduces or would have reproduce if it had survived and found a mate”. Since then, dispersal has become a subject of profound interest and the concept of dispersal has been considerably extended, allowing the definition of two dispersal processes: *i*) natal dispersal and *ii*) breeding dispersal.

Indeed, Howard (1960) described a dispersal that only refers to juveniles and concerns the permanent movement from birth site to the first breeding site or potential breeding site. However, older individuals may also disperse from one breeding site to another. This distinction between natal and breeding dispersal has been emphasized by Greenwood (1980) who described breeding dispersal as “the movements of individuals, which have already reproduced, between successive breeding sites”. While natal dispersal concerns individuals that have never reproduced, breeding dispersal obviously refers to individuals previously involved in reproduction.

Dispersal is usually defined as a three steps process. The movement is initiated by the decision to leave (i.e. emigration), which is followed by a movement phase that ends by a decision to settle in a new reproduction site (i.e. immigration). Because of the movement of individuals and because a successful dispersal is linked with reproduction, dispersal is thus defined as a process that has the potential to lead to gene flow (Clobert *et al.* 2001), which may have many and strong implications for a lot of ecological and evolutionary processes (Stenseth & Lidicker 1992).

DISPERSAL: A CORNERSTONE OF ECOLOGICAL AND EVOLUTIONARY PROCESSES

Dispersal is an important determinant of gene spread and is thus subject to strong natural selection. Through simply moving from one place to another, dispersing individuals not only influence the demography of populations but also population dynamics, population genetics, species distribution and individual fitness. Dispersal has therefore been widely recognized as a key life history trait affecting diverse and numerous ecological and evolutionary processes. The aim of this section is not to provide an exhaustive review of the potential effects of dispersal on ecological and evolutionary processes but to give an overview of the extent of the manifold effects of dispersal at different scale (i.e. demographic and genetic), and to illustrate why it would be particularly important to understand dispersal. These two scales first appeared to be of the highest importance when studying the effects of dispersal because individual movements modify populations' sizes and because dispersal leads to gene flow, which may have strong implications for population genetics.

DEMOGRAPHIC EFFECTS

Due to the movement of individuals between and within populations, the more intuitive effect of dispersal is maybe the effect on population dynamics via the effects of populations' demography. Indeed, by emigrating from a population

and immigrating in a new one, dispersing individuals affect spatial repartition of individuals and therefore impact population size via emigration, immigration and modifications of birth and dead rates (Diffendorfer 1998). Studies of population dynamics were therefore the first to point out the importance of dispersal in processes of extinctions and persistence (Levins & MacArthur 1966; Levins 1970; Gadgil 1971), particularly relevant in a metapopulation framework. The metapopulation concept refers to spatially delimited local populations, which interact via individuals moving among populations (i.e. especially via dispersal) (Levins 1969; Levins 1970; Hanski & Gilpin 1991). At the birth of the concept, Levins (1969) considered only the effects of dispersal on colonization processes (i.e. movement to empty patches). This has, lately, been extended with the idea that, at some point, all patches within a metapopulation are to some extent, exchanging individuals due to dispersal, also including those already occupied. At the metapopulation level, dispersal and establishment of new populations are often necessary for the long-term persistence of species, for instance, to compensate for local extinctions. By increasing the size of a small population, dispersal may thus buffer the extinction risk (Brown & Kodricbrown 1977; Hanski 2001) but may also increase this exact same risk if individuals disperse from a small population, already at higher risk of extinction (Andreassen & Ims 2001; Fowler 2009).

Importantly, spatial heterogeneity in patches quality may provide more suitable habitats than others. In that context, metapopulation models, where habitat suitability is spatially heterogeneous are commonly referred to as source-sink systems (Pulliam 1988). Sources designate habitat patches where the habitat is suitable enough for the population to persist in the absence of dispersal (i.e. positive *per capita* growth rate), and sinks are habitat patches where the population would become extinct in the absence of dispersal because of the low quality of the patch (Pulliam 1988; McPeck & Holt 1992; Amarasekare 2004). Obviously, the existence and persistence of sink populations depend on immigration from sources habitats. Besides, the rate of dispersal not only affects the growth rate in sources populations through emigration but also the dynamic and persistence of

the entire population and thus the whole metapopulation persistence (Ranta & Kaitala 2000; Gundersen *et al.* 2001).

There are two specific situations where the interaction between dispersal and population demography and spatial distribution or species range is particularly important: when the range is changing in response to an environmental change, or in the case of a biological invasion, two processes of particular interest nowadays. In the current global-warming context, one of the most efficient responses to climate change is range or habitat shifts (Kokko & Lopez-Sepulcre 2006; Parmesan 2006). A species dispersal characteristics and ability will therefore play a major role in its ability to escape degrading environment and therefore in determining its potential to adapt and persist (Berg *et al.* 2010).

Implicitly, the change of population size involves a change in local density, which has, in turn, many consequences (Clobert *et al.* 2012). For instance, access to resources is typically density-dependent. Dispersal out of the patch, by decreasing the density within the patch, may free up resources, leading thus to a better access to resources for non-dispersing individuals which may in turn lead to an increase in population growth (Keeley 2001). In an experimental study on root voles (*Microtus*), Gundersen, Andreassen and Ims (2002) demonstrated that the loss of dispersers from a population leads to an increase in the *per capita* recruitment rate of the remaining individuals. This effect is maybe particularly important among kin, where dispersal away from the natal patch decreases competition between siblings (Cote & Clobert 2007) (see §1.3.2.1 for further details about kin interactions as a proximate factor influencing the evolution of dispersal). Conversely, immigration increases density, which may, in turn, negatively affect density-dependent traits (e.g. growth rate, fecundity, survival, territorial acquisition and of course, dispersal). Overall, dispersal acts on the population level via density-dependent effects, and at a larger scale on the persistence of metapopulation.

GENETIC EFFECTS OF DISPERSAL

It is clear that dispersal have strong impacts on population genetics because of the resulting gene flow. It is however important to notice that genetic effects of dispersal can be de-coupled from demographic effects. Indeed, contrary to demographic effects, a single or a few migrants can have strong impacts on the genetic diversity of a population which depends on immigrants age, sex and life-history traits such as fecundity but which depends too on properties of the patch that the migrants enter (e.g. mate and resources availability, population size and density). To mention a single example, immigration to an inbred population can result in heterosis (i.e. hybrid vigour) in case of mating between a resident and an immigrant, which increases the realized gene flow (Ebert *et al.* 2002).

Globally, dispersal has been identified as counteracting the effects of genetic drift and mutations by increasing genetic variation within populations (Hartl & Clark 1997), which leads in the same time to a decrease of genetic variation between populations (Bohonak 1999). Indeed, spatially separated populations can become locally adapted (Kawecki & Ebert 2004) and gene flow is typically thought to act as a brake of local adaptation (Case & Taper 2000) because it homogenises allelic frequencies (Bohonak, Smith & Thornton 2004).

On the other side, dispersal can, under specific conditions, emphasizes genetic divergence between populations (Garant *et al.* 2005). Population divergence depends on the balance between diversifying natural selection and homogenizing gene flow (i.e. dispersal), with one force opposing the other (Felsenstein 1976; GarciaRamos & Kirkpatrick 1997). Until now, we saw that gene flow resulting from dispersal increases genetic variation within populations and thus decreases the divergences between populations. However, spatial variation in the expression of genetic variation will also generate differential evolutionary response.

To summarize, dispersal is a major process influencing diverse ecological and evolutionary processes. As highlighted by Dieckmann, O'Hara and Weisser

(1999), it is difficult to identify a single ecological or evolutionary process that is not affected by dispersal. Importantly, dispersal can produce ecological patterns, but these patterns can again influence the selective pressures acting on dispersive traits. It is only by closing this loop and by realizing that dispersal can act at the same time as both a cause and an effect that we will get a global idea of the evolutionary ecology of dispersal. Dispersal holds a central role for both the dynamics and evolution of spatially structured populations, allowing the genetic cohesion of species across space, its global persistence despite local extinction and the tracking of favourable environmental conditions in a changing world. However, dispersal remains a relatively cryptic process (Ronce 2007), partly because it is really challenging to consider the process as a whole. Usually, dispersal is considered as a ‘simple’ movement between two points. The reality is far more complex and a huge number of factors may influence dispersal propensity. Dispersal may be summarized as a set of interconnected processes influenced by many factors of different natures such as spatial and temporal heterogeneity or inter-individual variability (Ims & Hjermann 2001; Clobert *et al.* 2009).

THE EVOLUTION OF DISPERSAL UNDER MANY INFLUENCES

A fundamental question related to the effects of dispersal on the ecological and evolutionary processes mentioned above is: why do individuals disperse and which mechanisms cause the evolution of dispersal? There is classically two distinct answers to these questions: the ultimate and proximate causes (Stenseth & Lidicker 1992; Clobert *et al.* 2012). The ultimate causes are the selective forces shaping the evolution of the trait via the individual fitness. If dispersal enhances individual fitness, it will be selected for, independently of whatever proximate factors that may serve to trigger it. In contrast, proximate explanations are concerned with the mechanisms that underpin the trait or behaviour, that is: how it works?

ULTIMATE FACTORS

Particularly the evolution of dispersal has been the centre of much theoretical work aiming to identify *THE* ultimate factor driving the evolution of dispersal. Three main ultimate causes have been suggested to promote the evolution of dispersal: inbreeding avoidance, environmental stochasticity, kin interactions and competition and finally, habitat quality.

Inbreeding avoidance

The negative fitness consequences associated with breeding between relatives are well known as it results in an increased homozygosity and thus the risk of expression of deleterious recessive alleles (Pusey & Wolf 1996). Consequently, mechanisms to avoid such mating are expected to be selected and inbreeding avoidance has thus been demonstrated to promote the evolution of dispersal (Greenwood 1980). Although evidences for inbreeding avoidance are accumulating (e.g. Ebert *et al.* 2002), its impact on dispersal has been mainly correlative and the hypothesis that inbreeding avoidance is a major driving force favouring dispersal behaviour has been challenged on several grounds. For example, in practice, separating the evolution of dispersal as a mean to avoid inbreeding and opposing it to a mean to avoid kin competition is difficult (Perrin & Goudet 2001). Yet, in the great tit, Szulkin and Sheldon (2008) reported that individuals breeding with close relatives moved over shorter distances than those outbreeding and suggested thus that dispersal should be considered as a mechanism of prime importance for inbreeding avoidance in wild populations.

Kin interactions

Kin selection favours individuals exhibiting traits that increase the fitness of close relatives. By alleviating competition for resources and thus enhancing reproductive success of kin that do not disperse, it can select for dispersal.

Hamilton and May (1977) theoretically demonstrated the selection of dispersal in the absence of any other environmental factor (e.g. spatio-temporal variation), and even assuming a high cost of dispersal. Dispersal may be viewed as a mechanism to reduce kin competition at the natal site. Dispersal may therefore

be viewed as an altruistic trait that allows avoiding competition between related individuals within patches (Gandon 1999).

Habitat variability and environmental stochasticity

Many theoretical studies have identified spatiotemporal variations of local habitat as a key factor for the selection of dispersal (McPeck & Holt 1992). These variations in the environment have been suggested to be based on variations in habitat carrying capacity (McPeck & Holt 1992; Lemel *et al.* 1997), among patches of different qualities or as the result of stochastic local catastrophes. In that context, dispersal may be viewed as a way to escape locally degrading conditions (Ronce 2007). For instance, concerning the carrying patch capacity, individuals are better in populations with positive growth rate and should therefore disperse from populations with negative growth rate. Dispersal in response to temporal environment stochasticity can be view as a bet-hedging strategy, which allows a reduction of the variance in the expected fitness by distributing offspring from the same parents over different conditions (Ronce *et al.* 2001).

Importantly, in all of these cases, the spatiotemporal heterogeneity that favours dispersal is solely due to the external environment. But variations in demographic parameters of the metapopulation may be a source of heterogeneity among habitats as well (Cadet *et al.* 2003). However, when patch-capacity varies spatially but not temporally, most studies agree however, to say that dispersal should not be selected (Greenwood-Lee & Taylor 2001). Indeed, when quality varies over space but remains constant over time, dispersal should only be selected in poor-quality sites that individuals might have a strong interest to leave. However, because these low quality patches are those with the smallest population size, overall, dispersal is not expected to be selected (Bowler & Benton 2005). Consequently, the temporal heterogeneity is the only one thought to promote dispersal.

Given that change in the spatial variation of habitat quality is one of the

most important threats to biodiversity, understanding its evolutionary pressures on dispersal may be crucial in predicting how populations respond and adapt to a changing environment.

PROXIMATE FACTORS

Variations in fitness between patches can select for dispersal as a part of a life-history strategy at an evolutionary timescale. However, whether or not an individual disperse will depend on the environment that it has experienced itself. Study of the proximate causes of dispersal often yield insight into ultimate (i.e. evolutionary) causes of dispersal (Bowler & Benton 2005). Yet, proximate factors may thus influence each step of the dispersal process (i.e. emigration, travel, immigration) and will strongly influence individual probability to disperse and thus dispersal evolution.

Emigration

Density has been shown to influence emigration propensity in a wide variety of taxa. Matthysen (2005) highlighted that most of the 45 studies on birds and mammals testing density-dependent dispersal demonstrated a positive relationship between patch density and dispersal propensity. Increasing population density can reduce individual fitness via increased competition for resources availability (e.g. food, mates, nests sites) or direct interferences between individuals, and hence become a driving force for dispersal (Bowler & Benton 2005). In contrary, in small populations, Allee effects also favour dispersal as they lead to some density-dependent fitness decrease (Travis & Dytham 2002; Courchamp, Berek & Gascoigne 2008; Fowler 2009). Yet, a really few studies have found a negative relationship between density and dispersal rates (see Roland, Keyghobadi & Fownes 2000; Matthysen 2005 for a review). Such patterns can be explained by the fact that fitness benefits of living in groups may exceed the costs of competition.

In direct link with density, resources availability are also expected to play a key role in the decision to leave and many studies reported strong correlations between food availability and emigration rates (e.g. Kim 2000; Hanski *et al.* 2002;

Oro *et al.* 2004). Dispersal may indeed be a mechanism to avoid competition for resources.

Interspecific interactions have already been mentioned as ultimate causes of dispersal but have also been identified as a proximal mechanism promoting emigration. In that context, competition is not the only cause that may favour emigration out of the population but interactions with predators and/or parasites may also lead to dispersal. This has been experimentally demonstrated in the Tengmalm's owl (*Aegolius funereus*) in which male breeding dispersal rates increase when predation risk increases (Hakkarainen *et al.* 2001).

Finally, habitat characteristics are also recognized as influencing the emigration step of dispersal. First, patch size has been identified to be negatively correlated with emigration rate in a lot of empirical studies (e.g. Hill, Thomas & Lewis 1996; Poethke & Hovestadt 2002; see Bowler & Benton 2005 for others examples). For example, in both root voles, (*Microtus oeconomus*; Andreassen & Ims 2001) and field voles (*Microtus agrestus*; Crone, Doak & Pokki 2001) dispersal is more frequent from small patches than from larger patches (Wiens 2001). This has been explained by the probability for an individual to reach the edge and thus to leave its current patch. Still, the rate of dispersal is difficult to be distinguished from several other factors that may covary with patch size. Andreassen and Ims (2001) reported in their study that movement out of a patch was greater when the population density was low and more variable due to demographic stochasticity, both characteristics of small patches. Actually, patch size is likely to be an accurate descriptor of the patch carrying capacity, a parameter known to be negatively correlated with dispersal (Doncaster *et al.* 1997 and see previous section about ultimate causes of dispersal). Finally, the matrix habitat is expected to strongly influence emigration as it influences the costs of dispersal. Indeed, dispersal costs are expected to increase with the distance to travel and environments to cross. If a preliminary assessment of dispersal costs is possible, via, for example, preliminary exploratory behaviour, we could expect individuals to adjust their dispersal decision according to patches repartition (Wiens 2001; Bowler & Benton 2005).

Travelling phase

Of course, the proximate factors influencing the traveling phase of dispersal are not independent from those influencing the decision to leave. In the light of this, the matrix habitat is equally important in influencing travelling as the habitat type and spatial heterogeneity have been demonstrated to strongly influence animal movement and search strategies (Wiens 2001; Desouhant *et al.* 2003; Hein *et al.* 2003).

For instance, the gatekeeper butterfly (*Pyronia tithonus*) performs a “foray search” strategy by making petal-like loops and going back to their starting point each time (Conradt, Roper & Thomas 2001). This strategy may allow exploring the surrounding habitat but also to return back to the initial point if no suitable habitat is found. The use of habitat cues may also decrease search time and potentially increases dispersal success. In addition to increasing patch detectability, the use of habitat cues may provide information about patch quality (Danchin, Heg & Doligez 2001). In highly fragmented landscapes, for Eurasian red squirrels (*Sciurus vulgaris*), around 50% of individuals settle in a natal habitat type to 90% in least fragmented sites (Wauters *et al.* 2010). Increased habitat fragmentation seems thus to reduce reliable cues for habitat choice, illustrating the complex interactions between proximate factors on dispersal behaviour.

Immigration

The immigration in a new habitat is the last step of dispersal. Once again, factors influencing the previous steps are not independent from those influencing immigration and settlement and logically, habitat characteristics play, again, a key role in immigration and thus, settlement (Bowler & Benton 2005). In this way, as movement costs increase with moved distance, immigration (i.e. successful movement) is expected to increase as the between-patches distances decrease (e.g. Baguette, Petit & Queva 2000; Serrano & Tella 2003).

In this last but not least step, a central process is settlement and habitat selection, which have strong impacts on immigrants’ fitness, and habitat selection is really likely to influence immigration process and decision to settle. Two

behavioural mechanisms have been identified as key parameters in habitat selection and immigration process: conspecific attraction and natal habitat preference induction (Stamps 2001). Conspecific attraction occurs when the presence of conspecifics in a patch increases the probability of immigration and settlement. This process has been reported in several species including not only colonial species (Serrano *et al.* 2004), in which it was more expected but also solitary or territorial species (Doligez, Danchin & Clobert 2002; Doligez *et al.* 2003). Natal habitat preference induction (NHPI) is a really different mechanism, which occurs when common characteristics with the natal environment increase the probability of settlement (Stamps, Krishnan & Willits 2009).

The intensive theoretical work about the evolution of dispersal helped to identify these main causes of the evolution of dispersal. All of these factors are expected to act in concert and to drive the evolution of dispersal in a complex fashion.

The evolution of dispersal can be described by a balance between these forces, which may translate into benefits for dispersing individuals and costs of dispersal. Consequently, the understanding of the evolution of dispersal and therefore of its effects on the many ecological and evolutionary processes mentioned above strongly depends on the fitness of dispersing individuals (Belichon, Clobert & Massot 1996). This may explain why most theoretical models rely on strong and various assumptions about the costs and benefits of dispersal. Therefore, for both theoretical and practical purposes, we need to estimate fitness associated with both strategies. This context precisely describes the theoretical frame of this study.

A MATTER OF COSTS, BENEFITS AND LIFE-HISTORY STRATEGIES

Costs and benefits of dispersal at each step of the process are summarized in Table 1.1.

Suggested benefits result from ultimate and proximate factors

Ultimate factors are directly linked to potential fitness benefits of dispersal trait and we could thus expect that once an individual has become established in a new environment, it may actually perform better than it would have done if it had remain in its previous or natal breeding site. As expected, the main benefits of dispersal are inbreeding or kin competition avoidance. Yet the empirical demonstrations of inbreeding avoidance as a benefit of dispersal remained relatively scarce mainly because of several difficulties to test this hypothesis (Pärt 1996; Forero, Donazar & Hiraldo 2002; but see Banks & Lindenmayer 2014).

On the other side, proximate explanations of dispersal may explain how those fitness benefits are actually delivered. The suggested benefits of dispersal are thus the enhancement of breeding conditions, which may encompass various aspects such as the avoidance of predation, mate availability and/or quality, parasitism and intra- or inter-specific competition, including competition with kin (see Clobert *et al.* 2001 for a review). For instance, Brown and Brown (1992) reported that individuals coming from nests with higher ectoparasites load had a higher probability to disperse than individuals that fledged from nests without parasite. Yet, this study did not directly assess the relative fitness of philopatric and dispersing individuals according to parasitism environment. In a population of black kites (*Milvus migrans*), female dispersing farther did not exhibit a higher lifetime reproductive success but mated with more experienced male, which may enhance reproductive success (Forero, Donazar & Hiraldo 2002). Finally, dispersal can be beneficial for parents. Indeed, it may allow reducing offspring variance in success and dispersal can therefore be considered as a bet-hedging strategy (Ronce *et al.* 2001). Because of spatial heterogeneity and variability, the fitness of individuals is likely to differ because the quality of departure and settlement site may differ (Belichon, Clobert & Massot 1996). Then even though dispersal does not necessarily move individuals to better sites, its effects on global temporal variance in fitness has been shown to be beneficial (Ronce *et al.* 2001). Dispersal can thus be beneficial for parents that avoid putting all their eggs in the same basket. Empirical demonstrations of such hypothesis are difficult to found.

Yet, it has been suggested that hatching asynchrony may be a way to produce variation in offspring phenotype, notably in natal dispersal distances leading to a decrease of offspring variance in fitness in such heterogeneous environment (Laaksonen 2004).

However, if costs can be levied at each step of the process, it appears that benefits are mainly linked with post-settlement step or at least with settlement. Indeed, to our knowledge, no study suggested that travelling might be beneficial (Belichon, Clobert & Massot 1996).

TO DISPERSE CAN BE COSTLY

Contrary to benefits that are mainly linked with settlement or post-settlement steps, costs of dispersal can be paid immediately or deferred (Bonte *et al.* 2012). Dispersal costs can be first paid before dispersal movement in it. Pre-emigration costs arise during development to allow dispersal. In this section, I choose not to focus on potential costs linked with dispersal in passively dispersing organisms, such as seeds or fruits that develop specific morphologies (e.g. wings or floating seeds) to disperse. In actively dispersing species, an organism may invest in different morphologies and sensory structures, which are likely to improve its dispersal ability at one or more of the three stages. For instance, many insects display dispersing and non-dispersing morphs. Among these, aphids are one of the best examples of taxa that have evolved specialized morph for dispersal versus reproduction. The dispersal morph possesses a full set of wings as well as a sensory and reproductive physiology that is adapted to flight and reproduce in a new location while the non-dispersing morphs are wingless (Braendle *et al.* 2006). These investments involve energetic costs that may eventually reduce fitness and that are often linked with trade-offs with other life-history traits. For example, among seed-eating bud species, wing formation is negatively correlated with body size and subsequently increased development time (Solbreck 1986; Solbreck & Sillentullberg 1990). As a consequence, costs of being winged and able to fly are often associated with allocation of resources to wings and flying muscles as the expense of a poorer condition and or a decreased fecundity. However, such costs

are difficult to measure and no empirical quantification has been found in the literature (Bonte *et al.* 2012). Yet these kinds of costs have also been demonstrated in species with continuous variation in wings or wing muscles development rather than wing polymorphisms (e.g. Hanski *et al.* 2004). By paying such a cost at this stage, an individual can potentially reduce the realised costs of dispersal during later phases, and therefore increase the likelihood that dispersal will be successful. In vertebrates, however, no specific pre-departure costs for dispersive phenotypes have been recorded to date.

Costs that are strictly inherent to departure are rarely documented (Bonte *et al.* 2012), mainly because the decision to leave is really short-term and therefore really difficult to observe and study. Before departure, individuals may assess their environment to decide whether or not to disperse. Costs associated with exploring the surroundings, in term of time, energy and risks, even without actually dispersing may be substantial during the initiation of dispersal event (Young, Carlson & Clutton-Brock 2005; Young & Monfort 2009). Of course, there is a trade-off between acquiring information to optimize the decision to leave and the time, energy or risk costs associated with the information gathering. Indeed, by investing a lot in the assessment of the environment, an individual will call up for resources that will not be allocated in other life-history traits such as survival or subsequent reproduction or growth. For example, at birth, future dispersing female lizards (*Lacerta vivipara*) chased fewer prey and were thus less likely to eat than future non-dispersers (Meylan *et al.* 2009). Furthermore, exploring the surroundings is a risky behaviour. By spending a lot of time active or by adopting a behaviour, which improves information acquisition, individuals increase their probability of mortality, for example by predation. But assessing the environment may also be linked with attrition risks (i.e. non-recoverable damage that an individual may suffer on key structures) (Travis *et al.* 2012).

One of the most risky steps of dispersal is certainly the travelling phase. Travelling-related mortality may be owing to increased predation, aggression, stress, and energy depletion because moving through an unfamiliar environment (Greenwood & Harvey 1982; Bonte *et al.* 2012). In birds, direct mortality risk

during transfer appears to be a major cost of dispersal (e.g. Wiens, Noon & Reynolds 2006; Naef-Daenzer & Gruebler 2008). Among the different risks increasing the mortality probability during transfer, predation is often assumed to be a major cause leading to increased mortality (Greenwood & Harvey 1982). In the ruffed grouse, Yoder, Marschall and Swanson (2004) demonstrated that although the movement in itself may have some effects on the risks of being predated, moving through unfamiliar space has a much greater effect on risk. But costs may also be human-induced with for instance, increased mortality due to collision with wind-turbines or power lines (Real & Manosa 2001), road kills (Massemin, Le Maho & Handrich 1998) or human persecutions (Kenward 1999; Real & Manosa 2001). In mammals, increased mortality due to road kill and predation are well documented (Gillis & Krebs 2000; Boinski *et al.* 2005). Yet empirical evidences of such costs are difficult to demonstrate because of the difficulty to obtain data and to keep track of individuals during movements (Clobert *et al.* 2001; Nathan *et al.* 2003).

Once a dispersing individual reaches a potential area of suitable habitat, there are still numerous possible costs involved. First, individuals should acquire information about their new environment and this may be costly in term of time, energy and again risk (Pärt 1995; Bettinger & Bettoli 2002; Baker & Rao 2004; Stamps, Krishnan & Reid 2005). Further, it is likely that some costs can be associated with the familiarisation with the new breeding environment. Indeed, the lack of local knowledge may be linked with higher predation risk (Yoder, Marschall & Swanson 2004; Hoogland *et al.* 2006), lower probability of success in competition with conspecifics (Snell-Rood & Cristol 2005; Griesser *et al.* 2008; Kahlenberg *et al.* 2008; Milner *et al.* 2010) or lower foraging efficiency (Baker *et al.* 2011; Pascual, Carlos Senar & Domenech 2014). Moreover, dispersing individuals may suffer from maladaptation to local conditions (Dias & Blondel 1996). Dispersing individuals by emigrating may lose the advantage of being locally adapted, which has been developed through natural selection over former generations (Bonte *et al.* 2012). Maladaptation may concern various aspects such as mate selection (Bensch *et al.* 1998), parasite resistance (Boulinier, McCoy &

Sorci 2001) or breeding decisions (Postma & van Noordwijk 2005). For instance, Nussey *et al.* (2005) demonstrated a persistent difference in mean clutch size between two island subpopulations of great tits (*Parus major*) with a genetic basis. While in one subpopulation, immigrants that carry genes for larger clutches were strongly counter selected; a local adaptation and maintenance of small clutches have been highlighted on the other subpopulation. Local adaptation has been prevented due to higher gene flow leading thus to a maintenance of larger clutches. Importantly, the authors showed that these differences rest upon different levels of gene flow from outside the island.

To summarize, dispersal is risky because costs are diverse and might be levied at each step of the dispersal process. Importantly, among the dispersal costs that have been described, some are paid immediately, such as mortality from predation or failing to find a suitable habitat ("direct costs": Rousset & Gandon 2002; Stamps, Krishnan & Reid 2005; Soulsbury *et al.* 2008) but less obvious are those costs that gathered during movement or pre-dispersal phase but are experienced once the individual has settled ("deferred costs": Stamps, Krishnan & Reid 2005). Deferred costs (i.e. trade-offs) are particularly relevant, although overlooked, in the evolution of dispersal because, for realized connectivity to occur, individuals must not only arrive, but also survive and reproduce (Burgess, Treml & Marshall 2012). Such costs are expected to occur, for example, when time spent searching a suitable habitat to settle, reduces the amount of time available for post-settlement activities (Jakob, Porter & Uetz 2001; Marr, Keller & Arcese 2002) and the concept of trade-off appears therefore as central in the study of the fitness consequences of dispersal.

TRADE-OFFS AND DIFFERENCES IN LIFE-HISTORY STRATEGIES

The life-history theory predicts that life-history strategies should maximise the fitness of individuals (Stearns 1989). One possibility would be to live forever and to produce as much offspring as possible. However, individuals are limited by several trade-offs and constraints. In the context of dispersal, trade-offs may occur between and within dispersal-related phenotypic traits including

morphological, physiological, behavioural and life-history traits. For instance, winged male crickets experience costs in secondary sexual traits, like calling performance (Roff & Gelinas 2003).

Particularly deferred costs may translate into lower survival or fecundity or any other fitness component. Indeed, dispersal may be beneficial but mobilise resources that are potentially not invested subsequently in growth, survival or reproduction, either immediately or later in life. Because dispersing individuals do not experience the same constraints than philopatric individuals, we could expect individuals to adopt different strategies to deal with trade-offs according to their dispersal behaviour. These strategies may lead to different trajectories. For instance, individual may choose to invest more in reproduction at the cost of survival or to invest more in offspring quantity but at the cost of quality. According to this, compensations may occur between different fitness components or between reproductive events during an individual lifetime, in a different manner in dispersing and philopatric individuals (Lemel *et al.* 1997). This fact may have strong implications for the understanding of the link between dispersal and fitness and thus, the evolution of dispersal. A classic example of such trade-offs is between the quantity and quality of offspring. Classically this trade-off has first been studied in birds where the theory of clutch size predicts that the number of chicks in a clutch should be maximized given the number of young parents can recruit (Lack 1947). For instance, in a wild population of blue tit (*Parus caeruleus*), offspring quality was negatively correlated with brood size (Merila & Wiggins 1995). In the context of dispersal, if dispersing individuals suffer from reduced post-settlement survival and therefore shorter lifespan, they may invest more in reproduction and produce more offspring or offspring in better quality than philopatric individuals.

Table 1.1: Main proximal factors driving the evolution of dispersal at each step of dispersal process according to Bowler and Benton (2005), associated costs according to Bonte *et al.* (2012); Travis *et al.* (2012) and benefits.

Dispersal phase	Proximate factors	Associated costs	Associated benefits
Emigration	Within patch density Food availability Interspecific interactions Sex ratio Relatedness Patch size Matrix habitat Patch isolation	Energetic costs (development)	
Movement	Matrix habitat Search strategies Habitat cues Patch size Patch isolation	Risks costs: increased mortality predation risk wounding Energetic and time costs Risks costs:	Inbreeding avoidance Breeding conditions enhancement (food, mates, shelter availability)
Immigration	Patch size Patch isolation Habitat cues	- increased mortality - predation risk - non suitable habitat Energetic and time costs: - search costs to select optimal habitat Deferred costs: - decreased survival or reproductive success - unfamiliarity with the breeding environment - loss of social rank - maladaptation to local conditions	Bet-hedging

AIMS OF THE STUD

As we saw along this introduction, dispersal is a key life history trait, which may have particularly striking implications in the context of global warming as it represents a way to escape locally degraded conditions and may have strong impacts on how species will be able to face such sudden changes and therefore may be really useful in species conservation.

Because of these manifold and crucial effects, dispersal has been the subject of many theoretical and empirical studies over the past decades and still remains a very active field of research. If theoretical studies helped to identify the ultimate causes of dispersal, models always, implicitly or explicitly assume hypotheses about the relative costs and benefits entailed by dispersing individuals. The understanding of the fitness consequences of dispersal is a crucial aspect to better catch the evolution of dispersal. Many empirical studies were interested in comparing individual fitness prospects between dispersing and philopatric individuals. Yet no clear pattern between the costs and benefits of dispersal emerged from empirical studies and fitness consequences of dispersal remain difficult to predict, partly because of the multi-causality of dispersal. This PhD aims to get a better understanding of the fitness consequences of dispersal in a wild population of collared flycatchers (*Ficedula albicollis*) using both a correlative and experimental approach at several scales on an individual lifetime.

If many studies were interested in comparing the fitness consequences of dispersing and non-dispersing individuals, few considered fitness differences at a lifetime scale, even though recent evidences suggested that dispersal might translate into long-term costs. Using a correlative approach and the long-term data available, we first investigated whether dispersing and non-dispersing individuals differed in their in lifetime fitness output (**Chapter 3**). We therefore compared the Lifetime Reproductive Success (LRS) between dispersing and non-dispersing individuals. Because individuals may differ in their life-history strategies and because compensations may occur between components of fitness (i.e. between fecundity and survival), we also compared annual production of recruits and a proxy of survival.

However, as trade-offs processes may also occur at a finest scale, between fitness-related traits within a breeding event, we investigated whether fitness consequences differed according to dispersal status at the scale of the breeding event (i.e. annually) (**Chapter 4 and 5**). Most studies investigating the fitness consequences of dispersal did it at such short-term scale that they considered relatively rough fitness correlates, which may totally impede the possibility to detect differences in life-history strategies. The aim of the **Chapters 4 and 5** of this PhD is to dig deeper into the potential fitness differences between dispersing and non-dispersing individuals by considering the scale of the breeding event. In the chapter 3, we focused on early breeding decisions (i.e. before hatching) between dispersing and non-dispersing individuals while the chapter 4 was the focus of late breeding decisions.

Even if informative, the correlative approaches rarely allow a real discrimination of direct consequences of dispersal from consequences of other processes to which dispersal can be correlated (e.g. phenotypic quality). This confusion between correlates and consequences of dispersal has been highlighted earlier (Greenwood, Harvey & Perrins 1979; Clobert *et al.* 1988; McCleery *et al.* 2004) but remains largely ignored. Only five empirical studies reviewed in Belichon, Clobert and Massot (1996) and Doligez and Pärt (2008) are not correlative. In fact, only experimental approaches allowed testing the causality of relationships between dispersal and fitness outputs unambiguously. In the **Chapter 6**, we used an experimental approach with a translocation experiment to directly test for potential costs of being displaced in a non-familiar environment. Newly arrived males and females of different ages were either displaced between breeding plots or used as controls, and subsequent settlement decisions, return rates to the area of capture and fine breeding decisions were compared between groups. Even if dispersal is entirely artificial and do not account for any individual motivations to disperse, this approach however helps to identify the potential costs of displacement in a non-familiar environment and the relative importance of time and search costs.

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Chapter 2

What do we study and where?

STUDY SPECIES

The collared flycatcher (*Ficedula albicollis*, Temminck, 1795) is a small, insectivorous, cavity nesting, migratory passerine bird belonging to the Old World flycatcher family (*Muscicapidae*) that winter in sub-Saharan Africa.

Outside the breeding season, both sexes exhibit a cryptic plumage of dull brown, with white patches on the wings and stripes on the tail. For the breeding season, males' plumage turns to black with white patches on the wings and a white collar on the neck. During this period, males also possess this species characteristic, a white collar and a white patch on the forehead, which is a sexually selected trait (Gustafsson, Qvarnström & Sheldon 1995; Pärt & Qvarnström 1997).

Collared flycatcher breed in central and Eastern Europe but also on the Swedish Baltic island of Gotland and Öland, where they form well established populations. In Eastern Europe and on Baltic island, the collared flycatcher cohabits with its sister species, the pied flycatcher (*Ficedula hypoleuca*, Pallas, 1774) leading to hybrid zone as sexual selection between the two is not complete (Haavie *et al.* 2004). The collared population on the Swedish Baltic islands are at the western edge of the distribution and relatively isolated from the main species range (**Fig. 2.1**).

Males collared flycatchers arrive from their wintering quarters from late April to mid-May. Females tend to arrive shortly after males and older individuals arrive before young one (Pärt & Gustafsson 1989). Males quickly developed site-dominance and have never been observed to be expelled from their territories by intruders after one or a few days' ownership (Pärt 1994). Females mate choice is based upon males' territory quality (Alatalo, Lundberg & Glynn 1986) and secondary sexual characters such as the forehead patch size (Qvarnstrom & Forsgren 1998; Qvarnstrom, Griffith & Gustafsson 2000). Pair formation is seasonal, with really low mate fidelity between years. Collared flycatchers are mainly monogamous and exhibit bi-parental care, however, after attracting a primary female, male collared flycatchers may attempt to acquire a secondary

female in another territory (Qvarnström *et al.* 2003). It was estimated that approximately nine per cent of males attract a secondary female (Gustafsson & Qvarnström 2006). Polygyny is usually considered beneficial for male reproductive success while females mated with polygynous males suffered from a reduced reproductive success probably due to reduced parental care that polygynous males provide to their secondary nest (Gustafsson 1989; Garamszegi *et al.* 2004). The question of polygyny and the potential interaction with dispersal are addressed in the Chapter 2. Moreover, extra-pair copulations are not really frequent in this population as approximately 15% of nestlings distributed over 33% of nests were estimated to be extra-pair young (Sheldon & Ellegren 1999).



Figure 2.1: Distribution of the breeding areas of collared (black) and pied (light grey) flycatchers and areas of sympatry (dark grey). Baltic island of Gotland and Öland are marked with a circle. Figure adapted from Haavie *et al.* (2004).

In our population, individuals lay one clutch per year with clutches ranging from three to eight eggs and a mean of six eggs. At the beginning of May, the first eggs are laid with females laying one egg per day (mean laying date on the 1980-

2011 period: 23th May). Females start to incubate the day of laying the last egg and incubation is usually considered as a female task even if the question of courtship feeding remains open in the collared flycatcher. In the pied flycatcher, males feed their female frequently while they incubate, a behaviour that has been suggested to enhance female body mass and fledglings body condition (Lifjeld & Slagsvold 1986). Nestlings hatch after approximately 14 days, but incubation can last to 20 days according to various factors such as cold weather. Nestlings are subsequently feed in the nest by both parents for 14 to 16 days after hatching. After fledging, young flycatchers remain close to nest for two more weeks and are still fed by the parents.

Autumn migration and postnuptial moulting occur at the end of the breeding season (Hemborg 1998) and males exhibit their “non-breeding” plumage. Adults, but not yearlings, moult again before spring migration. This difference in moulting pattern allows a visual distinction between yearlings and older individuals (**Fig. 2.2**, Svensson 1992).

Collared flycatcher is particularly suitable biological model because i) it prefers nest-boxes to natural holes to nest, and thus large sample size and precise data can be acquired; ii) it tolerates disturbance at the nest well and thus manipulations (adults catching, measurement, offspring measuring and ringing) can be done without disturbing their breeding and iii) because of the high fidelity to the study site of both yearlings and older individuals.

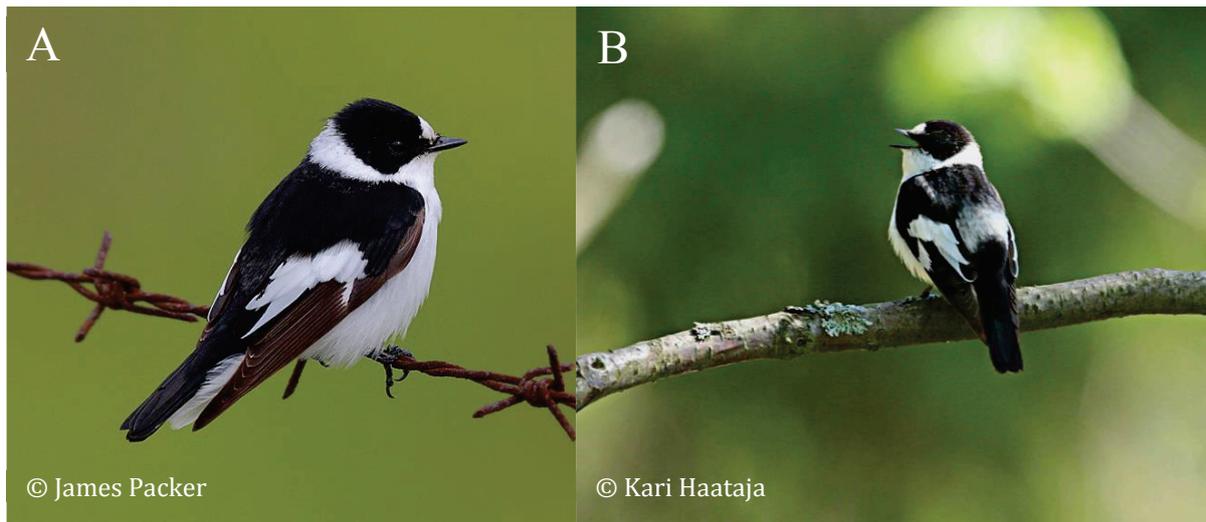


Figure 2.2: Difference in plumage between yearling (A) and older male (B). While yearling exhibit brown first primary feathers, older individuals show dark first primary feathers without distinction with the rest of the wing.

STUDY SITE

The field site is located in the southern part of the island of Gotland (57°10'N, 18°20'E), in the Swedish Baltic Sea. From 1980, nest-boxes have been settled in several woodlands. Nowadays, the field site in which the long-term monitoring is yearly performed consisted in 15 distinct nest-box areas including approximately 1800 nest-boxes including about 200 nest-boxes in inhabitants' gardens. However, several extra plots have been installed a little bit northern even if the long-term monitoring was mainly conducted on the 15 plots.

Most of these areas are deciduous woodlands dominated by oak (*Quercus robur*) and ash (*Fraxinus excelsior*) with a dense under storey of hazel (*Corylus avellana*) and hawthorn (*Crataegus sepp*). The others areas were part of a coniferous forest dominated by pine (*Pinus sylvestris*) with some birch (*Betula pubescens*). Nest-boxes are provided in excess of the total number of breeding birds that used them. Among the breeding birds, the collared flycatcher is the most abundant but other common species breed in nest-boxes: great tits (*Parus major*) but also blue tit (*Parus caeruleus*) and more rarely pied flycatcher (*Ficedula hypoleuca*) and coal tit (*Parus ater*).

The predation of eggs or nestlings is not really frequent as the area is free from mustelids, which are the main predators on the mainland, though clutches may be destroyed by woodpeckers notably great spotted woodpecker (*Dendrocopos major*), Eurasian red squirrels (*Sciurus vulgaris*) and eventually domestic cats (*Felis catus*).

Population monitoring and data collection

Breeding data are collected each year since 1980. All nest-boxes are visited regularly (every three days at least) to record whether individuals start to settle and build a nest, and to estimate the date of the laying of the first egg. Females lay one egg per day and it is thus possible to infer about real laying date according to the number of laid eggs. Data on clutch size were collected during incubation, during which the nest was not visited except for female capture. After 12 days of incubation, nests were visited again to determine the date of hatching and subsequently the number of fledglings.

Most females are caught inside nest-boxes during incubation using traps, and both parents were subsequently caught while feeding the young whenever possible (i.e. when the brood survived at least until 5-6 days). All individuals were ringed using unique aluminium ring, and morphological characters, such as tarsus length (to nearest 0.1mm), tail length, wing length, first primary and white stripes on primary feathers (to the nearest 1mm) were measured. Individuals were also weighed (to the nearest 0.1g). Forehead males patch was also measured (to the nearest 0.1mm; **Fig. 2.3**).

From years to years and depending on the projects in progress, this protocol may have been modified to collect complementary data, such as blood sample on two days-old chicks to determine both paternity and primary sex-ratio, blood sample on both parents to measure levels of parasitism and physiological parameters in relation to metabolic activity, oxidative stress but also mitochondrial activity and telomeres lengths.

To investigate the interaction between personality traits and dispersal behaviour and to link this with the possible fitness consequences of dispersal strategies, we performed several experiments across the breeding season to

measure *i*) aggressiveness, *ii*) neophobia and *iii*) risk taking (**Appendix 1**). These data have also been collected in the context of the translocation experiment we performed in 2012 and 2013 (**Chapter 4**) but are still under analysis.

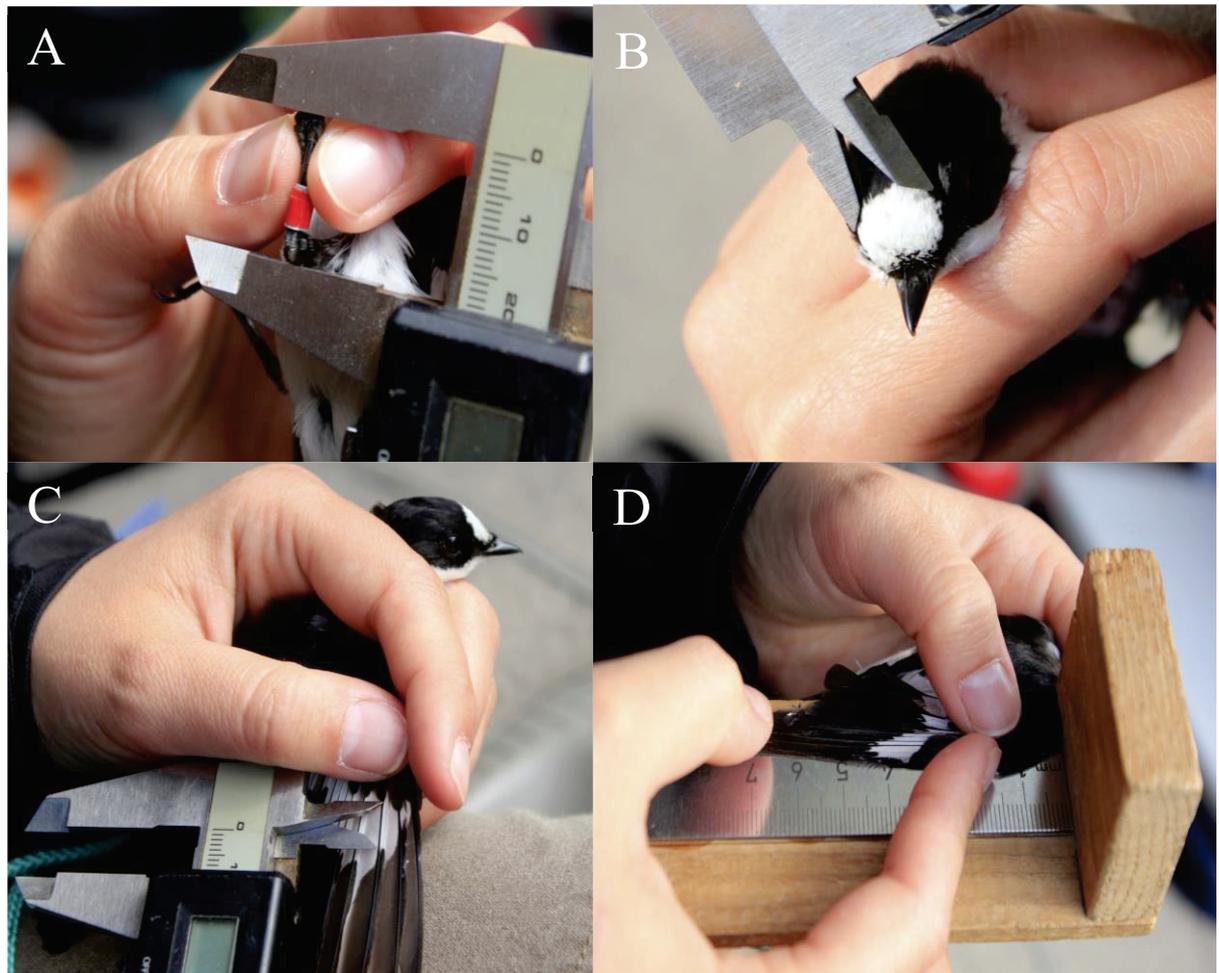


Figure 2.3: Morphological measures of (A) tarsus length, (B) forehead patch in males, (C) white stripes on the wing and (D) wing length.

DISPERSAL IN THE COLLARED FLYCATCHER OF GOTLAND: WHAT DO WE KNOW?

Dispersal in the studied population of collared flycatcher was mainly broached with Tomas Pärt and Blandine Doligez's projects, both under the supervision of Lars Gustafsson, among others. The two projects were based on different problematics. While Tomas Pärt was more interested in describing and the causality of dispersal patterns and understanding the potential fitness

consequences and the balance between the costs and benefits, that were largely unknown in the population, Blandine Doligez's project was more about information acquisition and individual decision making in dispersal and breeding context with a particular interest about public information.

Natal and breeding dispersal were found to be female-biased (**Fig. 2.4** and **2.5**), as in many birds' species, which is classically explained by the resources defence mating system (Greenwood & Harvey 1982). Young individuals dispersed more than older individuals resulting thus in a higher natal than breeding dispersal (Pärt & Gustafsson 1989; Pärt 1990).

Natal dispersal was shown to be linked to natal brood size but the distance of dispersal is not correlated to egg-laying of the mother, clutch size nor date of hatching or density in the natal area. Importantly, contrary to several others species, tarsus length, body weight and body condition before fledging were not correlated with natal dispersal distance in either sex (Pärt 1990). Concerning the fitness consequences, natal dispersal distance was reported to be negatively correlated with reproductive success in females and survival prospects in males, but only in individuals hatched late in the breeding season. According to Greenwood and Harvey (1982), males are expected to experienced higher costs of dispersal. Indeed, natal philopatric males chose higher quality nest-boxes, mated more quickly than dispersing individuals and were less likely to remain unmated (Pärt 1994). Yet, among mated males, no difference was found in reproductive success. The prior local knowledge of philopatric males may facilitate nest-box selection when high search costs force individuals to choose between a small number of alternative sites and natal dispersal has been suggested as a consequence of high time costs of searching and finding the way back home in this migratory specie (Pärt 1994).

Breeding dispersal, on the other side was also shown to be female-biased with really low nest-box fidelity. Indeed, only 2% and 8% of females and males respectively occupied their exactly same nest-box than previous year, showing thus that the definition of dispersal at the nest-box scale is not relevant in that specie. Again, individual size or body condition was not found related to breeding

dispersal propensity in either sex while previous reproductive success was found to strongly influence subsequent breeding dispersal in yearling females but not in older individuals. In males, however, previous reproductive success was not related with breeding dispersal propensity neither in older nor in yearlings even if unmated males dispersed more the next year (Pärt & Gustafsson 1989).

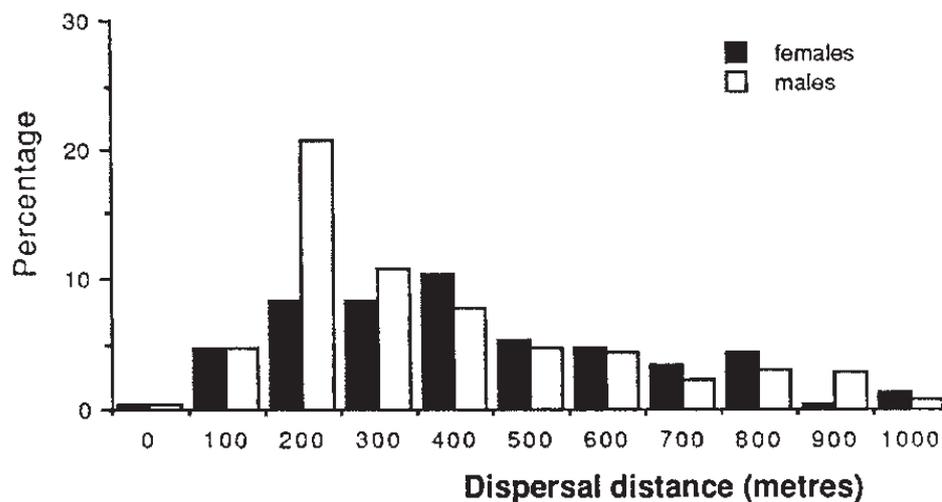


Figure 2.4: The distribution of natal dispersal distances of males and females collared flycatchers extracted from Pärt (1990). Upper histogram: natal dispersal distances for all individuals. Lower histogram: natal dispersal distance within 1000m.

The importance of local familiarity with the breeding environment and search costs has lately been highlighted by an experimental approach and it was demonstrated that older males returned more than other categories of individuals (i.e. yearling males and females).

Habitat selection strategies may have profound effects on animal distribution and dispersal processes but have also strong consequences upon individual fitness. Individuals are thus likely to select their habitat after gathering information about quality of potential breeding patches (Doligez *et al.* 1999). The patch reproductive success (PRS) was shown to influence both natal and breeding dispersal propensity but this effect depended on sex (Doligez *et al.* 1999). Indeed, female dispersal patterns were negatively correlated with PRS while the relation was positive in males with low competitive abilities. It was therefore suggested

that the observed patterns in the use of PRS differ in each sex in relation to intraspecific competition.

Finally, the question of heritability of dispersal was considered in our population (Doligez & Pärt 2008; Doligez, Gustafsson & Pärt 2009; Doligez *et al.* 2012). Because parent-offspring resemblance in the dispersal propensity may lead to bias in fitness estimates based on local adult survival and recruitment (Doligez & Pärt 2008), the estimation of heritability is of primary importance. The dispersal propensity displays a significant heritability with levels of heritability, which varied between 0.30 and 0.47, depending on parent-offspring comparisons made and correcting for a significant assortative mating with respect to dispersal status.

This PhD study is more in the line with Tomas Pärt's project as it aimed to investigate the fitness consequences of dispersal without considering habitat selection.

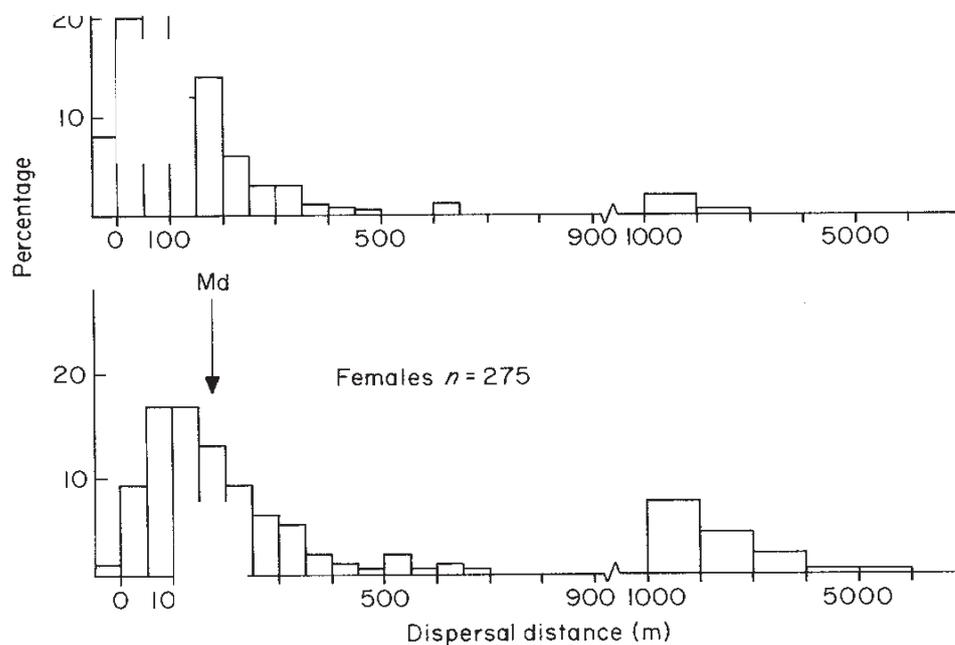


Figure 2.5: Breeding dispersal distance (m) for males and females. Figure extracted from Pärt (1990)

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Chapter 3

Natal dispersers pay a lifetime cost to increased reproductive effort in a wild bird population

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Tomas Pärt
Lars Gustafsson
Blandine Doligez

Abstract

Natal dispersal is a key life history trait shaped by multiple selective pressures. Despite decades of studies on natal dispersal, its consequences on individual fitness are not easy to predict since no clear costs and benefits pattern emerges from empirical studies. Natal dispersal is assumed to be costly, but in most situations it might be an adaptive decision, leading to the absence of differences detected in fitness components between dispersing and non-dispersing individuals. However, when reproductive effort increases suddenly following changes in the reproductive environment, natal dispersers may lack sufficient familiarity with the local environment to buffer negative effects, and thus costs of natal dispersal may be expressed in harsh conditions. We compared lifetime reproductive success (LRS) between natal dispersing and non-dispersing individuals in a wild patchy population of collared flycatchers (*Ficedula albicollis*). We specifically investigated whether LRS differed when reproductive effort was increased as a result of an experimental brood size manipulation or, for females, being the secondary female of a polygynous male. To test for possible compensations between fitness components, we also compared annual recruitment and return rates between natal dispersing and non-dispersing individuals. LRS did not differ between natal dispersing and non-dispersing individuals when reproductive effort was not increased. This is unlikely to result from compensations between reproductive success and survival over lifetime, since annual recruitment and return rates did not differ either. However, when brood size was experimentally increased, and for secondary females, natal dispersing individuals achieved lower LRS, and produced fewer recruits per year, than non-dispersing individuals. In contrast, annual return rate did not differ depending on natal dispersal status. Our results suggest a cost of natal dispersal paid immediately after the increase in reproductive effort, and not compensated for later in life. While natal dispersers may be able to adaptively adjust their breeding decisions when reproductive effort is as expected, they seem unable to efficiently face a sudden increase in effort, possibly because of a limited knowledge of their new environment and/or differences in phenotypic traits increasing their sensitivity to stressful situations.

Key words: lifetime reproductive success, annual reproductive success and return rate, natal dispersal, reproductive effort, dispersal cost, familiarity, polygyny, collared flycatcher

INTRODUCTION

Natal dispersal is classically defined as the movement of individuals between the natal site and the site of first breeding (e.g. if brood size enlargement have a positive effect on natal dispersal through a negative effect on body condition, Howard 1960; Greenwood & Harvey 1982). Because natal dispersal generates individual and gene flow among populations and sub-populations, it is considered as a crucial life-history trait affecting population genetics, dynamics and differentiation, and thus species distribution and evolution (Clobert *et al.* 2001; Kokko & Lopez-Sepulcre 2006; Clobert *et al.* 2012; Matthysen 2012). Consequently, many theoretical studies have investigated the factors affecting the evolution of natal dispersal (Johnson & Gaines 1990; McPeck & Holt 1992; Clobert *et al.* 2001), with many models relying on assumptions about the relative fitness of dispersing and non-dispersing individuals. Indeed, the consequences of natal dispersal on ecological and evolutionary processes, and thus its evolution, will strongly depend on dispersal success in terms of individual fitness (Lemel *et al.* 1997; Whitlock & McCauley 1999; Clobert *et al.* 2001).

Dispersal is assumed to be costly and can carry both direct and deferred costs during departure, travelling and settlement (for a review, see: Bonte *et al.* 2012; Duputie & Massol 2013) through (i) searching for suitable breeding sites, (ii) unfamiliarity with the new breeding habitat, affecting the ability to find high-quality sites, mates and/or resources, and (iii) maladaptation to local conditions in terms of mate selection, immunity or breeding decisions (e.g. Greenwood 1980; Stamps 1987; Pärt 1994; Bensch *et al.* 1998; Danchin & Cam 2002; Baker & Rao 2004; Postma & van Noordwijk 2005; Marr 2006). Some of these costs may be expected to be particularly important for natal dispersers, which are often younger, less experienced and less competitive individuals. Conversely, natal dispersal can benefit individuals by reducing the likelihood of negatively interacting with kin and therefore promoting avoidance of inbreeding and kin competition (Perrin & Mazalov 1999; Perrin & Goudet 2001; Szulkin & Sheldon 2008). Furthermore, dispersing individuals may escape locally unfavorable or degrading environmental conditions due to overcrowding, decreased food, mates

and breeding sites availability and/or quality, and increased predation or parasitism risk (see Clobert *et al.* 2001 for a review).

As a consequence of these opposite selective pressures potentially acting on natal dispersal, the fitness consequences of adopting different dispersal strategies are not easy to predict. No clear fitness costs and benefits pattern emerges from empirical studies investigating fitness correlates of natal dispersal (see Belichon, Clobert & Massot 1996 ; Doligez & Pärt 2008 for literature reviews). However, most of these studies focused on short-term fitness measures (i.e. hatching date, number of young fledged) and/or on single fitness components (Belichon, Clobert & Massot 1996; Doligez & Pärt 2008). Yet, recent evidence suggests that natal dispersal costs can be long-term, i.e. affect individual life history or fitness traits long after the dispersal event itself (e.g. Bouwhuis *et al.* 2010; Nevoux *et al.* 2013). Therefore, dispersal decisions early in life may generate small but accumulating fitness differences, detectable only at a lifetime scale. Nevertheless, because compensations may occur between different fitness components within breeding events (e.g. between young quantity and quality: Julliard, Perret & Blondel 1996) or between breeding events across an individual's lifetime (Belichon, Clobert & Massot 1996; Lemel *et al.* 1997), lifetime differences between dispersing and non-dispersing individuals may still be difficult to detect. For instance, lifetime fitness measures have been compared between dispersing and non-dispersing individuals in ten bird species so far to our knowledge (Appendix 1, Table S1); overall, these studies do not provide a clearer pattern of a costs and benefits balance of natal dispersal, although when detected, differences suggest a cost of natal dispersal (but see Doligez & Pärt 2008 for bias in parameters estimates in dispersing individuals). This suggests that that natal dispersal decisions are adaptive in most cases. However, the question remains whether individuals can adaptively adjust their investment in breeding and maintenance according to their natal dispersal decisions in all circumstances, in particular when sudden changes in the environment impose increased effort that may be buffered only through sufficient familiarity with the local environment. If

not, costs of natal dispersal may appear mainly in harsh conditions because natal dispersers a priori lack such familiarity.

Here, we investigated lifetime fitness differences according to natal dispersal behaviour in a wild patchy population of collared flycatchers (*Ficedula albicollis*). We compared the lifetime number of recruits produced between natal dispersing and non-dispersing individuals, accounting for individual characteristics known to affect lifetime reproductive success (LRS) in this population, i.e. sex, age at first reproduction and lifetime body condition index (Gustafsson 1989). We explored in particular LRS differences between natal dispersers and non-dispersers in two specific situations where breeding effort was increased, as a result of (i) an experimental brood size increase and (ii) a reduction in paternal care for secondary females of polygynous males in this facultatively polygynous species. To explore mechanisms underlying possible differences in LRS and possible compensations between fitness components, we further compared the annual number of recruits produced and return rate (as a proxy of local survival) between natal dispersing and non-dispersing individuals, again with a specific focus on the two situations of increased breeding effort (brood size increase and secondary mating status for females).

MATERIAL AND METHODS

STUDY SPECIES, STUDY POPULATION AND GENERAL FIELD PROCEDURES

The collared flycatcher is a small, short-lived hole-nesting migratory passerine bird. The data used here has been collected between 1980 and 2005 in a patchy population breeding on the island of Gotland, Southern Baltic, Sweden (57°10'N, 18°20'E), where artificial nest boxes have been regularly distributed in discrete woodland plots of varying sizes. Upon arrival from winter quarters, males choose a breeding territory and defend it to attract a female. Collared flycatchers typically recruit into the breeding population when either one or two years old (Gustafsson & Sutherland 1988) and once they have started breeding, most

individuals are thought to attempt to reproduce every year. Old birds (two years old or more) arrive before yearlings at the breeding grounds; they lay earlier and larger clutches and produce more surviving offspring than yearlings (Gustafsson & Pärt 1990; Sendecka, Cichon & Gustafsson 2007).

Each year, nest boxes have been monitored throughout the season, allowing laying date, clutch size, hatching date and number and condition of fledglings to be recorded. Breeding adults were trapped inside their nest box, identified with individually numbered aluminium rings, weighed (to the nearest 0.1 g), measured (tarsus length to the nearest 0.1 mm) and aged, based on their previous records in the population or morphological characteristics when previously unringed (yearling versus older individuals; Svensson 1992).

Most females were caught inside nest boxes during incubation, and both parents were subsequently caught while feeding young whenever possible (i.e. when the brood survived at least until 5-6 days). Therefore, capture in this population is linked to reproductive activity and success, with a sex bias (female capture rate being higher than male capture rate because of early brood failures, i.e. before males can be caught; Doligez *et al.* 2012). All nestlings were ringed, weighed and measured (tarsus length) when 12 days old. For details on the breeding ecology of the collared flycatcher, the study area and the long-term monitoring of the breeding population, see Pärt and Gustafsson (1989), Pärt (1990); Doligez *et al.* (1999); Doligez, Gustafsson and Pärt (2009).

NATAL DISPERSAL STATUS

We defined natal dispersal as a change of plot between the year of birth and the year of first breeding (Doligez, Gustafsson & Pärt 2009). This binary definition (dispersal versus philopatry) has been found to be biologically relevant in previous studies on this population (Doncaster *et al.* 1997; Doligez *et al.* 1999; Doligez, Danchin & Clobert 2002; Doligez, Pärt & Danchin 2004). Only adults whose natal site was known (i.e. individuals ringed as nestlings in the study population) were included in the analysis: unringed individuals were discarded

because they consisted of a mix of local birds previously missed and true immigrants.

LRS, ANNUAL RECRUITMENT AND RETURN RATE

We computed LRS as the total number of recruits produced by an individual during its life (Clutton-Brock 1988), for individuals caught as breeders at least once, i.e. with a natal dispersal status determined, and with complete records, i.e. dead at the end of the study period. An individual was assumed to be dead if it had not been seen for at least three consecutive years (i.e. last breeding record in 2003). For the period 1980-2005, we obtained LRS data for 2332 individuals (1160 females and 1172 males). When an individual was not caught, either at age 1 ($n = 852$) or later ($n = 123$), it was assumed to be a non- or failed breeder (i.e. no fledged young, thus no recruit).

In a second step, we considered separately annual recruitment and return rate to investigate possible compensations between the two main components of LRS, i.e. reproductive success and survival. We computed annual recruitment as the number of recruits produced by the individual at each breeding event. We used as a proxy of annual local survival the annual return rate, i.e. whether the individual returned (i.e. was caught as a breeder) in the study population in subsequent years. Because a fraction of individuals disperse beyond the limits of the study area (Doligez *et al.* 2012), and non- or failed breeders are rarely caught, this measure of survival is clearly underestimated, in particular for dispersal-prone individual (Doligez & Pärt 2008).

BROOD SIZE MANIPULATION

Brood size manipulations have been performed in different years across the long-term study to address in particular the costs of reproduction (Gustafsson & Sutherland 1988; Doligez *et al.* 2002). In all these experiments, pairs or triplets of broods sharing the same hatching date (and in some cases clutches with the same laying date) were randomly assigned to one of the experimental treatments and either (*i*) received extra young (eggs), in most cases one or two (increased

broods); (ii) had some young (eggs) removed and placed in another nest, in most cases one or two, but up to the whole brood (decreased broods); or (iii) had some young (eggs) exchanged with another brood without changing brood (clutch) size (control group). According to the treatment(s) an individual experienced during its life, we defined a lifetime brood size manipulation status with individuals having experienced at least once in their lifetime an increased brood size, a decreased brood size or a control treatment (i.e. three modalities). Because the collared flycatcher is short-lived, few individuals with known LRS experienced opposite treatments (i.e. both increased and decreased brood sizes) over their lifetime ($n = 36$). These individuals were excluded from the analysis because it was not possible to assess a priori which of the treatments, if any, may influence LRS more strongly. For the analyses including brood size manipulation status, individuals that had never been manipulated over their life were excluded (i.e. we considered only individuals that experienced either a brood size increase, a decrease or controls individuals; $n = 838$). This allowed us to control for spatial and temporal variation that may affect LRS or annual estimates of recruitment and return rate, since manipulations were not performed every year and in every plot. This implies that samples sizes vary between analyses. We used the lifetime brood size manipulation status when comparing LRS between natal dispersing and non-dispersing individuals, while we used the annual brood size manipulation status (i.e. the brood size manipulation treatment at a given breeding attempt) when comparing annual recruitment and return rate.

POLYGYNY STATUS

In facultative polygynous birds, some males attract and mate with a second female, but provide paternal care to the primary brood mainly (Kral, Saetre & Bicik 1996; Huk & Winkel 2006). Thus the reproductive output of the secondary brood is usually reduced (Huk & Winkel 2006). We defined polygyny status as follows. A male was considered polygynous if it was caught in two different nest boxes in the same year while feeding nestlings. A female mated with a male caught in one nest box only (i.e. considered monogamous) was defined as monogamously

mated. A female mated with a polygynous male was considered primary (resp. secondary) if she laid earlier (resp. later) than the other female mated with the same male. In the rare cases ($n = 5$) where laying date was the same for both females mated with the same male, the mating status of these females was considered unknown for the corresponding breeding season. Polygyny is thought to remain limited in this population (10-15% of males; Gustafsson & Qvarnström 2006). However, polygyny may be underestimated, because a fraction (approx. 30%) of males are missed each year and thus remain unidentified, mostly when the male was not attending the brood and/or the brood died before reaching the age of parents' capture (as is often the case for secondary nests). As for brood size manipulation, we defined a lifetime polygyny status according to the mating status an individual experienced during its life: a male was defined as polygynous if it was found polygynous at least once over its lifetime, and monogamous otherwise. Similarly, a female was defined as secondary if it was found to be a secondary female at least once over its lifetime, and monogamously mated or primary otherwise. To define lifetime polygyny status or analyze annual recruitment and return rate, we only included breeding events for which mating status was known (i.e. the male was caught). Consequently, a fraction of females were likely misclassified as lifetime monogamous or primary while being secondary, but our analyses should be conservative with respect to a potential lifetime cost of being secondary. Out of 83 females classified as lifetime secondary and 65 males as lifetime polygynous, only 1 female was secondary more than once and 10 males were polygynous more than once over their lifetime. We used the lifetime polygyny status when comparing LRS between natal dispersing and non-dispersing individuals, while we used the annual polygyny status (i.e. the polygyny status at a given breeding attempt) when comparing the annual recruitment and return rate.

STATISTICAL ANALYSES

To test whether LRS (lifetime number of recruits) and, in a second step, annual recruitment and return rate depended on natal dispersal status, we used a

generalized linear mixed model with a log-link function. Because LRS and annual recruitment data show a high number of zero values (i.e. a high number of individuals producing no recruits either over their lifetime or annually; Appendix S2; Fig. S1 and Fig. S2 respectively), we fitted a negative binomial model for these response variables (McCullagh 1984; Bolker 2008). We included as explanatory variables the natal dispersal status and several other phenotypic traits or factors that have previously been found to affect LRS: sex, age (binary variable), body condition index and mating status or brood size manipulation status. We computed body condition index as the ratio of body mass on tarsus length. Because female body mass markedly changes between incubation and nestling feeding, female body mass was standardized with respect to the capture period (i.e. centered relative to the mean body mass of females caught during the same breeding period and divided by standard deviation).

In the analyses of LRS, we used age at first breeding (binary variable: one year vs. one years or more) and lifetime variables for body condition index, polygyny status and brood size manipulation. Body condition index was averaged over the life of an individual to compute its lifetime body condition index. In the analyses of annual recruitment and return rate, we added the location of the breeding plot within the study area as a binary variable (plot on the edge *vs.* plot in the centre of the study area) to account for a potential edge effect and biases in fitness estimates due to dispersal outside of the study area (Doligez, Gustafsson & Pärt 2009; Doligez *et al.* 2012). It was not possible to add this information at the lifetime scale because of dispersal movements between plots.

The initial model included all main variables and first order interactions between each variable and natal dispersal status as fixed effects, and birth cohort and plot as random effects. For the analyses of annual recruitment and return rate, we added individual ring number as a random factor to account for multiple observations for a given individual over years. We do not subsequently detail random effects because they are not of primary interest here, however, they were kept in all the models. We backward removed non-significant terms starting with interactions. Because body condition index was never significant, either as a main

effect or in interaction with other variables, it was not retained in the final models of any of the response variables. Because our initial model was not over-parameterized for any of the response variable ($N > 3k$ in all cases), the risk of inflated type I error is negligible in our study (Forstmeier & Schielzeth 2011). Models were implemented in R v. 3.0.3 (R Core Team 2014). Parameter estimates are presented \pm one SE.

RESULTS

NATAL DISPERSAL STATUS AND LRS

LRS did not differ between natal dispersers and non-dispersers (**Table 3.1**), except when birds experienced at least once in their lifetime an increased brood size (interaction between natal dispersal status and lifetime brood size manipulation: $N=838$, $\chi^2_2 = 6.11$, $P = 0.048$, **Fig. 3.1A**) or, for females, when they were at least once in their lifetime secondary females of polygynous males (interaction between natal dispersal status and lifetime polygyny status: $N=1161$, $\chi^2_1 = 5.16$, $P = 0.023$, **Fig. 3.2A**), accounting for age at first breeding and sex when applicable.

Among individuals experiencing a brood size manipulation at least once in their lifetime, LRS did not differ between natal dispersers and non-dispersers experiencing a reduced brood (post-hoc test: $N=261$, $\chi^2_1 = 0.04$, $p = 0.85$) or a control treatment (post-hoc test: $N=257$, $\chi^2_1 = 0.16$, $p = 0.69$, **Fig. 3.1A**). However, among individuals experiencing an increased brood, natal dispersers had a lower LRS than non-dispersers (post-hoc test: $N=320$, $\chi^2_1 = 10.68$, $p = 0.001$, **Fig. 3.1A**).

In females, LRS did not differ between natal dispersers and non-dispersers when females were monogamously mated or primary females of polygynous males (post-hoc test: $N=1078$, $\chi^2_1 = 0.0001$, $P = 0.99$; **Fig. 3.2A**). However, among females that were secondary at least once in their lifetime, LRS was lower for natal dispersers compared to non-dispersers (post-hoc test: $N=83$, $\chi^2_1 = 7.09$, $P =$

0.007; **Fig. 3.2A**). The lifetime polygyny status did not interact with natal dispersal status in males ($N=1172$, $\chi^2_1 = 1.98$, $P = 0.16$), leading to a significant three-way interaction between sex, natal dispersal status and lifetime polygyny status on LRS in the analysis with both sexes ($N=2333$, $\chi^2_1 = 5.89$, $P = 0.015$).

NATAL DISPERSAL STATUS AND ANNUAL RECRUITMENT

Annual recruitment did not differ between natal dispersers and non-dispersers (Table 1) except when birds experienced an increased brood size (interaction between natal dispersal status and brood size manipulation: $N=990$, $\chi^2_2 = 6.11$, $P = 0.047$, **Fig. 3.1B**) or, for females, when they were secondary (interaction between natal dispersal status and polygyny status: $N= 1442$, $\chi^2_1 = 6.11$, $P = 0.012$, **Fig. 3.2B**), accounting for age and location of the breeding plot.

Among individuals experiencing a brood size manipulation, the annual production of recruits did not differ between natal dispersers and non-dispersers experiencing a reduced brood (post-hoc test: $N=278$, $\chi^2_1 = 0.21$, $p = 0.65$) or a control treatment (post-hoc test: $N=365$, $\chi^2_1 = 0.01$, $p = 0.92$, **Fig. 3.1B**). However, among individuals experiencing an increased brood size, natal dispersers produced fewer local recruits than non-dispersers (post-hoc test: $N=347$, $\chi^2_1 = 12.64$, $p = 0.004$, **Fig. 3.1B**).

In females, the annual production of recruits did not differ between natal dispersers and non-dispersers when females were monogamously mated or primary females (post-hoc test: $N=1358$, $\chi^2_1 = 0.65$, $p = 0.42$, **Fig. 3.2B**). However, among secondary females, the annual production of recruits was lower for natal dispersers compared to non-dispersers (post-hoc test: $N=84$, $\chi^2_1 = 8.65$, $p = 0.003$, **Fig. 3.2B**). The polygyny status did not interact with natal dispersal status in males ($N=1858$, $\chi^2_1 = 2.26$, $P = 0.13$), leading to a significant three-way interaction between sex, natal dispersal status and polygyny status on the annual production of recruits in the analysis with both sexes ($N=3300$, $\chi^2_1 = 7.82$, $P = 0.005$).

NATAL DISPERSAL STATUS AND ANNUAL RETURN RATE

Annual return rate did not differ between natal dispersers and non-dispersers ($N = 3296$, $\chi^2_1 = 1.78$, $P = 0.18$; no interaction including natal dispersal status was significant). In females, annual return rate was lower when breeding in plots at the edge of the study area compared to central plots ($N=1442$, estimate \pm SE = -0.40 ± 0.19 , $\chi^2_1 = 4.41$, $P = 0.036$) while this was not the case in males ($N=1858$, $\chi^2_1 = 0.006$, $P = 0.94$; interaction between plot location and sex: $N=3300$, $\chi^2_1 = 5.26$, $P = 0.022$). Annual return rate did not vary either with age ($\chi^2_1 = 0.07$, $P = 0.80$), polygyny status ($\chi^2_1 = 0.17$, $P = 0.68$) and brood size manipulation ($\chi^2_2 = 0.41$, $P = 0.81$).

DISCUSSION

In this study, we investigated whether lifetime reproductive success (LRS) and its annual components were linked to natal dispersal behaviour in our patchy population of collared flycatchers. Our results show that, in most situations, natal dispersing and non-dispersing individuals reached the same LRS. This absence of difference in LRS when reproductive effort was not increased was unlikely to result from compensations between reproduction and survival between breeding events because annual recruitment and return rate did not differ between natal dispersers and non-dispersers either. However, when individuals had to increase their reproductive effort (i.e. as the result of an experimental brood size increase or being the secondary female of a polygynous male), LRS and annual recruitment were lower for natal dispersing compared to non-dispersing individuals. Our results therefore suggest that natal dispersal is most often adaptive but can be associated to a cost when the negative impact of a sudden increase in reproductive effort cannot be buffered against. This cost translates into lower annual recruitment success and ultimately LRS.

CAN FITNESS ESTIMATES OF NATAL DISPERSING INDIVIDUALS BE BIASED?

Importantly, our results are unlikely to be explained by biases in fitness estimates due to non-random dispersal outside of the study area. When individuals disperse beyond the limit of the study area, both survival and offspring recruitment will be underestimated (Baker, Nur & Geupel 1995; Lambrechts *et al.* 1999; Lambrechts, Visser & Verboven 2000; Nathan 2001; Zimmerman, Gutierrez & Lahaye 2007). This is especially the case for dispersing individuals, which may be more prone to disperse again, and whose offspring may be more likely to disperse out of the study area, than non-dispersing individuals and their offspring, respectively (Doligez, Gustafsson & Pärt 2009; Doligez *et al.* 2012). Brood size enlargement may also lead to underestimated recruitment rate if young from increased broods are more likely to disperse (e.g. if brood size enlargement have a positive effect on natal dispersal through a negative effect on body condition; Tinbergen 2005). Here, however, LRS was similar for dispersing and non-dispersing individuals when reproductive effort was not increased. Among non-dispersing individuals, fitness estimates were also similar between individuals experiencing increased and decreased broods, and in our population, fledgling body condition was not related to dispersal behaviour (Pärt 1990). Birds breeding at the edge of the study area produced fewer local recruits, as a probable result of offspring dispersal out of the area, but the effect of breeding plot location on annual recruitment did not depend on natal dispersal status. Finally, results were qualitatively unchanged if individuals that were missed for at least one breeding season after the first breeding event ($N = 123$), which could have temporarily emigrated, were excluded from the analyses (results not detailed).

IS NATAL DISPERSAL COSTLY AND WHEN?

In our study population as in many others, capture and identification of parents are biased towards more successful individuals (see Doligez *et al.* 2012), thus probably higher quality individuals, which may more efficiently adjust breeding decisions. This could reduce our ability to detect fitness differences between natal dispersing and non-dispersing individuals. However, dispersing and

non-dispersing individuals probably most often reach the same fitness outcome, both annually and over lifetime, because natal dispersal is adaptive in many situations. Here, natal dispersers achieved lower LRS and annual recruitment compared to non-dispersers only when facing a considerable increase in reproductive effort. Brood size increase has been repeatedly shown to strongly increase breeding effort and energy expenditure when provisioning nestlings (Gustafsson & Sutherland 1988; Dijkstra *et al.* 1990; Pettifor 1993; Horak 2003). As a consequence, it can result in reduced subsequent parental and offspring fitness (Gustafsson and Sutherland 1988; Horak 2003). Similarly, in species with biparental care, secondary females of polygynous males face a strong increase in reproductive effort when provisioning nestlings, due to highly reduced paternal care (Weatherhead & Robertson 1979; Alatalo, Lundberg & Ståhlbrandt 1982; Lifjeld & Slagsvold 1989). As a consequence, secondary females have strongly reduced fledging success (Alatalo, Lundberg & Ståhlbrandt 1982) and fledge offspring with lower body condition, thus reduced survival prospects (Linden & Moller 1989), while male offspring from these broods do not benefit from a higher probability to become polygynous (Gustafsson & Qvarnström 2006).

In these two situations, natal dispersers paid a cost suggesting a higher sensitivity to the impact of an unexpected increase in reproductive effort, while they were able to adjust breeding decisions when they could predict reproductive effort. The reduced ability of natal dispersers to cope with an increase in reproductive effort could result from lower familiarity with the breeding environment (Greenwood & Harvey 1982; Bukacinski, Bukacinska & Lubjuhn 2000; Schjorring 2001; Brown, Brown & Brazeal 2008), and thus more limited knowledge on site quality, food resources, predation risk, etc., compared to non-dispersing individuals (Isbell, Cheney & Seyfarth 1990; Pärt 1995; Jacquot & Solomon 1997; Yoder, Marschall & Swanson 2004). In migratory species, several studies reported that young can acquire knowledge about the natal area by remaining near their birth site before the onset of migration (Nolan 1978; Rappole & Ballard 1987; Anders *et al.* 1997; Vega Rivera *et al.* 1998). Natal dispersers may therefore lack such knowledge about their settlement area. The post-fledging

period may be crucial for exploring the environment and acquiring knowledge about alternative breeding areas compared to the natal area; however it often remains one of the least studied period of life (Baker 1993). Recently, personality traits such as exploration and boldness have been shown to relate to natal dispersal behaviour (Dingemanse *et al.* 2003; Aragon *et al.* 2006; Korsten *et al.* 2013), and they could alleviate dispersal cost by helping individuals to familiarise more quickly with their new breeding environment. Further work would be needed to assess how and when dispersing young familiarize with their new environment, how individuals' phenotype may modulate this process and how this may affect lifetime fitness by buffering negative impacts of sudden environmental changes.

IS NATAL DISPERSAL COST LONG-LASTING?

Importantly, the implications of a natal dispersal cost resulting from an increased reproductive effort may strongly differ depending on when it occurs, i.e. just after the natal dispersal event only (short-term) or along the entire lifetime (long-term). Recently, long-term costs of natal dispersal have been reported in terms of accelerated reproductive senescence (Bouwhuis *et al.* 2010; Nevoux *et al.* 2013). However, costs due to a lack of familiarity with the new breeding environment can be expected to disappear later in life, once individuals acquired knowledge about their local environment. Here, we showed that annual recruitment of natal dispersing individuals was lower following an increase in reproductive effort without distinguishing whether the increase occurred in the year of settlement in the new habitat or later. Among individuals experiencing a brood size increase during their first breeding event, i.e. just after dispersal, natal dispersers achieved lower annual recruitment compared to non-dispersing individuals during the first breeding event only ($N = 47$, $\chi^2_1 = 3.54$, $P = 0.059$; interaction natal dispersal by brood size manipulation: $N = 127$, $\chi^2_2 = 8.57$, $P = 0.01$) and not later in life ($N = 72$, $\chi^2_1 = 1.66$, $P = 0.20$) interaction natal dispersal by brood size manipulation: $\chi^2_2 = 4.22$, $P = 0.12$). This could suggest that the lifetime cost of natal dispersal observed here in terms of reduced LRS when

experiencing an increased reproductive effort would be a legacy of costs paid early in life, when individuals have not yet familiarised with their new environment.

However, among individuals experiencing a brood size increase later in life, i.e. at least one year after the natal dispersal event, natal dispersers also achieved lower annual recruitment compared to non-dispersers in the year of the increase (N=72, $\chi^2_1 = 9.13$, P = 0.002; interaction natal dispersal status by brood size manipulation after the dispersal event: N = 390, $\chi^2_2 = 9.99$, P = 0.007). Thus the reduction in recruitment following increased reproductive effort in natal dispersers was observed only in the year of increase but could occur along the entire lifetime, reflecting a long-term cost of natal dispersal. Therefore, unless familiarity with the new environment takes longer than one year to acquire, the lack of familiarity was not the sole explanation for the observed natal dispersal cost, even though natal dispersers are more likely to disperse again (Doligez *et al.* 1999; Doligez *et al.* 2012), and thus encounter a new, unfamiliar, environment again later on. Natal dispersers could also bear phenotypic traits that increase over lifetime their sensitivity to stressful situations such as when facing an increased reproductive effort (e.g. a lower foraging ability: Aragon, Meylan & Clobert 2006; Meylan *et al.* 2009). Most likely, the effects of the lack of familiarity and the existence of behavioural syndromes associated to dispersal combine to result in the cost paid by natal dispersers when reproductive effort is increased. The above tests should however be interpreted with caution, because of limited sample sizes (in particular, we could not investigate the existence of a long-term cost of natal dispersal in secondary females because too few females were secondary after their first breeding event). Nevertheless, the cost of natal dispersal was not compensated for at the lifetime scale, either between breeding events or between fitness components, since natal dispersing individuals achieved lower LRS than non-dispersing ones even when their reproductive effort was increased early only. Dispersal decisions early in life thus translated into a fitness cost at a lifetime scale when reproductive effort was increased.

Overall, our results suggest that the lifetime consequences of natal dispersal costs are likely to depend on the spatio-temporal variability of habitat

quality, both between and within seasons. This variability may condition the ability of natal dispersing individuals to predict the expected reproductive effort and adjust decisions accordingly after dispersal, in the absence of sufficient familiarity with the habitat to buffer a sudden increase in the required effort and/or because of higher sensitivity to stressful situations. If natal dispersers cannot make such adjustments because of unpredictable environmental changes, they are at risk for paying a lifetime fitness cost.

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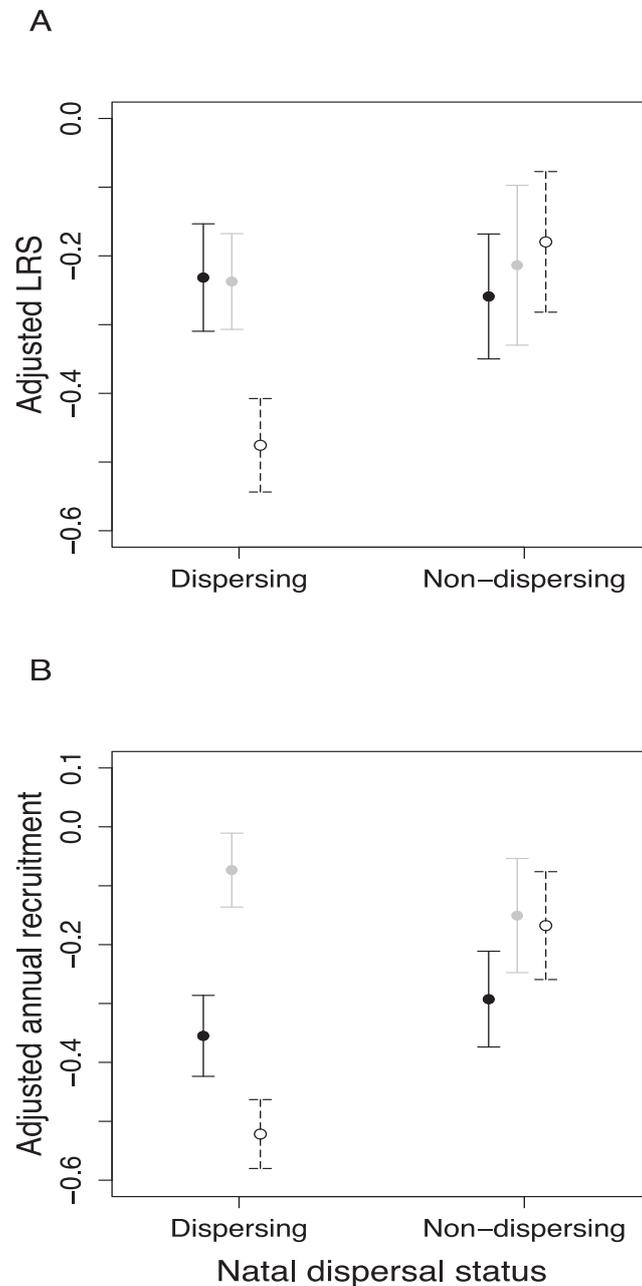


Figure 3.1: (A) LRS and (B) annual recruitment according to the interaction between natal dispersal status and brood size manipulation. The figure shows mean values (± 1 SE) adjusted for other significant effects in the model (i.e. residuals from the model without the interaction between natal dispersal status and brood size treatment). Black dots: individuals that experienced a brood size reduction (A) at least once during their lifetime or (B) in the year considered; grey dots: control individuals (A) at least once during their lifetime or (B) in the year considered; blue dots: individuals that experienced a brood size increase (A) at least once during their lifetime or (B) in the year considered.

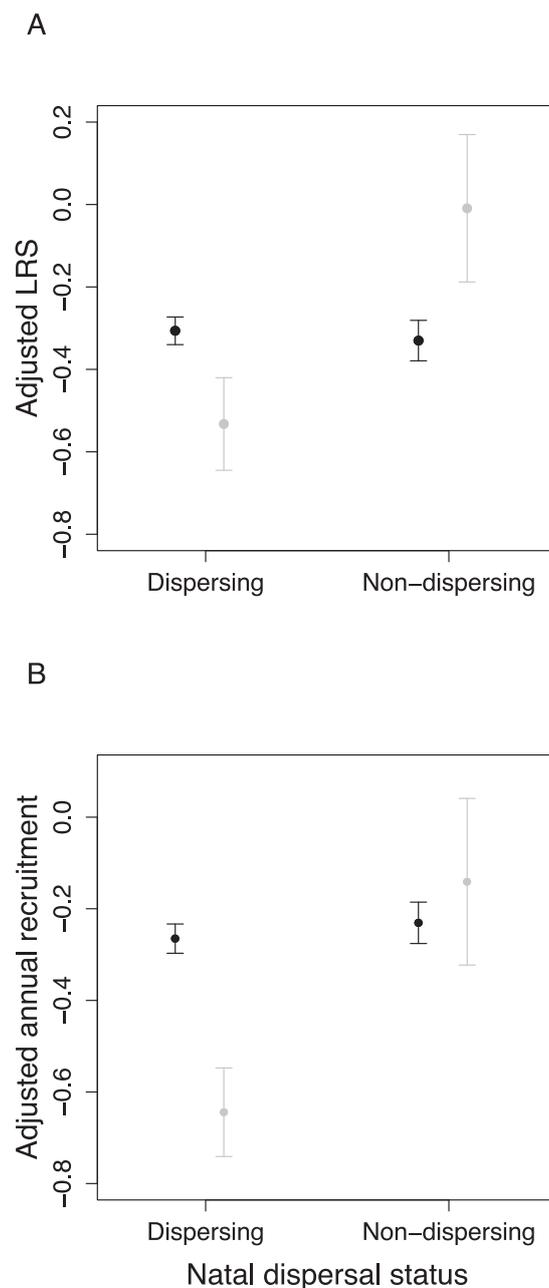


Figure 3.2: (A) LRS and (B) annual recruitment in females according to the interaction between natal dispersal status and polygyny status. The figure shows mean values (± 1 SE) adjusted for other significant effects in the model (i.e. residuals from the model without the interaction between natal dispersal status and polygyny status). Black dots: monogamously mated and primary females (A) over their entire lifetime or (B) in the year considered; grey dots: secondary females (A) at least once during their lifetime or (B) in the year considered.

Table 3.1: Effect of natal dispersal status (dispersing vs. non-dispersing individuals) on LRS (lifetime production of recruits), annual recruitment and return rate when all individuals are considered (i.e. not accounting for brood size manipulation or polygyny status; see text). X^2 and P-values refer to the LRT test. In all cases, $df = 1$. Significant cofactors in the final models are shown in bold. Test and p-values for the non-significant effects involving natal dispersal status correspond to the values when the effect or interaction was added to the final model (in the case of interactions, together with the main effects involved).

Variable	Estimate \pm SE	χ^2	P
LRS			
sex	0.22 \pm 0.06	15.06	< 0.001
age at first breeding	0.13 \pm 0.06	4.8	0.02
natal dispersal status	0.09 \pm 0.06	2.39	0.12
natal dispersal status*sex	0.12 \pm 0.12	1.03	0.31
natal dispersal status*age at first breeding	0.02 \pm 0.12	0.03	0.86
Annual Recruitment			
age	0.24 \pm 0.05	20.55	< 0.001
location of the breeding plot	-0.20 \pm 0.06	11.51	< 0.001
natal dispersal status	0.07 \pm 0.05	1.76	0.18
natal dispersal status*sex	-0.02 \pm 0.10	0.07	0.79
natal dispersal status*age	0.08 \pm 0.10	0.006	0.93
natal dispersal status*location of the breeding plot	0.03 \pm 0.11	0.08	0.78
Annual return rate			
natal dispersal status	0.11 \pm 0.08	1.78	0.18
natal dispersal status*sex	0.22 \pm 0.15	2.07	0.15
natal dispersal status*age	-0.22 \pm 0.15	2.05	0.15
natal dispersal status*location of the breeding plot	0.01 \pm 0.16	0.005	0.94

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Chapter 3

Appendix

APPENDIX 1 CHAPTER 3

Table 3.S1: Non-exhaustive list of recent studies reporting correlative comparisons of LRS measures between dispersing and non-dispersing individuals in avian species.

Species	Fitness Components	Type of Dispersal	Results	Dispersal variable	Notes	Ref
Great tit <i>Parus major</i> L.	F, S, LRS	Natal + Breeding	♂ S+LRS: D=P ♀ F: D=P ♀ S+LRS: D<P	Discrete	Correlative	1
Great Reed Warblers <i>Acrocephalus arundinaceus</i> L.	LRS	Natal	♂: D<P ♀: D=P	Discrete	Correlative	2
Savannah sparrow <i>Passerculus sandwichensis</i> Gmel.	LRS	Natal	♂: D<P ♀: D=P	Discrete	Correlative	3
Black kite <i>Milvus migrans</i>	F, S, LRS	Natal	F + S: D=P ♂ LRS: D<P ♀ LRS: D=P	Continuous	Correlative	4
Song sparrow <i>Melospiza melodia</i> Wils.	S, F, LRS	Natal	♀ F: D<>P ♂ F: D<P ♀ S: D=P ♂ S: D > P LRS: D=P	Discrete	Correlative	5
Great tit <i>Parus major</i> L.	S, LRS	Natal	♀ LRS: D < P ♂ LRS: D=P S: D=P	Discrete	Correlative	6

Great reed warbler	S, LRS	Natal + Breeding	♂ S, D<P ♀ S: D=P ♂ LRS: D<P ♀ LRS: D _s >P>D _l	Discrete	Correlative 2 classes of immigrants	7
Long-tailed tit <i>Aegithalos caudatus</i> L.	S, F, LRS, I	Natal	F: D<P S: D=P LRS: D<P	Discrete	Correlative	8
Red-cockaded woodpecker	F, LRS, S	Natal	♂ LRS: D<P ♀ LRS: D=P ♂ F: D=P ♀ F: D >=P ♂ + ♀ S: D=P	Continuous	Correlative	9
House sparrow <i>Passer domesticus</i>	F, LRS, S	Natal	F: D<P ♀ LRS: D=P ♂ F: D=P ♀ F: D >=P ♂ + ♀ S: D=P	Discrete	Correlative 2 classes of age	10
Great tit <i>Parus major</i> L.	F, S, LRS	Natal	F: D<=P S: D=P LRS: D<P	Discrete	Correlative Females only	11
Lesser kestrel <i>Falco naumanni</i>	F, S, LRS, I	Natal	F: D = P S: D<P LRS + I: D<P	Continuous and discrete	Correlative	12
Mauritiums kestrel <i>Falco punctatus</i>	F, LRS	Natal	♀ F: D<=P ♂ F: D=P ♀ LRS: D<P ♂ LRS: D=P	Discrete	Correlative	13

F = reproductive components, S = survival components, \square : individual fitness estimate (including inclusive fitness). Results of comparisons between dispersing (D) and non-dispersing or philopatric (P) individuals show whether parameters were higher (>), lower (<) or equal (=) for dispersing compared to non-dispersing individuals, separating sexes when results differ; <> means that some components were higher and some lower; \leq (resp. \geq) means that some components were lower (resp. higher) and some equal for dispersing compared to non-dispersing individuals. Dispersal variable analysed: discrete variable (dispersing status) or continuous variable (dispersal distance). D_s: short-distance dispersers, D_l: long-distance dispersers.

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1. (Verhulst & vanEck 1996),
2. (Van de Castele 2002),
3. (Bouwhuis *et al.* 2010),
4. (Bensch *et al.* 1998; Forero, Donazar & Hiraldo 2002) ,
5. (Hansson, Bensch & Hasselquist 2004),
6. (Wheelwright & Mauck 1998),
7. (Marr, Keller & Arcese 2002),
8. (Parn *et al.* 2009),
9. (Forero, Donazar & Hiraldo 2002),
10. (Maccoll & Hatchwell 2004)
11. (Pasinelli, Schiegg & Walters 2004),
12. (Serrano & Tella 2012),
13. (Nevoux *et al.* 2013)

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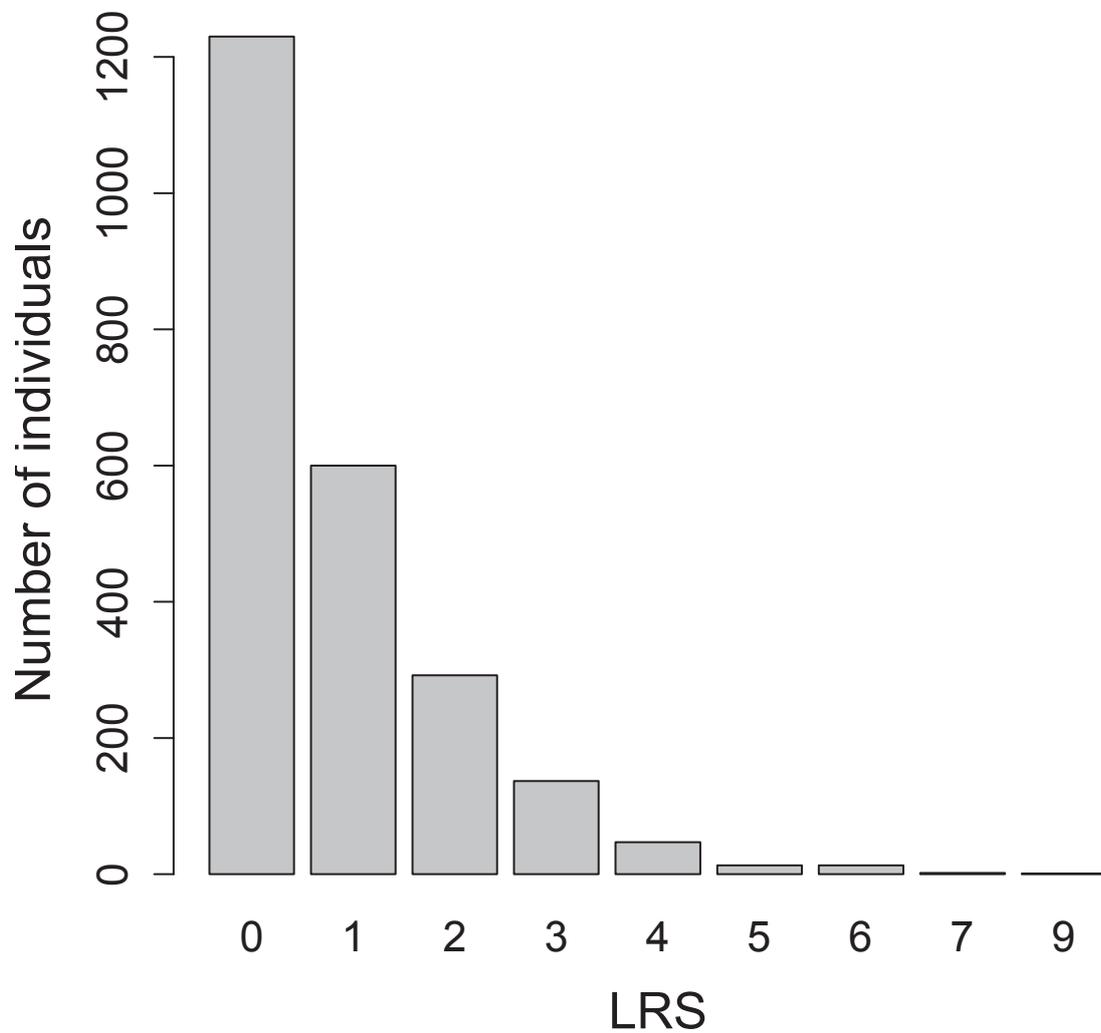
APPENDIX 2 CHAPTER 3

Figure 3.S1: Distribution of values of lifetime reproductive success, estimated as the total number of recruits produced over an individual's lifetime.

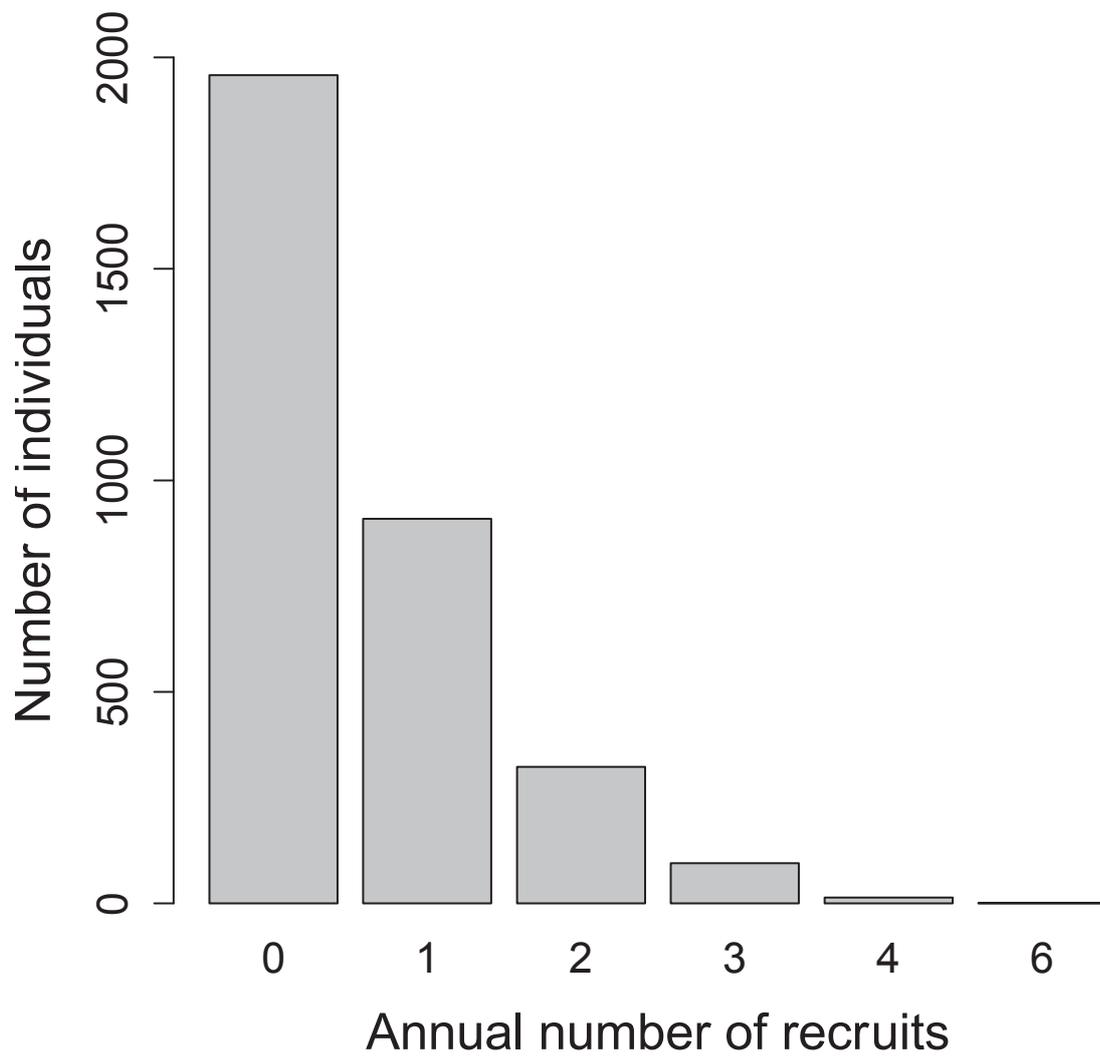


Figure 3.S2: Distribution of the annual number of recruits.

Chapter 4

**Dispersal and breeding decisions in a wild
population of collared flycatchers
(*Ficedula albicollis*)
Part 1: early breeding decisions**

Marion Germain
Tomas Pärt
Lars Gustafsson
Blandine Doligez

Abstract

Dispersal is widely recognized as a major trait for evolutionary processes. Yet, the balance between dispersal costs and benefits remains equivocal in empirical studies. The absence of a clear pattern may result from ignoring possible trade-offs among fitness components within breeding events and/or potential impact of mate characteristics on fitness output. Individuals may however be expected to adopt different breeding strategies depending on their dispersing status and their mate's characteristics. Here, we examined breeding decisions following dispersal in a wild population of a bird species with biparental care during the nestling phase. We compared a set of six early (i.e. until hatching) breeding decisions reflecting the timing of breeding, the investment in eggs and egg care, and the female body reserves between dispersing and non-dispersing individuals accounting for the dispersal status of the mate. In addition, we accounted for age and body condition of both parents, which are traits known to affect reproductive success. Dispersing and non-dispersing individuals differed in clutch size, egg mass and incubation length, i.e. three out of the six early decisions considered. However, the dispersal status most often interacted with body condition and/or age, suggesting phenotype-dependent effects of dispersal on breeding decisions. Furthermore, male dispersal status was involved in all differences observed, suggesting that male status influences even early breeding decisions as much as female status. However, male and female dispersal status were involved in interactions with different factors, in line with different selective pressures on dispersal for both sexes. Finally, dispersing individuals showed both higher and lower values of breeding variables compared to non-dispersing ones depending on other variables, without clear compensations among breeding decisions, suggesting no positive or negative net effect of being a disperser. Although our sample was necessarily biased towards successful individuals, these results suggest that the balance between the costs and benefits of dispersal is not fixed, but rather partly depends on the individual's and its mate's phenotypes. Late (i.e. from hatching) breeding decisions will be analysed elsewhere.

Key words: breeding decisions, pre-hatching, mate influence, trade-offs, patchy population, collared flycatcher, *Ficedula albicollis*

INTRODUCTION

Dispersal is commonly defined as the movement of an individual from its natal or previous breeding site to a new breeding site (Greenwood & Harvey 1982). Dispersal is widely recognized as a key life history trait affecting many ecological and evolutionary processes such as population dynamics and genetics, community structure and species spatial distribution (Clobert *et al.* 2001; Ellner *et al.* 2001; Bowler & Benton 2005; Garant *et al.* 2005; Postma & van Noordwijk 2005; Schliehe-Diecks, Eberle & Kappeler 2012). As a consequence, the evolution of dispersal has been extensively studied using theoretical models, often relying on strong assumptions about the relative fitness of dispersing and philopatric individuals (Johnson & Gaines 1990; McPeck & Holt 1992; Bowler & Benton 2005). Indeed, the evolution of dispersal and its impact on ecological and evolutionary processes will strongly depend on the success of dispersing individuals. Dispersal is often assumed to entail a survival cost during the transient phase (Johnson & Gaines 1990). However, once dispersing individuals have settled in a new habitat, their reproductive success can either increase or decrease as a result of the balance between costs and benefits of dispersal, which may strongly depend on both environmental factors (e.g. habitat quality) and individual's phenotypic traits (e.g. age, body condition) (Belichon, Clobert & Massot 1996; Clobert *et al.* 2001; Clobert *et al.* 2012).

Settling in a new area may involve both direct and deferred costs on reproduction (Bonte *et al.* 2012) such as search costs in terms of time and energy (Stamps, Krishnan & Reid 2005), unfamiliarity with the breeding environment, which may affect the ability to find high-quality sites, mates and/or resources (Pärt 1994; Pärt 1995b; Peron, Lebreton & Crochet 2010) or maladaptation to local conditions with regards to mate selection and breeding decisions (Greenwood 1980; Pärt 1994; Bensch *et al.* 1998; Baker & Rao 2004; Postma & van Noordwijk 2005). However, dispersers can also gain benefits by leaving a habitat patch declining in quality because of increasing predation or competition, including kin competition (Travis & Dytham 1999), and inbreeding avoidance (Greenwood 1980; Szulkin & Sheldon 2008; see reviews in Clobert *et al.* 2001).

Evidence for costs and benefits of dispersal remains equivocal in empirical studies, since only half of the studies investigating fitness correlates of dispersal have detected differences between dispersing and philopatric individuals (reviews in Belichon, Clobert & Massot 1996; Doligez & Pärt 2008). While survival after settlement was in most cases found equal between dispersing and non-dispersing individuals, the comparison of reproductive traits was less straightforward, with approximately the same number of studies showing no difference in the reproductive variables considered and showing lower or higher values for dispersing compared to non-dispersing individuals. Importantly, most of these studies (28 out of 38 most recent studies, i.e. 76%) compared only one or a few fitness related-traits between dispersing and non-dispersing individuals while the others analysed a lifetime fitness outcome. Therefore, one of the explanations for an absence of clear fitness costs and benefits patterns of dispersal in empirical studies may be the occurrence of compensations among different fitness components within breeding events (e.g. between offspring quality and quantity: Julliard, Perret & Blondel 1996) or among breeding events (e.g. between investment in reproduction and subsequent survival)(Lemel *et al.* 1997; Clobert *et al.* 2001). Such compensations may make fitness differences between dispersing and non-dispersing individuals difficult to detect using comparisons of a single or even a few fitness traits.

Another explanation for the absence of clear fitness costs and benefits patterns of dispersal may be the frequent ignorance of the potential impact of mate characteristics on the fitness output (e.g. Bensch *et al.* 1998; Spear, Pyle & Nur 1998). Life-history theory predicts that reproductive investment and breeding decisions should also be adjusted in response to mate quality and attractiveness, because it can influence fitness returns (Sheldon, Kruuk & Merila 2003; Gowaty 2008; Harris & Uller 2009; Braga Goncalves *et al.* 2010; Rios-Cardenas, Brewer & Morris 2013). Dispersing and non-dispersing individuals may differ in phenotypic traits (Clobert *et al.* 2009) but also in their knowledge of the local environment (e.g. Pärt 1994), and therefore they may differ in their breeding strategies (e.g. Julliard, Perret & Blondel 1996), with potentially different impact of the mate's

characteristics such as dispersal status, age, competitive ability or body condition. Dispersing and non-dispersing individuals may thus be expected to adjust breeding decisions differently according to their mate's characteristics, and such adjustments may blur comparisons of reproductive traits between dispersing and non-dispersing individuals.

Nevertheless, the role of males and females in reproductive decisions is often considered asymmetric, even species with bi-parental care (Sanz & Moreno 1995; Woodard & Murphy 1999; Sonerud *et al.* 2014). Early breeding decisions (e.g. timing of reproduction or number of eggs / foetus produced) are thought to be mainly under the direct control of the female. Yet, males have been shown to influence early breeding processes, e.g. through the defence of breeding resources of different quality, the provisioning or guarding of females during early breeding stages, and/or better access to information about local conditions compared to females (Slagsvold & Lifjeld 1990; Pärt 1994; Wendeln 1997; Korpimäki & Wiehn 1998). Furthermore, when males actively provide offspring care, paternal investment can strongly influence the output of reproduction (e.g. Pagani-Nunez & Carlos Senar 2014). Whether and to what extent early and late breeding decisions (i.e. pre- and post-birth or hatching) may be differently influenced by male and female traits depending on individuals' dispersal status remains poorly understood.

In this study, we investigated early breeding decisions (i.e. before hatching) following dispersal in a wild population of a small migratory passerine bird, the collared flycatcher (*Ficedula albicollis*). We compared laying date, egg mass, clutch size and incubation length between dispersing and non-dispersing individuals while accounting for the dispersal status of the partner and traits known to affect reproductive success, i.e. age and body condition (Forslund & Pärt 1995; Cichon, Olejniczak & Gustafsson 1998). We also compared female body mass before laying and during incubation between dispersing and non-dispersing females. This paper will be followed by a second paper focusing on late breeding decisions (i.e. after hatching). In our study species, dispersal has been shown to affect individuals' knowledge of local environmental conditions (nest site quality: Pärt

1994; nest predation risk: Doligez & Clobert 2003; social information: Forsman *et al.* 2014), with consequences on breeding decisions (nest site choice, laying date, clutch size). Dispersal is also linked in many species to phenotypic traits such as morphological, physiological and/or personality traits (De Fraipont *et al.* 2000; Duckworth & Badyaev 2007; Clobert *et al.* 2009; Korsten *et al.* 2013), or competitive ability, which may influence the use of information (e.g. Doligez *et al.* 1999; Doligez, Pärt & Danchin 2004; Kurvers *et al.* 2010) and thereby breeding decisions adjustments. We explored whether such adjustments could be detected here in early breeding decisions.

MATERIAL AND METHODS

STUDY AREA, STUDY SPECIES AND GENERAL POPULATION MONITORING

The collared flycatcher is a short-lived hole-nesting migratory passerine bird. Our study area is located on the Swedish island of Gotland, Baltic Sea (57°10'N, 18°20'E), where artificial nest-boxes have been regularly distributed in >15 spatially discrete forest plots of varying sizes, allowing an easy access to detailed breeding data of a large number of pairs.

Each year since 1980, the breeding population has been monitored throughout the breeding season. Laying and hatching date, clutch size and number of fledged young have been routinely recorded in all nests during regular visits to the nest boxes. Adult flycatchers breeding in nest boxes have been trapped, identified with individual aluminium rings, measured (tarsus length to the nearest 0.1 mm and body mass to the nearest 0.1g) and aged based on their previous records in the population or on plumage characteristics when previously unringed (yearlings versus older individuals: Svensson 1992). Most females were caught during incubation, and both parents were subsequently caught while feeding the young whenever possible (i.e. when the brood survived at least until 5-6 days of age). As a consequence, by including both male and female characteristics as explanatory variables in our analyses (see below), we *de facto* biased the sample

towards more successful individuals. Old birds arrive earlier on the breeding grounds, lay earlier and larger clutches, and fledge more offspring than yearlings (Gustafsson & Pärt 1990; Sendecka, Cichon & Gustafsson 2007). Because age differences strongly decrease after two years of age, we categorized age in two classes; yearlings (i.e. one-year-old) and “old” individuals (≥ 2 -years-old). For details on the breeding ecology of the collared flycatcher, the study area and long-term monitoring of the breeding population, see (Pärt & Gustafsson 1989; Pärt 1990; Doligez *et al.* 1999; Doligez, Gustafsson & Pärt 2009).

EARLY BREEDING DATA

The data used here were collected between 1980 and 2009. During the settlement and egg-laying period (beginning of May until beginning of June), nest-boxes were visited regularly (at least every third day) to determine the initiation of egg laying, assuming that females lay one egg per day. Final clutch size was recorded after the beginning of incubation. In 2003 and 2005 to 2009, clutches were visited daily during the egg laying period to determine the egg laying sequence. Eggs were individually marked according to the laying sequence and weighed to the nearest 0.01g. Here, we analysed the mass of the third egg laid because variation in egg mass is typically far larger among than within clutches (Christians 2002; Krist *et al.* 2004), and because not all eggs could be weighed for part of the clutches. Incubation length was calculated as the observed hatching date minus the sum of laying date and clutch size + 2 days, because incubation starts on the day when the last egg is laid.

A body condition index was computed for all individuals as the ratio of body mass on tarsus length (i.e. relative mass). Female body mass was however standardized to account for the period of capture (i.e. during incubation *vs.* when feeding young), because female body mass strongly differed between these two periods (incubation: $N = 812$, mean \pm SE: 15.46 ± 0.04 ; nestling feeding: $N = 1414$, mean \pm SE: 13.31 ± 0.02). Female body mass was therefore centred relative to the mean body mass of females caught during the same period and divided by the standard deviation of body mass of females caught during the same period. In

years 2006 and 2007, females were also caught in nest boxes during nest building for the purpose of another study, providing female body mass before laying in these two years.

DISPERSAL STATUS

Dispersal was defined as a change of forest plot between the year of birth and the first breeding event (natal dispersal) or between successive breeding events (breeding dispersal); philopatric (i.e. non-dispersing) individuals returned to the same plot. For the two largest plots, however, we adjusted this definition using dispersal distance, by categorising as dispersers individuals with a dispersal distance of > 700 m within these plots (see Doligez, Gustafsson & Pärt 2009 for a discussion). This binary definition of dispersal status (i.e. dispersing versus philopatric individuals) has been found to be biologically relevant in previous studies on this population (Doncaster *et al.* 1997; Doligez *et al.* 1999; Doligez, Danchin & Clobert 2002; Doligez, Pärt & Danchin 2004). Only adults whose natal or previous breeding site was known were included in the analyses: unringed individuals were discarded because they consisted of a mix of local birds previously missed and true immigrants. Furthermore, because natal and breeding dispersal are under different selective pressures (Clobert *et al.* 2001), we checked for differences in early breeding decisions depending on dispersal phase (natal vs. breeding) by including the dispersal phase as a covariate in the analyses (see below).

STATISTICAL ANALYSES

We investigated the links between early breeding decisions and dispersal status of both male and female accounting for both parents' age and body condition index. All response variables (laying date, clutch size, egg mass, incubation length and female body mass) were analysed using linear mixed models fitted using the function `lmer` in R package `lme4` (Bates & Maechler 2009; R Core Team 2014). For laying date (N=2 226), clutch size (N=2 222), egg mass (N=163) and incubation length (N=2 096), the starting model included as fixed effects

dispersal status, age and body condition index of both male and female, as well as all first-order interactions involving dispersal status of each parent (i.e. all first order-interactions except between age and body condition index). Year and breeding plot were included as random factors to control for non-independence of breeding events in the same year and/or plot due to environmental spatio-temporal variability. For laying date, clutch size and incubation length (but not egg mass because these data were collected over a smaller number of years), we added male and female ring number as random factors because many individuals appear several times in the dataset (e.g. for laying date, 873 individuals present at least twice over a total of 3254 individuals). We do not detail random effects because they are not of primary interest here; however, they were kept in all final models. In a second step, when differences were found between dispersing and philopatric individuals in breeding measures after the laying date, we included laying date and/or clutch size as explanatory variables in the final model to test whether the observed differences in the variable of interest could be explained by differences in earlier breeding measures. Sample sizes were close for the different breeding variables because we analysed mostly pairs successful in hatching eggs by including both parents' characteristics as explanatory variables (see above for catching timing of both parents).

For female body mass before laying (N=221) and during incubation (N=812), the female body condition index was replaced by female tarsus length to account for differences in mass due to structural size. For female body mass before laying, the dispersal status, age and body condition index of the male were not included as fixed effects (i.e. only female characteristics were considered), because they were not known in some cases, but the delay to laying (i.e. number of days between catching and laying the first egg) was included to account for the increase in female body mass with egg maturation. Here, sample sizes were smaller than for previous variables because female early catching (i.e. before laying) occurred only during a limited number of years, and female body mass was reported partly during incubation and partly during nestling feeding.

For each response variable, we used a stepwise backward elimination procedure starting with the initial model and removing non-significant terms starting with interactions, until the final model containing significant effects only (and all the main effects included in significant interactions). When the dispersal status of at least one parent was retained in the final model, we investigated potential differences in the effects of natal and breeding dispersal by adding a natal dispersal covariate indicating if the dispersal event considered was natal or breeding (i.e. a binary variable). We added male and/or female natal dispersal covariate and the corresponding interaction with male and/or female dispersal status. However, in our population, natal dispersal is strongly correlated to age (Doligez *et al.* 1999) and thus, we could not include this covariate in the initial model containing age, and therefore checked for the natal dispersal covariate in a second step only.

RESULTS

LAYING DATE, CLUTCH SIZE AND EGG MASS

Laying date did not differ between philopatric and dispersing individuals (Table 1a), alone or in interaction with other traits (all interactions with dispersal status, $\chi^2_1 < 2.80$, $P > 0.10$), but it was affected by male and female age as well as female body condition (**Table 4.1a**). Conversely, the dispersal status of both the male and the female affected clutch size, but always in interaction with body condition index or age (**Table 4.1b**). Clutch size of pairs with a dispersing male decreased with increasing male body condition ($N = 480$, estimate \pm SE: -1.81 ± 0.58 , $\chi^2_1 = 9.89$, $P = 0.002$) while there was no relation in pairs with a philopatric male ($N = 1742$, $\chi^2_1 = 0.03$, $P = 0.86$; **Fig. 4.1a**). Furthermore, clutch size of pairs with a philopatric male increased with female body condition (estimate \pm SE: 0.70 ± 0.34 , $\chi^2_1 = 3.34$, $P = 0.045$) while there was no relation in pairs with a dispersing male ($\chi^2_1 = 2.29$, $P = 0.13$; **Fig. 4.1b**). Finally, in pairs with an older male, philopatric females produced smaller clutches than dispersing females ($N = 1798$,

estimate \pm SE: -0.076 ± 0.036 , $\chi^2_1 = 4.30$, $P = 0.038$), whereas in pairs with a yearling male, clutch size did not differ between philopatric and dispersing females ($N = 424$, $\chi^2_1 = 0.31$, $P = 0.58$, **Fig. 4.2**). A difference in breeding timing is unlikely to explain the observed differences between dispersing and philopatric individuals as each interaction remained significant after including laying date in the final model (interaction between male dispersal status and male body condition: $\chi^2_1 = 4.00$, $P = 0.045$; male dispersal status and female body condition: $\chi^2_1 = 3.82$, $P = 0.050$; male age and female dispersal status: $\chi^2_1 = 3.99$, $P = 0.045$).

Females mated with philopatric males laid a heavier third egg in their clutch than females mated with dispersing males (**Table 4.1c**). Importantly, this effect did not either rely on difference in laying date ($\chi^2_1 = 1.59$, $P = 0.21$) or in clutch size ($\chi^2_1 = 0.02$, $P = 0.88$), as male dispersal status remained significant when including both variables ($\chi^2_1 = 7.69$, $P = 0.006$).

INCUBATION LENGTH

Incubation was longer in philopatric compared to dispersing females (**Table 4.1d**). Incubation length also differed between pairs with a philopatric and a dispersing male according to male age (**Table 4.1d**): for pairs with an older male, incubation was longer when the male was philopatric compared to dispersing ($N = 1703$, estimate \pm SE: 0.17 ± 0.08 , $\chi^2_1 = 0.17$, $P = 0.032$), while in pairs with a yearling male, incubation tended to be shorter when the male was philopatric compared to dispersing ($N = 393$, estimate \pm SE: -0.26 ± 0.13 , $\chi^2_1 = 3.68$, $P = 0.055$; **Fig. 4.3**). Again, these differences are not attributable to difference in the timing of laying or in clutch size. Indeed, even when correcting for laying date and clutch size, both female dispersal status ($\chi^2_1 = 4.20$, $P = 0.040$) and interaction between male dispersal status and male age ($\chi^2_1 = 6.76$, $P = 0.009$) remained significant.

FEMALE BODY MASS

Dispersing and philopatric females did not differ in their body mass before laying (**Table 4.1e**) and during incubation (**Table 4.1f**; in both cases, all interactions with dispersal status: $\chi^2 < 3.46$, $P > 0.06$). This accounted for the strong effect of tarsus length (**Table 4.1e;f**) and time interval until laying (for mass before laying; **Table 4.1e**) or female age (for mass during incubation, **Table 4.1f**).

DISCUSSION

In this study, we investigated early breeding decisions in relation to the dispersal status of both parents, along with their age and body condition, in a natural patchy population of collared flycatchers. In order to detect possible compensations between reproductive traits within breeding events, we analysed a set of six early breeding variables reflecting decisions regarding the timing of breeding (laying date), the investment in eggs and egg care (clutch size, egg mass, incubation length) and the female body reserves (mass before laying and during incubation). Our results reveal differences between dispersing and philopatric individuals in three variables: clutch size, egg mass and incubation length, i.e. half of the breeding variables considered. However, the effect of dispersal status always remains weak considering the sample sizes here, and often interacts with body condition and/or age, suggesting a phenotype-dependent impact of dispersal. Moreover, for all three variables, the dispersal status of the male was significant, suggesting that male status has an equally or even more important influence on early breeding decisions than female status. This is also in line with the idea that selective pressures on dispersal differ between males and females.

BIASES IN ESTIMATING REPRESENTATIVE BREEDING DECISIONS IN RELATION TO DISPERSAL?

Contrary to many previous studies, we investigated here the joint effect of dispersal status of both parents on early breeding decisions. Importantly, this implies that we investigated early breeding decisions of pairs having later reached a sufficiently advanced breeding stage to allow the capture and identification of males. Indeed, in our study population, as in many others, the capture of breeders is biased towards more successful individuals (see Doligez *et al.* 2012), particularly in males. Therefore, by analysing early breeding decisions in pairs for which characteristics of both parents are known, we biased our sample towards higher quality individuals, which may more efficiently adjust breeding decisions. This could reduce our ability to detect differences in breeding variables between dispersing and philopatric individuals, in particular when dispersing and philopatric individuals differ in capture probability depending on age (Doligez *et al.* 2012). In our population, age is linked to breeding success (Pärt 1995a) and our selection of individuals included in the analyses may therefore differ between dispersing and philopatric individuals. Although, overall, our sample also show that, even if dispersal entail some costs, a considerable number of dispersing individuals succeed to settle and to breed and to reach advanced stages as our sample encompasses more than 1 200 dispersing individuals. These individuals are maybe those contributing the more to ecological and evolutionary processes such as gene flow as the effects of dispersal on these processes require not only that individual disperse but survive and breed (i.e. effective dispersal; Greenwood & Harvey 1982).

PHENOTYPE-AND CONDITION-DEPENDENT EFFECTS OF DISPERSAL

Empirical studies have shown that dispersal propensity may depends on both individual's phenotypic traits, which may be either fixed or not (e.g. sex, age, fat reserves, competitive ability, personality traits) and environmental conditions (e.g. density of kin and non-kin, habitat quality) (Clobert *et al.* 2001; Clobert *et al.* 2009; Clobert *et al.* 2012). Therefore, phenotypic- and condition-dependence may

influence the balance between the costs and benefits of dispersal. However, to our knowledge, empirical demonstrations remained relatively rare as most studies focused on the link between dispersal propensity and phenotype or condition but did not directly consider the costs and benefits dispersal (Pasinelli & Walters 2002; Dingemanse *et al.* 2003).

Here we found that clutch size and incubation length differed between dispersing and philopatric individuals (both males and females) depending on male age and / or body condition index. This suggests phenotype- and condition-dependent effects of dispersal. Here we defined phenotype-dependent effects of dispersal as effects influenced by the individual own phenotypic traits and condition-dependence as effects based on external information (Clobert *et al.* 2009). In that sense, we considered that environmental conditions include the mate's phenotype. Dispersal was associated with both increased and decreased values of breeding variables, suggesting that the net effect of being a disperser was neither positive nor negative, but depended on many cases on the association with other phenotypic traits.

On the one hand, females mated with philopatric males laid more eggs when their own body condition increased, while this was not observed in females mated with dispersing males. Females mated with philopatric males also laid heavier eggs than females mated with dispersing males. The higher egg mass and increase in clutch size with female body condition for females mated with philopatric males suggest that male philopatry may allow pairs to benefit from better conditions, e.g. via higher quality territories (Pärt 1994), and/or adjust breeding investment according to their condition. Indeed, philopatric males were shown to acquire higher quality nest site (Pärt 1994) which may allow female to adjust breeding condition according to their own state, which may suggest a benefit of philopatry.

We also found that females mated with dispersing males laid more eggs than when mated with philopatric males when the male was old. Moreover, incubation was shorter for dispersing compared to philopatric females and for females mated with dispersing compared to philopatric males when the male was old. However, the larger clutch size of females mated with old dispersing males

also suggests that these females may benefit from favourable conditions and adjust decisions as early as during laying. Moreover the shortening of incubation by dispersing females and females mated with old dispersing males, which was not due to differences in laying date or clutch size, should allow them to benefit from higher success (Wiggins, Pärt & Gustafsson 1994; Verhulst & Nilsson 2008), and suggests that these females can also adjust their investment. In birds, reproductive success is known to increase with age (Newton 1989; Saetre *et al.* 1997; Sendecka, Cichon & Gustafsson 2007), as a result of increased breeding experience, foraging ability or again parental effort (Forsslund & Pärt 1995), which may be beneficial for females. In the pied flycatcher, females that choose old males as a mate has been shown to benefit in terms of a mate that is capable of a high performance of parental care (Saetre, Fossnes & Slagsvold 1995).

Importantly, if these differences (i.e. larger clutch size and/or shorter incubation period) may result in fitness benefits because of higher ability to access high resource quality / quantity, it is however also possible that these differences result from increased investment in order to compensate for lower expected quality/parental care ability of their partner (i.e. reproductive compensation, Gowaty 2008). However, because differences were observed for females mated with old, i.e. supposedly competitive, males rather than yearling males (independently of their own age), and because such higher investment did not seem to entail short-term costs on female body condition, such differences are more likely to reflect choices than constraints.

MALE DISPERSAL BEHAVIOUR

Early breeding decisions are often seen as mainly under the control of the female (Nilsson & Svensson 1993; Soler *et al.* 2001). Here, the dispersal status of the male was significantly related to more early breeding variables (clutch size, egg mass, incubation length) than the dispersal status of the female. This suggests that even if females make early breeding decisions, they base these decisions partly upon their mate's dispersal status. Again, this may arise either from direct effects of dispersal (e.g. different territory quality depending on the level of familiarity of the mate with its environment; Pärt 1994) or from indirect effects of mate's

phenotype (e.g. competitive ability, personality traits) on both dispersal decisions and resource holding potential for the female. Interestingly, male and female dispersal status had differential effects on early breeding variables; in particular they were overall involved in interactions with different variables. This may illustrate that males and females are under different selective pressures, in line with theories explaining sex-biased dispersal through social mating system (in birds, males defend resources to attract females and therefore should pay a higher cost to unfamiliarity with the breeding environment, i.e. to dispersal, than females; (Greenwood 1980; Greenwood & Harvey 1982), which are supported in the study species (Pärt 1995b). Nevertheless, the difference in effects of male dispersal between old and yearling males (with positive effects on clutch size and incubation length for females mated with old dispersing males) indicates that selective pressures depend on age, and old dispersing males may compensate costs due to lower familiarity by other means. The identification of selective pressures acting on dispersal in individuals with different phenotypic characteristics, such as sex and age, but also other behavioural traits such as personality traits (e.g. Duckworth et al. 2007), is therefore a crucial step in understanding the fitness consequences of dispersal depending on individuals' motivations to disperse.

CONCLUSION

Overall, our detailed investigation of a set of six fitness-related traits in the early stages of reproduction emphasized different points of importance to understand fitness consequences of dispersal. The different interactions between dispersal status and individuals' phenotypic traits and the presence of both positive and negative effects of dispersal status stress that the balance between the costs and benefits of dispersal is not fixed, but rather partly depends on the individual's phenotype. Accounting for the phenotype-dependent effects of dispersal as well as individuals' motivation to disperse depending on selective pressures acting on dispersal are critical steps for a better understanding of the possible consequences of dispersal on fitness-related traits. Furthermore, although we detected differences between dispersing and non-dispersing individuals in half of the breeding variables considered, we were not able to detect simple

compensations processes between decisions. This may suggest that other breeding decisions may be involved in the possible differences in reproductive strategies according to dispersal behaviour. These other decisions may occur either during the early stages of reproduction, such as nest construction, which is a potentially energy and time demanding activity seldom considered in avian life history (Moreno *et al.* 2010), or during the later stages of reproduction, i.e. during the nestling phase. To explore this possibility, we analysed a set of detailed late (i.e. after hatching) breeding decisions according to dispersal status in a similar way as our early decisions (next manuscript).

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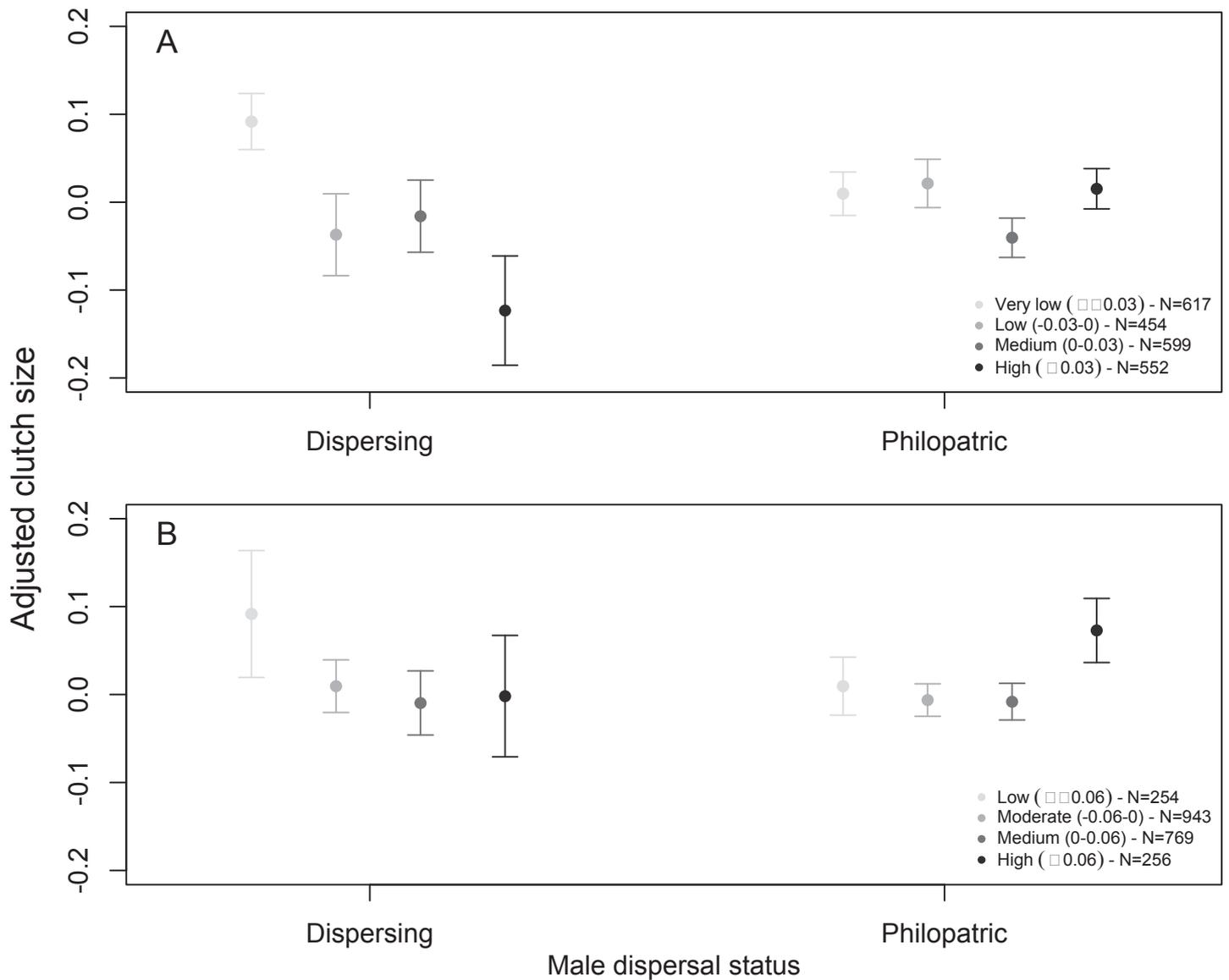


Figure 4.1: Clutch size according to male dispersal status and (A) male and (B) female body condition. The figure shows mean values (± 1 SE) adjusted for other significant effects in the model (i.e. residuals from the final model without the interaction between male dispersal status and the corresponding body condition). The categorisation of individuals according to body condition was done here purely for the purpose of illustration; see text for the statistics corresponding to the interactions.

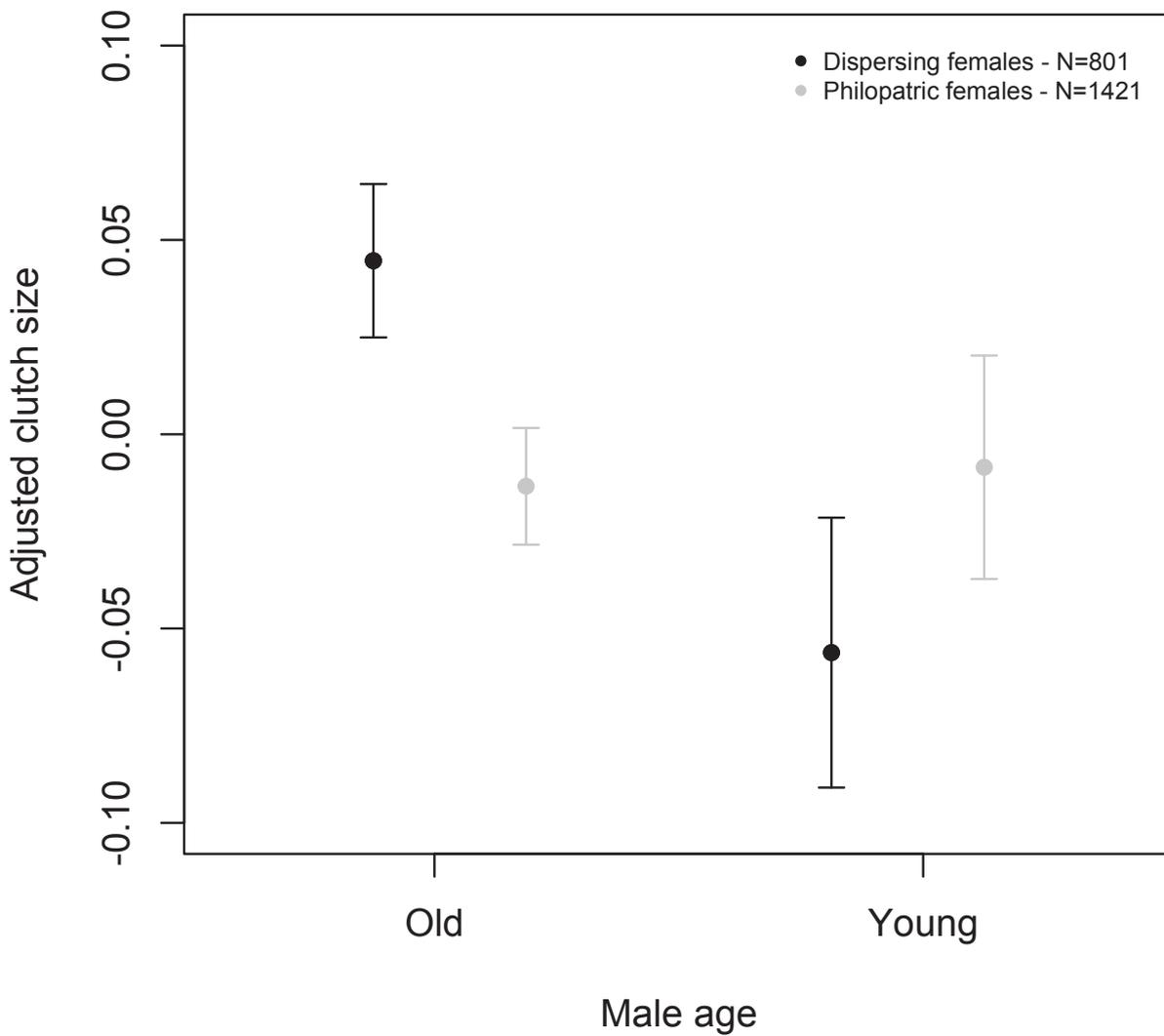


Figure 4.2: Clutch size according to female dispersal status and male age. The figure shows mean values (± 1 SE) adjusted for other significant effects in the model (i.e. residuals from the final model without the interaction between female dispersal status and male age).

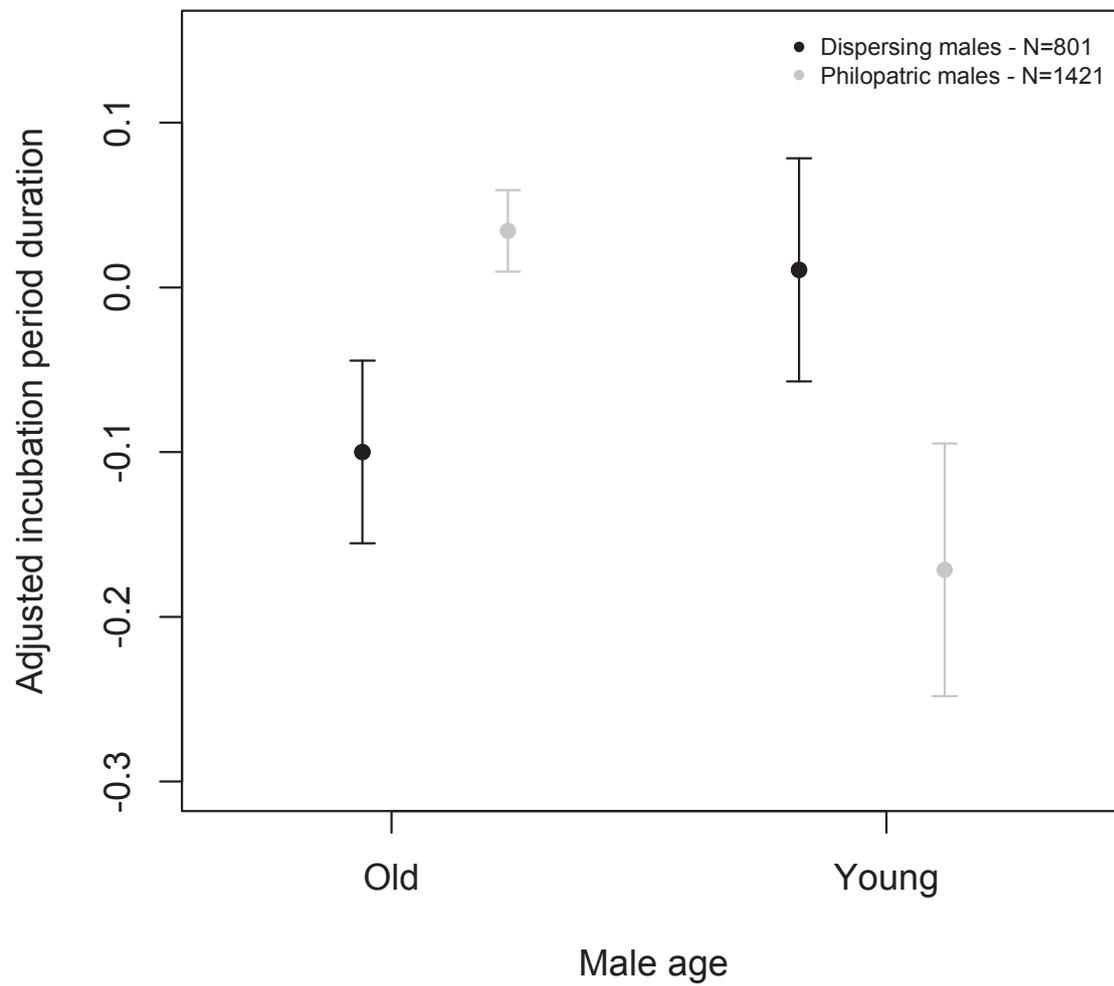


Figure 4.3: Incubation length according to male dispersal status and age. The figure shows mean values (± 1 SE) adjusted for other significant effects in the model (i.e. residuals from the final model without the interaction between male dispersal status and age).

Dispersal and early breeding decisions

Table 4.1: Effect of dispersal status (dispersing vs. philopatric individuals) on early breeding decisions. X^2 and P-values refer to the LRT test. In all cases, $df = 1$. The table shows final models without significant interactions that are detailed in the results. Test and p-values for the non-significant simple effects correspond to the values when the effect was involved in a significant interaction. For categorical variables, the estimate is given for one category (i.e. old individuals for age and dispersing individuals for dispersal status).

Variable	Estimate \pm SE	Chisq	P
(a) Laying date (N = 2 226)			
Male age	1.53 \pm 0.22	49.6	< 0.001
Female age	1.61 \pm 0.21	59.12	< 0.001
Female body condition index	-4.85 \pm 1.69	8.29	0.004
(b) Clutch size (N = 2 222)			
Male dispersal status	-0.06 \pm 0.04	2.88	0.09
Male age	-0.15 \pm 0.06	5.93	0.015
Female age	-0.33 \pm 0.04	80.71	< 0.001
Male body condition	-1.51 \pm 0.59	6.41	0.011
Female body condition	-0.64 \pm 0.57	1.26	0.26
(c) Egg mass (N = 163)			
Male dispersal status	64.90 \pm 24.09	7.26	0.007
Male age	111.40 \pm 42.57	6.85	0.008
Female body condition	718.76 \pm 203.74	12.45	< 0.001
(d) Incubation period duration (N = 2096)			
Female dispersal status	0.13 \pm 0.05	5.99	0.010
Male dispersal status	0.17 \pm 0.08	4.08	0.043
Female body condition index	-1.33 \pm 0.52	6.68	0.009
Male age	0.13 \pm 0.11	1.51	0.22
(e) Female early body mass (N = 220)			
Tarsus length	0.02 \pm 0.009	7.98	0.005
Interval before laying	- 0.25 \pm 0.022	134.32	< 0.001
(f) Female incubation body mass (N = 812)			
Female age	-0.02 \pm 0.09	9.75	0.002
Female tarsus length	0.49 \pm 0.07	52.34	< 0.001

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Chapter 5

Dispersal and breeding decisions in a wild population of collared flycatchers (*Ficedula albicollis*) Part 2: late breeding decisions

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Abstract

Dispersal is a major trait affecting evolutionary and ecological processes. Yet, the balance between the costs and benefits remains equivocal in empirical studies. The absence of a clear pattern may result from ignoring possible trade-offs among fitness components within breeding events and/or potential impact of mate characteristics on fitness output. Individuals may however be expected to adopt different breeding strategies depending on their dispersing status and their mate's characteristics. This study is a second part investigating the breeding decisions following dispersal in a wild population of a bird species with biparental care during the nestling phase. We compared a set of seven late (i.e. after hatching) breeding decisions reflecting the hatching success, the parental care, the fledging success and recruitment and finally both males and females reserves between dispersing and philopatric individuals accounting for the dispersal status of the mate. In this species, parental care is often considered as asymmetric. However, parents are supposed to equally share the parental effort during the nestling phase and both parents' characteristics are expected to be a strong determinant of breeding decisions. In addition, we accounted for age and body condition of both parents, which are traits known to affect reproductive success. Dispersing and philopatric individual differed in six over seven breeding decisions considered. However, as in early breeding decisions investigated in the previous paper, the dispersal status systematically interacted with body condition and/or age, are confirms therefore phenotype and condition-dependent effects of dispersal on breeding decisions. Furthermore, consistently with the results on early breeding decisions, male dispersal status is more involved in interactions with different factors than females' dispersal status. Finally, we did not detect a net positive or negative effect of dispersal, without clear compensations among breeding decisions. Although our sample was necessarily biased towards successful individuals, these results confirm that the balance between the costs and benefits of dispersal is not fixed. However, the picture is not yet completed and the analyse of two major late breeding decisions that are feeding rate and nest-defence is necessary.

Key words: breeding decisions, pre-hatching, mate influence, trade-offs, patchy population, collared flycatcher, *Ficedula albicollis*

INTRODUCTION

Dispersal is a major process, known to affect many ecological and evolutionary processes (Clobert *et al.* 2001), however consequences in terms of individual fitness remain poorly understood as illustrated by equivocal results from empirical studies (Belichon, Clobert & Massot 1996; Doligez & Pärt 2008). We suggested that this absence of clear pattern between the costs and benefits of dispersal may rely on at least two mutually but non-exclusive hypothesis: the frequent ignorance of the possible (i) occurrence of compensations between fitness components within a breeding event (Julliard, Perret & Blondel 1996) and (ii) the potential impact of mate characteristics on breeding decisions because mate quality and/or attractiveness may influence fitness returns (Harris & Uller 2009).

Because dispersing and philopatric individuals are thought to differ in several phenotypic traits but also in their knowledge of the breeding environment, they may differ in their breeding strategies (Julliard, Perret & Blondel 1996) with different impact of mate characteristics (e.g. age, condition or again dispersal status). In birds, biparental care is considered as the norm (Clutton-Brock 1991) but males and females often exhibited asymmetric roles with the female taking a larger part in early breeding decisions such as laying date, clutch size and incubation (Ketterson & Nolan 1994). In the previous chapter, we investigated early breeding decisions and the link between individuals' dispersal status and mate's characteristics. We found that mate characteristics were often involved in differences between dispersing and philopatric individuals. However, in biparental care species such as the collared flycatcher, after hatching parental care are shared between both sexes. Male parental care is therefore expected to have a strong impact on the fitness output but also on its mate's fitness and we could therefore expect individuals to adjust their breeding decisions according to their mate's characteristics (Alatalo, Lundberg & Ståhlbrandt 1982; Tinbergen & Boerlijst 1990; Bjornstad & Lifjeld 1996; Huk & Winkel 2006). For instance, male removal experiment in the great tit (*Parus major*) demonstrated that the absence of male was

linked to a significant reduced nestlings body mass as well as immune response. In addition the experimental nestlings showed a reduced probability to be found breeding the next year (Snoeijs, Pinxten & Eens 2005). Negative effects of an absence of male parental care is also well known in the context of polygynous mating in which secondary females received little or no help from their mate (Alatalo, Lundberg & Ståhlbrandt 1982; Alatalo & Lundberg 1984; Both 2002).

However, how late breeding decisions may differ from early breeding decisions and according to male and female traits depending on individuals' dispersal status has never been investigated and is poorly understood. This paper is the second part of the investigation of breeding decisions in relation with dispersal. If the first one considered early breeding decisions (i.e. before hatching), here, we investigated late breeding decisions (i.e. after hatching) following dispersal in a wild population of a small migratory passerine bird, the collared flycatcher (*Ficedula albicollis*). We compared hatching success, nestling body mass, fledging success, recruitment and finally male and female body mass between dispersing and non-dispersing individuals while accounting of the partner dispersal status and traits known to affect reproductive success, i.e. age and body condition (Forslund & Pärt 1995; Cichon, Olejniczak & Gustafsson 1998).

MATERIAL AND METHODS

STUDY AREA, STUDY SPECIES AND GENERAL POPULATION MONITORING

The collared flycatcher is a short-lived hole-nesting migratory passerine bird. Our study area is located on the Swedish island of Gotland, Baltic Sea (57°10'N, 18°20'E), where artificial nest-boxes have been regularly distributed in >15 spatially discrete forest plots of varying sizes, allowing an easy access to detailed breeding data of a large number of pairs.

Each year since 1980, the breeding population has been monitored throughout the breeding season. Laying and hatching date, clutch size and number of fledged young have been routinely recorded in all nests during regular visits to

the nest boxes. Adult flycatchers breeding in nest boxes have been trapped, identified with individual aluminium rings, measured (tarsus length to the nearest 0.1 mm and body mass to the nearest 0.1g) and aged based on their previous records in the population or on plumage characteristics when previously unringed (yearlings versus older individuals: Svensson 1992). Most females were caught inside nest boxes, and both parents were subsequently caught while feeding the young whenever possible (i.e. when the brood size survived at least until 5-6 days). As a consequence, by including male characteristics in our approach, we biased the sample size towards the most successful individuals. Old birds arrive earlier on the breeding grounds, lay earlier and larger clutches and fledge more offspring than yearlings (Gustafsson & Pärt 1990; Sendecka, Cichon & Gustafsson 2007). Because age differences strongly decrease after two years of age, we categorized age in two classes; yearlings (i.e. one-year-old) and “old” (≥ 2 -years-old). For details on the breeding ecology of the collared flycatcher, the study area and long-term monitoring of the breeding population, see (Pärt & Gustafsson 1989; Pärt 1990; Wiggins, Pärt & Gustafsson 1994; Wiggins, Pärt & Gustafsson 1994; Doligez *et al.* 1999; Doligez, Gustafsson & Pärt 2009).

LATE BREEDING DECISIONS

The data used in this study were collected between 1980 and 2005. After 12 days of incubation, nests were once again visited regularly (every two days) to determine the date of hatching of the first egg. Here we analysed the probability of hatching for each egg. From six days after hatching, both adults were caught when feeding the chicks whenever possible but females were mostly caught during incubation. A body condition index was computed for all individuals as the ratio of the body mass on tarsus length (i.e. relative mass). Chicks were weighed (to the nearest 0.1g) and measured (i.e. tarsus length to the nearest 0.1mm) 12 days after the hatching date. The number of fledglings was determined as the difference between the number of chicks measured and the number dead chicks found in the nest after fledging. Finally, the number of recruits was estimated based on the

number of fledglings recruited in the breeding population one or to years after fledging.

DISPERSAL STATUS

Dispersal was defined as a change of forest plot between the year of birth and the first breeding event (natal dispersal) or between successive breeding events (breeding dispersal); philopatric individuals returned to the same plot. For the two largest plots, however, we adjusted this definition using dispersal distance, by categorising as dispersers individuals with a dispersal distance of > 700 m within these plots (see Doligez, Gustafsson & Pärt 2009 for a discussion). This binary definition of dispersal status (i.e. dispersing versus philopatric individuals) has been found to be biologically relevant in previous studies on this population (Doncaster *et al.* 1997; Doligez *et al.* 1999; Doligez, Danchin & Clobert 2002; Doligez, Pärt & Danchin 2004). Only adults whose natal or previous breeding site was known were included in the analyses: unringed individuals were discarded because they consisted of a mix of local birds previously missed and true immigrants. Because natal and breeding dispersal are under different selective pressures (Clobert *et al.* 2001), we checked for differences in early breeding decisions depending on dispersal process (natal vs. breeding) by including the dispersal phase as a covariate in the analyses (see below).

STATISTICAL ANALYSIS

We investigated the links between late breeding decisions and dispersal status of both males and females also accounting for age and body condition. Hatching success ($N = 1\,418$) was modelled using generalized linear mixed models with a binomial distribution fitted using the function `glmer` in R package `lme4` (Bates & Maechler 2009; R Core Team 2014). Given that the causes of hatching success could be obscured by clutch size, we used a dependent variable in which the number of hatched eggs was the numerator and the whole number of eggs was the binomial denominator to not lose information about clutch size. The starting model included as fixed effects dispersal status, age and body

condition of both males and females, as well as first-order interactions involving natal dispersal of each parent (i.e. all first order interactions except between age and body condition index). Year and breeding plot were included as random effects to control for non-independence of breeding events in the same year and or/ plot due to environment variability. Male and female individual ring numbers were also included as random factor because many individuals may appear several times in the dataset (e.g. for hatching probability, 482 individuals present at least twice over a total of 2 217 individuals). We do not detail random effects because they are not of primary interest here; however they were kept in the final models. We backward removed non-significant terms starting with interactions using maximum likelihood ratio test and the approximate χ distribution of the test statistic.

Fledging success cannot be assessed using a normal distribution because it includes too many zeros corresponding to total failure. We therefore separated fledging success into two components: (i) the probability of fledging at least one chick (total failure rate), analysed using generalized linear mixed model using a binomial error ($N = 1\ 852$) and (ii) the number of fledgling, for nests with at least one fledgling ($N = 1\ 688$), which was implemented using a normal error.

Because the number of recruits ($N = 2\ 033$) showed a high number of zero values (i.e. a high number of individuals producing no recruits), we fitted a negative binomial model for this response variable (McCullagh 1984; Bolker 2008). Fledging success and recruitment were analysed using the same starting model than in hatching success analysis.

Finally, body masses were analysed using linear mixed models with a normal error. Starting models for nestlings ($N = 5\ 783$) were again the same than in hatching success and included both male and female dispersal status, age and condition plus nestling tarsus length to account for differences in body mass due to structural size. To account for the non-independence in nestling body mass from a same nest, we nested the nest-box number into breeding plot as a random factor but included also year and both male and female individual ring number. Starting models to analyse male ($N = 1\ 829$) and female ($N = 1\ 188$) body

condition included male and female dispersal status and age, female and male body condition and male and female tarsus length respectively. We added also chicks' age when parents were caught to account for increasing energetic demands across nestlings feeding. Random factors included in models to investigate male and female body mass remained unchanged (i.e. year, breeding plot, male and female individual ring numbers).

RESULTS

HATCHING SUCCESS

The probability of hatching differed according to the interaction between male dispersal status and whether dispersal fall under natal or breeding dispersal ($N = 1418$, $\chi^2_1 = 4.96$, $P = 0.026$, **Fig. 5.1**). Breeding philopatric males showed a higher hatching success than breeding dispersing males (estimate \pm SE: 0.53 ± 0.29 , $\chi^2_1 = 3.45$, $P = 0.063$) however, natal dispersing and philopatric males did not differ in hatching success. The difference in hatching success in nests with natal and breeding dispersing males did not rely on differences in laying date or in clutch size and was even more pronounced when laying date and clutch size were included in the final model ($\chi^2_1 = 5.15$, $P = 0.023$).

CHICKS BODY MASS

The status of both the male and the female affected chicks body mass at day 12 but always in interaction with mate dispersal status ($\chi^2_1 = 5.73$, $P = 0.017$; **Fig. 5.2A**) or age ($\chi^2_1 = 11.73$, $P < 0.001$; **Fig. 5.2b**; **Table 5.1B**). In pairs with dispersing females, chicks tended to be heavier when the male was also dispersing while the reverse pattern was observed in pairs with philopatric females (**Fig. 5.2A**). On the other side, in pairs with old male, chicks' body mass did not vary between philopatric and dispersing mothers while in pairs with yearling males, philopatric females tended to produce heavier chicks than dispersing females

(**Fig. 5.2B**). Finally, chicks body mass increased with both male and female body condition index (**Table 5.1b**). Again, differences were not due to differences in laying date or clutch size (interaction between male and female dispersal status: $\chi^2_1 = 7.29$, $P = 0.007$; interaction between female dispersal status and male age: $\chi^2_1 = 14.60$, $P < 0.001$).

FLEDGING SUCCES AND RECRUITMENT

The probability of fledging at least one chick did not differ between dispersing and non-dispersing individuals, alone or in interaction with other traits (all interactions with dispersal status; $\chi^2_1 < 3.38$, $P > 0.07$), but it was affected by female age (**Table 5.1c**).

The number of fledglings differs between nests with dispersing and philopatric males according to male body condition index ($\chi^2_1 = 6.14$, $P = 0.013$, **Fig. 5.3**). In pairs with low body condition index males (i.e. inferior to the mean body condition index value), the number of fledglings was lower in pairs with philopatric males than in pairs with dispersing males (estimate \pm SE: -0.35 ± 0.13 , $\chi^2_1 = 7.78$, $P = 0.005$). However, in pairs with high body condition index males (i.e. superior to the mean body condition index value), the number of fledglings did not differ between pairs with dispersing and philopatric male ($\chi^2_1 = 0.39$, $P = 0.53$). The number of fledglings also differed according to male and female age (**Table 5.1d**) and all of these differences remained even when controlling for laying date and clutch size (interaction between male dispersal status and body condition: $\chi^2_1 = 4.46$, $P = 0.034$).

Finally, the number of recruits did not differ between philopatric and dispersing individuals, alone or in interaction with other traits (all interactions involving dispersal status: $\chi^2_1 < 3.44$, $P > 0.06$). Still, the number of recruits tended to differ according to male dispersal status and female age ($\chi^2_1 = 3.44$, $P = 0.063$, **Fig. 5.4**). Indeed, in pairs with young females, the number of recruits tended to be lower when the male was philopatric (estimate \pm SE: -0.27 ± 0.16 , $\chi^2_1 = 2.70$, $P = 0.10$).

MALE AND FEMALE BODY MASS DURING NESTLINGS FEEDING

Male body mass when feeding the nestlings differed between dispersing and philopatric individual according to their age ($\chi^2_1 = 5.31$, $P = 0.021$, **Fig. 5.5A**). In older males, philopatric individuals were heavier than dispersing males (estimate \pm SE: 0.17 ± 0.04 , $\chi^2_1 = 14.60$, $P < 0.001$, **Fig. 5.5A**) while yearlings did not differ according to dispersal status ($\chi^2_1 = 0.67$, $P = 0.41$). Importantly, this effect did not depend upon laying date or clutch size as the interaction remained significant when both variables were included in the final model ($\chi^2_1 = 4.95$, $P = 0.026$).

Female body mass tended to differ according to male dispersal status and dispersal process ($\chi^2_1 = 3.45$, $P = 0.063$, **Fig 5.5B**). In pairs with males in their first breeding event, females mated with philopatric tended to be lighter than females mated with dispersing males (estimate \pm SE: -0.12 ± 0.08 , $\chi^2_1 = 2.54$, $P = 0.11$) while no difference was observed between females mated with dispersing or philopatric males that were not in their first breeding event (i.e. breeding dispersal process, $\chi^2_1 = 0.50$, $P = 0.48$).

Overall, both male and female body mass increased with tarsus length, mate body condition and decreased while chicks' age increased (**Table 5.1f and g**). Female body mass also differed between yearling and older females (**Table 5.1g**).

DISCUSSION

This study is the second part of an investigation of fitness differences in breeding decisions in relation with individuals' dispersal status and mates characteristics in a natural patchy population of collared flycatchers. As in the previous chapter, we investigated possible compensations between reproductive traits within breeding events and analysed a set of seven late breeding decisions regarding hatching success, parental care, fledgling success, recruitment and finally

male and female reserves (male and female body mass when feeding the nestlings) by accounting for both males and females characteristics.

Our results revealed that six over seven of these breeding decisions differed between dispersing and philopatric individuals, therefore indicating a more pronounced difference according to dispersal status than in early breeding decisions. Indeed, we found that every late breeding decisions investigated with the exception of the probability to fledge at least one chick differed or tended to differ between dispersing and philopatric individuals. However again, the effect of dispersal only depended on interaction with individuals or mates' phenotypic traits and confirmed condition- and phenotype-dependent effects of dispersal already found in the previous chapter (Clobert *et al.* 2009). Overall, we did not detect any positive or negative effect of being a disperser. Indeed, we found as much situations in which dispersal was positively associated with breeding decision as situations in which it was negatively correlated to breeding decision. For instance, consistently with our result on clutch size, we found that the number of fledglings differed according to male dispersal status and male body condition. Surprisingly, in pairs with low condition males, dispersing males fledged more young than philopatric males. Moreover, low condition dispersing males also fledged more young than pairs with high philopatric and dispersing males indicating thus that dispersing males with a low body condition index performed better concerning both the number of eggs and the number of fledglings. On the other side, we also found that nestlings body mass was lower for dispersing than for philopatric females mated with yearlings males.

Importantly, we did not detect direct compensations between breeding decisions. However it seems that dispersing and philopatric males and females may adopt different life-history strategies, as predicted by the classic sex-biased dispersal theory (Greenwood & Harvey 1982). For instance, we found that dispersing females mated with old males raised as heavy chicks as philopatric females. However, when mated with young males, chicks of philopatric females were heavier than chicks of dispersing females. On the other side, in yearlings, dispersing and philopatric males were found as heavy as each other. However, old

philopatric males were heavier than old dispersing males. In females, it seems therefore that costs of dispersal may be buffered by male age, which may be correlated with increased reproductive success (Forslund & Pärt 1995). Yet males did not seem to adopt the same strategy as natal dispersing males tended to be heavier than natal philopatric and breeding dispersing and philopatric males, suggesting maybe that heavier males may be more susceptible to overcome dispersal costs and therefore to access to reproduction.

Overall, our detailed investigation of seven late breeding decisions in complement of the investigation of the six early breeding decisions showed that dispersing and philopatric individuals differed more in late than in early breeding decisions. This difference may rely in the fact that the nestling phase is known as the more demanding phase in terms of parental effort, which may emphasize differences between dispersing and philopatric individuals. To date, we did not detect simple compensations between decisions. However, we did yet not investigate some major late breeding decisions such as male and female feeding rate or nest defence but as data will be soon available, I plan to compare both decisions using the same approach.

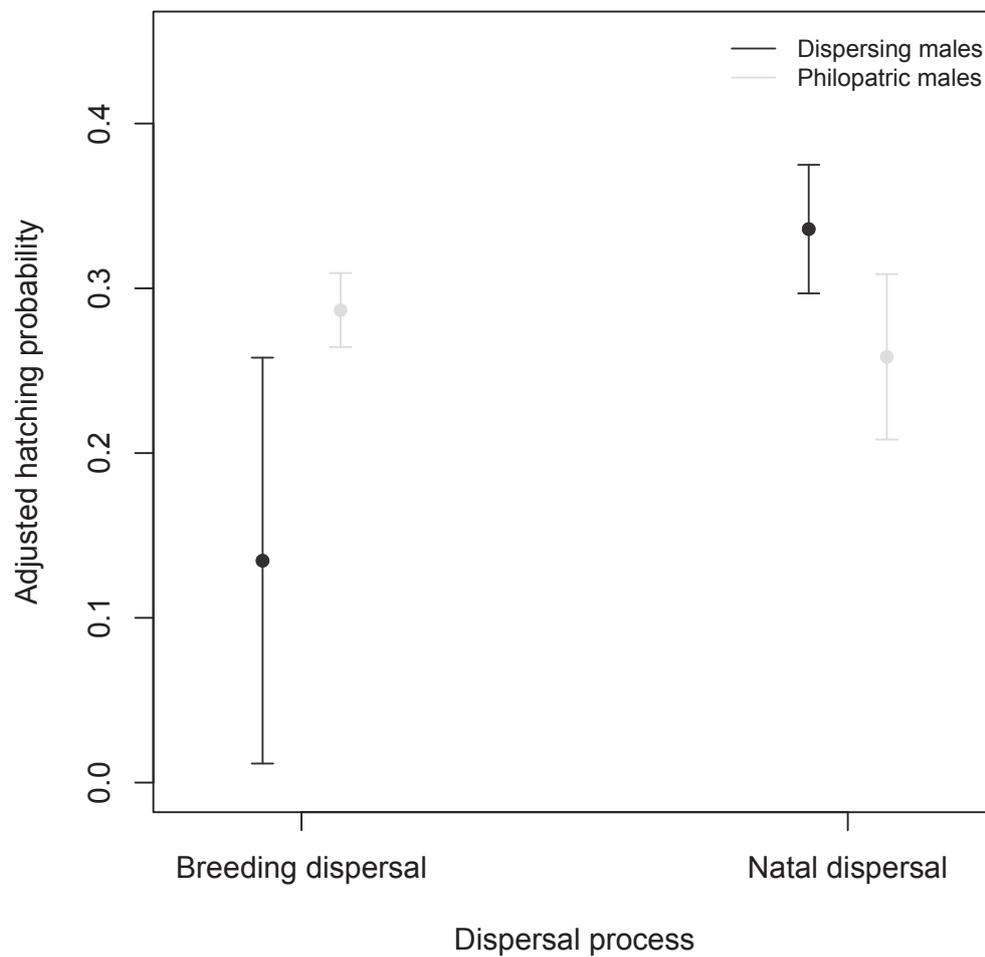


Figure 5.1: Hatching probability according to male dispersal status and dispersal process (i.e. natal or breeding dispersal). The figure shows mean value (± 1 SE) adjusted for other significant effects in the model (i.e. residuals from the final model without the interaction between male dispersal status and the corresponding body condition).

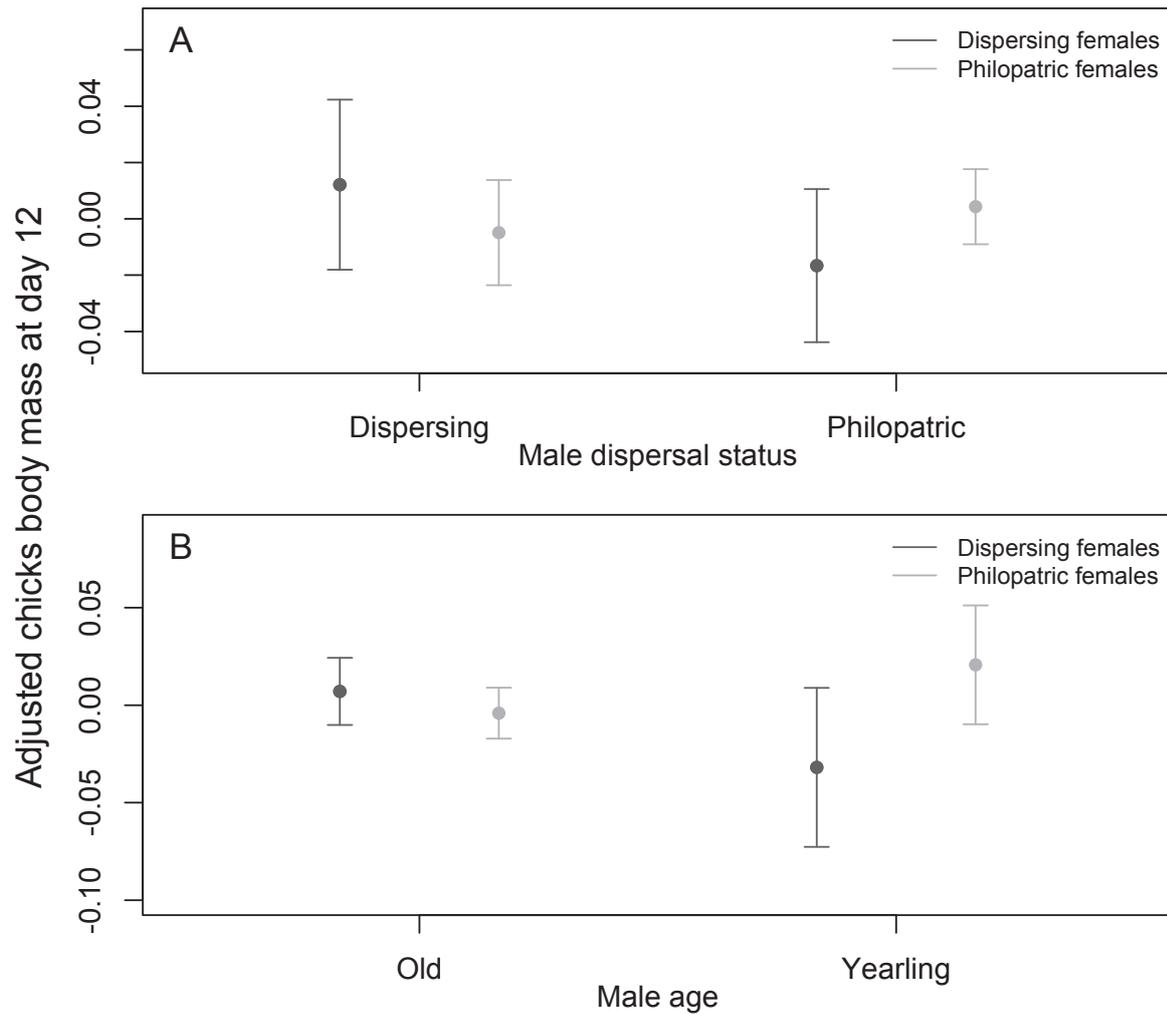


Figure 5.2: Chicks body mass according to female dispersal status and (A) male dispersal status and (B) male age. The figure shows mean values (± 1 SE) adjusted for other significant effects in the model (i.e. residuals from the final model without the interaction between male dispersal status and the corresponding male age).

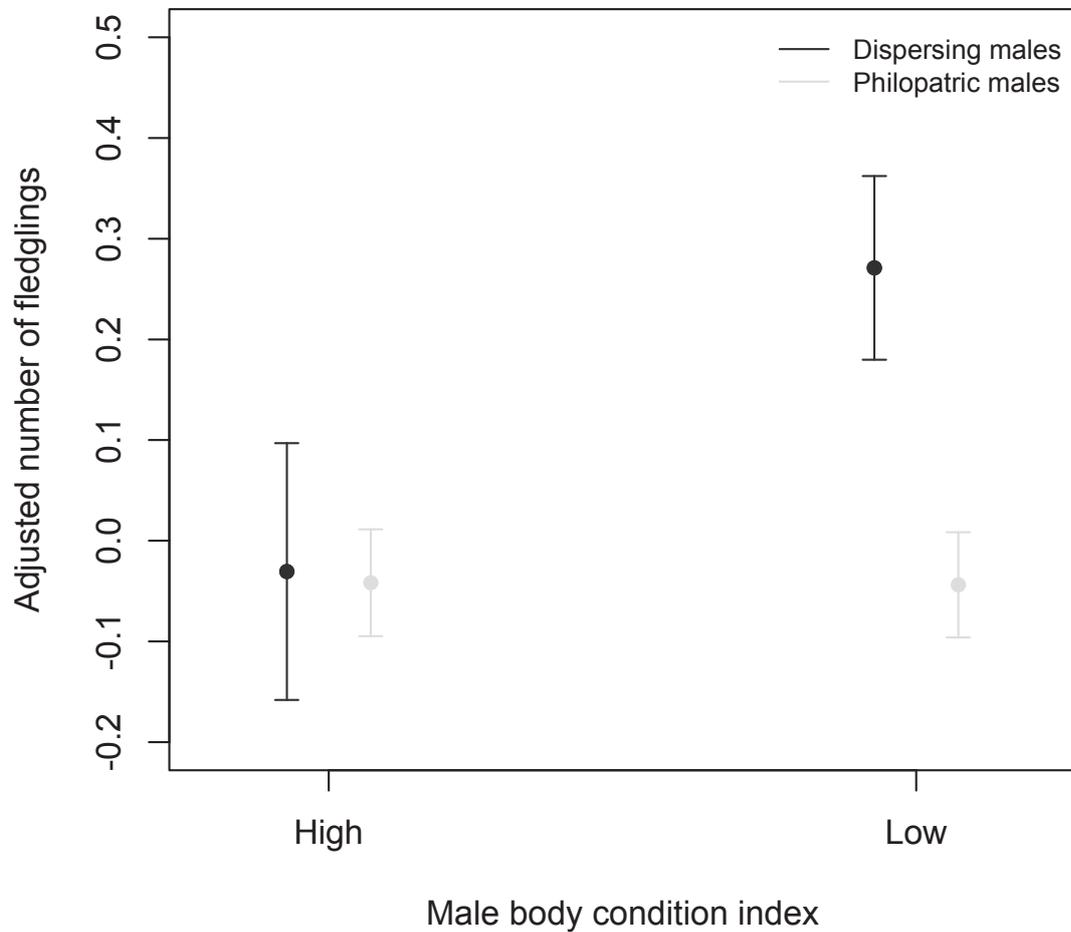


Figure 5.3: Number of fledglings according to male dispersal status male body condition index. The figure shows mean value (± 1 SE) adjusted for other significant effects in the model (i.e. residuals from the final model without the interaction between male dispersal status and the corresponding body condition). Low and high values of male body condition index have been determined relatively to the mean value of male body condition index. The low category encompasses males with body condition index value inferior to the mean, while high category encompasses males with a higher body condition index value compared to the mean.

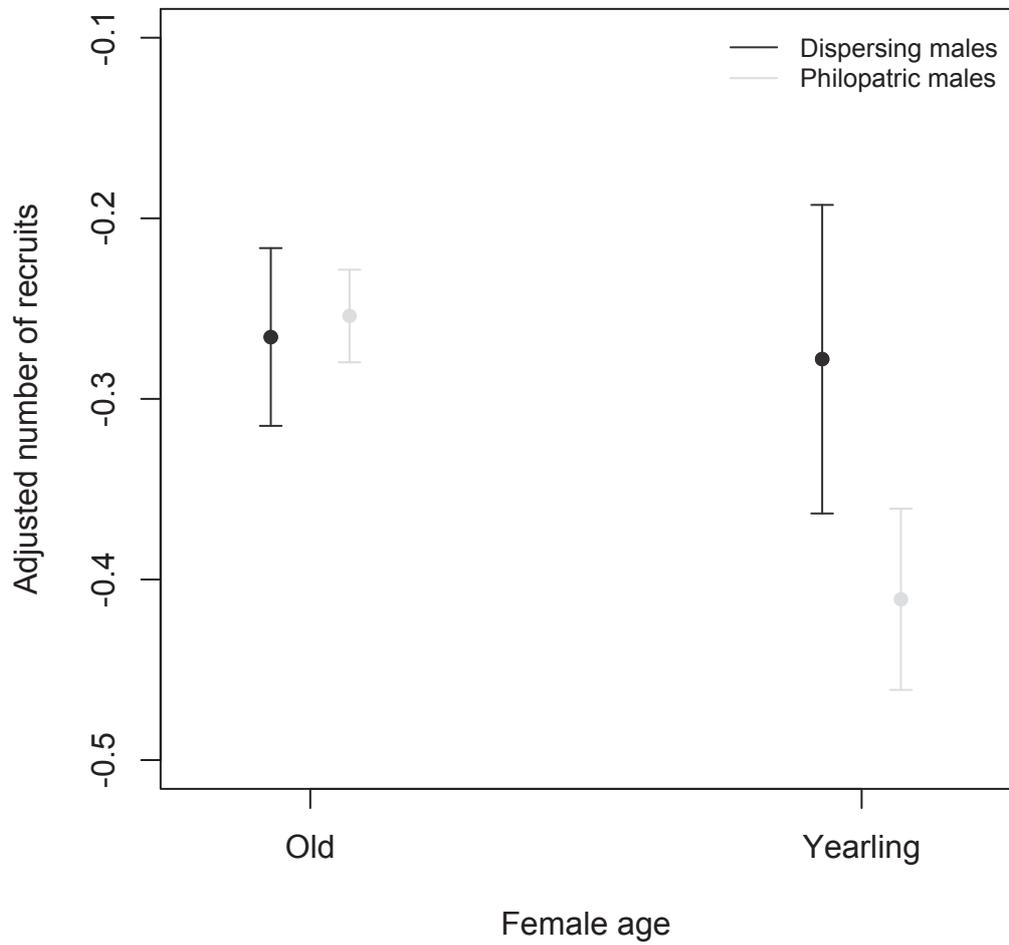


Figure 5.4: Number of recruits according to male dispersal status and female age. The figure shows mean values (± 1 SE) adjusted for significant effects in the model (i.e. residuals from the final model without the interaction between male dispersal status and the corresponding male age).

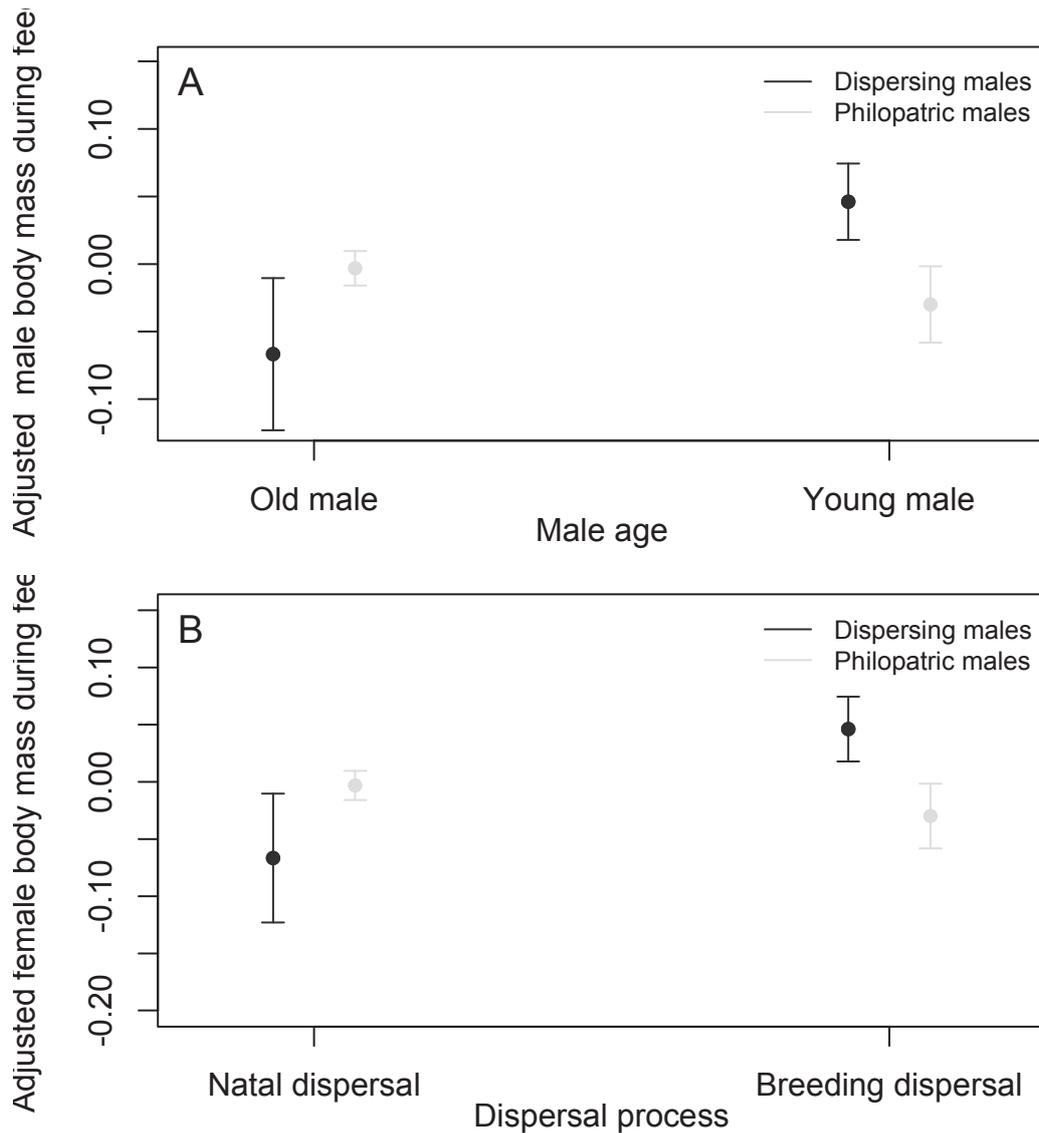


Figure 5.5: (A) Male body mass according to male dispersal status and age, and (B) female body mass according to male dispersal status and dispersal process (i.e. natal or breeding dispersal). The figure shows mean values (± 1 SE) adjusted for other significant effects in the model (i.e. residuals from the final model without the interaction between (A) male dispersal status and the corresponding male age and (B) male dispersal status and dispersal process).

Table 5.1: Effect of dispersal status (dispersing vs. philopatric individuals) on late breeding decisions. X^2 and P-values refer to the LRT test. In all cases, $df = 1$. Significant effects in the final models are shown in bold (first part).

Variable	Estimate \pm SE	Chisq	P
(a) Hatching success (N = 1418)			
Male dispersal status*dispersal process	0.53 \pm 0.29	4.96	0.026
Male dispersal status	0.46 \pm 0.28	2.70	0.10
Dispersal process	0.66 \pm 0.30	4.84	0.028
(b) Chicks body mass (N = 5783)			
Female dispersal status*male dispersal status	0.38 \pm 0.16	11.73	< 0.001
Female dispersal status*male age	0.61 \pm 0.18	5.73	0.017
Chicks tars length	1.03 \pm 0.023	1946.96	< 0.001
Male dispersal status	-0.17 \pm 0.12	2.03	0.15
Female dispersal status	-0.34 \pm 0.15	4.89	0.027
Male age	-0.37 \pm 0.14	6.91	0.008
Male body condition index	2.45 \pm 0.64	11.35	< 0.001
Female body condition index	4.88 \pm 1.44	11.43	< 0.001
(c) Fledging probability (N = 1852)			
Female age	-0.51 \pm 0.20	6.74	0.009
(d) Number of fledglings among successful individuals (N = 1688)			
Male dispersal status*Male body condition index	4.67 \pm 1.89	6.14	0.013
Male age	-0.25 \pm 0.11	5.23	0.022
Female age	-0.24 \pm 0.09	6.41	0.011
Male dispersal status	-0.25 \pm 0.10	6.03	0.014
Male body condition index	-4.31 \pm 1.70	6.44	0.011

Table 5.1: Second part.

Variable	Estimate \pm SE	Chisq	P
(e) Number of recruits (N = 2033)			
Female age	-0.18 \pm 0.08	5.53	0.018
(f) Male body mass during feeding (N = 1829)			
Male dispersal status*male age	-0.18 \pm 0.08	5.31	0.021
Male tarsus length	0.38 \pm 0.03	180.45	< 0.001
Female body condition index	2.80 \pm 0.62	20.59	< 0.001
Chicks' age at capture	-0.05 \pm 0.005	72.43	< 0.001
Male dispersal status	0.15 \pm 0.44	12.56	< 0.001
Male age	-0.05 \pm 0.06	0.71	0.40
(g) Female body mass during feeding (N = 1188)			
Female tarsus length	0.47 \pm 0.04	131.16	< 0.001
Female age	-0.17 \pm 0.05	11.81	< 0.001
Male body condition index	2.28 \pm 0.42	29.35	< 0.001
Chicks' age at capture	-0.09 \pm 0.008	134.83	< 0.001

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Chapter 6

Assessing the costs of dispersal: an experimental approach in a wild passerine bird population

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Abstract

Dispersal is widely recognized as a key life history trait impacting many ecological and evolutionary processes. Yet, the fitness consequences of dispersal remain poorly understood, in particular because most empirical studies are correlative and therefore do not allow discriminating direct effects of dispersal *vs.* other processes to which dispersal may be correlated. Using an experimental translocation performed on more than 600 individuals in a patchy population of a small migratory bird, the collared flycatcher *Ficedula albicollis*, we investigated behavioural responses to forced movement in terms of settlement in the study area and subsequent breeding decisions, accounting for the dispersal status of the individual before the translocation. Newly arrived birds of different sex, age and dispersal status were either experimentally translocated between woodlands within the study area or released in the patch of capture. We subsequently recorded and analysed (i) the probability of being subsequently caught in the study area (i.e. to settle as a breeder), (ii) the probability of accepting the displacement rather than returning to the area of capture for displaced birds and (iii) major breeding variables (laying date, clutch size, incubation length, probability to fledge young and number and condition of fledglings) according to sex, age and experimental categories. The probability of settling in the study area after the experimental treatment was lower for displaced individuals as well as for immigrants, suggesting either long-distance dispersal movements or non-breeding post-release, which could reflect costs of unfamiliarity. On the contrary, philopatric individuals were more likely to return to their patch of capture, supporting the idea of benefits of prior knowledge about the local breeding habitat. However, once settled, individuals from different experimental groups differed in none of the breeding variables measured, suggesting that once the decision to settle and breed is made, individuals are able to deal with local environmental conditions to adjust their breeding decisions. Overall, these results show that, on top of the costs of dispersal movements often found during transience, dispersal may also entail costs linked to settlement in a new habitat, which only some individuals may overcome.

Key words: translocation experiment, dispersal, cost, familiarity, collared flycatcher, settlement, breeding decisions

INTRODUCTION

Dispersal is commonly defined as the movement of an individual from its natal or previous breeding site to a new breeding site (Greenwood & Harvey 1982). Dispersal results in individual and gene flow, both within and between populations. As a consequence, dispersal influences processes as diverse as species distribution and range expansion, population dynamics and genetics, and community structure (Clobert *et al.* 2001; Kokko & Lopez-Sepulcre 2006; Clobert *et al.* 2012) and is therefore widely recognized as a key life history trait. Yet the consequences of dispersal remains poorly known (Ronce 2007), although such consequences largely depend on the success of dispersing individuals in terms of individual fitness (Belichon, Clobert & Massot 1996; Doligez & Part 2008), and therefore on the costs of dispersal. Dispersal can involve immediate and deferred costs on different individual fitness components during departure, transience and settlement (Bonte *et al.* 2012). Dispersal is often assumed to entail a survival cost during the transience phase (Baker & Rao 2004; Soulsbury *et al.* 2008). However, the effect of dispersal on subsequent reproductive success in the new habitat is less straightforward because it is likely to vary depending on the balance between multiple possible costs and benefits (Johnson & Gaines 1990; Belichon, Clobert & Massot 1996; Lemel *et al.* 1997). Suggested costs of dispersal include travelling and search costs, for example in terms of energy and time searching for a suitable breeding habitat or territory (Pärt 1995; Stamps, Krishnan & Reid 2005), predation risks (Yoder, Marschall & Swanson 2004), but also unfamiliarity with the new breeding habitat and lack of adaptation to local conditions leading to suboptimal decision-making in mate and site choice (Pärt 1994; Marr, Keller & Arcese 2002; Brown, Brown & Brazeal 2008).

So far, most studies aiming at investigating fitness consequences of dispersal have used direct comparisons of fitness estimates between dispersing and non-dispersing (philopatric) individuals (see Belichon, Clobert & Massot 1996; Doligez & Part 2008 for reviews). However, this correlative approach does not allow discriminating a causal link between dispersal and subsequent individual fitness from a correlation between dispersal and fitness estimates, on the one hand, and a third variable (e.g. phenotypic quality), on the other hand. Yet, empirical evidence for associations between dispersal and other phenotypic traits that may affect fitness is accumulating (Dingemanse *et al.* 2003; Snoeijs

et al. 2004; Duckworth & Badyaev 2007; review in Clobert *et al.* 2009), and these associations may be favoured by natural selection leading to genetic correlations at the population level (Fairbairn & Roff 1990; Korsten *et al.* 2013). The confusion between correlates and consequences of dispersal in previous studies has already been emphasized (Greenwood, Harvey & Perrins 1979; Clobert *et al.* 1988), but is still frequently ignored. Experimental manipulations of dispersal are needed to test the causality of relations between dispersal and fitness-related traits. However, experimental approaches to the fitness consequences of dispersal are often difficult to implement in wild populations and therefore remain rare. To date, most of these experiments consisted of translocating individuals, i.e. imposing a forced dispersal event to individuals by displacing them from one site to another. Translocation therefore mimics a dispersal movement to a new habitat independently from the individual's natural motivation to disperse. Most translocations have been performed in the context of conservation studies, in an attempt to establish new populations of endangered species (see Fischer & Lindenmayer 2000; Seddon, Armstrong & Maloney 2007 for a review), increase the size of small and declining populations (Griffith *et al.* 1989; Fisher, Lambin & Yletyinen 2009) and/or “rescue” inbred populations by introducing new alleles (Madsen *et al.* 1999).

However, the success of translocation programs strongly depends on whether displaced individuals settle and thrive in the new, unfamiliar habitat (Stamps & Swaisgood 2007). Overall, individuals translocated for conservation/restoration purposes usually suffered from a low survival rate (Beck *et al.* 1991), and thus most studies monitoring translocated individuals mainly focused on the factors harming survival (Calvete & Estrada 2004; Drees *et al.* 2009; Fisher, Lambin & Yletyinen 2009). Although these studies provided insights on some immediate costs that may prevent settlement (e.g. predation risk), they ignored most settlement and post-settlement costs (i.e. deferred costs; Pärt 1995; Pierre 2003; Stamps, Krishnan & Reid 2005). To date, only very few experimental studies allow investigating potential fitness costs associated with settlement in a non-familiar environment, by monitoring the breeding activity of displaced individuals (Burgess, Treml & Marshall 2012; Burger *et al.* 2013).

Furthermore, dispersal costs, are likely to depend on individuals' phenotype, such as personality traits (e.g. Dingemanse *et al.* 2003) or previous dispersal history (e.g.

Doligez *et al.* 2012). Therefore, the success of experimentally translocated individuals should be analysed in the light of their phenotype, which is rarely the case except for age and sex differences (e.g. Pierre 1999). To test for differential settlement behaviour and subsequent fitness estimates according to individuals' phenotype, and in particular previous dispersal status, translocation experiments need to be followed by the monitoring of breeding activity of forced dispersers (Burger *et al.* 2013). Such experiments can then allow investigating the behavioural changes induced by a novel environment (e.g. Doligez *et al.* 2012) and comparing costs of returning to original habitat (Cowan 2001) in particular depending on previous dispersal status.

We performed a translocation experiment during four years in a patchy population of a small hole-nesting migratory passerine, the collared flycatcher (*Ficedula albicollis*), to investigate behavioural responses to forced dispersal. Newly arrived birds from winter quarters were either displaced, i.e. released in a new patch within the study area (displaced group), or released in the patch of capture (control group; Pärt 1995). We subsequently recorded pre-breeding decisions (probability of settlement as a breeder and, for displaced birds, to return to the area of capture) and, for individuals that settled, the main measures of breeding success (laying date, clutch size, incubation length, probability to fledge young and number and condition of young), to investigate possible fitness consequences of forced movement. We tested whether these responses vary between experimental groups in relation to age, sex and previous dispersal status. Importantly, contrary to translocation experiments performed in a conservation context to establish new populations or rescue populations in deteriorated landscapes, we moved individuals within suitable and already occupied habitats, which may have strong implications for individual settlement. If familiarity with the habitat is advantageous, we could expect displaced individuals to be less likely to settle and breed successfully, and philopatric individuals to be more prone to return and settle in their patch of capture.

MATERIAL AND METHODS

Study species, study site, population monitoring and dispersal status

The collared flycatcher is a short-lived hole-nesting migratory passerine bird. The experiment was performed in 1989-1990 and 2012-2013 in a patchy population breeding on the island of Gotland, Southern Baltic, Sweden (57°10'N, 18°20'E), which has been monitored since 1980. In the study population, artificial nest boxes have been regularly distributed in discrete woodland patches of varying size, over a distance of approx. 15 km maximum (Pärt & Gustafsson 1989). Each year, nest boxes are visited regularly throughout the season, allowing us to record the main breeding variables. All adult birds caught are identified individually with aluminum rings, aged (based on their previous records in the population or plumage characteristics when previously unringed; Svensson 1992), weighed and measured. Young are ringed, weighed and measured a few days before fledging. The long-term monitoring of the population allows us to determine the successive breeding events of individuals over their life.

Dispersal was defined as a change of patch between the year of birth and of first breeding (natal dispersal) or between consecutive breeding events (breeding dispersal) (Doligez, Gustafsson & Pärt 2009). This binary definition of dispersal (*i.e.* dispersing vs. philopatric individuals) has been found to be biologically relevant in previous studies on this population (Doncaster *et al.* 1997; Doligez *et al.* 1999; Doligez *et al.* 2003; Doligez, Pärt & Danchin 2004). Here, we defined dispersal status of experimental individuals based on the patch of early capture (see below). Immigrants, *i.e.* unringed individuals, whose previous breeding or natal site was thus unknown (about 40% of individuals each year), were included in the analysis but were kept distinct from dispersing individuals because they consisted of a mix of local birds previously missed and true, potentially long-distance, immigrants.

Translocation experiment and subsequent individual settlement decisions

Upon arrival from winter quarters, males choose a breeding territory and defend it to attract a female. During breeding site choice, both sexes frequently visit nest boxes, where they can be caught using swing-door traps. In springs 1989, 1990, 2012 and 2013,

respectively four (1989 and 1990), height and again four experimental patches were thoroughly searched during at least 7h each day from late April until early June for locating newly arrived males and females and attempting to catch them on the same or the next day(s), between 0600 and 1500 hours (Swedish summer time). Among birds of a given age and sex category caught on a given day, we randomly attributed the experimental treatment, i.e. released in a different patch than the patch of capture ('displaced birds', N = 152 females and 357 males) or within the same patch (controls, N = 51 females and 97 males). As high return rates to the patch of capture are expected among displaced birds, we biased the sample towards displaced birds compared to controls.

In 1989 and 1990, control individuals were either released immediately after capture or 2-3 hours later, to control for the time delay of displacing birds ('time controls'). The subsequent probability of breeding in the patch of capture did not differ between controls and time controls (see Pärt 1995 for further details). Consequently, in 2012 and 2013, control individuals were systematically released 2-3h after capture, and all controls were pooled in one group. We displaced and released the same number of individuals in each patch to avoid modifying local patch density, a factor known to strongly affect individual dispersal decisions (Clobert *et al.* 2012). While complying with this constraint, displaced individuals were swapped between patches so as to maximize translocation distance and thereby minimize the probability that individuals return to their patch of capture. This distance, however, never affected return rate ($\chi^2_1 = 0.01$, $P = 0.92$) and will be not considered later.

Population monitoring during the breeding season allowed us to determine whether experimental individuals subsequently settled to breed in the study area and, if yes, in which patch. Experimental individuals that were not caught as breeders later on in the whole study area were considered "disappeared" (N = 266 out of 656, i.e. 40.5 %). Among experimentally displaced individuals later caught as breeders, we determined whether displaced individuals returned or not to their patch of capture to breed. Because not all individuals could be caught upon their arrival or on the next days (mean delay to laying \pm SE: 9.28 ± 0.26), we discarded from the analyses individuals caught less than four days before the laying date of the nest where they were subsequently caught as breeders (N= 30 out of 391). This time interval is supposed to correspond to the

minimum estimated time required for nest building because all displaced individuals that accepted the forced dispersal had an interval of at least four days. Thus we assumed that individuals caught less than four days before laying had already chosen their site and possibly started nest building, which should strongly affect their response to forced dispersal and in particular the probability to return to their previous site. The results however remained qualitatively unchanged when this time interval was either increased or decreased (0, 2 and 6 days, results not detailed).

Breeding decisions

During the egg-laying period, nest-boxes were visited regularly (at least every third day) as part of the general population monitoring to determine laying date. Clutch size was recorded after the start of incubation. Incubation length was calculated as follows: laying date – observed hatching date – clutch size + 2, because the female generally start incubating on the day of laying the last egg. Nests were checked for the presence of hatchlings from the 12th day of incubation to determine hatching date. Nestlings were weighed and their tarsus was measured when 12 days old. Finally, the number of fledged young was determined by counted dead nestlings remained in nest boxes after fledging. Regarding parents, females breeding in nest boxes were caught first during incubation and then both parents were caught in their box using swing-door traps when feeding young aged 5 to 12 days. Thus, males could not be caught at nests where the female deserted at incubation or where nestlings died early. Upon capture all adults were weighted (to the nearest 0.1 g) and measured (tarsus length to the nearest 0.1 mm).

Statistical analysis

We first investigated whether pre-breeding decisions differed between individuals depending on their experimental treatment, their original dispersal status, and their sex and age class (yearling *vs.* older individuals). In particular, we (*i*) compared the probability to settle as a breeder in the study population after the manipulation between displaced and control individuals depending on original dispersal status and, (*ii*) for displaced individuals, we compared the probability to return to the patch of capture between immigrants, dispersing and philopatric individuals. In both comparisons, we accounted

for sex and age, which have previously been found to affect fitness and dispersal decisions (Forslund & Pärt 1995; Pärt 1995). We analysed these probabilities using generalized linear mixed models with a binomial distribution with a logit link function in R 3.0.3 (R Core Team 2014). The starting model included as explanatory variables the individual's original dispersal status (i.e. philopatric, dispersing or immigrant individual), its date of capture (i.e. philopatric, dispersing or immigrant individual; Pärt 1995), sex and age, and, for the probability to settle as a breeder post-experiment, the individual's experimental treatment (i.e. displaced or control), as well as all pairwise interactions between treatment and original dispersal status, on the one hand, and other variables, on the other hand. The patch of release and year were included as random effects. We do not subsequently detail random effects because they are not of primary interest here, however, they were kept in all final models. We used a backward selection procedure to remove non-significant terms starting with interactions using maximum likelihood ratio test and the approximate χ distribution of the test statistic known to be relevant in large sample size as this one (Pinheiro & Bates 2000). To test for possible differences in body mass and therefore condition according to experimental treatment, we investigated whether body mass at early capture differed between individuals that later settled and those that disappeared, and, among displaced individuals, between individuals that returned to their capture patch and those that accepted the forced dispersal. All analyses of body mass accounted for tarsus length to control for differences due to structural size. We used linear mixed models with a normal error structure and identity link function based on the modified F test of Kenward and Roger (1997), known to produce a more accurate estimation of the F distribution when sample sizes are strongly unbalanced (Kenward & Roger 1997), as was the case here. Body mass data were available for 2012 and 2013 only, explaining the lower sample sizes for these analyses. Importantly, body mass did not differ between displaced and controls ($N = 302$, $F_{1,289} = 0.99$, $P = 0.32$). Furthermore, body mass at early capture was not found as significant to explain the probability to settle as a breeder in the study population ($\chi^2_1 = 0.0002$, $P = 0.98$) nor among displaced individuals to explain return rate to the patch of capture ($\chi^2_1 = 0.37$, $P = 0.54$) and were consequently non-included in starting models when considering these response variables.

To test whether breeding decisions differed between experimental individuals that were found as breeders in the study area after the manipulation, we compared a set of breeding variables between individuals of different treatments, but also, non-experimental individuals (i.e. unmanipulated breeders). We analysed laying date, clutch size, incubation length, probability of success (i.e. fledging at least one young) and number and condition (i.e. body mass at day 12) of fledglings. Continuous variables (laying date, clutch size, incubation length, chick body mass and number of fledglings among successful nests) were analysed using linear mixed models. The probability of success was analysed using a generalized linear mixed model with a binomial error. The starting model included as explanatory variables the individual's treatment (i.e. non-experimental, control, displaced and returned to the patch of capture, displaced and settled elsewhere after movement), its original dispersal status, and sex and age, as well as all pairwise interactions between individuals's treatment and each variable. The patch of breeding, year and individual ring number were included as random effects. Non-experimental individuals were included in all analyses except chick body mass because data were not yet available for year 2013. Again, we used a backward selection procedure to remove non-significant terms using here F-tests for continuous variables (linear models) and maximum likelihood ratio tests for the probability of success (generalized linear model). Importantly, none of the starting models were over-parameterized for any of the response variable ($N > 3k$ for every response variable), thus the risk of inflated error I should not be an issue in our study (Forstmeier & Schielzeth 2011).

RESULTS

Probability to settle in the study area and to return to the patch of capture

The probability for experimental individuals to be caught later as breeders in the study area differed between displaced and control individuals ($N = 623$, $\chi^2_1 = 4.09$, $P = 0.043$, **Fig. 6.1a**) and according to original dispersal status ($\chi^2_2 = 15.01$, $P < 0.001$, **Fig. 6.1b**). Displaced individuals and immigrants were significantly less likely to be caught again as breeders than control individuals (**Fig 6.1a**) and philopatric and dispersing

individuals, respectively (post-hoc test: immigrants vs. other individuals: $\chi^2_1 = 13.57$, $P < 0.001$; **Fig. 6.1b**). The difference between immigrants and other individuals did not depend on experimental treatment (interaction treatment by original dispersal status: $\chi^2_2 = 0.07$, $P = 0.96$). Besides the effects of treatment and original dispersal status, individuals captured late, females and older individuals were more likely to be caught again as breeders compared to individuals captured early ($\chi^2_1 = 7.67$, $P = 0.005$, estimate \pm SE: 0.028 ± 0.010), males ($\chi^2_1 = 8.67$, $P = 0.003$, estimate \pm SE: -0.61 ± 0.21) and yearlings ($\chi^2_1 = 11.12$, $P < 0.001$, estimate \pm SE: -0.64 ± 0.19), respectively (no significant interaction with treatment and dispersal status; all chi2 values < 3.03 and all p-values > 0.96).

Among displaced individuals, philopatric were more likely to return to their patch of capture than dispersers and immigrants ($N = 265$, $\chi^2_2 = 7.92$, $P = 0.02$, **Fig. 6.2**). This effect was observed while accounting for a lower probability to return to the patch of capture for yearlings individuals compared to older individuals ($\chi^2_1 = 13.97$, $P < 0.001$, estimate \pm SE: -1.23 ± 0.33) and for males compared to females ($\chi^2_1 = 12.64$, $P < 0.001$, estimate \pm SE: 1.14 ± 0.32).

Body mass did not either differ between individuals that were caught later as breeders in the study area and those that disappeared ($N = 302$, $F_{1,292} = 1.08$, $P = 0.30$) or between displaced individuals that returned to the patch of capture and those that did not ($N = 122$, $F_{1,109} = 0.89$, $P = 0.35$). Body mass at early capture tended to differ according to original dispersal status ($N = 112$, $F_{2,282} = 2.71$, $P = 0.068$): philopatric individuals were slightly heavier than dispersers and immigrants (post-hoc test: philopatric individuals vs. other individuals, estimate \pm SE: 0.23 ± 0.10 , $F_{1,260} = 5.26$, $P = 0.026$). This effect was observed while accounting for an increase of body mass with tarsus length ($F_{1,290} = 26.82$, $P < 0.001$, estimate \pm SE: 0.34 ± 0.07) and a lower body mass for yearlings compared to older individuals ($N = 136$, $F_{1,274} = 11.93$, $P < 0.001$, estimate \pm SE: -0.29 ± 0.08) and for males compared to females ($N = 241$, $F_{1,268} = 5.10$, $P = 0.024$, estimate \pm SE: -0.22 ± 0.09).

Breeding variables

Among individuals caught as breeders in the study area (including non-experimental birds), none of the breeding variables investigated differed between experimental treatments (**Table 6.1**; none of the interactions with treatment was significant: all F values < 7.22 and all p-values > 0.07). Breeding variables only depended on sex and age (see **Table 6.1**): yearlings laid later (estimate \pm SE: 1.59 ± 0.25 ; **Table 6.1**) and smaller clutches (estimate \pm SE: -0.25 ± 0.04 ; **Table 6.1**) than older individuals; they raised lighter young (estimate \pm SE: -0.34 ± 0.14 ; **Table 6.1**), showed a lower probability to fledge at least one young, estimate \pm SE: -0.54 ± 0.19 ; **Table 6.1**) and, among successful individuals, fledged fewer chicks (estimate \pm SE: -0.33 ± 0.11 ; **Table 6.1**) than older individuals. Males showed a higher probability to fledge at least one young than females (**Table 6.1**). Additionally, chick body mass at day 12 increased with tarsus length (**Table 6.1**).

DISCUSSION

In this study, we used here an experimental approach to investigate causal relations between dispersal and fitness related traits, and more specifically test for potential costs linked with displacement and settling in a new habitat. We translocated over 600 individuals within an intensively monitored study site (and used over 140 individuals as controls, released in the patch of capture), allowing us to record subsequent behavioural responses to the experimental displacement. Our results show that pre-breeding decisions (i.e. the probability to settle and breed in the study area and/or to return to the patch of capture for displaced individuals) differed between individuals' treatment and original dispersal status. We found that a large fraction of experimental individuals were not subsequently caught as breeders, i.e. did not settle to breed in the study area, and the probability to settle was lower for immigrants. Among displaced individuals, philopatric individuals were more likely to return to their patch of capture than dispersing and immigrant individuals. This shows that pre-breeding decisions

depend on individual's dispersal history, possibly reflecting differential costs and benefits balance of dispersal movements. However, once settled, individuals from different treatments did not differ in their main breeding decisions (laying date, clutch size, number and condition of young fledged), thus we did not detect costs linked with forced dispersal. This suggests that only individuals able to cope with a new habitat accepted the displacement in this highly mobile species, but does not preclude dispersal costs subsequent to settlement depending on individual's motivation to disperse in natural situations.

Pre-breeding decisions: cost of unfamiliarity

Overall, 265 out of 623 experimental individuals were caught as breeders in the study area during the breeding season following the manipulation, meaning that more than 42% of experimental individuals disappeared after the manipulation. This result is in line with the high disappearance of released individuals observed in many translocation studies performed for conservation purposes, particularly in avian species (Wolf *et al.* 1996). Such disappearance from the release population / site may be due to high mortality and/or large-scale movements of released animals (e.g. Griffith *et al.* 1989; Miller *et al.* 1999; Snyder, Pelren & Crawford 1999; Calvete & Estrada 2004; Mihoub, Le Gouar & Sarrazin 2009) and frequently leads to failure of translocation programmes. In our study, disappearance is unlikely to be due to mortality because the probability of recapturing experimental individuals in the following year was similar for individuals that settled and bred in the study area in the year of manipulation and those that did not (Pärt 1995). Therefore, experimental individuals may either have dispersed outside the study area (i.e. large-scale dispersal movements) or failed to breed. Whether this effect was partly due to the disturbance caused by early catching is difficult to know. However, because control individuals had a lower disappearance probability, this effect also reflected a potential cost of displacement itself.

Among experimental individuals, displaced individuals but also immigrants are the most susceptible to pay a cost of dispersal due to unfamiliarity with the breeding environment (Stamps 1987; Pascual, Carlos Senar & Domenech 2014). Large-scale post-release movements by translocated individuals have been documented, particularly in

highly mobile species such as birds (e.g. Coates, Stiver & Delehanty 2006; Le Gouar *et al.* 2008; Kesler & Walters 2012). Such movements probably result mainly from exploring the unknown environment to find suitable resources (Kesler & Walters 2012) but also from directional navigation towards the original capture site (Miller & Ballard 1982; Dickens *et al.* 2009; Tsoar *et al.* 2011). Here, immigrants disappeared more than dispersing and philopatric individuals. In our population, immigrants may include local birds previously missed but are most likely mainly long-distance (i.e. from outside the study area) dispersers, which may experience different costs compared to short-distance dispersers (e.g. Hansson, Bensch & Hasselquist 2004). These long-distance dispersers may be more prone to move again in response to disturbance (here, early capture) than short-distance dispersers or philopatric individuals. However, experimental individuals were not frequently found in patches surrounding the patch of release, even when released in the centre of the study area. Therefore the higher disappearance of immigrants is unlikely to be explained by local exploratory movements, but we cannot exclude that immigrants were transient individuals in the study area and returned to their original site beyond the study area. On the other side, failure to access to reproduction may be an extreme cost of dispersal (Danchin & Cam 2002). In our population, as in many others, the capture and identification of individuals is linked to reproductive activity, preventing us to distinguish between individuals that dispersed outside of the study area and individuals that failed to breed.

In conservation studies, individuals are often released in low-quality (e.g. highly fragmented) habitat patches and/or low-density patches, which may have a strongly negative impact on the probability of settlement in the release habitat (Gautier *et al.* 2006; Fisher, Lambin & Yletyinen 2009; Mihoub, Le Gouar & Sarrazin 2009). In particular, the presence of conspecifics has been shown to positively influence settlement probability of newcomers (e.g. Doligez *et al.* 2004; Fisher, Lambin & Yletyinen 2009; Mihoub *et al.* 2011). A review of studies on conspecific attraction reported that, in 20 of 24 studies, settlement increased in habitat patches where conspecific songs were broadcasted (Ahlering *et al.* (2010). Yet the presence of conspecifics may also induce stress in territorial species with high levels of competition for territory or mate acquisition (Ebrahimi & Bull 2014). Here, we released displaced individuals in habitat patches

occupied in the long-term and thus highly suitable, and we did not modify local (patch) density. The suitability of the release patch should thus not affect the probability of settling and breed in the new patch for translocated individuals, which may have reduce the probability of settlement of translocated individuals.

Among individuals later caught as breeders, the higher probability of returning to the patch of capture for philopatric compared to immigrants and dispersing individuals may also illustrate the benefits of familiarity with the environment. Because natal and breeding dispersal are under different selective pressures (e.g. the role of intraspecific competition; Doligez *et al.* 1999), the benefits of familiarity are likely to differ according to the dispersal phase considered (i.e. natal or breeding dispersal). Interestingly, when discarding immigrants, for which it is not possible to distinguish between natal and breeding dispersal for older birds, the probability to return to the patch of capture differ between natal and breeding individuals (interaction between original dispersals status and dispersal process: $N = 176$, $\chi^2_1 = 6.73$, $P = 0.009$). While the probability to return to the patch of capture did not differ between natal dispersing and natal philopatric individuals (post-hoc test comparing natal dispersing and philopatric individuals: $N = 72$, $\chi^2_1 = 0.40$, $P = 0.53$), breeding philopatric individuals, i.e. most experienced individuals, were more likely to return to their patch of capture than breeding dispersing individuals (post-hoc test comparing breeding dispersing and philopatric individuals: $N = 131$, estimate \pm SE: 1.15 ± 0.62 , $\chi^2_1 = 2.40$, $P = 0.065$; **Appendix Figure 6.S1**). This result support the idea that accruing knowledge of the environment are of great importance for the decision to return (Pärt 1995). All together, these results suggest that both the costs of non-familiarity but also the benefits of philopatry on the other side seem determinant to shape settlement decisions on our species.

Breeding decisions: no differences once settlement decision is made

Once settled, displaced, control and non-experimental individuals did not differ in the main breeding variables, thus suggesting that the balance between the costs and benefits of breeding in an unfamiliar environment mainly affects the settlement decisions. Hereafter, individuals seemed able to adjust their breeding decisions in relation to the breeding environment chosen. Our results are in line with a translocation experiment

performed on the pied flycatcher (*Ficedula hypoleuca*) from the Netherlands to Southern Sweden (Burger *et al.* 2013). In this experiment, the probability of settlement could not be analysed because individuals were released in pairs in large aviaries so that they were forced to stay and breed on site. However breeding variables did not differ between translocated birds and control birds that remained in the original site (Burger *et al.* 2013). This absence of differences was suggested to result from exceptionally cold weather and food availability conditions early in the season in the year of the experiment. However, with a larger sample size and replicating the translocation in four different years, we also found no difference in breeding variables between displaced individuals that stayed in their patch of release, those that returned and control individuals. Yet, in our study population, only individuals reaching a sufficiently advanced stage of breeding can be captured, especially males. Therefore, the identification of individuals is biased towards the most successful individuals (see Doligez *et al.* 2012), which are probably higher quality individuals, maybe more efficient in adjusting breeding decisions to local environmental conditions. This could reduce our ability to detect differences in breeding variables between treatments.

Our translocation experiment allowed us to investigate potential costs of dispersal. Although many factors are likely to shape individual's motivation to disperse in natural situations while we experimentally imposed the displacement here, our results suggest that translocating individuals to an unfamiliar environment impacts more pre-breeding than breeding decisions. Our results supported the hypothesis that familiarity with the environment is beneficial. Yet, to better understand the consequences of forced movement, monitoring individuals that failed to access reproduction and individuals that moved outside the study area following the translocation would be critical. Furthermore, the impossibility to constrain displaced birds to stay on their patch of release limited our ability to investigate the costs of breeding in a non-familiar environment following dispersal movement. Nevertheless, our study provides insights on factors driving individuals to settle in a new habitat independently from the processes involved in the movement itself. Especially the role of familiarity with the environment seems to play a key role, which could have implications, in particular on shifts of species spatial range in response to environmental changes (Kokko & Lopez-Sepulcre 2006).

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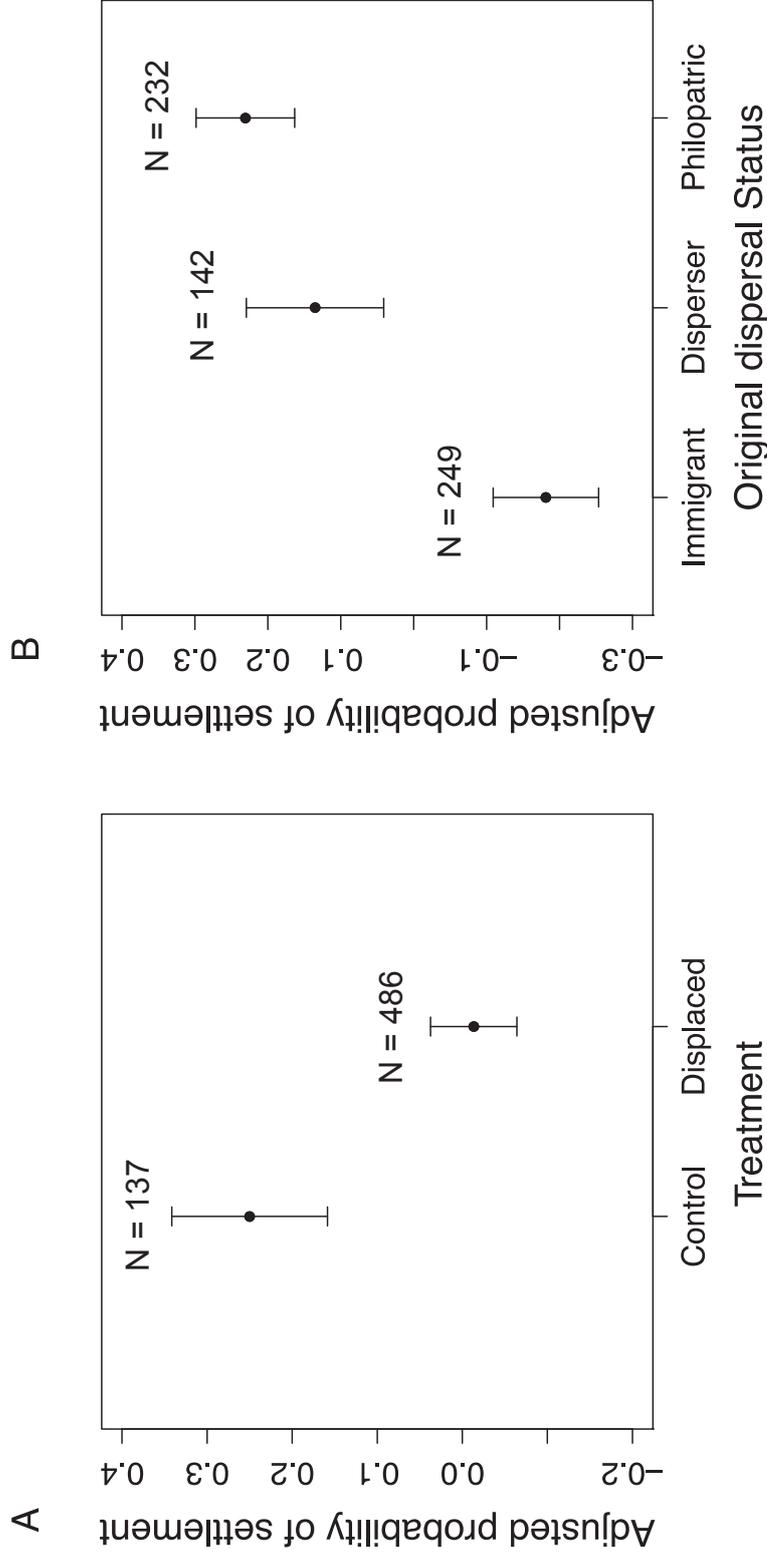


Figure 6.1: Probability for individuals to be caught as breeders in the study area after the experimental manipulation according to their (A) experimental treatment and (B) original dispersal status. See text for the description of treatments. Immigrants: unringed individuals upon early capture; dispersers: individuals that were caught early in a patch different from their natal or previous breeding patch; philopatric individuals: individuals that were caught early in their natal or previous breeding patch. The figure shows mean values (± 1 SE) adjusted for other significant effects in the model (i.e. residuals from the same model without the effect on the X-axis) and sample size for each category.

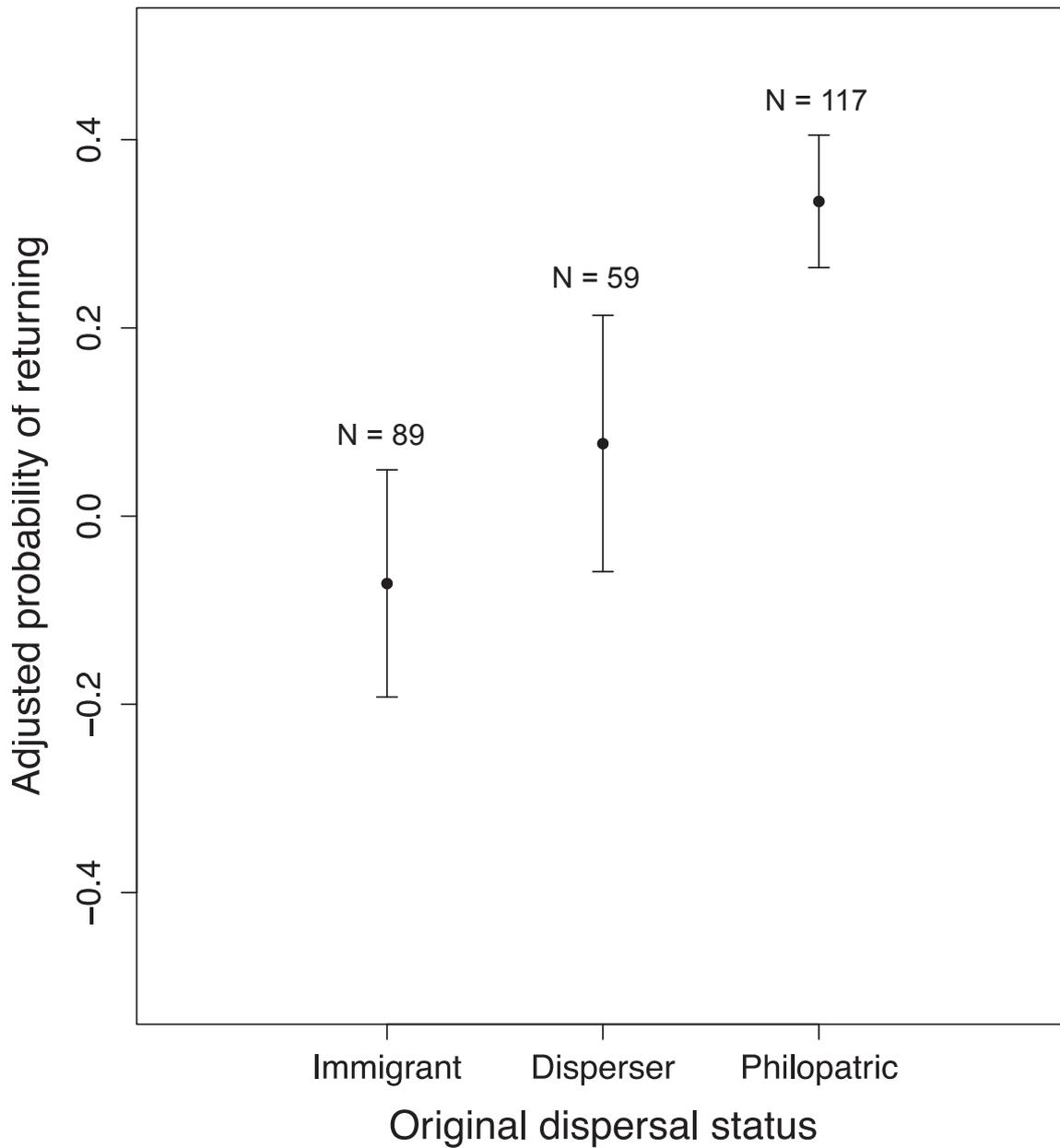


Figure 6.2: Probability for displaced individuals to return to the patch of capture according to original dispersal status. The figure shows mean values (± 1 SE) adjusted for other significant effects in the model (i.e. residuals from the same model without original dispersal status).

Table 6.1: Final models when investigating the effect of treatment on breeding decisions. F and χ^2 and P-values refer to the modified F test performed in cases of linear mixed models and to LRT tests in cases of generalized linear mixed models respectively. The table shows final model. The estimate is given for one category, i.e. yearlings for age and males for sex.

Variable	Estimate \pm SE	F or χ^2	Residual ddl	ddl	P
Laying date (N = 1024)					
Age	1.59 \pm 0.25	39.23	1199	1	< 0.001
Clutch size (N = 1195)					
Age	-0.25 \pm 0.04	32.17	1188	1	< 0.001
Clutch size (N = 999)					
Nestling's tarsus length	0.70 \pm 0.05	209.64	985	1	< 0.001
Age	-0.35 \pm 0.14	5.84	541	1	0.016
Probability to fledge at least one chick (N = 1102)					
Sex	1.10 \pm 0.21	29.01	-	1	< 0.001
Age	-0.51 \pm 0.19	7.21	-	1	0.007
Number of fledglings (N = 934)					
Age	-0.32 \pm 0.10	9.22	928	1	0.002

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Chapter 6

Appendix

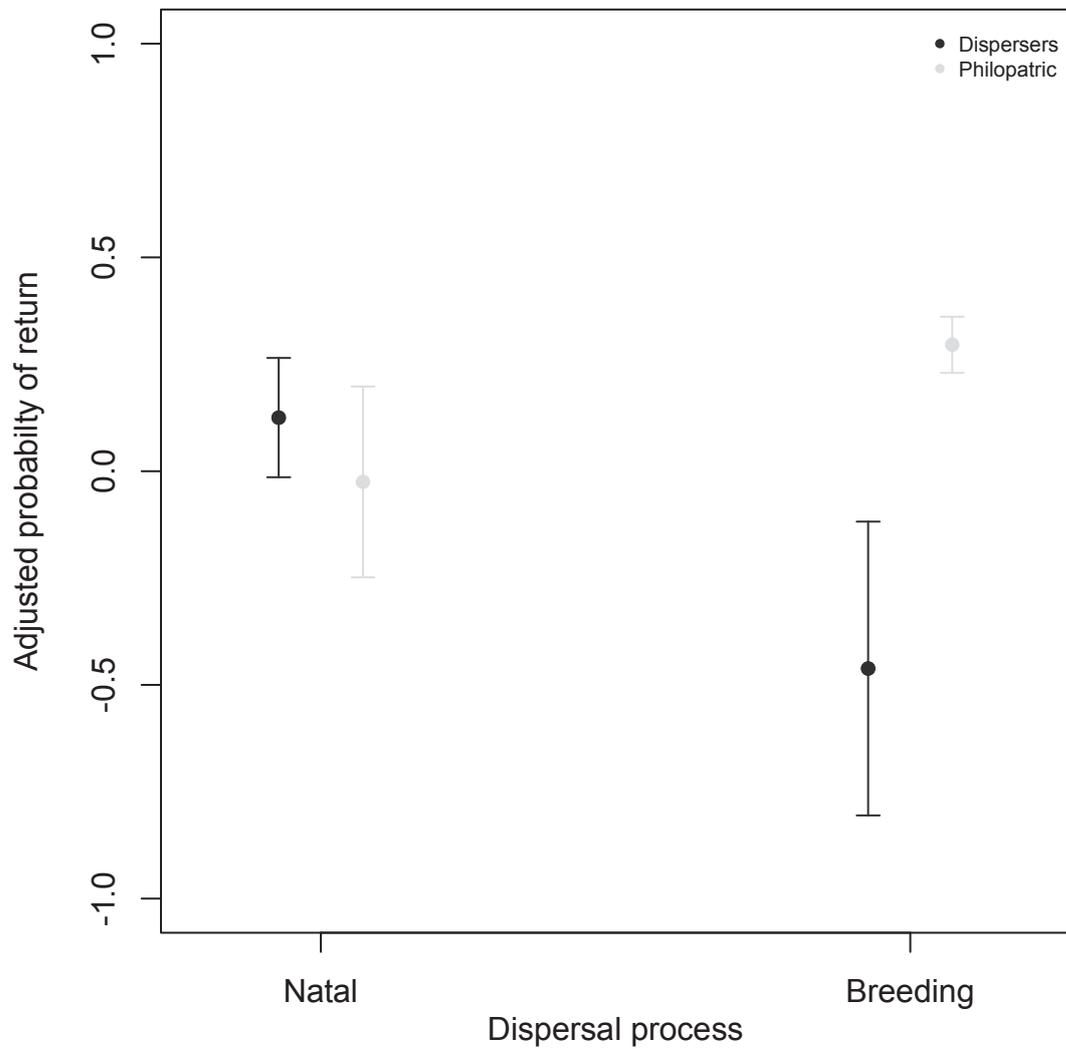
APPENDIX CHAPTER 6

Figure 6.S1: Probability to return to the patch of capture according to original dispersal status and dispersal process (i.e. natal *vs.* breeding dispersal). The figure shows mean value (± 1 SE) adjusted for other significant effects in the model (i.e. residuals from the final model without the interaction between dispersal status and the corresponding dispersal process).

Chapter 7

General discussion

SUMMARY OF THE RESULTS

The evolution of dispersal is at the heart of many concerns; notably because dispersal impacts more ecological and evolutionary processes and represents a solution to escape the degradation of local environment conditions, which may be of particular interest in the current context of global warming. If a lot of factors driving the evolution of dispersal have been identified thanks to a large theoretical work, the evolution of dispersal strongly depends upon the fitness of dispersing individuals. However, little is known about the balance between the costs and benefits of dispersal and the fitness consequences of dispersal are really difficult to predict. Using both correlative and experimental approaches at different scales (i.e. annual and lifetime scales), we aimed to get better insights in the fitness consequences of dispersal. Overall, I showed differences between dispersing and philopatric individuals at each scale investigated both at a lifetime scale, at the annual scale in early and late breeding decisions but also in the experiment.

When investigating the lifetime fitness differences between natal dispersing and philopatric individuals (**Chapter 3**), we showed that dispersing and philopatric individuals differed in their lifetime reproductive success when reproductive effort was strongly increased (i.e. for secondary polygynously mated females and when brood size was experimentally increased) with individuals that experienced a brood size increased and secondary polygynously mated females that exhibited a lower LRS and annual recruitment. Thus, despite the fact that in most situations, natal dispersal might be adaptive, in harshest situations, lack of prior knowledge about the environment of dispersing individuals may be particularly prejudicial. Moreover, we highlighted that *i*) differences according to natal dispersal status and *ii*) absence of differences in the most classic situations are not due to compensations (i.e. trade-offs) between fitness components or between breeding attempts during an individual lifetime.

In the **Chapter 4**, we focused on early breeding decisions and reported not only that clutch size, egg mass and incubation period differed between dispersing

and philopatric individuals, but also that male dispersal status was at least as much involved in these differences than female dispersal status. This illustrates that (i) the importance of the implication of the male in early breeding decisions, usually assumed to more under the control of the female, (ii) that different selective pressures shape dispersal behaviour in each sex (see discussion in **Chapter 4**). Yet, differences between dispersing and non-dispersing individuals mostly rely on interactions between dispersal status and individual's phenotypic traits and/or mate's phenotypic traits.

When investigating late breeding decisions (**Chapter 5**), we found that hatching date, chicks body mass, the number of fledglings and both male and female body mass when feeding the young significantly differed between dispersing and philopatric individuals, with as much differences showing an advantage for dispersing individuals as differences showing an advantage for philopatric individuals. We therefore did not detect a net positive or negative effect of being a disperser. Rather differences relied on interactions with individual's or mate's phenotypic traits, which therefore confirms the phenotype- and condition-dependent effects of dispersal and underline the importance of both parents in adjustment of breeding decisions, particularly in the context of dispersal. Furthermore, male dispersal status was once again at the heart of the differences between dispersing and philopatric individuals as differences according to dispersal status mostly rely on differences between pairs with dispersing and philopatric males. On the other side, we did not detect simple compensations between breeding traits within a breeding event.

I finally used an experimental approach with a translocation experiment to directly test for consequences of displacement in a non-familiar environment (**Chapter 6**). We reported that decisions before settlement, i.e. the decision to settle in the breeding area and the decision to return to the plot of capture or to settle in a new environment, differed between experimental treatment and a priori dispersal status while breeding decisions did not. Indeed on the one side, displaced birds and immigrants settled less often than control and philopatric or dispersing individuals. Among settled individuals, I found that philopatric

individuals returned more to the area of capture than dispersers and immigrants. On the other side, once settled, individuals did not differ in none of the breeding decisions investigated. Overall, these results may reflect costs of non-familiarity in terms of settlement but also confirms that the benefit of familiarity with the breeding environment is a strong determinant of dispersal in this population.

In this general discussion, I do not aim to address again the points that have already been discussed in each chapter and that are briefly summarized here. I rather would like to emphasize some specific aspects that appeared as important to me when considering all the results but that were not really discussed before, over the chapters. These points are maybe more speculative but are something worth thinking about. First of all, I would like emphasizing the importance of the multi-determinism of dispersal and potential importance in our ability to detect and identify fitness differences between dispersing and philopatric individuals. Particularly, natal and breeding dispersal are known to be under different selective pressures and considering natal and breeding dispersing and philopatric individuals may also impede the detection of fitness differences according to dispersal behaviour. In a second part, I therefore would like to discuss specifically the potential differences between natal and breeding dispersal using notably complementary analysis investigating potential differences in LRS between dispersing and philopatric females. Thirdly, I found that body condition was strongly involved in differences between dispersing and non-dispersing individuals at least at the annual scale. However, I showed unexpected results concerning body condition and the interaction with dispersal status. Body condition is considered as an important trait in ecology and strong assumptions are often assumed about the link between condition and fitness. However, these assumptions are maybe questionable in the light of the results and in the context of dispersal. Finally, as stated previously, I found that fitness differences between dispersing and philopatric individuals often relied on interactions with phenotype, such as body condition. The evolution and existence of correlations between phenotypic traits and dispersal is now well documented. Particularly, I would like

to discuss the possible importance of correlations between dispersal and behavioural traits and their implication for fitness consequences of dispersal in the light of preliminary analysis based on behavioural tests in the context of the translocation experiment.

MULTI-CAUSALITY OF DISPERSAL IS NOT LIKELY TO HELP TO SEE CLEAR

The fitness consequences of dispersal are not easy to predict and this is also visible in the results of empirical studies investigating the fitness consequences of dispersal. Indeed, half of the empirical studies investigating fitness consequences of dispersal reviewed in Belichon, Clobert and Massot (1996) and in Doligez and Pärt (2008) did not detect differences between dispersing and philopatric individuals. Furthermore, when detected, differences were as much in favour of dispersing individuals as in favour of philopatric individuals.

In this study, I find differences between dispersing and non-dispersing individual, both at the lifetime and breeding event (i.e. annual) scales. At the lifetime scale, I highlighted differences when breeding effort was increased following an experimental brood size increase or a polygynous mating for secondary females. However, at a finest scale, even if I detected differences between many breeding decisions, the effects were relatively weak considering sample sizes and did not showed strong effects of dispersal behaviour. Such relative absence of differences could result from two different (but not mutually exclusive) processes: (i) within individuals adjustment of breeding decisions allowing dispersing and non-dispersing individuals to reach similar fitness (e.g. via a trade-off between quantity and quality; Julliard, Perret & Blondel 1996) and/or (ii) between-individual differences, with part of dispersing individuals reaching higher values of fitness components and part reaching lower values, resulting in similar average fitness values. The occurrence of compensations between fitness components or breeding events is unlikely to explain this relative absence of

difference as trade-offs were deeply investigated between breeding events without support. On the other side, our ability to detect fitness differences between dispersing and non-dispersing individuals may be hampered notably because, in our population, capture and identification of parents is biased towards more successful individuals (see Doligez *et al.* 2012 and Chapter 2). Yet, I truly think that between-individual differences among dispersing individuals may also occur because of the multiple causes shaping natal dispersal decisions. This multi-determinism may rely on the different causes addressed in the introduction but may also involve phenotype- and/or condition-dependence (Dobson & Jones 1985; Ims & Hjermann 2001; Bowler & Benton 2005; Matthysen 2005 and see below for a discussion about dispersal syndromes).

Theoretical studies that aim to identify *THE* ultimate cause shaping the evolution of dispersal considered the effect of one factor at a time. However, in the wild, it is really likely that individuals are affected simultaneously by multiple factors that may be involved in the decision to leave or to stay, how far it will move or even where it will settle (Clobert, Anker Ims & Rousset 2004). Dispersal is therefore really likely to be expressed under a complex interaction of the organism with its environment and results of a combination of individual characteristic and environmental effects (Lambin, Aars & Piertney 2001; Bowler & Benton 2005). As a consequence, dispersal can be viewed as common response or process that derives from really different mechanisms, which may lead to some confusion when considering the fitness consequences of dispersal. Indeed little is known about the influence of each factor on the evolution of dispersal and therefore how they influence the balance between the costs and benefits of dispersal and we still do not know if these factors act independently, synergistically, or on the contrary, suppress each other's factors (Gandon & Michalakis 2001; Massot *et al.* 2002).

Given the heterogeneity and complexity of dispersal mechanisms and the variety of proximal factors involved, different aspects of the environment are likely to act together in altering the costs and benefits of dispersal. Yet, in our study as in many others, dispersers were considered as a single group irrespective

of the main causes of dispersal (e.g. inbreeding avoidance, kin competition, previous breeding failure). In our population, Pärt and Gustafsson (1989) already reported that this might be particularly important when investigating the fitness consequences of breeding dispersal. Indeed, when all individuals, irrespective of the possible causes of dispersal were analysed together, no correlation was found between dispersal distance and any of the considered life-history variables (i.e. laying date, clutch size, number of fledglings, and recruits and survival to subsequent breeding seasons). However, they show that in females, reproductive outputs tended to differ according to dispersal motivations, depending mostly on the breeding success in the previous year. Among females failing to fledge young in the previous year, there was a positive correlation between dispersal distance and subsequent reproductive success while the corresponding correlation among successful females was negative.

To illustrate these idea, I would like to emphasize that, among the possible differences in dispersal motivation that may lead to differences in fitness consequences is whether individuals were forced to disperse or not (Greenwood & Harvey 1982; Pärt & Gustafsson 1989). Individuals may be forced to disperse because of disappearance of their previous breeding or natal patch or, for instance, because of low competitive ability or lack of experience when trying to acquire and secure a territory (Greenwood & Harvey 1982). In birds and mammals, cases of forced natal dispersal have been documented (Sarno *et al.* 2003; Stokes, Parnell & Olejniczak 2003), with possible implications for future fitness components. For instance, the ability of young to compete for food resources in their natal area has been found to influence the timing of natal dispersal (Ellsworth & Belthoff 1999). Nilsson and Smith (1988), early dispersing marsh tits (*Parus palustris*) are heavier than individuals that disperse later, and marsh tits in poorer condition forage longer in the natal area than birds in good condition. In that case, early dispersing individuals may be expected to have a better access to high-quality territories or favourable habitats that are limited and are acquired on a first-come, first-served basis (Dufty & Belthoff 2001).

This shows how distinguishing individuals based on their motivation to disperse or at least to identify several “profiles” of dispersing individuals may be important to investigate the balance between the costs and benefits of dispersal. Yet, the identification of the causes of dispersal remains challenging, particularly in a wild population of migratory birds. Adult body size than in high-quality patches, which may increase fitness. An interesting perspective would be to develop tools from e.g. genetics or social networks research fields to identify individuals’ motivation to dispersal for investigating the fitness correlates of dispersal.

NATAL AND BREEDING DISPERSAL

In our comparison of early and late breeding decisions within a breeding event, we first considered natal and breeding dispersers as a single group. In the light of the previous section, this may impede our ability to distinguish clear fitness consequences between dispersing and philopatric individuals as natal and breeding dispersers did not moved for the same reason, at least part of them.

The distinction between natal and breeding dispersal has been emphasized by (Greenwood 1980) almost 20 years after Howard (1960). A first fact when considering both processes, is that many species dispersed only once in their lifetime and even in species showing a breeding dispersal propensity, natal dispersal is mostly more extensive than breeding dispersal (Paradis *et al.* 1998; but see Dale, Lunde & Steifetten 2005). This has obviously resulted in a higher difficulty to study this process empirically while it is more “easy” to collect data about natal dispersal in many species. This may explain why breeding dispersal has been far less studied than natal dispersal and why breeding dispersal remains the most mysterious dispersal process (Berteaux & Boutin 2000; Pasinelli *et al.* 2007; Calabuig *et al.* 2008; Eeva *et al.* 2008; Peron, Lebreton & Crochet 2010; Cline *et al.* 2013). This bias towards natal dispersal is also true in our species, which lead to smaller sample size when considering breeding dispersal (Pärt & Gustafsson 1989;

Pärt 1990; Doncaster *et al.* 1997). For instance, when investigating the difference in laying date between dispersing and philopatric individuals, we observed only 69 events of breeding dispersal in males (i.e. about 5% of the total number of dispersal events) in a data set including more than 20 years of data showing thus the required effort in data sampling to investigate such behaviour.

Yet, as suggested by this difference between both processes, it is commonly assumed that natal and breeding dispersal are shaped by different selective pressures (Clobert *et al.* 2001; Duputie & Massol 2013). Indeed, it is likely that factors influencing natal dispersal may be of a much more involved nature than those influencing breeding dispersal (Danchin, Heg & Doligez 2001). For instance, maternal effects are probably mostly, if not only, involved in natal dispersal (at least as a major factor influencing decisions; Clobert *et al.* 2012). In the same way, kin competition and risks of inbreeding are probably predominant in natal dispersal but much less in breeding dispersal. On the other hand, the use of individual experience in the decisional process cannot be as much implied in natal dispersal than it is in breeding dispersal (Danchin, Heg & Doligez 2001). This is the reason why the greater mobility of young individuals may result of the less risk averse of yearlings compare to old individuals. Indeed, young individuals do not yet have established a territory and they have less to loose by moving (Starrfelt & Kokko 2012). Furthermore, the usual increasing site fidelity (i.e. philopatry) with age has been interpreted as a result of increased benefits of local knowledge with the breeding environment (Desrochers & Magrath 1993; Pärt 1995; Forero *et al.* 1999; Serrano *et al.* 2001). In the Chapter 6, I found that breeding philopatric individuals returned significantly more to the plot of capture after displacement than breeding dispersers while I did not detect any difference between natal dispersing and philopatric individuals. According to this, we therefore could expect differences in the fitness outcome according to dispersal process.

In the investigation of early breeding decisions, I did not detect any difference between dispersing and philopatric individuals according to the process considered. Even if sample sizes concerning breeding dispersal are much smaller

(e.g. for laying date, we observe 69 and 343 dispersing males and females respectively) than for natal dispersal, we have nevertheless a large number of dispersing individuals. On the other side, in the investigation of late breeding decisions, I reported that hatching success and female body mass differed in pairs with dispersing or philopatric males depending on the dispersal process. However, because natal dispersal is strongly correlated with age in our population, we only included the interaction between dispersal status and dispersal process as a binary variable in the final model. By doing this, we investigate possible differences between natal and breeding dispersers and/or philopatric individuals, we did not consider the possibility that natal and breeding dispersing and philopatric individuals differed in their interactions with phenotypic traits or conditions. Considering that we found mostly condition- and/or phenotype-dependent effects of dispersal, it would be interesting to investigate such differences between natal and dispersing individuals.

When studying LRS between dispersing and philopatric individuals (**Chapter 3**), I distinguished natal and breeding dispersal for several reasons. First, the definition of dispersal status at a lifetime scale is more questionable than the annual definition of dispersal. Indeed, it is easy to determine whether an individual was or not a natal disperser and it may fit a binary definition, found as relevant in our population (Doncaster *et al.* 1997; Doligez, Pärt & Danchin 2004). However, concerning breeding dispersal, individuals may be either breeding disperser and/or philopatric during their lifetime. Using a binary definition of breeding dispersal (i.e. individuals were considered as dispersers if they dispersed at least once as breeder), we observed that, our dataset only encompasses 16 breeding males born in the study area and for which the whole lifetime was known, which impedes any investigation of the fitness differences of dispersal at a lifetime scale in males. However, to dig deeper into the potential differences between natal and breeding processes, we compared LRS, annual recruitment and return rate as proxy of survival between breeding dispersing and philopatric females. Breeding dispersing and philopatric females did not differ in LRS (dispersal status: $N = 356$, $\chi^2_1 = 0.003$, $P = 0.96$) and LRS was only positively correlated to mean body

condition during the lifetime (estimate \pm SE: 2.91 ± 1.37 , $\chi^2_1 = 4.49$, $P = 0.034$). We did not detect any effect of brood size manipulation in interaction with dispersal status ($N = 187$, $\chi^2_1 = 0.93$, $P = 0.82$) or mating status (i.e. secondary *vs.* monogamous/primary females) in interaction with dispersal status ($N = 187$, $\chi^2_1 = 0.51$, $P = 0.48$), which differ from natal dispersal pattern. Similarly, the annual production of recruits did not differ between breeding dispersing and non-dispersing females ($N = 506$, $\chi^2_1 = 0.76$, $P = 0.38$). Again we did not detect any interaction between brood size manipulation and dispersal status ($N = 161$, $\chi^2_1 = 2.95$, $P = 0.23$) and we were not able to test the interaction between dispersal status and mating status as only five breeding dispersing females were secondary. Overall, we found that annual recruitment was again strongly positively correlated with condition (estimate \pm SE: 3.31 ± 1.14 , $\chi^2_1 = 8.35$, $P = 0.004$). Finally, we found that breeding philopatric females returned more the next year than dispersing females ($N = 506$, estimate \pm SE: 0.50 ± 0.23 , $\chi^2_1 = 4.42$, $P = 0.04$). However, even if we did not detect any effect of the location of the breeding plot (i.e. central or on the edge), it is likely that this pattern resulted from a methodological bias because dispersing individuals are more prone to disperse out of the study area (Baker, Nur & Geupel 1995). Nevertheless, this result would deserve to be deeper investigated maybe using capture-recapture multi-state capture-recapture models that may allow accounting for the imperfect detectability of individuals according to their dispersal status

Overall, this complementary investigation about the potential differences in LRS, annual recruitment and return rate between breeding and philopatric females highlighted different patterns than those found when considering natal dispersal and the link with LRS. However, it is important to highlight that we were not able to investigate as much situations as in natal dispersal because of restricted sample sizes of secondary females for example. Moreover, the absence of breeding dispersal males is really symptomatic of a difference between the costs and benefits of dispersal in both sexes, as already suggested in this population (Pärt & Gustafsson 1989).

CONDITION: FROM CLASSIC ASSUMPTIONS TO UNEXPECTED RESULTS

Body condition is usually considered as a key organismal characteristic strongly influencing individual fitness (Jakob, Marshall & Uetz 1996). In our study, as in many others, we found that several fitness related traits were correlated with individual body condition on the one side but also that body condition was involved in differences between dispersing and non-dispersing individual. Indeed, we found that laying date, clutch size, incubation period, chicks body mass, number of fledglings and male and female body mass when feeding the nestlings were all correlated with male and/or female body condition (**Chapter 4 and 5**). On the other side, however, body condition did not appear as significant when comparing LRS according to natal dispersal behaviour (**Chapter 3**; but see discussion above concerning breeding dispersal and LRS).

The use of body condition is a matter of some debate from a statistical and biological point of view (e.g. Green 2001; Labocha & Hayes 2012; Labocha, Schutz & Hayes 2014). Here, I do not aim to discuss the potential statistical bias of the use of the ratio between body mass and body size as body condition. We are aware that several pitfalls in the use of such method have been highlighted, notably because this index has been demonstrated to be correlated with body mass, which may weakened the strength of conclusions that could be drawn (Jakob, Marshall & Uetz 1996). But it seems that there is no consensus about the most appropriate condition to use (Peig & Green 2010). Moreover, in the investigation of early breeding decisions (Chapter 4), the use of four different methods to estimate body condition leads qualitatively the same results (i.e. both residuals and simple ratio and log transformations).

Beyond the statistical considerations, the biological meaning of condition may be questionable, particularly when considering my results. Condition often referred to a pool of resources that an individual has acquired and presumably assimilated and that can be allocated among life-history traits and particularly in reproduction (Tomkins *et al.* 2004; Peig & Green 2009). It is therefore consider as

indicative of the health or at least physiological state of an individual and assumed to be positively related to fitness. Indeed, many studies have related body conditions of birds to their survival (Bergan & Smith 1993; Blums *et al.* 2005) or reproduction (Blums, Clark & Mednis 2002; Bustnes, Erikstad & Bjorn 2002). It is therefore really easy to make a quick way between condition and quality and the idea that individual of higher quality may exhibited higher body condition has become widespread (Clancey & Byers 2014). Indeed, individuals of superior quality are expected to be relatively more successful in acquiring resources vital for improving their realized fitness (Milenkaya, Legge & Walters 2014). The results of both Chapter 4, 5 and complementary investigation of LRS and breeding dispersal females supported this idea concerning female condition. We found that female with high condition value lay earlier, incubate longer and exhibit larger clutch size when mated with philopatric males (**Chapter 4**). But female body condition was also positively correlated with chicks' body mass (i.e. a proxy of nestlings' quality; **Chapter 5**) and finally; LRS was positively correlated with mean body condition. However, the trend is less obvious concerning males, particularly when considering the link with dispersal status.

We found that old male condition was positively correlated with chicks' body mass (**Chapter 5**), which tend to support the idea that condition is positively correlated with fitness at least in older individuals. On the other side, we also found that lower body condition was correlated with larger clutch size and number of fledglings in pairs with dispersing males, while we did not detect any effect of male body condition in pairs with philopatric males (**Chapter 4 and 5**). Surprisingly, this last result would indicate that pairs with unfamiliar males of lowest quality perform “better” than the other. It is first important to notice that we are not able to exclude reproductive compensation as a potential explanation for this pattern. In such case, female may increase reproductive effort to buffer the negative effect that mate quality may have on offspring fitness (Harris & Uller 2009). Yet this possibility is not the only one to explain my results and is not likely to explain with dispersing individuals with low condition performed actually better

than dispersing males with high condition or than philopatric males, whatever the condition (**Fig.4.1** and **5.3**).

The difference of condition when feeding the nestlings between dispersing and philopatric males may be explained by differential costs of reproduction. In birds, it is well known that feeding the young require large daily energy expenditures (DEE) to forage for rapidly growing nestlings. The reproductive costs hypothesis postulates that condition results from a trade-off between self-maintenance and offspring condition and survival (i.e. cost of reproduction; Stearns 1992). In such case, energy stores are hypothesis to be depleted in much the same way a car burns fuel and heavier individuals are consequently expected to better be able to cope with the particularly demanding nestling feeding stage and the induced energy stress (Lima 1986; Merila & Wiggins 1997). Philopatric individuals are more familiar with the breeding environment and/or may own higher quality territory, which may translate in increased foraging efficiency or higher access to food resources (Pärt 1994). As a consequence, they may be better able to maintain their body condition when feeding the young compared to dispersing individuals.

Overall however, this hypothesis is also unlikely to explain that dispersing males with a low condition showed both larger clutch size and number of fledglings than pairs with dispersing high condition males or philopatric males, irrespective of their condition. This does not explain either the negative relationship between condition and the probability to fledge at least one chick in dispersing individuals (complementary analysis: $N = 575$, estimate \pm SE: -27.85 ± 12.52 , $\chi^2_1 = 4.95$, $P = 0.02$). The observed difference in condition between dispersing and philopatric individuals on the one side and the higher fitness prospects of low condition dispersing males on the other side, may also suggest that condition in dispersing male reflect the investment in reproduction, which in turn, results in a greater body mass loss than in philopatric individuals. Indeed, we could expect dispersing individuals to invest more in foraging activities to respond to the nestlings demand which may translate into lower condition at capture without any implication about individual quality. However, as we ignore individual

condition at arrival on the breeding grounds, it is so far not possible to determine whether dispersing males lose more weight than philopatric males and if it may be due to higher daily energy expenditure and investment into reproduction. The analysis of longitudinal data of body condition along nesting between dispersing and philopatric individuals should help to shed light on the different conditions when feeding the nestlings. However, this hypothesis is unlikely to explain why we observed larger clutch size and number of fledglings in dispersing males with low condition.

On the other side, being heavier is not always beneficial. Indeed, large energy stores may compromise foraging abilities while exposing heavier individuals to greater predation risk (Gosler, Greenwood & Perrins 1995; Kullberg, Fransson & Jakobsson 1996). For instance, fat blackcaps (*Sylvia atricapilla*) have shown to have 17% lower velocity than blackcaps carrying no fat load and therefore increased predation risk (Kullberg, Fransson & Jakobsson 1996). It has thus been suggested that parents may actively modulate their condition according to the changing costs and benefits of carrying energy stores at different stages of reproduction (Norberg 1981). Prior to the period of peak (*i.e.* when feeding the nestlings), individuals are hypothesized to reduce energy stores to increase the effectiveness and reduce the cost of foraging (*i.e.* flight efficiency hypothesis; Norberg 1981; Merila & Wiggins 1997; Boyle, Winkler & Guglielmo 2012). Again, because dispersing individuals are less familiar with their breeding environment or own lower quality territory, feeding the nestlings may require more intense foraging ability and individuals that are able to adjust their condition in relation with foraging and flight costs may be able to improve their realized fitness. This however, may explain why lower condition individuals perform better in dispersing males. In the collared flycatcher, an experimental manipulation of prolonged incubation demonstrated that females did not suffer from prolonged incubation in terms of condition despite the potential costs of prolonged incubation. However, control females that successfully hatched their eggs dropped their mass significantly. This difference has been interpreted as stage dependent mass adjustment, which support the flight efficiency hypothesis (Cichon 2001).

Finally, it is also possible that the observed pattern simply result of an increased investment of dispersing male in reproduction. Indeed, male body mass loss may reflect investment in reproduction and has been found correlated with nestlings' body size and/or body mass in the pied flycatcher (Moreno, Potti & Merino 1997). The observed difference between dispersing and philopatric individual in both condition when feeding the nestlings and higher clutch size and number of fledglings of low condition dispersing males may therefore be interpreted as a difference of parental effort but remain difficult to investigate with our data.

So far however, we cannot definitely conclude as for the mechanisms underlying the observed differences. From what I know, body condition and body mass loss when feeding the nestlings have not been investigated in relation to dispersal behaviour and would really deserve it. A first step would be to investigate if the simple ratio between body mass on structural size really reflects energy reserves in terms of fat and/or proteins in the collared flycatcher repeatedly throughout the breeding season, as it has been shown that the correlation between reserves and ratio strongly varies according to species (Labocha & Hayes 2012). In the collared flycatcher, it has been suggested that lighter individuals have a better winter body condition (i.e. measured in terms of tail feathers grown) because of an increased foraging ability due to better flight manoeuvrability (Hargitai *et al.* 2014). This example illustrates how different condition definitions may lead to opposite conclusions and highlight the importance of investigating the true meaning of the condition index used.

On the other side, distinguishing the potential effects of reproductive costs hypothesis from the potential flight efficiency hypothesis remains really challenging, including when using an experimental approach, as, for instance, both hypothesis would predict less mass loss in response to supplemental feeding because feeding would help both maintain female condition as well as lower the costs of feeding chicks (Merila & Wiggins 1997; Nagy, Stanculescu & Holmes 2007). Consequently, such investigation requires a specific design (Boyle, Winkler & Guglielmo 2012). Finally, the investigation of the loss of body mass at several

step of the reproductive season (e.g. when arriving at the breeding ground, during egg laying, incubation, hatching and when feeding the nestlings) should be really indicative of the possible differences between dispersing and philopatric individuals and may be a first step to dig deeper into the mechanisms underlying these differences. The understanding of the meaning of condition and the use of a relevant method to describe condition would be therefore crucial as dispersal is often correlated with several phenotypic traits, including condition.

DISPERSERS ARE NOT ANYBODY: PHENOTYPE-DEPENDENT DISPERSAL

Most results in this PhD suggested phenotypic- and/or condition-dependent effects of dispersal. Here, I would like to emphasize the importance of phenotype-dependent effects of dispersal and possible implications in our study. A recurrent finding of evolutionary models of dispersal is that the balance between the costs and benefits of dispersal strongly depends on the factor driving the evolution of dispersal behaviour but also on the internal state of the individual (e.g. body condition, sex, age; Bowler & Benton 2005). As a consequence, even when experiencing the same environment, the balance between the costs and benefits of dispersal is likely to differ according to individual's phenotype (Clobert *et al.* 2009). It therefore appears that variation between individual is also a key component in the understanding of the costs and benefits of dispersal.

It has been shown that dispersing and philopatric individuals differ in several phenotypic traits and that phenotypic-dependent dispersal is a widespread phenomenon in many animals and even in plant species (Clobert *et al.* 2012). A particular striking phenotypic trait often highlighted as correlated with dispersal is body condition. The mechanisms of underlying body condition dependent dispersal are manifold and difficult to survey. For example, if larger body size allow higher competitive ability or larger fat reserves, then heavier or larger individual might be able to better survive to the most risky phases of dispersal

(van der Jeugd 2001; Delgado et al. 2010). On the other hand, lighter and smaller individuals might do better than heavier when dispersing if, their body condition implies agility to escape predators (Witter, Cuthill & Bonser 1994; Kullberg, Fransson & Jakobsson 1996) or again if increased flight capacity is negatively correlated with body mass (Gu & Danthanarayana 1992). Both examples perfectly illustrated that correlations between phenotypic traits and dispersal can be viewed as adaptive in the sense where they increase dispersal success (i.e. dispersal syndromes) by reducing potential dispersal costs. But that may also revealed some constraints that shape dispersal behaviour, an important idea to keep in mind when considering the correlation between phenotypic traits and dispersal and particularly when considering the balance between the costs and benefits of dispersal.

Among the phenotypic traits described as correlated with dispersal, behavioural traits have recently received a lot of attention with the result that a lot of studies demonstrated a covariation between several behavioural traits (behavioural syndrome) and dispersal propensity with the idea that dispersing individuals are not a random subset of the population (O'Riain, Jarvis & Faulkes 1996; Dingemanse *et al.* 2003; Cote & Clobert 2007).

For example, Duckworth and Badyaev (2007) reported that dispersal in the western bluebirds (*Sialia mexicana*) was strongly correlated with aggressiveness, which facilitate the range expansion (i.e. large scale dispersal) across the northwestern United States over the last 30 years. In the great tit (*Parus major*), dispersal propensity has been shown to be correlated with higher exploratory behaviour (Dingemanse *et al.* 2003). In general, phenotypic correlations between dispersal and behavioural traits or personalities are thought to have evolved because they allow to increase dispersal success by overweighing dispersal costs but also by leading to several advantages for dispersing individuals (Clobert *et al.* 2012). Indeed, more aggressive dispersing western bluebirds are able to exclude both less aggressive conspecifics and less aggressive individuals of the competing species, from breeding territories (Duckworth 2006). In contrast, less aggressive western bluebird males, which show a lower level of aggression, are poorly suited

for colonizing new areas. Similarly in the great tit, faster explorer individuals are more susceptible to find high quality territories than slower explorers but are also expected to be better able to cope with non-familiarity which may strongly enhance realized fitness of these individuals.

It is therefore really likely that these interactions among traits lead to some selection for functional integration and trait coexpression, which may, in turn, result in genetic correlations at the level of the population (Duckworth & Kruuk 2009; Korsten *et al.* 2013; but see van Overveld *et al.* 2014).

However, not all individual disperse with respect to same environmental factor (Clobert *et al.* 2001). For example, competition among conspecifics or among kin can lead to the departure of particular phenotype (Lena *et al.* 1998; Le Galliard, Ferriere & Clobert 2003) suggesting therefore that this is not the decision to leave or to stay that may be adaptive but rather that dispersal strategies are likely to differ according to conditions and individuals' internal state (Clobert *et al.* 2009). In that case, we could therefore expect that dispersing and philopatric individual reach the same fitness outcome, as it was the case when comparing the LRS between dispersing and philopatric individuals. On the other side, these correlations may impede our ability to distinguish fitness differences between dispersing and philopatric individuals without considering individuals' phenotypic traits as illustrated by the results in the **Chapter 4 and 5**, without considering the phenotypic traits of dispersing and philopatric individuals, it is probable that we would not have detect differences in early or late breeding decisions.

In the context of the translocation experiment, we know that displaced individuals that settled in the new environment in which they were released and individuals that decided to return to the area of capture are not a random subset of the sample of displaced individuals in terms of age, sex but also in terms of a priori dispersal status (Pärt 1995). It is therefore really likely that these individuals differ also in several behavioural traits. For instance, as demonstrated in the great tit, we could expect that displaced individuals that settled in the area of release were more explorer and/or aggressive than individuals that decided to return to the plot of capture. However, it would be therefore interesting to match individual

a priori dispersal status with the response to the experimental treatment. To investigate this possibility, we recorded several behavioural traits known to be relevant in the context of dispersal on experimental and non-experimental individuals in 2012 and 2013 (**Appendix 2**). We specifically recorded (i) aggressiveness in the context of con- or heterospecific competition, (ii) neophobia and the response to the presence of a novel object in terms of feeding rate and finally (iii) risk taking in a nest defence context. Preliminary analysis showed that individuals returned to their area of capture decreased significantly the feeding rate in the presence of a novel object ($t_{53,1} = 6.56$, $P < 0.001$), suggesting therefore that individuals that settled in a non-familiar environment are less neophobic than individuals that returned to the area of capture. On the other side, these analyses did not allow to demonstrate other differences between groups of individuals in terms of aggressiveness or risk taking. However, to date, I did not account for a priori dispersal status or for others phenotypic traits. The investigation of the link between behavioural traits and dispersal in the context of the translocation experiment deserves therefore deeper analysis.

CONCLUSIONS AND SOME PERSPECTIVES

In this study, I showed differences between dispersing and philopatric individuals both at a lifetime scale and at the scale of the breeding event and using correlative and experimental approaches, suggesting therefore that the observed differences are not only due to correlations with phenotypic traits. However, despite the numerous differences, I did not detect a net positive or negative effect of being a disperser but highlighted that the balance between the costs and benefits of dispersal often depends on the conditions an individual experience but also on its internal state and phenotype. However, among early breeding decisions, at least two yet remain to be investigated to complete the picture: brood sex ratio and paternity. Brood sex ratio has already been found to depend on local environmental conditions in this population (Forsman *et al.* 2008). However, the

effect of parental dispersal status was never considered in previous studies. Parental dispersal status could however affect sex ratio directly, through differences between dispersing and non-dispersing individuals in their familiarity with their local habitat and thus their ability to optimally exploit this habitat. Parental dispersal status could also affect sex ratio indirectly, through the adjustment of offspring natal dispersal probability depending on the local conditions offspring may encounter when recruiting (Julliard 2000). It would therefore be particularly interesting to test whether breeders may adjust brood sex ratio depending on their dispersal status. Furthermore, extra-pair paternity occurs in this population (Sheldon & Ellegren 1996) and parental dispersal status may also affect the female decision to engage in extra-pair copulations, depending on her familiarity with the neighbours or the phenotype of her own partner. However, whether dispersal status is linked to extra-pair paternity remains poorly investigated and completing the picture of early breeding decisions by investigate the link between extra-pair paternity would be particularly interesting.

On the other side, the results of the experimentation tended to show that, on the top of the costs of dispersal movements often found during transience, dispersal may also entail cost linked to settlement in a new habitat. However, in the experiment and more generally when monitoring the population, we estimated fitness differences between dispersing and philopatric individuals only considering individuals that, at least, succeed to settle and to attract a mate. It has been suggested that non-breeding may be an extreme cost of dispersal (Danchin & Cam 2002). Yet, to date, how individual's dispersal status affects territory and mate acquisition is poorly understood, particularly because it is really difficult to track individuals during this step. In the light of the results of the translocation, it would be particularly relevant to be able to monitor philopatric and dispersing individuals before settlement and maybe, ideally to determine the potential differences between dispersing and philopatric individuals at the wintering quarters. Indeed, it has been demonstrated that winter condition for instance may have long-term consequences on the reproductive success of collared flycatcher (Hargitai *et al.* 2014). However, the relation between dispersal status during the

breeding season and subsequent winter behaviour and/or condition has never been investigated to our knowledge.

All together, these two possible lines of approach may help to foster understanding of the fitness consequences of dispersal in our population of collared flycatcher but may also help to better understand how the individual's fitness costs and benefits of dispersal influence the evolution of dispersal.

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APPENDIX

APPENDIX 1

TRANSLOCATION EXPERIMENT PROTOCOL

This experiment is part of my PhD investigating the evolution of dispersal in a wild bird population and the consequences of dispersal on fitness. Familiarity with potential breeding site may increase the probability of acquiring a site of high quality. Despite, the potential benefits of philopatry, individuals frequently disperse and dispersal patterns are believed to be the result of the balance between benefits and costs of dispersal and philopatry (Greenwood, 1980). To investigate possible fitness consequences of dispersal, we will perform an experiment of “forced dispersal” by translocating birds between woodlands in which nestboxes have been provided. Birds will be caught and either moved in another woodland (moved individuals) or released in the same woodland (control individuals). Moved and control individuals will be monitored, early and late reproductive data will be recorded throughout the reproductive season (laying date, clutch size, hatching date, hatching success, nestlings growth, feeding rate, behavioral tests...). We will thus able to compare moved and control individuals to investigate possible different strategies according to dispersal status within a single reproductive event. To investigate the link between search costs for age- and sex-biased philopatry, Tomas Pärt already performed the same kind of translocation experiment (Pärt, 1995). He found among control individuals, most individuals stayed and bred within the plot they were caught, the remaining ones disappeared without being resighted elsewhere in the study area during the same year. Among displaced birds, 54% returned to their plot of capture and arrival, while 20% were found in other plots and 26% disappeared. Return rate to the area of capture was not homogeneous: in both sexes, older individuals returned to their area of capture more often than yearlings, and males returned more often than females (Pärt 1995). We also did this experiment last year and 220 individuals were

caught. Among displaced birds, 38% returned to their plot of capture and arrival, while 11% were found in other plots and 51% disappeared.

Translocation experiment

Each day, from late April to early June, ideally all experimental plots will be thoroughly searched for newly arrived males and females. Newly arrived males are easily recognizable; they sing a lot. Walking in the woodlands (while waiting for birds to get trapped or checking boxes, in particular), we will locate newly arrived birds and attempt to capture them in the same or next day(s) by setting traps in nestboxes around the point where they have been seen. Of all birds captured on a particular day we will randomly choose within sex and age, those to be translocated or used as controls. We will use a randomization-by-block design within each category (4 categories in total: 2 age classes x 2 sexes), with 4 individuals per block, 3 translocated individuals and one control individual per block. The ratio 3 experimental birds / 1 control is chosen to account for the large proportion of birds returning to their capture site (we keep the same ratio as in Pärt's study). In order to balance the two treatments between plots and within plot, each day the cumulative number that have been attributed to each treatment in each plot are recorded to make sure that the numbers are balanced.

Individuals will be caught in the nestboxes using different kind of traps (iron thread trap and swing-door trap). Individuals caught will be released 2-3 hours later maximum either in another plot (displaced birds) or within the same plot (time controls birds).

To ensure that experimental (both displaced and control) birds are not included again in the experiment, we will stick a piece of colored adhesive on top of the ring of each captured bird, identified with its ring number (and ringed if unringed), to recognize birds already included in the experiment straight upon recapture and release them immediately.

The experiment will be conducted in forest plots from the south to the norther part of the study area. Forests plots where the birds will be caught and released are :

- Tuviken (TU)
- Öja (OJ)
- Ronnarve-Powerstation (RO-PS)
- Falluden (FA)

(around 160 expected pairs in total)

Captures will be mainly conducted in the morning and the early afternoon when birds are most active, by 4 to 5 persons (10 traps each, trying to catch 2 birds at a time, for a time frame of 2 to 3 hours), one in each plot (possibly 2 in TU and /or OJ depending on the number of new individuals detected). Individuals will be captured and released in all plots. All caught birds will be identified and measured before release to record all the regular morphological measurements for the data base. Individuals will be translocate to different plots to randomize translocations in space. However, because birds should be translocate to maximize distance of dispersal in order to minimize the return rate, there are some impossible association.

Table S.1: % of individuals of each sex to be released in each patch, based on the number of pairs expected in each plot, and depending on where they have been caught. In parentheses, the corresponding nb of birds for each sex based on the assumption that the number caught equals the number expected.

From/To	TU	OJ	FA	RO-PS	Total
TU	20% (12)	60% (36)	10% (6)	10% (6)	100% (60)
OJ	60% (24)	20% (8)	20% (8)	0	100% (40)
FA	30% (6)	40% (8)	20% (4)	10% (2)	100% (20)
RO-PS	65% (14)	0	15% (3)	20% (5)	100% (22)

On the diagonal of the table are the controls (released in the same plot as where they were caught)

Breeding monitoring and data collected

Nest building stage and laying:

Between end of April and early June, plots will be visited every 2 days to record nest building stage, laying date and clutch size (nests where laying has started will be visited a bit later when the clutch is expected to be complete). To investigate possible correlation between several personality traits and dispersal status, we will measure three personality traits: (1) aggressiveness (agonistic reaction towards a con- or heterospecific competitor); (2) neophobia (defined here as individuals' reaction to a new situation represented by the presence of a novel object in a known environment; Greenberg & Mettke-Hoffman 2001); (3) risk taking (reaction to a risky situation, here, the presence of a nest predator; Réale et al. 2007).

During nest building stage (between building stage 2/4 and 4/4), aggressiveness tests will be performed (**Appendix 2**). Two aggressiveness tests will be conducted on each

nest, one using a conspecific lure and one using a heterospecific competitor lure (great tit).

Incubation:

To estimate egg size, we will take pictures of clutches after completion, i.e. at the beginning of incubation.

Between 8 and 10 days after the beginning of incubation (females start to incubate on the day of laying the last egg), females will be caught to be identified, ringed if necessary, measured for all the standard morphological measurements and blood and feather sampled (for other purposes than this experiment, but DNA will be used to check extra-pair paternity). Stress level can be measured from feathers, so we plan to collect feathers and possibly check this later.

Nestling rearing period:

From the 12th day of incubation onwards, nests will be checked daily to record hatching date of the first chick. If all eggs have not hatched, nests will be visited again on the next day to record the number of hatchlings and eggs.

After hatching, several measures and behavioral tests are planned (cf following planning).

- Day 2: Counting of the number of nestlings and remaining egg(s). Blood sample are taken on chicks to determine sex ratio and extra-pair paternity.
- Day 5: Chicks weighing. Chicks will be weighted regularly throughout the season to measure chicks' growth. To have a good estimate of growth, chicks will be weighted. The feeding rate and neophobia level will be measured following Greg's protocol.
- Day 8: Chicks are ringed and weighed.
- Day 10: Chick are weighed.
- Day 12: Chicks will be measured (tarsus length and possibly wing growth) and weighed.

- Day 13 and 14: Risk taking measurement in the context of nest defense following Greg's protocol.

Fledge checks (after 18 days after hatching) to record final breeding success.

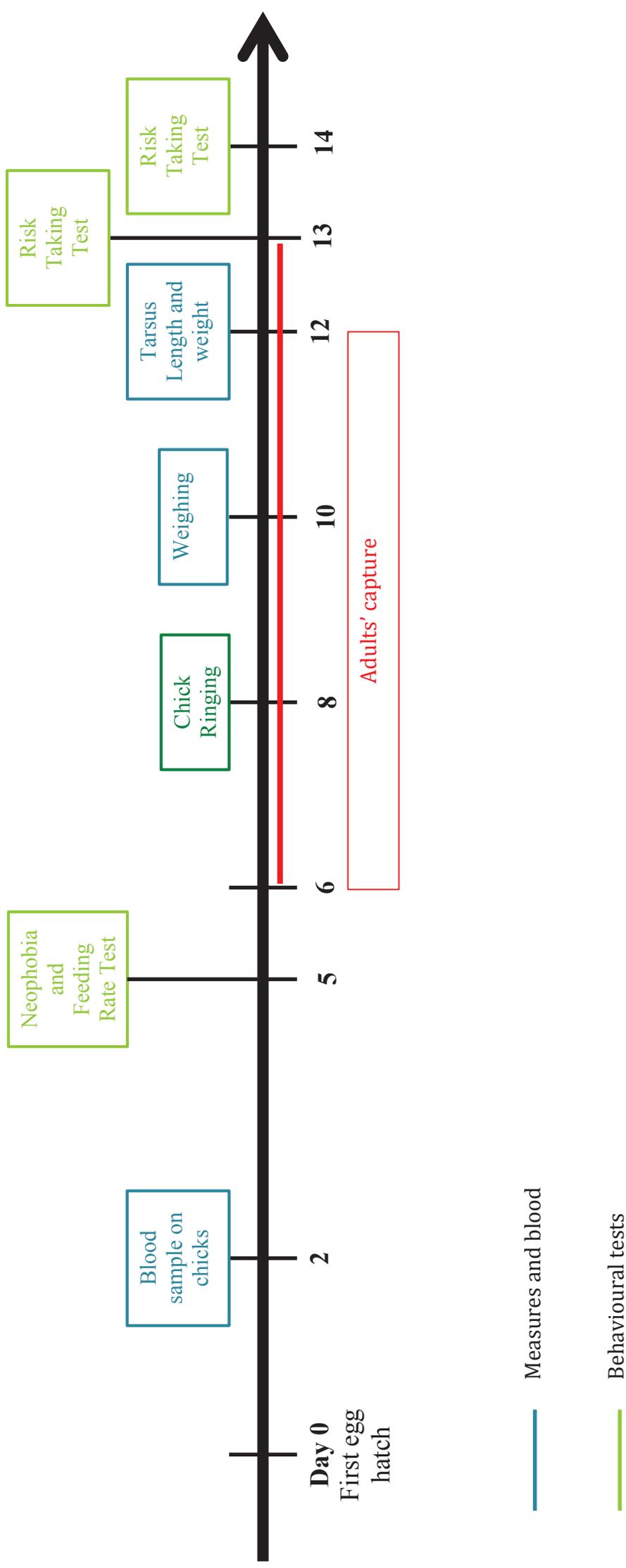


Figure S.1: Timeline of the different behavioural tests, measures and sampling performed on adults and nestlings during the breeding season in the context of the experiment.



Figure S.2: Patches between which individuals will be moved in 2013.

APPENDIX 2

DISPERSAL BEHAVIOURAL SYNDROME IN THE COLLARED FLYCATCHER: PROTOCOLS FOR MEASURING PERSONALITY TRAITS IN THE FIELD

Gregory Daniel PhD project

AGGRESSIVENESS

We will measure the level of aggressiveness towards (1) a conspecific and (2) a main heterospecific competitor (the Great tit, *Parus major*). To elicit an aggressive response, we will simulate an intrusion into the territory of the tested pair using either dummy flycatchers or great tits that will be placed on the top of the focal pair's nest box. At the same time, songs of the corresponding species will be played back using a portable broadcast set at the bottom of the tree where the nest box is attached. The test will be conducted preferentially during the nest building stage (between building stages 2/4 and 4/4) and possibly during the first days of laying, but before the beginning of incubation. Nest building and egg laying are indeed the periods during which individuals are the most susceptible to lose their nest box (or partner) to a conspecific or heterospecific and therefore are expected to defend most their nest box / partner.

We will measure the level of aggressiveness against a con- and a heterospecific individual twice on each individual, in order to decrease the effect of random variations on the measure of aggressiveness (e.g. of external origin); the average of the two measures will be used as the response variable in the analyses. In total, each individual will therefore be tested four times (2 intraspecific and 2 heterospecific tests), each test being conducted on a different day (i.e. for each individual, the tests will be conducted over four possibly non consecutive days). Furthermore, the intraspecific and heterospecific tests will be alternated, the first test being chosen

randomly by blocks of two nests. Five different dummies and playback songs of each species will be used to avoid pseudoreplication problems (dummy and playback number will be included as a covariate in statistical models, along with order of the tests). In order to measure responses of both pair members, we will present male dummies for great tits and both male and female dummies simultaneously for flycatchers, so that both the male and the female should react to the presence of a same-sex intruder. The dummy(ies) of the specific species will be chosen for each test using a random-by-block procedure (with blocks of five nests) (but see below).

We expect that each test will last 15 min maximum. In the beginning of the season, we will make 20 to 40 trials tests of 25 to 30 min, and check whether most of the between-individual variation in measured aggressiveness is captured (as we expect) within the first 15 min. The rest of the tests will therefore be reduced to 15 min, possibly 10 min if this appears to be sufficient. If we conclude from the trial tests that tests should last more than 15 min (20, 25 or even 30 min), we will use video recordings to record the tests. The video recorders will be placed at a distance of 7-8 meters away from the nest and covered by a camouflage net. The image frame will be set to 1 m around the nest box, in order to record both direct interactions with dummies and behaviour at a close distance. If direct observations are possible (which would be preferred), each test will be performed as follows: *(i)* after having decided where he/she would observe the scene from (from a distance of 7-8 m away from the nest box), the observer sets the dummy on the box (firmly attached to the box to avoid falling in case of attacks) and the playback on as quickly and quietly as possible; *(ii)* the observer returns to his/her observation spot and covers him/herself with camouflage net; *(iii)* the observer records the behaviour of the focal pair during the test. The behavioural variables that will be recorded are: *(i)* number of direct attacks of the dummy, *(ii)* number of times each member of the focal pair is flying or hovering around the dummy within 0.5 m, and *(iii)* time when each attack / flight takes place; in each case, the sex of the bird will be recorded. These measures will allow us to compute an aggressiveness score for each individual tested as done in

Duckworth 2006 (score of 1 = non- aggressive to 6 = most aggressive). Variables that may affect the observed behaviours, such as date, time of the day, weather conditions, nest building stage, etc. will be recorded and included as covariates in analyses.

We aim at testing aggressiveness level of 250 to 300 pairs, mostly in the central and Southern part of the study area, from FA South up to FK North; this part of the study area should indeed be less prone to immigration from the new study plots located North (see Doligez et al. 2009), therefore optimizing the information about parentage relationships between individuals. Tests should take place from the first days of May until the first days of June for the new very late nests, with an expected peak between 5th and 20-25th of May approximately.



Figure S.3: Measure of aggressiveness behaviour in case of conspecific competition. Male and female dummies flycatchers were positioned on the nest-box and song are broadcasted.

NEOPHOBIA

Measuring exploration behaviour by placing individuals into a new environment requires catching individuals and using field cages (a standard field test is currently under development on blue tits in several field sites), and can therefore not easily be done on a large number of individuals. Here, we will therefore not measure exploration behaviour but level of neophobia, by placing a novel object on the nest box of the birds, i.e. in a known environment (see Garamzezi et al. 2009). The novel object chosen will be determined during the first 20 trial tests by choosing among different colorful objects of about 8 cm high, and whose shape should not be close to objects that the birds may experience in nature. Neophobia tests conducted on great tits in the same study site in 2010 used toy hockey players (around 7cm high, blue and red colors), which elicited a good response when placed on the front of the box, close to the entrance hole (1-2 cm), left side. Trial tests will therefore start with these toy hockey players. If they elicit no or little response in flycatchers, possible alternative objects could be black and yellow streaked bead crocodile, orange vinyl leaves, colored dummy feathers...

The neophobia test will be performed when nestlings are 4 or 5 days old, i.e. before the parents are caught for identification and measurements. It will be coupled with a temerity test and recording of the parental feeding rates. The test will last a total of two hours, and will therefore be video recorded. The test will be performed as follows: (1) the observer prepares the video recorder; (2) the observer walks to the nest box and opens it to (i) check the presence of alive nestlings and (ii) standardize the time present at the box; (3) the observer walks away from the box (>300 m) during 1 h, paying attention not to elicit alarming behaviour from other pairs (that could be heard by the focal pair) if standing in one place; (4) the observer comes back after one hour, walks again to the nest box, and this time he/she attaches the novel object on the front side of the nest box, always at the same place (same distance to the entrance hole); (5) the observer walks away for another hour (tapes last 2h15). Temerity will be measured by the latency for individuals to return to their nest box

after the departure of the observer during the first step of the test. Neophobia will be measured by the difference in the latencies for individuals to return to the box in the absence and presence of the novel object (thus controlling for the presence of the observer at the nest box). We will also measuring any aggressiveness reaction to the novel object using the same score as for aggressiveness tests based on potential flying/hovering and attacking behaviours if any are observed. We aim at testing temerity and neophobia level of at least 250 pairs among those for which aggressiveness level has been measured. Parental feeding rate will be determined for each pair member using the video recordings of the first (and possibly second) step of the test, once parents have returned to the box.

Tests should take place from the very first days of June until the first days of July for the very late nests, with an expected peak between 5-8th and 20-22th of May approximately.



Figure S.4: Nest-box with the novel object positioned in order to evaluate neophobia.

RISK TAKING (NEST DEFENCE)

We will measure risk taking behaviour within the context of nest defense, by mimicking a nest predation event. We will place dummies of two common passerine nest predators in the study population, the great spotted woodpecker (*Dendrocopos major*) and the red squirrel (*Sciurus vulgaris*) on the nest box of the focal breeding pair. Gotland is indeed free from mustelids, which are the main nest predators on the mainland. However, woodpeckers and squirrels can also injure adults during nest defense. Previous observations in this population clearly show that flycatchers can respond to the presence of these predators on their nest box by alarming and/or attacking them.

The test will be conducted during the second half of the nestling rearing period, e.g. when nestlings are 11 to 13 days old, a period when parental investment in nest defense has been shown to be high in different hole-nesting passerine (and other) species. The idea would be to avoid interactions with adult catching and nestling measuring, thus the test may be better scheduled when nestlings are 13 days old, i.e. when most parents should have been caught and nestlings have been measured (day 12). The nest predator dummies will be attached to the entrance hole, mimicking a nest predation event with predators trying to pick up nestlings. As for aggressiveness tests, several (3 to 5) dummies of each nest predator species will be used to avoid pseudoreplication problems (dummy number will again be included as a covariate in statistical models). The sex of the dummy should not matter here although if possible male woodpeckers will be preferred due to their red plumage coloration (to standardize the stimulus). If not all dummies are of the same sex, sex of the dummy can be included as a covariate in the statistical analyses. The dummy of the specific species will be chosen for each test using a random-by-block procedure (with blocks of 3 to 5 nests, i.e. number of different dummies used) (but see below). As for aggressiveness tests, we plan to measure risk taking level twice on each focal pair, once for each nest predator species (we will use either the two different measures or the average of the two measures as the response variable in the analyses).

Each risk taking test will again be conducted on different days, and the order of the tests for a given focal pair will be determined at random by blocks of two nests.

We will record nest defense behaviour during 15 minutes after attaching the dummy nest predator to the nest box. As for aggressiveness tests, we indeed expect that each test will last 15 min maximum. On the earliest nests, we will make 20 trials tests of 25 to 30 min, and check whether most of the between-individual variation in measured nest defense is captured (as we expect) within the first 15 min. The rest of the tests will therefore be reduced to 15 min, possibly 10 min. If we conclude from the trial tests that tests should last more than 15 min (20, 25 or even 30 min), we will use video recordings to record the tests (see above). If direct observations are possible (which here again would be preferred), each test will be performed as follows: (i) after having decided where he/she would observe the scene from (from a distance of 7-8 m away from the nest box), the observer attaches the dummy nest predator on the nest box of the focal pair (firmly attached to the box to avoid falling in case of attacks) as quickly and quietly as possible; (ii) the observer returns to his/her observation spot and covers him/herself with camouflage net; (iii) the observer records the behaviour of the focal pair during the test. The behavioural variables that will be recorded are the same as during the aggressiveness tests, i.e. (i) number of direct attacks of the dummy, (ii) number of times that each member of the focal pair is flying or hovering around the dummy within 0.5 m, and (iii) time when each attack / flight takes place; in each case, the sex of the bird will again be recorded. Again, variables that may affect the observed behaviours, such as date, time of the day, weather conditions, brood size on the test day, fledgling condition (measured on day 12) etc. will be recorded and included as covariates in analyses. In particular, at the end of the test, when taking the dummy nest predator away, the observer will open the box to check brood size. These measures will allow us to compute a risk taking score for each individual tested. We aim at testing risk taking behaviour of 200 pairs minimum among those for which both aggressiveness and neophobia has been measured.

Tests should take place between the 10th of June until the first days of July for the few very late nests, with an expected peak between 15th and 25th of June approximately.



Figure S.5: Risk taking behaviour was tested in the context of predation using a dummy positioned at the entrance of the nest-box.