

# INTRASPECIFIC VARIATION IN MIGRATORY PATTERN OF A PARTIAL MIGRANT, THE BLUE TIT (*PARUS CAERULEUS*): AN EVALUATION OF DIFFERENT HYPOTHESES

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**ABSTRACT.**—To evaluate hypotheses explaining intraspecific variation in migratory behavior in partial migrants, a local population of Blue Tits (*Parus caeruleus*) was studied in southern Sweden. Birds born in the study area and recaptured there in winter were compared with birds recaptured at a nearby bird station where a large number of migrant Blue Tits were passing.

By comparing sex ratios among migrants and residents, we concluded that, among juveniles, more than 40% of the females and a significant proportion of the males migrated, while considerably fewer adult females and virtually no adult males did so. Migrant and resident Blue Tits did not differ in size as nestlings, but more late- than early-hatched males migrated. No differences in hatching date were determined for females, presumably because most of them migrated.

Our findings are consistent with the "dominance hypothesis" as an explanation of partial migration, i.e. that the individuals lowest in rank migrate. The fitness gain that leads dominants to stay as residents may be lower winter mortality or a higher probability of establishing a territory in spring. In either case, keener competition for breeding territories among males than among females as a cause for higher residency cannot be excluded. Received 26 February 1986, accepted 4 September 1986.

SOME species show great intraspecific variation in migratory behavior, e.g. differential and partial migrants. In partial migrants some birds migrate while other fractions of the population remain sedentary (Lack 1944, Gauthreaux 1982). Among migrants, females and juveniles normally predominate (Gauthreaux 1982).

Three hypotheses have been proposed to account for differences in migratory tendency between age and sex classes (Ketterson and Nolan 1976, 1982, 1983; Myers 1981). According to the "body-size hypothesis," more small than large individuals migrate because of different abilities to endure starvation (Ketterson and Nolan 1976, Ketterson and King 1977, Ketterson 1979). If energy stores are proportional to body size, larger individuals should have greater reserves relative to their basic metabolic rate (Calder 1974) and thus better survive temporary food shortages. The "arrival-time hypothesis" states that if members of one sex (or some other class) experience more intense competition for breeding resources than do members of the other, then individuals of the former sex should benefit by returning to the breeding grounds earlier, i.e. to winter closer to or on the breeding grounds (Ketterson and Nolan 1976, Myers

1981). Finally, the "dominance hypothesis" holds that the subdominant members of a local population are forced to leave and migrate because of experienced or expected competition with more dominant conspecifics (Kalela 1954; Gauthreaux 1978, 1982; Ketterson and Nolan 1979; Sutherland and Parker 1985).

These hypotheses are not mutually exclusive but generate partly overlapping predictions. For example, all predict that more females than males should migrate in species where males are larger than and dominant over females. By determining differences in migratory tendency within age and sex classes, the hypotheses may be separated. However, information of this kind is scanty (Ketterson and Nolan 1985).

The Blue Tit (*Parus caeruleus*) is an abundant partial and irruptive migrant in Sweden (Lindskog and Roos 1979). In some years large-scale migration takes place, especially when population density is high and the beech mast crop low (Ulfstrand 1962, Ulfstrand et al. 1974, Svensson 1981). The tendency to migrate differs among age and sex classes (e.g. Lindskog and Roos 1979, Karlsson et al. 1986).

We capitalized on a situation where a nest-box and ringing program was carried out in the

vicinity of a bird station. Some of the birds from our study area were recaptured among the large numbers of tits that passed the station on migration. This enabled us to compare residents and migrants.

#### METHODS

The study was carried out in the Revinge area, 20 km east of Lund, south Sweden, in 1984 and 1985. The study area (64 km<sup>2</sup>) consists of woods and groves, interrupted by permanent pastures and agricultural fields. There were 359 nest boxes with an entrance hole small enough (26 mm) to exclude Great Tits (*Parus major*). In 1984, 143 pairs of Blue Tits produced first-brood young in these nest boxes. This population size was about twice as large as any recorded in 1982–1983 and 1985.

The date the first egg was laid, clutch size, date of hatching, and brood size were recorded for each clutch. All nestlings were ringed with an aluminum ring. Altogether, 1,367 first-brood and 16 second-brood nestlings fledged in 1984. Body mass and wing length were taken 13 days after hatching, and at the same time most of the parents were caught. In 1985 we also caught as many breeding Blue Tits as possible.

During the winter Blue Tits were caught at night in the nest boxes and at feeders placed in the central part of the study area. Each feeder was supplied with sunflower seeds until tits started using it. Mist-netting was then carried out during one or a few periods lasting 30–90 min, whereafter the feeder was removed. This was done to avoid attracting transient birds. We netted for a total of 89 h, 89% of it in October and November. A total of 441 nest-box inspections was done, 97% of them in December–February. The age of juveniles was determined by the method described in Svensson (1983). Only 2 juveniles and 1 adult were not sexed.

For the analysis of migration we relied on recoveries made by Falsterbo bird observatory 50 km south-southwest of the Revinge area, and by two private ringers. Because migrating Blue Tits follow leading lines (e.g. coast lines), a high concentration was achieved at Falsterbo bird observatory, which is on a peninsula in southwesternmost Sweden. Netting was conducted between 21 July and 5 November, a period that exceeds the migration period of Blue Tits (Roos et al. 1985).

All statistical tests were according to Sokal and Rohlf (1981). Unless otherwise stated, G-tests with Williams correction and Mann-Whitney U-tests were used.

#### RESULTS

*Sex ratio among migrants.*—During the autumn of 1984, 5,709 Blue Tits were netted at

Falsterbo, which was more than twice the number caught in any season since 1947 (Roos et al. 1985). The median catching date for juveniles (males and females) was 10 October, and 11 October for adult females (Karlsson in litt.). Seventy-five percent of the Blue Tits captured at Falsterbo were yearling females, 21% first-year males, 3% adult females, and 0.1% adult males. Only 0.4% (juveniles) were not sexed (Karlsson et al. 1986).

Nineteen juvenile Blue Tits, ringed as nestlings in the Revinge area, were caught during migration: 12 females and 5 males at Falsterbo, 1 individual near Falsterbo, and 1 in Denmark 150 km southwest of Revinge. The latter 2 were not sexed. There was no difference in age and sex composition between the recaptured Blue Tits from Revinge and all migrants ( $G = 1.39$ ,  $P > 0.1$ ).

The expected frequency distribution if there was no difference in migratory tendency among age and sex categories for Revinge birds recaptured on migration was calculated by applying data on postfledgling survival for the Great Tit in England (applicable data on Blue Tits are lacking) (Krebs and Perrins 1978). Survival of juveniles relative to adults until October was 0.47. This figure was conservative as Dhondt (1979) calculated that only 22% of Great Tits fledged in southern Sweden were alive at the beginning of September. Ninety-one male and 94 female parent Blue Tits and 1,367 fledglings were marked. This gives expected frequencies of 6.6 juveniles of each sex and 3.8 adults. This differs from the frequencies observed (12 juvenile females, 5 juvenile males, no adults) ( $G = 11.1$ ,  $P < 0.005$ ). To calculate the expected frequency distribution among all migrants, the total number of parents was used instead of the number of ringed parents (all parents were not ringed). The expected frequencies then are 933 adults of each sex and 1,910 juveniles of each sex. This differs from the observed frequencies ( $G = 5,120$ ,  $P < 0.001$ ). In both comparisons juvenile females were most prone to migrate, followed by juvenile males. For the comparison between adult males and females only the distribution among all migrants could be used; more adult females than males migrated ( $G = 204$ ,  $P < 0.001$ ). Actually, no adults ringed at Revinge were recaptured at Falsterbo, but with the same distribution as for all migrants only 0.3 Revinge adults were expected to have been caught.

TABLE 1. Sex ratio among juvenile Blue Tits of different categories: individuals caught in the study area during October–February that were previously unmarked (local unmarked), individuals caught in the study area during October–February that were marked as nestlings in the same area (local recoveries), and individuals recovered on migration that were marked as nestlings in the study area (recoveries migration).

	Males	Females	P
Local unmarked	30 (61.2%)	19 (38.8%)	<0.05
Local recoveries	14 (87.5%)	2 (12.5%)	
Recoveries migration	5 (29.4%)	12 (70.6%)	<0.001

We conclude that juvenile females show the largest tendency to migrate, followed by, in turn, juvenile males, adult females, and, finally, adult males.

*Sex ratio among residents.*—Sixteen juvenile Blue Tits, ringed as nestlings at Revinge, were recaptured subsequently in winter in the same area, and an additional 51 unringed juvenile Blue Tits were trapped. Of those, all but 2 were sexed. Juvenile sex ratios did not differ between birds caught at feeders (70% males) and in nest boxes (67% males) or between birds caught early in winter (October–November: 69% males) and late in winter (December–February: 68% males) (some birds were included in both categories).

The proportion of females (70.6%) among juvenile Blue Tits ringed as nestlings at Revinge and recaptured on autumn migration at Falsterbo ( $n = 17$ ) was significantly higher than among those recaptured while wintering at Revinge (12.5%,  $n = 16$ ;  $G = 12.29$ ,  $P < 0.001$ ) (Table 1). Males may have been captured more easily at Revinge than females because they were dominant. However, among breeding adults ringed in 1984 an equal proportion of each sex was recaptured in the subsequent winter (5.5% for males, 5.3% for females). Furthermore, the adult sex ratio during winter (68% males) approximated the sex ratio among Blue Tits older than 1 yr that bred in the subsequent spring (61% males, corrected for the total number of each sex caught).

The proportion of females among juveniles recaptured at Revinge was lower than among previously unringed juveniles (38.8%,  $n = 49$ ;  $G = 4.13$ ,  $P < 0.05$ ) (Table 1). Thus, a higher

TABLE 2. Sex ratio among first-year breeders of the Blue Tit in relation to whether they were previously marked as nestlings in the study area (recoveries) or not (unmarked) ( $G = 0.15$ ,  $P > 0.1$ ).

	Males	Females
Recoveries	4 (28.6%)	10 (71.4%)
Unmarked	14 (34.1%)	27 (65.9%)

proportion of females than males migrated from the local population at Revinge. At the same time, other females arrived in the Revinge area.

*Proportion that migrated.*—The proportion of juvenile males and females of the local population at Revinge that took part in migration can be calculated assuming that there is no differential mortality between the sexes before migration. Let  $N$  be the number of birds alive just before migration,  $F$  the number of birds migrating,  $S$  the number of birds remaining as residents,  $x$  the proportion of males among migrants, and  $y$  the proportion of males among residents. Then,  $N/2 = xF + yS$ .  $S = N - F$ , so the proportion of juvenile Blue Tits that migrated is  $F/N = (1 - 2y)/(2x - 2y)$ , and the proportions of males and females that migrated are  $2xF/N$  and  $2(1 - x)F/N$ , respectively.

Using the figures above, 65% of the total population (91% of the females and 38% of the males) migrated. A 95% confidence interval for the proportion of males captured at Falsterbo and at Revinge yields a lower limit of 23% of the total juvenile population (5% of the males and 42% of the females). We conclude that a large proportion of the juveniles migrated, among juvenile females at least half the population.

Among first-year breeders in 1985, the proportion of females did not differ between ringed and unringed birds (Table 2). This may be the result of a return of ringed females during spring, the emigration of unringed females, or both.

*Characteristics of migrants.*—There was no difference in hatching date of broods that produced female recoveries at Falsterbo (migrants) and those that did not. Males from late-hatched broods had a higher tendency to migrate (Table 3). Conversely, males that subsequently established themselves in the breeding population were born earlier than those that migrated (Table 3). The lack of influence of hatching date on females probably depends on the fact that

TABLE 3. Hatching date for Blue Tit broods for different recovery categories: during autumn migration, in the study area during winter (October–February), during subsequent breeding in the study area, and all broods that did not produce recoveries of the sexes in question during migration.

	Median date <sup>a</sup>	Range	n	p <sup>b</sup>
<b>Males</b>				
Migration	56.5	51–58	5	
Study area	52.8	47–56	14	<0.05
Breeding	52.5	49–53	4	=0.06
All broods	53.6	43–73	138	<0.05
<b>Females</b>				
Migration	52.5	44–66	12	
Breeding	51.3	46–58	10	>0.1
All broods	53.8	43–73	132	>0.1

<sup>a</sup> Day 1 = 1 April.

<sup>b</sup> Differences between individuals recovered on migration and other categories.

the majority of females migrated. Hence, we should not expect the proportion among the migrants to differ from that of the population as a whole.

There was no tendency for migrants to come from broods that weighed less at fledging or from broods of short mean wing length (Table 4). Thus, neither males nor females recaptured at Falsterbo tended to be from clutches of lesser mean mass or with shorter mean wing length, to have less mass or shorter wing length as nestlings, or to have less mass or shorter wing length than their nest mates, than juveniles recovered at Revinge in winter or during subsequent breeding (Table 5). Because nestling size correlates with fledgling size (Garnett 1981), we conclude that size had no effect on the probability that an individual would migrate.

Neither migrating males nor females came from broods of any particular size. The age of parents of broods with detected migrants did not differ from the age of parents without detected migrants.

#### DISCUSSION

We found that juveniles and females were overrepresented among migrant Blue Tits. This age- and sex-specific migration is consistent with patterns found elsewhere for the Blue Tit (e.g. Frelin 1971, Hildén 1974, Winkler 1974, Ehrenroth 1976, Lindskog and Roos 1979), as well as for other partial migrants and irruptive species (Gauthreaux 1982).

TABLE 4. Mean mass (g) and wing length (mm) of Blue Tit broods with and without detected migrants (one-sided *t*-test,  $P > 0.1$  for all comparisons). Standard deviations are given in parentheses.

	Mass	n	Wing length	n
With migrants	11.05 (0.62)	16	37.01 (2.28)	16
Without migrants	11.09 (0.82)	125	37.12 (2.91)	124 <sup>a</sup>
Total	11.08 (0.80)	141	37.11 (2.84)	140 <sup>a</sup>

<sup>a</sup> Sample size varies because wing length was not measured for one brood.

Late-hatched juvenile males migrated more frequently than did early-hatched ones (Table 3). This is, as far as we know, the first time it has been shown that phenotypic differences within a sex and age class promote migration in a partial migrant, although Dhondt and Hurlé (1968) hinted at that in their analysis of Belgian ringing recoveries of Great Tits. Kluyver (1971) showed that second-brood young of the Great Tit disperse longer distances than do first-brood young. These authors, however, failed to distinguish between dispersal and migration. We use our results to evaluate the different hypotheses about the selective agent responsible for differences in the tendency to migrate.

The "body-size hypothesis" predicts that migrants should be smaller than residents. At Revinge, juvenile male Blue Tits were heavier and had longer wings than adult female Blue Tits (11.5 vs. 10.9 g,  $P < 0.02$ ; 65.9 vs. 64.1 mm,  $P < 0.001$ ; two-tailed *t*-test). This contradicts the body-size hypothesis because a higher proportion of juvenile males than of adult females migrate. Furthermore, because body size among Blue Tit nestlings was independent of hatching date (correlation coefficient between brood mean mass and hatching date = 0.096,  $P > 0.1$ ,  $n = 141$ ) the body-size hypothesis does not explain why a larger proportion of late- than of early-hatched males should migrate.

The "arrival-time hypothesis" was suggested primarily as an explanation for the difference in migratory pattern between the sexes. It would be valid if, for example, only males compete for territories during spring and those arriving early would have a competitive advantage. For females, which do not compete for males to the same extent, an early arrival gives little or no competitive edge. The hypothesis

TABLE 5. Size differences between migrant and resident juvenile Blue Tits. Mean mass (g) and wing length (mm) for broods and for individual nestlings are given, and the deviation of individual nestlings from their brood mean (one-sided *t*-test,  $P > 0.1$  for all comparisons within sex). Standard deviations are given in parentheses.

Category*	Brood mean		Individual value		Deviation		n
	Mass	Wing length	Mass	Wing length	Mass	Wing length	
Males							
Migration	11.42 (0.48)	38.20 (0.57)	11.60 (0.80)	38.25 (1.32)	0.18 (0.54)	0.05 (1.49)	4
Study area	11.31 (0.92)	37.29 (2.46)	11.60 (1.01)	37.46 (3.28)	0.25 (0.48)	0.12 (1.76)	14 <sup>b</sup>
Breeding	10.93 (0.89)	36.87 (1.31)	11.45 (0.81)	37.00 (2.58)	0.53 (0.71)	0.13 (1.83)	4
Females							
Migration	10.98 (0.66)	36.74 (2.58)	10.78 (0.67)	36.76 (3.36)	−0.21 (0.43)	0.02 (1.89)	14 <sup>b</sup>
Breeding	11.37 (0.82)	37.23 (2.18)	10.91 (0.89)	37.56 (2.28)	−0.46 (0.43)	0.33 (1.37)	9

\* Categories are defined in Table 3.

<sup>b</sup> For brood mean  $n = 12$ .

thus could explain the difference in migratory tendency between the sexes in the Blue Tit, but not the difference between the age classes.

The "dominance hypothesis" holds that when competition for food or some other nonbreeding resource is intense, socially dominant individuals will be more likely to obtain an adequate supply and subdominant individuals will depart (Ketterson and Nolan 1983). Males are dominant over females within each age class and adults over juveniles within each sex in many species of tits (Perrins 1979). A crucial question is whether adult females are dominant over juvenile males. To answer this, information on flock membership is required because, in most species of tits, dominance is site dependent (Saitou 1982, Drent 1983, Nilsson and Smith in prep.). We found no information on this dominance relationship in the Blue Tit. Instead, we rely on comparisons with other species of tits. The evidence here is conflicting. Kluyver (1957) found that adult Great Tit females are dominant over juvenile males, but Saitou (1979, 1982) found no consistent trend. In the Marsh Tit (*Parus palustris*) adult females dominate juvenile males (Nilsson and Smith in prep.), whereas in the Black-capped Chickadee (*P. atricapillus*) males are dominant over females (Glase 1973). In the Willow Tit (*P. montanus*) juvenile males normally dominate adult females (Hogstad 1986). The survival of dominant females (nearly always adults) is higher than that of subdominant males (which are always juveniles) [60% vs. 23% in flocks studied by Ekman and Askenmo (1984)]. Thus, even if adult females are subdominant to juvenile males, they may not be forced to migrate be-

cause, for other reasons, they survive winter better.

The dominance hypothesis also may explain why late-hatched males show a stronger migratory tendency than do early-hatched males. Prior occupancy may confer a dominance advantage (Maynard Smith and Parker 1976, Maynard Smith 1982, Yasukawa and Bick 1983). In the Great Tit, territory owners can maintain territories because of prior occupancy, regardless of differences in size and age (Krebs 1982), and newcomers in Great Tit flocks are confined to low positions in the dominance hierarchy (Krebs et al. 1972, Saitou 1979, Drent 1983). In the Marsh Tit late-established juveniles are consistently subdominant to early-established individuals regardless of size (Nilsson and Smith in prep.). Late juveniles also have problems getting established in winter flocks. Furthermore, Arcese and Smith (1985) showed that in fledgling Song Sparrows (*Melospiza melodia*) dominance depended on age, so that early-hatched juveniles were dominant over late-hatched ones. Therefore, according to the dominance hypothesis, late-hatched individuals should show a higher tendency to migrate. The reason we find this pattern among juvenile male but not juvenile female Blue Tits is probably that any tendency in this direction is diluted because the majority of the juvenile females migrate.

Size is generally regarded as the main factor determining dominance hierarchies among birds. In the Black-capped Chickadee and the Marsh Tit, however, size does not predict rank when age and sex are taken into account (Glase 1973, Nilsson and Smith in prep.). This may be

the reason we found no difference in size between migrant and resident Blue Tits.

The pattern found is also consistent with an alternative version of the dominance and arrival-time hypotheses. If birds can hold a territory or a high dominance position in winter flocks because of prior occupancy, then resident adults will be more likely to obtain a breeding territory than will resident juveniles. Thus, the incentive to be resident is higher for adults than for juveniles. Likewise, early-hatched juveniles will have a higher probability of obtaining a breeding territory than will late-hatched juveniles, if they are more dominant in winter flocks because of earlier establishment. Therefore, early-hatched juveniles should show a higher tendency to be residents. The difference between males and females may be due to males competing more for breeding territories (arrival-time hypothesis). The difference from the original statement of the dominance hypothesis lies in when fitness gains are achieved. Thus, detailed data on survival and probability of territorial establishment for different sex and age categories have to be collected to separate the hypotheses. The different hypotheses are not mutually exclusive, however.

Unringed females from other places seemed to immigrate into the Revinge area and spend the winter there (local unmarked vs. local recoveries in Table 1). These females were not just on passage as they were caught from the last few days of October onwards, when migration had virtually ceased at Falsterbo (Roos 1985). Thus, females from presumably more northerly areas wintered at Revinge at the same time that other juveniles were forced to leave. The dominance and the arrival-time hypotheses may explain partial migration from a local population of Blue Tits, but more knowledge is needed to understand the distance traveled by migrants.

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