

Genetic transmission of migratory behavior into a nonmigratory bird population

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Summary. Crossbreeding experiments with blackcaps from a nonmigratory population (of the Cape Verde Islands) and a migratory population (from southern Germany) demonstrated that the urge to migrate as well as orientation behavior can be transmitted rapidly into a nonmigratory bird population and thus have a substantial genetic basis. **Key words.** Bird migration; behavioral genetics; blackcap; crossbreeding; orientation.

Over the last twenty years, the role of endogenous factors in the control of bird migration has found increasing support from both field and laboratory research¹. Experimental studies in several species of European warblers have suggested a genetic basis for 1) the amount of migratory activity in migrating populations with different lengths of migration routes, and 2) for residency versus migration in partially migratory populations². In addition, the preference for specific migratory directions appears to have a strong endogenous component³. However, it is not clear whether the urge to migrate and the accompanying orientation can be transmitted into a nonmigratory animal population, and if so how rapidly transmission would occur or even whether migratory activity and orientation behavior would be inherited together⁴. We therefore conducted crossbreeding experiments with the blackcap, *Sylvia atricapilla*, which has resident, partially migratory and fully migratory populations. This species has a wide distribution from the Cape Verde Islands in the tropics to subarctic areas in northern Eurasia. It is also one of the few wild passerines that can be successfully bred on a large scale in captivity².

Material and methods

30 blackcap nestlings from Cape Verde and 31 from S. Germany were hand-raised in S. Germany in 1982 and kept under photoperiodic conditions simulating those of their home areas during the first fall and winter. During spring 1983 and 1984, 9 pairs of birds were selected whose migratory activity had been recorded the previous autumn; in 5 pairs the female was from Cape Verde and the male from S. Germany, and in 4 pairs the opposite. The birds were put into large outdoor aviaries to breed, and a total of 35 F₁-hybrids was obtained. These offspring were also hand-raised; the 21 birds born in 1983 were kept under photoperiodic conditions simulating those of Cape Verde (CV), the 14 birds born in 1984 under the conditions found in S. Germany (SG). All birds were kept in registration cages where their migratory activity (nocturnal restlessness or zugunruhe) could be recorded continuously^{4,5}. We calculated the mean number of hours with restlessness per night with standard error over the subsequent 10-day periods.

To study the migratory orientation, 7 F₁-hybrids which had shown migratory activity during the autumn were transferred to Frankfurt in the following winter where they were tested for orientation. This was done in spring and autumn using automatic registration cages for orientation in closed rooms with the local geomagnetic field (46 000 nT, 66° incl.) but without visual cues^{6,7}. It was not possible to test the birds for migratory activity and for orientation simultaneously, because it was initially necessary to determine which of the F₁-hybrids would develop nocturnal migratory activity in undisturbed conditions. With respect to orientation, we calculated from the distribution of hops the bearings of the recordings (with n > 10) by vector addition. These bearings showed a bimodal distribution, a phenomenon which is not seldom observed in orientation experiments with hand-raised birds⁸. Because of this, we calculated the axis of orientation for each individual bird from the bird's bearings by the method of doubling the angles⁹. For a second-order statistic, the modes of these axes had to be transferred into a distribution covering 360°, which was achieved by again doubling the angles of one mode. The resulting distribution was tested with the Rayleigh test for directional preference.

Results and discussion

All birds of S. German origin showed nocturnal migratory activity, a mean of 370 ± 288 (SD) h was found during the first autumn migration (fig. 1). At the same time none of the birds from the Cape Verde showed any migratory activity, hence they were nonmigratory. Of the 35 F₁-hybrids, 7 individuals (from 21 under CV conditions) in 1983 and 6 individuals in 1984 (from 14 under SG conditions), or 33 and 43%, respectively, showed migratory activity, with means of 241 ± 133 and 283 ± 105 h migratory restlessness (fig. 1). This amount of activity was numerically lower but not significantly different from that of the migratory S. German parent group (U-test). 5 of the F₁-birds (raised in 1984) that had shown migratory activity in autumn produced a suitable number of orientation recordings in the following spring and the second autumn migratory period, and the axial means of these birds show a significant directional preference

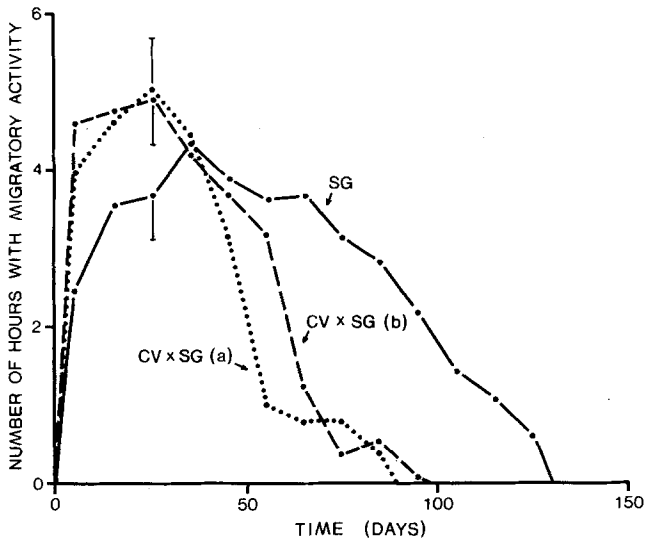


Figure 1. Patterns of migratory activity during the first autumn migratory period of groups of hand-raised blackcaps *Sylvia atricapilla* of different origin: SG, data from southern German birds, CV x SG, data from F₁-hybrids of S. German birds with those from the Cape Verde Islands; a under simulated photoperiodic conditions of S. Germany, b under photoperiodic conditions of Cape Verde. The curves show mean values for 10-day intervals and, for the sake of clarity, standard errors of only representative examples. The dependence of the amount of migratory activity on photoperiodic conditions is treated in Berthold².

Directional behavior of hand-raised F₁-hybrids of blackcaps. n = number of tests with more than 10 hops; α_a = direction and r_a = lengths of axial vector. * = $p < 0.05$; ** = $p < 0.01$, Rayleigh test.

| Bird | Spring | | | Autumn | | |
|---------|--------|------------|--------|--------|------------|-------|
| | n | α_a | r_a | n | α_a | r_a |
| 725 | 6 | 14°–194° | 0.87** | 15 | 54°–234° | 0.10 |
| 726 | 8 | 341°–161° | 0.41 | 4 | 62°–242° | 0.09 |
| 748 | 12 | 27°–207° | 0.25 | 14 | 16°–196° | 0.43 |
| 766 | 12 | 34°–214° | 0.12 | 13 | 62°–242° | 0.35 |
| 767 | 6 | 14°–194° | 0.32 | 5 | 52°–232° | 0.36 |
| Summary | 5 | 15°–195° | 0.81* | 5 | 51°–231° | 0.84* |

(table and fig. 2). This preference was in good agreement with the principal axis of migration of the S. German blackcap population as revealed by ringing recoveries¹⁰ and by outdoor cage tests with hand-raised blackcaps in autumn (224°)¹¹. The large amount of scatter shown by most individuals was not atypical for the orientation of hand-raised birds tested in the absence of visual cues¹². An additional individual (raised in 1983) yielded an axial preference of 58°–238° on its second migration. The results indicate that in the blackcap the development of migratory behavior, i.e. the urge to migrate as well as its orientation, are to a great extent inherited. There is but a small influence of the conditions under which the hybrids were raised. With respect to the genetic mechanism it can be concluded that: a) a single locus determination is unlikely (because this would lead to the F₁ being either all migrants or all nonmigrants), b) a multi-locus system with a threshold is the most likely (because otherwise one would have expected all F₁ to show a small

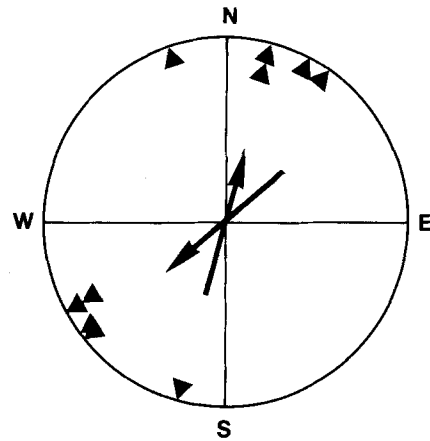


Figure 2. Directional means of individual hand-raised F₁-hybrids of blackcaps. The northern ends of the spring axes are given in the northern semicircle, the southern ends of the autumn axes are given in the southern semicircle. The arrows in the center represent the respective mean vector based on the transformed ends of these axes (see methods, above); for numerical values, see table, summary line.

amount of activity). Other analyses also suggest a threshold model². These findings shed light on how rapidly avian migratory behavior or resident behavior could spread or be genotypically altered if environmental circumstances forced reproductive contact between migratory and more or less sedentary populations. There are two possible mechanisms for the inheritance of the preferred direction that cannot be discriminated: either its inheritance is coupled to that of the migratory urge, or all birds have a similar directional preference, which does, however, not come to be expressed in cases where there is no migratory unrest. To what extent first generations of migrants are fully equipped with a complete set of programmed migratory activity and orientation systems needs further investigation, as do the rules for genetic transmission of migratory traits^{1,3}.

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