HERITABILITY OF WING LENGTH AND WEIGHT IN EUROPEAN BEE-EATERS (MEROPS APIASTER)

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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, Möller 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.

<table>
<thead>
<tr>
<th></th>
<th>Wing length (mm)</th>
<th>Weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males x ± SD (n)</td>
<td>Females x ± SD (n)</td>
</tr>
<tr>
<td>Juveniles</td>
<td>152.9 ± 2.93 (227)</td>
<td>147.9 ± 2.96 (185)</td>
</tr>
<tr>
<td>Adults</td>
<td>152.5 ± 3.27 (116)</td>
<td>147.5 ± 3.32 (135)</td>
</tr>
</tbody>
</table>

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

(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: $F_{1,342} = 3.58, P < 0.001$). 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)$^3$, $F_{3,342} = 61.4, P < 0.001$. (Date = days after 30 April, i.e., 1 = 1st May, etc.)](image-url)
A heritable component of variation in weight was also significantly repeatable in males, and weight was calculated using a regression of offspring on mid-parent; 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 based on the 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 all years (males: mean of repeatability values calculated separately for each of the years 1983–1987 = 0.682, range = 0.497–0.762; females: $x = 0.359$, range = 0.29–0.756).

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 ($r$ of offspring-mid-parent, $r_{OM}$). The offspring-mid-parent regression was slightly, but not significantly, higher than that obtained when combining data from all years ($r_{OM} = 0.89, P > 0.5$). Because of these differences, the offspring-mid-parent regression may reveal sex linkage or sex-limited expression of genes.
TABLE 3. Heritability of wing length and weight in European Bee-Eaters.

<table>
<thead>
<tr>
<th>Regression</th>
<th>n</th>
<th>Heritability ± SE</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing length</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Offspring-Father</td>
<td>33</td>
<td>0.579 ± 0.256</td>
<td>0.042</td>
</tr>
<tr>
<td>Offspring-Mother</td>
<td>34</td>
<td>0.564 ± 0.258</td>
<td>0.036</td>
</tr>
<tr>
<td>Offspring-Mid-parent</td>
<td>31</td>
<td>0.734 ± 0.210</td>
<td>0.0015</td>
</tr>
<tr>
<td>Weight</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Offspring-Father</td>
<td>44</td>
<td>0.280 ± 0.303</td>
<td>0.36</td>
</tr>
<tr>
<td>Offspring-Mother</td>
<td>47</td>
<td>-0.046 ± 0.298</td>
<td>0.88</td>
</tr>
<tr>
<td>Offspring-Mid-parent</td>
<td>43</td>
<td>0.212 ± 0.212</td>
<td>0.32</td>
</tr>
</tbody>
</table>

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

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 Emlyn 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, Möller 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

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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 previ-ously unknown species for southern Mexico. Both species were found in the southern part of the Montes Azules Biosphere Reserve (16°06'S, 90°56'W) along the Lacantun river, approximately 4 km southwest of the town of Boca del Chajul, Ociosoing County, Chia pas, 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