# ARRIVAL TIME FROM SPRING MIGRATION IN MALE PIED FLYCATCHERS: INDIVIDUAL CONSISTENCY AND FAMILIAL RESEMBLANCE[1]

JAIME POTTI

*Departamento de Biología Animal, Universidad de Alcalá, E-28871 Alcalá de Henares (Madrid), Spain,*
*e-mail: bnjps@bioani.alcala.es*

*Abstract.* The timing of arrival from spring migration was studied in 4 years for male Pied Flycatchers (*Ficedula hypoleuca*) in central Spain. Heritability and repeatability analyses were performed at several levels of familial resemblance and male age in order to determine whether arrival times are consistent within individuals between years and are similar between relatives. Oldest males arrived earlier. Arrival time explained much of the variation in laying time and number of young fledged. Age-independent variation in wing length also affected arrival date, the males with longest wings settling earlier. Arrival times were not repeatable within individuals across years and were not similar between relatives (parents-sons, full-sibs). Although genetic variation may exist in departure dates of long-distance migrant birds, the close connection of an early arrival to high reproductive success may have depleted genetic variation in arrival time. In addition, environmental variation probably is too high to detect significant heritability in arrival times without very large sample sizes.

*Key words: age, Ficedula hypoleuca, heritability, migration, Pied Flycatcher, repeatability.*

## INTRODUCTION

Each year migratory birds must find, occupy, and defend a breeding territory on their arrival from winter quarters. Among passerines, a common pattern is for males to arrive earlier than females, most likely due to within-sex competition for access to resources vital for reproduction, and older birds arrive earlier than younger ones (Francis and Cooke 1986, Hill 1989, Lozano et al. 1996). Early arrival at the breeding sites increases reproductive fitness through more nest sites (Potti and Montalvo 1991a) or better resources (Slagsvold 1986, Aebischer et al. 1996), earlier pairing (Slagsvold and Lifjeld 1988, Potti and Montalvo 1991a) and, in promiscuous and/ or facultatively polygynous species, greater opportunity to attract additional females (Alatalo et al. 1981, Potti and Montalvo 1993). Early arrival enhances male and female breeding success which is accentuated by a widespread tendency for early breeders to have a greater chance to fledge and/or recruit more offspring (Hochachka 1990, Møller 1994, Aebischer et al. 1996).

Although much research has been conducted on intrinsic and extrinsic factors affecting bird migration, the evolutionary important question

whether components of migratory behavior in animals are heritable, and thus capable to respond to selection, has only recently come under study (Berthold 1991, Dingle 1994). Experimental work with captive European Blackcaps (*Sylvia atricapilla*) has shown that some components of the migratory syndrome, such as migratory restlessness (*Zugunruhe*) or migratory direction, are inherited and are probably polygenic traits with threshold effects (Berthold 1991, Pulido et al. 1996).

Data on individual (ontogenetic) and familial variation in migratory behavior in wild bird populations are scant (Rees 1989) and hard to obtain, due to high dispersal, low site fidelity, short life spans, and long-term work required. Here, I report data on one component of migratory behavior, the timing of arrival of males on the breeding grounds, that were obtained across four years for a population of Pied Flycatchers (*Ficedula hypoleuca*). Pied Flycatchers are small (~ 12 g) long-distance migrants overwintering south of the Sahara and breeding across the western Palearctic (Lundberg and Alatalo 1992). I investigate whether there exist individual consistency or stability (repeatability) and familial resemblance (heritability) of male arrival time. I found no clear evidence that arrival date of males is a heritable trait in this species.

## METHODS

I studied the arrival times of male Pied Flycatchers through the spring and early summer from 1988–1991 in a population breeding in nestboxes in a mature deciduous (*Quercus pyrenaica*) oakwood in central Spain (Potti and Montalvo 1991a). The area was censused daily from mid April onwards to document exact arrival dates and identity of males. Soon after arrival, males start to sing at one or more nestboxes, making census of males a relatively easy task. Since 1987 most arriving males were previously color-banded, allowing their quick identification. The majority of remaining males only wore a metal band or were unbanded and were distinguished until capture by age-distinctive plumage traits (Potti and Montalvo 1991a), by idiosyncratic features of their plumage color (Potti and Merino 1995), by the size and form of the white patch on the forehead (Potti and Montalvo 1991a), or by the position of a metal band put on them as a fledgling in previous years (since 1984). It is very rare for a Pied Flycatcher to lose its preferred nestbox to a conspecific or interspecific competitor and, when this occurred, the same male was usually observed again singing in a neighbor nestbox. Hence, it is likely that few errors were made in the *a posteriori* assignment of arrival times to previously unbanded birds.

Males were captured inside their nestboxes while feeding nestlings. All birds were individually marked with color bands and aged as yearlings or older (Karlsson et al. 1986, Potti and Montalvo 1991a), and their wing length (flattened chord; Svensson 1992) was measured. Immigrant birds aged as "older" at first capture were assigned a minimum age of two years (Potti and Montalvo 1991b). The laying date of a particular nest was defined as the day the first egg in the clutch was laid. Laying dates and number of young fledged varied across years and were standardized by using the deviations of individual values from median annual values (laying date) or the residuals (deviations from calculated group averages) of an analysis-of-variance (ANOVA) in relation to study year (young fledged). To calculate repeatabilities (see below) of laying dates in nests of individual males in different years, I used the entire data set from my long-term population study, comprising breeding records from 1987 to 1995.

Arrival times were standardized within years by subtracting data points from median annual values and then transforming them to $z$-scores with 0 mean and unit variance (hereafter standardized arrival time). I first estimated familial resemblance in arrival times by calculating the repeatability. Repeatability is estimated by making repeated (annual, in this case) measures of a sample of individuals and then calculating the ratio of the among-individual variance to the sum of both the among-individual and within-individual variances (the intraclass correlation coefficient; Zar 1996). Components of variance are estimated by one-way ANOVA. A high repeatability indicates that variation within individuals is much smaller than among individuals. If measurements within individuals are very different, repeatability is low.

I used linear regression to compute heritability ($h^2$) of the arrival times of sons on those of their presumptive fathers. Twice the slope of the regression estimates the heritability (Falconer 1986); the standard error (SE) of the regression slope also was doubled. Arrival times of full sibs also were compared using one-way ANOVA, as in the analysis of repeatability. Heritability was computed as twice the intraclass correlation coefficient (Falconer 1986). In the analyses of parent-son resemblance, when two or more data points for a particular parent or family (sibships) were available, I used averages of standardized data to avoid pseudoreplication.

To estimate the power (Thomas and Juanes 1996, Zar 1996) of heritability estimates, that is, the probability of correctly rejecting the null hypothesis on absence of heritability given a specified significance level (alpha = 0.05) and sample sizes, as well as the sample sizes needed to detect heritabilities of specified magnitude with a given power, I used program PS of Dupont and Plummer (1990) for linear regression (available as freeware on the Internet; ftp://ftp.vanderbilt.edu/pub/biostat/ps.zip). The power of analyses of repeatability was estimated by means of the Pearson correlation coefficient, using only males with arrival dates known in two years. Statistical tests are two-tailed.

## RESULTS

The first males arrived on the study area in the third week of April; successfully pairing males can arrive as late as 12 June (Potti and Montalvo 1991a). Arrival times of males gradually ad-
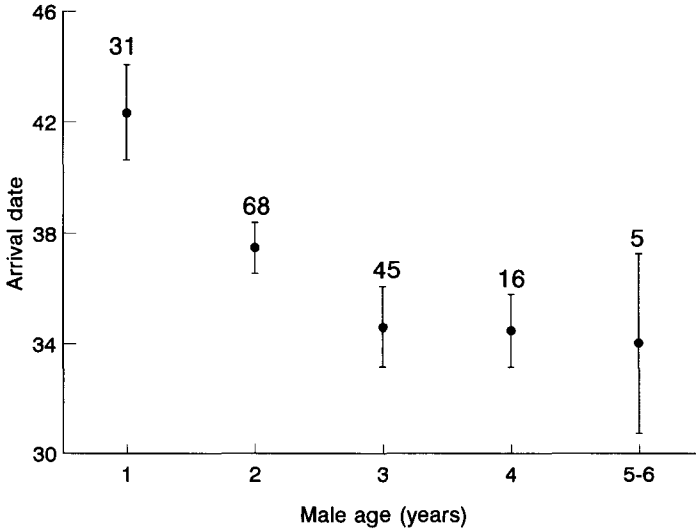
FIGURE 1. Arrival times (means ± SE) of male Pied Flycatchers in relation to age. Date 30 is April 30. Numbers above lines are sample sizes.

vanced with increasing age (Fig. 1), although significant differences were apparent only between yearlings and older birds (Tukey *a posteriori* tests). Standardized arrival times were earlier for longer-winged males ($r = -0.30$, $n = 164$, $P < 0.001$), which might be confounded by age due to the significantly longer wings of older birds (Alatalo et al. 1984a). However, arrival time was earliest for males with longer wings even after controlling for the effect of age (partial correlation, $r = -0.21$, $P = 0.006$). This indicates that the effects of increasing age and wing size on an earlier arrival date were at least partially independent.

Being early was advantageous for male fitness as the number of young fledged was lower for males that arrived later in the season ($r = -0.38$, $n = 138$, $P < 0.001$, Fig. 2). There was no cost in being too early, as indicated by the nonsignificant quadratic regression term (quadratic coefficient $= -0.002$, $P > 0.10$; Fig. 2).

In order to remove variation in arrival times due to age, I further standardized arrival times for familial comparisons by using the residuals of an ANOVA of standardized arrival time (see Methods) in relation to male age (hereafter residual arrival times). Residual scores of arrival time were normally distributed (Kolmogorov-Smirnov tests, $P > 0.25$) and their distribution did not differ between young and older birds (Kolmogorov-Smirnov two-sample tests, $P =$ 0.22, $n = 31$ and 133 birds, respectively), nor between presumptive fathers and sons within the subsample of familial data ($P = 0.21$, $n = 22$ families).

I obtained repeated records of arrival time for 39 males, 32 of which had 2 records in different, usually successive years, 4 males had 3 annual records, and 3 males had 4 records. The repeatability ($R$) of arrival times was very low and not significant ($R = 0.04$; mean number of data per individual, $n_0 = 2.25$, $F_{38,87} = 1.10$, $P > 0.30$). The same was true when standardized ($R = 0.08$; $F_{38,87} = 1.19$, $P > 0.25$) and residual arrival times ($R = 0.08$; $F_{38,87} = 1.21$, $P = 0.27$; power $> 0.10$) were used. In order to remove any potential confounding effects of variation in age and arrival time among males, I selected, for further confirmatory analysis, repeated records of arrival only for males 2 or more years old. The repeatability of residual arrival time in this data set was again nonsignificant ($R = 0.09$; $n_0 = 2.18$, $F_{26,58} = 1.22$, $P > 0.25$), indicating that individual adult males are not consistent in the relative timing of their arrivals on the breeding grounds as they age.

There were 32 male sons in 22 families for which one or more arrival times of the sons and their presumptive male parents were known. Although the relationship was positive, the heritability of residual arrival times did not differ significantly from zero ($h^2 = 0.34 \pm 0.73$, $P >$
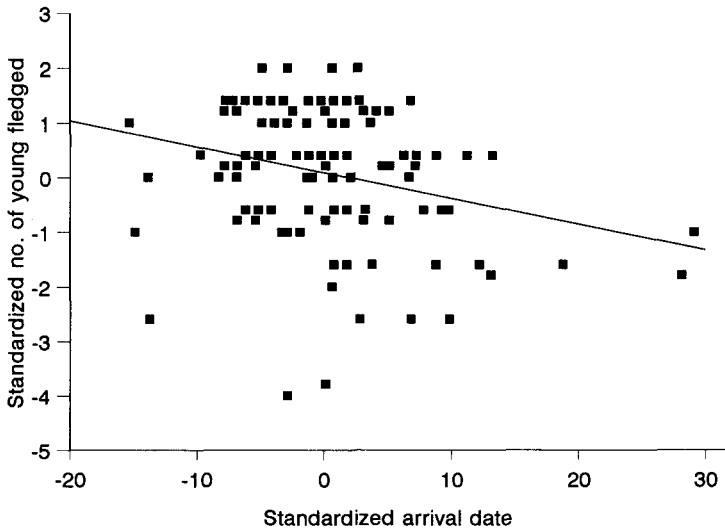
FIGURE 2. Relation between standardized date of arrival of male Pied Flycatchers and standardized number of young fledged (see Methods for standardized computations). The line is the least-squares regression line (regression function: $y = 0.11 - 0.05x$).

0.60, $n = 22$, Fig. 3). However, given the large variances of arrival dates, the power of this test at the customary alpha level of 0.05 is very low (power = 0.07). Furthermore, that value of $h^2$ is entirely due to the "pull" of an outlier (Fig. 3); when this point is excluded a "no sense," negative heritability is obtained ($h^2 = -0.50 \pm 1.00$, $P > 0.60$, $n = 21$).

There were 9 families for which the arrival times of 2 or 3 (presumptive) full-sib males were known. The heritability of residual arrival dates calculated on the basis of (presumptive) full-sib resemblance was $h^2 = 0.08$ ($n_0 = 2.25$, $F_{8,19} = 1.09$, $P > 0.40$).

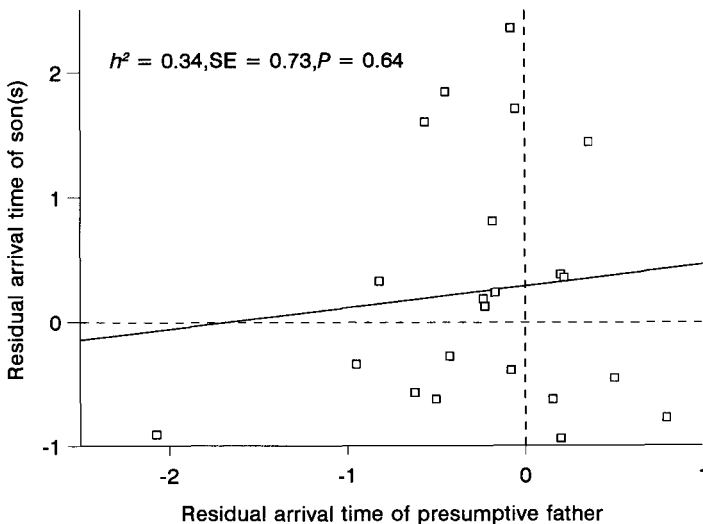As there were more data available on laying dates, which are closely related to male arrival



FIGURE 3. Relationship between standardized arrival times of male Pied Flycatchers and their presumptive sons (see Methods for standardized computations). The line is the least-squares regression line (regression function: $y = 0.29 + 0.17x$).

and pairing dates (Potti and Montalvo 1991a), I investigated whether laying times for 142 males with 2–6 breeding records were repeatable. The repeatability was −0.00 ($F_{141,347}$ = 0.99, $P$ > 0.50) after standardizing the data set for significant variation with respect to year and female and male ages by using residuals of a factorial ANOVA. I also correlated the average residual laying dates in nests of sons with those of their presumptive male parents. The resemblance in laying date in nests of male parents and male offspring was nil ($r$ = −0.01, $n$ = 74, $P$ > 0.90; power = 0.05) and the same was true when the comparison was made with average residual laying dates of their mothers (controlling for significant variation of laying date with female age; $r$ = −0.07, $P$ > 0.70, $n$ = 103 males in 71 families; power = 0.06). Hence, there is no evidence that arrival and laying times may be both repeatable or heritable in male Pied Flycatchers. However, the chances to correctly reject the null hypothesis of no heritability of male arrival and laying dates were very low (power = 0.05–0.12).

## DISCUSSION

I have presented what to my knowledge are the first data obtained on familial resemblance in timing of arrival to the breeding sites in a long-distance migrant passerine. The estimates were not confounded by the social environment (Rees 1989) because Pied Flycatchers live solitary lives after they become independent of their parents, and they migrate alone (Lundberg and Alatalo 1992). Using a large data set, Rees (1989) showed that arrival and departure times of wintering social Bewick's Swans (*Cygnus columbianus* [*bewickii*]) had a slight heritability ($h^2$ = 0.10–0.19), although in this case the estimate could to some degree be confounded by the social habits of swans and their tendency to migrate in groups, hence cultural, not genetic transmission. This problem did not exist in my study, and I still was unable to find evidence for genetic variation in the arrival times from spring migration in male Pied Flycatchers.

One may argue that lack of father-son resemblance in arrival dates may be due to genetic analyses being plagued by a high frequency of extra-pair fertilizations (EPF), which are known to occur in the Pied Flycatcher at variable rates (Lifjeld et al. 1991, Gelter and Tegelström 1992). No DNA fingerprinting estimates of ge-

netic parentage are available for my population and, unfortunately, the method to compute EPF rates on the basis of differences in heritability estimates of morphological traits using mother- and father-on-offspring regressions (Alatalo et al. 1984a) has proven unreliable to that end (Hasselquist et al. 1994, Potti and Merino 1994). However, misassigned parentage is not a problem for repeatability estimates, which indicated an overall inconstancy of male arrival and laying dates, and hence a likely absence of detectable genetic variation (Boake 1989). Checking for the existence of repeatability is a first step in proposed protocols to detect genetic variation because repeatability sets an upper limit to the heritability of a trait, which cannot be larger than the former (Falconer 1986, Boag and van Noordwijk 1987). In addition, because genetic variation within individuals is absent, EPFs are not a confounding factor in the computations of repeatability, although they certainly are a problem for the quantification of heritability. In spite of this, the consistency of nonsignificant repeatability and heritability estimates in this study indicates that, whatever may be the rate of EPFs in my population, genetic variation for arrival time, if present, must be low.

There are, however, further reasons to be cautious about the absence of genetic variation, because it may exist but be masked by genotype-environment interactions, which are likely to be present in such a complex "trait" as arrival date. Arrival times must depend to some degree on distances migrated and departure dates from winter quarters, which in turn depend upon environmental variables, including photoperiod and weather conditions there. In addition, the predictably high environmental variation met by the birds while on passage in their migratory journey, and the likely important roles played in migration performance by bird age and previous experience with both the migration route and the area (Montalvo and Potti 1992, Cantos and Tellería 1994), may sum up to a high stochastic variance in timing of arrival (Aebischer et al. 1996). Body condition (Arvidsson and Neergard 1991), including lack of infection by hematozoan parasites (Rätti et al. 1993), and body size (wing and first primary lengths; Alatalo et al 1984b, Potti and Montalvo 1991a) also are related to early arrival in at least some bird species. For instance, male flycatchers with the longest wings arrived earlier independently of their

age, which may be interpreted as evidence that a size constraint may operate on migration speed and counters the argument that late arrivals by young, small-winged birds are due to their relative inexperience with the migratory journey.

An analytical problem in this study was the low power of statistical tests to detect significant heritability (Falconer 1986, Arnold 1994). Power calculations indicate that very large sample sizes are necessary to detect a low heritability with the sample variance observed. For example, to detect a low heritability of, say, 0.10 (regression slope = 0.05) with a reasonably high (Thomas and Juanes 1996) power of 0.80 (that is, an 80% chance of getting a significant result given that the null hypothesis of no heritability is false), it would be necessary to have data on arrival dates for 641 families, implying about 32 years of data collection at the current recruitment rate in my population (Potti and Montalvo 1991b). If heritability of arrival date was larger, say 0.50 (a common heritability for morphological traits, Boag and van Noordwijk 1987), then 335 father-son pairs (about 17 years of field work) would have to be sampled to detect it at alpha = 0.05 and power = 0.80. Similar computations for detecting a low ($h^2$ = 0.10) heritability of "male laying dates" result in unwieldly figures (> 13,000 and > 295,000 data pairs, using laying dates of mother and father Pied Flycatchers, respectively).

The fact that male arrival time in spring is closely connected to male fitness in the Pied Flycatcher (Fig. 2) might be taken as a priori evidence in support of a predictable absence of genetic variation in this characteristic. Genetic variance might have been depleted by the close association of early breeding to fitness due to strong and constant selection, with all remaining variation being environmentally caused ("Fisher's fundamental theorem;" Mousseau and Roff 1987). The evidence presented here and background information on this population are consistent with this interpretation. An early date of breeding is the most important determinant of recruitment in this population (Potti and Montalvo 1991b; unpubl. data), imposing a strong selection pressure to settle and breed early. Alternatively, as discussed above, low heritability of arrival date may be due to the predominant importance of environmental variables affecting it (Price and Schluter 1991), i.e., arrival times may be subject to all the variation in the traits

that affect it plus additional environmental variation, such that a low heritability is to be expected (Price and Schluter 1991). For instance, wing length seems to retain genetic variance in this population (around 0.50; unpubl. data), whereas corresponding variation in arrival time, one of its correlates, is almost undetectable. This illustrates that the link from genes to wing length to a life-history trait such as arrival date is long: much environmental variance is added at each step in the path of morphological to life-history traits, so that even though there may be a genetic component to arrival date via its connection with heritable body traits, this must be very small (Price and Schluter 1991, Roff 1997). It is not possible to distinguish between the "exhaustion of genetic variance hypothesis" and the "environmental noise hypothesis" with the data at hand and, most likely, both may be true.

Genetic variation may underlie the proximate control of departure dates in long-distance migrants, as well as in birds migrating shorter distances (Berthold 1991), but still be undetectable with arrival times to the breeding grounds. Individuals may not be consistent in their time of arrival from one year to another because complex interactions between environmental factors affecting arrival date and migration performance. Demonstrating among-population genetic variation in major traits, such as circannual rhythms (Berthold 1991, Pulido et al. 1996), can help to explain within- and between-species variation in the urge to migrate and hence on departure dates to breeding or wintering areas (Ellegren 1990). However, environmental variation will likely make it difficult to demonstrate within-population genetic variation in arrival times of migrant birds in natural settings.

## ACKNOWLEDGMENTS

## LITERATURE CITED

AEBISCHER, A., N. PERRIN, M. KRIEG, J. STUDER, AND D. R. MEYER. 1996. The role of territory choice, mate choice and arrival date on breeding success in the Savi's Warbler Locustella luscinioides. J. Avian Biol. 27:143–152.

ALATALO, R. V., A. CARLSON, A. LUNDBERG, AND S. ULF-STRAND. 1981. The conflict between male polygamy

and female monogamy: the case of the Pied Flycatcher *Ficedula hypoleuca.* Am. Nat. 117:738–753.

ALATALO, R. V., L. GUSTAFSSON, AND A. LUNDBERG 1984a. High frequency of cuckoldry in Pied and Collared Flycatchers. Oikos 42:41–47.

ALATALO, R. V., L. GUSTAFSSON, AND A. LUNDBERG. 1984b. Why do young passerines have shorter wings than older birds? Ibis 126:410–415.

ARNOLD, S. J. 1994. Multivariate inheritance and evolution: a review of concepts, p. 17–48. *In* C. R. B. Boake [ed.], Quantitative genetic studies of behavioral evolution. Univ. Chicago Press, Chicago, IL.

ARVIDSSON, B. L., AND R. NEERGARD. 1991. Mate choice in the Willow Warbler—a field experiment. Behav. Ecol. Sociobiol. 29:225–229.

BERTHOLD, P. 1991. Genetic control of migratory behaviour in birds. Trends Ecol. Evol. 6:254–257.

BOAG, P. T., AND A. J. VAN NOORDWIJK. 1987. Quantitative genetics, p. 45–78. *In* F. Cooke and P. A. Buckley [eds.], Avian genetics. Academic Press, London.

BOAKE, C. R. B. 1989. Repeatability: its role in evolutionary studies of mating behavior. Evol. Ecol. 3: 173–182.

CANTOS, F. J., AND J. L. TELLERÍA. 1994. Stopover site fidelity of four migrant warblers in the Iberian peninsula. J. Avian Biol. 25:131–134.

DINGLE, H. 1994. Genetic analyses of animal migration. p. 145–164. In C. R. B. Boake, [ed.], Quantitative genetic studies of behavioral evolution. Univ. Chicago Press, Chicago.

DUPONT, W. D., AND W. D. PLUMMER JR. 1990. Power and sample size calculations: a review and computer program. Controlled Clinical Trials 11:116–128.

ELLEGREN, H. 1990. Timing of autumn migration in Bluethroats *Luscinia s. svecica* depends on timing of breeding. Ornis Fennica 67:13–17.

FALCONER D. S. 1986. Introducción a la genética cuantitativa. Cecsa, Mexico D.F., Mexico.

FRANCIS, C. M., AND F. COOKE. 1986. Differential timing of spring migration in wood warblers. Auk 103:548–556.

GELTER, H. P., AND H. TEGELSTRÖM. 1992. High frequency of extra-pair paternity in Swedish pied flycatchers revealed by allozyme electrophoresis and DNA fingerprinting. Behav. Ecol. Sociobiol. 31:1–7.

GWINNER, E. 1977. Circannual rhythms in bird migration. Annu. Rev. Ecol. Syst. 8:381–405.

HASSELQUIST, D., S. BENSCH, AND T. VON SCHANTZ. 1994. Estimating cuckoldry in birds: the heritability method and DNA fingerprinting give different results. Oikos 72:173–178.

HILL, G. E. 1989. Late spring arrival and dull nuptial plumage: aggression avoidance by yearling males? Anim. Behav. 37:665–673.

HOCHACHKA, W. 1990. Seasonal decline in reproductive performance of Song Sparrows. Ecology 71:1279–1288.

KARLSSON L., K. PERSSON, AND G. WALINDER. 1986. Ageing and sexing in Pied Flycatchers *Ficedula hypoleuca.* Vår Fågelvärld 45:131–146.

LIFJELD, J. T., T. SLAGSVOLD, AND H. M. LAMPE. 1991. Low frequency of extra-pair paternity in pied flycatchers revealed by DNA fingerprinting. Behav. Ecol. Sociobiol. 29:95–101.

LOZANO, G. A., S. PERREAULT, AND R. E. LEMON. 1996. Age, arrival date and reproductive success of male American Redstarts *Setophaga ruticilla.* J. Avian Biol. 27:164–170.

LUNDBERG, A., AND R. V. ALATALO. 1992. The Pied Flycatcher. T. & A. D. Poyser, London.

MØLLER, A. P. 1994. Phenotype-dependent arrival time and its consequences in a migratory bird. Behav. Ecol. Sociobiol. 35:115–122.

MONTALVO, S., AND J. POTTI. 1992. Breeding dispersal in Spanish Pied *Flycatchers Ficedula hypoleuca.* Ornis Scand. 23:491–498.

MOUSSEAU, T. A., AND D. A. ROFF. 1987. Natural selection and the heritability of fitness components. Heredity 59:181–197.

POTTI, J., AND S. MERINO. 1994. Heritability estimates and maternal effects on tarsus length in Pied Flycatchers, *Ficedula hypoleuca.* Oecologia 100:331–338.

POTTI, J., AND S. MERINO. 1995. Some male Pied Flycatchers *Ficedula hypoleuca* in Iberia become collared with age. Ibis 137:405–409.

POTTI, J., AND S. MONTALVO. 1991a. Male arrival and female mate choice in Pied Flycatchers *Ficedula hypoleuca* in central Spain. Ornis Scand. 22:45–54.

POTTI, J., AND S. MONTALVO. 1991b. Return rate, age at first breeding and natal dispersal of Pied Flycatchers *Ficedula hypoleuca* in central Spain. Ardea 79:419–428.

POTTI J., AND S. MONTALVO. 1993. Polygyny in Spanish Pied Flycatchers *Ficedula hypoleuca.* Bird Study 40: 31–37.

PRICE, T., AND D. SCHLUTER. 1991. On the low heritability of life-history traits. Evolution 45:853–861.

PULIDO, F., P. BERTHOLD, AND A. J. VAN NOORDWIJK. 1996. Frequency of migrants and migratory activity are genetically correlated in a bird population: evolutionary implications. Proc. Natl. Acad. Sci. 93:14642–14647.

RÄTTI, O., R. DUFVA, AND R. V. ALATALO. 1993. Blood parasites and male fitness in the Pied Flycatcher. Oecologia 96:410–414.

REES, E. C. 1989. Consistency in the timing of migration for individual Bewick's Swans. Anim. Behav. 38: 384–393.

ROFF, D. A. 1997. Evolutionary quantitative genetics. Chapman and Hall, New York.

SLAGSVOLD, T. 1986. Nest settlement by the Pied Flycatcher. Does the female choose her mate for the quality of his house or himself? Ornis Scand. 17: 210–220.

SLAGSVOLD, T., AND J. T. LIFJELD. 1988. Plumage colour and sexual selection in the Pied Flycatcher *Ficedula hypoleuca.* Anim. Behav. 36:395–407.

SVENSSON, L. 1992. Identification guide to European passerines. Svensson, Stockholm.

THOMAS, L., AND F. JUANES. 1996. The importance of statistical power analysis: an example from *Animal Behaviour.* Anim. Behav. 52:856–859.

ZAR, J. H. 1996. Biostatistical analysis. 3rd ed. Prentice Hall, Englewood Cliffs, NJ.