Should I stay or should I go?

Breeding dispersal decisions in a young avian hybrid zone
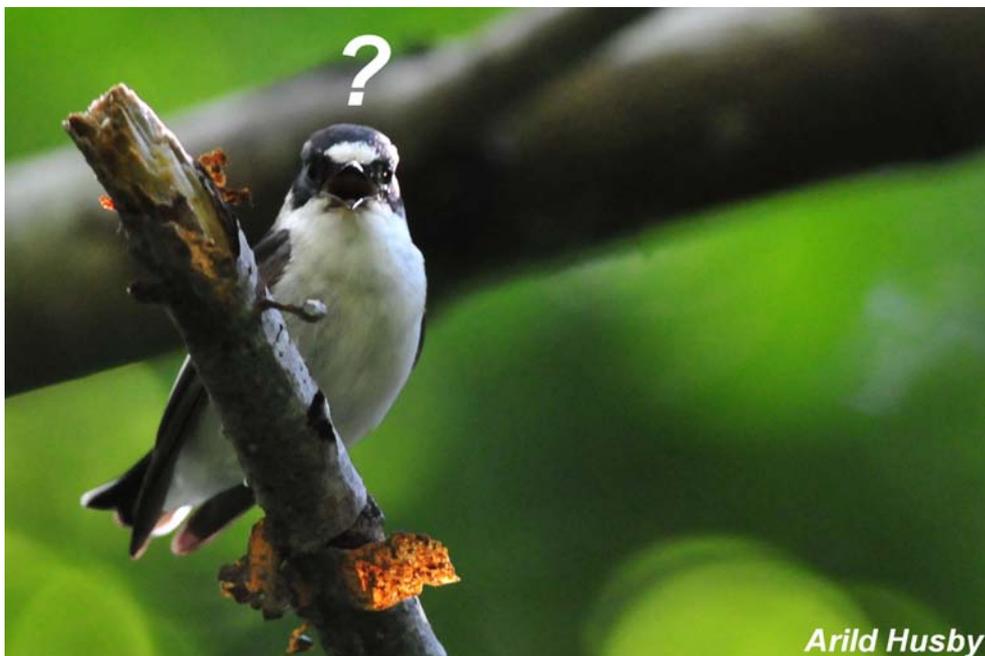
Jakub Rybinski

To Marek Keller

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Abstract

The study of speciation holds an exceptional place in evolutionary biology, as it answers the questions about mechanisms responsible for the origin of biodiversity. Natural hybrid zones provide us with an opportunity to witness the speciation machinery in action and are often assumed to be maintained by the migration-selection balance. However, the role of smaller scale movements in hybrid zone dynamic remains not fully understood, i.e. to what extent they facilitate or impede gene flow between populations. In this study I investigated the role breeding dispersal plays in a *Ficedula* hybrid zone on Ö land. I found that the probability of changing breeding sites between years was significantly related to a b ird's sex, age and reproductive success in the previous breeding season, but not to the density of breeding birds or to estimates of the overall quality of the sites. Moreover I found no di fference in breeding dispersal propensity between the two interacting flycatchers (i.e. *Ficedula hypoleuca* and *F. albicollis*). High site fidelity of both species therefore appears to be a factor promoting stability of this young hybrid zone.

Introduction

Speciation lies at the very core of modern research in evolutionary biology. It is not only of theoretical importance, but the knowledge about how species originated is essential also for conservation of biodiversity (Freeman and Herron 2007). Since the "modern evolutionary synthesis" done by Huxley (1942), the concept of species and the way they form has been extensively advanced (e.g. Kirkpatrick and Ravigné 2002; Servedio and Noor 2003; van Doorn et al. 2009), and a variety of different species concepts are nowadays used in biological studies (Mallet 1995; Mayr 1996). Despite the fact that scientists agree upon the basic definition of what a species is – the smallest unit that evolves independently (Freeman and Herron 2007) – there are approximately 26 species concepts used in the literature (Wilkins 2006)**.** Three of them are most widely used: the morphospecies concept, the phylogenetic species concept and the biological species concept (Freeman and Herron 2007).

The morphospecies concept focuses on i nsightful analysis of phenotypic differentiation. It has wide application, as it can be used to identify both present and extinct species. However it may be prone to arbitrariness and cryptic species will not be classified separately with this method (Freeman and Herron 2007).

The phylogenetic species concept builds upon the common ancestry of individuals. Evolutionary independence is inferred from the existence of diagnostic traits that while being shared by a group also differentiate it from another group. The main advantage of this concept is its versatility and the main limitation is time and cost of building phylogenies (Freeman and Herron 2007).

The biological species concept, since being championed by Mayr in 1942, is probably the most meaningful species concept to many zoologists, and it is also applied in legislation around the world (Freeman and Herron 2007). The main criterion for identifying species under this concept is reproductive isolation. Because evolutionary independence is inferred, among other factors, from the lack of gene flow, this concept offers a logical classification. The biological species

concept has, however, many limitations. If ranges of the populations do not overlap, or if the species is extinct, or if it is asexual, reproductive isolation cannot be examined, and has to be hypothesised (Freeman and Herron 2007).

In speciation research the biological species concept is particularly useful. This is because the common theoretical framework for speciation focuses on t he development of reproductive isolation (Mayr 1996) since reduced gene flow is essential for separate evolution of the forming species. The first step in the speciation process is population divergence. Population divergence can be driven by genetic drift, natural and sexual selection. Divergence in traits such as mating or foraging behaviour (e.g. Uy and Borgia 2000; Benkman 2003) leads to the build-up of reproductive isolation thorough reduced likelihood of crossing between two populations (i.e. assortative mating) and selection against hybrids (e.g. because their intermediate phenotype makes them poorly adapted to either parental niche). As population divergence proceeds and the differences between populations accumulate genetic incompatibilities will also accumulate over time. This proposed two-steps framework is a simplification. It is also possible that the evolution of sexual isolation and the build-up of genetic incompatibilities precede major ecological divergence and that young species go through niche differentiation when they come into periods of secondary contact (Rundell and Price 2009).

Much of the debate in the speciation literature focuses on the external conditions needed for speciation to occur. Allopatric speciation is believed to be the most common in nature and under this model geographic isolation of populations is a prerequisite for independent evolution of populations (i.e. for the cut off of gene flow). There are many well studied examples where either dispersal or vicariance triggered the speciation process (see Bonacum et al. 2005; Knowlton et al. 1993). When considering vicariance we cannot forget habitat fragmentation by glaciers during the Pleistocene (e.g. Hoskin et al. 2005). Peripatric speciation is a variation of allopatric one, the difference lays in the size of the populations – in this case a smaller population becomes isolated at the edge of the larger one. In models of parapatric speciation there are no clear cut barriers to gene flow and new species are formed from a continuous population, however individuals do not mate randomly. The fact that individuals are more likely to mate with nearby partners reduces gene flow, which may be additionally impeded by different selection regimes in different parts of population range. In models of parapatric speciation new species are formed from a continuous population. Recently Heinz and co-workers (2008) analysed the coevolution of an ecological trait and dispersal patterns and revealed the importance of dispersal evolution in how populations distributed along environmental gradients can respond to selection. Sympatric speciation happens within the range of the ancestral population. The main difference is that this mode of speciation does not require geographic isolation; here events like utilizing new habitat are responsible for reduced gene flow. Sympatric speciation has been for years the most controversial one (e.g. Mayr 1963), well explained by theoretical models (Maynard-Smith 1966), but only recently empirically demonstrated (Bolnick and Fitzpatrick 2007, and references therein).

During the last years, studies on speciation have shifted the focus from geographical factors, to the mechanisms of speciation (i.e. the relative importance of genetic drift, natural and sexual selection in driving populations apart). Genetic drift used to be considered as an important factor in speciation (e.g. Templeton 1996), however recently there has been a shift towards recognition of natural selection as the most important force behind the divergence of populations (Schluter 2001; Tonnis et al. 2005; Via 2002; Via 2009). Moreover, theoreticians provided us with models

showing that sexual selection can also drive speciation (e.g. Lande 1981) and there is empirical evidence for this to happen (e.g. Uy and Borgia 2000). The way in which natural and sexual selection interact in speciation has become nowadays of major interest to scientists studying speciation (Schluter 2000), because they allow us to combine all steps of speciation into a more logical framework based on the concept of the so called ecological speciation (Schluter 2001) which builds on the assumption that reproductive isolation evolves through the divergence of ecological traits.

The main obstacle in studying speciation is time. Mutations and genetic differences responsible for species genetic isolation accumulate over time. However in some cases recently diverged populations meet again during secondary contact and interbreed. This process is called hybridization and results in the creation of hybrid zones, where hybrid offspring is frequent. The importance of hybrid zones in the study of speciation has been acknowledged by many scientists (e.g. Barton 2001) as hybrid zones provide unique opportunities to study speciation mechanisms in action (Via 2009). They are formed mostly between species that diverged in allopatry and can have various results. The possible outcomes depend on the fitness of the hybrids relative to their parents (Freeman and Herron 2007).

First, if the hybrids are inferior to the parental forms then the hybrid zone will be narrow and short lived, due to the selection pressure acting against hybrids, eventually resulting in reinforcement. The theory behind reinforcement states that when closely related species meet and hybridize, mechanism acting against hybridization will evolve. It has been hypothesised by Dobzhansky (1937) that populations evolving towards different optima when interbreeding will produce offspring of lower fitness. Due to selection against hybrids, the evolution of any trait preventing interbreeding will be promoted, and result in prezygotic isolation (Kirkpatrick and Ravigné 2002). Reinforcement can be an important factor in speciation, although not essential (Servedio and Noor 2003). Another way of maintaining genetic isolation without reinforcement is postzygotic isolation (Freeman and Herron 2007). This may happen when hybrids are sterile (Haldane 1922).

Second, if the hybrids are equal to the parental forms, then the hybrid zone will be wide and long lived. As the equality of fitness between interbreeding species and hybrids enhances gene flow, parental populations may eventually coalesce (Freeman and Herron 2007).

Finally, if the hybrids are superior to the parental forms, then the hybrid zone will be stable or a new species will be formed. The first will happen if the superiority is related to intermediate habitat where parental species meet, the latter if the superiority is related to a novel habitat (Freeman and Herron 2007).

As the climate changes and species' ranges shift, existing hybrid zones will move (e.g. Krosby and Rohwer 2010) and new hybrid zones will emerge. Therefore the nature of species interactions within hybrid zone is of great importance to predict the outcome of future hybridization events and the stability of present hybrid zones (Barton and Hewitt 1985; Barton and Hewitt 1989). To date, however, the studies of hybrid zones focused on theoretical aspects of gene flow (Barton and Hewitt 1985) and the structure of the hybrid zone itself (Durrett and Zahle 2007). Only recently the effort has been put into studying what role ecology and behaviour play in hybrid zone maintenance (Arnold 1997; Adamík and Bures 2007). It is remarkable how

fast their importance has been proved by recent studies (e.g. Saetre et al. 2003; Patten et al. 2004; Vallin et al. 2012).

Among hybridizing species, flycatchers hold a special place. Birds in general provide scientists with an opportunity to study speciation, as they hybridize often and produce fertile hybrid offspring (Grant and Grant 1992). Collared flycatcher (*Ficedula albicollis*) and pied flycatcher (*Ficedula hypoleuca*) are passerine hole-nesting birds that probably diverged in allopatry approximately 1 million years ago, when during the last glaciation period ancestral populations took shelter in separate refuges (Saetre et al. 2001). When they co-occur they hybridize to some extent producing viable offspring that follows Haldane's rule (1922) – the heterogametic sex (females in birds) is sterile while the homogametic sex suffers from reduced fertility. The opportunity presented by this system, meaning a chance to study evolution of reproductive barriers in action, has been widely recognized and today we have detailed knowledge about the interactions between flycatcher species (reviewed in Qvarnström et al. 2010; Saetre and Saether 2010).

The uniqueness of the flycatcher system lays in the fact that the species in question form hybrid zones of different types. As sister species diverged in separate refuges (Saetre et al. 2001) they evolved separately and now differ in habitat use (Qvarnström et al. 2009). As the result of the climate change, collareds expanded to the north and began interacting with pieds, apparently excluding them from their environment (Saetre et al. 1999). In the light of the fact, that collared flycatcher is among the species expected to expand their territory further on, as the climate changes (Huntley et al. 2007) the nature of this exclusion is of particular interest. A Central European hybrid zone was formed as a consequence of the collareds expansion. This zone dynamics has been studied and in literature it has been referred to as a clinal zone (Saetre et al. 1999), however according to Barton and Hewitt (1985) in order to prevent confusion in terminology such zones should be rather named tension zones to prevent confusion. The discrepancy roots in the fact, that at the beginning term cline was used to describe only hybrid zones maintained by balance between selection and dispersal, although later its' use became confounded (see Barton and Hewitt 1985). Therefore, new term "tension zone", coined by Key (1968), was suggested to distinguish clines maintained by mentioned balance from clines that are not (as clines driven by selection-migration balance tend to minimize their length, Key 1968). The theory behind their dynamics is extensive (see Barton 1979; Barton and Hewitt 1985; Durrett et al. 2000; Durrett and Zahle 2007) and far beyond the scope of this thesis.

As the Central European hybrid zone is a relatively old, the mechanisms facilitating competitive exclusion or coexistence had enough time to evolve and nowadays it might be difficult to infer their very nature. The isolated hybrid zone on the Swedish islands of Gotland and Öland offers a much better chance of success. On Gotland collareds arrived approximately 150 years ago (Lundberg and Alatalo 1992) and until today almost completely excluded native pieds (L. Gustafsson, personal communication). The first collared pairs were recorded on Öland in the 1960s (Qvarnström et al. 2009). Since then the proportion of pieds breeding in suitable habitat decreased (Qvarnström et al. 2009). The question about the future of this island hybrid zone remains open. Such isolated hybrid zones are hypothesised to be maintained by a selection-migration balance. The dynamics of both, clinal and island, hybrid zones have been compared by Sætre and co-workers (1999). The focus of the mentioned study was on the patterns of gene flow and the authors suggested that the difference in gene flow patterns between the two types of

hybrid zones may be accredited to the accumulation of fertile hybrid individuals (Sætre et al. 1999). This does not seem to hold true anymore for the Baltic populations. Recent studies provided evidence for selection against hybrids (Svedin et al. 2008; Podevin et al. unpublished data), that remains in later generations (Wiley et al. 2009). Mechanisms promoting stable coexistence of the flycatcher species have also been proposed (Qvarnström et al. 2009; Vallin et al. 2011) and among them behaviour plays an important role.

Dispersal decisions are important, because they directly affect animal fitness (i.e. staying in the area that guarantees high reproduction success, or abandoning the poor quality one). Theory behind the evolution of dispersal behaviour (Greenwood and Harvey 1982, and references therein) suggests kin-competition and inbreeding avoidance as evolutionary drivers promoting dispersal and philopatry and area familiarity as drivers impeding dispersal. Studies of flycatcher species provided an evidence for resemblance between parents and their offspring in their dispersal propensity (Doligez et al. 2009); moreover there is an evidence of non-random habitat choice when dispersing (Doligez et al. 2004a; Doligez et al. 2004). The question is how dispersal patterns can be affected by recent hybridization events and what role previous experience plays in hybrid zone dynamics.

Here I investigate the role dispersal has in shaping the flycatcher hybrid zone. The common practice is to distinguish between two types of dispersal behaviours: natal and breeding dispersal (Greenwood and Harvey 1982). They correspond to movement between the natal area and area of first breeding, and movement between breeding areas in consecutive years, respectively. I follow this classification in my master thesis and limit my analysis to breeding dispersal.

Material and methods

Study system

Ecology of *Ficedula* flycatchers

Collared (Figure 1) and pied flycatchers (Figure 2) are small migratory songbirds that spend the winter in Africa. In late April, the first males arrive at the breeding grounds in Europe and start competing for natural nest holes or artificially placed nest boxes. Approximately one week later females arrive. Males defend chosen territories with breeding holes/boxes and sing to attract females. Females evaluate a number of males before choosing one of them. Shortly after the decision is made the female builds a nest. The most common breeding system in flycatchers is monogamy, although polygyny (Gustafsson and Qvarnström 2006) and extra-pair copulations (Sheldon and Ellegren 1999) occur. When the nest is ready, females lay five to seven eggs and then incubate them. The eggs usually hatch in the beginning of June, and both parents feed the chicks with insects. Flycatchers try to optimize laying date in such way that clutches hatch when the availability of food is the highest. After hatching the chicks stay in the nest for approximately 15 days. After they have left the nest, their parents provide them with food for one more week. At the end of breeding season, after fledging of the offspring, birds moult feathers and migrate to Africa in the middle of August.

Figure 1 Collared flycatcher male.

Figure 2 Pied flycatcher male.

Collared males are slightly bigger than pied males and share a similar black-and-white plumage. However, the white patches on the forehead and wings are bigger in collared males. In addition, collared males have a distinctive white collar around their neck, which is absent in pied males. On the contrary pied males display bigger variation in plumage shade, which ranges from jet-black, typical for collareds, to a more brownish, female alike, coloration. Females of both species are a bit harder to distinguish. Again collareds are a bit bigger, but plumage differences are much more subtle. Collared females are more greyish, while pied females more brownish. The two flycatcher species can be easily distinguished by species-specific alarm calls and songs.

Range of *Ficedula* flycatchers

The breeding ranges of collared and pied flycatchers overlap in two European hybrid zones (Figure 3). The oldest one, is dated 12 000 years back and is located in Central and Eastern Europe (Sætre et al. 1999). A much younger hybrid zone is located on the Swedish islands of Gotland and Öland. These islands were initially inhabited only by pied flycatchers. Around 150 years ago the first collared individuals arrived on Gotland (Lundberg and Alatalo 1992) probably as a result of range expansion caused by climatic changes. They consecutively excluded pieds from their habitat and nowadays Gotland is inhabited mostly by collared flycatchers. Later on (during 1960s) collared flycatchers arrived on Öland (Qvarnström et al. 2009), where they still co-occur and hybridize with pied flycatchers. In my thesis I evaluated data collected on Öland during the last 10 years.
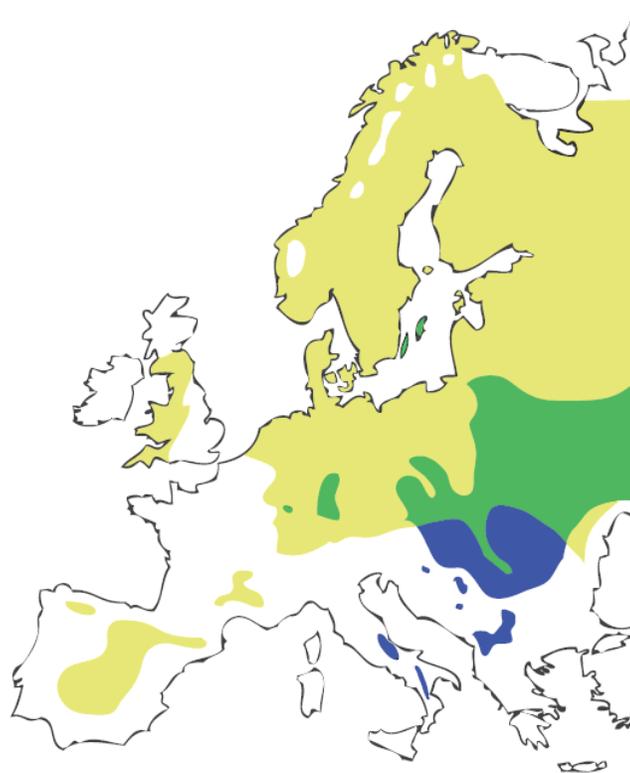

Figure 3 Breeding range of the two flycatcher sister species (yellow represents pieds breeding range, blue represents collareds breeding range and green represents areas where both species co-occur). Reprinted after Qvarnström et al. 2010, with permission from the publisher.

Hybridization in *Ficedula* flycatchers

Most of the breeding pairs on Öland are conspecific. Occasionally (4% of the breeding pairs, Svedin et al. 2008) heterospecific mating happens and hybrid offspring is produced. Several mating barriers reducing gene flow have been identified in this study system. Among premating barriers we can distinguish:

1. Assortative mating – females' choice is based on distinct, species-specific traits, such as plumage or song (Wiley et al. 2005; Qvarnström et al. 2006).
2. Habitat segregation – collared flycatcher choose to breed in the fine quality deciduous forests, and as they are superior competitors, they push away pied flycatchers from this type of habitat into lower quality mixed forest or pine areas (Qvarnström et al. 2009; Vallin et al. 2011).
3. Different breeding time – collared flycatcher breed earlier (Alatalo et al. 1990).

There is also evidence for postzygotic isolation between two flycatcher species. Hybrid females are sterile, while hybrid males suffer from reduced fertility (Svedin et al. 2008, Podevin et al. unpublished data). Despite all mentioned barriers, reproductive isolation is still not complete. Maladaptive mate choice is caused by imperfect species recognition (for example due to mixed songs, Qvarnström et al. 2006) or shortage of both conspecific males and good territories.

Dispersal of *Ficedula* flycatchers

Dispersal patterns of birds have been extensively studied over past years (for reviews see (Greenwood and Harvey 1982; Paradis et al. 1998; Jenkins et al. 2007). General studies for flycatchers boil down to three papers discussing the evidence for most common dispersal predictors: sex, age and reproductive success.

In the first study, Harvey and coworkers (1984) analyzed the breeding dispersal of pied flycatchers *F. hypoleuca*. Median dispersal distances between consecutive breeding attempts in the study population in the Forest of Dean in Gloucestershire varied from 52 to 133 meters, which was approximately equal to 1 to 3 nest boxes (see Harvey et al. 1984). In addition they observed that older birds are more likely to move shorter distances, females are less likely to breed in the same area after their partners' death, divorce or breeding failure (Harvey et al. 1984).

In the second study, Pärt and Gustafsson (1989) investigated similar patterns in collared flycatchers on the Swedish island of Gotland. Their results showed significant difference in breeding dispersal between the sexes, a lack of correlation between breeding dispersal and body morphology or condition, and in case of yearling females – significantly longer distances travelled after reduced breeding success or breeding failure, while for males – significantly longer distances travelled after remaining unmated throughout the breeding season. Pärt and Gustafsson (1989) proposed that breeding dispersal to some extent can be explained by availability of territories and on prior knowledge of the quality of breeding sites.

In the third study, Montalvo and Potti (1992) studied breeding dispersal patterns of a Spanish population of pied flycatchers. In their population there was no difference in dispersal between the sexes. Females tended to disperse shorter distances with age, while for males this pattern was

not significant. However, males that travelled shorter distances acquired territories of better quality that individuals travelling longer distances. There was no evidence for similar pattern in females. The authors concluded that their results are consistent with the hypothesis that the choice of breeding site is based on prior experience, in accordance to the work done by Pärt and Gustafsson (1989).

To summarize, in flycatchers several factors seem to play a significant role in determining dispersal decisions. Among them are: the bird's sex and age, previous reproductive success and prior knowledge of the breeding grounds. To my knowledge, the link between dispersal decisions and risk of hybridization has never been investigated so far.

Data gathering

The study population on Öland is monitored each year since 2002. At the beginning of the breeding season, over 2000 nest boxes are cleaned, and then checked every 4th day for the evidence of nest building. After a nest has been found, it is monitored throughout the breeding season. For each breeding attempt we record the laying and hatching date, number of laid eggs, number of hatched eggs, number of fledged chicks, etc. Each breeding adult is captured at least once during the breeding season and morphological traits are measured. Sex, species, age and ring number of each captured bird are recorded. Individuals without a ring are ringed. From each individual a blood sample is taken. Chicks are also measured and sampled for blood. I visited Öland for two months during the breeding season in 2011 and helped with data gathering.

Data analysis

In order to investigate the factors influencing breeding dispersal of flycatchers I used data from Öland collected during the whole study period 2002-2011.

I focused on the distances the birds dispersed between consecutive breeding seasons. Statistical modelling of distance in meters has been proven difficult. Firstly, response variables in patchy environment are not independent. The distribution of distances is determined by the distribution of suitable habitat, as the birds do not decide freely how far to go. Different solutions to this problem have been proposed, among them are: log transformation of the variable, which deals only with the statistical side of the problem, and randomization (Noordwijk 1984; Noordwijk 1995). Secondly, there is a bias in dispersal estimates, caused by non-random distribution of observers (Noorwijk 1995). Study areas are usually limited by the number of human observers, which may result in underestimation of dispersal – animals dispersing longer distances may leave the study area. In this case the animal is treated as dead, what may lead to a false conclusion about high mortality of dispersers or lower dispersal propensity of a certain group of animals. By no means have these problems been definitely solved, and in any analysis of animal dispersal we should keep them in mind. To minimize the impact of the first issue, I decided to statistically analyse only the distances travelled within areas. As this decision resulted in the exclusion of birds that shifted areas between consecutive breeding seasons, I performed a second round of analyses, this time modelling a binary response of area change (yes or no). All statistical analyses were performed in SAS JMP 9.0 statistical software.

Results

Dispersal within area

In order to analyse dispersal within study plots between years I used 604 independent records containing data from two consecutive seasons for each bird. I found that the median dispersal distance was 129 m and that the mean dispersal distance was 181 m (SD 170 m, mean SE 7 m). Since the distance distribution was strongly right tailed, I did two separate analyses: one non-parametric of distance in meters and a second parametric test using log transformed distances (base 10; Osborne 2002). Transformation improved the distribution of distances, although individuals that bred subsequently in the same nest box still caused statistical problems. Therefore I decided to label them as outliers and exclude them from the parametric analyses. Further I investigated if there is an evidence of difference in probability of breeding in exactly the same nest box between species.

Collared flycatcher

Non-parametric tests

In total, there was information about 516 consecutive breeding attempts of collared flycatcher individuals (CF) including 268 females and 248 males. Females on average dispersed 233 meters (SD 193 meters, mean SE 12 meters), and males on average dispersed 124 meters (SD 109 meters, mean SE 7 meters). Hence, females dispersed significantly further inside the area than males (K-W one way analysis of variance, χ^2=55.7534, df=1, p<0.0001).

The dispersal distances of collared flycatchers after their first breeding season were not significantly different from those after later breeding attempts (K-W one way analysis of variance; for CF females χ^2=0.1036, df=1, p=0.7475; for CF males χ^2=0.9279, df=1, p=0.3354).

Collared flycatcher females dispersed significantly further after experiencing a complete breeding failure when compared to females that fledged at least one chick (K-W one way analysis of variance, χ^2=7.5169, df=1, p=0.0061), while for males there was no significant difference (K-W one way analysis of variance, χ^2=0.6923, df=1, p=0.4054).

Parametric tests

Female collared flycatchers dispersed significantly further than males (One-way ANOVA; R^2=0.101738, F-ratio=55.9314, df=1, p<0.0001). There was no evidence for different dispersal propensity of different age classes (yearling or older; One-way ANOVA; R^2=0.000664, F-ratio=0.3215, df=1, p=0.5710) or different ages *per se* (One-way ANOVA; R^2=0.003716, F-ratio=0.2977, df=6, p=0.9379).

Pied flycatcher

Non-parametric tests

In total, there was information about 88 consecutive breeding attempts of pied flycatcher individuals; among them were 40 females and 48 males. Females on average dispersed 203 m (SD 189 m, mean SE 30 m), and males on average dispersed 170 m (SD 186 m, mean SE 27 m). The difference in dispersal distances between the sexes was not significant (K-W one way analysis of variance, χ^2=55.7534, df=1, p=0.1653).

The breeding dispersal distance of pied flycatchers (PF) did not differ between their first breeding season and after later breeding attempts (K-W one way analysis of variance; for PF females χ^2=0.0264, df=1, p=0.8710; for PF males χ^2=1.3611, df=1, p=0.2433).

Pied flycatcher males and females did not differ in dispersal distances in respect to breeding success or failure (K-W one way analysis of variance; for females χ^2=0.7625, df=1, p=0.3825; for males χ^2=0.6087, df=1, p=0.4353).

Parametric tests

Female pied flycatchers dispersed further than males, but the difference was not statistically significant (One-way ANOVA; R^2=0.01191, F-ratio=1.9523 df=1, p=0.1663). In pieds there was no evidence for different dispersal propensity of different age classes (yearling or older, One-way ANOVA; R^2=0.000953, F-ratio=0.0744, df=1, p=0.7857) or different ages *per se* (One-way ANOVA; R^2=0.015971, F-ratio=0.3043, df=4, p=0.8742).

Between species comparison

Non-parametric tests

As the data set was dominated by records of collared flycatchers (among 308 female records, 268 were collared and only 40 pied; among 296 male records, 248 were collared and only 48 pied), I randomly sampled a subset of 40 collared individuals to make the groups equal. For both sexes there was no significant species specific difference in distances travelled within areas (K-W one way analysis of variance; for males χ^2=2.5773, df=1, p=0.1084; for females χ^2=0.2362, df=1, p=0.6270). Mean male dispersal distance was 102 m (SD 95m, mean SE 14 m) for collareds, and 169 m (SD 186 m, mean SE 27 m) for pieds. Mean female dispersal was 201 m (SD 158 m, mean SE 25) for collareds, and 203 (SD 189 m, mean SE 30 m) for pieds.

Parametric tests

I performed a one way ANOVA on log transformed dispersal distances to investigate the possible difference between species. For both sexes there was no indication of significant differences in distance travelled within the area between consecutive breeding seasons (One-way ANOVA; females R^2=0.000954, F-ratio=0.2780, p=0.5984; males R^2=0.009401, F-ratio=2.5720, p=0.1099).

In general, the mean dispersal distances after reproduction failure were bigger than the mean dispersal distances of successful individuals, however only in collared females this difference was significant (One-way ANOVA, R^2=0.025071, F-ratio=6.4290, p=0.0118). In addition dispersal distance was significantly negatively correlated with the number of fledged chicks in females of both species. Linear regression of number of fledged chicks as an explanatory variable and log transformed dispersal distance as a response variable indicated a weak decrease of dispersal propensity with the increase of number of fledged chicks (for collared females R^2=0.028765, slope=-0.03194, se=0.011738, t-Ratio=-2.72, p=0.0070; for pied females R^2=0.121375, slope=-0.066645, se=0.027922, t-Ratio=-2.39, p=0.0229). The same linear regression performed for males of both species showed no correlation between number of fledged chicks and log transformed dispersal distance.

Probability test

I investigated whether one of the flycatcher species is more likely to breed subsequently in the same nest box than the other. In general it is not common for flycatchers to breed in exactly the same box. Pärt and Gustafsson (1989) reported that only 8% and 2% of males and females respectively reoccupied nest box from the previous season. I found no significant difference between species in probability of occupying the same nest box in two consecutive breeding seasons (Fisher's exact two-tailed test; females p=0.4242; males p=0.5533).

Dispersal between areas

I investigated the propensity to change areas between breeding seasons using records of consecutive breeding attempts. Firstly I evaluated each factor separately, then I followed a bottom up procedure, adding one predictor after another starting with the most meaningful and leaving only the ones that improved model fit or significantly explained variance in the data. In total, there were 940 independent records of subsequent breeding events (Table 1).

Table 1 Number of collared and pied individuals breeding in two subsequent years and their between sites dispersal decisions.

		Dispersed	Stayed
Collared flycatcher			
Male	384	**13** (3%)	**371** (97%)
Female	429	**72** (17%)	**357** (83%)
Pied flycatcher			
Male	62	**3** (5%)	**59** (95%)
Female	65	**13** (20%)	**52** (80%)

I used the following explanatory variables: species, sex, age (in years), reproductive success (number of chicks fledged from the nest), the quality of the breeding area (standardized by year average number of chicks that fledged from nests in the area, - "out" stands for situation in the area the bird was breeding, "in" stands for situation in the area bird chose to disperse to), conspecific male and female percentage in the area (standardized by year), heterospecific male and female percentage in the area (standardized by year), nest density (number of nests in the

area per square meter standardized by year), collared and pied nests' density (as previously, but for each species). With nominal logistic model I tested individually all explanatory variables (EV, Table 2).

Table 2 Evaluation of the impact each explanatory variable has on the area change between consecutive breeding seasons.

Explanatory Variable	Model -LL	Model DF	Model χ^2	Model P	Model R^2	Model AIC	EV P
Species	0.25277	1	0.505535	0.4771	0.0008	644.858	0.4689
Sex	24.90424	1	49.80849	**<0.0001**	0.0777	595.555	**<0.0001**
Age	3.21905	1	6.438097	**0.0112**	0.0103	638.925	**0.0150**
Fledged chicks	7.99455	1	15.98909	**<0.0001**	0.0262	597.94	**<0.0001**
Patch quality – out	0.01678	1	0.033561	0.8546	0.0001	645.33	0.8544
Patch quality – in	0.4969	1	0.993975	0.3188	0.0015	644.369	0.3228
Conspecific male percentage	0.05366	1	0.107327	0.7432	0.0002	645.256	0.7432
Conspecific female percentage	0.04593	1	0.091866	0.7618	0.0001	645.271	0.7618
Heterospecific male density	0.31291	1	0.625825	0.4289	0.0010	644.737	0.4289
Heterospecific female density	0.14375	1	0.287501	0.5918	0.0004	645.076	0.5914
Total nest density	0.39726	1	0.794522	0.3727	0.0012	644.569	0.3751
CF nest density	0.09744	1	0.194871	0.6589	0.0003	645.168	0.6587
PF nest density	2.27080	1	4.541593	**0.0331**	0.0071	640.821	**0.0441**

I evaluated all factors mentioned above by adding one after another; moreover, I evaluated higher level interactions when possible. The final model included sex, number of fledged chicks, age, and second level interaction between sex and age. From all other combinations of explanatory variables this one had the strongest explanatory power and lowest information criterion score. The whole model fit was significant (-LL=37.80163, DF=4, χ^2=75.60326, p<0.0001) and it explained 12% of the variation in the data (R^2=0.1240, AIC=544.379). The model's parameter estimates are presented in the Table 3.

Table 3 Estimates of the parameters in the nominal logistic model of dispersal decisions.

Parameter	Estimate	SE	χ^2	P
Sex [F]	-1.0760731	0.2063147	27.20	**<0.0001**
Fledge	0.1874876	0.0480873	15.20	**<0.0001**
Age	1.00433418	0.0.393843	6.53	**0.0106**
Age * Sex[F]	-0.6706339	0.3930673	2.91	0.0880

The model of Öland's flycatchers indicated that females are more likely to change areas between breeding seasons. Moreover, an increase in number of fledged chicks or in age decreases the probability of changing area in subsequent years. Moreover older females are more likely to change areas than older males, although this result is only close to significance. After adding basic explanatory variables none of the factors related to the quality or density of birds in a breeding area significantly explained the remaining variation.

Discussion

Breeding dispersal can be defined as permanent movement from the site where an animal bred in the previous season to an area where it reproduces in the following season (Greenwood 1980; Greenwood et al. 1979). Although flycatchers travel more than 7000 kilometres to spend the winter in Africa and the same distance back to bred in Europe, their breeding dispersal is very limited. On the Swedish island of Öland, I found that collared males dispersed on average 124 m, while females dispersed on average 233 m within individual study areas. These values are similar to ones reported by Pärt and Gustafsson for the Gotland's population in 1989 (breeding dispersal for males close to 100 m, for females close to 200 m; more accurate data available only for distinct categories examined in the mentioned study). Pied flycatchers on Öland dispersed on average 170 m and 203 m for males and females respectively. These values are similar to the ones reported by Montalvo and Potti for their Spanish population in 1992 (median dispersal distance equal to 112.5 m in males and 159 in females) or to the ones reported by Harvey and co-workers in 1984 for British population in Gloucestershire (breeding dispersal varied from 52 to 133 m). On Öland, most of the local flycatcher population breeds in our study sites, which consists of woodlots located in a farmland landscape. I found that females of both species were more likely to change breeding sites between consecutive breeding attempts as compared to males. Another important determinant of breeding dispersal was reproductive success. A higher number of fledged chicks increased the probability of a female returning to the same area. However, the average number of chicks fledged in the area where the bird previously bred, or in the area to which bird dispersed, did not explain site changes between years. The probability of returning to the same site increased with the age and there was a tendency for older females to be more likely to change sites than older males.

In general, within sites movements were rather limited and restricted to neighbouring boxes. The situation flycatcher face on arrival in the spring depends on many random factors, such as nest box condition (individuals that arrive early may find that their previous nest box is damaged or broken) or occupancy by tits or other flycatchers. Therefore, within area movements are more likely to be a result of a non-active choice to disperse. By contrast, between sites dispersal appears to be much less random, mostly based on previous experience (e.g. Doligez et al. 2004a; 2004b). I therefore focus the rest of my discussion on breeding dispersal between sites.

Migratory birds such as flycatchers experience reduced fitness in response to bad timing of breeding (Both et al. 2005) hence for males it is crucial to establish a territory shortly after arrival, and for females to quickly find the best available male and start building a nest. Under these circumstances, dispersal decision should be efficient (i.e. both fast and accurate) in order to maximize reproductive success. In case of the flycatcher there is an evidence of prospecting, i.e. meaning that individuals acquire information about other individuals' reproductive success, and

base the dispersal decision on such prior knowledge of quality of particular nesting site on the quality of the whole breeding area (Doligez et al. 2004a).

In birds males are known to be the sedentary sex, as the most common mating system enforces males to defend resources in order to attract females (Emlen and Oring 1977; Greenwood 1980). Comparing to mammals, female birds invest less in each offspring; therefore they are not constrained to the same level by resources' availability (Emlen and Oring 1977). In case of mammals, where in most cases females are selected to defend adequate quality territories, mating systems based on mate defence evolved as a natural response (Greenwood 1980). Flycatchers seem to follow the well-established pattern of female dispersal in birds, although site fidelity seems to be much lower than in other studied species (Greenwood et al. 1979). This difference is partially explained by the fact, that dispersal decisions are affected by the situation during the onset of the breeding season. Some males face the necessity to disperse after their box is taken, but for majority of them it is more beneficial to defend their previous box if available, or look for a better one close by. Doing so, males minimize the risk that suitable breeding territory will be taken over by a new arriving male while they spend time on evaluating different sites. Moreover, long dispersal is costly and may result in lowered fitness (Pärt and Gustafsson 1989), therefore once familiar with a habitat patch they faithfully stick to it whenever it is possible. The fact that we see more females than males breeding consecutively in different sites may suggest that it is hard to establish a territory in a novel area. It might be that males who decided to change areas between seasons apparently fail in acquiring a new breeding territory. This conclusion is supported by the fact that some of those males breed in the next season, although it remains unclear whether their absence is evidence for a failed breeding season, or if these individuals actually bred but remained not captured throughout the entire season. Recently another explanation for female-biased dispersal in birds emerged, suggesting that female propensity to dispersal can be explained by availability of males (Arlt and Pärt 2008). Differences between sexes in both flycatcher systems works in accordance with the new supplementary theory, as males arrive on the breeding grounds earlier. Their choice of breeding site is limited only by box availability. On the other hand females are limited by the availability of males. They utilize the ability to evaluate males before making a decision. Competition between females is also a limiting factor, however I argue that its' effect is weaker. When a previously available male will be chosen by another female, while the choosy female inspects nearby sites, a reasonable assumption would be that it is still easier for the female to find a male in a preferred site (e.g. less rewarding secondary box of a good quality male), than for the male to establish a territory under those conditions. As a result, costs for females are lower. Moreover, in situations when there are no available males in the preferred site, it is better to decide on a male in another site, than to wait for a new opportunity, as flycatcher fitness is negatively correlated to egg laying date (Qvarnström et al. 2005).

I also expected evidence for reproductive success, prospecting or intra- and interspecific interactions playing an important role in the decision-making process. Indeed I found that breeding success of an individual female influenced her breeding dispersal. After total breeding failure, female collared flycatchers dispersed further than females that fledged at least one chick. This pattern was not visible in pied females. There are at least two possible explanations for this. First, pied females are much stronger constrained by availability of males than collared females. It is due to the fact, that pied males were subsequently excluded from most of the sites, and nowadays it is very hard for them to establish a territory in sites with many collared males.

Therefore pied males are breeding in the poorer quality parts of the sites, and pied female after breeding failure can choose from a limited set of dispersal options. Second, for the relative low number of pied flycatchers breeding in our study sites may prevent us from discovering this pattern. However, additional support for the first option exists. In both species I found weak but significant negative correlation between number of fledged chicks and dispersal distance. It suggests that breeding dispersal of both collared and pied flycatchers is indeed affected by reproductive success in the previous season, although pied females have fewer possibilities of dispersal within site. In the entire island perspective, the distribution of breeding flycatchers across woodlots is strongly affected by their reproductive success in the previous year.

Prospecting studies show that birds observed while inspecting nest boxes with higher than average reproductive success one year were more likely to breed in or around those particular nest boxes in the following season (Doligez et al. 2004b). Moreover woodlots with increased reproductive quality in general attracted more individuals (Doligez et al. 2004a). Hence, the quality of a woodlot should play an important role for a bird's dispersal decision. However, the average number of chicks fledged in the plot where the bird previously bred, or in the plot to which bird dispersed did not explain site changes in my study. The reason for that could be the fact, that in the mentioned prospecting studies the brood size was artificially enlarged to boost the reproductive quality of the nest box or area. In my case – the differences between sites are very subtle hence the interaction remains undiscovered. In my study the variation in reproductive success within sites was comparable to variation between sites. Large scale manipulation could probably reveal the patterns described in the literature (Pärt and Doligez 2003; Doligez et al. 2004a; Doligez et al. 2004b). In addition one could include all the background variation caused by environmental factors or performed experiments. Only then it will be possible to answer the questions about use of public information by flycatchers on Öland.

The lack of significance for all density proxies (besides pied flycatcher nest density, which is significant only when considered alone, and its' explanatory power is negligible) may be accredited to the crude resolution of the analysis. Assuming the same situation for the entire area, based on the number of occupied nest boxes per square meter or relative percentage of the species in the area, renders subtle differences between parts of the area invisible. However I found it impossible to increase the resolution of the analysis and include such within-site spatial variation in density, due to the fact, that I did not have the geographic coordinates of all the boxes in the sites. Though, even with accurate data for all the boxes, discovering density dependent dispersal in flycatchers could be a major discovery, as investigating density dependent dispersal has been proven to be challenging in vertebrates. Recently Matthysen (2005) reviewed studies in birds and mammals, concluding that positive density dependence (meaning individuals moving from patches as a result of competition), rather than negative density dependence (meaning overcrowding being a factor preventing individuals from dispersing to a novel site), seems to explain most of the up to date studies. However for flycatchers the fact that birds are attracted to the higher quality patches (Doligez et al. 2004a) contradicts the expectations from positive density dependence models, therefore further investigation is necessary in order to asses to what extent conspecific or heterospecific densities can affect dispersal decisions.

The final explanatory variable in my model was age. It was not significant on the level of within sites dispersal, probably due to the mentioned previously strong variation in conditions at the onset of breeding. However, it explained well the between site shifts. This result work in

accordance with previous flycatchers studies (e.g. Pärt and Gustafsson 1989). The increase in site-fidelity with age can be explained with the balance between benefits and costs of dispersal decisions. First, in general older individuals arrive earlier hence older males have higher chances of finding an available box in their preferred site. Younger males arrive later and in result experience stronger competition over boxes. In general it is unlikely that a male who has established a territory will be outcompeted by a later arriving one (Pärt 1995; Pärt and Qvarnström 1997), therefore younger males may be forced to leave the area. When they do, they possess less knowledge about the breeding grounds than older individuals and hence visit more territories in order to evaluate them (Pärt and Gustafsson 1989). One may argue that early in life it is more advantageous to visit more sites in order to gather as much information as possible. As youngsters do not have knowledge to benefit from, they do not gain more by competing over any particular box. This renders them more dispersive. In the similar manner, younger females' dispersal is limited by males' presence. They also possess limited knowledge about breeding grounds, therefore they benefit from gathering as much information as possible early in their life. On the other hand, with age both sexes become more familiar with the site they breed in. Acquired knowledge about food resources or shelters from predator allows them to utilize the site more efficiently, therefore the benefits of staying in a known site increase (Pärt and Gustafsson 1989). The tendency for older females to change sites more frequently than older males can be explained by lower risks associated with dispersal. Females therefore can use gathered public information to a larger extent that males, even later in life, although they still remain constrained by the number of available males.

All the factors I have discussed above explained 12% of the variation in the data. Have I therefore missed inclusion of important factors that could have explained more of the observed variation? Investigating dispersal of migratory birds is a difficult task. Flycatchers are most likely to make breeding dispersal decisions before they leave for wintering grounds in Africa, as after breeding they gather public information. There is evidence for prior experience and gathered knowledge to affect this choice (Pärt and Doligez 2003, Doligez et al. 2004a, 2004b). Previous studies (e.g. Harvey et al. 1984) discussed flycatcher dispersal propensity in comparison to tit dispersal patterns. However migratory flycatchers are driven by entirely different forces. Each year they make a long journey back from wintering grounds in Africa. Both global climate change and weather condition during the migration (Both et al. 2005) affect the distance birds cover each year. The common problem that burdens dispersal studies (e.g. Noorwijk 1995) is the lack of knowledge on whether individuals disperse a long distance and end up outside the study area or if they die between breeding seasons. On Öland however collared flycatchers are at the range of their breeding distribution hence they do not have many additional options. This provides us with an opportunity to overcome this problem. Moreover in migratory birds the establishment of a territory depends strongly on site availability, which may vary between years. Within area movement is a flexible behaviour. On arrival males can easily assess their previous breeding territory and evaluate the availability of the boxes they find interesting at the end of the previous season. The consequences of a preferred nest box being occupied are much lower, as they can quickly discard their decision and compete for a previously owned box. On the other hand, this type of movement is strongly driven by density at the time of arrival. Males with no intention of dispersing may end up far away from their previous nest boxes if it is occupied and there is no available site close to it. In my study I had no knowledge of males' arrival dates hence it was impossible to include site occupancy in my analysis. Due to the fact that many boxes are occupied by tits, this missing information can have a profound effect that is not yet included in

the models. One could want to include it in the future analysis, as flycatcher sister species may respond different to tit presence. On one hand, there is an evidence for colonizing individuals to differ in behavioural phenotype when compared to the rest of the population, pointing towards increased aggression of the former (Duckworth 2006; Duckworth 2008). Collared flycatcher population on Öland can be described as being on the edge of the species range hence it might be that they are more aggressive and - to some extend – capable of competing with tits over nest boxes or nesting closer to the ones occupied by them. On the other hand, a recent study (Quinn et al. 2011) suggested a linkage between personality and dispersal, which remains to be investigated in more detail. Based on that one may argue if colonizing species reacts different towards interspecific competitors and what role this interaction plays in dispersal decisions. Keeping all the uncertainties in mind, I would say that for a unique hybrid zone my model's fit is satisfying.

What role does dispersal have in hybrid zone dynamic?

Collared flycatchers only recently colonized Öland (Qvarnström et al. 2009), and since then they have been competing with pied flycatchers over available breeding sites (Qvarnström et al. 2009; Vallin et al. 2011). Whether dispersal propensity of collared flycatchers was related to other behavioural traits, which affected the pace of colonization, remains unknown. For other species, as for example western bluebirds (Duckworth 2008), it has been shown that adaptive dispersal strategies have an impact on the species range expansion. The follow up study suggested maternal effect as the key factor in this process (Duckworth 2009). On top of that a recent study of great tits (Quinn et al. 2011) identified links between individual's personality and dispersal propensity. How can all these discoveries be related to the study of flycatcher hybrid zone?

On Öland there is a strong evidence for competitive exclusion of pieds from rich deciduous habitats driven by interspecific interactions and hybridization (Vallin et al. 2011). In addition it has been shown that imprinting plays an important role in forced habitat shifts (Vallin and Qvarnström 2011), but to what extent distinct dispersal strategies are responsible for the maintenance of *Ficedula* hybrid zone remains to be investigated. It is surprising that pied flycatchers on Öland do not disperse longer distances. There may be several explanations for the lack of a difference between the two species. First, in my analyses I focused on study of breeding dispersal. In the next step one might investigate how natal dispersal and recruitment differ between species in *Ficedula* hybrid zone. Second, only successful breeders were analysed in my study. The next step would be the inclusion of individuals that arrive on Öland but do not breed. To do that large scale capture of individuals early in the breeding season could be conducted. Then one might analyse the difference between the individuals that breed within the same area as they were caught in early in the same season and the ones that breed in a different area. Afterwards tests of probability of breeding in relation to arrival time, site availability, species' proportion and dispersal decision could reveal more about interspecific interactions driving the dynamics of the *Ficedula* hybrid zone. Third, I analysed pooled data for all years, because distances did not differ between years. However, after including individuals that did not acquired a box or failed in attracting a female, new pattern may be revealed. It is possible that dispersal after experiencing higher than average heterospecific densities is adaptive. In this case during the first years of interspecific interactions only pied individuals that dispersed from areas of high collared density areas managed to get a box and attract a female. Therefore I did not see the pattern in the data – as I used only males that bred, due to the fact that complete data for arriving individuals that either failed to establish a territory or even dispersed away from the island is

missing. Another question would be how to disentangle the individuals that failed from the ones that left the island. My suggestion is to additionally capture individuals at the end of the season. As flycatchers display prospecting behaviour (Pärt and Doligez 2003) birds that remained on island should be still in the area, while dispersers from island not.

Sex differences in dispersal could affect the patterns of hybridization. Collared flycatchers are superior competitors when compared to pied flycatchers (Qvarnström et al. 2009). Therefore, pied flycatchers have been consequently excluded from the best sites. With the increase of relative proportion of collared males within the sites the chances of finding conspecific mates by pied females decreased, while at the same time risk of heterospecific pairing increased (Sætre et al. 1999). It has been shown, that pied females, when given a limited choice between a yearling and an adult collared flycatcher, chose the yearling (Wiley et al. 2005). Previous studies in this hybrid zone have shown that young pied males faced more difficulties in establishing territories, when young pied females faced a higher risk of hybridization (Vallin et al. 2011). When we consider that females are more dispersive sex, we may conclude that the pattern of hybridization on Öland (young collared males interbreeding with young pied females) can be partially explained by different dispersal propensity of both sexes.

Conclusion

In concordance with previous studies I found that both pied and collared flycatchers show a low degree of breeding dispersal and generally can be found within the same breeding woodlot in consecutive years. I found no difference in breeding dispersal propensity between the two flycatcher species, suggesting that consistency in where adult birds breed once they have established themselves promote stability of this young hybrid zone. Future fine scale analysis can reveal patterns that remained undiscovered by my analysis. One of possible pathways to improvement leads through a comprehensive analysis of both populations experiencing secondary contact and allopatric ones. The recent trend of integrating geographic information systems (GIS) into evolutionary research can provide us with a useful tool in refining patch reproductive quality or density proxies (e.g. Kozak et al. 2008). The benefits one can get from such interdisciplinary approach to speciation study has been recently reviewed (Swenson 2008), what remains is to improve the quality of the information by collecting updated coordinates and using models that account for spatial and temporal variation of breeding sites availability. With mentioned approach we could get more insight into hybrid zone dynamics, and study similar to the one by Carling and Zuckerberg (2011, evidence of Passerina bunting hybrid zone narrowing over time) should be possible also for *Ficedula* hybrid zone on Öland.

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