

Contemporary Evolution of Reproductive Isolation and Phenotypic Divergence in Sympatry along a Migratory Divide

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Summary

Understanding the influence of human-induced changes on the evolutionary trajectories of populations is a fundamental problem [1, 2]. The evolution of reproductive isolation in sympatry is rare, relying on strong selection along steep ecological gradients [3–7]. Improved wintering conditions owing to human activities promoted the recent establishment of a migratory divide in Central European blackcaps (*Sylvia atricapilla*) [8, 9]. Here, we show that differential migratory orientation facilitated reproductive isolation of sympatric populations within <30 generations. The genetic divergence in sympatry exceeds that of allopatric blackcaps separated by 800 km and is associated with diverse phenotypic divergence. Blackcaps migrating along the shorter northwestern route have rounder wings and narrower beaks and differ in beak and plumage color from sympatric southwest-migrating birds. We suggest that distinct wing and beak morphologies are ecomorphological adaptations resulting from divergent, multifarious selection regimes during migration. We hypothesize that restricted gene flow accelerates the evolution of adaptive phenotypic divergence toward the contrasting selection regimes. Similar adaptive processes can occur in more than 50 bird species that recently changed their migratory behavior [10, 11] or in species with low migratory connectivity. Our study thus illustrates how ecological changes can rapidly drive the contemporary evolution of ecotypes.

Results and Discussion

There is growing recognition that ecological and evolutionary dynamics can occur on the same timescales and thereby influence each other [12–14]. A good example is the contemporary evolution of a migratory divide in Central European blackcaps (*Sylvia atricapilla*) that was favored by warmer climate and increasing food supply provided by humans in the United Kingdom [8, 9]. Part of the blackcap population breeding in southern Germany and Austria established a new migratory direction toward the northwest (NW) in the 1960s. The new wintering areas are 1200–1800 km north of the traditional western Mediterranean overwintering sites of sympatrically breeding southwest (SW)-migrating blackcaps [8, 9]. Within

less than 30 generations, the proportion of NW-migrating blackcaps breeding in southern Germany has increased to approximately 10% [15]. Crossbreeding experiments established that hybrids between birds with the two migratory directions migrate in an intermediate direction and that the inheritance pattern is consistent with migratory orientation being controlled by one or only a few major genes [15]. Further experiments showed that migratory behavior in blackcaps can evolve within a few generations owing to substantial additive genetic variation for migratory traits [16]. Blackcaps form seasonal pair bonds upon arrival at the breeding grounds. Differences in migratory orientation lead to temporal segregation upon spring arrival and, consequently, assortative mating between birds with the same migratory orientation [8, 17]. As such, divergence in migratory orientation could potentially lead to premating isolation mediating the evolution of ecotypes and, possibly, even incipient ecological speciation in the blackcap.

Evidence for migratory behavior promoting speciation in birds is limited. Previous studies on avian populations with distinct migratory orientation reported little genetic divergence in neutral markers [18, 19], and, although there are some possible exceptions [20, 21], divergence in sympatry is thought to be rare in birds [22, 23]. Given that migratory birds are the prime example of highly mobile organisms, the lack of genetic diversification might be caused by interbreeding among different populations. Also, it may reflect the limited genetic response of populations that experience differential selection along a single ecological dimension [23]. Here, we investigated potential adaptive divergence in the contemporary evolution of migratory behavior of the blackcap. We used stable isotope analysis to assign sympatric populations to their wintering quarters and measured various phenotypic traits as well as neutral genetic differentiation to determine whether divergent selection occurs along one or multiple ecological dimensions.

Population Genetics

Consistent with the low amount of genetic structuring in migratory birds, previous analyses of mitochondrial DNA (mtDNA) haplotypes revealed no genetic structure among Western European blackcaps indicating that any differences in migratory behavior are of very recent origin [24].

The recent establishment of a NW migratory route in Central European blackcaps resulted in genetic divergence of neutral markers from sympatrically breeding SW migrants within <30 generations (Table 1). Log-likelihood estimations of population affiliation for individual genotypes [25] assigned more than 85% of the individuals correctly to their respective populations (Figure 1). The presence of two distinct genetic clusters was supported with the software STRUCTURE [26] (see Figure S1 available online), but STRUCTURE did not assign individuals to their source population. This result was expected because STRUCTURE is not a powerful tool when genetic differentiation is slight. Importantly, the low but significant genetic divergence in sympatry ($F_{ST} = 0.008$; $p < 0.005$) exceeds the genetic divergence of these populations and an allopatric population of SW migrants from northern Germany separated by 800 km

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Table 1. Pairwise F_{ST} Comparisons between Five Different Blackcap Populations from Europe

	Southern Germany	Southern Germany	Spain	Northern Germany	Russia
n	142	55	49	27	20
Migratory orientation	SW	NW	Sedentary	SW (north)	SE
SW		0.028	0.094	<0.001	0.187
NW	0.008*		0.051	<0.001	0.131
Sedentary	0.019**	0.012*		0.085	0.197
SW (north)	<0.001	0.004	0.02**		0.163
SE	0.048**	0.037**	0.05**	0.044**	

Pairwise F_{ST} comparisons are shown below the diagonal, standardized F_{ST} comparisons above it. We genotyped 293 individuals that included a random sample of the SW migrants (comprising 50% of these birds) and all NW migrants except for 6 birds that were excluded owing to insufficient DNA material. Data are based upon ten microsatellites [35]. * $p < 0.005$; ** $p < 0.001$; adjusted nominal level (5%) for multiple comparisons: 0.005.

($F_{ST} = 0.0001-0.004$; all $p > 0.5$; Table 1). The genetic divergence in sympatry was consistently found in different years and different sampling sites (Table S1). Interestingly, genetic differences are larger within years than when years are pooled, a result that corroborates our conclusions on the genetic divergence in sympatry.

We thus conclude that, owing to assortative mating, the evolution of a migratory divide has initiated reproductive isolation among the sympatric blackcap populations. Drift seems unlikely to be a powerful mechanism creating genetic divergence within <30 generations or even <60 generations if the NW migratory orientation evolved 100 years ago but remained undetected because few individuals were initially involved. More likely, the genetic divergence might be attributable to founder effects because NW migrants had a higher proportion of homozygotic individuals than SW migrants (G.R., unpublished data).

A drift-immigration equilibrium between NW and SW migrants is unlikely owing to the recent origin of reproductive

isolation. Consequently, the F_{ST} values do not necessarily indicate the current level of gene flow. The migratory divide might thus either cause further divergence between sympatric populations or collapse owing to hybridization between birds of different migratory direction.

Analysis of molecular variance (AMOVA) of five blackcap populations from Europe with distinct migratory strategies (Figure 2) indicated low but significant levels of genetic structuring (overall $F_{ST} = 0.016$; 95% confidence interval = 0.005–0.028; $p = 0.00228$, AMOVA). Pairwise F_{ST} comparisons revealed the strongest genetic differentiation between SE migrants from Rybachy, Russia and the other populations ($F_{ST} = 0.037-0.050$; all $p < 0.00001$). This differentiation reflects the secondary contact zone of populations from different Pleistocene refugia where a migratory divide separates SW and SE migrants at 12°E–13°E in Central Europe [24]. Similarly, sedentary blackcaps from southern Spain differed from the three migratory Central European populations ($F_{ST} = 0.012-0.020$; all $p \leq 0.005$). Our results suggest that genetic divergence in blackcap populations is determined mainly by migratory behavior (Mantel test of genetic and geographic distance: $r = 0.504$, $p = 0.255$).

Apart from the well-known examples of introduced species and populations, this is among the few studies to provide evidence that ecological changes associated with human activities are strong enough to initiate evolution of reproductive isolation among sympatric populations. The alternative hypothesis of an allopatric origin of the NW-migrating population is not supported by our data and previous genetic data from other European blackcap populations [24]. Furthermore, this hypothesis is unlikely because NW-migrating blackcaps were not recorded in Europe or elsewhere prior to the 1960s.

Phenotypic Divergence

We found divergence in various phenotypic traits among sympatric SW and NW migrants. Blackcaps migrating along the shorter NW route (~1090 km) had rounder wings than birds traveling the longer SW route (~1640 km). The observed difference in wing shape among sympatric populations is consistent with the Europe-wide pattern that a shorter migratory route is associated with a decrease in wing pointedness (Holynski index) of blackcaps (Figure 3). We consider founder effects as unlikely to have caused the difference in wing shape because NW migrants would have then originated from a more southern population with an originally shorter migratory route (resulting in a longer current NW route), a pattern that is not confirmed by ringing records. Birds from both populations molt their wing feathers in a common garden situation on the

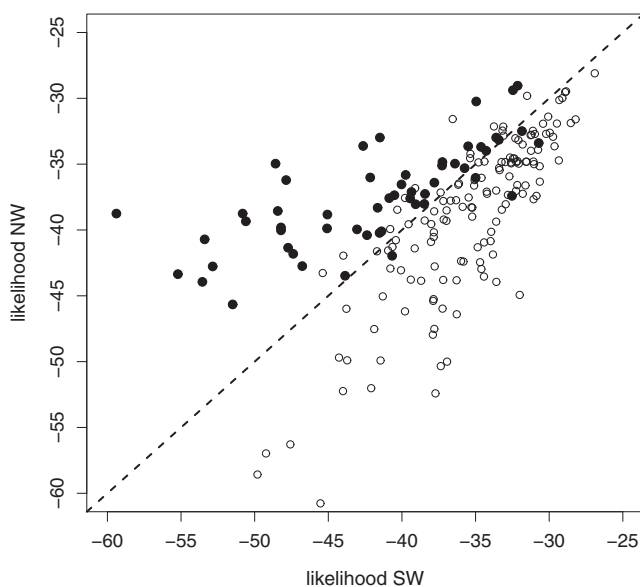


Figure 1. Log-Log Plot of the Likelihood of Genetic Assignment to the Source Population in Sympatric Blackcaps

We used multilocus assignment of individual birds without any a priori information other than isotope signature. Black circles (●) indicate northwest (NW) migrants; white circles (○) indicate southwest (SW) migrants. The dashed line depicts 1:1 correspondence. Note that the two populations are genetically similar because a large proportion of individuals cluster close to the 1:1 correspondence line.

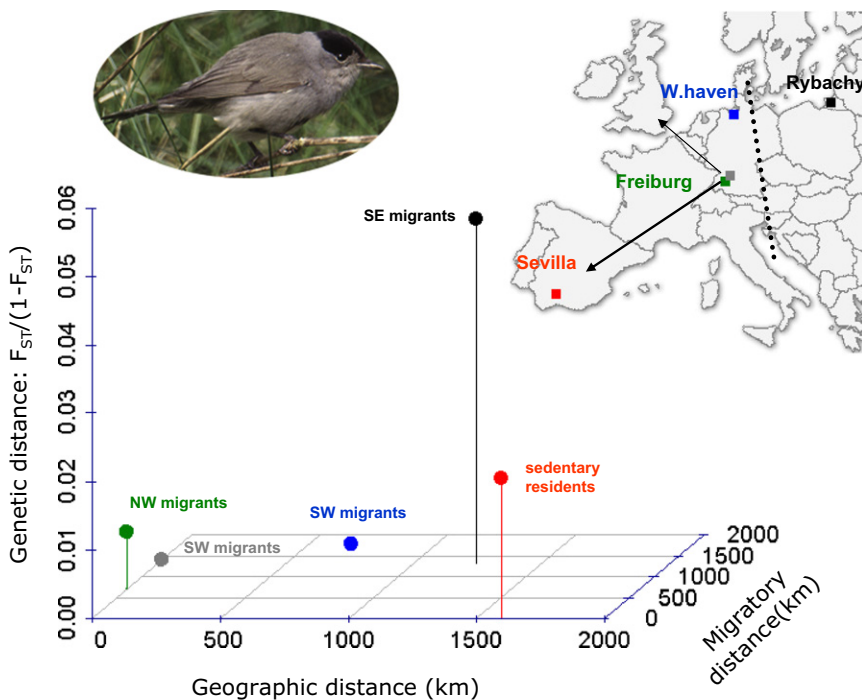


Figure 2. Genetic Distance among Blackcap Populations Is Primarily a Function of Migratory Orientation Rather Than Geographic Distance

Genetic and geographic distances are illustrated relative to the SW-migrating blackcaps from southern Germany (gray dot). The respective migratory distances are denoted on the z axis. Each population is characterized by a given color. The map of Europe shows the breeding grounds of the sampled populations and the two pronounced migratory divides in the blackcap. The dotted line corresponds to the migratory divide at 12° E–13° E separating SE- from SW-migrating populations [24]. The arrows indicate the distinct migratory orientations in the recently established Central European migratory divide. “W. haven” indicates Wilhelmshaven.

breeding grounds prior to migration [27]. Although birds do not necessarily molt at the same time, it is unlikely that different environmental conditions during molt alone determine the differences in wing shape. Rather, we suggest that incipient reproductive isolation of NW and SW migrants has facilitated

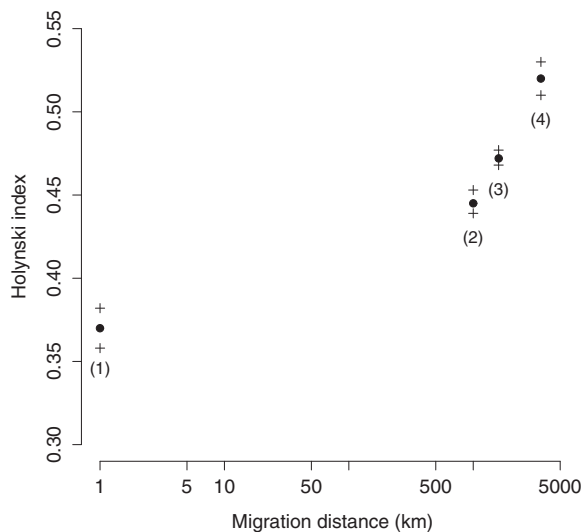


Figure 3. Wing Pointedness as Measured by the Holynski Index Changes According to Migratory Distance

Short-distance migrants (<500 km) or sedentary blackcaps ([1]; $n = 99$) from the Mediterranean area (additional data from [38]) have rounder wings than long-distance migrants (1800–5000 km, [4]; $n = 315$, $\text{mean}_{\text{Holynski}} = 0.52 \pm 0.009$ standard error). NW-migrating blackcaps ([2]; $n = 61$) have rounder wings than sympatric blackcaps that migrate along the longer SW route ([3]; $n = 264$; $F = 6.23$, $p < 0.05$, type II analysis of variance; see Figure S2 for the distribution of the Holynski index among the two sympatric populations). Wing traits have a heritability of >0.6 in southern German blackcaps [38]. Note the logarithmic scale of the x axis. Means and standard errors are shown.

adaptive phenotypic divergence toward the new migratory route.

NW and SW migrants also differ in beak morphology, but not in tarsus length ($p > 0.4$). Beak shape differed among populations and sexes (beak PC2: $F = 12.32$, $p < 0.001$), and there was a sex effect in beak size (beak PC1: $F = 10.05$, $p < 0.01$; $n_{\text{NW migrants}} =$

61, $n_{\text{SW migrants}} = 264$, type II analysis of variance): females of both populations had larger beaks than males. Divergence in beak shape in birds can reflect adaptation toward differential exploitation of food resources [28], a scenario that might also hold for the blackcap. In the Mediterranean area, fruits make up 95% of the diet of blackcaps [29], whereas blackcaps wintering in Britain are known to feed primarily on seeds and fat at garden feeders [30]. Given that gape width is the main constraint determining the size of fruits that a bird can exploit [31], we hypothesize that the relatively broader bills of SW migrants are adapted to a more specialized, frugivorous diet. In contrast, the relatively narrower and longer beaks of NW migrants likely reflect a more generalistic feeding behavior at bird feeders.

Analysis of beak and plumage colors revealed significant differences between NW and SW migrants in avian visual color space. The beak and the feathers of the back were relatively browner (with a tinge of olive in males) in NW migrants, whereas they were relatively greyer in SW migrants independent of sex or age (Table S2). The browner coloration of NW migrants suggests a different ratio of eumelanin and pheomelanin. Alternatively, and unlike the differences in wing shape, differences in feather color may be explicable by differential molt strategies. Different wear and tear of feathers may explain the color differences because blackcap populations wintering farther north renew fewer feathers during the prenuptial molt than those wintering further south [27]. Unlike feathers, beaks constitute a fast-responding tissue sensitive to fluctuation in abiotic stress, health, and diet [32]. Differences in beak color might therefore reflect various divergent ecological constraints that are partly associated with distinct foraging in both wintering areas.

In total, five traits that were uncorrelated among each other (wing morphology, beak shape, back plumage color, head plumage color, and bill color; all $p > 0.2$; see Table S2) differed between the two populations. The diverging traits correspond to multiple ecological dimensions: wing shape is associated

with migratory distance, beak shape is associated with foraging, and plumage coloration is associated with molting strategies or melanin synthesis.

Because selection on and the heritabilities of the five traits probably differ, distinct evolutionary mechanisms are likely to contribute to the phenotypic divergence among sympatric blackcaps. First, reproductive isolation might facilitate adaptive phenotypic divergence in response to contrasting, multifarious selection regimes associated with each migratory route. In this case, divergence is adaptive and evolved owing to the establishment of the migratory divide. We suggest that this scenario is particularly likely for divergence in wing and beak shape. Second, phenotypic differences might have been caused by drift following incipient reproductive isolation. Third, founder effects might explain phenotypic differences that would have been present before—and might have even facilitated—the evolution of the migratory divide. Because an adaptive role of beak and back coloration is unknown, a combination of drift and founder effects might explain the differences in these traits.

Even if we assume that divergence evolved after the evolution of the migratory divide, microevolutionary rates (measured in haldanes) are high, but not exceptionally so. The rates of phenotypic divergence in wing morphology ($h_{p(1.43)} = 0.014$) and beak shape ($h_{p(1.43)} = 0.020$) in blackcaps would be at the upper limit of the third quartile of studies on microevolutionary rates summarized by Hendry et al. ([33]; quartiles from haldane database: first: 0.002; second: 0.006; third: 0.014). If the migratory divide is twice as old as the first sightings of blackcaps wintering in the United Kingdom suggest, the microevolutionary rates would be lower (Table S3) but still above the median given in [33].

It is unknown whether selection will lead to further divergence among NW and SW migrants. We note, however, that the evolution of differential plumage coloration in NW and SW migrants provides a proximate mechanism for reinforcement allowing for the evolution of active recognition and further premating isolation. If the intermediate migratory routes of hybrids lead them to unsuitable wintering grounds, mate selection according to migratory orientation could override assortative mating as a by-product of differential migratory behavior.

We suggest that alternative migratory behavior can initiate reproductive isolation in sympatry, leading to the evolution of genetically distinct ecotypes. We hypothesize that the ecotypes experience different selection regimes that are temporarily restricted to an allopatric phase during the annual cycle but that can entail significant carryover effects upon the sympatric breeding phase. In this scenario, a single trait, migratory orientation, initially restricts gene flow but concomitantly results in divergent multifarious selection during migration. Adaptive divergence might then secondarily lead to a further reduction in gene flow and—owing to positive feedback loops between reduction in gene flow and adaptive divergence—a scenario of incipient ecological speciation.

Theoretical considerations predict that if multifarious selection causes divergence, the resulting widespread evolutionary response might be more effective in driving speciation than the more limited response caused by single-trait selection. Because migratory orientation in the blackcap can potentially result in subsequent multifarious selection upon other, uncorrelated traits, the distinction between single-trait selection and multifarious selection might be less pronounced than recently suggested [7].

Our study illustrates the profound impact of human activities on the evolutionary trajectory of populations. Food provided during winter in the United Kingdom contributed to the establishment of the NW migratory route that would probably have been maladaptive previously. Because anthropogenic changes occur in general concomitantly on multiple ecological dimensions, they can result in multifarious selection upon multiple traits and thereby drive contemporary evolution.

We propose that the evolution of migratory ecotypes is a subtle but potentially widespread process that improves adaptive responses toward the diverse ecological settings that migrants experience. We predict that the evolution of migratory ecotypes occurs in species with low migratory connectivity where individuals disperse to different overwintering quarters or habitats.

Experimental Procedures

We caught birds in four regions. In spring 2006–2008, we caught blackcaps upon arrival at their breeding grounds in southern Germany in Radolfzell (47°45'N 08°59'E) and Freiburg (48°00'N 07°51'E). These birds comprised SW migrants (main migratory direction southern Spain) and NW migrants (wintering in Britain) that were caught at each site within an area of ~50 hectares in the same mist nets. We also sampled sedentary blackcaps caught in winter 2006–2008 near Sevilla, Spain (37°39'N 5°35'W); northern German blackcaps caught in summer 2007 at their breeding grounds in Wilhelmshaven (53°31'N 08°07'E); and blackcaps caught in spring/summer 2007 at Rybachy, Russia (55°09'N 20°51'E). Blackcaps from Wilhelmshaven are SW migrants traveling to the Mediterranean and to sub-Saharan Africa, whereas blackcaps from Rybachy migrate along the eastern route to Africa [24]. We calculated the number of generations separating the sympatric populations by dividing the time since the appearance of the migratory divide (noted in 1959) by the mean age (1.8 years) of southern German blackcaps [27].

We recorded the following phenotypic traits of blackcaps from southern Germany and Sevilla: lengths of tarsus and wing; lengths of all long primaries and the first secondary (P1–P9, S1); length, width, and height of beak; plumage coloration of back, breast, and head feathers; and beak coloration. Variation in beak morphology was analyzed via a principal component analysis (PCA) on the beak measurements. PC1 was interpreted as beak size (50% variance explained; loadings: length: –0.31, width: –0.64, height: –0.69) and PC2 as beak shape (33% variance explained; loadings: length: –0.91, width: 0.39, height: 0.04). Moreover, we obtained 2–4 distal claw sections from each individual for individual assignment via stable isotope analysis of deuterium (see Figure S3).

We measured plumage and beak coloration with an AvaSpec 2048 spectrometer and AvaLight-DH-S deuterium halogen lamp (Avantes). We took five measurements per body part per bird and averaged spectra in 5 nm intervals from 300 to 700 nm. Using an avian eye model [34], we modeled the probability of photon catches of the four avian cone types used for color vision.

Genetic Analyses

DNA was extracted from blood samples with a DNeasy Blood and Tissue Kit (QIAGEN). Locus characteristics, amplification of loci, and polymorphic information content were as described in [35] and Table S4. We conducted calculations of pairwise F_{ST} , partitioning of molecular variance (AMOVA), and individual genotype–population assignment. To account for variation in heterozygosity within populations that differ in degree of isolation [36], we used a standardized measure of differentiation scaling F_{ST} into the same range (0–1) for all levels of variation among loci and populations [37]. We report the standardized measure together with the original F_{ST} values. Moreover, we tested for robustness of our set of ten loci because our estimates may be biased by low sample sizes relative to the number of alleles (Table S5).

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures, five tables, and three figures and can be found with this article online at [http://www.cell.com/current-biology/supplemental/S0960-9822\(09\)01925-3](http://www.cell.com/current-biology/supplemental/S0960-9822(09)01925-3).

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