

POSITIVE FEEDBACK BETWEEN ECOLOGICAL AND REPRODUCTIVE CHARACTER DISPLACEMENT IN A YOUNG AVIAN HYBRID ZONE

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Character displacement can reduce costly interspecific interactions between young species. We investigated the mechanisms behind divergence in three key traits—breeding habitat choice, timing of breeding, and plumage coloration—in *Ficedula* flycatchers. We found that male pied flycatchers became expelled from the preferred deciduous habitat into mixed forest as the superior competitor, collared flycatchers, increased in numbers. The peak in food abundance differs between habitats, and the spatial segregation was paralleled by an increased divergence in timing of breeding between the two species. Male pied flycatchers vary from brown to black with brown coloration being more frequent in sympatry with collared flycatchers, a pattern often proposed to result from selection against hybridization, that is, reinforcement. In contrast to this view, we show that brown male pied flycatchers more often hybridize than black males. Male pied flycatcher plumage coloration influenced the territory obtained in areas of co-occurrence with collared flycatchers, and brown male pied flycatchers experienced higher relative fitness than black males when faced with heterospecific competition. We suggest that allopatric divergence in resource defense ability causes a feedback loop at secondary contact where male pied flycatchers with the most divergent strategy compared to collared flycatchers are favored by selection.

KEY WORDS: Collared flycatcher, ecological character displacement, pied flycatcher, reinforcement, reproductive character displacement, sexual isolation, speciation.

Speciation is generally assumed to be facilitated by some degree of geographic isolation between the diverging populations (Coyne and Orr 2004; Price 2008). However, most young species sooner or later come into secondary contact with each other and may then compete over similar resources (Hardin 1960) and/or interact during mating (reviewed by Gröning and Hochkirch 2008). Such harmful interactions can be reduced by divergence in resource use or in reproductive phenotypes, that is, through char-

acter displacement (Brown and Wilson 1956). Ecological character displacement (evolution resulting from selection to reduce interspecific resource competition) and reproductive character displacement (evolution resulting from selection to minimize interspecific reproductive interference) can result in a pattern of geographical variation where populations in sympatry with a closely related heterospecific differ from conspecific populations in allopatry (Butlin 1987; Howard 1993; Sætre et al. 1997; Noor 1999;

Pfennig and Pfennig 2009). The interactions between ecological and reproductive character displacement have rarely been studied, although closely related species that compete for resources are also likely to interact during mate acquisition (Pfennig and Pfennig 2009). A possible reason for the lack of studies may be that empirical tests aiming to investigate the selective forces underlying character displacement are faced with the classical problem of inferring processes from patterns.

Character displacement at secondary contact is facilitated if the populations involved are already somewhat differentiated due to divergence in periods of allopatry (Milligan 1985; Schluter 2000), and if the traits involved show some degree of phenotypic plasticity (Pfennig and Pfennig 2009). If the strength of selection to avoid ecological or reproductive interactions at secondary contact differs between the two populations, asymmetric character displacement can arise, that is, when one of the species shows more displacement than the other (Cooley 2007). This appears to be a general pattern, sometimes also associated with a trade-off between the benefits of avoiding heterospecifics and the costs of having a displaced character (Cooley 2007; Pfennig and Pfennig 2009).

When character displacement results in stronger pre-mating reproductive barriers between sympatric populations than allopatric populations with similar genetic divergence, the pattern is often assumed to arise through a process called reinforcement (Coyne and Orr 1989; Howard 1993; Butlin 1995; Hostert 1997; Noor 1999; Ortiz-Barrientos et al. 2009). According to the reinforcement theory, stronger pre-mating reproductive barriers evolve at secondary contact between populations in response to natural selection against maladaptive hybridization (Dobzhansky 1940). However, there have been several theoretical objections against the likelihood of this process. One of the major problems is that reinforcement can only work under a narrow window of conditions: hybridization must be fairly common to exert a significant selection pressure (Moore 1957), yet not so prevalent that recombination breaks down the association between genes influencing hybrid fitness and genes coding for traits important for assortative mating (Barton and Hewitt 1985). Advocates of the importance of reinforcement have generally considered reproductive character displacement to be a pattern resulting from the process of reinforcement (see Servedio and Noor 2003 and references therein), whereas others consider reinforcement rather as a special case of the process of reproductive character displacement (Blair 1974; Pfennig and Pfennig 2009). One difficulty with inferring process from pattern is that character displacement driven by competition, either for resources or mates, could create a similar pattern of greater divergence in sympatry than in allopatry to that produced by character displacement through reinforcement. Moreover, an evolutionary response to competition over resources may lead to reproductive isolation as a by-product, for example, through

displacement in habitat choice (e.g., Feder et al. 1994; Schluter 2000) or breeding time (Théron and Combes 1995; Hendry and Day 2005).

We are not aware of any study estimating the relative roles of competition for resources and selection against hybridization in driving the process of character displacement. In this study, we describe a snapshot of ongoing processes of character displacement between two closely related species of birds: pied (*Ficedula hypoleuca*) and collared (*F. albicollis*) flycatchers. Our main aims are to investigate the relative importance of potential mechanisms underlying ecological and reproductive character displacement, and to pinpoint interactions between the processes, using data on pairing patterns, reproductive success, onset of breeding, and habitat composition collected during eight years in a young hybrid zone.

The breeding ranges of pied and collared flycatchers overlap in a broad hybrid zone in central and eastern Europe and in a more isolated hybrid zone on the Baltic islands of Öland and Gotland in Sweden (Sætre and Sæther 2010; Qvarnström et al. 2010). The Swedish hybrid zone is relatively young; collared flycatchers have bred on Gotland for around 150 years (Lundberg and Alatalo 1992), and on Öland for around 50 years, where they now are excluding their predecessors, pied flycatchers, from the most favorable breeding sites (Qvarnström et al. 2009). Pied flycatchers prefer to breed in deciduous forests (Lundberg and Alatalo 1992; Siikamäki, 1995) but are often found in coniferous forests on Öland (Qvarnström et al. 2009; Veen et al. 2010). In this study, we investigate whether there is ongoing reproductive character displacement in breeding time, as well as ecological character displacement in habitat use, between the two flycatcher species on Öland. Optimizing the date of egg laying so that the nestlings are brought up under optimal feeding conditions is crucial for maximizing reproductive success in birds (Perrins 1970; Lundberg and Alatalo 1992). As the peak in food abundance is lower and occurs later in coniferous forests compared to deciduous forests (Veen et al. 2010, Fig. 1), we expect that a potential change in timing of breeding and habitat should act in concert; a shift in the breeding habitat of pied flycatchers should influence their optimal timing of breeding and vice versa.

We also investigated the relationship between male breeding plumage coloration, timing of breeding, and habitat composition of the defended territory. Reproductive character displacement in the sexually selected plumage trait between pied and collared flycatchers (Sætre et al. 1997) is often cited as one of the most convincing examples of reinforcement. The two flycatcher species exhibit pronounced spatial variation in plumage coloration across their ranges, and there is greater plumage divergence in sympatry (i.e., in central Europe and the Swedish Baltic islands) compared to allopatry (Drost 1936; Roskaft and Järvi 1992; Sætre et al. 1993; Huhta et al. 1997). Most strikingly, the

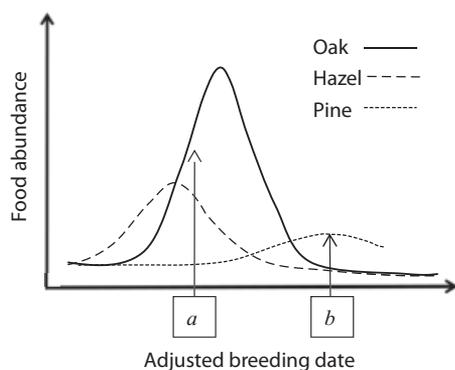


Figure 1. Relative food abundance, in terms of caterpillar biomass, associated with three common tree species across the breeding season (dates of egg laying adjusted for variation between years) in the Swedish *Ficedula* flycatcher hybrid zone (data from Gotland). The food peak is markedly lower and later in pine habitats (b) as compared to hazel/oak habitats (a). Modified from Veen et al. 2010.

breeding plumage of male pied flycatchers varies from black to brown (Fig. 2). The brown coloration is more common in areas where the two species co-occur, although some allopatric populations are also biased toward relatively brown coloration (Lehtonen et al. 2009). Four of Howard's (1993) five proposed requirements for demonstrating reinforcement have been fulfilled in studies of *Ficedula* flycatchers. (1) Heterospecific pairings regularly occur (Qvarnström et al. 2010; Sætre and Sæther 2010) and result in genetic introgression (Borge et al. 2005); (2) there is strong selection against hybridization such that heterospecific pairs experience a fitness reduction of 97%, mainly due to female hybrid sterility and sexual selection against male hybrids (Svedin et al. 2008; Wiley et al. 2009); (3) female flycatchers have changed their preference in parallel with the character displacement in male coloration (Sætre et al. 1997); and (4) plumage coloration is a heritable trait (Alatalo et al. 1994). Howard's (1993) fifth requirement for demonstrating reinforcement is that displacement has not occurred for other reasons. However, field experiments have previously shown that brown male pied flycatchers are subdominant to blacker male pied flycatchers (Slagsvold and Sætre 1991), and allowed to settle nearer resident male collared flycatchers in sympatry (Gustafsson and Pärt 1991; Alatalo et al. 1994) compared to black male pied flycatchers. This suggests that selection pressures other than avoidance of hybridization could also drive divergence in plumage coloration.

The Swedish hybrid zone on Öland provides a unique opportunity to disentangle the causes and consequences of both ecological and reproductive character displacement, because pied flycatchers breed in woodlots both where collared flycatchers occur and where collared flycatchers are still absent on the same

island. Using detailed data on habitat composition and breeding records collected between the years 2002 and 2009, we tested how the increasing numbers of collared flycatchers relates to the breeding habitat composition, onset of breeding, and coloration of pied flycatchers. We also investigated how the presence versus the absence of breeding collared flycatchers in the woodlots influences the selection operating on these key characters in male pied flycatchers breeding with conspecific females. Finally, we investigated whether ecological and/or reproductive character displacement affect the risk of hybridization.

Materials and Methods

STUDY SYSTEM AND SAMPLING OF LONG-TERM DATA

Pied and collared flycatchers are closely related passerine bird species. According to mitochondrial DNA sequence differences, the two species started to diverge 1–2 million years ago and were probably periodically isolated in separate glacial refuges during the Pleistocene, before they expanded their breeding ranges northward (Sætre et al. 2001). The Swedish hybrid zone probably arose when collared flycatchers expanded their breeding range northward where pied flycatchers were already present. The two species feed their offspring with a similar diet (Wiley et al. 2007) but they differ in several life-history traits: collared flycatchers are more successful in competition over breeding sites (Sætre et al. 1993; Alatalo et al. 1994; Sætre et al. 1999) and their offspring have a higher growth potential under favorable environmental conditions (Qvarnström et al. 2005, 2007, 2009). However, pied flycatchers are relatively more robust to harsh environments and declining food availability. Because pied flycatchers can escape interference competition by breeding in poorer habitats, life-history divergence appears to promote regional coexistence of the two species (Qvarnström et al. 2009).

Flycatchers obtain their breeding plumage during a partial molt before migrating back to Europe from their African winter quarters (Svensson 1992). Male collared flycatchers have black and white plumage, with large white patches on the wing and forehead and a distinctive white collar. As mentioned above, male pied flycatchers exhibit a great degree of intraspecific variation, ranging from bright black and white, similar to that of the adult collared flycatcher male but with smaller white patches and no collar, to a dull female-like brown plumage (Fig. 2). Females of both species are dull grayish brown and differ slightly in the tone of their upperparts (female pied flycatchers are generally browner than female collared flycatchers) and in the amount of white at the base of their neck feathers (Svensson 1992). The first males arrive at the breeding grounds in northern Europe in late April and immediately start competing over natural breeding holes

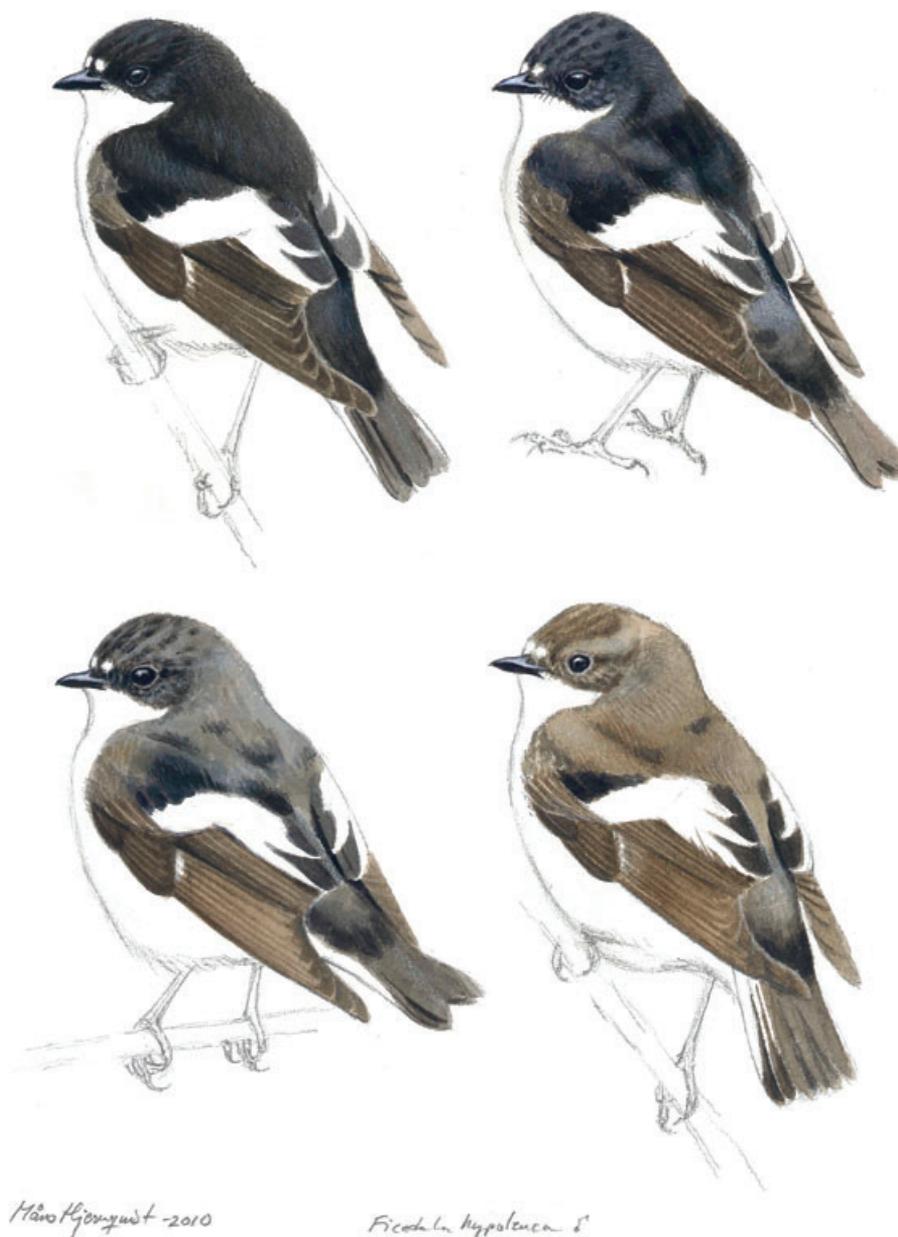


Figure 2. The breeding plumage of male pied flycatchers (*Ficedula hypoleuca*) varies from black to brown, with the browner plumage being more common in areas of sympatry with the closely related collared flycatcher (*F. albicollis*). Artwork by Måns Hjernerquist.

or nest-boxes (Alatalo et al. 1994; Pärt and Qvarnström 1997; Qvarnström 1997). Females generally arrive one week later and select their partner based on a number of characteristics of the male and the territory he defends (Alatalo et al. 1986; Dale and Slagsvold 1996). Females lay five to seven eggs, which hatch in the beginning of June and the young are fed with insects by both parents. Nest-box areas on Öland have been monitored during the periods 1981–1985 and from 2002 onwards. Yearly records are kept on breeding performance, and all breeding birds and their offspring are marked individually with numbered metal rings. Adult

birds are caught once every breeding season (females when incubating, males when feeding nestlings) and morphological characters are measured. Coloration of male pied flycatchers is estimated by scoring the percentage of plumage that is brown. To account for variation between years, we standardized these brown scores using *z*-scores (e.g., Quinn and Keough 2002) calculated within each year. All of the analyses were carried out using R 2.10.1 (www.r-project.org) except where otherwise noted. Model simplifications were performed throughout by removing nonsignificant terms, starting with the least significant interaction terms.

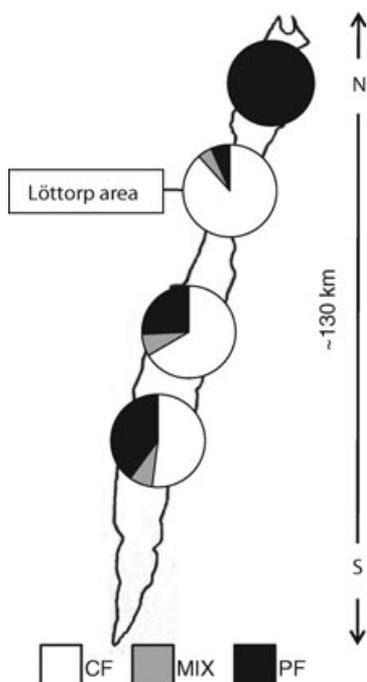


Figure 3. Relative proportions of pied flycatchers (PF), collared flycatchers (CF), and heterospecific pairs (MIX) on the Swedish island of Öland in the years 2002–2009. “Löttörp area” refers to the most densely populated study plots surrounding the town of Löttörp where collared flycatchers started to colonize the island in the 1960s.

IS ECOLOGICAL AND REPRODUCTIVE CHARACTER DISPLACEMENT ONGOING IN THE YOUNG HYBRID ZONE?

The landscape on Öland is characterized by a mixture of agricultural land and deciduous forest, except for the very northern-

most part of the island, which is dominated by coniferous forest. The colonization history of the collared flycatcher on Öland is well known. Since the arrival of the first collared flycatcher immigrants during late 1950s to early 1960s, pied flycatchers have quickly been replaced in the rich deciduous forests (Qvarnström et al. 2009). The relative proportions of the species now vary across the island, with the highest density of collared flycatchers found near the town of Löttörp, whereas areas solely inhabited by pied flycatchers can be found in the very north (Fig. 3). To test if the increasing numbers of collared flycatchers has affected the breeding conditions for pied flycatchers, we investigated how the composition of tree species in pied flycatcher territories (proportion of deciduous versus coniferous forest) has changed across the study period, using least squares linear regression with arcsine-transformed response variable. Breeding habitat was measured during 2007–2009 as the abundance of each tree species 360° around the nest-boxes using a “relascope” (see Veen et al. 2010), assigning individual trees into three categories (0; 0.5; 1) based on trunk size (tree diameter at breast height) and distance from the nest-box. Assuming that the tree species composition is constant across the study period, we linked the habitat measurements to breeding attempts in previous years. We then analyzed trends in the onset of breeding across the study period between the two species. The mean date of egg laying was used as a response variable with year and species as explanatory variables in an ANCOVA. We excluded the first year of the study as the number of breeding flycatchers was low and applied weighted least squares in the model to reduce the influence of years with high variation in breeding dates. All nests with conspecific pairs (pied or collared), including experimental nests not manipulated before the onset of egg laying, were included in this analysis (the total

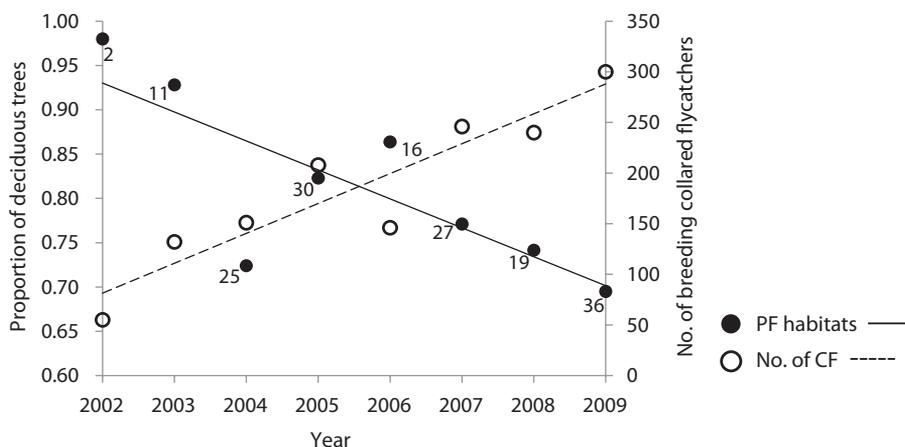


Figure 4. The relative proportion of deciduous trees in pied flycatcher territories on the Swedish island of Öland has declined across the study period as the number of breeding collared flycatchers (secondary y-axis) has rapidly increased. The number of sampled pied flycatcher habitats/year is given below the points.

sample size was 1599 nests). Lastly, we investigated whether there have been any changes in male pied flycatcher coloration during the study period using linear regression with the untransformed brown score as response variable. In this analysis, we included all measured (breeding and nonbreeding) male pied flycatchers ($N = 298$).

WHAT ARE THE RELATIONSHIPS BETWEEN MALE COLORATION, BREEDING HABITAT COMPOSITION, AND TIMING OF BREEDING IN PIED FLYCATCHERS IN THE PRESENCE/ABSENCE OF COLLARED FLYCATCHERS?

We then investigated the relationships between male coloration, habitat composition of the breeding territory, and timing of breeding among male pied flycatchers. First, we performed an ordination of the habitat variables through nonmetric multidimensional scaling using the Bray–Curtis similarity measurement in PAST (palaeontological statistics; <http://folk.uio.no/ohammer/past>, Hammer et al. 2001). Here, we also included an estimation of the relative abundance of Hazel bushes (*Corylus avellana*) and Juniper shrubs (*Juniperus communis*) by scoring them in four categories: absent, ≤ 10 , $> 10 \leq 20$, or > 20 . We subsequently used the values of the first axis of the ordination to compare the habitat composition in areas with collared flycatchers present and in areas with collared flycatchers absent using a Wilcoxon signed-rank test. We then investigated how plumage coloration influenced the habitat composition in the breeding territory obtained, and how habitat composition and plumage coloration influenced breeding time, using linear regression. In areas without collared flycatchers, the habitat composition was biased toward a few coniferous species and we applied Spearman's rank correlation to analyze how plumage coloration influenced the habitat composition of the obtained territory. Annual variation in laying date was controlled for by using the residuals from ANOVAs with laying date as response and year as a factor from all breeding pairs. Spearman's rank correlation was used to investigate the relationship between the proportion of deciduous trees and the habitat variable obtained from the ordination. In addition, to achieve a more detailed understanding of the differences in terms of habitat composition between differently colored male pied flycatchers and collared flycatchers in areas of co-occurrence, we divided the habitat measurements into four groups based on species identity of the male defending the territory and, when defended by a male pied flycatcher, on brown score as well (collared flycatchers and three pied flycatcher groups: low brown, 0–33%; medium brown, 34–66%; and high brown, 67–100%). We thereafter performed a SIMPER (Similarity Percentage, Clarke 1993) test on the habitat composition between the different groups in PAST. The total sample size was 275 nests.

IS SELECTION ON THE REPRODUCTIVE CHARACTERS OF MALE PIED FLYCATCHERS BREEDING WITH CONSPECIFIC FEMALES DEPENDENT ON THE PRESENCE/ABSENCE OF COLLARED FLYCATCHERS?

The presence of a superior competitor is likely to affect the selection pressures operating on pied flycatchers. We therefore tested if the relationship between plumage coloration of male pied flycatchers and their relative fitness (w) was affected by the absence/presence of collared flycatchers in the same woodlot. To estimate relative fitness, we standardized the fledging success of each nest by dividing it with the mean fledging success of all conspecific pairs within the same year. We measured selection on plumage using the selection gradients (β), defined as the covariance between relative fitness and trait value divided by the phenotypic variance in the trait (Lande and Arnold 1983). Relative fitness was used as the response variable in an ANCOVA with brown score and the categorical variable absence/presence of collared flycatchers as explanatory variables. Only conspecific pairs not subject to any experiments were included in the analyses ($N = 104$).

HOW DO ECOLOGICAL AND REPRODUCTIVE CHARACTER DISPLACEMENT INFLUENCE THE RISK OF HYBRIDIZATION?

The low numbers of heterospecific pairings compared to conspecific resulted in a very unbalanced dataset that made fitting a logistic regression model to examine hybridization risk difficult. Therefore, to test how variation in different ecological and reproductive characters (habitat composition, breeding time, and plumage coloration) influenced the risk of hybridization, for each character, we performed a two-tailed Fisher exact test on the likelihood of hybridizing with the characters transformed into categorical variables based on whether they were higher or lower than the average using a dataset including information on all three variables ($N = 112$).

Results

PATTERNS OF ONGOING ECOLOGICAL AND REPRODUCTIVE CHARACTER DISPLACEMENT IN THE YOUNG HYBRID ZONE

We found a significant shift in the proportion of deciduous forest in the territories defended by pied flycatchers across the study period ($N = 8$, slope = -0.068 , SE = 0.021 , $F_{1,6} = 10.356$, $P = 0.02$, Fig. 4). The mean onset of breeding differed significantly between the species ($N = 14$, $F_{1,10} = 8.786$, $P = 0.01$), and the change in the onset of breeding over time also differed between the species as indicated by a significant interaction between species and year ($N = 14$, $F_{1,10} = 5.214$, $P = 0.05$). To examine the

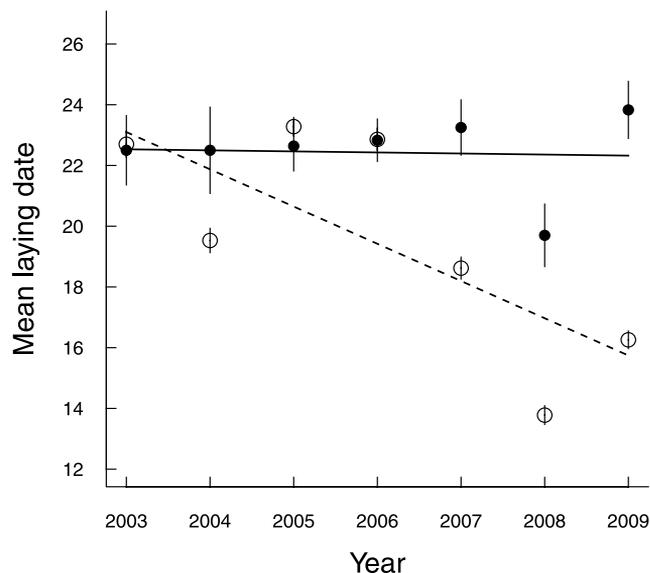


Figure 5. There has been rapid divergence in the onset of breeding (mean day off egg laying in May) between pied (solid circles and trend line) and collared (open circles, dashed trend line) flycatchers on the Swedish island of Öland across the study period.

interaction in more detail, we repeated the analysis within each species and found that the two species appear to show different temporal responses over a relatively short period of time with collared flycatchers advancing their onset of breeding during the study period more rapidly compared to pied flycatchers ($N = 7$, slope = -1.220 , SE = 0.473 , $F_{1,5} = 6.655$, $P = 0.05$, and $N = 7$, slope = -0.035 , SE = 0.266 , $F_{1,5} = 0.018$, $P = 0.90$ for collared and pied flycatchers, respectively). Hence, over the study period, the mean onset of breeding has diverged between collared and pied flycatchers (Fig. 5). After excluding the nonsignificant interaction term between year and presence/absence of collared flycatchers, we did not detect any significant change in brownness of male pied flycatcher plumage across the study period ($N = 298$, $F_{1,296} = 0.664$, $P = 0.416$).

COVARIATION BETWEEN BREEDING HABITAT COMPOSITION, ONSET OF BREEDING, AND COLORATION OF MALE PIED FLYCATCHERS

We analyzed the relationships between male plumage coloration, habitat composition in the defended breeding territory, and timing of breeding in pied flycatchers. Habitat composition was estimated by using the first axis of a nonmetric multidimensional scaling ($N = 188$, stress = 0.22 , $R^2 = 0.535$). There was a highly significant difference in habitat composition between areas where collared flycatchers were present compared to areas where collared flycatchers were absent ($N = 166$, $Z = 9.263$, $P < 0.0001$). For that reason, we proceeded with separate analyses in the two different types of areas. In the areas without collared flycatchers, there was a significant relationship between the habitat composi-

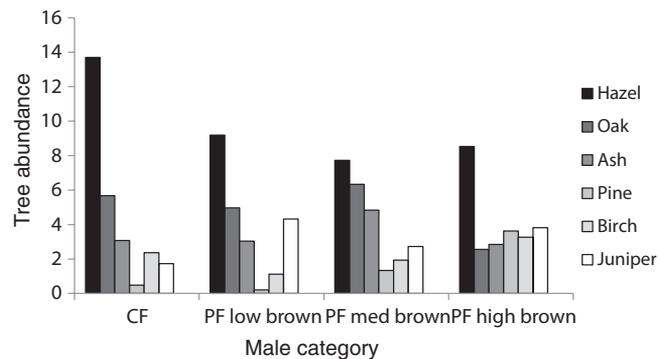


Figure 6. Relative mean abundance (m^2/ha , except hazel and juniper—see Material and Methods) of the most common tree species found in breeding territories defended by collared (CF) and pied flycatchers (PF) co-occurring on the Swedish island of Öland. Male pied flycatchers are divided into three categories of plumage coloration; low brown (0–33%), medium brown (34–66%) and high brown (67–100%). The total sample size was 275 breeding pairs.

tion in the territory obtained and breeding time ($N = 39$, slope = -90.4 , SE = 41.8 , $F_{1,37} = 4.684$, $P = 0.04$) whereas the brown score of male pied flycatchers was not related to either the habitat composition in the territory ($N = 31$, $r_s = 0.009$, $P = 0.96$) or to breeding time ($N = 44$, $F_{1,42} = 0.168$, $P = 0.68$). By contrast, in areas where collared flycatchers were present, the brown score of male pied flycatchers was significantly related to the habitat composition in the obtained territory ($N = 100$, slope = -0.010 , SE = 0.003 , $F_{1,98} = 8.623$, $P = 0.004$), and also to timing of breeding ($N = 144$, slope = 1.232 , SE = 0.53 , $F_{1,142} = 5.320$, $P = 0.02$, and $N = 143$, slope = 0.96 , SE = 0.49 , $F_{1,141} = 3.858$, $P = 0.05$ after excluding a late breeding outlier). Black male pied flycatchers bred earlier than brown males.

The habitat variable obtained from the nonmetric multidimensional scaling was significantly positively correlated with the proportion of deciduous trees ($N = 188$, $r_s = 0.740$, $P < 0.0001$), that is, browner male pied flycatchers were more likely to breed in habitats with a lower proportion of deciduous trees compared to blacker males in areas shared with collared flycatchers. To assess and illustrate more explicitly which tree species contributed most to the observed differences among males, we additionally performed a SIMPER test on the habitat composition for four categories of males (male collared flycatchers and low, medium, and high brown colored male pied flycatchers). The overall average dissimilarity was 65.33%, with hazel contributing the most (16.3%) to the observed difference ($N = 275$). Although hazel was the most common tree species in the territories defended by all groups of males, the highest abundance was found in territories defended by male collared flycatchers (Fig. 6). In the habitats occupied by the brownest male pied flycatchers, oak was less abundant whereas pine was relatively more abundant than in habitats occupied by the other groups of males (Fig. 6). Thus,

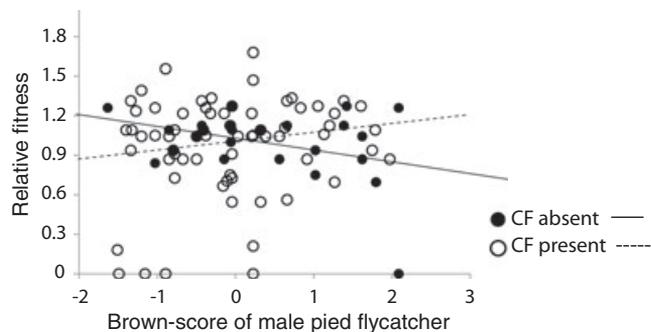


Figure 7. Relative fitness (w) in relation to coloration of male pied flycatchers within the Swedish island of Öland. Browner males have relatively higher breeding success than black males in woodlots where collared flycatchers are present (dashed trend line), but relatively lower breeding success in woodlots where collared flycatchers are absent (solid trend line). See text for descriptions on the estimation of relative fitness and color score. The sample size was 104 breeding pairs.

relatively brown male pied flycatchers bred in territories most different from collared flycatchers, with a habitat composition associated with a lower absolute abundance of food, but a more stable seasonal access to food (Veen et al. 2010; Eeva et al. 2011) compared to the territories defended by collared flycatchers and darker male pied flycatchers.

SELECTION ON THE REPRODUCTIVE CHARACTERS—BROWNER MALE PIED FLYCATCHERS EXPERIENCE HIGHER REPRODUCTIVE SUCCESS IN THE PRESENCE OF COLLARED FLYCATCHERS

To compare the strength of selection on plumage in male pied flycatchers in areas with and without collared flycatchers, we performed a formal selection analysis testing the interaction between presence/absence of collared flycatchers and the brown score of male pied flycatchers.

This interaction was significant ($N = 104$, $F_{1,100} = 4.191$, $P = 0.04$) showing that for male pied flycatchers relative fitness increased with increasing brownness when collared flycatchers were present, but decreased in areas where collared flycatchers were absent (Fig. 7). Hence, the standardized selection gradient on plumage brownness in male pied flycatchers was positive in areas of co-occurrence with collared flycatchers ($\beta = 0.068$, $SE = 0.042$) and negative in areas without collared flycatchers ($\beta = -0.084$, $SE = 0.061$).

CHARACTER DISPLACEMENT AND HYBRIDIZATION—NO EVIDENCE FOR REINFORCEMENT

The number of breeding pairs (excluding hybrids) where both sexes were captured across the study period totaled 1478 pairs of collared flycatchers, 274 pairs of pied flycatchers, and

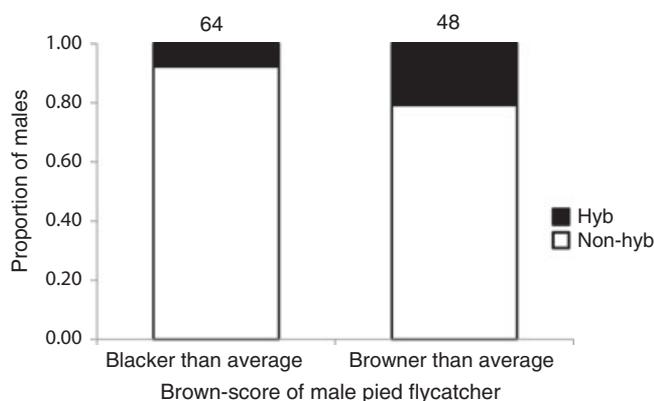


Figure 8. The proportion of hybridizing male pied flycatchers on the Swedish island of Öland in relation to color score (blacker or browner than average). Sample sizes are given above the bars. Hyb, heterospecifically paired male, Non-hyb, conspecifically paired male.

100 heterospecific pairs. These numbers include secondary females (secondary females with an unknown mate were excluded). In total, 7.7% of the male pied flycatchers and 5% of the male collared flycatchers were paired with a heterospecific female. There were no significant differences in the habitat scores or timing of breeding between conspecifically paired versus heterospecifically paired male pied flycatchers ($N = 112$, odds ratio = 1.37, $P = 1.0$, and odds ratio = 0.252, $P = 0.08$, respectively). Neither did we find any evidence in accordance with the reinforcement hypothesis of browner male pied flycatchers experiencing a decreased risk of hybridization. On the contrary, heterospecifically paired male pied flycatchers were significantly browner than conspecifically paired male pied flycatchers ($N = 112$, odds ratio = 3.073, $P = 0.05$, Fig. 8).

Discussion

Collared flycatchers colonized the Baltic island of Öland about 50 years ago and are now rapidly excluding their pied flycatcher predecessors from certain parts of the island (Qvarnström et al. 2009). We show here that the increasing numbers of breeding collared flycatchers has led to a shift in the breeding habitats of pied flycatchers from deciduous forest toward mixed or coniferous forest (Fig. 4). The displacement in habitat occupancy has furthermore been paralleled by a divergence in breeding time between the two *Ficedula* flycatchers (Fig. 5). Previous studies have shown that the breeding plumage of male pied flycatchers is browner in populations occurring in sympatry with collared flycatchers than in allopatry (Drost 1936; Roskaft and Järvi 1992; Sætre et al. 1993; Huhta et al. 1997), including both the two Baltic isles compared to the mainland of Sweden (e.g., Alatalo et al. 1994). However, we did not find any significant further change in plumage coloration across this study period, perhaps

because plumage coloration is a largely genetically determined trait (Alatalo et al. 1994) whereas habitat choice and timing of breeding are highly plastic traits (Lundberg and Alatalo 1992; Przybylo et al. 2000; Sheldon et al. 2003). In contrast to the main expectation of reinforcement, we found that relatively brown male pied flycatchers hybridized more often than black males under similar conditions (Fig. 8). Furthermore, the relationship between male coloration and relative fitness among conspecific pairs of pied flycatchers changed depending on the presence or absence of collared flycatchers breeding within the same woodlot. Browner male pied flycatchers experienced higher reproductive success when collared flycatchers were present, whereas the opposite was true in nearby woodlots lacking collared flycatchers (Fig. 7). We also found that the brownness of male pied flycatchers in areas of co-occurrence with collared flycatchers was significantly related to the habitat composition of the territory defended as well as timing of breeding. Relatively brown male pied flycatchers bred later than black males and occupied territories that were most dissimilar in habitat composition from the ones occupied by collared flycatchers (Fig. 6).

RELATIONSHIP BETWEEN ECOLOGICAL AND REPRODUCTIVE CHARACTER DISPLACEMENT

Collared flycatchers advanced their onset of breeding more across the study period compared to pied flycatchers (Fig. 5). This is likely a plastic response of collared flycatchers to keep up with an advancing peak in food abundance due to recent climate change (Przybylo et al. 2000; Sheldon et al. 2003). The finding that pied flycatchers have not adjusted their onset of breeding as markedly may reflect a direct interaction with collared flycatchers resulting in pied flycatchers being forced out into a new habitat, and an indirect effect of differences in timing of the food peak in the different habitats. As the two flycatcher species are both long-distance migrants but with different migration routes and winter quarters (Lundberg and Alatalo 1992; Veen et al. 2007), one may argue that they are differentially affected by ongoing climate change through, for example, a differential change in arrival date. However, among males caught prior to breeding, there is rather a tendency for pied flycatchers to arrive at the breeding sites at an earlier date than collared flycatchers and there is no significant difference in adult survival between the two species (Vallin 2011). Thus, different migration routes are an unlikely alternative explanation to the rapid character displacements occurring on Öland. Adamik and Bureš (2007) suggested that pied and collared flycatchers exhibit divergent habitat preferences and diet in the central European hybrid zone. However, an earlier study on Öland indicated highly overlapping diets between the two species (Wiley et al. 2007), even though pied flycatchers appear to have a wider niche breadth (Reif et al. 2010). Our recent data show that the composition of the breeding habitat of pied flycatchers

on Öland is currently approaching the habitat composition observed in the older central European hybrid zone (Sætre et al. 1999). Our results therefore imply that interspecific competition can cause rapid changes in breeding time and habitat choice, presumably aided by other factors such as phenotypic plasticity and imprinting (e.g., Thibert-Plante and Hendry 2011).

SELECTION ON THE DISPLACED CHARACTERS OF MALE PIED FLYCATCHERS BREEDING WITH CONSPECIFIC FEMALES DEPENDS ON THE PRESENCE/ABSENCE OF COLLARED FLYCATCHERS

The fact that the relationship between male coloration and relative fitness among conspecific pairs of pied flycatchers changed depending on the presence or absence of collared flycatchers breeding within the same woodlot is consistent with the evolution of browner plumage of male pied flycatchers in sympatry. That relatively black male pied flycatchers experience higher relative fitness in the absence of collared flycatchers is consistent with earlier findings showing that black male pied flycatchers are dominant to brown ones in allopatric populations (Slagsvold and Sætre 1991). But why do browner male pied flycatchers enjoy higher reproductive success than blacker males in the presence of collared flycatchers (Fig. 7)? Previous experiments have shown that interspecific aggression is relaxed for browner male pied flycatchers (Král et al. 1988; Sætre et al. 1993), and that they are allowed to settle nearer to collared flycatchers than blacker males (Gustafsson and Pärt 1991). However, we found that relatively brown male pied flycatchers settled in habitats most different from the ones defended by collared flycatchers in areas of co-occurrence (Fig. 6). A relatively low abundance of oak and high abundance of pine imply a comparatively lower, later, and broader peak in food abundance (Veen et al. 2010) suggesting that brown males may experience relatively higher reproductive success because the black male pied flycatchers have become severely mistimed in relation to the peak in food abundance in the breeding habitat they occupy. Further studies are needed to pinpoint detailed differences in prey diversity and abundance in different microhabitats, as well as the effect of direct interference from collared flycatchers. Paradoxically, by breeding later than black male pied flycatchers (Lundberg and Alatalo 1992; this study) and by settling in the less-preferred habitat (this study), browner male pied flycatchers in sympatry appear to end up in a better breeding situation. Abundant standing genetic variation and intraspecific character displacement (through disruptive selection caused by, e.g., intraspecific competition) are considered to facilitate character displacement (Rice and Pfennig 2007; Pfennig and Pfennig 2009). The fact that male pied flycatchers vary in plumage coloration also in allopatric populations (Lehtonen et al. 2009) indicates that they could be predisposed

to character displacement in plumage coloration when there is strong selection against black male pied flycatchers, that is, in areas of sympatry with collared flycatchers.

A FEEDBACK LOOP BETWEEN ECOLOGICAL AND REPRODUCTIVE CHARACTER DISPLACEMENT

Our results illustrate that secondary contact between closely related species can lead to rapid displacement in several important characteristics. In the young Swedish *Ficedula* hybrid zone, heterospecific competition quickly resulted in pied flycatchers being displaced from their preferred deciduous habitat, which also delayed the advancement in their onset of breeding, compared to collared flycatchers. We suggest that with this delay in breeding time, the initially less-preferred habitat fits better in terms of food availability for that particular timing of breeding, and that the browner less-competitive pied flycatchers do best simply because they are not challenging the superior collared flycatchers. The older hybrid zone in central Europe likely represents a later step in habitat segregation and reproductive character displacement (with larger habitat segregation and a higher frequency of brown males). A relevant question then becomes how the asymmetry in interference competitive ability between males of the two flycatcher species evolved in the first place. We have previously suggested that the two flycatcher species have solved the trade-off between aggressive competitive ability and stress tolerance differently (Qvarnström et al. 2005, 2009). There are trends toward competitive exclusion of pied flycatchers from the most preferred breeding sites where the two species co-occur in central Europe (Sætre et al. 1999), on Öland (Qvarnström et al. 2009) and on Gotland (Alerstam et al. 1978). However, collared flycatchers produce slightly smaller clutches, their nestlings beg more intensively, and their young are more sensitive to poor environmental conditions (Qvarnström et al. 2005, 2007, 2009). The most likely explanation for the divergence in life-history traits (of both nestlings and adult birds) is that pied flycatchers have been selected to breed under more harsh environmental conditions because their overall breeding distribution is more northern. Because pied flycatchers can escape interference competition by breeding in poorer habitats, life-history divergence appears to promote regional coexistence of the two species (Qvarnström et al. 2009). The divergence in life history appears to promote pre-mating isolation by facilitating habitat segregation on a regional scale. However, reproductive character displacement in plumage coloration rather seems to act against pre-mating isolation, by prolonging coexistence through a reduced risk of exclusion by male aggressive interactions, and by facilitating habitat segregation also on a local scale.

Although evidence consistent with reinforcement is supported by empirical examples (Noor 1995; Sætre et al. 1997; Rundle and Schluter 1998; Higgie et al. 2000; Nosil et al. 2003;

Hoskin et al. 2005), there is also an increasing awareness that species interactions, such as predation, pollination, brood parasitism, mimicry, and competition for signal space, can cause direct selection on mating traits, potentially causing the pattern of reproductive character displacement (Hoskin and Higgie 2010). In particular, the importance of interspecific aggression in causing selection on secondary sexual characters is gaining increasing support (Butcher and Rohwer 1989; Seehausen and Schluter 2004; Tynkkynen et al. 2004, 2005; Grether et al. 2009; Anderson and Grether 2010), and our results are more compatible with this view than with a role for reinforcement in causing male breeding plumage divergence in *Ficedula* flycatchers. We furthermore argue that interspecific competition among males over resources necessary to attract females (i.e., suitable nest sites) may give rise to a feedback loop between ecological divergence and reproductive character displacement. Ecological divergence in allopatry is likely to influence aggressive competitive abilities at secondary contact. In the case of the flycatchers, this link arises through a trade-off between tolerance to harsh environment and competitive ability, but there are many other possible links (an obvious example being divergence in body size, which directly influences resource use and competitive ability). At secondary contact, the link between reproductive character displacement and future ecological divergence can occur both through a correlated evolutionary response (or through a dual function of traits such as body size), and through the fact that interspecific competition among males over resources necessary to attract females also determines in what type of environment offspring are raised. In birds, allopatric divergence is thought to be the most common mode of speciation, and male resource defense is the most common mating pattern (Price 2008). We therefore suggest that a feedback loop between ecological divergence and reproductive character displacement through male interspecific competition may, in general, play an important role during the final stages of speciation. This mechanism by which the speciation process could be finalized in sympatry could moreover act over a much wider range of conditions than reinforcement (e.g., selection for avoiding heterospecific male competition can remain high even when the rate of hybridization is low).

Conclusions

In summary, we present results consistent with competition-mediated ecological divergence between two closely related flycatcher species. We suggest that the reproductive character displacement, observed in the plumage and the timing of breeding, and ecological character displacement in terms of a shift in habitat occupancy, of male pied flycatchers co-occurring with collared flycatchers are initially driven by intense social and ecological interactions with a dominant competitor rather than by avoidance

of hybridization (i.e., reinforcement). Within a young zone of secondary contact on the island of Öland, Sweden, we found that pied flycatchers were rapidly excluded from their preferred breeding habitats, as the numbers of breeding collared flycatchers increased. Furthermore, the relationship between the brownness of male pied flycatchers and relative fitness depended on the presence/absence of breeding collared flycatchers in the area. Relatively brown male pied flycatchers had higher relative fitness than black males when faced with the superior competitor, even though browner male pied flycatcher territories were associated with nonpreferred habitat characteristics. However, these brown males were also faced with a high risk of hybridizing with female collared flycatchers. Thus, there is no evidence suggesting that selection against hybridization is driving character displacement at this early stage of co-occurrence but we do not exclude the possibility that reinforcement could be operating at later stages of co-occurrence between these two species. Character displacement driven by competition between heterospecific males at an early stage of co-occurrence may even facilitate reinforcement at a later stage of co-occurrence. We conclude that competition between heterospecific males functions as a major driving force causing fast ecological and reproductive character displacement at secondary contact between two young *Ficedula* flycatcher species. In addition, our results imply a feedback loop between ecological divergence and reproductive character displacement, which in general may have important consequences during the final stages of the speciation process.

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