

SEXUAL SIZE DIMORPHISM AND SOURCES OF VARIATION IN THE GROWTH OF WING FEATHERS IN NESTLING PIED FLYCATCHERS (*FICEDULA HYPOLEUCA*)

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SUMMARY.—*Sexual size dimorphism and sources of variation in the growth of wing feathers in nestling Pied Flycatchers Ficedula hypoleuca.* I report a 5-year field study of the growth of flight feathers, as scored by the lengths of the wing and first-primary feather, of Pied Flycatcher nestlings when they were 13 days old. Further evidence to that already published for gender differences in growth of different traits (fledgling tarsus length, mass and body condition) being already present early in the ontogeny in a passerine species with slight adult size dimorphism is presented. Familial and environmental sources of resemblance in both feather traits are suggested by highly significant correlations of feather growth within siblings, and within individual nestboxes independently of the identity of parents breeding therein. Retrospective analyses of gender differences in feather growth at the nest for a sample of recruited young show that feather traits of female fledglings were, on average, larger than those of males. However, the difference is reversed at recruitment due to compensatory gains in males that may be related with positive directional selection on wing length in males related to an early settlement in spring in this long-distance migrant.

Key words: *Ficedula hypoleuca*, growth, nest ectoparasites, Pied Flycatcher, sex differences, sexual size dimorphism, wing length.

RESUMEN.—*Dimorfismo sexual en el tamaño y fuentes de variación influyentes sobre el crecimiento de las plumas del ala en volanderos de Papamoscas Cerrojillo Ficedula hypoleuca.* Se estudia durante cinco años la longitud del ala y de la primera pluma primaria, como índices de crecimiento del plumaje de vuelo, en pollos de Papamoscas Cerrojillo de 13 días de edad. El trabajo aporta evidencia añadida a la ya conocida previamente sobre la existencia de diferencias sexuales durante el crecimiento de algunos caracteres (tarso, peso y condición corporal de los pollos) desde la ontogenia temprana en un paseriforme con ligero dimorfismo sexual en el tamaño. Se demuestra la existencia de fuentes de parecido en el crecimiento de las plumas alares debidas a los genes, al ambiente común y, presumiblemente, a la calidad del territorio. Este último aspecto lo sugiere el hecho de que el crecimiento del ala de diferentes nidadas en diferentes años fue repetible para nidales concretos, independientemente de los adultos que criaron en ellos. Se realizan análisis retrospectivos del crecimiento del plumaje para una amplia muestra de pollos que fueron recuperados (y sexados) como adultos reproductores. Las hembras tuvieron las alas más largas que los machos a los 13 días de vida, pero la diferencia se invierte en la vida adulta, probablemente debido a la selección direccional positiva sobre la longitud del ala en los machos, que se relaciona con las ventajas derivadas de un asentamiento temprano de la migración primavera en este migrante de larga distancia.

Palabras clave: crecimiento, diferencias sexuales, dimorfismo sexual en el tamaño, ectoparasitismo de nido, *Ficedula hypoleuca*, Papamoscas Cerrojillo, tamaño del ala.

INTRODUCTION

Much evidence has accumulated in the last few years on the role played by the environment experienced during early life in shaping patterns of variation in morphological and life-history traits in animals (Boag, 1987; van Noordwijk *et al.*, 1988; Larsson & Forslund, 1991; Haywood & Perrins, 1992; Bernardo, 1993, 1996; Hórák, 1994; Potti & Merino, 1996; de

Kogel, 1997; Merilä & Svensson, 1997; Lindström, 1999; Potti, 1999a, b). In birds, most of the information gathered to date has been based on recaptures of marked nestlings at the adult stage, sexing them by dimorphic plumages or differences in size and behaviour due to the difficulty, if not impossibility, of reliable sexing of nestlings in many species until recently. Novel approaches relying on molecular sexing techniques (Ellegren & Sheldon, 1997)

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are likely to overcome these limitations and to reveal additional examples of sex differences in growth rates at the nest. In addition to being of interest in their own right and for applied reasons (Williams, 1975; Short & Balaban, 1994; Zuk & McKean, 1996), sex differences in growth and survival are a central part in contemporary theories of sex-ratio variation and parental investment (e.g. Trivers, 1972, 1985; Clutton-Brock, 1991) and should accordingly be thoroughly investigated.

Previous research has shown that sex differences at the nestling stage exist in many strongly size-dimorphic species (Richner, 1991), and even in slightly size dimorphic bird species as, e.g., Great Tits *Parus major* (Smith *et al.*, 1989), Blue Tits *Parus caeruleus* (Merilä & Svensson, 1997) and Pied Flycatchers (Potti & Merino, 1996; Potti, 1999b). However, other studies have not found such a difference (Sheldon *et al.*, 1998). Conclusions derived from some of these studies are plagued by two facts. First, retrospective analyses are made after survival selection has occurred between fledgling and recruitment (Grant & Grant, 1989), which may confound interpretation, because it may occur that one gender has to be larger or be in better condition in order to survive than the other (Hochachka & Smith, 1991; Merilä & Svensson, 1997; Merilä *et al.*, 1997; Potti, 1999b). Second, most previous research has paid little attention to differential patterns of growth depending on the traits examined (Potti, 1999b).

Here I report a field study of the growth of flight feathers, as scored by the lengths of the wing and first-primary feather, of Pied Flycatcher *Ficedula hypoleuca* nestlings when near to fledge. My main objective was to see if there exist gender differences in early life in these indices of plumage growth and, if so, whether they translate into differences that persist through lifetime (Potti, 1999a; Thomas *et al.*, 1999). I present further evidence for between-sex differences in growth of different traits being already present early in the ontogeny in a passerine species with slight adult size dimorphism.

MATERIAL AND METHODS

Data were obtained during a long-term study of Pied Flycatchers in central Spain from 1987

to 1992 (Potti, 1999a). Pied Flycatchers are single-brooded, mostly socially monogamous (Potti & Montalvo, 1993), long-distance migrants that arrive at the study area from late April to May (Potti & Montalvo, 1991a; Potti, 1998a). Males do not defend foraging territories, but only one or more breeding holes and their close surroundings (Lundberg & Alatalo, 1992). All studied nests were in nestboxes which were cleaned after reproduction in all years (see Møller, 1989), although this had no effect on the prevalence of nest ectoparasites (Merino & Potti, 1996).

In the Pied Flycatcher, some males become polygynous and do not adequately attend their nestlings in some nests (Lundberg & Alatalo, 1992; Potti & Montalvo, 1993). This is reflected in undernourishment of nestlings and diminished growth of fledglings (Alatalo & Lundberg, 1986; Lifjeld & Slagsvold, 1989b) but, in my population, only for the offspring of secondary, not primary females (Potti & Montalvo, 1993). To eliminate this source of variation, all secondary nests were excluded from analyses.

All fledglings were ringed at day 13 post-hatch, day 1 being that of hatching of the majority of the brood. Wing length (flattened chord) and length of the first primary feather (counted in ascending order; Svensson, 1992) of fledglings were measured with a top ruler to the nearest 0.5 mm. While the wing length was measured in all years, first-primary length was measured only in 1987-1989. Mass (to the nearest 0.1 g) and tarsus length (to the nearest 0.01 mm) were also recorded (Potti, 1999a; Potti & Merino, 1994a). To control for the fact that young in a nest are not statistically independent (see below, and Results), I used within-nest averages of all measurements in the analyses of correlates of feather growth. No data were available on fledgling measurements in 1990 due to a heavy episode of predation by weasels *Mustela nivalis* (Potti & Merino, 1994b).

To see whether there exists a maternal effect on fledgling wing feather growth via egg size (Potti & Merino, 1994a), I related the average measurements of fledglings to the mean egg volume of the clutch from which these fledglings hatched. To this end, all eggs (range 3-8) were measured for maximum length (L) and breadth (B) and an average egg volume

(V , in cm^3) was calculated for each clutch using Hoyt's (1979) formula ($V = 0.51 L \times B^2$; Potti, 1993, 1999a).

Within-nest resemblances among young in a nest were used to estimate heritabilities by means of the intra-class correlation coefficient (R) of wing measurements using variance components from one-way ANOVAs with family as a factor (Sokal & Rohlf, 1981; Lessells & Boag, 1987). The intraclass correlation thus estimates the fraction of the total phenotypic variance attributable to factors causing resemblance between sibs of the same family. Assuming an absence of environmental effects on trait expression, twice the estimate of R gives the value of heritability (Falconer, 1986).

The sex of the nestlings was known only for those that recruited to the breeding population in later years, usually at one (females) or two years (males) of age (Potti & Montalvo, 1991b). Here I analyse the recruitment of fledglings from the 1987-1989 and 1991-1992 cohorts, which was followed until 1995. The birds were captured and identified while incubating (females) or feeding nestlings (all males, some females).

Adult wing and first-primary lengths are consistent across years (i.e. repeatable) in both males and females but nevertheless vary significantly with bird's age (range 1-8 years; J. Potti, unpublished data). To compare fledgling and adult lengths of feather traits I used mean adult wing length and first primary length recorded across lifetime (range 1-7 records per individual), as conclusions were the same when mean residual scores, after controlling for age by means of one-way ANOVAs, were used.

As an index of territory quality, I used an index of nestbox attractiveness over the period 1984-1990 (see Askenmo, 1984; Potti & Montalvo, 1991a, b), after which a major spatial rearrangement of nestboxes in the study area took place. Scoring of nestbox attractiveness was based on the frequency of nestbox occupation by Pied Flycatchers in relation to availability (i.e. excluding nestboxes occupied by other species) during the seven year period. Nestboxes were classified for the purposes of analyses into two classes, i.e. high and low quality, in relation to the median attractiveness score.

The wing feathers were not fully grown at the time of measurements, a fact that discouraged from estimating heritability by means of

parent-offspring regressions, which nevertheless have been presented elsewhere (Potti, 1999a). More indirect approaches were used here to demonstrate familial resemblance in indices of feather growth (see above), as well as to know whether territory quality has any influence on average fledgling feather growth that is independent of the parents breeding therein. To this end, I selected for analyses only those nestboxes which remained in the same spatial arrangement until 1990. In calculations of repeatability of wing length and first-primary, re-matings between birds that were paired in former years and re-occupations of nestboxes used in former years by either of the parents (Montalvo & Potti, 1992) were discarded in order to partially separate effects of parents from those due to habitat quality. Repeatability, i.e. consistency in measurements of feather growth, is estimated by making repeated (at yearly intervals in this case) records of average wing and first-primary lengths for the offspring reared in different years in the same nestboxes and then calculating the ratio of the among-subjects (nestboxes) variance to the sum of both the among-subjects and within-subjects variances (Falconer, 1989; Lessells & Boag, 1987). A high repeatability indicates that variation in average offspring's feather growth within nestboxes is lower than among different nestboxes.

To control for yearly variation in breeding dates, I used hatching dates standardised as deviations from yearly medians as an index of breeding phenology. To quantify ectoparasite abundance, I used categorical scores of mite (*Dermanyssus gallinoides*) abundance (low versus high) recorded on the day the measurements of fledglings were made. These scores were available only since 1988, and were highly predictive indices of intensities of mite infestations as shown by mite counts in Berlese funnels (Merino & Potti, 1995).

Statistics (Statsoft, 1996) are two-tailed. Means are given with 1 S.D.

RESULTS

At day 13 of age, wing length of fledglings was only $60.0 \pm 6\%$ ($n = 100$) and $63.8 \pm 6\%$ ($n = 87$) of the mean value for the same males and females measured as breeding adults, respectively. On the contrary, lengths of the first

primary feather had reached $92.9 \pm 5\%$ ($n = 68$) and $96.0 \pm 4\%$ ($n = 59$) of average adult length, for males and females, respectively. In both sexes, first primary feather length at fledgling was significantly related to the same trait when adult (Fig. 1; males: $r = 0.26$, $n = 68$; females: $r = 0.38$, $n = 59$, $P < 0.001$ in both). However, wing-length as an adult was not predicted by measurements taken at fledging (males: $r = 0.13$, $n = 100$, $P = 0.17$; females: $r = 0.00$, $n = 87$, $P = 0.97$).

Average within-brood fledgling wing and first-primary length were highly and significantly correlated ($r = 0.76$, $n = 120$, $P < 0.0001$), as well as with fledgling tarsus length ($r = 0.54$, $n = 295$ and $r = 0.52$, $n = 120$, respectively, $P < 0.0001$ in both). The correlations of feather traits with fledgling mass were significantly (or marginally so) weaker ($r = 0.42$, $n = 294$, and $r = 0.35$, $n = 119$, $P < 0.0001$, respectively; tests for differences between correlation coefficients: $P = 0.059$ and $P = 0.015$, respectively). Mean within-brood feather growth decreased with hatching date (Fig. 2). In addition, wing-length was the only measure-

ment taken at fledgling that decreased significantly with an increasing number of young in the nest ($r = -0.13$, $n = 295$, $P = 0.029$), although broods of two young also had reduced feather growth (Fig. 3). However, the length of the first primary feather was unrelated to the number of young in the nest ($r = -0.03$, $n = 120$, $P = 0.73$). Neither was there any relationship between maternal egg volume and average fledgling wing measurements ($r = 0.10$, $n = 169$, $P = 0.22$, and $r = 0.11$, $n = 80$, $P = 0.33$, for wing and first-primary length, respectively).

Within-nest resemblance in feather growth

Table 1 summarizes within-nest resemblance in feather growth. Intraclass correlation coefficients indicated a high resemblance between young in a nest in the indices of feather growth. Values of intraclass correlations transform to heritabilities of about 1.50 and 1.26, for wing and first-primary length, respectively. As heritability ranges from 0 to 1, these high values indicate that intraclass sibship correlations ove-

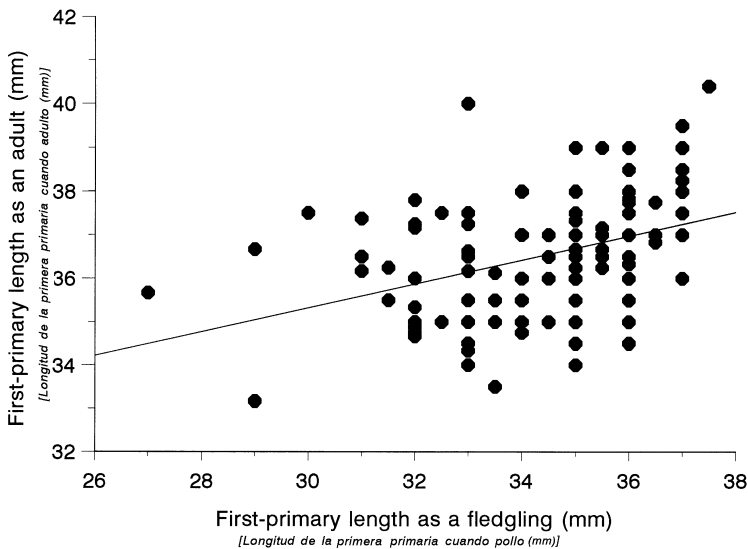


FIG. 1.—Relationship between length of the first-primary feather in the same individual measured in the nest and later as an adult. The least-squares regression line is shown. Note that some observations are hidden due to overlap of data points.

[Relación entre la longitud de la primera primaria de los mismos individuos medida cuando eran pollos en el nido y como adultos reproductores. Se muestra la línea de regresión de mínimos cuadrados; nótese el número de datos aparentemente menor al tamaño de muestra, debido al solapamiento de puntos.]

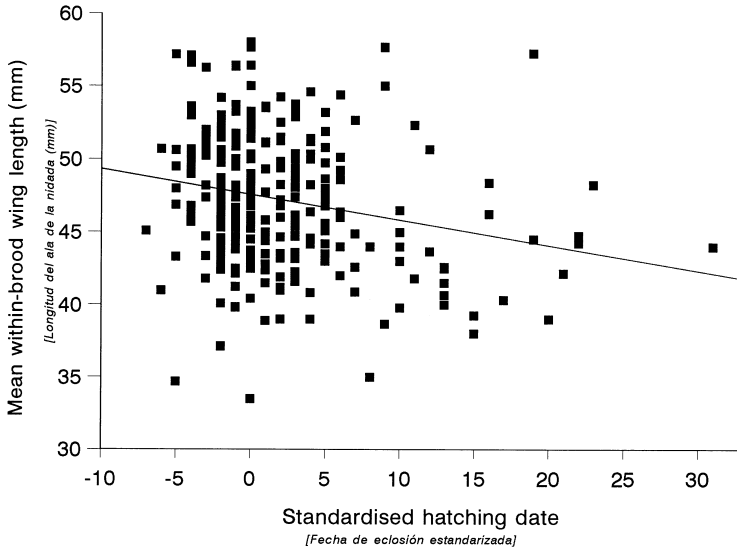


FIG. 2.—Relationship between mean within-brood wing-length and standardised hatching date ($n = 295$). Note that some observations are hidden due to overlap of data points.
 [Relación entre la media de la longitud del ala de las nidadas y la fecha de eclosión estandarizada para la variación anual. Nótese el número de datos aparentemente menor al tamaño de muestra ($n = 295$), debido al solapamiento de puntos.]

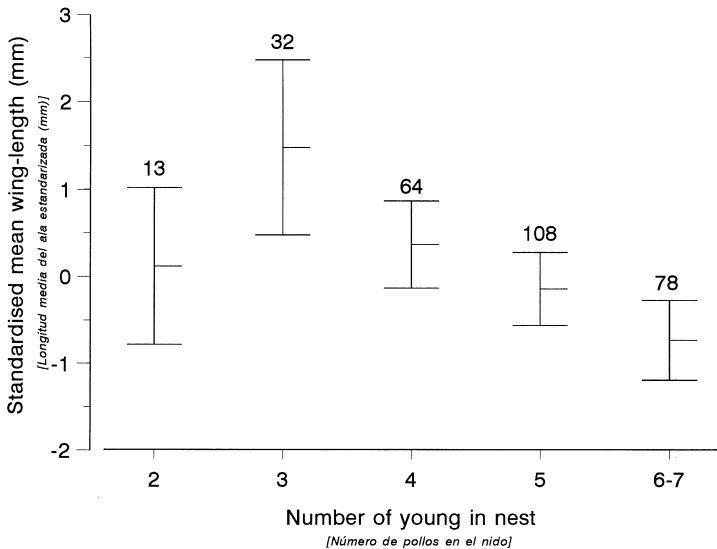


FIG. 3.—Relationship between average residual wing length of Pied Flycatcher broods (standardised for variation with hatching date) and number of young at day 13 of age. Figures are numbers of nests.
 [Relación entre la longitud del ala media (estandarizada para la variación negativa con la fecha de eclosión) de las nidadas de Papamoscas Cerrojillos en función del número de pollos en el día 13 de vida. Las cifras indican número de nidos en cada caso.]

TABLE I

Values of intraclass correlation coefficients (R) testing for resemblance of wing-length and first-primary length among fledgling sibships Pied Flycatchers in five and three different years, respectively. All correlations are highly significant ($P < 0.001$). Also shown are the mean number of fledglings (N_0), degrees of freedom (nests, fledglings) and F statistics.

[Valores de los coeficientes de correlación intraclass que estiman el parecido entre hermanos, en el nido, en la longitud del ala y la primera primaria en cinco y tres años de estudio, respectivamente. Todos los coeficientes son altamente significativos ($P < 0.001$). Se muestran también el número de pollos (N_0), los grados de libertad (d.f.: nidos, pollos) y los valores del estadístico F .]

Wing length [Longitud del ala]	1987	1988	1989	1991	1992	Total
R	0.79	0.66	0.76	0.45	0.40	0.75
N_0	4.87	4.22	4.62	5.00	4.63	4.67
d.f.	40,159	53,174	65,239	61,248	75,276	222,819
F	19.70	9.36	15.54	5.15	4.12	15.04
First-primary length [Longitud de la primera primaria]						
R	0.63	0.58	0.68	—	—	0.63
N_0	4.74	4.22	4.62	—	—	4.50
d.f.	35,135	53,174	65,239	—	—	155,546
F	8.95	6.80	10.80	—	—	8.81

reestimate heritabilities, probably due to common environmental effects (see below).

Sex differences in feather growth

Female fledglings had almost significantly larger wings than male fledglings ($F_{1,212} = 3.71$, $P = 0.056$; Fig. 4a) while the between-sex difference in the length of the first primary feather was significant ($F_{1,142} = 4.01$, $P = 0.042$; Fig. 4b). However, both differences are reversed at breeding age (ANCOVAs with sex as a factor and fledgling measurements length as a covariate; $P < 0.001$ in both; Fig. 4c, d). Although all nestlings are included in Fig. 4, the same conclusion is reached if within-nest averages for each sex are calculated and then compared thus avoiding pseudoreplication (paired t -tests, $n = 43$, $P < 0.002$).

Unlike tarsus length (Potti & Merino, 1996) or body mass and condition (Potti, 1999b), feather traits were unaffected by mite ectoparasite abundance (wing length: $F_{1,101} = 0.01$, $P = 0.93$; first-primary length: $F_{1,80} = 0.46$, $P = 0.51$), nest quality (wing length: $F_{1,162} = 2.53$, $P = 0.11$; first-primary length: $F_{1,80} = 0.46$, $P = 0.51$) or their interactions with nestling sex (all $P > 0.40$).

Feather growth influenced by nestboxes?

The repeatability of average fledgling wing length within «territories» (nestboxes) was low, but significant ($R = 0.15$, $F_{77,117} = 2.50$, $P = 0.036$). This was not the case for first-primary length although sample size was small ($R = 0.02$, $F_{20,43} = 1.04$, $P = 0.46$; rematings and re-occupation of nestboxes (Montalvo & Potti, 1992) excluded in these analyses). The consistency of measurements of different young means that, despite the apparent lack of impact of the measured environmental factors on feather growth for the sample of recruited offspring, nestboxes occupied by different individuals in different years were consistent at least in the mean wing-length of the fledglings raised in them. This was true irrespective of whether rough mean values or values standardised for variation with hatching date were used in computations, thus excluding the possibility that consistency in measurements of wing length were due to consistency of breeding date in particular nestboxes. This suggests an influence of conditions around the nest affecting the growth of wing of the young Pied Flycatchers reared nearby, which could be mediated by food quantity and/or quality.

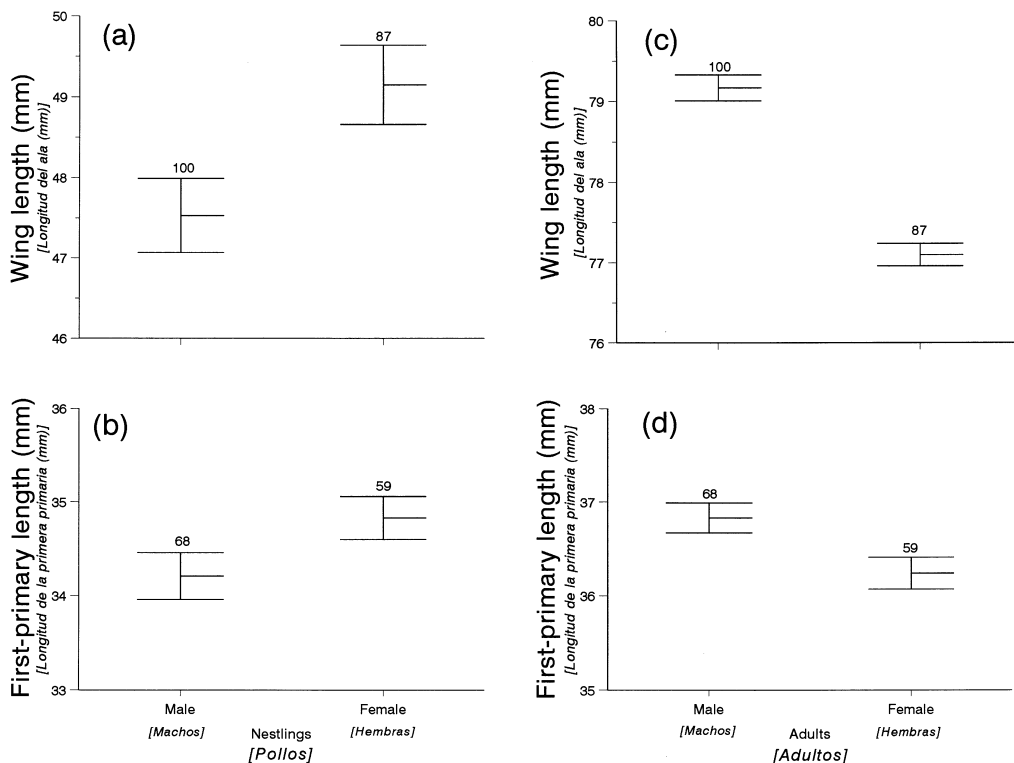


FIG. 4.—Between-sex differences in wing length (a, c) and length of the first-primary feather (b, d) in 13 days old fledgling Pied Flycatchers and in the same individuals when they became adult. Shown are means \pm 1 SE. Figures are numbers of individuals.

[Diferencias entre sexos en la longitud del ala (a, c) y de la primera primaria (b, d) en pollos de Papamoscas Cerrojillos de 13 días de edad y en los mismos individuos cuando llegaron a adultos. Se muestran las medias \pm 1 S.E. Las cifras indican números de individuos.]

DISCUSSION

Together with evidence presented elsewhere (Potti, 1999a), results in this paper suggest that feather growth of Pied Flycatchers near to fledgling is dependent on both genetic transmission and environmental characteristics of natal territories and their surroundings, so that the former might *a priori* be predicted as being responsible for about 30-50% of the variation in wing and first-primary lengths (from Table 1 in Potti, 1999a). In other words, in addition to resemblance by shared genes, resemblance among related individuals may arise from a variety of non-genetic causes (e.g. Boag & van Noordwijk, 1987; Schluter & Gustafsson, 1993; Cheverud & Moore, 1994; Potti & Merino,

1994a; Lynch & Walsh, 1998; Potti, 1999a). I have previously used sex-specific heritabilities of wing and first-primary lengths as a means to ascertain the possible importance of maternal effects and/or extra-pair fertilizations in biasing heritability estimates (Potti & Merino, 1994a; Hasselquist *et al.*, 1995; Potti, 1999a). I found that, when fully grown, both wing length and first-primary length retain significant heritabilities which apparently are not distorted by a maternal effect related to egg size or misassigned parentage (Potti, 1999a), as opposed to an apparently permanent impact of egg size on fledgling tarsus length in the same population (Potti & Merino, 1994a). However, apart from those due to egg size, other maternal effects which were not addressed in this study are still

capable to affect nestling feather growth, as we have documented elsewhere for other traits in the same population (see Merino *et al.*, 1996; Moreno *et al.*, 1997).

Environmental and genetic variation in feather growth at the nest were made manifest in the present study by several trends. As to environmental factors affecting nestling feather growth these are revealed, on the one hand, by the significant decrease in average wing-length of broods with increasing number of young, which suggests within-brood competition limiting feather growth (e.g. Merilä & Wiggins, 1995). In fact, I have previously shown that reduced growth, including that of wing length, is associated to large clutch sizes that hatch asynchronously (Potti, 1998b). On the other hand, an environmental source of resemblance is suggested by the significant consistency in the size of wings of different broods reared in the same nestboxes in different years by different adult flycatchers (it is worth mentioning that nestboxes were not repeatable in the mean tarsus length or mass of fledglings; J. Potti, unpublished data). Common rearing environments are a demonstrated cause of an increased resemblance among young in a nest, as the high heritabilities of feather growth here reported, based on full-sib resemblance estimates, and its comparison with parent-offspring estimates (Potti, 1999a) indicate. Comparison of regressions of offspring across generations (van Noordwijk *et al.*, 1981; Grant & Grant, 1996; Potti, 1999a) and breaking the correlation between genetic and environmental effects by swapping eggs or young between nests may reveal this kind of effects (e.g. James, 1983; Rhymer, 1992; Smith & Wettermark, 1995; Potti *et al.*, 1999). However, the latter technique alone does not allow for identification of sources of environmental variation without further experimental manipulations (e.g. Merilä, 1996, 1997).

Contrary to other traits in the same individuals, there was no differential feather growth depending on an interaction between host fledgling sex and parasites, as previously reported in the same population for fledgling tarsus length (Potti & Merino, 1996) and fledgling mass and condition (residual mass; Potti, 1999b). On the other hand, I found that in the total data set, i.e. that including non-recruiting individuals of unknown sex, a significant re-

semblance existed in the size of wings and first-primary feathers of different broods reared in the same nestboxes in different years by different adult Pied Flycatchers. This means that the growth of fledgling feathers in particular nestboxes was predictably different from that in other nestboxes, suggesting a role for environmental conditions in the immediate surroundings of the nestboxes in determining fledgling feather growth independently of parental characteristics. The results presented here suggest therefore that growth of flight feathers of nestling Pied Flycatchers may be predicted from unspecified aspects of territory (nestbox) quality, in whose vicinity parent Flycatchers search for prey to feed their young (Lundberg & Alatalo, 1992). The index of territory quality used here presumably scores quality of foraging habitats, and not more immediate, readily measured aspects of habitat quality as infestations of nests by parasites. In fact, prevalence and intensity of nest ectoparasitism are not consistent across years in different nestboxes, which supports this interpretation (Merino & Potti, 1995; 1996). Thus, those unmeasured components of quality differences among microhabitats do not translate into differences in feather growth between the sexes among fledglings.

I found that, irrespective of environmental influences, feather tracts grow larger in female than male Pied Flycatcher nestlings near to fledging. This study thus adds further evidence to the size dimorphism that is observed in Pied Flycatchers in both nestling and adult birds, but with a different directionality in each case. Adult females have longer tarsi and are slightly, though significantly, heavier than males (Lundberg & Alatalo, 1992; Potti & Merino, 1994a), while adult males have longer wings and tails than adult females (Potti, 1999b). Therefore, as regards skeletal size, as estimated by tarsus length (Garnett, 1981) and mass, females are the larger sex in the Pied Flycatcher. However, at 13 days of age, female Pied Flycatchers are apparently larger than their male counterparts in both tarsus length (Potti & Merino, 1996) and wing and first-primary feather (this study), but are lighter and in poorer condition (residual mass) than male fledglings, in particular under stressful conditions (Potti, 1999b). Thus, nestlings seem to differentially allocate incoming energy gains in growth of skeletal

and plumage structures or increases in body mass depending on gender. The reasons for differential allocation to growth of structures according to sex are not yet clear and several explanations have been advanced, including differential selection pressures on each sex (Merilä *et al.*, 1997), variable susceptibility to parasitism (Potti & Merino, 1996) and varying allocation to growth of different traits (Hochachka & Smith, 1991; Potti, 1999b). Differential selection pressures depending on gender may apply in this case, as the between-sex difference in feather growth is already reversed at first breeding the following year. Thus, there is a «catch-up» of feather growth in males. I have shown elsewhere that selection for longer wings probably applies to male Pied Flycatchers and is probably responsible for the differential growth of wing feathers depending on sex, as, other things being equal, males with longer wings arrive earlier from spring migration and enjoy greater reproductive success than males with shorter wings (Potti, 1998a; Potti & Montalvo, 1991a). Female Pied Flycatchers, on the other hand, apparently lack this selective pressure as their settlement date from spring migration, while strongly covarying with age, is independent of wing-length (Potti, 1999c; J. Potti, unpublished data). On the other hand, by knowing the sex of fledglings by molecular techniques and performing analyses similar to those I have presented here, Merilä *et al.* (1997) showed that post-fledgling selection varied in sign depending on sex in Collared Flycatchers *Ficedula albicollis*, thus confounding the interpretation of size dimorphism at the nest, which they showed to be absent *before* recruitment selection. Thus, only by knowing already from hatching the sex of nestlings (e.g., Lessells *et al.*, 1996) will we be able to gain further insight into the likely pervasive influences of environmental variation experienced during development (itself potentially containing influences of genetic origin; see reviews in Mousseau & Fox, 1998), on variation in sex-dimorphic traits of birds.

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