ENDOCRINE CORRELATES OF AUTUMNAL BEHAVIOR IN SEDENTARY AND MIGRATORY INDIVIDUALS OF A PARTIALLY MIGRATORY POPULATION OF THE EUROPEAN BLACKBIRD (*TURDUS MERULA*)

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ABSTRACT.—Plasma levels of luteinizing hormone (LH), testosterone, 5α-dihydrotestosterone (5α-DHT), estradiol-17β, and corticosterone were measured in free-living and captive European Blackbirds (*Turdus merula*) during autumn. Free-living birds were designated as sedentary or migratory according to whether they remained in or disappeared from the study area during the winter season. Captive birds that increased body weight, deposited fat, and developed *Zugunruhe* in autumn were designated as migratory, whereas those that failed to do so were regarded as sedentary. The results do not support the hypothesis that plasma levels of gonadal hormones are elevated in sedentary birds, thus inhibiting autumnal migration. Plasma levels of LH and of testosterone were low in both adult and first-year free-living males, although testosterone levels were higher in migratory than in sedentary free-living first-year males. In captivity, however, testosterone levels were not different between first-year sedentary and migratory males. In both free-living and captive first-year females levels of 5α-DHT were higher in migratory than in sedentary individuals. Our analyses suggest that the sedentary and migratory habit may be a consequence of different reactions of genetically different individuals to a slightly increased secretion of gonadal hormones in autumn. The variable plasma levels of corticosterone suggest that this hormone is not directly involved in the initiation of migratory behavior, although circulating levels of corticosterone may be influenced by energetic demands during migration. *Received 26 September 1983, accepted 23 February 1984.*

FOR many species of mid- and high latitudes, migration is an adaptation that permits avoidance of the unfavorable hibernal conditions of the breeding area. Within a given species, the fraction of individuals that migrate frequently increases as a function of the latitude of the breeding area of the population. Thus, in areas in which winter conditions are unpredictable, populations are likely to be "partially migratory," some individuals remaining on the breeding grounds and others migrating to distant wintering areas.

The endocrine mechanisms that regulate the physiological events associated with migratory behavior, like premigratory fat deposition and changes in the diurnal pattern of locomotor activity, have been studied until recently largely during spring migration. It has been demonstrated that, at least in some species, gonadal hormones are involved in the deposition of fat before spring migration (Lofts and Marshall 1960, Morton and Mewaldt 1962, Weise 1967, Mattocks 1976, Yokoyama 1976). It might be assumed that these hormones would have no role in the events associated with autumnal migration, because the gonads are regressed and plasma levels of gonadal hormones are basal at this time (Farner 1950, Wingfield and Farner 1980).

For partially migratory species, it has been hypothesized that gonadal hormones, particularly testosterone, might inhibit migratory behavior in the sedentary individuals in fall (Lack 1943, 1968). This hypothesis is derived from observations that more males than females remain in the breeding grounds during winter and that first-year birds are more prone to migrate than adults. Although it is now known

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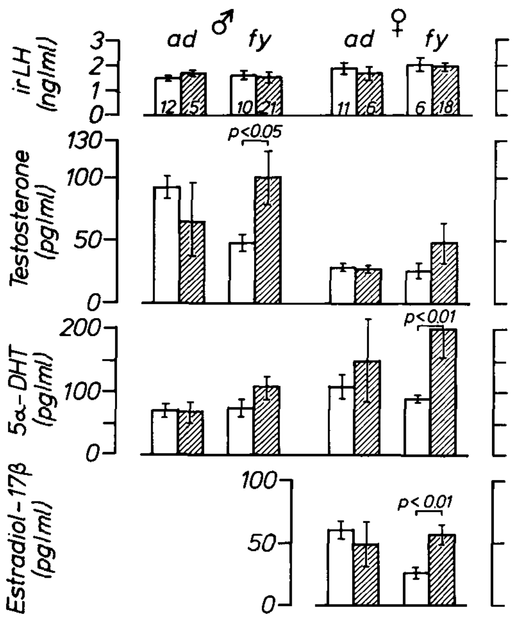

Fig. 1. Mean plasma levels (SE) of LH, testosterone, 5α-DHT, and estradiol-17β in free-living European Blackbirds in September and October. Unhatched columns depict levels in sedentary birds and hatched columns levels in migratory birds. Numerals indicate the sample sizes. fy, first-year birds; ad, adult birds.

that the endocrine activity of the testes of some sedentary species increases in late summer or autumn (e.g. Dawson 1983, Temple 1974, Paulke and Haase 1978, Lincoln et al. 1980), the endocrine activities of the gonads of migrants and nonmigrants within a population of a single species have not, as yet, been compared. To test the hypothesis that plasma levels of gonadal steroids are higher in sedentary than in migratory birds, we measured luteinizing hormone (LH), testosterone, 5α-dihydrotestosterone (5α-DHT), estradiol-17β, and plasma levels of corticosterone in European Blackbirds (*Turdus merula*) of a partially migratory population (Schwabl 1983). We report here plasma levels of these hormones in free-living and captive birds during the time of autumnal migration.

MATERIALS AND METHODS

Field investigations.—A partially migratory population of European Blackbirds, consisting of about 40 breeding pairs, was studied from 1976 to 1979 in southwestern Germany near Radolfzell (47°46'N, 9°00'E). Up to 31 October 1977, a total of 351 individuals had been color banded on the study area. For this investigation, we designated as migratory those individuals that disappeared from the study area during the following winter. Birds trapped or observed between 1 November 1977 and 20 February 1978 were designated as sedentary. To account for birds that may have moved only locally in response to feeding conditions, we also made observations at several feeding sites outside the study area; we designated banded individuals observed therein as sedentary. Of the 50 birds that were designated as migratory and from which we had obtained blood samples in autumn, 14 were recaptured or observed in the study area after 20 February 1978. This did not provide a sample large enough for a detailed analysis of hormone levels according to sex and age. It must be noted that our method, although reliable for the designation of sedentary behavior, produces a rather heterogeneous group of "migrants." Possible differences in plasma levels of hormones between the groups designated as sedentary and migratory may be masked. The blood samples collected in autumn 1977 were obtained according to methods described by Schwabl et al. (1980).

Laboratory studies.—Forty-two birds from the same population, hand-reared indoors during the breeding season of 1979, were subsequently held under the outdoor conditions of their breeding grounds in individual cages (120 cm × 50 cm × 150 cm). Chick-starter mash and water were available *ad libitum;* the diet was supplemented daily with about five mealworms per bird. Body weight and postjuvenal molt were monitored weekly, and locomotor activity was recorded continuously. We estimated premigratory fat deposition by using an arbitrary index for the amount of visible fat deposited in the furcula clavicularis: 1, no fat visible; 2, furcula up to about ⅓ filled with fat; 3, furcula up to about ⅔ filled with fat; 4, furcula completely filled with fat. Postjuvenal molt was assessed by inspection of various pterylae for the fraction of growing new feathers. Blood samples were taken between 1500 and 1700 and at 0200–0500, when some of the birds were in *Zugunruhe.* Blood samples during postjuvenal molt were taken between 19 August and 4 September; samples during the migratory period, as indicated by the occurrence of *Zugunruhe,* were drawn from mid-September until 25 October from birds in *Zugunruhe* as well as from those inactive at night. Our captive birds developed *Zugunruhe* at the time of migration of free-living conspecifics. Samples for the postmigratory period were taken between 14 and 23 November.

Measurement of plasma levels of hormones.—The radioimmunological methods for the measurement of the hormones and the validation of the system for the European Blackbird have been described in previous reports (Wingfield and Farner 1975, Schwabl et al. 1980).

Statistics.—The data were analyzed for repeated measurements by an analysis of variance (Winer 1971). The Student-Newman-Keuls test was used to compare mean levels within one group at different stages when ANOVA indicated a significant variation. The Mann-Whitney *U*-test was used to compare levels between sedentary and migratory birds.

Results

Free-living Birds

The seasonal variations in the plasma levels of LH, testosterone, 5α-DHT, estradiol-17β, and corticosterone in free-living European Blackbirds have been reported in a previous paper (Schwabl et al. 1980). Data from this previous study have been reanalyzed here according to the sedentary or migratory status of these birds.

Plasma levels of LH in sedentary and migratory birds of all sex and age groups were low and not different in September and October before fall migration (Fig. 1). Although plasma levels of testosterone in males were low compared with those during the breeding season, they were significantly higher in migratory than in sedentary first-year males. In sedentary and migratory females of both age classes, levels of testosterone were basal and significantly lower than those of males. Levels of 5α-DHT were significantly higher in migratory than in sedentary first-year females but were not different in the other sex and age groups. Plasma levels of estradiol-17β were also higher in first-year female migrants than in sedentary first-year females.

Circulating levels of corticosterone were greater in first-year migratory males than in first-year sedentary males but did not differ significantly between sedentary and migratory individuals in all other groups (Fig. 2). Body weight as a measure of premigratory fat deposition was significantly greater in migratory than in resident adult males and first-year females. This did not hold for adult females or first-year males (Fig. 2).

Classification of Captive Birds

We used nocturnal activity and body weight to designate each bird as either sedentary or migratory. About half of the caged birds developed migratory restlessness (*Zugunruhe*) in autumn at the time of migration of their free-living conspecifics. Body weight, which was high during postjuvenal molt, decreased thereafter (Fig. 3). There was considerable variability in body weight after molt, when some of

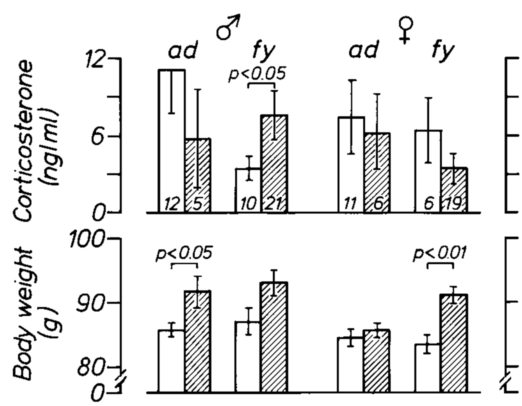

Fig. 2. Mean plasma levels (SE) of corticosterone and mean body weight (SE) of free-living European Blackbirds in September and October. For details see Fig. 1.

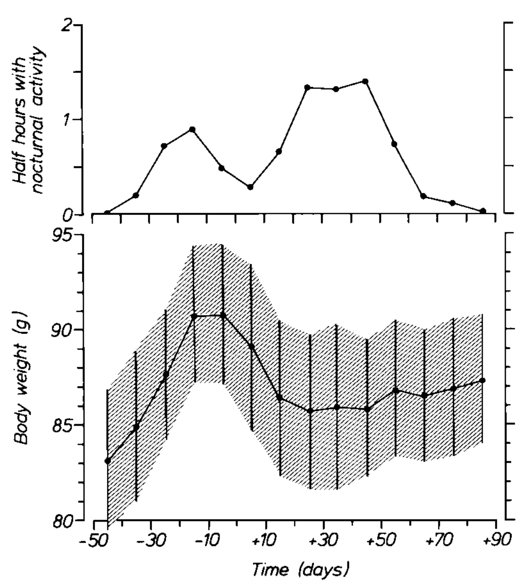

Fig. 3. Body weight (lower panel) and amount of nocturnal activity (upper panel) of caged European Blackbirds in autumn. The data for individual birds are normalized to the day (0) when their molt score was 75% of the score of completed molt. In case of body weight, SD is shown. The calculation of nocturnal activity includes birds that did not show any nocturnal activity.

the birds developed intense nocturnal activity. The decrease in body weight from a maximum during postjuvenal molt to a minimum after molt was assessed for each bird. The magnitude of this decrease was negatively correlated with the amount of visible fat deposited in the furcula clavicularis during the migratory period ($r^2 = 0.56$; $P < 0.01$; Fig. 4). A small decrease in body weight, therefore, represents deposition of reserves of fat, whereas a large decrease indicates that there was no deposition. Thus, the magnitude of decrease in body weight appeared to be an appropriate measure for premigratory fat deposition. Figure 5 illustrates the relationship between the intensity of *Zugunruhe* and the decrease in body weight in individual birds.

For analysis of plasma concentrations of hormones, we defined birds with more than the median amount of nocturnal activity as migrants and those with less than median nocturnal activity as sedentary. Six females were excluded from the analysis, because they had greater than median fat deposition but failed to develop significant nocturnal activity.

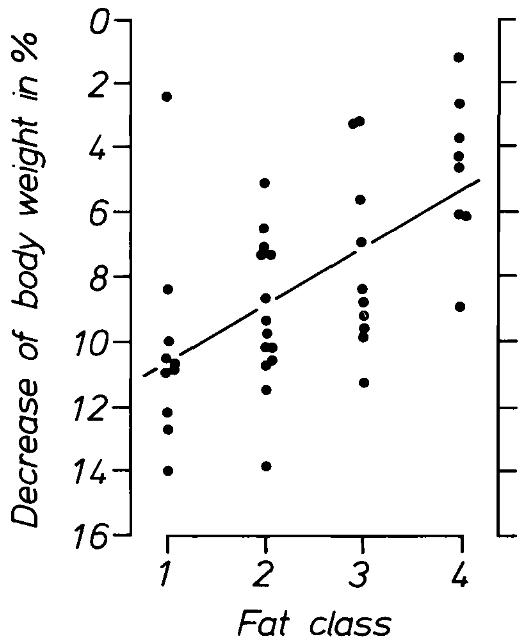

Fig. 4. Correlation between the decrease in body weight from maximum during postjuvenal molt to minimum after the end of molt and the amount of fat deposited in the furcula clavicularis after postjuvenal molt. 1, no visible fat; 2, furcula filled to about ⅓ with fat; 3, furcula filled to about ⅔ with fat; 4, furcula filled to more than ⅔ with fat.

Plasma Levels of Hormones in Captive Birds

The following section presents hormone levels from two aspects. We report (1) whether or not there was variation in the plasma levels of hormones with time within the sedentary and migratory groups and (2) whether or not there were differences in plasma levels of these hormones between sedentary and migratory birds at each stage.

Males (Fig. 6).—There was no significant variation in plasma levels of LH in autumn in either sedentary or migratory birds ($P > 0.10$, $P > 0.25$), but mean levels at night were significantly higher ($P < 0.05$) in sedentary than in migrant males in *Zugunruhe.* Also, testosterone levels did not vary significantly within either group ($P > 0.05$, sedentary; $P > 0.25$, migratory) and were not different between the two groups at any stage. Levels of 5α-DHT, however, varied significantly with time in sedentary males ($P < 0.05$), with levels during postjuvenal molt being lower than during the migratory and postmigratory period ($P < 0.05$). In migrants, the plasma levels of 5α-DHT were relatively stable throughout autumn ($P > 0.25$). At none of the stages, however, were levels significantly different between sedentary and migrant birds. Plasma concentrations of corticosterone varied with time ($P < 0.01$) in both groups; but the only difference was the relatively higher level during the night ($P < 0.05$, sedentary; $P < 0.01$, migratory). Corticosterone levels of sedentary and migrant birds were never different.

Females (Fig. 7).—Plasma levels of LH, testosterone, and 5α-DHT did not change significantly from postjuvenal molt to the postmigratory period among both sedentary and migratory females (LH: $P > 0.25$; testosterone: $P > 0.25$, sedentary; $P > 0.10$, migratory; 5α-DHT: $P > 0.25$); mean levels of LH and testosterone were the same in migrant and sedentary females at all stages. Concentrations of 5α-DHT, however, were significantly higher in migratory than in sedentary females during daytime in the migratory period ($P < 0.05$), as in free-living females. The mean plasma concentrations of corticosterone varied in both groups ($P < 0.01$). In migrants, significant differences

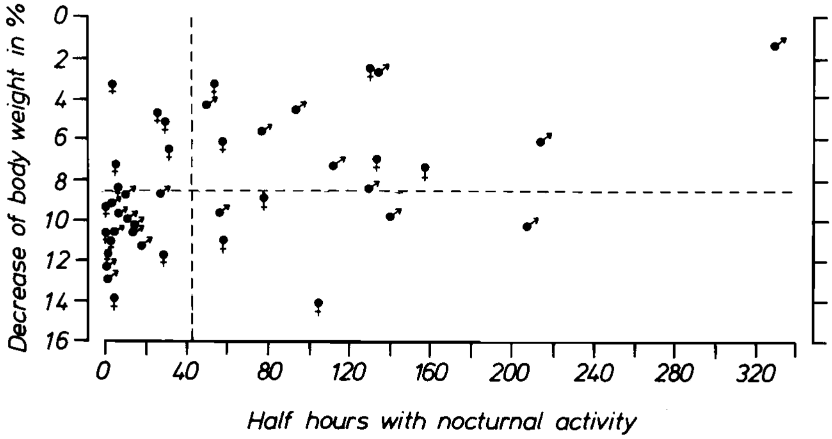

Fig. 5. Relationship between the amount of nocturnal activity and the decrease in body weight from maximum during postjuvenal molt to minimum after postjuvenal molt. The broken lines represent the medians of nocturnal activity and decrease in body weight.

were found between the mean concentrations during the nights of the migratory period and the mean concentrations during daytime of other stages. There was no significant difference between nocturnal and daytime levels, however, when females showed *Zugunruhe* ($P > 0.05$). In contrast, sedentary females had higher nocturnal levels during this time ($P < 0.05$). Corticosterone levels in sedentary and migratory females were different only during daytime in the migratory period ($P < 0.01$).

Discussion

Gonadal hormones.—The analyses of our data do not demonstrate higher plasma levels of gonadal hormones in sedentary than in migratory adult or first-year European Blackbirds in fall, under both natural and captive conditions. At least for this species, these results are contrary to the hypothesis of Lack (1943, 1968) that elevated plasma levels of sex hormones in autumn inhibit migration.

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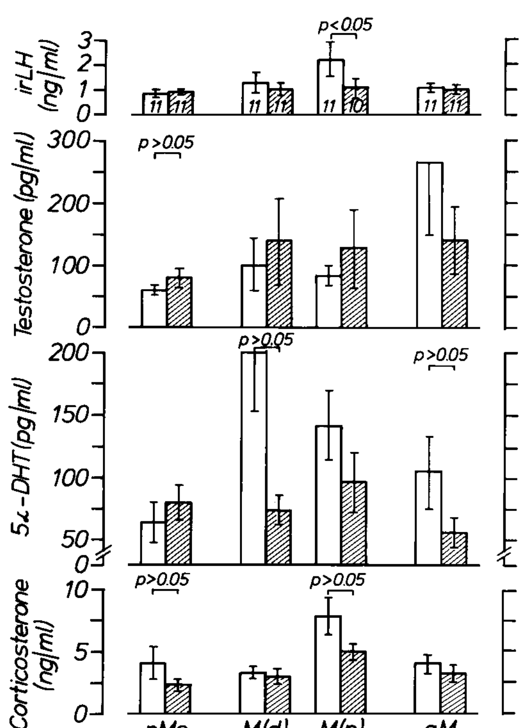

Fig. 6. Mean plasma levels (SE) of luteinizing hormone, testosterone, 5α-DHT, and corticosterone in captive male European Blackbirds during the events of the first autumn of life. pMo, postjuvenal molt (August/September); M(d), migratory period (September/October), samples taken during late afternoon; M(n), migratory period (September/October), samples taken during late night; aM, after migratory period (November). The unhatched columns represent mean plasma levels in birds classified as sedentary and the hatched columns mean plasma levels in birds classified as migratory. Sample sizes are indicated in the columns for LH.

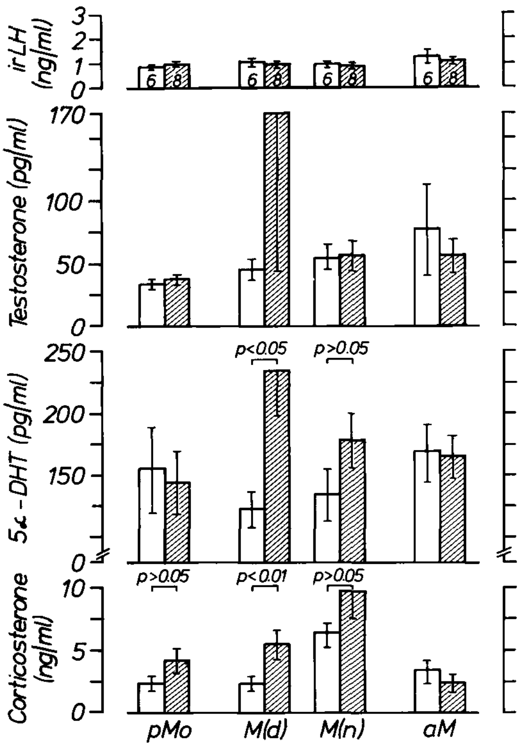

Figure 7. Mean plasma levels (SE) of LH, testosterone, 5α-DHT, and corticosterone in caged female European Blackbirds during the events in the first autumn of life. For explanations see Fig. 6.

The only significant difference in plasma levels of LH was the higher nocturnal concentration in sedentary than in migratory caged males during the migratory period. This may indicate a daily rhythm of LH, with high concentrations during the night and low concentrations during the day, like that reported for roosters (*Gallus domesticus*, Scanes et al. 1978, 1980) and White-crowned Sparrows (*Zonotrichia leucophrys gambelii*, Wingfield et al. 1981). Testosterone levels, however, did not differ between these birds.

Among possible explanations for the lack of difference in plasma levels of testosterone between captive first-year "migrant" and "sedentary" males in comparison with the higher plasma levels in free-living migratory versus sedentary first-year males are that (1) circulating levels of testosterone in free-living birds are the result of social interactions among individuals (captive birds are deprived of this social environment, which may influence plasma levels of testosterone and behavior), or (2) free-living and captive males may have different clearance rates for testosterone, which are related to metabolic differences between the sedentary and migratory habit under these two conditions.

The high plasma levels of 5α-DHT in migratory first-year females under natural and restricted conditions resemble the transient increases of plasma levels of this hormone in female *Zonotrichia leucophrys gambelii* before the onset of vernal migration (Wingfield and Farner 1980) and in first-year females before late-summer migration (Wingfield et al. 1980). Although the function of 5α-DHT in females is unknown, it appears to be a major circulating androgen, which is often in higher concentrations in females than in males. Possibly it has some role in the control of migratory behavior and associated functions in females. The higher levels of 5α-DHT and the detectable concentrations of estradiol-17β may indicate at least that ovarian steroidogenesis is enhanced more in migratory than in sedentary first-year females.

There are several lines of evidence that suggest a function for testosterone or for one of its metabolites in the physiology of migration. Testicular hormones are involved in premigratory fat deposition in male migratory birds, although this has been demonstrated only for spring migration (Lofts and Marshall 1960, Morton and Mewaldt 1962, Weise 1967, Mattocks 1976, Yokoyama 1976). Also, one of the hormones produced by the ovary, possibly testosterone, appears to have the same effect on female *Zonotrichia leucophrys gambelii* (Schwabl and Farner unpubl. data). Experiments by Wagner (1961) on several migratory species suggested that exogenous testosterone can induce *Zugunruhe* at any time in the annual cycle except during postnuptial molt; in the European Starling (*Sturnus vulgaris*) injections of testosterone also cause splitting of the circadian rhythm of locomotor activity, producing a pattern similar to that during *Zugunruhe* (Gwinner 1974, 1975). In the long-distance migrant *Zonotrichia leucophrys gambelii*, however, an endocrine role of the gonads in the induction of late-summer or autumn migration has been excluded, because by this time the gonads have regressed and plasma levels of gonadal hormones are minimal (Farner 1950, Wingfield and Farner 1980), and also because castrated birds show autumnal fattening and *Zugunruhe* (e.g. Mattocks 1976, Schwabl and Farner unpubl. data). We do not have evidence yet that physiological and behavioral events associated with autumn migration are also independent of gonadal hormones in a short-distance partial migrant like the European Blackbird.

On the other hand, the differences in plasma levels of gonadal hormones between sedentary and migratory European Blackbirds conceivably might reflect different pathways of steroid metabolism. The rate of catabolism of testosterone in the anterior pituitary gland and in the hypothalamus of *Sturnus vulgaris*, for example, changes during the annual cycle, with respect to the activity of 5α- and 5β-reductase (Bottoni and Massa 1980, Massa et al. 1977), and the 5β-reduction of testosterone is thought to serve as an inactivation shunt for physiologically active androgens (Steimer and Hutchison 1981, Hutchison and Steimer 1981, Massa and Sharp 1981).

From our results we conclude that we must abandon, at least in the case of the partially migratory European Blackbird, the hypothesis that elevation of plasma levels of gonadal hormones in sedentary birds, as compared with migratory birds, prevents these birds from migration. A new hypothesis about the involvement of gonadal hormones in the regulation of partial migration must account for the following. (1) Plasma levels of testosterone are low in autumn but higher in migrant than in sedentary first-year males; plasma levels of 5α-DHT are high in migratory first-year females; and levels of estradiol-17β appear to be increased in migratory females. (2) Migration is not initiated in sedentary European Blackbirds in spring despite increased plasma levels of gonadal hormones (Schwabl unpubl. data). (3) There appears to be a hereditary difference between sedentary and migratory individuals in partially migratory populations (Berthold and Querner 1982, Biebach 1983). (4) Hand-raised European Blackbirds, deprived of their natural social environment after they have become independent, develop a migratory or sedentary habit, suggesting that social interactions in autumn are apparently not required for the expression of the two behaviors. (5) The tendency to migrate decreases with increasing age of an individual (Lack 1944, Schwabl 1983). If gonadal hormones have a role in the expression of the wintering strategy of European Blackbirds in autumn, it must be effected by very low plasma levels of these hormones. Other species that display sexual and territorial behavior in autumn have elevated plasma levels of gonadal hormones at this time, but levels are below those of the breeding season (cf. Balthazart and Hendrick 1976, Paulke and Haase 1978, and Donham 1979 on *Anas platyrhynchos;* Lincoln et al. 1980 on *Corvus frugilegus;* Temple 1974 and Dawson 1983 on *Sturnus vulgaris*). We suggest that the hypothalamo-adenohypophysio-gonadal axis may be activated slightly after postjuvenal or postnuptial molt, which causes gonadal hormones to have different effects on genetically different sedentary and migratory members of the population, i.e. those overwintering at the breeding grounds or those migrating. There is some evidence that there may be a genetic component in the difference in winter behavior of first-year European Blackbirds (Schwabl unpubl. data). This genetic difference could be expressed through differing reactions to slightly elevated levels of gonadal hormones or through differing metabolic pathways of these hormones in specific brain centers, which then lead to different behaviors and physiological events. This hypothesis, however, cannot explain the decreasing tendency to migrate with increasing age of an individual.

Corticosterone.—Because our results on plasma levels of corticosterone in sedentary and migratory European Blackbirds are variable, they do not indicate a role of corticosterone in partial migration. Only in free-living first-year males did we find higher levels in migratory than in sedentary birds. In caged birds, however, levels of corticosterone were higher only in migratory as compared with sedentary females, whereas there was no difference between levels in males of the two categories. A possible explanation for these seemingly anomalous results could lie in differing responses of males and females to blood-sampling procedures and captivity. A sex difference in the reaction to stress of capture has been reported recently for *Zonotrichia leucophrys* (Wingfield et al. 1982), and an influence of hand raising on the increase of corticosterone levels caused by the blood-sampling procedure has been demonstrated in geese (Dittami 1981).

It has been shown, however, that the secretion of corticosterone *in vitro* is higher in the adrenal glands of migratory than in those of nonmigratory species in fall (Peczely 1976) and that exogenous adrenocortical hormone augments the promotion of fat deposition and nocturnal activity by prolactin in *Zonotrichia leucophrys gambelii* (Meier et al. 1965). If corticosterone secretion is elevated only during actual migration, which is also suggested by investigations of White-crowned Sparrows (Wingfield and Farner 1978, Wingfield et al. 1980), then it is not surprising that we were unable to find conclusive differences in free-living European Blackbirds, because blood samples were taken before the migrant birds left the study area. In that case, however, our caged birds should have had different corticosterone plasma levels, according to whether they developed or failed to develop fat deposits and *Zugunruhe*. That we did not find differences in caged males may be related to influences of captivity on the endocrine activity of the adrenal gland, although this did not appear to influence the expression of the nonmigratory or migratory habit of these birds in captivity. Therefore, we conclude that increased levels of corticosterone in migratory as compared with sedentary species during the time of migration may reflect a response to the energetic demands of migration rather than a direct role in preparation for and initiation of migration.

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