Bill morphology reflects female independence from male parental help

Wolfgang Forstmeier^{1,3*}, Bernd Leisler¹ and Bart Kempenaers²

¹Max Planck Research Centre for Ornithology, Vogelwarte Radolfzell, Schloss Moegglingen, Schlossallee 2, D-78315 Radolfzell, Germany

²Max Planck Research Centre for Ornithology, Postfach 1564, D-82305 Seewiesen, Germany

³Theodor Boveri Institute, Department of Animal Ecology and Tropical Biology, Würzburg University, Biozentrum, Am Hubland, D-97074 Würzburg, Germany

The study of territorial polygyny in birds has been influential in the development of the theory of social mating systems. Alternative female mating options have been studied within the framework of the polygyny-threshold model and later as the outcome of conflicts of interest between individuals. However, little attention has been given to variations between individual females, and how this affects their mating behaviour. Here, we test the hypothesis that some females are better adapted to raise nestlings without male assistance, and thus to mate polygynously. Specifically, we investigate whether intraspecific variation in female bill morphology is related to mating behaviour. This hypothesis is derived from earlier studies showing that, in both intra- and interspecific comparisons, uniparental care by females is correlated with the catching of larger prey items than when both parents provision the young. Using the polygynous dusky warbler (*Phylloscopus fuscatus*) as a model species, we found that, in accordance with our prediction, females with deep bills were more likely to mate as a secondary female. Moreover, regardless of mating status, females with deep bills settled in territories with more food and they received less male assistance in feeding their offspring. We argue that females with stronger bills are better adapted to exploit the abundance of large food items in rich territories and thus to raise young on their own. Our results demonstrate the importance of studying variations between individual females, and provide evidence for an extended version of the 'constrained-female hypothesis'. As bill depth is a highly heritable trait, our study strongly suggests that variation in female mating behaviour is not only related to ecological factors and female condition (as shown elsewhere) but also to heritable morphological traits.

Keywords: mating system; parental care; *Phylloscopus fuscatus*; polygyny-threshold model; prey size; territory quality

1. INTRODUCTION

The study of territorial polygyny in birds has been influential in the development of the theories of social mating systems and individual reproductive strategies (Searcy & Yasukawa 1989; Slagsvold & Lifjeld 1994; Ligon 1999). Females usually suffer from having to share resources such as male parental care, so the main question has been why should females mate with already-paired males if other breeding options are available? The polygyny-threshold model (Verner 1964; Verner & Willson 1966; Orians 1969) provides an answer: it suggests that females do better (in terms of fitness) by mating with an already-paired male in a high-quality breeding situation (e.g. territory) than by settling with an unpaired male in a low-quality breeding situation. The polygyny-threshold model and its derivatives have been used to explain most social mating systems in passerine birds (Wittenberger 1979; Ligon 1999), even though the assumptions made by these models have rarely been tested and may be unrealistic (Davies 1989). Davies' (1989) paper and subsequent studies led to the development of a new conceptual framework in which variable mating systems are considered to be the outcome of sexual conflicts between individuals. However, little attention has been given to variation between individual females and to how this affects their reproductive options (see Gross 1995).

Many studies of social polygyny have shown that secondary females differ from primary females in that they arrive later on the breeding grounds and/or are younger (Slagsvold & Lifjeld 1994). However, to date, no field study has focused on the differences between females that mate with an already-paired male (secondary females) and simultaneously settling monogamous females. In socially polygynous systems, the decision of where to settle is often characterized by a trade-off between the food abundance in a territory and the amount of male assistance that can be expected (Whittingham & Robertson 1994; Hoi-Leitner *et al.* 1999). The importance of this trade-off clearly depends on the importance of male parental assistance for a female's reproductive success. This is known to vary geographically (e.g. Dunn & Robertson 1992) but may also depend on the quality of the female. Thus, some females might be more 'emancipated' from male help than others (Gowaty 1996; see also Gowaty 1997). The general hypothesis we test here is that some females are better adapted to raise nestlings without male help and that these females are more likely to settle with an already-paired male. Our hypothesis is an extension of the 'constrained-female hypothesis' (Gowaty 1996), which predicts that females should seek extra-pair copulations when they can rear offspring with little help from their mate, because the cost of the (possible) reduced male care would be lower.

A specific hypothesis can be derived based on a comparative study by Leisler & Catchpole (1992), who

*Author for correspondence (forstmeier@mail.uni-wuerzburg.de).

investigated the evolution of mating systems in *Acrocephalus* warblers. Six closely related species of similar ecology display a variety of mating systems ranging from monogamous pair bond and biparental care to promiscuity without pair bonds and uniparental care by females. Between these extremes, there are species with facultative polygyny, where a variable proportion of secondary females raise their broods without, or with very little, male assistance. The higher the abundance of food in a species' habitat, the smaller the contribution of males to the care of the offspring and the higher the frequency of unassisted females. Species with uniparental care feed their nestlings with larger prey items than species in which biparental care is the rule. Moreover, these species have stronger bills, presumably as an adaptation for catching larger prey (Leisler & Catchpole 1992). Recently, Sejberg *et al.* (2000) showed that in polygynous great reed warblers (*Acrocephalus arundinaceus*, which were also included in the study of Leisler & Catchpole (1992)) secondary females feed larger prey items to their nestlings than monogamous and primary females, which receive a much larger amount of male assistance. This means that, in both inter- and intraspecific comparisons, female emancipation from male assistance was correlated with catching larger prey.

Based on these two studies, we investigated whether intraspecific variation in bill morphology is related to female mating behaviour. We predicted that, in insectivorous passerines, females choosing uniparental care in optimal habitats (i.e. secondary females) should have bills better adapted to catching larger prey than do simultaneously settling monogamous females in lower-quality habitat. To test this hypothesis, we studied the dusky warbler (*Phylloscopus fuscatus*), a species with a variable social mating system where, on average, 21% of the males mate polygynously. The foraging behaviour of dusky warblers is similar to that of *Acrocephalus* warblers (Forstmeier & Keßler 2001) and the two genera are closely related (Sibley & Ahlquist 1990). Here, we test the hypothesis that bill morphology is correlated with intraspecific variation in female emancipation from male parental care. First, we compare the bill depths of secondary females with those of simultaneously settling monogamous females. Second, we test whether female bill depth is correlated with a continuous variable describing female independence from male assistance.

2. METHODS

The study was conducted at the mouth of the Malkachan river, 190 km east of Magadan, in the far east of Russia (154°14' E; 59°51' N). The area is characterized by bushlands of *Pinus pumila* with some mixtures of *Betula middendorffii* and *Alnaster fruticosus*, typically 1–2 m in height. On rich soils in close proximity to the Malkachan river these bushes are replaced by faster growing *Salix* sp. and *Alnus hirsuta* bushes. These low bushes are the habitat occupied by the dusky warbler.

We studied the mating system of this dusky-warbler population in the breeding seasons of 1997–1999. Males and females were captured using mist-nets as soon as possible after their arrival and were marked with a unique combination of plastic colour rings. We measured the bill depths of all birds at the proximal margin of the nostrils, to the nearest 0.1 mm, using

callipers. We also measured wing, tail and tarsus lengths, foot span (including claws) and body mass. A principal component ('PC body size') was extracted from these five measurements reflecting individual variation in body size (Rising & Somers 1989). All morphological measurements were taken by the same person (WF) to prevent observer-specific variation. Measurements were taken blind with regard to the hypotheses tested here. In the analyses, multiple values for the same individual were averaged. Many studies have found significant effects of year and season on bill morphology (e.g. Davis 1954; Gosler 1987; Morton & Morton 1987; Matthysen 1989). To control for these possible confounding effects, we tested for seasonal and annual changes in bill morphology. Bill depth (first measurements from 76 individual females) showed no increase over the breeding season ($r = 0.12$, $p = 0.32$). Mean bill depth did not differ significantly across years (analysis of variance (ANOVA), $F_{2,73} = 0.84$, $p = 0.44$). Nevertheless, we performed all analyses with and without controlling for capture date and year. Since this did not make any difference to the results, we report only the tests where we did not control for these factors.

Male age was determined as first year or older, partly based on ringing data and partly based on a discriminant analysis using morphological characteristics (tail length, wing length and wing shape). The latter analysis classified 91% of males of known age ($n = 65$) correctly. Female age was determined in a similar way, using tail length and patterns of tail moult (Forstmeier *et al.* 2001).

Male territories were usually visited every day or second day, and song posts were plotted on a detailed map. For each polygynous male, female mating status (primary or secondary) was determined based on the order in which females laid their first egg. All non-primary females were classified as 'secondary females', including second, third, fourth and fifth females. We observed almost no individual variation in the time between female arrival and clutch initiation (7 or 8 days; Forstmeier *et al.* 2001), so we used the date of the first egg minus eight as the arrival date. Within each year, monogamous females were divided into early and late settlers in such a way that the late settlers showed maximal overlap in arrival date with secondary females.

To quantify the amount of paternal investment we recorded the feeding behaviour of parents at nests during the nesting period. For a total of 72 nests, we collected data on the number of feeding trips performed by males and females. When the young were 1–15 days old, we counted male and female feeding trips during short (5–60 min) observation periods. Observations were made between 05.00 and 21.00 (local time) and some nests were observed more than once a day. For each day and each nest, we calculated the proportion of male feeds (out of the total number of feeds). These values were then averaged over the nesting period to obtain an estimate of male participation in brood care. The proportion of male feeds was independent of time of day ($p = 0.23$) but declined with mean nestling age at observation ($r = -0.25$, $n = 72$, $p = 0.036$). To control for this effect we took residuals from the regression $y = 0.433 - 0.0203x$, where y is the proportion of male feeds and x is the mean number of days after hatching.

During the nesting period (late July) in 1998 and 1999 we sampled the arthropod fauna of the bush vegetation by beating branches (of a standardized volume of vegetation) with a stick and collecting arthropods from a tray held below the branch. The volume sampled was measured relative to the size of the tray. To standardize the volume of sampled vegetation, we

selected only branches with dense foliage and estimated the volume when branches were in their natural positions. The foraging activity of dusky warblers is almost exclusively restricted to this vegetation type. Within each of 45 male territories we collected at least 30 samples in each year. We summed the volumes of all arthropods in a sample (measuring individual length, width and depth on millimetre paper) and calculated the mean arthropod volume per sample for each territory and year. As values were highly correlated between the 2 years ($r^2 = 0.929$) we assumed that the average values reflected the food abundances of the territories for all 3 years of the study. The richest and poorest territories differed by a factor of 47. Averages were $\log_{10}$ transformed to approach a normal distribution (Kolmogorov–Smirnov test after transformation, $Z = 1.1$, $p = 0.17$). Using a telescope (30 $\times$), we observed the food items carried to the nestlings by their parents. We did this to check whether the sampled arthropods were fed by dusky warblers to their nestlings. We used arthropod densities per volume of bush as a measure of territory food abundance because the foraging success of warblers seems to depend more on arthropod abundance than on the amount of bush in the territory. The latter is not so variable and birds cannot deplete their territories.

Data are given as mean $\pm$ s.e.m. Statistical analyses were performed with SPSS 9.0 (SPSS Inc., Chicago, IL, USA) and SAS 6.12 (SAS Institute Inc., Cary, NC, USA). All tests were two-tailed.

3. RESULTS

Female mating status (secondary females versus simultaneously settling monogamous females) was nearly significantly related to female bill depth (logistic regression, $\chi^2 = 3.60$, $p = 0.058$). Thus, females with deep bills were more likely to settle as secondary females than were females with shallower bills. Note that this two-tailed test is conservative, because we made a clear one-tailed prediction. Overall, secondary females had deeper bills than simultaneously settling monogamous females (figure 1) but the difference was not significant ($t_{38} = 1.86$, $p = 0.07$). Three out of the 40 females shown in figure 1 bred in two seasons. These females had the same status in both years but are included only once. The difference in bill depth between the two female groups was consistent across all three study years (data not shown). When using a statistically more powerful test (i.e. a pair-wise comparison between secondary and monogamous females matched for study year and arrival date) we found that secondary females had significantly deeper bills (paired t -test, $t_{15} = 2.30$, $p = 0.036$). In this test, the sample of 16 pairs of females included the secondary female with the smallest bill depth (2.3 mm; figure 1).

Secondary females received significantly less male assistance in raising nestlings than simultaneously settling monogamous females (percentage of feeds by the male, comparing observations at the same nestling age: secondary females, $2.2 \pm 1.2\%$, monogamous females, $40.1 \pm 5.0\%$; Mann–Whitney U -test, $Z = -4.8$, $n = 36$, $p < 0.001$). On the other hand, secondary females bred in territories with higher food abundances (volume of arthropods per sample: secondary females, $254 \pm 77 \text{ mm}^3$, monogamous females, $117 \pm 31 \text{ mm}^3$, $t_{34} = -2.28$, $p = 0.029$). As both the proportion of male assistance and food abundance are continuous variables, the relationship between

Figure 1. Distribution of the bill depths of 19 secondary females and 21 simultaneously settling monogamous females.

them can be investigated for all females irrespective of their social status and date of arrival at the breeding grounds. In general, females breeding in territories with higher food abundances received less paternal assistance ($r = -0.35$, $n = 61$, $p = 0.005$). This pattern of declining male participation in care with increasing food availability reflects a common trade-off found within populations (Whittingham & Robertson 1994; Hoi-Leitner *et al.* 1999), between populations (Dunn & Robertson 1992) and between species (Leisler & Catchpole 1992). We therefore decided to summarize this trade-off by using a single variable that describes how female independence increases as food becomes more abundant. We calculated the bivariate major axis (BMA; see Sokal & Rohlf 1995) of the variables 'amount of food' and 'proportion of male help'. This is equivalent to performing a principal-component analysis (PCA) to summarize a set of correlated variables but is used when only two variables are to be summarized.

Female bill depth and female emancipation (BMA) are highly significantly correlated (figure 2; $r = 0.41$, $n = 61$, $p = 0.001$) and the correlation is consistent across the three study years (data not shown). This correlation is independent of individual variation in body size: first, bill depth is only weakly correlated with body size (correlation with tarsus length: $r = 0.16$, $n = 75$, $p = 0.17$; correlation with PC body size: $r = 0.19$, $n = 70$, $p = 0.12$); and second, bill depth corrected for body size (using the residuals of bill depth on PC body size) is also strongly correlated with the BMA ($r = 0.42$, $n = 57$, $p = 0.001$). The correlation shown in figure 2 does not simply reflect the difference between secondary and monogamous females because positive correlations are also present when each group of females is considered separately (secondary females: $r = 0.49$, $n = 18$, $p = 0.039$; primary and monogamous females: $r = 0.37$, $n = 43$, $p = 0.014$). Evaluating each variable of the BMA separately using partial correlation shows that females with deeper bills tend to settle in territories with more food ($r_{\text{constant help}} = 0.23$, $n = 61$, $p = 0.073$) and receive less male help ($r_{\text{constant food}} = -0.29$, $n = 61$, $p = 0.024$).

We investigated various factors that influence how much care a male provides using an analysis of covariance (ANCOVA) with individual nests as the statistical unit ($n = 68$). Using a step-wise procedure we determined the best subset of factors explaining variance

Figure 2. Female bill depth in relation to the bivariate major axis (BMA, see § 3) 'emancipation'. Increasing values indicate territories with increasing food abundance and decreasing male parental assistance (factor loadings, food $r = 0.79$, help $r = -0.79$). The larger symbols represent two individuals with identical scores.

in the amount of male help. This analysis shows that secondary females receive less help than other females, that male help declines over the season, that males with long tails help less than males with short tails, and that females with deep bills receive less help than females with shallower bills. Food abundance (factor loadings, food $r = 0.79$, help $r = -0.79$). The effect of female bill depth is significant in any reasonable variant of the presented model and remains when male characters (age and tail length) are excluded ($F_{1,64} = 7.1$, $p < 0.01$).

4. DISCUSSION

Our main finding is that, in the polygynous dusky warbler, females with stronger bills were more likely to breed in territories with high food abundances where they received less paternal care. This result at the intraspecific level corroborates evidence from a comparative study of *Acrocephalus* warblers' mating systems (Leisler & Catchpole 1992), which showed that species with strict biparental care had relatively slim bills, bred in unproductive habitats and fed their nestlings with small prey items. Polygynous and promiscuous species with a high degree of uniparental care had stronger bills, bred in habitats with more food and fed their nestlings with larger prey. Our results suggest that female emancipation from male help in raising the brood, through female bill morphology and territory quality, is an important factor determining the mating system of this species. Thus, the 'decision' to become polygynous cannot be viewed independently from the ability of the female to raise her young without male assistance. Our study thus supports the 'constrained-female hypothesis' (Gowaty 1996). However, we do not claim that female mating behaviour in the dusky warbler can be reliably predicted from bill measurements. Other factors, such as the availability of unmated males, will also affect the outcome of a female's mating decision. This renders it less likely that a significant effect of bill

Table 1. ANCOVA explaining the amount of male assistance in brood provisioning at 68 dusky-warbler nests ($r^2 = 0.64$).

(A nested design is used because male tail length strongly depends on male age. This means that a separate regression coefficient of tail length is estimated within each level of the factor male age (dichotomized into first-year males and older males). Therefore, the factor male age, although non-significant, cannot be omitted from the model. When 'food abundance' is entered as a covariate, its effect is non-significant and the p values for the other variables remain basically the same.)

factor/covariate	d.f.	sum of squares	F	p
hatching date	1	0.333	16.59	0.0001
female status	1	0.316	15.79	0.0002
female bill depth	1	0.185	9.22	0.0035
male age	1	0.000	0.01	0.9150
male tail length (nested within male age)	2	0.270	6.74	0.0023
food abundance*	1	0.016	0.80	0.3750
(residual)	61	1.223		

*Excluded from the presented model.

morphology on mating status will be observed within a limited sample of females (see the effect of a single outlier in figure 1). We now discuss possible mechanisms by which deeper bills may facilitate uniparental care by the female. We then consider how the intraspecific correlation between bill morphology and mating behaviour may be caused.

There is little doubt that intraspecific variation in bill morphology is correlated with individual prey-size preferences (e.g. Grant *et al.* 1976; Herrera 1978; Grant 1985; Gosler 1987; Price 1987; Smith 1987; W. Forstmeier, unpublished data). There are three possible explanations of why females in rich habitats with little male help may, on average, catch larger prey items than other females. First, birds in rich habitats may specialize in large prey. Small prey items are always much more abundant than large prey items (e.g. Leisler & Catchpole 1992; W. Forstmeier, unpublished data). It is likely that in poor habitats all sizes of prey have to be used, whereas in rich habitats the absolute abundance of large prey may be high enough to allow the birds to specialize in it (Leisler & Catchpole 1992). Second, unassisted females may catch larger prey further away from the nest. Sejberg *et al.* (2000) found that female great reed warblers with little or no male assistance fed their young with larger prey items than did assisted females. The authors hypothesized that unassisted females may be forced to travel longer distances than assisted females in order to compensate for the lack of male help. According to the central-place-foraging theory (Orians & Pearson 1979), prey size should increase with travelling distance. Consequently, unassisted females should catch larger prey. However, this hypothesis is weakened by contradicting results from studies that showed that widowed females foraged closer to the nest (Sasvári 1986; Aho *et al.* 1997). A combination of different mechanisms is probably required to explain fully the findings of Sejberg *et al.* (2000) with regard to the prey-size choice of males and females. Third, prey

size may increase with time constraints. Unassisted females need to catch prey at a higher rate than assisted females (Sasvári 1986; Pinxten & Eens 1994; Aho *et al.* 1997) and they may achieve this by increasing search speed (Sasvári 1986; Aho *et al.* 1997; W. Forstmeier, unpublished data) and by using more energy-consuming foraging manoeuvres (Nyström 1990; W. Forstmeier, unpublished data). Interspecific comparisons suggest that, in small foliage-gleaning passerines, increased speed of search should result in the capture of predominantly large prey items (e.g. *Regulus ignicapillus* versus *Regulus regulus*, Leisler & Thaler 1982; Thaler & Thaler 1982; *Parus cristatus* versus *Parus ater*, Mattes *et al.* 1996; M. Pollheimer and B. Leisler, unpublished data). Brood-size manipulations in starlings and pied flycatchers produced equivocal results with regard to the effects of increased workload on prey size (Lifjeld 1988; Wright & Cuthill 1990; Siikamäki *et al.* 1998; Wright *et al.* 1998). However, these results do not necessarily contradict our hypothesis, as much depends on the foraging techniques used by the respective species and neither starlings nor pied flycatchers are foliage-gleaners like the dusky warbler. For any of the above reasons, unassisted females in rich territories may catch larger prey items than assisted females in poor territories (as in the study by Sejberg *et al.* 2000), and females with stronger bills may be better adapted to do so.

The observed correlation between female bill morphology and her decision of where to breed (figure 2) is unlikely to be due to chance ($p=0.001$). It is also unlikely to be explained by confounding variables such as female body size (see § 3), age (bill depth is independent of age; W. Forstmeier, unpublished data; see also Gosler (1987)), competitive ability (females do not compete aggressively for breeding sites; Forstmeier *et al.* 2001) or timing of arrival (bill depth is not correlated with arrival date; data not shown). Therefore, the correlation between bill morphology and mating strategy can probably be explained in one of the following ways. First, behavioural differences may induce morphological change. Numerous studies have shown that seasonal variation in bill morphology is associated with dietary changes (e.g. Davis 1954; Gosler 1987; Morton & Morton 1987; Matthysen 1989), apparently through differences in wear of the constantly growing bill. However, in contrast to the pattern we found, the bill depth in females catching larger prey should become smaller rather than larger because larger items are harder and require extended handling times. Thus, this explanation can be rejected. Second, individuals might adjust their behaviour depending on their morphology. We suggest that females with deep bills settle in richer habitats than shallow-billed females. This may be a consequence of between-female differences in estimates of habitat quality. A shallow-billed female would gain less from moving to a richer habitat and suffer more from a lack of male assistance than would a deep-billed female because it cannot use the abundance of large prey items with the same efficiency. On the other hand, a deep-billed female would suffer more from moving to a poorer habitat because its bill might not be optimized for collecting small prey items. The observation that females with deep bills receive less male assistance than females with shallow bills may be the result of deep-billed females being better able to

compensate for a lack of male help. Males may adjust their paternal effort to the female's ability to feed nestlings alone. Third, morphology and behaviour may be genetically correlated. Pleiotropic effects of genes on both the morphological and the behavioural traits could cause such genetic correlations (Falconer 1989).

In most bird species the heritability of bill depth is high ($h^2 > 0.5$ in four out of five species; Smith & Zach 1979; Grant 1983; Gosler 1987). Females inheriting a relatively deep bill should (either through learning from experience or through inherited behavioural differences) show a higher disposition to mate as a secondary female. Demonstrating that female mating strategy is heritable is, however, virtually impossible. We agree with Dominey (1984) that the vast majority of alternative mating tactics are due neither to a simple genetic polymorphism of alternative strategies nor to a single conditional strategy with genetic uniformity of all individuals. Ecological circumstances and condition-dependent and heritable components may all simultaneously influence a female's mating decision. In conclusion, the polygyny threshold might differ for two females of the same age and condition arriving at the same time but differing in heritable components of bill morphology.

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