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HERITABILITY OF WING LENGTH AND WEIGHT IN EUROPEAN BEE-EATERS (*MEROPS APIASTER*)[1]

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Key words: European Bee-Eater; morphometrics; weight; wing length; heritability; repeatability; quantitative genetics.

In recent years, an increasing number of studies have demonstrated the existence of significant heritable variation in morphological and other ecologically important traits in wild bird populations (van Noordwijk et al. 1980, Boag and van Noordwijk 1987). These heritability values have not only revealed the previously unexpected presence of considerable amounts of genetic variance, and hence the potential for populations to show microevolutionary change in response to selection (Boag and Grant 1981, van Noordwijk et al. 1981), but have also been used as a tool to estimate other variables of interest, such as the frequency of successful extra-pair copulation (Alatalo et al. 1984, Grant and Grant 1987, Møller 1987). Here we report repeatability and heritability values for wing length and weight in the European Bee-Eater, *Merops apiaster*.

METHODS

Fully-grown bee-eaters were caught at the colony at Mas des Sarcelles (8 km south of Arles) in the Camargue region of southern France between mid-May and early August from 1983 to 1987. Birds were given a numbered aluminum band and were individually marked for field identification. Birds were reliably classified as 'juvenile' (born the previous calendar year) or 'adult' (born at least two calendar years ago) on the basis of plumage characteristics (Lessells and Krebs, unpubl.). Birds were also sexed in the hand on the basis of plumage characteristics; this technique was not completely reliable, but the sexes of most birds were confirmed from their breeding attempts. The wing length (flattened, straightened wing; Spencer 1984) was recorded to the nearest 1 mm, and weight was recorded to the nearest 0.1 g using a 100-g range Pesola balance. Chicks were banded from a third to a half of all nests each year, so parent-offspring relationships were known for these birds. Analyses were carried out using SAS

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TABLE 1. Age and sex differences in wing length and weight in European Bee-Eaters.

	Wing length (mm)	
	Males $\bar{x} \pm$ SD (n)	Females $\bar{x} \pm$ SD (n)
Juveniles	152.9 ± 2.93 (227)	147.9 ± 2.96 (185)
Adults	152.5 ± 3.27 (116)	147.5 ± 3.32 (135)

2-way ANOVA: Age: $F_{1,659} = 3.05$, $P = 0.08$. Sex: $F_{1,659} = 425.3$, $P < 0.001$. Age × sex interaction: $F_{1,659} = 0.00$, $P = 0.97$.

	Weight (g)	
	Males $\bar{x} \pm$ SD (n)	Females $\bar{x} \pm$ SD (n)
Juveniles	56.57 ± 2.936 (355)	56.91 ± 5.383 (286)
Adults	56.50 ± 2.864 (186)	56.66 ± 5.683 (196)

2-way ANOVA: Age: $F_{1,1019} = 0.33$, $P = 0.56$. Sex: $F_{1,1019} = 1.04$, $P = 0.31$. Age × sex interaction: $F_{1,1019} = 0.10$, $P = 0.75$.

(SAS Institute 1985) on the University of Sheffield's IBM 3083 computer.

RESULTS

Male bee-eaters had significantly longer wings than females, but there was no difference in wing length between juveniles and adults (Table 1). On average, males had wings that were about 5 mm longer than those of females. There were no significant differences in the weights of males and females, or juveniles and adults (Table 1). However, the weights of females were significantly more variable than those of males (variance ratio: $F_{319,342} = 3.58$, $P < 0.001$). Females weighed more during the laying period (Fig. 1), and their weights were also more variable at this time (see SDs in Fig. 1) because individual females laid for only part of the laying period of the colony as a whole and the weight of a female who was laying varied greatly depending on whether or not she was carrying an egg in her oviduct. Both the greater seasonal variation in the female weights, and the greater variation of female weights during the laying period contributed to the greater overall variance in female weights. During July and August, females weighed less than males (males: weight

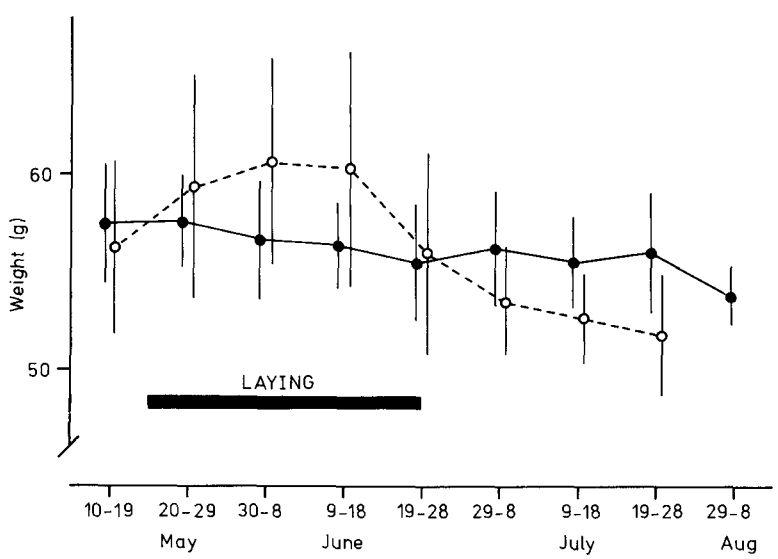

FIGURE 1. Seasonal variation in the weights of male and female European Bee-Eaters. Filled circles and unbroken lines: males. Unfilled circles and broken lines: females. Vertical bars are standard deviations. Least squares polynomial regressions: Males: weight (g) = 59.1 − 0.0894(date) + 0.00599(date)^2, $F_{2,538} = 19.9$, $P < 0.001$. Females: weight (g) = 40.0 + 1.495(date) − 0.03273(date)^2 + 0.0001988(date)^3, $F_{3,478} = 61.4$, $P < 0.001$. (Date = days after 30 April, i.e., 1 = 1st May, etc.)

TABLE 2. Repeatability of wing length and weight in European Bee-Eaters.

	F-ratio (df)	P	Repeatability
Wing length			
Males	11.2 (38,43)	***	0.829
Females	10.0 (34,38)	***	0.812
Both	10.5 (73,81)	***	0.820
Weight			
Males	5.20 (124,197)	***	0.620
Females	2.43 (104,158)	***	0.364
Both	3.64 (229,355)	***	0.509

*** $P < 0.001$.

= 55.9 ± 2.82 [SD] g, $n = 147$; females: weight = 52.9 ± 2.67 [SD] g, $n = 123$; $F_{1,268} = 79.3$, $P < 0.001$) and their weights were no more variable than those of males ($F_{122,146} = 0.89$, $P > 0.5$). Because of these differences between males and females in mean wing length and variation in weight, standardized measurements have been used in the repeatability and heritability analyses. Standardized wing length was: (measured wing length − mean for birds of that age and sex)/SD for birds of that age and sex (see Table 1 for age- and sex-specific values used). Standardized weight was: (measured weight − mean for birds of that sex caught during the same 10-day date category)/SD for birds of that sex caught during the same 10-day date category (see Fig. 1 for sex- and date-specific values used). The results of analyses of weight standardized for age and sex (not presented here) did not differ qualitatively from those presented below for weight standardized for sex and date. Weight and wing length were correlated (actual measurements: males: $r = 0.295$, $n = 299$, $P < 0.001$; females: $r = 0.177$, $n = 279$, $P = 0.003$. Standardized measurements: males: $r = 0.270$, $n = 299$, $P < 0.001$; females: $r = 0.155$, $n = 279$, $P = 0.01$).

Wing length was significantly repeatable in males, females, and both sexes combined (Table 2). In general, differences between individuals accounted for over 80% of the variation in wing length. The only four repeat measurements within a year (one male and three females) were excluded from the analysis, so these repeatability values reflect the constancy of the lengths of primaries grown in different molts (as well as consistency within and between measurers).

Weight was also significantly repeatable in males, females and both sexes combined (Table 2). Differences between individuals accounted for over 60% of the variation of male weights, but less than 40% of the variation in female weights (t for difference in repeatability between males and females = 3.01, $P < 0.01$; SEs calculated after Becker 1984). The difference in repeatability between males and females reflected the higher variance in female weights. Unlike wing length, repeat measures were made within as well as between years; the birds used for this analysis were each weighted a mean of 1.56 times in each of a mean of 2.05 years. When repeatability values were calculated separately for each of the 5 years, the mean value obtained was close to that obtained when combining data from all years (males: mean of repeatability values calculated separately for each of the years 1983–1987 = 0.682, range = 0.497–0.762; females: $\bar{x} = 0.359$, range = 0.029–0.756).

Sixty-seven males and 17 females banded in the nest were caught in subsequent years. Of these, 57 males and 16 females from 48 broods were measured at least once as a juvenile or adult, and had at least one parent who had been measured. Heritability of wing length and weight were calculated using a regression of offspring on each parent and on the mid-parent; heritability is equal to the regression coefficient of offspring on mid-parent or twice the regression coefficient of offspring on a single parent (Falconer 1981). In the analysis, mean standardized values of wing length and weight were calculated for each individual, and, when more than one offspring from a brood was measured, a single mean value for all the offspring in the brood (independent of their sex) was used. Offspring included in the analysis survived at least 1 year, and during this time selective death of offspring whose growth was adversely affected by environmental conditions may have occurred. As a result, heritability may be higher than it would have been if measured at the termination of growth (van Noordwijk 1984). Heritabilities calculated from offspring–single parent regressions will be inflated by assortative mating for the character (Falconer 1981). This may be detected by comparing heritability values based on offspring–single parent and offspring–mid-parent regressions. There is no direct evidence that bee-eaters mate assortatively for wing length or weight (correlation between members of pairs: wing length: $r = 0.02$, $n = 180$, $P = 0.78$; weight: $r = 0.09$, $n = 209$, $P = 0.21$). Maternal effects (for instance via egg size) will increase heritability values calculated from offspring–mother regressions. The extent of such effects can be assessed by comparing heritability values based on offspring–mother and offspring–father regressions. Similarly, a comparison of single-sex offspring–single parent regressions may reveal sex linkage or sex-limited expression of genes.

Wing length was significantly heritable; about 60% of the variation in wing length was genetic (Table 3). Heritability based on the offspring–mid-parent regression was slightly, but not significantly, higher than that based on either of the offspring–single parent regressions. When the data were subdivided, and the analysis performed separately for sons and daughters, heritability based on offspring–mid-parent regressions remained high (sons: $h^2 = 0.75$, $P = 0.004$; daughters: $h^2 = 0.83$, $P = 0.06$). When heritability was calculated using offspring–single parent regressions, heritabilities were higher when based on parents of the opposite sex (sons: $h^2 = 0.67$, $P = 0.02$; daughters: $h^2 = 1.03$, $P = 0.03$) than if based on parents of the same sex (sons: $h^2 = 0.43$, $P = 0.18$; daughters: $h^2 = -0.28$, $P = 0.73$), but these differences were not significant.

A heritable component of variation in weight was not detected whether calculated from regressions of offspring on a single parent or a mid-parent value (Table 3). However, given our small sample sizes only heritability values greater than about 0.5 would have been statistically significant.

The above calculations of heritability assumed that

TABLE 3. Heritability of wing length and weight in European Bee-Eaters.

Regression	n	Heritability ± SE	P[1]
Wing length			
Offspring–Father	33	0.579 ± 0.256	0.042
Offspring–Mother	34	0.564 ± 0.258	0.036
Offspring–Mid-parent	31	0.734 ± 0.210	0.0015
Weight			
Offspring–Father	44	0.280 ± 0.303	0.36
Offspring–Mother	47	−0.046 ± 0.298	0.88
Offspring–Mid-parent	43	0.212 ± 0.212	0.32

[1] Two-tailed probability: such a probability value is conservative in the face of a clear hypothesis allowing only positive regression coefficients.

resemblances between relatives were due to shared genes alone. However, there may have been an environmental correlation between relatives, and the resemblance thus caused will be incorrectly attributed to shared genes, resulting in heritability being overestimated. Environmental and genetic sources of resemblance may be separated in fostering experiments (Smith and Dhondt 1980, Dhondt 1982, Alatalo and Lundberg 1986). We have not carried out large-scale fostering experiments for this purpose, but 14 of the offspring in the above analysis had been fostered into different broods at less than 23 days of age (a few days before fledging). (Fostering sometimes led to an increase in brood size.) Within this sample, there were no significant correlations between the wing lengths of offspring and foster parents. However, offspring weight was significantly correlated with the weight of the foster mother ($r = 0.65$, $n = 10$, $P = 0.040$), but not of the foster father ($r = 0.48$, $n = 9$, $P = 0.19$). This result should be treated with caution, as it has not been confirmed in the larger sample including offspring raised by their own parents (r, with female who raised the brood = 0.08, $n = 50$, $P = 0.58$; r, with male who raised the brood = 0.24, $n = 47$, $P = 0.10$). Moreover, offspring were fostered relatively late in the nesting period when environmental correlations may already have been established.

DISCUSSION

The repeatability values for wing length and weight fall within the published ranges of values and also confirm the tendency for wing length to be more repeatable than weight (Boag and van Noordwijk 1987). In this study, the heritability of wing length was high (0.6), and the heritability of weight was not significant. In previous studies, heritabilities of wing length and weight were rather variable, with no consistent difference between wing length and weight (Boag and van Noordwijk 1987). The high heritability of wing length in European Bee-Eaters may indicate that this character is rather poorly related to fitness in this species (Falconer 1981, Gustafsson 1986, Mousseau and Roff 1987).

Cross-fostering experiments on other species suggest that there is little environmental correlation between relatives for linear body measurements (Smith and Dhondt 1980, Dhondt 1982, Alatalo and Lundberg 1986). Our limited results confirm this for wing length. The results for weight are suggestive of an environmental correlation.

The heritability calculations above assumed that chicks in a nest were the biological offspring of the breeding pair, but this may not have been the case if extra-pair copulations, intraspecific nest parasitism, or quasi-parasitism (offspring the child of the putative father, but not of the putative mother; Wrege and Emlen 1987) occurred. At the study colony, at least 4% of copulations in the colony, and 14% of copulations at a feeding site, were extra-pair copulations (M. I. Avery, pers. comm.) and intraspecific nest parasitism also occurred (C.M.L., pers. observ.). In European Bee-Eaters, there is also the (currently unsupported) possibility that the helpers that attended approximately 25% of nests were the biological parents of some of the chicks, as has occurred in the White-fronted Bee-Eater, *Merops bullockoides* (Emlen and Wrege 1986).

Recently differences between heritability values based on offspring–mother and offspring–father regressions have been used to assess the frequency of extra-pair fertilization (Alatalo and Lundberg 1986, Grant and Grant 1987, Møller 1987). In bee-eaters, these heritability values for wing length are virtually identical, suggesting that extra-pair fertilization is a rare event. However, we know from DNA fingerprinting (Burke and Bruford 1987, Wetton et al. 1987) that extra-pair fertilization occurred in the study colony (T. Burke, pers. comm.). Whether the heritability values are equal despite the known occurrence of extra-pair fertilization because true heritability values are dependent on the sex of the parent (for instance because environmental variance is greater in one sex, or the expression of the character is sex limited) or because a decrease in the offspring–father regression caused by extra-pair fertilization is being balanced by a decrease in the offspring–mother regression caused by quasi-parasitism can only be determined when the true parentage of each chick is known. We intend to carry out this analysis in the future using DNA fingerprinting to determine parentage.

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TWO NEW RECORDS OF BIRDS FOR SOUTHERN MEXICO[1]

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Key words: Neotropical species; tropical rain forest; resident bird; winter visitor; Nyctibius grandis; Lymnothlypis swainsonii.

During a 9-month study on avian diversity in the Lacandona tropical rain forest, we recorded two previously unknown species for southern Mexico. Both species were found in the southern part of the Montes Azules Biosphere Reserve (16°06′N, 90°56′W) along the Lacantun river, approximately 4 km southwest of the town of Boca del Chajul, Ocosingo County, Chiapas, Mexico.

NYCTIBIUS GRANDIS (GREAT POTOO)

A tape recording of the vocalization from a single bird was obtained at 22:30 on 30 October 1987. It was

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