

DIFFERENTIAL TIMING OF SPRING MIGRATION IN ROSE-BREASTED GROSBEAKS

CHARLES M. FRANCIS AND F. COOKE

*Biology Department
Queen's University
Kingston, Ontario K7L 3N6, Canada*

Abstract.—We used banding data to examine the timing of spring migration of Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) at Prince Edward Point, Ontario. Males arrived significantly earlier than females, in common with most passerines, and contrary to a previous report based upon field observations at the same site. However, the difference between the sexes in mean arrival dates was only 1 d. Adult males arrived on average, 3 d before second-year males. There was also some evidence, based on wing length, that adult females arrived before second-year females. Among second-year males, individuals with the most adult-like plumage tended to arrive earlier, but there was no relationship between wing length or body mass and arrival date. Data on recoveries of grosbeaks, obtained from the Canadian Wildlife Service, showed an extensive overlap between the sexes in wintering distribution, but insufficient data were available to detect differences in mean wintering latitude. The small difference between arrival times of males and females, and the later arrival of young birds, suggests that both sexes are selected to arrive relatively early because of competition for territories on the breeding grounds, although females may benefit by waiting until males are on territories.

DIFERENCIAS EN EL PERÍODO DE MIGRACIÓN PRIMAVERAL EN INDIVIDUOS DE *PHEUCTICUS LUDOVICIANUS*

Sinopsis.—Utilizamos datos obtenidos de aves anilladas para examinar el tiempo particular de migración de *Pheucticus ludovicianus* en Prince Edward Point, Ontario. Los machos llegan primero que las hembras, en común con otros passeriformes, y contrario a informes previos, al mismo lugar. Sin embargo, la diferencia de las fechas promedios de llegada entre los sexos fue de tan sólo un día. Los machos adultos llegan en promedio tres días antes que los machos de segundo año. Basado en el largo del ala, hay alguna evidencia que tiende a indicar que las hembras adultas llegan primero que las de segundo año. Entre los machos de segundo año, aquellos individuos que tienen el plumaje más parecido a los adultos tienden a llegar más temprano, pero no se encontró relación entre el tamaño del ala, peso y fecha de llegada. Datos obtenidos del Servicio de Vida Silvestre Canadiense sobre la recaptura de *P. ludovicianus*, muestra un extensivo solapamiento entre los sexos en su distribución invernal. Los datos resultaron insuficientes para detectar diferencias en la latitud promedio invernal. La pequeña diferencia entre las fechas de llegada de machos y hembras, y la llegada más tarde de las aves jóvenes, sugiere que la selección actúa sobre ambos sexos para llegar temprano debido a la competencia por territorios en los lugares donde crían. Las hembras muy bien podrían beneficiarse de esperar a que llegasen primero que ellas los machos a ocupar sus respectivos territorios.

In most species of migratory birds that have been studied in North America, males tend to arrive before females on spring migration (Francis and Cooke 1986, Gauthreaux 1982, Myers 1981). However, in a few species, such as Spotted Sandpipers (*Actitis macularia*; Oring and Lank 1982) and phalaropes (Reynolds et al. 1986), the females arrive earlier, whereas in others the sexes appear to arrive at the same time (Myers 1981, Orians 1980, Rohwer and Anderson 1988). The most widely accepted explanation for this differential migration is that individuals of

the territorial sex, or at least the sex with the strongest intrasexual competition for mates, are selected to arrive as early as possible to increase their chances of obtaining a good territory or mate (Francis and Cooke 1986, Myers 1981, Reynolds et al. 1986). The other sex, usually the female, may benefit by waiting until the first sex has settled its disputes and the weather and feeding conditions have improved. The only documented cases where the sexes migrate at the same time are when pairing takes place before arrival on the breeding grounds, such as in waterfowl (Rohwer and Anderson 1988).

If this explanation is valid, and the earliest birds to arrive obtain the best territories, then competitively superior birds within the early sex might be expected to arrive first. Because older birds are generally dominant over younger individuals (Gauthreaux 1978), adults (after second year or ASY) might be predicted to arrive before second year (SY) birds. On the other hand, Ketterson and Nolan (1983) postulated that young birds may be under greater selection pressure to arrive early than adults, because the latter can often reclaim their previous year's territory even if it is already occupied (Nolan 1978, Jakobsson 1988). Studies on several species have shown that adults arrive before younger birds, supporting the first hypothesis (Francis and Cooke 1986, Jakobsson 1988). However, Ketterson and Nolan (1983) found that younger male Dark-eyed Juncos (*Junco hyemalis*) winter farther north than adults. Because differences in wintering latitude are often correlated with arrival times (Myers 1981), this suggests that young juncos may migrate earlier than adults in spring, although data are not available to confirm this. If variation in competitive ability within age classes is correlated with other traits, such as body size or plumage, one might also expect a relation between these characters and arrival date. Hill (1988) found that more brightly-colored male Black-headed Grosbeaks (*Pheucticus melanocephalus*) within each age class obtained better quality territories, although he failed to detect any differences in their arrival times on the breeding grounds. Ketterson (1979) found that larger juncos were generally dominant over smaller individuals, but again had no data on arrival dates in spring.

Although the phenomenon of early male arrival is thought to apply to most passerines, relatively few species have been studied in detail and even fewer species have been examined for differences between and within age classes. In this paper, we examine differences in arrival times between and within sex and age classes of Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) on migration through Prince Edward Point, Ontario. We chose to study this species for two reasons. First, Weir (1989) reported that the average arrival date near Kingston, Ontario of male and female Rose-breasted Grosbeaks appeared to be the same, based upon data on the first sightings of the species each spring. This suggests that the species may not fit the general pattern for other passerines. The only other passerine in which the sexes are reported to migrate at the same time is the Brewer's Blackbird (*Euphagus cyanocephalus*), which is non-territorial (Orians 1980), unlike the Rose-breasted Grosbeak (Dunham 1966). Sec-

ond, SY male Rose-breasted Grosbeaks can be readily distinguished from ASY males by the retention of brown juvenal primaries, but they also vary considerably in the amount of juvenal plumage retained in other feather tracts (Cannell et al. 1983). Thus we can examine differences in arrival dates between and within age classes of males in this species. In addition to using data on arrival times, we also used recoveries of banded birds to test for differences in the wintering distribution of each sex, to determine whether these are related to arrival times.

METHODS

Ideally, to test hypotheses about arrival times and competition, one should measure the arrival times on the breeding grounds. Unfortunately, it is very difficult to ascertain exact arrival dates on the breeding grounds, as well as to sample a sufficiently large number of birds for statistical analysis. In contrast, at a migration stopover, large numbers of birds can be captured, and the capture time fairly accurately reflects arrival time as long as birds do not remain more than 1–2 d in the study area. As a result, we have used data from birds on active migration for the analysis, making the assumption that arrival times on migration reflect arrival on the breeding grounds.

We used data for Rose-breasted Grosbeaks caught and banded on spring migration at Prince Edward Point National Wildlife Area, Ontario (43°57'N, 76°54'W). Birds were caught using 15 to 30 standard (12 × 2-m) mist nets, most of which had 30 mm mesh. Nets were set daily, when the weather permitted, in small woodlots near the tip of the point, from early May until at least June in 1976–1981, 1988, and 1989. Most grosbeaks were caught before the end of May, which has been previously noted as the main migration period of grosbeaks near Kingston (Sprague and Weir 1984). A few birds of both sexes were caught in June, but we excluded these from analysis because they may have been local breeders that had completed migration (the results were essentially the same if these birds were included). Few birds were recaptured after they were banded and most birds that were recaptured stayed no more than 1 or 2 d after banding, suggesting that capture times fairly accurately reflect arrival times in the area.

Captured birds were banded, their wing was measured, most individuals were weighed, and the age of males was determined based on the retention of brown juvenal primaries. In 1989, the plumage of each yearling male was scored to estimate the amount of adult-like plumage. The percentage of black feathers on the head, back, and shoulder, and the percentage of white and black feathers on the rump were estimated (rump color was not recorded until the third day after SY males started arriving). The number of new (black) tail feathers was also counted, and the brightness of the pink on the breast was estimated in relation to a bright adult. The latter ranged from 30% for a small dull patch of pink mixed with brown, to 100% for a large bright pink triangle. All birds were scored by the same person (C. M. Francis).

To look for possible differences in the wintering latitude of the sexes, we obtained data from the Canadian Wildlife Service on recoveries of Rose-breasted Grosbeaks that had been banded in North America. Data were available for all recoveries reported up to the middle of 1987. We restricted the analysis to birds recovered between the months of November and February inclusive, to exclude any birds that may have been on migration.

RESULTS

Differences between the sexes.—We initially examined the first capture dates for the sexes in each year at Prince Edward Point to compare with the results of Weir (1989). In six of eight years, the first bird captured was a male, while in the other two years it was a female (Table 1). This suggests that males may arrive earlier, but is certainly not conclusive. However, first arrival dates only represent one individual, which may not even be the first to arrive, because not all birds are caught. A better measure of arrival dates is the mean arrival date for all individuals of each sex. This takes into account information for all individuals caught, rather than just the few that were first. Altogether, 538 males, and 450 females were caught during the 8 years we examined.

In every year for which we have data, the mean arrival date of males was earlier than that of females, although in a few years the difference was very slight (Table 1). Even in years when the first arrival was a female, the average arrival for females was later than for males. Pooled over all years, the difference between the sexes was highly significant statistically (Wilcoxon $U = 137857$, $P < 0.0001$), as was also true for four of eight years. These results unambiguously show that males do, in fact, arrive earlier than females on migration, contrary to the observations of Weir (1989). Nevertheless, in two years the average arrival date for males and females was virtually the same, and the overall difference between the means was only 1.1 d.

Differences between age classes.—The age was not recorded for all male grosbeaks in some of the early years, but data on arrival times are still available for 188 ASY males, and 311 SY males. In six of the eight years, the first male caught was an adult, in one year a SY and ASY male were caught on the same first date, and in 1979 a SY was caught first (Table 2). These results suggest that adults may arrive earlier, but as was noted in the sex analysis, first arrival dates only use information from a very small number of birds. For a more powerful analysis, we examined the average arrival times for each age class. In every year, adult males arrived before young males, and in the three years with the largest sample sizes, this difference was statistically highly significant (Table 2). Overall, ASY males arrived an average of 2.6 d before SY males.

The age of females is much more difficult to determine, and while it apparently can be worked out (Pyle et al. 1987), most birds were not aged in our study. However, there was indirect evidence to support the hypothesis that young females were also delayed in their arrival relative

TABLE 1. First captures and mean arrival times of male and female Rose-breasted Grosbeaks on spring migration at Prince Edward Point, Ontario (all dates are in May).

Year	Number of birds		First dates		Mean dates		Comparison of dates ^a
	Males	Females	Males	Females	Males	Females	
1976	30	42	10	11	17.5	18.5	n.s.
1977	82	72	5	10	15.8	17.4	$P < 0.003$
1978	65	47	9	11	16.3	17.7	$P < 0.05$
1979	49	50	12	9	17.9	18.3	n.s.
1980	100	74	5	12	19.1	19.3	n.s.
1981	18	15	13	5	18.6	19.7	n.s.
1988	64	63	8	9	15.4	17.8	$P < 0.01$
1989	129	86	1	10	17.1	18.1	$P < 0.05$
Total	537	449	1	5	17.1	18.2	$P < 0.0001$

^a Wilcoxon-Mann-Whitney *U*-test.

to adults. Early arriving females tended to have longer wings than later birds, as indicated by a negative correlation between wing length and arrival date ($r = -0.15$, $P < 0.001$, $n = 445$). At least within males, adults have significantly longer wings than younger birds (101.7 mm compared with 99.5 mm, $F = 58.6$, $P < 0.0001$), and there was no relationship between wing length and arrival date within age classes (see below). Assuming the same relationships between wing length and age in females, this suggests that early females included a higher percentage of adults than late females.

Variation within age classes of males.—Except for one bird that had replaced some of its outer primaries, the SY males all retained their juvenal primaries and most of their secondaries. However, in other measures of plumage brightness, SY males varied considerably. Many individuals strongly resembled adults, but other individuals were very dull with less than 50% black on their head and back (although none resembled females). The median values for the percentage of adult-like feathers on the head, back, rump, and breast ranged from 90 to 95%, although the median for black on the shoulder was only 80%. About half of the birds had replaced all their rectrices, a few had replaced none of them, and the remainder retained 1–10 juvenal tail feathers.

Overall, there was a significant tendency for brighter individuals to arrive earlier, as indicated by negative correlations between capture date and the amount of adult plumage for all six characters measured, two of which were significant (percent white on rump, $r_s = -0.29$, $P = 0.02$, $n = 62$; and relative brightness of pink on the breast, $r_s = -0.26$, $P = 0.02$, $n = 80$). However, the correlations were not particularly strong, indicating that there was considerable variation in arrival dates for birds of similar brightness.

As noted above, young males were significantly smaller than adults. However, within each age class, there was no apparent relationship between size and arrival date (yearling wing length: $r = 0.05$, $P = 0.4$, n

TABLE 2. First captures and mean arrival times of yearling (SY) and adult (ASY) male Rose-breasted Grosbeaks on spring migration at Prince Edward Point, Ontario (all dates are in May).

Year	Number of birds		First date		Mean date		Comparison of dates ^a
	ASY	SY	ASY	SY	ASY	SY	
1976	7	14	10	11	16.0	18.3	n.s.
1977	36	35	5	12	14.3	16.7	$P < 0.002$
1978	38	26	9	11	15.9	17.0	n.s.
1979	9	31	14	13	17.0	18.8	n.s.
1980	24	74	5	11	16.8	19.9	$P < 0.0001$
1981	8	7	13	18	16.1	20.3	n.s.
1988	18	42	8	8	14.6	15.7	n.s.
1989	48	81	1	10	15.4	18.1	$P < 0.0001$
Total	188	310	1	8	15.5	18.1	$P < 0.0001$

^a Wilcoxon-Mann-Whitney U -test.

= 307; yearling body mass: $r = 0.02$, $P = 0.7$, $n = 236$; adult wing length: $r = -0.09$, $P = 0.23$, $n = 187$; adult body mass: $r = 0.06$, $P = 0.5$, $n = 118$).

Wintering distribution of males and females.—Although more than 68,000 Rose-breasted Grosbeaks have been banded in North America (up to the end of 1986), only 20 birds of known sex (10 males and 10 females) have been recovered on the wintering grounds between the months of November and February. The recovery locations ranged from southern Mexico through northern Columbia and Venezuela. The recovery latitudes of males ranged from 6°20'N to 18°0'N, while those of females ranged from 8°0'N to 14°30'N. While the two most northerly records were males, there was no significant difference between the mean recovery latitudes of males (13°10'N) and those of females (12°50'N; Wilcoxon $U = 57.5$, $P > 0.6$).

DISCUSSION

Overall, this study has shown that male Rose-breasted Grosbeaks arrive earlier than females, in common with most other passerines, and contrary to the findings of Weir (1989). These results highlight the difficulties of using first arrival dates to analyze migration timing, and the advantages of quantitative banding data for this purpose. Nevertheless, the difference in mean arrival dates between the sexes was only 1.1 d, less than has been reported for other passerines, such as paruline warblers (Francis and Cooke 1986). The small difference could mean that male grosbeaks experience relatively less intrasexual competition than other species, or that ecological constraints prevent them from arriving early. Alternatively, females may also experience strong intrasexual competition, a hypothesis supported by Dunham's (1966) observations that adult female Rose-breasted Grosbeaks actively defended territories against other females on breeding grounds in New York. However, Dunham found that the first females arrived "several days" after the first males.

Differences in arrival dates between age classes of males may partly explain the discrepancy between Dunham's observations and ours. Whereas Dunham did not report the age of his males, he did record many aspects of variation in plumage among males without mentioning differences in primary color. This suggests that all of his breeding males were adults. In a study of Black-headed Grosbeaks in Arizona, Hill (1988) also found that most breeding males, especially in good quality territories, were adults. In our study the difference between adult males and females (of all ages) was about three days, which is similar to that for other passerines (Francis and Cooke 1986). Of course, if only adults among females are breeding, then it would be appropriate to compare adults of both sexes, which would reduce the difference in arrival dates. Even if SY females do breed, the evidence that adult females arrive earlier suggests that adults will get first choice of territories.

If few SY males are able to obtain territories, this may explain their late arrival relative to ASY males. There may be little advantage to arriving until after the ASY males have settled, and the vacant territories, if any, are apparent. Adult males may benefit by arriving early for two reasons. Although previous residents are usually able to reclaim a territory even if it is already occupied, the cost of obtaining and holding the territory increases with time and can result in greatly escalated fights (Jakobsson 1988). In addition, early arrival may result in early pairing (Jakobsson 1988), which could both increase the chances of obtaining a mate, and advance the date of breeding. Several studies have shown that early nesting results in greater reproductive success (Price et al. 1988).

The early arrival of brighter SY males suggests that they may be more likely to obtain territories, as was found by Hill (1988) for Black-headed Grosbeaks. If bright individuals are more likely to obtain territories, why are some individuals less bright? Dull birds were generally those with the least extensive pre-alternate molt. They may have been competitively inferior individuals that were unable to obtain sufficient nutrition on the wintering grounds for a complete molt. Thus dull plumage may be an epiphenomenon of poor condition. Dull plumage may also serve as a signal of subordination, reducing aggression from territorial males on the breeding grounds (Lyon and Montgomerie 1986), although Dunham (1966) found that singing behavior was the main signal provoking aggressiveness in grosbeaks. Finally, second-year plumage may be correlated with variation in plumage brightness that has been observed within adult males (Smith 1966). If so, this could indicate that grosbeaks of different plumages use alternative reproductive tactics, as has been demonstrated for Yellow Warblers (*Dendroica petechia*, Studd and Robertson 1985). Further data are required to test these hypotheses.

While several studies have found that males tend to winter farther north than females (reviewed in Gauthreaux 1982), few have examined species that winter in the Neotropics. Sexual differences in habitat preference have been found in some warblers (Lynch et al. 1985) which could lead to geographic segregation. Pearson (1980) found some evidence to

suggest that adult male Summer Tanagers (*Piranga rubra*), a neotropical migrant, winter farther north than females, but the data were not conclusive. In this study, we found no evidence for sexual differences in wintering grounds of Rose-breasted Grosbeaks. However, while our data indicate that the sexes overlap extensively in wintering ranges, the number of recoveries was not adequate to detect small differences in the center of distribution for each sex.

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NORTH AMERICAN BLUEBIRD SOCIETY RESEARCH GRANT AWARDS 1990

The North American Bluebird Society is pleased to announce the presentation of the seventh annual research grant awards. The 1990 recipients are as follows:

BLUEBIRD GRANTS

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Topic: Field tests of acceptance of Eastern Bluebirds of nest boxes which deter raccoon predation.

GENERAL GRANTS

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STUDENT GRANTS

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Topic: Parental investment and the maintenance of monogamy in Eastern Bluebirds.

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