GENETIC DETERMINATION OF PARTIAL MIGRATION IN THE EUROPEAN ROBIN (*ERITHACUS RUBECULA*)

HERBERT BIEBACH

*Max-Planck-Institut für Verhaltensphysiologie, Vogelwarte Radolfzell, Radolfzell und Andechs,
D-8138 Andechs, FRG*

Abstract.—Partially migratory behavior, the occurrence of resident and migratory individuals in a population, has been reported in free-living birds. I examined this behavior in the European Robin (*Erithacus rubecula*) under controlled experimental conditions. In an offspring group from a partially migratory field population, 36 (78%) individuals exhibited migratory restlessness (migrants), whereas 10 did not (residents). There were more migrants (89%) in an offspring group from exclusively migratory parents and fewer migrants (53%) from an offspring group from mostly resident parents than there were in the field population. A heritability value of 0.52 was found under the experimental conditions. A connection between the genetic determination of migratory behavior and unpredictable winter weather in the breeding area is discussed. *Received 5 November 1981, accepted 20 December 1982.*

THE occurrence of different and genetically distinctive morphs within a population (polymorphism) has been recorded in a variety of avian species (Huxley 1955). Most such cases involve morphological characters such as color pattern (Mock 1980). Polymorphisms in behavior or physiology have been documented less frequently, perhaps due, in part, to difficulties in quantifying these characters. One of the few examples of polymorphic behavior to have been described is partial migration (Lack 1943, 1944), in which a fraction of an avian population is migratory, whereas another fraction is sedentary. The frequency of the migratory morph increases at higher latitudes (Lack 1943, Berthold 1978), with the result that most individuals in a northern-breeding population are migrants and most in a southern-breeding population are residents.

It has been proposed that polymorphism in the migratory behavior of insects has an adaptive significance in an unstable environment, because it reduces wide fluctuations in population density (Den Boer 1968). The effect upon an entire population of a fraction of the population experiencing extreme conditions in one place is reduced to some degree by the fact that the other fraction is experiencing less extreme conditions in another place. The same might be true of some avian species. One fraction of the population would winter in the breeding area, chancing unfavorable winter conditions that could not be predicted from the environmental conditions current at the time of migration. The other fraction would migrate to normally mild wintering areas. Cox (1968), however, suggested that "Evolution of partial migration may thus result from high overall competition or high intraspecific competition alone."

To understand the primary selective agents in the evolution of partial migration, it is necessary to know how the decision to migrate or to remain is made. There are two hypotheses. Based on ring recoveries, Lack (1943, 1968) proposed a mainly genetic determination of the two morphs, although he did not exclude environmental influences. On the other hand, Kalela (1954) concluded from field observations of behavior that the losers in territorial fights in autumn migrate, whereas the winners stay, which implies that the result of such fights is important in determining migratory behavior. Gauthreaux (1978) interpreted the available data in the same way and stressed the importance of behavioral dominance in partial migration. Conclusive experiments with offspring bred and tested in the laboratory, however, have only recently been undertaken for the first time (Berthold and Querner 1981).

In this paper I report on the genetic determination of two migratory behavioral morphs in the European Robin (*Erithacus rubecula*) from southwestern Germany.
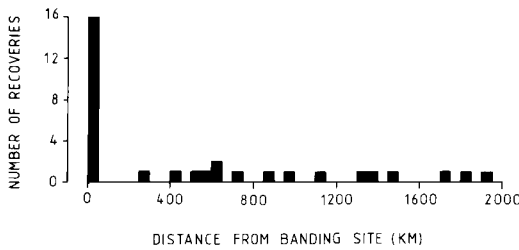
Fig. 1.   Frequency distribution of the distance of ring recoveries of 32 robins banded in the breeding area in southern Germany (from May to July) and found in the wintering areas in Germany, France, Spain, Algeria, Tunisia, Portugal and Italy (November to February) for the years 1947–1980 (data from Vogelwarte Radolfzell). The two groups, those recovered within 50 km of and those recovered beyond 250 km from the breeding area, correspond to residents and migrants.

MATERIALS AND METHODS

In 1978 and 1979, 46 robins were taken as nestlings from nine nests in a field population in southwestern Germany and hand-raised at the Vogelwarte Radolfzell (47°46′N, 09°00′E). From 1979 to 1981, 10 pairs of these birds were selected and bred on the basis of migratory behavior, and they produced 42 offspring. All birds were hand-raised from an age of 5–8 days indoors with a natural daylength and at an ambient temperature of 20 ± 2°C (mean ± SD). All clutches hatched between 14 May and 27 July. Incubation and parental care for as long as 7 days after hatching were entrusted to free-living nesting Great Tits (*Parus major*) as foster parents, because robins breeding in captivity often abandon their nests and because hand raising of newly hatched young robins is difficult. At age 4–7 days these young were brought into the laboratory and raised further by hand. The adult robins could thus produce up to five clutches in captivity during the breeding season. After the birds were self sufficient, they were given a mixture of dried insects (Aleckwa feed), mashed boiled eggs, water, and mealworms *ad libitum*. All were housed in individual recording cages (54 cm × 31 cm × 40 cm) in windowless rooms with a simulated natural light-dark cycle (250 lx during day time, 0.05 lx at night) at an ambient temperature of 20 ± 3°C. Some of the hand-raised birds from 1978 and 1979 were used for breeding experiments the following year. In early April they were placed in outdoor aviaries (1.3 m × 7 m × 2.8 m).

In this study only the data from the migratory period of the first autumn are presented. Every week animals were weighed to the nearest 0.1 g and scored for molt and body feathers with a molt score of 0–5 (Evans 1966).

Using two microswitches mounted beneath one of the two perches, I made a continuous record of hopping activity on event-recorders. In this research I used a single-threshold criterion to designate the presence or absence of nocturnal activity. If a bird hopped more than eight times during each of more than two 30-minute periods during one night, I considered nocturnal activity to have occurred. The total number of all such nights was taken to represent the duration of migratory activity. The purpose of the threshold was to exclude occasional hops during the night when the bird only changed its sleeping place or cases in which the tickmark on the event-recorder was caused by a movement on the same perch. By introducing this threshold, I omitted not more than about 9% of all hops during the night.

For many long-distance migrants, it has been shown that the activity during the night (*Zugunruhe*) of birds in captivity is a useful quantitative representation of migratory activity in free-living conspecifics (Gwinner 1968, Berthold 1973). In contrast, short-distance migrants or resident birds in captivity often show more night activity than would be expected from their natural behavior (Berthold 1973, Helms 1963, Smith et al. 1969). This raises the question of whether or not night activity in the robin, a short-distance migrant, correlates quantitatively with the migratory activity of free-living conspecifics. A comparison of the onset and maximum amount of night activity of birds in captivity with that of birds captured in the field (Dorka 1966) showed a good correlation on both an annual and a daily scale.

RESULTS

DISCONTINUOUS VARIATION IN MIGRATORY BEHAVIOR: FIELD DATA

Banding records show that there is discontinuous variation in migratory behavior within the southern German population of robins. The winter recoveries of birds that were originally banded during the breeding season in southern Germany can be separated into one group of birds that remains within 5 km of the banding site and a second group found 285–1,950 km ($\bar{x} \pm$ SD = 1,032 ± 525 km) from the breeding area (Fig. 1). This discontinuous distribution corresponds to residents (within 5 km of breeding site) and migrants (more than 285 km of breeding site). The wintering areas of migrants are in France, Spain, Algeria, Tunisia, Portugal, and Italy. Because the chance of recovering the banded birds from these countries varies with the intensity of hunting and many other factors (Zink 1973) and because the records of resident birds are mainly from the ring-
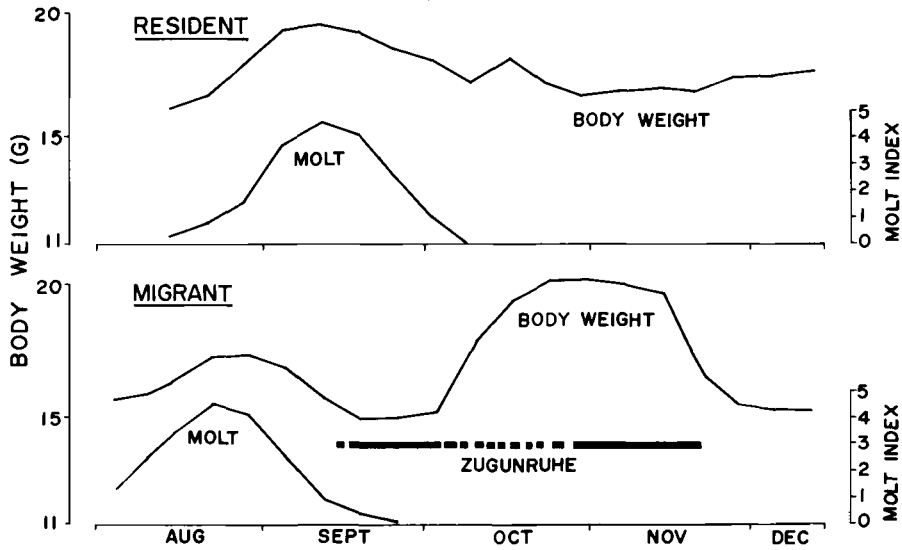
Fig. 2. Body weight, molt, and *Zugunruhe* of a representative resident (upper graph) and a representative migratory robin (lower graph) measured in the laboratory during their first autumn. Only the migrant shows a pronounced increase in body weight (fattening), which is associated with *Zugunruhe*.

ers themselves, we cannot determine on the basis of these data the fraction of the southern German population that is migratory or resident. Moreover, it is possible that the southern German population is composed of subpopulations with very different migratory behavior. The roughly equal distribution of the banding sites of the migratory birds and the resident birds, however, supports the idea that the resident-migratory behavior is typical of the whole population.

DISCONTINUOUS VARIATION IN MIGRATORY BEHAVIOR: LABORATORY DATA

The same discontinuity in the migratory behavior of birds found in the field can also be demonstrated in hand-raised birds in the laboratory by measuring *Zugunruhe*. The difference between migrant and resident robins is illustrated by two examples in Fig. 2. Molt of body feathers is maximal at the beginning of September and is finished by early October. Migratory activity begins toward the end of molt and lasts until mid-November. Body weight increases during molt in both migrants and residents, but only migrants show a pronounced time of fattening that is associated with *Zugunruhe*. The frequency distribution of

the duration of *Zugunruhe* in the offspring sample from a field population shows one group of birds with up to 4 nights of *Zugunruhe* and and a second group with between 5 and 64 nights of *Zugunruhe*; these two groups are thus defined as residents and migrants, respectively (Fig. 3). By this procedure about 20% of the birds ($n = 10$, 95% confidence interval = 11–36%) are allotted to the group of residents and 80% ($n = 36$, 95% confidence interval = 64–89%) to the group of migrants. Six birds of the group of residents showed no *Zugunruhe* at all.

The mean $\pm$ 1 SD of *Zugunruhe* in migrants was 29.86 $\pm$ 15.94 nights and in residents 0.80 $\pm$ 1.14 nights.

HOW ARE THE TWO MORPHS DETERMINED?

Genetics.—To answer this question, breeding experiments were carried out with 5 pairs of migrant $\times$ migrant, 4 pairs of resident $\times$ migrant, and 1 pair of resident $\times$ resident birds. The parents were chosen from the hand-raised birds from the field population on the basis of the intensity of their *Zugunruhe*. Migrant/migrant pairs showed *Zugunruhe* for a mean of 44 nights, resident/migrant pairs for 11 nights, and the resident/resident pair for 2.5 nights. Migrant pairs produced 24 migrant offspring (89%)
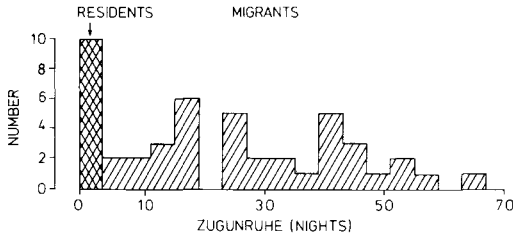
HERBERT BIEBACH

Fig. 3. Frequency distribution of the duration of *Zugunruhe* of 46 hand-raised robins from nine nests chosen randomly from a field population in southern Germany. The *Zugunruhe* was measured in the laboratory during the first autumn. Robins with up to 4 nights with *Zugunruhe* are classified as residents and those with more than 4 nights with *Zugunruhe* as migrants.

and only 3 resident offspring (11%), a significantly higher proportion ($P = 0.0096$, Chi-square test) of migrants than was produced by the combined resident/resident and resident/migrant pairs, which had 8 migrant offspring (53%) and 7 resident offspring (47%). The percentage of migratory offspring (89%) from the migrant/migrant pairs was slightly higher ($P = 0.2943$, Chi-square test) than that of the sample from the field population (78%), which had 36 migrant offspring and 10 resident offspring. On the other hand, the percentage of migratory offspring from the combined resident/resident and resident/migrant pairs (53%) was less ($P = 0.0614$ Chi-square test) than that of the field population. This confirms the genetic hypothesis, which predicts the frequency of migratory offspring from the field population to be between the frequencies of migratory offspring from the migrant/migrant parents and from the combined resident/migrant and resident/resident parents. The sex of a bird has some effect on its migratory behavior (see below), but, as the proportion of males and females in the offspring groups of migratory/migratory pairs, resident/resident plus resident/migrant pairs, and the field population is very similar (13 ♀/ 14 ♂, 7 ♀/8 ♂, 25 ♀/19 ♂, respectively), the results described above are not caused by an uneven sex ratio.

The number of nights with *Zugunruhe* for migratory offspring from migratory/migratory pairs was 50.5 ± 28.3 ($\bar{x} \pm 1$ SD, $n = 23$), as compared to 38.4 ± 23.3 ($\bar{x} \pm 1$ SD, $n = 9$) for offspring from resident/resident plus resident/

migratory pairs. The different is not significant (U-test, $P < 0.4$).

A genetic determination of migratory behavior is also demonstrated by the heritability value (van Noordwijk et al. 1980). The birds are not separated into residents and migrants; rather, the behavior is regarded as having a continuous variation ranging from 0 to 104 nights with *Zugunruhe*. The heritability value is defined as the slope of the linear regression of the *Zugunruhe* of offspring on the mean *Zugunruhe* of parents ("midparent value"). If the heritability value is 1, all phenotypic variation in the offspring is genetic; if it is 0, all the variation is environmental. The slope of 0.524 for the calculated regression of all 42 offspring (from resident pairs, migrant pairs, and resident/migrant pairs) is significantly different ($P < 0.05$, regression coefficient = 0.094) from a slope of zero. This again indicates a genetic effect on the *Zugunruhe* of the offspring. The probability of a difference from a slope of 1 is between 0.1 and 0.05 and thus points also to a nongenetic component.

Effect of sex.—To evaluate the effect of sex on migratory behavior, I used the amount of *Zugunruhe* of males and females of all birds from the field population and from breeding experiments. There is a higher proportion of residents to migrants among males (29:71%, $n = 41$) than among females (20:80%, $n = 45$). These proportions are not significantly different from each other ($P = 0.317$, Chi-square test), but the tendency for males to be more sedentary than females has previously been reported in banding data (Lack 1946).

DISCUSSION

Genetic basis and adaptive significance of migratory behavior.—Based on banding recoveries of many bird species, including the European Robin, Lack (1943) proposed that partial migration might be determined in part by a genetic polymorphism. The data of Nice (1937) on the Song Sparrow (*Melospiza melodia*) also lead one to infer that partial migration has a genetic basis. In Blackcaps (*Sylvia atricapilla*), the proportion of birds with and without *Zugunruhe* is, under experimentally constant conditions, different for samples from populations with different proportions of residents and migrants (Berthold 1978). These results lead to the hy-

pothesis that partial migration in Blackcaps is based on polymorphism. Berthold and Querner (1981) crossed Blackcaps from an exclusively migratory German population (100% migrants) with Blackcaps from a partially migratory African population (23% migrants); 56% of the hybrids were classified as migrants and were thus intermediate to the parental population. These results indicate that the capacity of a bird to migrate is genetically determined. Because partial migration is defined as the occurrence of two different modes of migratory behavior within *one* population, however, those experiments are only indirectly related to the problem of partial migration. The breeding experiments from the present study show a genetic component in the determination of the two morphs from the same population. The data strongly suggest that individuals in local populations can produce both migrant and resident offspring and that this variation in behavior is due to a genetic polymorphism.

The possibility that the expression of migratory behavior in the general population of robins might be gradual, in contrast to the dimorphic pattern expressed within the experimental sample, cannot be excluded completely, however. That all individuals within a population are either resident or migratory and that there are no individuals whose behavior is intermediate is clearly demonstrated for a few bird species under free-living conditions (Lack 1943). This seems also to be true of robins in southern Germany, as shown in Fig. 2, but, based on these data, it is possible, although not very likely, that the laboratory samples were drawn from small, local subpopulations that were purely resident or purely migratory. Indications of two different morphs are less obvious in the laboratory than in the field, however. Berthold (1978) separated captive Blackcaps from southern France into residents and migrants according to their *Zugunruhe* and had no difficulty in classifying them. In robins the frequency distribution of *Zugunruhe* (Fig. 3) is better described by two different distributions than by a gradual change in behavior.

Taken together, the field and laboratory data on the robins justify a discussion of the ecological relevance of residents and migrants. Why should individual birds be able to produce offspring not only of their own migratory disposition but also of the opposite behavior? This

kind of genetic programming of migration appears to be an adaptation to the unpredictability of winter weather. Unpredictable climatic conditions in winter may have a more significant impact on survival than do food supply, body condition, or population density because of the overriding effect of spells of bad weather upon the above. During weather extremes of high snow cover and low ambient temperatures, foraging is extremely difficult due to the scarcity of food, and the risk of death in residents may be high. From the point of view of the parents, the probability that all their offspring of a reproductive season, and thus their own genetic information, would perish during such severe winters would be very high if they were to produce only residents. During a mild winter, however, most of the resident offspring will survive and, compared to the migrants, should have a higher reproductive rate during the following season (von Haartmann 1968, Schwabl 1981). Parents who produce both types of offspring have the advantage of resident offspring during mild winters and of migrant offspring during severe winters in the breeding area. Migrant offspring provide security against an elimination of parents' genetic information, because the migrants, in their more southern wintering area, should, in general, have a higher survival rate than do the residents in the northern wintering area (Ketterson and Nolan 1982). Producing migrants as well as residents can thus balance the high risk of unpredictable winter conditions and can be more successful than producing either migrants or residents.

As a consequence, the extent of environmental variability in different winters and thus the survival rate might not correlate precisely with the frequencies of the two morphs in the population. The stability of the population is increased by this strategy of migratory polymorphism. Over the long term, however, the frequencies of the morphs may well reflect winter conditions, because each morph produces more offspring of its own type than of the other type.

Effect of sex.—Though the effect of sex on migratory behavior was not significant in this study, the hypothesis of a sex difference is strongly supported by field data on robins (Lack 1946) and many other species (Gauthreaux 1978, Ketterson and Nolan 1982). "In all those par-

tially migratory species so far investigated, females migrate more than males" (Lack 1943). This is confirmed to some extent by the observation from the present study of 80% migrants among females and 71% migrants among males. The small sample size might be the reason for the difference being not significant. Environmental factors might also be effective in the field and produce the uneven relationship among males and females in their migratory behavior, but these effects lie outside the scope of the experiments reported here.

LITERATURE CITED

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

———. 1978. Endogenous control as a possible basis for varying migratory habits in different bird populations. Experientia 34: 1451.

———, & U. QUERNER. 1981. Genetic basis of migratory behavior in European warblers. Science 212: 77–79.

COX, G. W. 1968. The role of competition in the evolution of migration. Evolution 22: 180–192.

DEN BOER, P. J. 1968. Spreading of risk and stabilization of animal numbers. Acta Biotheor. 18: 165–194.

DORKA, V. 1966. Das jahres- und tageszeitliche Zugmuster von Kurz- und Langstreckenziehern nach Beobachtungen auf den Alpenpässen Cou/Bretolet (Wallis). Ornithol. Beob. 63: 165–223.

EVANS, P. R. 1966. Autumn movements, moult and measurement of the Lesser Redpolls (*Carduelis flammea cabaret*). Ibis 108: 183–216.

GAUTHREAUX, S. A., JR. 1978. The ecological signif-icance of behavioral dominance. Pp. 17–54 *in* Perspectives in ethology, vol. 3 (P. P. G. Bateson and P. H. Klopfer, Eds.). New York, Plenum Publ. Corp.

GWINNER, E. 1968. Circannuale Periodik als Grundlage des jahreszeitlichen Funktionswandels bei Zugvögeln. J. Ornithol. 109: 70–95.

HAARTMANN, L. VON. 1968. The evolution of resident versus migratory habit in birds. Some considerations. Ornis Fennica 45: 1–7.

HELMS, C. W. 1963. The annual cycle and Zugunruhe in birds. Proc. 13th Intern. Ornithol. Congr. Ithaca: 925–939.

HUXLEY, J. 1955. Morphism in birds. Acta 11th Congr. Intern. Ornithol. Basel: 309–328.

KALELA, O. 1954. Populationsökologische Gesichtspunkte zur Entstehung des Vogelzuges. Ann. Zool. Soc. Vanamo (Helsinki) 16: 1–30.

KETTERSON, E. D., & V. NOLAN JR. 1982. The role of migration and winter mortality in the life history of a temperate-zone migrant, the Dark-eyed Junco, as determined from demographic analysis of winter populations. Auk 99: 243–259.

LACK, D. 1943. The problem of partial migration. Brit. Birds 37: 122–130.

———. 1944. The problem of partial migration. Brit. Birds 37: 143–150.

———. 1946. The life of the robin. London, H. F. & G. Witherby Ltd.

———. 1968. Bird migration and natural selection. Oikos 19: 1–9.

MOCK, D. W. 1980. White-dark polymorphism in herons. Proc. 1st Welder Wildl. Found. Symp. 1: 145–161.

NICE, M. M. 1937. Studies in the life history of the Song Sparrow. A population study of the Song Sparrow. Trans. Linnaean Soc. New York 4: 1–247.

NOORDWIJK, A. J. VAN, J. H. U. VAN BALEN, & W. SCHARLOO. 1980. Heritability of ecologically important traits in the Great Tit (*Parus major*). Ardea 68: 193–203.

SCHWABL, H. G. 1981. Untersuchungen über das Zugverhalten einer südwestdeutschen Population der Amsel (*Turdus merula*): Zur Physiologie und Ökologie des Teilzugs. Unpublished Ph.D. dissertation, München, Ludwig-Maximilians-Universität.

SMITH, R. W., I. L. U. BROWN, & L. R. MEWALDT. 1969. Annual activity patterns of caged nonmigratory White-crowned Sparrows. Wilson Bull. 81: 419–440.

ZINK, G. 1973. Der Zug europäischer Singvögel. Stuttgart, DBV-Verlag.