



Polygyny in the dusky warbler, *Phylloscopus fuscatus*: the importance of female qualities

WOLFGANG FORSTMEIER*†, DRIES P. J. KUIJPER‡ & BERND LEISLER*

*Max Planck Research Centre for Ornithology, Vogelwarte Radolfzell

†Department of Animal Ecology and Tropical Biology, University of Würzburg

‡Zoological Laboratory, University of Groningen

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The polygyny threshold model states that secondary females gain benefits from high territory quality that outweigh the costs of sharing a male. We aimed to test this prediction using the dusky warbler as a model species. We first showed that neither the shifted sex ratio hypothesis nor the no-cost models were likely to apply to our study. Secondary females settled in territories of higher quality (high food abundance, low predator density) and had a nonsignificantly higher reproductive success than simultaneously settling monogamous females. However, there were strong indications that these two groups of females differed intrinsically. Secondary females were older than late monogamous females, and while they replaced lost clutches more often, they also suffered from a nonsignificantly higher winter mortality. Consequently, it was impossible to tell whether differences in reproductive success were caused by differences in territory quality or in female qualities. Our study suggests that female choice may also depend on characteristics that are specific to the individual, and may therefore be more sophisticated than allowed for in traditional polygyny models. In other words, the polygyny threshold may be not the same for all individuals. We suggest that prior breeding experience may help older females to profit more from the benefits and to suffer less from the costs of polygyny than young females.

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Social monogamy is the prevalent mating system for the vast majority of bird species, and it is usually combined with biparental care of the offspring (Lack 1968; Ligon 1999). The most common deviation from monogamy is polygyny, which has been recorded in 39% of well-studied European passerine species (Møller 1986). More than 30 years ago, the polygyny threshold model (PTM) was developed (Verner 1964; Verner & Willson 1966; Orians 1969), which explained territorial polygyny as an adaptive strategy originating from female choice. According to this model, a female can gain higher fitness by mating with an already paired male in a high-quality territory than by joining an unpaired male in a poor territory. The cost of sharing the male's parental efforts with his primary female is offset by direct or indirect benefits from high breeding situation quality (BSQ), which may include territory quality, male parenting abilities and male genetic quality (sexy son hypothesis; Weatherhead & Robertson 1979).

Correspondence: W. Forstmeier, Vogelwarte Radolfzell, Am Obstberg, D-78315 Radolfzell, Germany (email: forstmeier@mail.uni-wuerzburg.de). D. P. J. Kuijper is now at the Laboratory for Plant Ecology, Rijksuniversiteit Groningen, Postbus 14, NL-9750 AA, Haren, The Netherlands.

Numerous field studies have been conducted to test the assumptions and predictions of the PTM empirically (reviewed in Davies 1989; Searcy & Yasukawa 1989, 1995; Ligon 1999; Slagsvold & Lifjeld 1994), and interest in this topic is still active (Bensch 1996; Hansson et al. 2000; Pribil & Searcy 2001). Generally it has been recognized that a single model is unable to explain all cases of territorial polygyny in birds (Searcy & Yasukawa 1989, 1995; Ligon 1999). According to Searcy & Yasukawa (1989), the most important alternatives that need to be considered are the skewed sex ratio model (Skutch 1935), the no-cost models (Lightbody & Weatherhead 1987) and the no-compensation models (Haartman 1969; Alatalo et al. 1981). Few studies have supported the PTM (e.g. Pleszczyńska 1978; Temrin & Jakobsson 1988; Petit 1991; Bensch 1996), while the majority have found that secondary females breed less successfully than simultaneously settling monogamous females (reviewed in Slagsvold & Lifjeld 1994; see also Johnson et al. 1994). The approach these studies have usually taken is to compare the reproductive success of secondary females with that of monogamous females settling simultaneously in the study area. This approach assumes that a key prediction of the PTM is that the breeding success of

secondary females should at least equal that of simultaneous monogamous females. However, this is the case only if these two groups of females do not differ in their intrinsic qualities (Altmann et al. 1977; Davies 1989). If secondary females are of low quality, this might alternatively explain their low reproductive success as found in many studies (Slagsvold & Lifjeld 1994).

However, few studies have investigated the possibility that individual females may differ in their decision rules (but see Bakker et al. 1999; Qvarnström et al. 2000). Female choice may depend on qualities and characteristics that are specific to the individual, such as breeding experience or body condition (a conditional strategy; Caro & Bateson 1986). A similar idea was proposed by Gowaty (1996): according to the constrained-female hypothesis some females may depend more on the assistance of the male in rearing offspring than others. This implies that the polygyny threshold might differ between females.

We studied (mono-) territorial polygyny in a migrant passerine, the dusky warbler, and in particular the importance of individual variation between females. We first tested whether the PTM can explain the occurrence of polygyny in the dusky warbler. We followed the instructions of Searcy & Yasukawa (1989) in testing between the possible alternative explanations. Assuming that polygyny in territorial birds is never based on male coercion (Searcy & Yasukawa 1989), the procedure consists of three steps. We have rearranged the order of these steps to make them easier to follow.

(1) We analysed whether secondary females were forced to pay the cost of polygyny because of the unavailability of unmated males (skewed sex ratio model) or whether there were unmated males present that could provide secondary females with monogamous alternatives (balanced sex ratio models). (2) We investigated whether polygyny is costly to secondary females (cost models) or whether possible benefits from increased harem size immediately outweigh these costs (no-cost models). (3) To distinguish between compensation (PTM) and no-compensation models is inherently difficult (Davies 1989; Searcy & Yasukawa 1989), but some predictions of the PTM can be tested. First, do secondary females experience higher BSQ than simultaneously settling monogamous females? Second, is the occurrence of polygyny related to the magnitude of the difference in BSQ between the best and worst territories?

Following the argument that intrinsic female qualities might influence female mating decisions (assuming that females actively decide about their status) we tested whether secondary females differ from simultaneously settling monogamous females in age or in other characteristics possibly related to their readiness to rear nestlings without male assistance.

METHODS

Study Area and Species

We conducted the study in pristine landscape at the mouth of the Malkachan river, 190 km east of Magadan,

in the Russian Far East (154°14'E; 59°51'N). The area holds extensive bushlands of *Pinus pumila* with some admixture of *Betula middendorffii* and *Alnaster fruticosus*, typically 1–2 m in height, which is the habitat occupied by the dusky warbler.

We studied this dusky warbler population over three consecutive breeding seasons between 1997 and 1999. The dusky warbler is an insectivorous long-distance migrant passerine. It has a sexually monomorphic dull brown plumage and there is little sexual dimorphism (Forstmeier 2001). Dusky warblers winter in southeast Asia (Glutz von Blotzheim & Bauer 1991) and are present in the study area from late May to early September. We followed the birds throughout the breeding season, which comprises only a single brood (second attempts are made only when the first brood is lost early in the season) and an obligatory postnuptial, premigratory moult. In 1997 we restricted our investigations to the central part of the study area described above (area A), and extended it during the following 2 years to the north (area B) and south (area C).

Breeding Data

Male dusky warblers, which arrived on average 6 days in advance of the females, were captured with mist nets as soon as possible after their arrival, and fitted with a unique combination of plastic colour rings. We usually visited male territories every day or second day, and plotted song posts on a detailed map drawn from a 1:5000 scale satellite photograph of the area.

Females were mist-netted and ringed either at arrival, when they moved through the different territories, or (mostly) later at their nests, when incubating or feeding nestlings. We could not trap 16% of females, for example because they deserted their nests early in the season as a result of nest predation. In contrast, we ringed all the males that held territories in the area and also mist-netted a small number of additional males that were thought to be nonterritorial floaters. Unringed floaters could be recognized in the field as being males rather than females, first, by the aggressive behaviour of territorial males towards them and, second, with some confidence, by the 15% difference in tail length between the sexes (Forstmeier 2001).

Dusky warbler nests, which are built by the females in low bushes near to the ground, were mapped and frequently checked to determine the date of laying of the first egg. In all cases where we were able to determine the date of female arrival, the first egg was laid either 7 ($N=1$) or 8 ($N=5$) days after arrival. As a result of the short breeding season females are constrained to start the clutch as soon as possible, and we assume that an interval of 7 or 8 days is the minimal time required for nest building and egg formation. As we found hardly any variation in the length of this period, we defined the date of female settlement as being 8 days before the first egg of the first clutch is laid.

Male polyterritoriality does not occur. We can unambiguously define the social partner of a female as the owner of the territory where she builds the nest. We

determined female ranks in polygynous relations by the order of female settlement. All nonprimary females are referred to as secondary females, including the third, fourth and fifth females.

We inspected each nest frequently (every day or second day during egg laying and around hatching, otherwise about once per 5 days), and determined clutch size, hatching date, hatching success, fledging date, fledging success and incidence of nest predation. On the 12th day of the nestling period, that is, 2.5 days (range 1–4, $N=35$) before fledging, all nestlings were measured and ringed. We measured body mass, wing, tail and tarsus length, and fitted nestlings with metal and colour rings.

In the dusky warbler, nest building and incubation are done solely by females. Male parental effort is restricted to feeding of nestlings and, to a minor extent, fledglings. Nest defence by the male is restricted to warning of predators and was observed only at nests where the male was also feeding. To quantify the amount of paternal investment we recorded feeding behaviour of parents at nests (between 0500 and 2100 hours local time) when the nestlings were 1–15 days old. Feeding trips were counted during short (mean 24 min, range 5–60 min) observation periods at 72 different nests (mean 4.0 observation periods per nest, range 1–11). For each nest we calculated the percentage of feeds by the male. For details see Forstmeier et al. (2001). For a subsample of 20 nests in 1998, absolute feeding rates (feeds/h) were recorded during 1-h periods when nestlings were 10 days old.

This study includes a total of 97 breeding seasons of 84 individual females. Eleven females were included twice and one female three times. We used female breeding seasons as independent observations. We feel this is justified as there was no strong association between individual females and their status in different years. In eight of 13 replications females changed their status in successive years. Retention of status between years was no more frequent than expected by chance (probability of five or more cases of retention occurring by chance is $P=0.335$). The same methodology was adopted by Bensch (1996), who also found no repeatability of status in a sample of 40 females breeding more than once.

Territory Quality

To estimate the quality of territories we measured aspects of (1) food availability, (2) potential nest predation pressure and (3) availability of potential nest sites.

(1) During the nestling period (late July) in 1998 and 1999 we sampled the arthropod fauna of bush vegetation by shaking the content of branches into an umbrella. We summed the volumes of all arthropods in a sample (measuring length, breadth and height on millimetre paper) and calculated mean arthropod volume per sample ($N=30$) for each territory ($N=45$) and year ($N=2$). For details see Forstmeier et al. (2001).

(2) The most important predator of dusky warbler nests in the study area appears to be the Siberian chipmunk, *Tamias sibiricus*, occurring in densities of ca. 20 individuals/ha (Weiß 2000). We estimated chipmunk densities by carrying out line transect counts (Burnham

et al. 1980) for each territory in 1998 and 1999 (mean 4.5 counts per territory and per year; Weiß 2000). We applied a square-root transformation of resulting values to fit the density estimates to a normal distribution.

(3) On the basis of experience gained from a total of 101 dusky warbler nests found in the study area we estimated the approximate number of potential nest sites (number of bushes capable of holding a well-concealed nest) for each territory. Estimated numbers, ranging from 5 to 250 per territory, were log transformed.

Morphology

The same person (W.F.) measured all the birds, to prevent observer-specific variation. The following morphological characters of females were measured: wing length, tail length, tarsus length, footspan with claws, bill depth, bill width and body mass. Using the tarsus, footspan and bill measurements we extracted one principal component (PC body size) that reflects body size independently of body mass and feather measurements.

Body mass was strongly dependent on the stage in the breeding cycle of individual females ($r^2=0.60$, $N=89$ measurements). Body weight tended to increase from day 8 to day 3 prior to the laying of the first egg but not significantly so ($\bar{X} \pm \text{SE}=0.18 \pm 0.09$ g/day; $r_6=0.62$, $P=0.10$). During egg laying, females were a mean \pm SE of 1.9 ± 0.19 g ($N=6$) heavier than the average weight outside the egg-laying period ($\bar{X} \pm \text{SE}=9.33 \pm 0.08$ g, $N=83$; t test, two tailed: $t_{87}=9.9$, $P<0.001$). From the day of laying of the last egg to the day of fledging of the young, female body mass decreased by a mean \pm SE of 0.065 ± 0.006 g/day ($r_{73}=-0.76$, $P<0.001$). Female weight measurements were standardized with the residuals from the above regressions, to eliminate the influence of stage of breeding cycle. In addition, weights were corrected for differences attributable to visible fat deposition, which varies markedly with time of day. Fat deposition, estimated in nine distinct classes (according to Kaiser 1993), accounted for 14% of the variation in weights that had been corrected for stage in breeding cycle as described above. Weights increased by 0.136 g per class of fat score ($r_{87}=0.38$, $P<0.001$). The influence of fat score was eliminated by standardizing weights with the residuals from this regression. When available, multiple values for the same female were averaged within seasons. Repeatability (calculated following Lessells & Boag 1987) of lean mass estimates for individual females was still low, but substantially higher than repeatability of untreated weight measurements (+0.23 versus -0.36).

For each bird we recorded states of active moult and the extent of moult that had taken place in the winter quarters. Dusky warblers undergo a complete postnuptial moult of body and flight feathers on the breeding grounds, which, in our study area, usually started around 25 July. However, late-breeding females, which were still feeding their offspring at this time, delayed the onset of moult until their young were independent, which was as late as 20 August. A variable number of tail feathers (most commonly the central pair) and tertials (usually all of them) can be moulted in mid or late winter (unpublished

Table 1. Occurrence of polygyny in study areas A, B and C from 1997 to 1999

	A 1997	A 1998	A 1999	B & C 1998	B & C 1999
Number of territories	17	16	7	42	21
Unmated males	3	2	1	4	1
Monogamous males	9	12	5	23	19
Polygynous males (2 females)	4	1	1	4	1
Polygynous males (3 females)	1	1	0	2	0
Polygynous males (5 females)	0	0	0	1	0
Status unknown	0	0	0	8	0
Floating males*	+	+	–	+	–
Rate of polygyny (%)	36	14	17	23	5
Breeding density (males/ha)	0.58	0.54	0.24	0.46	0.23
Secondary females	6	3	1	12	1

*Floating males were present in low numbers in 1997 and 1998, but were absent in 1999.

data). These fresh feathers are easily distinguished from older feathers by marked regular growing bars (these are always absent in feathers of postnuptial moult) and their better condition.

Statistical Analysis

For statistical analysis we used the exact permutation null distribution in chi-square tests (using StatXact 4.0 for Windows, Cytel Software Corporation, Cambridge, Massachusetts, U.S.A.) and in logistic regressions (using LogXact 4.1 for Windows, Cytel Software Corporation), since the use of an asymptotic distribution for inference is problematic when sample sizes are small.

RESULTS

Skewed Versus Balanced Sex Ratio

Table 1 lists the numbers of territorial males and their mating status for various parts of the study area and for each year separately. The population size and especially the number of secondary females decreased dramatically from high levels in 1997 and 1998 to low levels in 1999. This population decline was apparently caused by unusually high mortality outside the breeding season. As a consequence, in 1999, only territories of high quality were occupied by males (shown below in detail).

In 1997 and 1998 the number of secondary females exceeded that of unmated territorial males, suggesting a slightly unbalanced sex ratio (Table 1). However, in these years, we also observed a small number of unringed males in the study area that were thought to be floating males without territories. Unmated males were available to secondary females within a mean radius \pm SD of 380 ± 139 m ($N=22$, range 60–740 m) from the place where they nested. This means that they would have needed to sample a mean \pm SD of 4.3 ± 2.2 neighbouring males (range 1–10, but 6 or less in 20 out of 22 cases) to meet an unmated male (i.e. the number of males within the above given circle around the nest). Circumstantial evidence suggests that this might be feasible. Three females were mist-netted elsewhere, the day before they were observed

on their nesting territory for the first time. These had to move at least 660, 880 and 1370 m through dusky warbler habitat and thereby pass at least three, five and nine dusky warbler territories to reach the place where they started nest building 1 or 2 days later.

Cost Versus No Cost of Polygyny

Figure 1 shows how much males contributed to the feeding of nestlings. The data presented are raw means, not adjusted for differences in average nestling age and time of day at observation. Adjusting for these factors did not lead to any significant change of mean value. Polygynous males concentrated their feeding effort almost exclusively on their primary female. Secondary females received no male help in the majority of cases. Out of 16 secondary nests (11 secondary, four tertiary and one quarternary), where feeding data are available, only four nests (three secondary and one tertiary) received a small amount of male help (on average 10 and maximally 18% of the feeds observed at the nest).

The fact that secondary females encountered a clear cost of polygyny in terms of reduced male assistance was

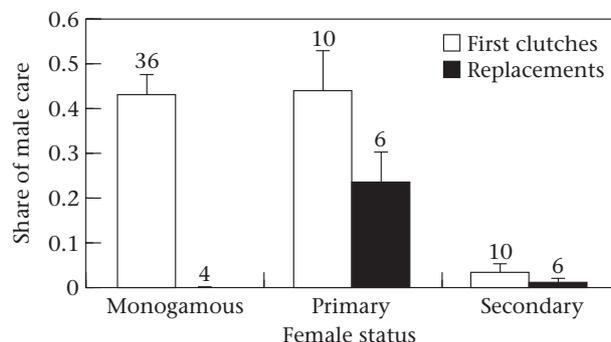


Figure 1. Proportion of male assistance (feeds at the nest) at nests of monogamously mated females, primary females of polygynous males and all secondary females (second to fourth) of polygynous males. Sample sizes (number of nests) and SE are given. Replacement clutches made after predation of the first clutch are depicted separately, as the intensity of male help declined significantly over the season (Forstmeier et al. 2001).

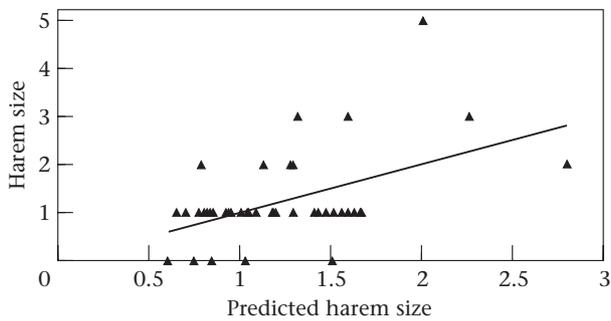


Figure 2. Multiple regression between harem size of 45 territories in 1998 and three measures of territory quality: arthropod density (standardized regression coefficient: $\beta=0.36$), predator density (Siberian chipmunks, $\beta=-0.28$) and abundance of possible nesting sites ($\beta=0.20$). The line indicates where harem size equals predicted harem size.

not a by-product of paternal care declining as the season progresses, but was clearly due to their social status (ANCOVA with date and status as main effects: date: $F_{1,69}=17.7$, $P<0.0001$; status: $F_{1,69}=23.5$, $P<0.0001$; male care adjusted for nestling age, see Forstmeier et al. 2001). In contrast, there appeared to be little or no cost of polygyny to the primary females. Males always appeared to be reluctant to feed at a secondary nest, even when the nest of the primary female was depredated. We therefore did not find much potential for conflict between primary and secondary females. Aggressive encounters between females were never observed.

From 18 nests of secondary females we found nine situated within and nine outside a circle covering 50% of the territory area around the primary female's nest, suggesting a random distribution with regard to between-nest distances. The average distance between primary and secondary nests was 72 m (range 15–160 m). To human ears, alarm calls are perceptible only within 50–100 m. These findings indicate that benefits from communal predator defence are marginal (Picman et al. 1988).

Do Secondary Females Experience Higher BSQ?

Because of small sample sizes in 1997 and low rates of polygyny in 1999 (Table 1), we concentrated on the data from 1998 to analyse how harem size depends on territory characteristics. A test for consistency in female choice (see below) indicates that the patterns were similar between years. Harem size increased with arthropod and nest site densities and decreased with predator (Siberian chipmunk) densities (Fig. 2). A multiple regression with these variables explained 24% of the variation in harem size and was significant at $P=0.009$ ($N=45$ territories). In a stepwise multiple regression, the first variable entering the model was predator density ($R=-0.33$, $F_{1,43}=5.17$, $P=0.028$). After accounting for variation in predator density, inclusion of arthropod density significantly improved the model ($R=0.32$, $F_{1,42}=5.57$, $P=0.025$). Finally, availability of potential nest sites improved the model further, although not significantly ($R=0.20$, $F_{1,41}=4.41$, $P=0.178$). The three factors used to explain

variation in harem size were largely uncorrelated with each other (not shown).

The PTM predicts that polygyny will occur only if the difference in BSQ between the best and the worst territories exceeds a certain threshold value. In 1999, when population density was much lower than the year before (Table 1), only the best territories were occupied by males. Territories occupied in 1999 had a mean predicted harem size (from the relationship between harem size and territory quality in 1998; see Fig. 2) of 1.35, which differed significantly from those remaining unoccupied in 1999 (predicted harem size of 0.97; t test, two tailed: $t_{32}=-2.38$, $P=0.023$). The fact that the rate of polygyny was also lower in 1999 (Table 1) is in accordance with the PTM.

The low rate of polygyny in 1999 and the small study area covered in 1997 render analysis of consistency of female choice between years difficult. Furthermore, patterns can be influenced by the same females returning to the same territory in consecutive years. Therefore, we looked at those secondary females that were new to study area A in 1998 or to the overall area in 1999 ($N=4$). All four settled on territories that had been polygynous before in a previous year. The one-tailed probability of this occurring by chance is $P=0.04$. In all four cases the owners of polygynous territories were different from those that had occupied these territories in previous years.

Another prediction of the PTM is that polygynous territories are settled by primary females earlier than females settle on monogamous territories. Analysing the order of mating for 29 territorial males (five polygynous and 24 monogamous males) in 1998, we found that polygynous males mated significantly earlier than monogamous males (t test: $t_{28}=3.78$, $P<0.001$). Four days after the arrival of the first female all polygynous males were mated, while only 25% of the monogamous territories were settled by females.

In conclusion, BSQ for secondary females depended solely on territory quality (not on male quality), and secondary females experienced higher territory quality than monogamous females.

Are Secondary Females Different?

Table 2 compares reproductive and morphological data between different groups of females. Note that morphological data reflect female traits, while reproductive data may depend on both BSQ and intrinsic female qualities. As this comparison is aimed to make sure that female groups did not differ intrinsically, we highlighted all differences with $P<0.1$ and did not apply a Bonferroni correction (Rice 1989). Although this approach reduces the probability of statistical errors of type II, marginally significant results will require corroboration by other data sets. Monogamous females were split into two groups, depending on settlement date. Within each year, we selected those monogamous females (late monogamous) that best matched the secondary females of that year with regard to arrival date. There were no primary females arriving simultaneously with secondary females.

Table 2. Reproductive and morphological data for four groups of females: primary (P1) and secondary (P2) females of polygynous males and early- and late-breeding monogamous (M) females

Female group	Date of first clutch	Clutch size	Clutch size corrected	Renesting frequency	Age class	New tail feathers	Tail length (mm)	Wing length (mm)	PC body size	Mass residuals (g)
P1	18.6 (15)	5.13 (15)	5.06 (15)	79% (7)	1.75 (8)	2.14 (7)	46.02 (15)	57.13 (15)	-0.50 (14)	0.015 (14)
M early	18.6 (20)	5.52 (20)	5.28 (20)	36% (11)	1.67 (12)	3.31 (16)	46.62 (20)	57.35 (20)	0.14 (18)	-0.012 (18)
M late	22.6 (22)	5.05 (21)	4.98 (21)	0% (2)	1.44 (16)	4.50 (19)	46.03 (22)	56.92 (22)	-0.01 (21)	-0.018 (21)
P2	23.6 (22)	4.97 (17)	5.26 (17)	100% (10)	1.79 (14)	2.19 (16)	46.52 (22)	57.27 (22)	0.09 (20)	0.043 (20)
Test	<i>t</i> test	<i>t</i> test	<i>t</i> test	χ^2 exact	χ^2 exact	Wilcoxon	<i>t</i> test	<i>t</i> test	<i>t</i> test	<i>t</i> test
P2 vs non-P2	0.001	0.209	0.482	0.011	0.352	0.104	0.534	0.691	0.518	0.507
P2 vs M late	0.720	0.770	0.259	0.015	0.072	0.036	0.322	0.403	0.788	0.454

Sample sizes (in parentheses) are numbers of females. Clutch size corrected is clutch size after removal of effects of laying date. Age class is mean age of females classified with significance by discriminant analysis as 1 (first year) or 2 (older), including ringed birds of known age. New tail feathers is the number of tail feathers moulted in winter. Tail length was measured on old feathers, not moulted in winter. PC body size is a principal component on hindlimb and bill measurements. Mass residuals are from a regression on PC body size. Bold print highlights P values <0.1 .

Variation in clutch size depended strongly on laying date and thereby also on the frequency of clutch replacement. When we corrected for effects of laying date (clutch size declined by 0.069 eggs/day; $r_{80} = -0.563$, $P < 0.001$), secondary females did not lay fewer eggs than late monogamous females. For a medium effect size of $D = 0.5$ (i.e. here a difference of 0.34 eggs) the two-tailed power of this test is 0.32. More significantly, secondary females differed from monogamous females in their ability or readiness to replace lost clutches. Because of the brevity of the breeding season, replacement clutches were undertaken only when predation occurred early in the season. Nests lost after 12 July were never replaced and therefore excluded from the analysis. The data in Table 2 reflect how often clutches lost before 13 July were replaced. The validity of the finding that both secondary and primary females replaced a much higher percentage of lost clutches than monogamous females is not affected by differences in the mean date of nest predation. However, the relatively large clutches and the renesting ability of secondary females may be due either to differences in intrinsic female qualities, or to differences in environmental conditions, such as high food density in polygynous territories.

There were also morphological differences between secondary and late monogamous females. Secondary females moulted significantly fewer tail feathers on their wintering grounds than late monogamous females. There are strong indications that tail growth is related to age (Fig. 3). Out of 15 females that were captured in 2 consecutive years, 13 increased their tail length by more than 0.8 mm (on average by 1.31 mm; paired t test: $t_{14} = 5.6$, $P < 0.001$). Tail length therefore increased with age. Furthermore, none of 13 females that were known (by ringing) to be older than 1 year had moulted more than two tail feathers in winter. In contrast, three first-year females (ringed as nestlings the year before), had

moulted two, four and eight tail feathers. While only 54% of females had tails longer than 44.5 mm and no more than two winter-moulted tail feathers, this population included all 13 females known to be older than 1 year and 13 out of 16 secondary females (Fig. 3).

We used tail length and winter moult in a discriminant analysis to assign females of unknown age to one of the two age groups (first-year versus older; Fig. 3). The discriminant function classified 15 out of 16 females of known age correctly and 51 females of unknown age were grouped into: 17 'confident' first-years ($P < 0.05$), five 'uncertain' first-years ($P > 0.05$), 20 'confident' older and

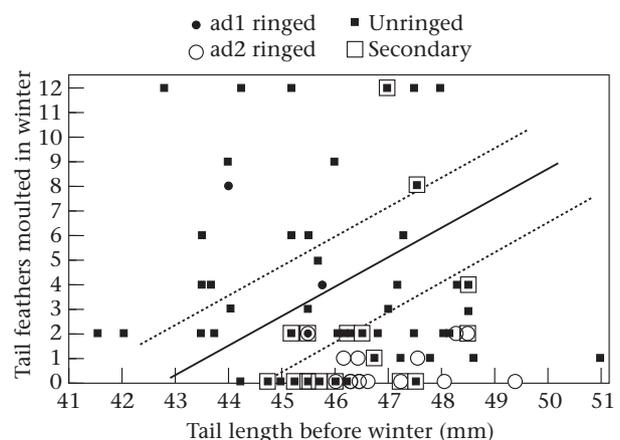


Figure 3. Scatterplot of tail length and winter moult for 68 females. Tail length was measured on unmoulted feathers unless all 12 feathers were moulted. Three females were known to be first-year birds (ad1 ringed), 13 were known to be older than 1 year (ad2 ringed) and 52 were of unknown age (unringed). Tail characteristics of 16 secondary females (one ad1 ringed, two ad2 ringed, 13 unringed) are shown. A discriminant analysis was used to separate females into first year and older (continuous line). Individuals outside the dashed lines were assigned with significance ($P < 0.05$).

Table 3. Parameters of breeding success for four groups of females: primary (P1) and secondary (P2) females of polygynous males and early- and late-breeding monogamous (M) females

Female group	Clutches per season (females)	Fledging success (nests)	Fledged young (females)	Fledging mass (nests)	Winter survival of females (%)
P1	1.44 (16)	0.52 (21)	3.31 (16)	10.33 (10)	46 (13)
M early	1.17 (24)	0.44 (27)	2.17 (24)	10.26 (12)	42 (15)
M late	1.03 (34)	0.40 (35)	1.91 (34)	10.61 (16)	32 (13)
P2	1.52 (23)	0.47 (30)	2.83 (23)	10.57 (12)	17 (20)
Test	χ^2 exact	χ^2 exact	<i>U</i> test	<i>t</i> test	χ^2 exact
P2 vs M late	<0.001	0.588	0.177	0.859	0.164

Sample size of females or nests included in the analysis is given in parentheses. The number of clutches includes first clutches and possible replacement clutches. Fledging success is the proportion of nests producing at least one fledgling. Fledging mass increased by 0.543 g/mm of tarsus length ($r_{233}=0.67$, $P<0.001$), and was adjusted to fit the mean tarsus length of 24.0 mm (tarsus measured as shown in Schmid & Spitznagel 1985) to eliminate effects of brood sex ratio and heritable components of body size. Survival data are taken from Table 4 and the test between P2 and M late was calculated as in Table 4. The *P* value is for a difference in the 2 years combined. Bold print highlights *P* values <0.05.

nine 'uncertain' older. Those that were determined with significance (later referred to as 'confident') plus those of known age class (referred to as 'certain') were included in the numbers given in Table 2, while those determined at $P>0.05$ (referred to as 'uncertain') were excluded from the table. According to this, there was a nonsignificant tendency for secondary females to be older than late monogamous females (χ^2 exact test, two tailed: $\chi^2=3.77$, $P=0.072$).

We tested whether the probability that a female will mate as a secondary female depended on her age, while controlling for the effect of arrival date. A logistic regression explaining female status (secondary versus nonsecondary) showed that the effect of age was significant (arrival date: $\beta=5.8$, $P=0.0004$; female age: $\beta=2.4$, $P=0.028$; $N=50$ females as in Table 2; entering year as a stratum variable; exact computation using LogXact 4.1 for Windows, Cytel Software Corporation, Cambridge, Massachusetts, U.S.A.). This result is robust to whether 'uncertain-aged' females are included or excluded ($N=67$ versus $N=50$), and to whether 'year' is entered as a factor or as a stratum variable (*P* values for the effect of age range from 0.019 to 0.028).

One additional finding supports the validity of our ageing technique. Ten out of 17 females breeding in study area A in 1998 (see Table 1) were ringed there in the previous year, nine as adults and one as a nestling. Taking into account the high site tenacity of adult female dusky warblers (Forstmeier 2001), the remaining seven unringed females should be newly recruited first-years. A discriminant analysis (Fig. 3) assigned five of them as confident first-year, one as uncertain older and one could not be trapped.

Measurements of wing length, body size and residual body mass (as a measure of body condition) revealed no significant differences between secondary and late monogamous females (Table 2). For a medium effect size of $D=0.5$ the two-tailed power of these tests is between 0.35 and 0.37, depending on the respective sample sizes.

Compensation versus No Compensation

Since secondary females differ from late breeding monogamous females in being older and in replacing lost clutches more frequently, comparing the reproductive success of these two groups is not a legitimate test of the PTM, as effects of BSQ cannot be distinguished from effects of intrinsic female qualities. Nevertheless it is worth examining the factors that contribute to differences in reproductive success.

Table 3 gives parameters describing the reproductive success of the different groups of females. Secondary females tended (but nonsignificantly) to fledge more young per season than late-breeding monogamous females. To a minor extent, this was caused by a higher fledging success of nest attempts as a result of slightly lower rates of nest predation. Nest predation was the most important factor determining fledging success, as there was no case of nestling starvation. The main factor leading to between-group differences in the number of fledged young was the number of clutches laid per season, that is, the ability or readiness of females to replace lost clutches. Secondary females laid significantly more replacement clutches than late monogamous females (χ^2 exact test, two tailed: $\chi^2=18.9$, $P<0.001$). The fact that primary females also tended to lay more replacement clutches than early monogamous females, although not significantly so (χ^2 exact test, two tailed: $\chi^2=3.53$, $P=0.08$), suggests that all females in polygynous territories might have been facilitated in the replacement of lost clutches by the same factor or combination of factors. Candidate factors shared by primary and secondary females are (1) age, both groups consisting mainly of females older than 1 year (Table 2), and (2) territory quality.

(1) Out of 32 clutches that were lost before 13 July, 69% were replaced. There was no indication that the frequency of clutch replacement was lower in first-year females (6 of 8 replaced). For a medium effect size of $W=0.3$ the power of this test is 0.40.

Table 4. Return rates of ringed females

Female group	Ringed 1997	Returned 1998	Ringed 1998	Returned 1999	Returned 1997–98 (%)	Returned 1998–99 (%)	Mean rate (%)
P1	5	4	8	1	80	13	46
M early arrive	3	2	12	2	67	17	42
M late arrive	3	1	10	3	33	30	32
All but P2	11	7	30	6	64	20	42
P2	6	2	14	0	33	0	17
χ^2 P	1997–1998:	0.335	1998–1999:	0.155	Years combined:		0.044
Early finish	12	9	26	6	75	23	49
Late finish	4	0	21	0	0	0	0
χ^2 P	1997–1998:	0.019	1998–1999:	0.027	Years combined:		0.001
Early finish non-P2	10	7	20	6	70	30	50
Early finish P2	2	2	6	0	100	0	50
χ^2 P	1997–1998:	1.000	1998–1999:	0.280	Years combined:		0.646

Female groups: primary (P1) and secondary (P2) females of polygynous males, and early- and late-breeding monogamous (M) females. Late finish comprises females that fledged young only after 25 July. The first χ^2 exact test is between P2 and all non-P2 females. The P value for years combined was calculated by stratified crosstabulation according to [Robins et al. 1986](#).

(2) There are indications that the territory per se influenced whether females replaced their lost clutches. Two out of 14 monogamous females that lost clutches before 12 July in 1998 and 1999 bred in territories that had been polygynous in one of the previous years. Both of these replaced their clutches, compared to three of the remaining 12 (χ^2 exact test, two tailed: $\chi^2=4.2$, $P=0.11$). Furthermore, there were 10 cases of clutch loss in territories where the clutch of another female had been lost before (in this or in earlier years). In nine of these 10 cases the decision of the two females was identical, which differs significantly from random (binomial test: $P=0.011$). However, BSQ, measured as predicted harem size (see [Fig. 2](#)), did not differ significantly between territories where replacements always occurred and territories where they never occurred (t test, two tailed: $t_{16} = -1.23$, $P=0.24$; the one-tailed power for $D=0.5$ is 0.26).

The weights of nestlings at 11 days of age (and also wing and tail length; data not shown) produced by secondary females did not differ from those of young from late monogamous broods (the two-tailed power for $D=0.5$ is 0.24), indicating that secondary females compensated for the lack of paternal assistance by working harder. Feeding rates of unassisted females were significantly higher than those of assisted females ($\bar{X} \pm \text{SE} = 12.4 \pm 2.0$ feeds/h, $N=7$ nests versus 7.3 ± 0.5 feeds/h, $N=13$ nests; $t_{18}=3.2$, $P=0.005$). Even though high food densities in polygynous territories may have facilitated this, secondary females tended to suffer higher winter mortality ([Tables 3, 4](#)). Survival data for late monogamous females are scanty, making comparisons with secondary females unreliable (χ^2 exact test, two tailed: $P=0.164$; years combined). In a comparison with all other females, secondary females had significantly lower return rates (χ^2 exact test, two tailed: $P=0.044$; years combined). The main reason for this appeared to be their tendency to delay postnuptial moult when replacing a clutch. Females that still had to feed their offspring late in the season

delayed the onset of moult (by about 10–30 days, $N=5$ females) until the independence of young. At the extreme, such females started to moult only when other females had mostly already left the study area. We therefore looked at the return rates of females whose young fledged later than the normal date of onset of moult (25 July). None of 25 females with late-fledging young returned, while 15 of 38 earlier-finishing females were seen in the following year (χ^2 exact test, two tailed: $P<0.001$; years combined; [Table 4](#)). Secondary females with early-fledging young showed no reduction in winter survival compared to nonsecondary, early-finishing females (χ^2 exact test, two tailed: $P=0.646$; years combined).

In conclusion, females faced a clear trade-off between current and future reproduction. Those that replaced a lost clutch had a low chance of survival to the next breeding season. Whether females replaced lost clutches was correlated with both female status and unidentified territory properties.

DISCUSSION

Testing between Polygyny Models

We followed the stepwise procedure proposed by [Searcy & Yasukawa \(1989\)](#) to test between alternative models possibly explaining the occurrence of territorial polygyny in the dusky warbler.

First, our data show that, contrary to the skewed sex ratio hypothesis ([Skutch 1935](#)), there were unmated males available when females decided to mate polygynously. Our study site was chosen to comprise the areas of highest breeding densities. This makes it likely that more unmated males could have been present in the surrounding habitats, as harem size and breeding density tended to be positively correlated (see e.g. [Petit 1991](#); [Kempnaers 1994](#)).

Second, being a secondary female was costly in terms of greatly reduced male assistance, and these costs were unlikely to be outweighed by direct benefits resulting from increased harem size. Ideally, we would need experimental evidence that the lack of male help negatively affects female fitness (Searcy & Yasukawa 1989; Bensch 1997). However, this has been shown for several bird species with comparable amounts of male assistance (reviewed by Bart & Tornes 1989) and the review by Searcy & Yasukawa (1995) indicates that no-cost models apply only to those species with little male help and very large harems. Therefore, it is highly unlikely that the no-cost models could explain polygyny in the dusky warbler.

Third, secondary females settled in territories of high quality, with low predator density, high food abundance and a large number of potential nest sites. The direction of correlation between territory characteristics and harem size suggests that secondary females chose the territory to maximize their chances of breeding success. The negative influence of high Siberian chipmunk densities on reproductive success was shown by Weiß (2000), and the positive effects of high food abundances and numerous nest sites to choose from are intuitive. Other studies have found that food availability is a prime factor in territory selection by secondary females (e.g. Verner & Engelsen 1970; Ewald & Rohwer 1982). Differences between monogamous and polygynous territories in nest predation pressure were found to be important in compensating for the costs of polygyny in many studies (Knapton 1988; Temrin & Jakobsson 1988; Askenmo & Neergaard 1989; Bell et al. 1997; Hansson et al. 2000). With regard to the dusky warbler, we conclude that secondary females are compensated, at least to some degree, by high BSQ.

Whether benefits from high territory quality are large enough to outweigh the cost of polygyny is difficult to answer. The reproductive success of secondary females exceeded that of simultaneously settling monogamous females, although not significantly so. This might be the result of both high BSQ and high female quality. We found that secondary females were more experienced individuals than simultaneous monogamous females, and reproductive success is often age dependent (Dhondt 1989; Gustafsson 1989; Newton 1989; Saether 1990). In addition, secondary and late monogamous females may differ in other respects as is suggested by the differences in relaying behaviour. We discuss this in more detail below.

Despite these difficulties, it should still be possible to rule out the major no-compensation models. The correlation between harem size and BSQ and the temporal patterns of female settlement are consistent with the predictions of the PTM, but not so easy to explain by the deception hypothesis. Furthermore, we observed primary and secondary females simultaneously building nests as close as 15 m from each other. This also contradicts the deception hypothesis, where females are unaware of the presence of other females. The clearest evidence comes from annual variation. In years of low population density the range of used habitat was restricted to the optimal sites and differences in territory qualities did not reach

the polygyny threshold. Neither the female deception hypothesis nor the search cost models (Searcy & Yasukawa 1989; Slagsvold & Dale 1994) can explain why there should be no or almost no polygyny in years of low population size.

The Role of Female Age and Condition

Our data indicate that a female's decision to mate monogamously or as a secondary female was not independent of her age. We can envisage three reasons why this might be.

(1) Older females might be better able to bear the costs of rearing a brood without male assistance. There is an extensive literature indicating that breeding performance improves with age (reviewed in Newton 1989; Saether 1990) and increased foraging ability is certainly one of the main factors leading to this relationship (Desrochers 1992; Forslund & Pärt 1995; Martin 1995).

(2) A female's ability to estimate BSQ may increase with age (see the experience-based choice hypothesis of Wootton et al. 1986), so the benefits a female can gain from mating as a secondary female may also be age dependent. Earlier studies have suggested that individuals may use the breeding success of birds in previous years to evaluate territory quality (e.g. Boulinier & Danchin 1997).

(3) If the residual reproductive value of a female decreases with age (Williams 1966; Pianka & Parker 1975), the cost of polygyny, in terms of a reduction in female condition, should decrease with age as well. There is accumulating evidence that, even in short-lived passerines, annual mortality increases with age after the first breeding season (Newton 1989; Ricklefs 1998). Old females should therefore be more ready to concentrate all reproductive effort in the current breeding season, in what is sometimes termed 'big-bang reproduction' (the residual reproductive value hypothesis; Williams 1966; Pianka & Parker 1975; Pugesek 1981; Curio 1983).

The last point indicates that not only age but also female body condition might influence mating decisions. Females in good condition may be able to bear the costs of polygyny without seriously impacting their residual reproductive value, or only such females may be able to compensate for the lack of male assistance. Females in good condition might therefore more often decide to breed in a secondary position. Under certain ecological conditions, however, the opposite might also occur. Given that body condition is crucial for winter survival, but does not seriously affect a female's ability to rear nestlings, females returning from winter quarters in poor physical condition may do best by going for 'big-bang reproduction'. As such a female will not benefit much from investing in her own condition, she might rear higher-quality offspring as a secondary female than she could have done with the help of a male in a low-quality territory. The nature of the relationship between female quality and the readiness to rear broods without male help depends on the actual selection regime.

In our study, all secondary females replaced their clutches if these were lost before 13 July. An apparent

consequence of this was that none of them returned the next breeding season. We can therefore reject the hypothesis that secondary females chose this mating option because they could tolerate the lack of male help without impacting their winter survival. Rather, the readiness of secondary females to go for 'big-bang reproduction' suggests that females of low residual reproductive value decided to mate as secondary females. The willingness of secondary female dusky warblers to increase the fitness of their offspring at the expense of their own survival may be further supported by the fact that females do not overlap reproduction with moult. The trade-off between these two activities has been demonstrated before (Nilsson & Svensson 1996; Svensson & Nilsson 1997) and overlapping may greatly reduce offspring fitness (Hemborg & Lundberg 1998). Secondary female dusky warblers seem ready to reproduce in the current breeding season at any cost.

We have no way of estimating the residual reproductive value of females when they arrive in our study area. Nevertheless, condition may well play a part in their decision making. During the short period of female settlement, old females arrived an average of 3 days earlier than first-year females (t test: $t_{43}=3.48$, $P=0.001$). While it is normal for a first-year female to arrive rather late, late arrival in old females may be indicative of poor condition. Differences in body condition and future reproductive expectations may therefore lead late-arriving, old females to prefer good territories, while young females mate monogamously to maximize their chances of survival.

Evidence from Other Studies

Of the 16 papers reviewed by Slagsvold & Lifjeld (1994) that compared reproductive success of secondary females with that of simultaneously breeding monogamous females, only Simmons et al. (1986) provided data on female age: 81% of 16 secondary female hen harriers, *Circus cyaneus*, and 58% of monogamous females were older than 2 years (χ^2 exact test, two tailed: $\chi^2=2.57$, $P=0.129$). Searching several journals (*Animal Behaviour*, *Behavioral Ecology*, *Behavioral Ecology and Sociobiology*, *American Naturalist*, *Journal of Animal Ecology*) for polygyny studies published since 1994, we found only one additional study that mentions the age of females. The data published by Bensch (1996) showed that significantly fewer secondary female great reed warblers, *Acrocephalus arundinaceus*, were first-year birds (24% of 71 females) than were simultaneous monogamous females (42% of 55 females; χ^2 exact test, two tailed: $\chi^2=4.57$, $P=0.036$).

To test for a relationship between age and mating status once more, we used our own data on a German population of great reed warblers (data only partially published in Leisler et al. 1995). In contrast to the findings of the Swedish study (Bensch 1996, see above), the group of secondary females did not contain fewer first-year birds than the group of simultaneously breeding monogamous females (χ^2 exact test, two tailed: $\chi^2=0.89$, $P=0.430$). However, in our study, significantly more secondary

females were older than 3 years (21% of 57 females; simultaneous monogamous females: 9% of 163 females; χ^2 exact test, two tailed: $\chi^2=5.51$, $P=0.023$).

Conclusion

Our study suggests that individuals might behave in a more sophisticated way than allowed for in traditional models of polygyny. The finding that individual variation in females may also affect mating decisions renders tests of the PTM even more complicated than already suggested (e.g. Davies 1989). However, the general idea behind the PTM would be supported if we were able to show that the costs and/or benefits of polygyny differ between first-year and older females, and that females make their choices accordingly. Costs could be measured experimentally by widowing monogamous females of different age classes. Whether older females make better choices than inexperienced females could be studied by removing unmated males and so forcing females to mate polygynously. The idea that some females may depend less than others on male assistance (Gowaty 1996) opens a whole field of challenging questions, as age is certainly not the only candidate feature possibly related to female independence from the male.

Further analysis of female mating behaviour indicates that, besides the effects of female age shown here, there may also be heritable components contributing to the variation observed between females (Forstmeier et al. 2001). Our findings remain valid despite such possible additional effects, as both heritable and nonheritable components appear to contribute to female behaviour independently of each other.

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