

Combined effects of interspecific competition and hybridization impede local coexistence of *Ficedula* flycatchers

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Abstract At secondary contact closely related species may both compete over similar resources and/or hybridize. Simulation models suggest that hybridization increases the risk of extinction beyond the risk resulting from interspecific competition alone, but such combined effects are rarely studied empirically. Here, we use detailed records on pairing patterns, breeding success, local recruitment and immigration collected during 8 years (2002–2009) to investigate the underlying mechanism of the rapid displacement of pied flycatchers by collared flycatchers on the Swedish island of Öland. We found no differences in average reproductive success or reproductive lifespan between the two species. However, we show that young male pied flycatchers failed to establish new territories as the density of male collared flycatchers increased. In addition, as the relative frequency of collared flycatchers increased, the risk of hybridization dramatically increased for female pied flycatchers, which speeds up the exclusion process since there is a high fitness cost associated with hybridization between the two species. In a nearby control area, within the same island, where pied flycatchers breed in the absence of collared flycatchers, no decline in the number of breeding pairs was observed during the same period of time. Our results demonstrate the crucial importance of studying the combined effects of various types of heterospecific interactions to understand and predict the ecological and evolutionary implications of secondary contact between congeneric species. These findings are particularly interesting in the light of recent climate change since the expected range shifts of many taxa will increase competitive and sexual interactions between previously separated species.

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Introduction

Classical studies on competitive exclusion and coexistence of ecologically similar species usually focus on resource competition (e.g., Hutchinson 1978). Typically, individuals belonging to the dominant species are more efficient in utilizing shared resources or can by other means prevent individuals belonging to the subordinate species from getting access to resources (Tilman 1982). The subordinate species is therefore excluded and driven to local extinction. This trend is often shown in laboratory experiments, but environmental heterogeneity and/or life-history trade-offs may lead to prolonged co-existence in nature, at least on a regional scale (e.g., Chesson and Huntly 1997; Amarasekare and Nisbet 2001).

Since closely related species are expected to have similar ecological requirements, newly formed species are especially likely to compete over resources (Hardin 1960). Closely related species are also likely to hybridize, but even though about 10% of animal and 25% of plant species are known to be involved in natural interspecific hybridization (Mallet 2005), the relative role of hybridization in species replacement remains largely untested. Secondary contact between formerly separated species is hence expected to be “revitalizing the ghosts of competition and evolution” (Confer 2006) and simulation models suggest that hybridization increases the risk of extinction beyond the risk resulting solely from competition (Wolf et al. 2001). Still, the role of reproductive interference, defined as any heterospecific sexual interaction that reduces the fitness of individuals (including hybridization), is greatly overlooked in relation to species replacements (Gröning and Hochkirch 2008). There are several different explanations for this lack of attention. One possibility is that many scientists have viewed species as discrete units of reproduction, rarely interacting sexually (Mallet 2005). In addition, reproductive interference may in many cases be hard to detect since it may also operate in the absence of hybridization (Kishi et al. 2009). The detrimental effects of reproductive interference include: loss of mating options with conspecifics (Hochkirch et al. 2007), hybridization (Rhymer and Simberloff 1996), and wastage of reproductive efforts in terms of gametes (Rozhnov 1993), time, energy or nutrients (Gröning and Hochkirch 2008). Because these fitness effects can be both large and asymmetrical, reproductive interference may have a major influence on population dynamics (Gröning and Hochkirch 2008). It has been suggested that the frequency dependent effect of reproductive interference leads to more efficient exclusion of populations as compared to density-dependent resource competition (Ribeiro and Spielman 1986; Kuno 1992; Yoshimura and Clark 1994). In fact, many examples of species exclusions attributed to resource competition may instead have been caused by reproductive interference (Kishi et al. 2009). We investigated the effects of interspecific male competition (over nest sites and food used for reproduction) and hybridization on the exclusion process of pied flycatchers (*Ficedula hypoleuca*) by collared flycatchers (*F. albicollis*) on the Swedish island of Öland. We assume that the effects of interspecific competition over the different types of resources (i.e., nest sites and food) will manifest themselves at different stages of the reproductive cycle of the birds. More precisely, a low ability to compete over nest boxes will result in lower establishment of breeding pied flycatchers, while a lower ability to compete over food to feed the nestlings will manifest itself in lower reproductive success among the established pairs of pied flycatchers.

Collared and pied flycatchers co-occur during the summer breeding season in central and eastern Europe and on the Baltic isles of Öland and Gotland in Sweden. On Öland, the number of breeding pied flycatchers has been drastically reduced in woodlots where they co-occur with collared flycatchers (Qvarnström et al. 2009). Because collared flycatchers started to colonize Öland only 50 years ago, it is possible to examine the process of the replacement of pied flycatchers in detail. Moreover, these species both compete over resources and occasionally hybridize, making this system ideal for addressing the importance of competitive and reproductive interactions in driving species exclusion.

Pied and collared flycatchers winter in Africa, but the two species exhibit divergent migration routes, and segregated, but probably slightly overlapping, winter quarters. Pied flycatchers winter in western to central Africa and migrate along the Iberian Peninsula, whereas collared flycatchers take a more eastern route through Italy, or further east, and winter in central to southeastern Africa (Lundberg and Alatalo 1992; Veen et al. 2007). There is no evidence of hybrids having an intermediate route or winter quarters: instead, hybrids appear to cluster with pied flycatchers, which potentially contributes to the high annual survival of hybrid flycatchers (Veen et al. 2007).

Males of the two species compete fiercely for access to nest-boxes when arriving at the breeding grounds after spring migration from their African winter quarters (Alatalo et al. 1994; Pärt and Qvarnström 1997; Qvarnström 1997). The crucial resource, i.e., the prerequisite for breeding, is the nest-box in a suitable habitat. There is extensive overlap in timing of breeding (Qvarnström et al. 2009) as well as feeding habits (Wiley et al. 2007) between the two species, suggesting strong interspecific competition may be present. Gustafsson and Pärt (1991) reported that collared flycatchers are dominant to pied flycatchers in interspecific competition for nest holes on the Swedish island of Gotland, and Sætre et al. (1999) found that the breeding density of pied flycatchers was negatively correlated with the density of collared flycatchers in a Czech flycatcher population.

Females arrive slightly later than the males to the breeding grounds and select their partner among the established males (Lundberg and Alatalo 1992). Females of both species prefer conspecific males (Sætre et al. 1997, 2007). Still, hybridization (which can be viewed as a form of sexual competition; e.g., Yoshimura and Clark 1994) occurs at a moderate rate and approximately 2–7% of the breeding flycatchers in different mixed populations are hybrids (reviewed in Qvarnström et al. 2010; Sætre and Sæther 2010). The level of gene flow is low between the two species; female hybrids are sterile, in accordance with Haldane's rule, while male hybrids mainly experience a disadvantage in competition over mates (Svedin et al. 2008). This reduction in fitness remains for several backcrossed generations (Wiley et al. 2009). Even so, introgression from pied to collared flycatchers has been observed (at higher rates on Öland and Gotland compared to the older Central European hybrid zone), whereas introgression from collared to pied flycatchers is seemingly absent in all populations (Borge et al. 2005).

Coexistence of these two apparently very similar species is facilitated through divergent life-history adaptations, which likely arose during historical allopatry. Nestling pied flycatchers are more robust towards harsh conditions (i.e., low food abundance late in the breeding season), providing them an opportunity to prolong coexistence with the otherwise more aggressive collared flycatchers (Qvarnström et al. 2005, 2009). Collared flycatchers are more dependent on a high abundance of caterpillars for their reproductive success, whereas pied flycatchers can settle in areas with lower caterpillar abundance, thereby reducing interspecific competition (Veen et al. 2010). However, apart from these windows in time and space where they can prosper, the number of breeding pied flycatcher pairs is rapidly declining in the most favourable breeding sites, which consist of deciduous forest

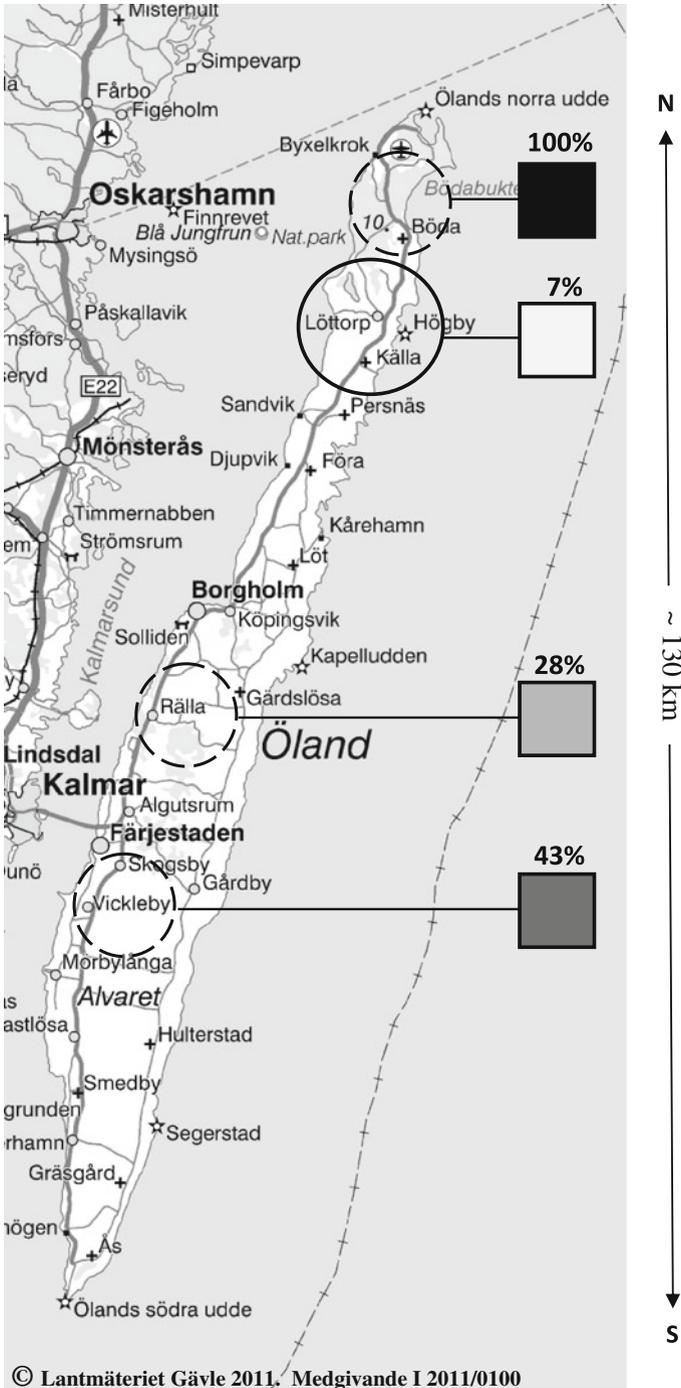
Fig. 1 The proportion of pied flycatchers (vs. collared flycatchers) varies along a north–south gradient on the Baltic island of Öland, Sweden. The breeding density of pied flycatchers is indicated by the gray to black shading (black = highest density). In the far north the habitat changes into coniferous forest, which so far is solely inhabited by pied flycatchers. A couple of areas in the south were also only inhabited by pied flycatchers at the start of the study period. The numbers are based on data collected from 21 nest-box areas during 2002–2009. The solid-line circle around Löttorp represents the 10 nest-box areas included in this study

with high caterpillar abundance, on Öland (Qvarnström et al. 2009). Here we investigate the underlying mechanisms of this rapid exclusion.

Materials and methods

Study population

We used breeding and recruitment data from a long-term population monitoring study to investigate the combined effects of hybridization and interspecific competition on species exclusion. A subset ($n = 10$) of the current nest-box study plots ($n = 21$) on Öland (57°10'N, 16°58'E) was used for all analyses, including the largest study plots where flycatchers breed at the highest densities. The landscape on Öland is characterized by a mixture of agricultural land and deciduous forest, except for the very northernmost part of the island which is dominated by coniferous forest and contains areas solely inhabited by pied flycatchers (Fig. 1). The selected study plots for this study are surrounding the town of Löttorp (Fig. 1), the area where collared flycatchers colonized Öland in the 1960's, and where there has been a rapid decline of pied flycatchers (Qvarnström et al. 2009). Within these study plots, there have been sympatric occurrences of collared and pied flycatchers, in varying proportions, ever since nest-boxes were put up in 2001 and 2002 (see Qvarnström et al. 2009). A subset of males is usually caught prior to breeding for different experimental purposes (e.g., song recordings). All birds are individually marked with numbered metal rings and detailed yearly records on breeding performance are kept. All breeding birds are caught once every breeding season with a trap inside the nest-box (or occasionally with a net), whereupon the birds' morphological characters are measured. Females are caught during incubation, and males when feeding nestlings. Nestlings are measured at day 7 and 13, and every nest-box is visited a couple of days after expected fledging to achieve an accurate estimate of breeding success. Species assignment of males is usually straightforward since they differ in song and plumage traits. Males of both species exhibit a black and white plumage, but the male collared flycatchers are slightly bigger (with longer wings and tail) and have larger white patches on the wings and on the forehead as compared to pied flycatchers (Svensson 1992). Juvenile males are recognized by their brownish wings and shoulders, and already banded males are matched against prior capture data for an exact age. The females are more similar to each other. However, female collared flycatchers are slightly bigger and more greyish in colour (female pied flycatchers are more brownish), have larger white patches on their wings and a rudimentary white colour hidden at the base of the feathers on the neck (Svensson 1992). The females are also easily separated by species-specific alarm calls. Male hybrids are identified through their intermediate plumage pattern and female hybrids through their complete sterility. Later generation backcrosses are extremely rare due to accumulated costs of hybridization (Wiley et al. 2009). The species identity of expected hybrids is later confirmed by pedigree data or by the use of species-specific molecular markers.



Habitat characteristics and density of breeding birds

Pied flycatchers prefer to breed in deciduous forests (Lundberg and Alatalo 1992), but on Öland it seems that pied flycatchers are becoming increasingly associated with coniferous forests with lower food abundance (Veen et al. 2010; Vallin et al. 2011). In these areas, pied flycatchers can avoid competition since collared flycatchers are less tolerant of harsh environments (Qvarnström et al. 2009). For a general description of the habitats within this study, an estimation of the dominant tree species was performed with a ‘relascope’ (see Veen et al. 2010), assigning individual trees into three categories based on trunk size and distance from the nest-box. High quality deciduous forests characterized by a high food peak early in the breeding season (Veen et al. 2010) dominated the habitat within the ten selected study plots, with the most common tree species, in descending order of abundance, being Hazel (*Corylus avellana*), Oak (*Quercus* sp.), Ash (*Fraxinus excelsior*), Alder (*Alnus glutinosa*) and Birch (*Betula* sp.). The area of these study plots combined was approximately 220 ha., as calculated with ArcMap 9.2, using GPS coordinates of the location of nest-boxes, and including a 50 m buffer around the outermost boxes. The average breeding densities increased across the study period from 0.3 pairs/ha in 2002 to 1.0 pairs/ha in 2009. We analyzed how the number of breeding male and female pied flycatchers has changed across the years in relation to the number of breeding collared flycatchers in this preferred habitat using generalized linear models (glm) with binomial errors and a logit link. The models were tested and corrected for overdispersion. We thereafter analyzed trends in the number of breeding pied flycatchers in nearby coniferous dominated forests (within the same island) using linear regression. The area of these two study plots combined were 55 ha, with an average breeding density of 0.16 pairs/ha in 2004 (nest-boxes were put up in 2002) and 0.24 pairs/ha in 2009.

Establishment of breeding territories and pairing patterns

We investigated in which phase of the breeding cycle that pied flycatchers are having a competitive disadvantage in comparison to collared flycatchers. We first compared the abilities of males to establish breeding territories. The different migration patterns of the two species could explain the competitive asymmetry (i.e., displacement of pied flycatchers) if male collared flycatchers arrive earlier at the breeding grounds and thereby experience an advantage when establishing breeding territories within the preferred habitat. We tested this possibility by comparing trends in arrival dates after migration between the two species across the study period using ANCOVA. As the response variable, we extracted the first yearly observations by species on Öland from the Swedish report system for birds (administrated by the Swedish species information centre; <http://artportalen.se/birds/>). Another, not mutually exclusive possibility is that male collared flycatchers experience an advantage because they are more aggressive than male pied flycatchers. During some years, we catch a subset of males prior to breeding for different experimental purposes. We used this data to compare the dates the males were caught and the ages of the early caught males between the two species using Wilcoxon signed-rank tests. We also investigated the ability of early caught males to subsequently establish a territory across the study period, using logistic regression with establishment (1 or 0) as the response variable and male species and year as the explanatory variables. The extensive monitoring and the high site fidelity of flycatchers also enabled us to compare long-term trends in the general patterns of establishment of breeding males in the area. If interspecific male competition over nesting sites is the main mechanism behind the exclusion of pied flycatchers, we would expect the rate of establishment of male pied

flycatchers to decline over the years and to be negatively related to the increasing numbers of breeding male collared flycatchers. To test this, we analyzed trends in the establishment of first time breeding males, i.e., recruits (males born in the area and then returning to breed) and immigrants (breeding males not banded in previous years) combined, between the two species using ANCOVA. As the sample sizes were largely unequal between the species (the number of male collared flycatchers breeding for the first time increased from 58 in 2002 to 122 in 2009, whereas the number of male pied flycatchers breeding for the first time decreased from 12 in 2002 to 3 in 2009), the numbers of males breeding for the first time were standardized using z-scores, which represent values from a normal distribution with a mean of zero and a standard deviation of one (e.g., Quinn and Keough 2002). We thereafter analyzed how the proportion of first time breeding male pied flycatchers has changed across the years in relation to the number of breeding collared flycatchers using a generalized linear model (glm) with binomial errors and a logit link. The model was tested and corrected for overdispersion.

We investigated the relative success in the next step of the breeding cycle, i.e., getting a conspecific mate, from the female perspective since it is the females who select their mate among the established males (Lundberg and Alatalo 1992). Choosy individuals are expected to accept heterospecific mates only when conspecifics are unavailable or rare in the subset of males they choose their mates among (e.g., Wirtz 1999), while the reverse combination is expected to occur at a much lower rate. It may, however, take a longer time for the males that occur in low frequency to be found by conspecific females. This latter problem should then be reflected in a longer time period passing between arrival of the males and the onset of breeding. We used a Wilcoxon signed-rank test to compare potential differences in breeding time (i.e., laying date of first egg) between the two species.

The role of demographic factors and/or competition over food

In order to test whether the decline of pied flycatchers was caused by differences in demographic factors, more specifically in lower annual reproductive success or due to a shorter reproductive lifespan once they have established themselves in the area, we compared reproductive lifespan (maximum age) and reproductive success (clutch size and number of fledged offspring) for all nesting birds using Wilcoxon signed-rank tests. If competition over food is the underlying mechanism for the decline of pied flycatchers, we would then also expect this to be reflected in lower reproductive success (clutch size and/or fledging success) as compared to collared flycatchers. Fledging success was analysed only for conspecific pairs not subject to any experiments, whereas clutch size and maximum age were analyzed using the complete data set. All statistical analyses were carried out using JMP 8 (SAS Institute, Cary, North Carolina, USA).

Results

The number of breeding pairs with certain species identity and where both sexes were captured were in total: 1,164 pairs of collared flycatchers (ranging from 55 pairs in 2002 to 199 pairs in 2009), 86 pairs of pied flycatchers (decreasing from 12 pairs in 2002 to 3 pairs in 2009) and 60 heterospecific pairs (increasing from 3 pairs in 2002 to 9 pairs in 2009). Among these heterospecific pairs, female pied flycatchers were significantly overrepresented, as compared to female collared flycatchers ($N = 60$, $df = 1$, $\chi^2 = 12.004$, $P < 0.001$). There was a significant decrease in the proportion of male pied flycatchers in

Fig. 2 The proportion of male pied flycatchers (“PF”, *filled bars*) has declined significantly in recent years within the area where collared flycatchers (“CF”, *empty bars*) colonized the Swedish Baltic island of Öland in the 1960’s. Sample sizes are given above the *bars*

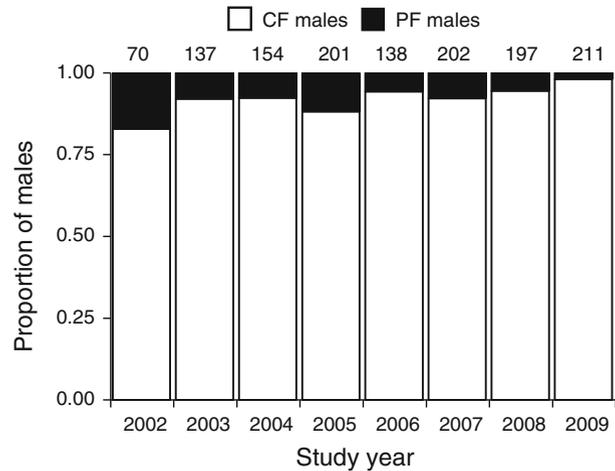
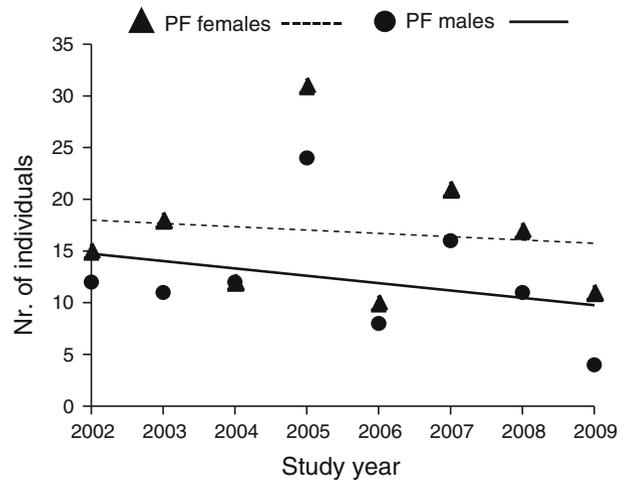


Fig. 3 Within the areas shared with collared flycatchers in rich deciduous forest surrounding the town Löttorp on Öland, female pied flycatchers (*filled triangles, dashed line*) follow the same pattern of decline as the male pied flycatchers (*filled circles, solid line*), but with a time lag



favour of male collared flycatchers across the study period ($N = 8$, $df = 1$, slope = -0.195 ± 0.065 SE, $\chi^2 = 9.103$, $P = 0.003$, Fig. 2). The proportion of female pied flycatchers also showed a significant decline in favour of female collared flycatchers across the study period ($N = 8$, $df = 1$, slope = -0.149 ± 0.058 SE, $\chi^2 = 6.734$, $P = 0.01$). The decline of female pied flycatchers lagged behind the decline of male pied flycatchers (matched pairs t test; mean difference: 4.75 ± 0.881 SE, $N = 8$, $df = 7$, $t = 5.389$, $P = 0.001$, Fig. 3). In nearby lower-density study plots dominated by coniferous forest (within the same island) where collared flycatchers were absent, no decline in the number of breeding pied flycatcher pairs was observed. Here, the number of pied flycatcher pairs changed from 9 in 2004 to 13 in 2009, but this increase was not statistically significant ($N = 6$, $df = 1$, $F = 1.449$, $P = 0.30$).

We investigated possible mechanisms underlying the decline of pied flycatchers within the preferred habitat. We found no significant interaction between species of the male and year on earliest arrival date ($N = 16$, $df = 1$, $F = 1.380$, $P = 0.26$), nor was there a significant overall difference between the species after removing the non-significant

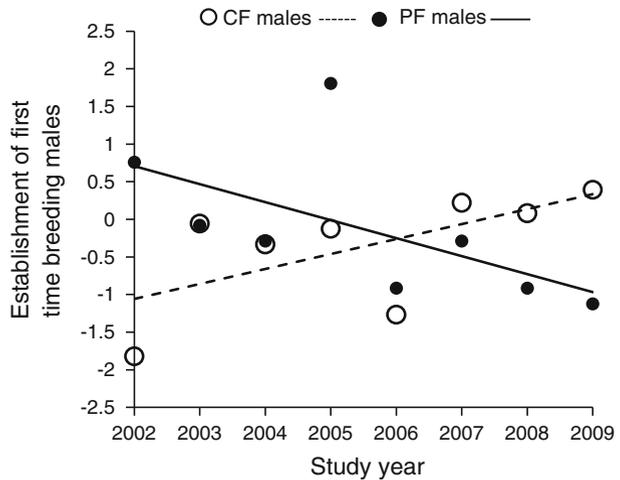
Table 1 A comparison of breeding performance (mean values and s.d.) at different stages of the breeding cycle of male collared (CF) and pied flycatchers (PF) monitored in a subset of nest-box areas in high quality deciduous forests surrounding the town Löttorp where collared flycatchers first colonized the Baltic island of Öland, Sweden

Breeding cycle event	CF	PF
Arrival date in April	22.75 ± 3.45 (<i>N</i> = 8 years)	20.88 ± 3.97 (<i>N</i> = 8 years)
Mean date of early caught males in May	11.07 ± 6.50 (<i>N</i> = 430)	11.11 ± 6.50 (<i>N</i> = 61)
Probability of establishment 2005–2007*	0.52 ± 0.05 (<i>N</i> = 349)	0.57 ± 0.04 (<i>N</i> = 46)
Probability of establishment 2008–2009*	0.50 ± 0.08 (<i>N</i> = 54)	0.21 ± 0.06 (<i>N</i> = 14)
Onset of breeding in May**	19.00 ± 5.73 (<i>N</i> = 1129)	22.36 ± 6.01 (<i>N</i> = 84)
Clutch size	6.36 ± 0.79 (<i>N</i> = 1146)	6.29 ± 0.83 (<i>N</i> = 84)
Number of fledged offspring	4.84 ± 2.02 (<i>N</i> = 716)	5.21 ± 1.54 (<i>N</i> = 39)
Male reproductive lifespan	2.38 ± 1.25 (<i>N</i> = 790)	2.36 ± 1.62 (<i>N</i> = 60)

The detailed records on breeding performance were collected during the time period 2002–2009. Bold text indicates stages in the breeding cycle when pied flycatchers have a significantly lower success compared to collared flycatchers. * Probability of establishment is based on whether males caught prior to breeding subsequently established a territory or not (no males were caught prior to breeding in 2002, 2004 or 2006, and only a few in 2003). The proportion of male collared flycatchers managing to establish a territory increased over the study period, whereas the opposite was true for pied flycatchers (significant interaction between species of male and year on the probability of establishment). ** Onset of breeding is based on the laying date of the first egg (significant difference between the species)

interaction term (*N* = 16, *df* = 1, *F* = 0.965, *P* = 0.34, Table 1). We did not find any overall differences between the species in the dates when we caught males prior to breeding (*N* = 491, *df* = 1, *Z* = 0.062, *P* = 0.95, Table 1). To investigate if there were age-dependent differences in arrival between the two species, we repeated the analysis for one-year old birds and adult birds (2 years or older) separately. Juvenile male pied flycatchers were caught slightly earlier than juvenile male collared flycatchers, but the difference was not significant (*N* = 196, *df* = 1, *Z* = -1.753, *P* = 0.08, mean = 12.43 ± 0.43 SE and 10.12 ± 1.12 SE, for collared and pied flycatchers respectively). We did not find any differences among the adult males (*N* = 284, *df* = 1, *Z* = 1.189, *P* = 0.24, mean = 10.14 ± 0.44 SE and 11.71 ± 1.18 SE, for collared and pied flycatchers respectively). Overall, there was no significant difference between the two species in the mean age of the males caught before breeding (*N* = 483, *df* = 1, *Z* = 0.329, *P* = 0.74, mean = 2.13 ± 0.06 SE and 2.27 ± 0.16 SE, for collared and pied flycatchers respectively). However, there was a significant interaction between species of the male and year on the probability of establishment in the breeding area among the subset of males caught prior to breeding (*N* = 494, *df* = 1, χ^2 = 4.065, *P* = 0.04, slope = 0.169 ± 0.065 SE and -0.200 ± 0.174 SE for collared and pied flycatchers respectively). A higher proportion of male collared flycatchers that were caught when they arrived to the breeding grounds managed to establish a territory and attract a female at the end of the study period (Table 1). Our analysis of the long-term data showed further support for a difference in ability to establish a territory between males of the two species. Collared and pied flycatchers showed opposing trends in the pattern of establishment of males in the area during the study period: there was a significant interaction between male species and year on the standardized number of males breeding for the first time across the study period (*N* = 16, *df* = 1, *F* = 6.959, *P* = 0.02, Fig. 4). The proportion of male pied flycatchers breeding for the first time in relation to resident male pied flycatchers was negatively correlated to the increasing numbers of male collared flycatchers over the years of the study (*N* = 8, *df* = 1,

Fig. 4 The pattern of establishment of male collared flycatchers (CF) and male pied flycatchers (PF) breeding for the first time (i.e., immigrants and recruits) differs in the area with the highest densities of collared flycatchers on the Swedish island of Öland. While the number of young male collared flycatchers breeding for the first time is increasing, the number of young male pied flycatchers breeding for the first time is decreasing. Values on y-axis are standardized z-scores



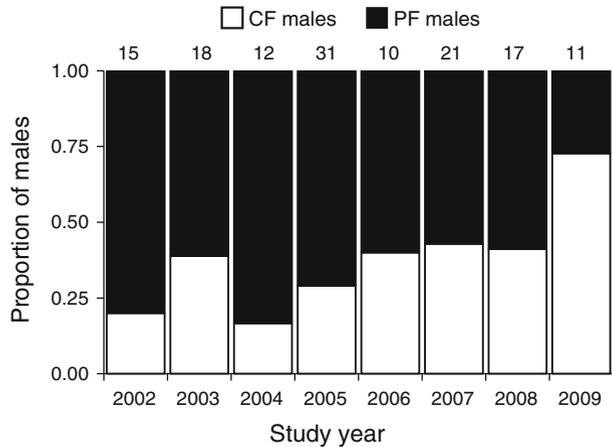
$\chi^2 = 4.670$, $P = 0.03$). Males breeding for the first time were significantly younger than resident males ($N = 1306$, $df = 1$, $Z = 21.535$, $P < 0.0001$, mean 1.81 ± 0.03 SE for first time breeding males and 3.44 ± 0.05 SE for resident males among collared flycatchers ($N = 1211$), mean 1.62 ± 0.13 SE for first time breeding males and 3.97 ± 0.18 SE for resident males among pied flycatchers ($N = 95$)). In summary, young male pied flycatchers that have not bred in the area before appear to have increasing problems establishing themselves.

The proportion of hybridizing female pied flycatchers increased significantly across the study period ($N = 8$, $df = 1$, slope = 0.219 ± 0.088 SE, $\chi^2 = 6.547$, $P = 0.01$) and was positively correlated with the proportion of male collared flycatchers ($N = 8$, $df = 1$, slope = 12.519 ± 4.994 SE, $\chi^2 = 6.976$, $P = 0.008$). In 2009, most of the female pied flycatchers breeding in this area paired with a male collared flycatcher (Fig. 5). Collared flycatchers bred significantly earlier than pied flycatchers ($N = 1213$, $df = 1$, $Z = 4.693$, $P < 0.0001$, mean date of first egg laying in May = 19.00 ± 0.17 SE and 22.36 ± 0.63 SE for collared and pied flycatchers respectively, Table 1). There was no significant difference in reproductive success between the two species in terms of clutch size ($N = 1230$, $df = 1$, $Z = -0.530$, $P = 0.60$, mean 6.36 ± 0.02 SE and 6.29 ± 0.09 SE for collared and pied flycatchers respectively, Table 1) or the number of fledged offspring from each breeding event ($N = 755$, $df = 1$, $Z = 0.619$, $P = 0.54$, mean 4.84 ± 0.07 SE and 5.21 ± 0.32 SE for collared and pied flycatchers respectively, Table 1), and no difference in the maximum lifespan of breeding males ($N = 851$, $df = 1$, $Z = -1.073$, $P = 0.28$, mean 2.38 ± 0.05 SE and 2.36 ± 0.17 SE for collared and pied flycatchers respectively, Table 1). Thus, male pied flycatchers that have managed to establish themselves in the area have a similar reproductive success as male collared flycatchers, and they also come back to breed as many times as collared flycatchers.

Discussion

We have previously shown that the proportion (and absolute number) of pied flycatchers declined between two separate study periods (1981–1985 and 2002–2007) in our central

Fig. 5 Pairing patterns of female pied flycatchers in the areas where collared flycatchers breed in high density on the Swedish island of Öland. The proportion of female pied flycatchers that hybridize has increased across the study period, and in 2009 most of them paired with a heterospecific male (“CF”, *open bars*). Sample sizes are given above the *bars*



study sites close to the town of Löttorp where collared flycatchers colonized the island of Öland during the 1960's (Qvarnström et al. 2009). In this study we have focused on the last 8 years (i.e., 2002–2009) and show that pied flycatchers are approaching local extinction in these woodlots dominated by insect rich deciduous forest (Fig. 2). This is quite a remarkable trend considering that pied flycatchers were almost as common as collared flycatchers as late as the early 1980's in this area (Qvarnström et al. 2009). We subsequently investigated the underlying mechanisms for this decline. Reproductive lifespan and annual breeding success did not differ significantly between the two species (Table 1). However, the two species show strikingly opposing trends in terms of the establishment of males breeding for the first time (immigrants and recruits, Fig. 4), with the establishment of male pied flycatchers being negatively correlated to the number of male collared flycatchers. The finding that younger male pied flycatchers are having trouble establishing themselves is also apparent among the males caught before breeding. We found a significant interaction between species of the male and year on the probability of establishment implying that young pied flycatchers were less likely to establish a territory than young collared flycatchers, and that this asymmetry in probability of establishment increased over time as the density of collared flycatchers increased (Table 1). Hence, young male pied flycatchers are present at the breeding grounds but they are having increasing troubles in establishing a territory. Taken together, these results imply that male pied flycatchers that have established themselves in the area are equally efficient at utilizing the available resources (for self maintenance and offspring production) as male collared flycatchers, but young male pied flycatchers appear to be less able to establish themselves. Occurring in relatively lower frequency appears to impose problems per se. We interpret the longer time period passing between the arrival date and the onset of breeding in male pied flycatchers, as compared to male collared flycatchers, as a disadvantage in mating success by becoming “flooded” by heterospecific individuals. During the last year of the study some male pied flycatchers remained unmated for the whole breeding season and kept on singing long into June when the other birds had reached an advanced stage of breeding (author's personal observations). The number of breeding female pied flycatchers declined with a time-lag behind the male pied flycatchers (Fig. 3), resulting in a steady increase in the proportion of hybridizing female pied flycatchers. During the last year of the study, most female pied flycatchers paired with male collared flycatchers (Fig. 5).

One may argue that the observed reduction in the number of breeding pied flycatchers could result from lower survival at the winter quarters or during migration as compared to collared flycatchers. However, there are at least four facts not compatible with this alternative explanation. First, the absence of a difference in lifespan between males of the two species suggest that differences at the wintering grounds or during migration are not causing the rapid local decline of pied flycatchers observed in this study. Second, the number of breeding pied flycatchers did not decline in a nearby woodlot (within the same island) where collared flycatchers were absent. Thirdly, although pied flycatchers have declined moderately in Europe since the 1980's (e.g., Gregory et al. 2007), the number of pied flycatchers breeding on the mainland in Sweden (where collared flycatchers, except for a few pairs, are absent) seems to have stabilized in recent years. According to the standardized monitoring performed by the Swedish bird survey (<http://www.zoo.ekol.lu.se/birdmonitoring/>), the pied flycatcher population in Sweden is actually showing a significant (although slight) increase in numbers since 1998 (a 2.5% increase per year on average, based on a mean of 1,032 observations per year, $P < 0.001$). Lastly, we did not find any differences in spring arrivals or in the dates when we caught males prior to breeding between the two species across the study period. We therefore argue that a lower competitive ability of first-time breeding male pied flycatchers is the most likely explanation for why pied flycatchers are becoming almost completely excluded from these rich deciduous woodlots. Thus, interspecific competition over breeding sites (which is a prerequisite for attracting females) rather than competition over food appears to be the main mechanism behind the exclusion of pied flycatchers. However, even if this is the main mechanism of local exclusion in recent years, there are likely to be other factors that have helped collared flycatchers to colonize the island so successfully. For example, pied and collared flycatchers differ slightly in their breeding strategies, so that collared flycatchers generally breed in higher densities than pied flycatchers (e.g., Lundberg and Alatalo 1992), which initially could contribute to causing local breeding asymmetries. Another exciting possibility is that there has been an adaptive introgression of alleles from pied to collared flycatchers as suggested by Borge et al. (2005), facilitating the colonization success of collared flycatchers at the very fringes of their breeding distribution. This is a scenario that hopefully, with the rapid advancement of genomic methods and analytic tools, can be explored in more detail in the near future.

Since male pied flycatchers are being excluded prior to the females (Fig. 3), female pied flycatchers face a large risk of hybridizing with male collared flycatchers. In addition, choosy individuals are expected to accept heterospecific mates only when conspecifics are unavailable or rare in the subset of males they choose their mates among (e.g., Wirtz 1999), while the reverse combination is expected to occur at a much lower rate. Therefore, we expected an increased risk of hybridization to be more evident for female pied flycatchers. Searching for mates is costly and females find several singing males easier to locate than single singing males (Alatalo et al. 1988). Females to a large extent base their choice of mate on the quality of the territory he is defending (Alatalo et al. 1986), and competition between females restricts the time and energy spent on mate search (Dale et al. 1992). If the prime territories are mainly occupied by collared flycatchers, the risk of choosing a heterospecific mate increases. In the breeding season of 2009, the majority of the female pied flycatchers breeding in the high quality core areas paired with male collared flycatchers (Fig. 5). Hybridization is associated with large costs in flycatchers (a fitness reduction of approximately 97%, Wiley et al. 2009), and especially so for female pied flycatchers. Collared flycatcher females compensate the costs of heterospecific pairing by extra-pair copulations with conspecifics (Veen et al. 2001; Wiley et al. 2007), but due to

the rarity of conspecific mates, this strategy is not available to hybridizing pied flycatcher females. Therefore, most of their offspring are low-fitness hybrids, rendering them almost no descendants over time (Wiley et al. 2009). Since genetic introgression from collared to pied flycatchers is seemingly absent (Borge et al. 2005), genetic dilution (Levin et al. 1996; Wolf et al. 2001) of the pied flycatcher population is unlikely and the main negative effect of hybridization is lost reproductive opportunity. However, due to the frequency dependent nature of reproductive interference (e.g., Kishi et al. 2009), the costs of hybridization increase for the rarer species with increasing differences in abundance between the involved species (Gröning and Hochkirch 2008). Hence, “sexual exclusion” through hybridization is more likely if one of the species is more abundant than the other, or if the associated costs are asymmetric so that reproductive success is more reduced for one of the species (Ribeiro and Spielman 1986; Kuno 1992). Here, we have shown that as one of a hybridizing species pair becomes very rare, females of the rare species frequently mate with males of the common species, even though there is a high associated fitness cost. In addition, if the males of the rarer species are excluded prior to the conspecific females, as in our study, this will further enhance the likelihood of the conspecific females making the “wrong” choice. A majority of female pied flycatchers hybridizing must be seen as the coup de grâce of local exclusion.

Pied flycatchers, although preferably breeding in deciduous forests, are often found in coniferous forests on Öland (Veen et al. 2010), suggesting that habitat segregation is currently taking place. From a conservation management perspective, this means that habitat heterogeneity may be important per se, i.e., maintaining a variable environment is a prerequisite in allowing for habitat segregation. However, this increasing habitat segregation may also have additional negative effects on the population dynamics of the pied flycatcher. When breeding in coniferous forests pied flycatchers nest later and lay smaller clutches (Gezelius et al. 1984; Siikamäki 1995) with lower egg-yolk carotenoid levels (Eeva et al. 2011) as compared to when breeding in deciduous forests. Because of competition over limited breeding habitat, the two flycatcher species have undergone asymmetric niche segregation; only the competitively inferior pied flycatcher has been forced to utilize the lower-quality coniferous territories. The lower food availability in the coniferous forests (Veen et al. 2010) may support a smaller population of pied flycatchers than would be possible in the deciduous forests. Indeed, the breeding densities of pied flycatchers observed in the coniferous forests were very low, consistent with earlier observations of lower breeding densities in coniferous versus deciduous forests (Lundberg and Alatalo 1992). Small populations risk extinction due to stochastic demographic or environmental effects. Once hybridization and interference competition lead to local extinction of the pied flycatcher, because of the asymmetric niche segregation, these forces may continue to indirectly influence the population dynamics of this species and enhance the likelihood of a more regional extinction.

Our results in this study highlight the importance of considering the combined effects of interference competition over breeding territories and hybridization when interpreting the population dynamics of congeneric species experiencing secondary contact. This is because closely related species are likely to be both ecologically and phenotypically similar, thus increasing the risk of similar resource requirements and sexual interference. We further show that it is important to investigate the sex-specific responses of such encounters. Here, increased interference competition negatively influences the likelihood of young male pied flycatchers to establish a territory, resulting in a sharp decline in male pied flycatchers defending territories in the prime habitat and increased heterospecific pairing of female pied flycatchers. Female reproductive success may be reduced by mating

with heterospecific males (Gröning and Hochkirch 2008), which indeed is the case in flycatchers (e.g., Wiley et al. 2009).

Although hybridization has led to the extinction of many populations (Rhymer and Simberloff 1996), hybridization and species replacement are often treated as independent subjects in conservation biology (Konishi and Takata 2004). Further, interactions between ecological replacement and hybridization are often overlooked. Global change is supposed to increase the prevalence of biological invaders (Dukes and Mooney 1999) and previously separated species are being brought together at an increasing speed (Parmesan and Yohe 2003), with collared flycatchers being one of the species predicted to expand its breeding range (Huntley et al. 2007). Although evidence is accumulating that global change is providing opportunities for invasive species (generally considered to be generalists), it remains largely untested how the interactions between different elements of global change might affect interactions between closely related species. The relative effects of inter-specific competition and hybridization could vary in relation to biotic as well as abiotic factors. Our findings will contribute to the base of knowledge required for more reliable tools in, for example, theoretical modelling and decision making in this growing field of concern.

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