Inheritance of migratory direction in a bird species: a cross-breeding experiment with SE- and SW-migrating blackcaps (*Sylvia atricapilla*)

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Summary. Young avian migrants of many species are able to find their species- or population-specific wintering area without the help of conspecifics. In orientation tests hand-raised birds have been demonstrated to choose appropriate population-specific migratory directions, suggesting a genetic basis to this behaviour. I here report results of a cross-breeding experiment between individuals of two blackcap (*Sylvia atricapilla*) populations with widely different migratory directions. The orientation of the F1 offspring was intermediate between and significantly different from that of both parental populations (Fig. 2). The variance of individual mean directions in the F1 generation did not increase compared with the parental groups, and the inheritance of migratory directions was not sex-linked. The data provide direct evidence for a genetic basis of migratory directions in birds and demonstrate a phenotypically intermediate mode of inheritance.

Introduction

Many passerine bird species are nocturnal migrants in which young of the year often migrate very long distances individually (without social guidance) to well-defined, species- or population-specific wintering areas. A classic large-scale displacement experiment with starlings (*Sturnus vulgaris*) demonstrated among other things that juveniles on their first migration possess no knowledge about the geographic coordinates of the wintering area (Perdeck 1958). There is substantial evidence that such inexperienced migrants rely largely on innate information about distance and direction in which to migrate. An approximate measure of distance is encoded in an endogenous circannual programme as the duration of migratory activity per season (Gwinner 1968; Berthold 1973). This behavioural character is known to have a genetic basis (Berthold and Querner 1981) and responds

rapidly to selection (Berthold et al. 1990a). The migratory direction seems to be encoded as an angle with respect to an external reference (Emlen 1969; Wiltschko and Gwinner 1974).

The compass mechanisms by which such vector orientation is achieved have been subject to intensive research during the past 40 years and are reasonably well understood (Wiltschko 1983; Wiltschko and Wiltschko 1988a). However, little is known about the basis of the directional information beyond the assumption that it must be "innate". Young birds of several species have been hand-raised in the laboratory from an early age onward. When tested during their first migration season in circular orientation cages, such inexperienced birds generally chose southerly directions, as expected from ringing recoveries, irrespective of whether they could see the natural sky or not (e.g. Emlen 1969; Wiltschko and Gwinner 1974; Beck and Wiltschko 1982). The geomagnetic field and the rotational center of the starry night sky seem to serve as ontogenetically independent references in relation to which birds can find a migratory direction (Wiltschko and Wiltschko 1988b).

While such experiments provided strong circumstantial evidence that directional information has a genetic basis, the single, more direct support comes from a cross-breeding experiment between migratory and sedentary blackcaps (*Sylvia atricapilla*): the F1 offspring oriented bimodally in a NE-SW direction, i.e. along the same axis as their migratory parents (Berthold et al. 1990b). I crossbred blackcaps from two Central European populations which differ considerably in autumn migratory direction to study the mode of inheritance of this behavioural trait. The results are one of the very few cases in which the genetic basis as well as the mode of inheritance of a behavioural character have been elucidated in a non-domesticated vertebrate species.

Material and methods

The species. The blackcap is a common and widespread Palearctic representative of the species-rich muscicapid subfamily Sylviinae,
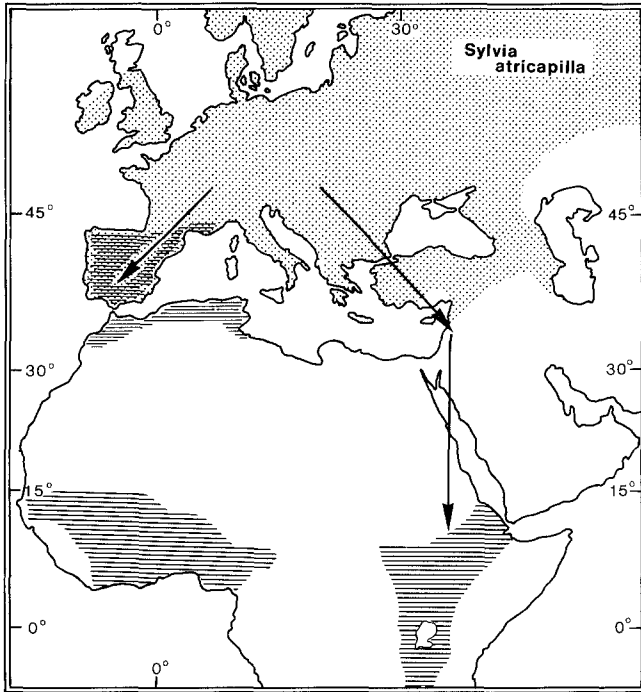
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Fig. 1. Breeding (*stippled*) and main over wintering (*hatched*) areas of the blackcap. *Arrows* show schematically the autumn migratory directions of central European SW- and SE-migrating populations (after Klein et al. 1973) which were the subjects of this study

comprising many long-distance nocturnal migrants. Central European populations of this species winter in widely separated areas (western Mediterranean region and NW Africa, East Africa and recently the British Isles) and display within their continuous range a corresponding variety of autumn migratory directions ranging from SE to SW to NW (Klein et al. 1973; Zink 1973; Berthold and Terrill 1986). While the W to NW migrants (a minority) seem to originate from central Europe, a rather distinct migratory divide exists between SE and SW migrants south of 52°N (Fig. 1). According to ringing recoveries the initial autumn migratory directions of these two populations differ by about 70° (Klein et al. 1973).

Raising of test birds and orientation tests. I hand-raised groups of 50 nestlings (up to four siblings per nest) from west of the divide near Frankfurt/M. (50°04'N; 8°41'E) and Radolfzell (47°46'N; 8°59'E), FRG, and from east of the contact zone near Bruck/Leitha and Halbturn (47°46'N; 17°01'E), eastern Austria. Birds were taken out of the nest at 7–8 days of age, i.e. 3–4 days after opening their eyes, and were raised to independence in the laboratory at Radolfzell. Prior to the migration season they were exposed to natural day and night skies by placing them in individual cages in outdoor aviaries. After becoming migratorily active the orientation of each bird was tested 15–20 times outdoors at dusk in round funnel-shaped cages (Emlen and Emlen 1966) lined with typewriter correction paper and covered with clear plexiglass (cf. Helbig et al. 1989). Next spring the birds were transferred to outdoor breeding aviaries (2.5 × 2.5 × 2 m) where 35 mixed pairs were formed, comprising one bird each from east and west of the divide. During 1987 and 1988 16 pairs produced a total of 68 F1 offspring (maximum 8 young per pair). These were again hand-raised and their orientation tested during the first autumn of life. Treatment during raising and testing as well as their prior experience of natural skies was exactly the same as for the 2 parental groups.

Data analysis and statistics. During the orientation tests birds produced scratches on the typewriter correction paper. Papers were divided into 24 sectors and scratches counted on a light screen.

From each recording with a minimum of 40 scratches, a heading (α_i) was calculated by vector addition. For treatment of axially bimodal activity distributions see Helbig et al. (1989). For each individual bird a mean vector of orientation was calculated from all its α_i values (regardless of the dispersion of hopping activity) during October and November. For each individual and month, the distribution of α_i values was checked for axial bimodality by doubling the angles (see Batschelet 1981). If the vector length of the resulting axis exceeded that of the unimodal vector by more than 0.01, the axis of orientation provided a better fit to the data. In such cases the more southerly end of the axis was taken as the bird's mean direction, because over the entire season every individual had more southerly than northerly directional choices. Occasional northerly directional choices probably correspond to reverse orientation, which is frequently observed in nature (Schüz 1971).

The season had to be divided into 2 parts, because 1 parental group changed direction around the end of October (see below). Statistical analysis follows Batschelet (1981). Mean directions were compared between samples using the Watson-Williams test. All samples to which this parametric test was applied had concentration parameters larger than 2 and did not differ significantly from a von-Mises distribution, thus satisfying the underlying assumptions. Average deviations from the mean angle between 2 samples were compared using the non-parametric Mann-Whitney U test.
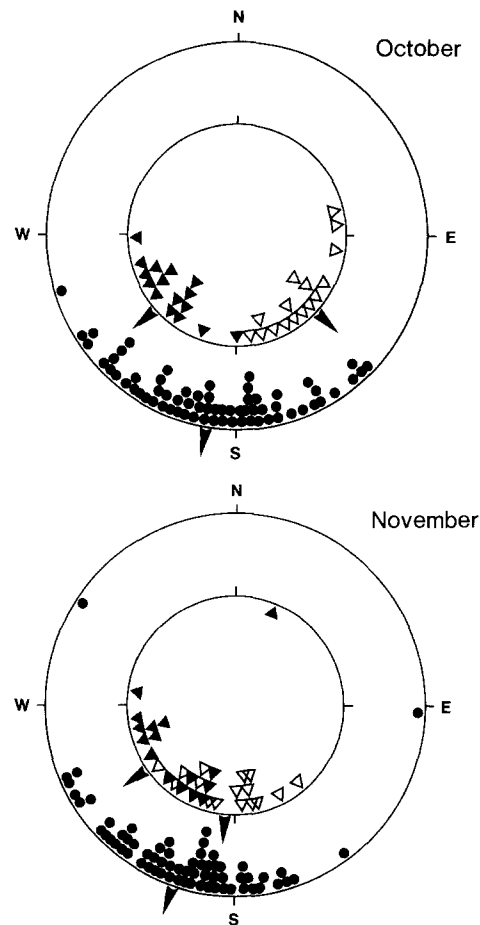

Fig. 2. Individual means of directional choices of hand-raised blackcaps during the early and late part of the autumn migration season. *Inner circle,* parental generation; *solid triangles,* birds from the FRG; *open triangles,* birds from eastern Austria. *Outer circles* (*full dots*), F1 generation. *Arrowheads,* group mean directions. Compare Table 1. Each symbol is based on an average of 8.1 orientation tests per bird in the parental generation (data from first and second autumn of life combined) and 6.2 tests per bird and month in the F1 (first autumn only)

Table 1. Orientation of two parental groups (P1 = FRG birds, P2 = east Austrian birds) and their F1 offspring (F1)

Group	Month	n	α	r	Sample pair	WW test	MW test
P1	October	16	228°	0.933	P1 Oct. vs. Nov.	n.s.	*
	November	16	234°	0.779	P2 Oct. vs. Nov.	***	n.s.
					P1 vs P2 Oct.	***	n.s.
P2	October	16	134°	0.892	P1 vs. P2 Nov.	***	n.s.
	November	16	185°	0.912	P1 vs. F1 Oct.	***	n.s.
					P2 vs. F1 Oct.	***	n.s.
F1	October	68	189°	0.898	P1 vs. F1 Nov.	***	*
	November	66[a]	199°	0.889	P2 vs. F1 Nov.	$P = 0.061$	n.s.
					F1 Oct. vs. Nov.	*	n.s.

[a] For two F1 birds November data are missing (died, escaped)

n = number of birds; α = direction, r = length of mean vector. All six samples are significantly oriented ($P < 0.001$ for all cases, Rayleigh test). The right part of the table shows results of pairwise comparisons between samples with respect to differences in mean direction (Watson-Williams test = WW test) and average deviations from the mean direction (Mann-Whitney U test = MW test). * $P < 0.05$; *** $P < 0.001$; n.s. = not significant

Results

The birds from eastern Austria (i.e. one of the parental groups) showed a significant shift in orientation during the course of the autumn ($P < 0.001$, Watson-Williams test): individual mean vectors clustered around an overall mean direction of 134° in October and 185° in November (Fig. 2). This probably corresponds to a change of direction from SE to S-SSW when the birds fly around the eastern Mediterranean and on toward East Africa (Helbig et al. 1989). The birds from the FRG oriented SW with no difference between months (Table 1). For this population, migration toward its winter quarters in the western Mediterranean region involves no major change of direction (Klein et al. 1973; Zink 1973).

During both months of their first migration season, the F1 offspring oriented toward mean directions intermediate between those of the parental populations. They performed a shift of only 10° from October to November (compared with 51° in the SE migrating parental group). This difference was, however, significant due to the high degree of concentration [$F(1; 132) = 5.25$; $P < 0.05$; Watson-Williams test]. The orientation of the F1 generation differed significantly from both parental populations during October and from the FRG parents in November (Table 1); the difference from the Austrian parents in November was suggestive [$F(1; 80) = 3.70$; $P = 0.061$]. There were no differences in the scatter of mean directions between parental and F1 groups in either month ($P > 0.05$ for all pairwise comparisons; Mann-

Whitney U test). Directional choices of F1 hybrids were not linked to the sex of their respective SE- or SW-migrating parent (Table 2). An analysis of variance showed no greater similarity of mean directions among siblings than among non-siblings [ANOVA: $F(15; 52) = 1.32$; $P = 0.228$; Kruskal-Wallis test: $H = 20.96$, $P = 0.138$], thus revealing no significant genetic component to the variation in individual mean directions.

Discussion

The results show that the population-specific migratory directions in the blackcap have a genetic basis and can be altered by cross-breeding. The behavior of the F1 generation was phenotypically intermediate between the parental groups with no increase in variance. This suggests either a polygenic (polyallelic) basis to the trait or – less likely – a single locus without dominance. The change of direction performed by one but not the other parental population during the course of the season also seems to have been transferred to the offspring but was much smaller in extent. An endogenous basis of intraseasonal changes of migratory direction had previously been demonstrated for *Sylvia borin* (Gwinner and Wiltschko 1978) and *Ficedula hypoleuca*; in the latter, however, changes in magnetic field parameters are also involved in its control (Beck and Wiltschko 1988).

Information on the genetics of compass orientation in other organisms is scarce (Scapini 1988). Seaward migration of salmonid fishes has been reported to be based on inherited directional information either with respect to a compass reference or to the water current (Brannon 1972, 1984). As with my Austrian blackcaps, the directions preferred by seaward migrating *Oncorhynchus nerka* fry changed during the season and paralleled the course of rivers the fish are known to follow (Groot 1965). Cross-breeding of positively and negatively rheotactic parental populations of the same species resulted in intermediate behaviour in the F1 generation with a strong increase in variance (Brannon 1972). Similarly, Pardi and Scapini (1983) found an intermediate mode

Table 2. Orientation of F1 offspring depending on sex of SW-orienting parent. There are no significant differences in mean direction (Watson-Williams test) or scatter (Mann-Whitney U Test) between any of the six samples ($P \gg 0.05$ in all cases)

Period	Male parent			Female parent		
	n	r	α	n	r	α
October	36	0.913	187°	32	0.881	190°
November	35	0.880	197°	31	0.903	202°
Whole season	36	0.902	190°	32	0.925	196°

of inheritance for the escape direction of the littoral amphipods *Talitrus saltator*.

My results obtained with blackcaps agree with previous findings that suggest a quantitative genetic basis for other physiological and morphological characters related to migration, such as amount of migratory restlessness (Berthold and Querner 1981), timing and duration of post-juvenile moult, body weight and wing length (Berthold and Querner 1982). Heritabilities of migratory activity derived from selective breeding experiments were high in the blackcap (Berthold 1988). An important question is how much genetic variability exists with respect to migratory directions in natural populations. Among the relatively small sample of birds bred in this experiment, no significant genetic component of the variability could be demonstrated. This may be due to the difficulties of accurately measuring small individual differences between innate migratory directions with the relatively crude funnel technique.

Taken together, the available evidence indicates a rather strong genetic control of migratory adaptations in avian nocturnal migrants. Given sufficient intra-population genetic variability, these adaptations may respond readily to selection and explain the high degree of population-specific differentiation and rapid rate of evolutionary change observed in some cases (Berthold and Terrill 1988). However, it is at present unclear how the differentiation between (sub)populations with different migratory directions is maintained in areas of contact. Some assortative mating probably takes place and could be achieved by slightly different arrival times in spring (cf. the similar situation in SW- and SE-migrating white storks *Ciconia ciconia* in central Europe; Schüz 1964), differences in physiological condition or habitat preferences during the mating stage. If mixed matings, as simulated in this breeding experiment, occur in the contact zone, strong selection is likely to act against the offspring: my orientation data indicate that such young would attempt to cross the Alps, the Mediterranean Sea and parts of the Sahara Desert, several formidable geographical and ecological barriers. Given the fact that both parental populations avoid crossing these barriers, it is unlikely that the F1 hybrids would be sufficiently adapted physiologically to cross them successfully. Following such a course would seem to lower their chances of survival significantly.

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