Heritability of migratory activity in a natural bird population

PETER BERTHOLD AND FRANCISCO PULIDO

Max Planck Institute for Behavioural Physiology, Vogelwarte, Schloss Moeggingen, D-78315 Radolfzell, Germany

SUMMARY

The presence of additive genetic variation is a prerequisite for changes in migratory behaviour through selection. Previous work with the blackcap, *Sylvia atricapilla*, has shown that the urge to migrate and the migratory direction are under genetic control. Here we examine whether migratory activity in this species has a significant additive genetic component, with the aim of predicting micro-evolutionary changes in migratory distance. Migratory activity was recorded in 280 southern German blackcaps from 69 families. We calculated heritabilities by parent–offspring regressions and by full-sibling correlations. Heritability estimates obtained by different methods were significantly different from zero and in good agreement with each other ($h^2 = 0.37$–0.46). This suggests that in the expression of migratory activity maternal and dominance effects are negligible. The high amount of phenotypic and additive genetic variation found for migratory activity in this population could lead to rapid evolutionary changes of migratory habits. Under moderate selection intensities and environmental conditions similar to those presented in this study, the southern German blackcap population could evolve into a short-distance migrant in 10–20 generations.

1. INTRODUCTION

In the last 25 years, numerous field observations of migratory birds and an increasing number of experiments with caged migrants have provided evidence that genetic factors play an important role in the control of bird migration. Migration appears to be based to a large extent on heritable programmes, and genetic variability of such programmes seems to allow for remarkably rapid adaptations through evolutionary processes (Berthold 1993). The blackcap *Sylvia atricapilla* has become a model among bird species for the experimental study of control mechanisms and micro-evolution of migratory behaviour (Berthold 1988*a*; Sutherland 1988; Berthold *et al.* 1992). There are two main reasons for its suitability: (i) the pronounced geographic differentiation of this Eurasian–African passerine species into populations of non-migrants, partial migrants and migrants with different migratory habits; and (ii) the ability to breed the species in captivity on a large scale (Berthold 1988*a*). Cross-breeding and selection experiments have revealed significant genetic components to the control of the occurrence of migratory activity, the formation of spatiotemporal migration programmes and reproductive cycles (Berthold & Helbig 1992; Berthold & Querner 1993). Recent changes in migratory habits have thus been shown to be inherited (Berthold *et al.* 1992).

Here we report on the first study of the heritability of the amount of migratory activity within a natural migratory bird population. In previous studies it was demonstrated: (i) that the amounts and patterns of migratory activity in this species are heritable, population-specific characteristics (Berthold & Querner 1981); and (ii) that they are likely to function in many species as time programmes that enable young birds to reach their species-specific (and to them unknown) winter quarters on their first migratory journey (Berthold 1988*a*). The amount of genetic variation in migratory activity within a migratory blackcap population is worth knowing, especially in view of recent changes in migratory behaviour in Europe and elsewhere. In Europe, short- and middle-distance migrants (including the blackcap) tend to reduce migratoriness progressively, probably in response to global warming and related environmental changes (see, for example, Gatter 1992). Evidence for this ongoing process has accumulated from the observation that many migratory species progressively leave their breeding areas later in autumn and return to them earlier in spring; short-distance migrants start to winter within their breeding grounds, partial migrants increase steadily the proportion of non-migrants, and other species reduce the distance they migrate (Berthold 1991). Most spectacular is the case of central European blackcaps which have established a novel wintering area on the British Isles within the last 30 years. The migratory distance to this novel wintering area is one third shorter than to the traditional areas around the Mediterranean (Berthold *et al.* 1992). In this context we will discuss to what extent the amount of additive genetic variation for migratory activity may provide an evolutionary potential for rapid shifts in migratory distance and winter quarters, and consequently change the future composition of European bird communities.

2. MATERIALS AND METHODS

From 1988 to 1992 a total of 186 blackcaps from 47 nests were collected at the age of 4–6 days from the vicinity of our institute in southern Germany (47.46° N, 09.00° E), hand raised and kept under identical controlled conditions. Simulated light–dark cycles mimicked the natural photoperiodic conditions of this population. Migratory activity was quantitatively recorded in registration cages during each bird's first autumn migratory period as so-called 'migratory restlessness' or 'zugunruhe'. This nocturnal restlessness is a reliable measure of migratory activity in the wild (Berthold 1973; Berthold & Querner 1981; Berthold 1988*b*). From ringing recoveries it is known that the main wintering area of German blackcaps lies in the area around the western Mediterranean; a small proportion of birds winter south of the Sahara in West Africa. The distances covered by southern German blackcaps during migration thus range from about 700 km (southern France) to 4500 km (Ivory Coast).

In a second approach we mated these birds assortatively with respect to their migratory activity in outdoor aviaries. Their offspring were hand raised, kept and studied in the same way as the parental birds. From 1989 to 1992 a total of 94 individual blackcaps from 22 different pairs were bred in aviaries.

Migratory restlessness was normally distributed across all samples and within each cohort. Hence, for all further calculations, untransformed data were used. Narrow sense heritabilities (h^2) for the different cohorts of parental birds were obtained by computing the intraclass correlations of full sibs derived from a one-way analysis of variance (Falconer 1989). Standard errors were computed according to Becker (1992). When data from different years were pooled for obtaining a population estimate, migratory activities within each year were set equal to the population mean, thus removing the between-cohort variance component. With these corrected data we estimated the population heritability, its variance and confidence interval by using a delete-one-family jack-knife procedure which has been shown to give robust estimates for a variety of distributions and heterogeneous variances (see, for example, Knapp *et al.* 1989).

A second heritability estimate was obtained from the weighted least-square regression of offspring on midparent values for migratory activity (Falconer 1989). The regression coefficient of this regression line yields an unbiased estimate of h^2 with a small standard error (Reeve 1961). Heritabilities from weighted regressions on single parents (mother or father) were computed for detecting possible maternal effects. These estimates were corrected for the bias caused by the correlation between the phenotypic values of the mates (r) by dividing the regression coefficient (b) by the factor $(1+r)$. Heritabilities are equivalent to twice this corrected regression coefficient (Falconer 1989). Regressions for each parental cohort (1988–1991) and offspring cohort (1989, 1990, 1992) were calculated separately and tested for the equality of slopes by the procedure proposed by Sokal & Rohlf (1981, box 14.8). Following the same procedures, we computed pooled regression coefficients as population means.

3. RESULTS

The average number of half hours of migratory restlessness in the parental generation was 913±370. Migratory activity differed significantly between the cohorts (one-way ANOVA, $F = 92.0$, d.f. = 4, $p < 0.0001$). The activities in the 1988 and 1990 cohorts were significantly higher than in the 1989, 1991 and 1992 cohorts (Scheffé's multiple range test, $p < 0.05$).

Table 1. *Amount, variation and heritability of migratory activity in different years*

(Migratory activity (MA) was measured as half hours of nocturnal activity (n = number of full sibs studied, k = number of families studied, CV = coefficient of variation). Heritability estimates (h^2) were calculated as twice the intraclass correlation between migratory activities of full sibs obtained in one-way ANOVA; p gives the significance of the F value in the test for an added variance component among families.)

year	n	k	MA	CV	h^2	s.e.	F	p
1988	50	12	1045	0.359	0.444	0.308	2.18	0.037
1989	38	9	843	0.379	0.421	0.355	2.12	0.066
1990	30	7	1074	0.305	−0.279	0.188	0.48	0.818
1991	20	5	772	0.360	0.653	0.520	3.02	0.052
1992	48	14	788	0.493	0.477	0.321	2.06	0.045

Within these groups there were no significant differences in activity (table 1). The differences in migratory activity among different cohorts are paralleled by significant differences in mean hatching dates between the 'early cohorts' (mean hatching date: 1988, 22 May±5 d; 1990, 23 May±5.5 d) and 'late cohorts' (mean hatching date: 1989, 30 May±8 d; 1991, 20 June±4 d; 1992, 29 May±4 d; Scheffé's multiple range test, $p < 0.01$). This suggests that the differences in migratory activity are due to photoperiodic effects: the onset of migratory activity of birds hatched later in the season (but before the summer solstice) is later than in birds hatched early. Thus, in late-hatched birds, migratory activity is expressed under shorter day lengths which cause a reduction of the amount of migratory activity (Berthold *et al.* 1972; Berthold 1988*a*). There were no sex-specific differences in the expression of migratory activity (males, 917±384 half hours; females, 909±359 half hours of activity; in 22 out of 38 families, activity in males was lower than in females, sign test, n.s.).

In all years except 1990, heritabilities derived from full-sib correlations were consistently greater than zero. However, due to large sampling variances, significant added variance components among families were found only in the years with the largest sample sizes (1988 and 1992; see table 1). The combination of the results for the five years by the test proposed by Lancaster (1961) yields an overall error probability of 0.004 for the hypothesis $h^2 > 0$. The mean of the heritabilities for five years weighted by the number of families studied is 0.364±0.285. The mean for the two significant values is 0.461±0.017. The overall jack-knifed heritability estimate for the complete data set (using corrected means) is 0.367±0.173 ($\mathrm{CI}_{95\%}$, $0.022 < h^2 < 0.713$).

Heritability estimates derived from the weighted regression of offspring on mid-parent activities were consistently different from zero in all years. There was neither a significant influence of parental birth (= test) year ($F_{3,86} = 0.137$, n.s.) nor of offspring birth (= test) year ($F_{2,88} = 0.695$, n.s.) on the regression coefficients. The average heritabilities derived from pooling re-

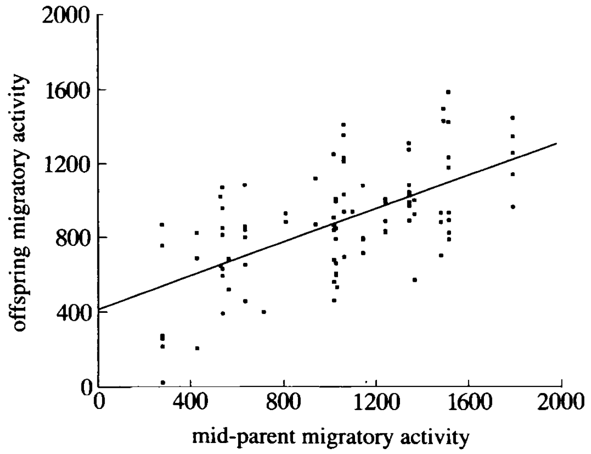

Figure 1. Weighted mid-parent–offspring regression for migratory activity (given in half hours of night activity). The equation of the regression line is $y = 409+0.453x$ ($n = 94$, $r^2 = 0.614$).

gression coefficients over offspring cohorts and over parental cohorts are in good agreement (0.417 ± 0.092 and 0.408 ± 0.076, respectively), but are a little lower than the estimate obtained by the weighted regression of all mid-parent–offspring values ($h^2 = 0.453 \pm 0.080$, $p < 0.0001$; figure 1).

Also in single-parent regressions there was no significant effect of parental cohort (father–offspring, $F_{3,86} = 0.310$, n.s.; mother–offspring, $F_{3,86} = 0.234$, n.s.) or offspring cohort (father–offspring, $F_{2,88} = 0.520$, n.s.; mother–offspring, $F_{2,88} = 0.873$, n.s.) on regression coefficients. The heritabilities derived from pooling the single-cohort coefficients over parental and offspring cohorts are 0.432 ± 0.081 and 0.440 ± 0.095 for the mother–offspring regression, and 0.392 ± 0.075 and 0.395 ± 0.090 for the father–offspring regression. Using the complete data set, the weighted regressions of mother on offspring ($b = 0.450 \pm 0.082$, $p < 0.0001$) and father on offspring activities ($b = 0.439 \pm 0.079$, $p < 0.0001$) yielded, when corrected for the correlation between the phenotypic values of the mates ($r = 0.96$), h^2 estimates of 0.460 and 0.448, respectively.

4. DISCUSSION

The present study is the first report of a heritability estimate on migratory activity in a natural, distinctly migratory bird population. Biebach (1983) obtained a heritability estimate ($h^2 = 0.52$) for a partly migratory population of European robins, *Erithacus rubecula*, but only by using a fairly rough comparison of whole 'nights with migratory activity'. The heritability found in this complex trait ($h^2 = 0.37$–0.46) is in the range of published h^2 estimates on behavioural traits in animals ($h^2 = 0.374 \pm 0.25$ (Mousseau & Roff 1987)), and of traits related to migration (range 0.20–0.88 (Dingle 1991)). Studies on heritabilities of behavioural characters in wild birds are almost lacking (Boag & van Noordwijk 1987). In poultry, h^2 estimates for behaviours are low: most are in the range 0.05– and 0.25. Nevertheless, many behavioural traits in poultry have responded to artificial selection (Siegel & Dunnington 1990).

Heritabilities derived from the phenotypic resemblance of full sibs include dominance and large common environment components of variance. This tends to inflate these h^2 estimates (Falconer 1989). We minimized this 'common-environment bias' by raising and keeping all birds under the same controlled conditions. In four out of five years there is close correspondence between heritability estimates derived from the analysis of full-sib families and the estimates based on the regression of offspring phenotypes on parental phenotypes. Nevertheless, the population mean is, contrary to expectation, lower for the full-sib correlations than for the parent–offspring regressions. This is due to the negative value obtained for the intraclass correlation of full sibs in 1990, which was probably caused by sampling error. However, as we cannot completely exclude the possibility of environmental influences on migratory activity during egg formation, incubation or the early nestling period, this difference in heritabilities among years could also be due to genotype–environment (G × E) interactions (see, for example, Gebhardt-Henrich & van Noordwijk (1991) for the influence of environmental conditions on heritabilities of fledgling mass). In general, heritability estimates obtained by three different methods and for different cohorts are in good agreement. We can thus assume that dominance and maternal effects (resemblance due to the common maternal environment) are negligible under the environmental conditions of our study. This seems to be the rule in quantitative genetic studies in wild bird populations (Boag & van Noordwijk 1987; but see Larsson & Forslund (1992) for maternal effects found in birds).

With the populational estimate of the heritability of migratory activity in southern German blackcaps, we can now tentatively predict the response to directional selection for longer or shorter migration distances. For this, several assumptions have to be made: (i) that there are no G × E interactions; and (ii) that in the wild, phenotypic variance is similar to the variance observed in our birds, i.e. that environmental variation does not substantially enlarge phenotypic variance. We can say little about the first assumption, as nothing is known about the reaction norms of different genotypes for this trait (but see the above-mentioned possibility of G × E interaction during early development). In wild birds, both parallel reaction norms (for example, for laying date in blue tits (Lambrechts & Dias 1993)), and significant G × E interactions (see, for example, Gebhardt-Henrich & van Noordwijk 1991; Larsson 1993; see Sheridan (1990) for G × E interactions in poultry) have been found. One good indicator of whether G × E interactions are to be expected is the susceptibility of the trait to environmental influence. Environmental factors seem to play only a minor role in the expression of migratory activity in distinctly migratory *Sylvia* warblers. In the garden warbler, *Sylvia borin*, for instance, the pattern of migratory activity is fairly insensitive to changes in food availability (as long as birds are not severely starved) or weather conditions (Berthold 1985; Gwinner 1986). However, the photoperiod modifies the amount of night activity, although the effects are

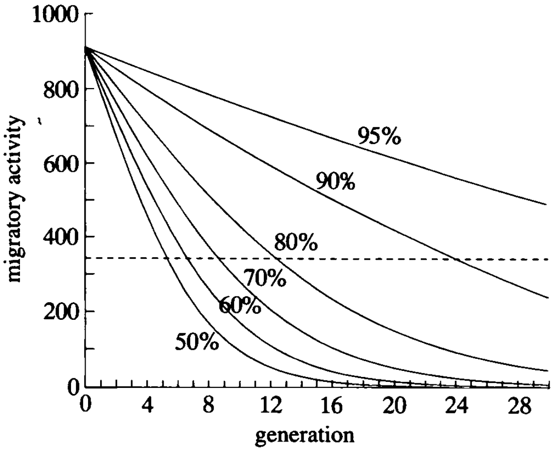

Figure 2. Predicted responses of southern German blackcaps to downward selection on migratory activity (given in half hours of night activity), assuming a heritability of 0.41 and variable coefficients of variation (35–70%). Selection intensities are indicated by the proportions of birds selected per generation (from a population of infinite size). The broken line gives the average amount of migratory activity in a short-distance migrant (southern French population).

small unless the light phase is distinctly prolonged (see Berthold *et al.* 1972). The influence of this potentially confounding factor was probably minimal in our study, as experimental birds were kept under the same photoperiod as they would have experienced in the wild. Moreover, for the estimation of resemblance between relatives, this environmental factor is probably of minor importance as all birds experience the same photoperiodic conditions (but note that there is an influence of different hatching dates). Heritability estimates obtained under laboratory conditions are to a certain extent transferable to environmental conditions in the wild (see, for example, Coyne & Beecham 1987; also discussion in Barton & Turelli 1989). Furthermore, cross-fostering experiments have shown that different environments may not significantly alter family resemblances (see, for example, Dhondt 1982).

A further assumption is that the phenotypic variance, as measured by the coefficient of variation (cv), and the additive genetic variance remain unchanged over the period of selection. There is much empirical evidence for the relative constancy of the response to directional selection over several generations (see Falconer 1989), yet we do not know to what extent the change in the amount of migratory activity would be accompanied by changes in its variance. However, the analyses of migratory activity in different cohorts of southern German birds (see table 1), and in a population of short-distance migrants (southern France (F. Pulido & P. Berthold, unpublished results)), show that the coefficient of variation is negatively correlated with the amount of migratory restlessness within populations. We account for this decrease of the cv with increasing migratory restlessness (b for the linear regression of cv on the amount of migratory restlessness is -0.048) in the prediction of responses to variable selection intensities (figure 2). Thus, by using a conservative heritability estimate ($h^2 = 0.41$) and assuming that in each generation only those 50% of southern German blackcaps with the lowest migratory activities would reproduce, a population of short-distance migrants with migratory activities similar to southern French birds (mean activity is 325 half hours; range of migratory distance, 0–1300 km) could evolve within six generations. Under weaker selection, allowing, for example, 70% or 90% of the birds to breed, we would obtain the same response in 9 and 24 generations respectively (figure 2). Hence, even assuming moderate selection intensities (annual mortality in the southern German blackcap is about 55% (Bairlein 1978)), the evolution from middle-distance to short-distance migrants could take place within only a few generations. Such a change would be theoretically predicted as an evolutionary response of migratory birds to global warming (Berthold 1991). Our results support the following earlier hypothesized scenario in case of global warming: population increase in resident bird species, increase of the resident fractions in partial migrants and, in accordance with our results, shortening of migration distances and earlier return in middle-distance migrants. As a consequence, population declines in long-distance migrants due to the loss of ecological niches are to be expected (Berthold 1991). Although significant additive genetic variation for migratory activity has so far only been demonstrated for the blackcap and the European robin, we predict that many other middle-distance migrants possess a similar potential for rapid evolutionary change, since the endogenous nature of the control of migratory activity has already been shown for a considerable number of bird species (Gwinner 1986).

We thank H. Dingle, P. J. Jones, A. van Noordwijk, T. Städler and an anonymous reviewer for valuable comments on the manuscript. This study was supported by a research grant from the Deutsche Forschungsgemeinschaft (to P.B.) and a predoctoral fellowship from the University of Constance (to F.P.).

REFERENCES

Bairlein, F. 1978 Über die Biologie einer südwestdeutschen Population der Mönchsgrasmücke (*Sylvia atricapilla*). *J. Orn.* **119**, 14–51.

Barton, N. H. & Turelli, M. 1989 Evolutionary quantitative genetics: how little do we know? *A. Rev. Genet.* **23**, 337–370.

Becker, W. A. 1992 *Manual of quantitative genetics*, 5th edn. Pullman, Washington: Academic Enterprises.

Berthold, P. 1973 Relationships between migratory restlessness and migration distance in six *Sylvia* species. *Ibis* **115**, 594–599.

Berthold, P. 1985 Endogenous components of annual cycles of migration and moult. *Acta XVII Congr. Int. Ornithol.*, pp. 922–929.

Berthold, P. 1988*a* The control of migration in European warblers. *Acta XIX Congr. Int. Ornithol.*, pp. 215–249.

Berthold, P. 1988*b* Evolutionary aspects of migratory behavior in European warblers. *J. evol. Biol.* **1**, 195–209.

Berthold, P. 1991 Patterns of avian migration in light of current global "greenhouse" effects: a central European perspective. *Acta XX Congr. Int. Ornithol.*, pp. 780–786.

Berthold, P. 1993 *Bird migration.* Oxford University Press.

Berthold, P. & Helbig, A. J. 1992 The genetics of bird migration: stimulus, timing, and direction. *Ibis* **134**, (Suppl. 1), 35–40.

Berthold, P. & Querner, U. 1981 Genetic basis of migratory behavior in European warblers. *Science, Wash.* **212**, 77–79.

Berthold, P. & Querner, U. 1993 Genetic and photoperiodic control of an avian reproductive cycle. *Experientia* **49**, 342–344.

Berthold, P., Gwinner, E., Klein, H. & Westrich, P. 1972 Beziehungen zwischen Zugunruhe und Zugablauf bei Garten- und Mönchsgrasmücke (*Sylvia borin* und *S. atricapilla*). *Z. Tierpsychol.* **30**, 26–35.

Berthold, P., Helbig, A. J., Mohr, G. & Querner, U. 1992 Rapid microevolution of migratory behaviour in a wild bird species. *Nature, Lond.* **360**, 668–670.

Biebach, H. 1983 Genetic determination of partial migration in the European robin (*Erithacus rubecula*). *Auk* **100**, 602–606.

Boag, P. T. & van Noordwijk, A. J. 1987 Quantitative genetics. In *Avian genetics* (ed. P. A. Buckley & F. Cooke), pp. 45–78. London: Academic Press.

Coyne, J. A. & Beecham, E. 1987 Heritability of two morphological characters within and among natural populations of *Drosophila melanogaster*. *Genetics* **117**, 727–737.

Dhondt, A. A. 1982 Heritability of blue tit tarsus length from normal and cross-fostered broods. *Evolution* **36**, 418–419.

Dingle, H. 1991 Evolutionary genetics of animal migration. *Am. Zool.* **31**, 253–264.

Falconer, D. S. 1989 *Introduction to quantitative genetics*, 3rd edn. London: Longman.

Gatter, W. 1992 Zugzeiten und Zugmuster im Herbst: Einfluß des Treibhauseffekts auf den Vogelzug? *J. Orn.* **133**, 427–436.

Gebhardt-Henrich, S. G. & van Noordwijk, A. J. 1991 Nestling growth in the great tit. I. Heritability estimates under different environmental conditions. *J. evol. Biol.* **4**, 341–362.

Gwinner, E. 1986 *Circannual rhythms*. Berlin: Springer-Verlag.

Knapp, S. J. W., Bridges, W. C. & Yang, M.-H. 1989 Nonparametric confidence interval estimators for heritability and expected selection response. *Genetics* **121**, 891–898.

Lambrechts, M. M. & Dias, P. C. 1993 Differences in the onset of laying between island and mainland blue tit *Parus caeruleus*: phenotypic plasticity or genetic differences? *Ibis* **135**, 451–455.

Lancaster, H. O. 1961 The combination of probabilities: an application of orthonormal functions. *Aust. J. Statist.* **3**, 20–33.

Larsson, K. 1993 Inheritance of body size in the barnacle goose under different environmental conditions. *J. evol. Biol.* **6**, 193–208.

Larsson K. & Forslund, P. 1992 Genetic and social inheritance of body and egg size in the barnacle goose (*Branta leucopsis*). *Evolution* **46**, 235–244.

Mousseau, T. A. & Roff, D. A. 1987 Natural selection and the heritability of fitness components. *Heredity* **59**, 181–197.

Reeve, E. C. R. 1961 A note on non-random mating in progeny tests. *Genet. Res.* **2**, 195–203.

Sheridan, A. K. 1990 Genotype × environment interactions. In *Poultry breeding and genetics* (ed. R. D. Crawford), pp. 897–912. Amsterdam: Elsevier.

Siegel, P. B. & Dunnington, E. A. 1990 Behavioral genetics. In *Poultry breeding and genetics* (ed. R. D. Crawford), pp. 877–895. Amsterdam: Elsevier.

Sokal, R. R. & Rohlf, F. J. 1981 *Biometry*, 2nd edn. San Francisco: W. H. Freeman.

Sutherland, W. J. 1988 The heritability of migration. *Nature, Lond.* **334**, 471–472.

Received 8 June 1994; accepted 21 June 1994