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CORSICAN FINCHES HAVE LESS POINTED WINGS THAN THEIR MIGRATORY CONGENERS ON THE MAINLAND

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BIRD MIGRATION
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CARDUELIS CORSICANUS
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NICHE EXPANSION
WING SHAPE

ABSTRACT. – It is assumed that trade-offs between the costs of energy-efficient flight during migration and the costs of manoeuvrability cause wing shape to vary among birds that differ in migratory status. Migrants generally have more pointed wings than more sedentary species or populations. Here, we compare wing morphology between two closely related, allopatric passerine species, the migratory citril finch (*Carduelis [citrinella] citrinella]* and the sedentary Corsican finch (*Carduelis [citrinella] corsicanus*), drawing on morphometric measurements from museum specimens. In line with the general expectation, we show that the migratory citril finch has longer, more pointed wings than the sedentary island form. However, this morphological divergence may not have resulted from selection on migration-related wing characteristics alone, but also from selection towards rounder wings (increased manoeuvrability) in the island form that inhabits a more densely vegetated terrain than its mainland counterpart. We discuss the roles of habitat quality and niche exploitation in shaping wing morphological differences between island and mainland species.

INTRODUCTION

The design of the avian wing constitutes a trade-off between various selection pressures that act on its aerodynamic and mechanical properties (Norberg 1990, Videler 2006). The evolution of wing size and shape is affected by the energy demands of migration, by take-off ability in response to predator attacks and by the density of obstacles that constrain flight manoeuvrability (Mönkkönen 1995, Lockwood et al. 1998, Swaddle & Lockwood 2003). One of the common generalizations is that birds which migrate over longer distances have more pointed wings (i.e. longer distal and shorter proximal primaries and a wing tip positioned closer to the leading edge of the wing) than less migratory birds (also known as "Seebohm's rule"; Seebohm 1901, Niethammer 1937, Mönkkönen 1995, Fitzpatrick 1998, Calmaestra & Moreno 2001), because pointed wings enable a more energy-efficient flight (Norberg 1990, Videler 2006, Bowlin & Wikelski 2008). This principle of wing shape variation is evident at the interspecific level (e.g. Tiainen 1985, Winkler & Leisler 1992, Mönkkönen 1995, Keast 1996) and has been established in several intraspecific studies comparing wing shape of differentially migrating individuals within and among populations (e.g. Mulvihill & Chandler 1990, 1991, Wiedenfeld 1991, Carrascal et al. 1994, Copete et al. 1999, Pérez-Tris et al. 1999, Pérez-Tris & Tellería 2001, Fiedler 2005, Seki et al. 2007).

The citril finch (*Carduelis [citrinella] citrinella*) and the Corsican finch (*Carduelis [citrinella] corsicanus*) are two closely related members of the super-species *Cardu-*

elis [citrinella] (Pasquet & Thibault 1997, Sangster et al. 2002, Förschler & Kalko 2007) that differ considerably in their migratory behavior (Cramp & Perrins 1994). The Corsican finch is restricted to perform small-scale altitudinal movements within its Mediterranean island habitat (Thibault & Bonaccorsi 1999), whereas the citril finch is a regular, short- to medium-distance migrant in most parts of its northern breeding range (Alps, Black Forest) and spends the winter in mountainous habitats of central France and north-eastern Spain (Cramp & Perrins 1994). Both subspecies also differ in their habitat selection. The Corsican finch has expanded its niche on the Mediterranean islands into densely vegetated scrublands, especially maquis dominated by Erica arborea (Blondel et al. 1988, Förschler & Kalko 2006a). In contrast, the habitat of the citril finch is restricted to semi-open coniferous forests in subalpine and montane zones with only little undergrowth (Förschler & Kalko 2006a).

In this study, we compare wing morphology between the citril and the Corsican finch, drawing on measurements from museum specimens. There are three, not mutually exclusive reasons for assuming that Central European citril finches should have longer, more pointed wings than their Mediterranean congeners. First, an increase in the proportion of migrants during the postglacial range expansion of this species could have resulted in selection of birds with more pointed wings as part of the migratory syndrome (Dingle 2006). Secondly, we may expect the Mediterranean form to show more rounded wings as an adaptation to increased manoeuvrability demands in their more densely vegetated maquis habitat.

Third, wing shape might be related to differences in resource allocation strategies, with longer flight distances predicted for the citril finch that exploits more patchy habitats (Förschler & Kalko 2006b, Förschler & Siebenrock 2007) and is prone to undertake longer facultative movements in response to adverse, northern temperate weather conditions (Förschler 2001).

MATERIAL AND METHODS

We measured a total of 21 well-preserved museum specimens sampled at the beginning of the 20th century in the Vosges mountains and the Black Forest (10 individuals), and on Corsica (11 individuals). Museum specimens stemmed from three collections in Germany: Zoologische Staatssammlung München (Munich), Zoologisches Museum der Humboldt Universität (Berlin) and Naturkundemuseum Rosenstein (Stuttgart). Since the overall number of available skins was considerably limited, we confined our analysis to adult male individuals to render comparable wing measurements.

We measured the distance between the carpal joint and the tip of the nine larger primaries on the folded wing, following the definitions given in Lockwood *et al.* (1998). Primary distances are defined as the length of the line between the wingtip and the relevant primary feather tip projected onto a line parallel to the wing chord on a folded wing in which all primaries are approximately parallel (Lockwood *et al.* 1998). All measurements were carried out by the same person.

For comparing wing shape among subspecies, we selected

three conventional indices of "pointedness", which control for interspecific difference in absolute feather length (reviewed in Lockwood *et al.* 1998, see Table II): (1) Kipp's index, (2) Holynski's index, (3) Busse's index (Kipp 1959, Holynski 1965, Busse 1967, 1986). Primary 10 was excluded from calculations due to its extremely small size.

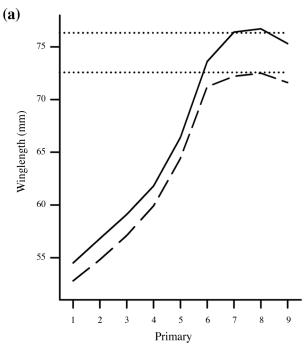
RESULTS

We found significant differences in wing size and shape between mainland citril finches and insular Corsican finches. Mean values of primary distances and wing length differed significantly between subspecies (Table I, Fig. 1).

Both subspecies differed significantly in three indices of wing pointedness, with the citril finch generally showing a more pointed wing tip than the Corsican finch (Table II, Fig. 1). Indices of wing pointedness were significantly positively correlated with total wing length across subspecies (Spearman's rank correlations, Kipp's index, $r_s = 0.56$, p < 0.05, Holynski's index, $r_s = 0.45$, p < 0.05, Busse's index, $r_s = 0.60$, p < 0.01), indicating that individuals with longer wings tend to have more pointed wings (Fig. 2).

DISCUSSION

Migratoriness is generally associated with a tendency



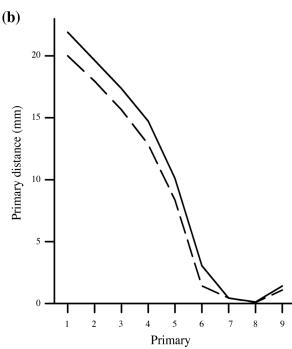


Fig. 1. – Graphical representation of differences in wing size and shape between adult male citril finches (solid lines) and Corsican finches (broken lines) as derived from measurements of the nine larger primaries (P1 to P9, proximal to distal) on folded wings: a, Wing diagram showing differences between wing length and primary distances. The dotted line gives the average total wing length for the respective subspecies. b, Size-independent, mean primary distances. Among-species differences in primary distance are significant for primaries P1 to P6 (see Table I).

Table I. – Mean values (± SD, in mm) of primary distances (defined as the length of the line between the wingtip and the relevant primary feather tip projected onto a line parallel to the wing chord, cf. Lockwood et al. 1998) and wing length measured on folded wings of 10 citril finches (*Carduelis* [citrinella] citrinella] citrinella] citrinella] corsicanus). Statistic and level of significance of the Wilcoxon 2-sample Test.

	C.c.citrinella	C.c.corsicanus	Wilcoxon Test
P1	22.30 ± 0.79	19.81 ± 1.08	Z = 3.61; p = 0.0003
P2	20.00 ± 1.05	17.77 ± 1.25	Z = 3.18; p = 0.0013
P3	17.75 ± 0.79	15.45 ± 1.31	Z = 3.28; $p = 0.0010$
P4	15.05 ± 1.34	12.72 ± 1.17	Z = 3.13; p = 0.0018
P5	10.40 ± 2.16	8.23 ± 1.21	Z = 2.60; p = 0.0092
P6	3.23 ± 2.75	1.40 ± 0.60	Z = 2.84; $p = 0.0045$
P7	0.44 ± 056	0.43 ± 0.44	Z = -0.36; p = 0.7176
P8	0.13 ± 0.22	0.07 ± 0.17	Z = 0.61; p = 0.5083
P9	1.54 ± 0.80	0.99 ± 0.77	Z = 1.53; p = 0.1265
Wing length	76.80 ± 1.27	72.59 ± 2.21	Z = 3.57; p = 0.0004

Table II. – Differences between wing-tip shape indices as calculated from measures based on folded wings of 10 citril finches (*Carduelis* [citrinella] citrinella] citrinella] and 11 Corsican finches (*Carduelis* [citrinella] corsicanus). Median values, statistic and level of significance of the Wilcoxon 2-sample Test.

	Source	C. c. citrinella	C.c. corsicanus	Wilcoxon Test
Kipp's Index	Kipp 1959	29.42	27.45	Z = 2.22; p = 0.0264
Holynski's Index	Holynski 1965	109.05	103.62	Z = 2.78; p = 0.0221
Busse's Index	Busse 1967	114.99	104.05	Z = 2.29; $p = 0.0049$

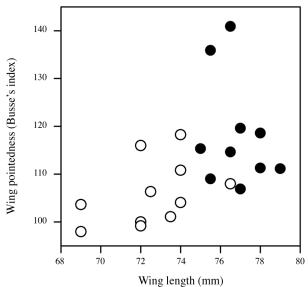


Fig. 2. – Correlation between wing pointedness as expressed by Busse's index (cf Busse 1967, 1986) and total wing length of adult male citril finches (black dotts) and Corsican finches (open circles).

towards elongated and pointed wings. Our result shows that the non-migratory Corsican finch has shorter, more rounded wings than its migratory mainland counterpart, the citril finch. This confirms the general pattern of wingshape variation among populations of different migratory

status (e.g. Pérez-Tris & Tellería 2001, Fiedler 2005, Seki *et al.* 2007).

Wing pointedness may have evolved in the citril finch during its postglacial range expansion into northern temperate, seasonal environments, with selection acting on a suit of co-adapted migratory traits or a 'migratory syndrome' (Dingle 2006, van Noordwijk *et al.* 2006), including wing morphology. Recent studies on house finches *Carpodacus mexicanus* have shown that morphological differentiation of the wing-tip shape among populations with different migratory habits can take place even on a microevolutionary time scale (Egbert & Belthoff 2003). Consequently, the observed morphological divergence between the migratory citril and non-migratory Corsican finch could be explained solely by a microevolutionary process within the migratory population.

However, seasonal migration may not be the only reason for the observed pattern. The morphological divergence among subspecies may have also arisen from divergent effects of habitat quality and niche occupancy (e.g. Leisler & Winkler 1991), because both subspecies inhabit contrasting environments that impose different selection pressures on wing morphology. In contrast to the mainland citril finch, the insular Corsican finch has expanded its niche into densely vegetated maquis dominated by *Erica arborea* (Blondel *et al.* 1988, Förschler & Kalko 2006a). The rounder wings of the Corsican finch may thus reflect an adaptation to the need for improved manoeu-

vrability in a densely vegetated habitat, making individuals less susceptible to predators (e.g. Pérez-Tris & Tellería 2001). Furthermore, an energy-efficient wing shape may not only be favorable during long-distance seasonal migrations, but also during daily movements between habitat patches. Corsican and citril finches differ in the mean distance between their nesting and foraging grounds, with significantly shorter distances covered by the Corsican finch (Förschler & Kalko 2006a, b). Thus, besides selection for wing pointedness within migratory citril finch populations, differences in resource allocation and exploitation on the breeding grounds may have reinforced the morphological divergence between both species. This is further supported by among-species differences in morphological characteristics associated with feeding and foraging performance (Förschler & Siebenrock 2007). The Corsican finch has proportionally a smaller bill and shorter legs, toes and claws than the citril finch, suggesting that overall morphology has been adapted to suit local habitat conditions (Förschler & Kalko

To conclude, wing pointedness in relation to migratoriness may not have been the only target of selection leading to this morphological divergence. The directionality and relative strength of the potential selective forces remain ambiguous. Given that patterns of wing-shape variation are not always related to the extent of migration (e.g. Mulvihill & Chandler 1991), further research is needed to distinguish between morphological adaptations that are associated with the demands of seasonal migration and those resulting from habitat heterogeneity (e.g. Clegg & Owens 2002, Scott et al. 2003, Sacher et al. 2006, Seki et al. 2007). Rounder wings are commonly found in bird populations inhabiting island habitats, representing one facet of the so-called 'insular syndrome' (Blondel 2000). At the macroevolutionary scale, some bird taxa colonizing islands even became completely flightless, presumably as a consequence of reduced predation. But exceptions from this rule (e.g. Acrocephalus warbler species, see Komdeur et al. 2004) show that it is far from clear why birds inhabiting islands should differ in wing morphology from (migratory) mainland congeners. Fossil records provide evidence that citril finch forms were present on Corsica during the late Pleistocene (Alcover et al. 1992), yet it is unknown whether these represent ancestors of today's Corsican finch or whether the divergence took place on a microevolutionary time scale during later periods. The evolutionary history of both the Corsican and the citril finch is still uncertain (Pasquet & Thibault 1997, Sangster 2002, Förschler & Kalko 2007). Molecular genetic work may clarify this problem. Further questions that remain to be resolved are whether wing morphology and migration behavior can evolve independently and whether the insular (Blondel 2000) and the migratory syndrome (Dingle 2006, van Noordwijk et al. 2006) represent extremes along a phenotypic continuum.

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