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Thomas W.P. Friedl · Georg M. Klump

Determinants of male mating success in the red bishop (*Euplectes orix*)

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Abstract We studied sexual selection in the red bishop, *Euplectes orix*, a colonial, polygynous weaverbird widely distributed over sub-Saharan Africa. Male reproductive success measured in terms of the number of nests accepted by females and the number of eggs and nestlings in all the nests on a male's territory varied considerably. The standardized variance (variance/mean^2) in male reproductive success ranged from 0.505 to 1.737 in different years, indicating a high potential for sexual selection in this species. An analysis of genetic parentage for 432 nestlings by non-radioactive, multilocus DNA fingerprinting confirmed that male reproductive success (number of young sired on the territory) in this species can be reliably estimated by the measures introduced above. In all 4 study years there was a strong positive correlation between male mating success and the total number of nests that males built in their territories. The number of nests built can be partitioned into the number of weeks a male held a territory and his nest-building performance. Both factors exert a significant positive effect on male mating success and in combination explained between 53.3 and 86.3% of the variation in male reproductive success. Male morphological characters were found to be of no importance. Males that established a territory in the following season built more nests and held their territories for longer than males that did not establish a territory in the following season, suggesting that these measures might be indicators of male condition and quality. Male nest-building performance (number of nests built per week) seems to be unrelated to male condition or quality.

T.W.P. Friedl (✉) · Georg M. Klump
Institut für Zoologie,
Technische Universität München, Lichtenbergstraße 4
D-85747 Garching, Germany
e-mail: thomas.friedl@bio.tum.de
Tel.: +49-89-28913669, Fax: +49-89-28913674

Supplementary material Figure S1 showing the relationship between bandsharing rates and number of novel fragments is available in electronic form on Springer Verlag's server at http://link.springer.de/journals/bes

Key words Weaverbird · Male reproductive success · DNA fingerprinting · Number of nests built · Male quality · Female choice

Introduction

Both the mating system and the amount of parental investment by the sexes are known to affect variation in male mating success which, per se, is regarded as an indicator of the strength of sexual selection (e.g. Wade and Arnold 1980; Arnold and Wade 1984). The variation in male reproductive success is rather limited in monogamous birds with biparental care, being mainly determined by brood size and the quality of the offspring. Nevertheless, females have been shown to prefer males with more elaborate secondary sex traits as social mates (e.g. Møller 1988; Hill 1990; Sætre et al. 1994; Mountjoy and Lemon 1996), indicating the significance of sexual selection in many monogamous species. Moreover, by seeking extra-pair copulations, males can escape the limitations set by the monogamous mating system and thus increase the variation in male mating success. Several studies have provided evidence for direct benefits for females choosing mates with better parental ability (e.g. Norris 1990; Palokangas et al. 1994) or better territories (e.g. Catchpole 1986) in terms of higher fledgling number. However, evidence for indirect (genetic) benefits can also be found in monogamous species as was demonstrated, for example, by studies on ectoparasite susceptibility in the barn swallow (*Hirundo rustica*, reviewed by Møller 1994). In many polygynous species, only the females are responsible for raising the young and male parental care is not essential for offspring survival. In such species, male reproductive success is mainly determined by the number of females attracted for mating, which usually leads to a higher variation in male mating success than in monogamous species – at least in terms of within-season variance in male mating success. As in monogamous species, the

variation in male reproductive success and thus the opportunity for selection can be further increased by extra-pair fertilizations (e.g. Webster et al. 1995; Møller and Ninni 1998). Thus, intense sexual selection can be expected in polygynous species (for examples see review by Andersson 1994).

We studied sexual selection in the red bishop (*Euplectes orix*), a sexually dimorphic and polygynous passerine which occurs widely over sub-Saharan Africa. The red bishop belongs to the weaverbird family (Ploceidae), which comprises sparrows, weavers, bishops and widows. The breeding males have a black bill, forecrown, face and throat; the rest of the head, breast and rump are brilliant orange-scarlet. The belly is black, the mantle orange-brown, and wings and tail are brown. Females and immatures are boldly streaked buff and dark brown above, below white, with the breast and flanks washed buff and streaked brown. Wings and tail are dark brown. They show a distinctive whitish to yellowish eyebrow stripe, and the bill is pinkish horn. In the non-breeding season, males have an eclipse plumage that resembles that of the females.

Males in breeding plumage establish and defend small territories of a few square metres in colonies located in reedbeds or bullrush stands around water, where they construct several nests during a breeding season to which they try to attract females. When a female enters a territory, the male performs courtship displays until the female either flies off or permits copulation. Most of the males are polygynous, mating with several females within a single breeding season. Males do not guard their mates to assure paternity, but copulate frequently with them during the fertile period, that is shortly before and during the egg-laying stage. After the egg-laying phase, the female is usually ignored by the territory owner and is solely responsible for incubating and feeding nestlings. Territories often contain nests with eggs and chicks and empty nests simultaneously, and most territories contain one or more empty nests of different age at any time during the breeding season. While adults are almost exclusively granivorous, chicks are fed mainly with insects, spiders and other animal material, only occasionally also with seeds. Foraging always takes place away from the territories. The main cause for nestling mortality in our colony was predation by the cape cobra (*Naja nivea*). Nest defence by males against cape cobras is restricted to mobbing behaviour and does not prevent the cobras from robbing eggs or nestlings. (For a more general description of red bishop breeding behaviour see, for example, Skead 1956; Craig 1974; Friedl 1998).

Female red bishops can choose among males, since copulations are always initiated by the female showing the typical copulation solicitation display of passerine birds (King and West 1977). We have never observed a copulation without a preceding copulation-solicitation display by the female, and if a male tries to mount a female without being solicited, he is repulsed by vigorous pecks (Craig 1974; personal observation).

Since red bishop incubation and feeding of nestlings is done by the female without any male assistance, and foraging usually takes place away from the breeding site, the potential material benefits that females could gain from mate choice seem to be limited. In the absence of material (i.e. immediate) effects of female mate choice on her fitness, it is more likely that female choice evolves for the effect on the genotypes of her offspring (Maynard Smith 1991). That is, in such a mating system, females might choose their mates based on traits that indicate male genetic quality to gain indirect genetic benefits in terms of offspring with higher viability ('good genes' model for the evolution of female mating preferences; see for example Andersson 1994; Johnstone 1995; Andersson and Iwasa 1996). Thus, the red bishop appears to be an ideal species for studying variation in male mating success that might result from the decision of the choosy female. Here we investigate (1) the extent to which the component of reproductive success that is acquired on the territory varies between males, (2) male traits that might explain the variation in male mating success, and (3) whether these traits might indicate male quality. Finally, we discuss whether the variation in male mating success is likely to be explained by active female choice of particular males.

Methods

Study colony

We studied a colony of red bishops at the Addo Elephant National Park, Eastern Cape, South Africa (33°26′ S; 25°45′ E) during four consecutive breeding seasons (1993/1994 to 1996/1997) lasting approximately from October to April. The breeding colony was located in the vegetation at a small dam (approximately 250 m^2) comprised of bullrushes (*Typha capensis*) and common reeds (*Phragmites australis*).

In the colony, all territorial males had the conspicuous orange-scarlet and black breeding plumage. During the four breeding seasons 32, 41, 33 and 36 of such males in breeding plumage held territories; 24 (75%), 36 (87.8%), 31 (93.9%) and 33 (91.7 %) of these males, respectively, were marked with legbands and could be identified individually. On average, 43% of these territorial males were observed during consecutive breeding seasons. Throughout the breeding season, additional males in breeding plumage visited the colony but did not succeed in establishing a territory. Besides males in breeding plumage, 1-year-old males in a plumage resembling that of females and the eclipse plumage of territorial males were frequently observed in the colony. The delayed plumage maturation of male red bishops in their first breeding season has been previously observed (e.g. Skead 1956). One-year-old males never establish a territory for more than a week. However, they occasionally built nests in areas not occupied by territorial males and they courted females (personal observation, see also Skead 1956). Birds with territories or nests at the breeding site or other red bishops visiting the breeding site were usually not observed foraging within the limits of the colony.

General field methods

Throughout the study, nest counts were conducted daily to register new nests built by the territory holders. These nests were

marked with numbered yellow plastic tags attached to a reed or bullrush stem close to the nest. Nests built by 1-year-old, non-territorial males were not marked, since females never accepted nests from these males constructed at the edge of the colony (Skead 1956; personal observation). Throughout the breeding season, all tagged nests were checked daily to collect data on the laying date for the eggs in the nest, clutch size, hatching dates, number of hatchlings and number of fledglings. Detailed observations of territorial behaviour and aggressive interactions between males throughout the breeding season provided information on the location of the territories and identities of the territory holders. Based on these data, territory maps were drawn and updated fortnightly. Social parents of nestlings were assigned through behavioural observations, identifying the putative father as the owner of the territory in which the nest was located and the putative mother as the female incubating the eggs or feeding nestlings.

Adult red bishops were caught either with mist nets that were set up close to the colony or with a walk-in trap positioned approximately 10 m from the border of the colony that was baited with commercially available mixed bird seeds. We measured wing length, tarsus length, and the weight of every red bishop that was captured. The red bishop is a moderately size-dimorphic species. Although the differences between the sexes with regard to wing length, tarsus length and weight were highly significant (*t*-test, all $P < 0.001$), the ranges of all three variables overlapped considerably (male wing length: 75.09 ± 1.86 mm, range 70–80 mm, $n = 308$; female wing length: 69.03 ± 1.84 mm, range 63–75 mm, $n = 377$; male tarsus length: 24.07 ± 0.78 mm, range 22–26 mm, $n = 308$; female tarsus length: 22.07 ± 0.78 mm, range 20–24 mm, $n = 377$; male weight: 25.87 ± 1.69 g, range 21.5–31 g, $n = 297$; female weight: 22.1 ± 1.79 g, range 17.5–29 g, $n = 367$). Each individual was legbanded with a unique combination of four colour rings and a stainless steel ring with an engraved number provided by the South African Bird Ringing Unit. Several studies in birds have shown that colour rings might affect male as well as female mating behaviour, and that rings matching the colour of secondary sexual ornaments are most likely to exert such effects (e.g. Burley et al. 1982; Metz and Weatherhead 1991; Johnson et al. 1993; Zann 1994; Burley et al. 1996; Johnsen et al. 1997). Therefore, the colour combination of every bird was chosen to contain one red ring regardless of sex and age, thereby excluding any possible effects of red rings closely matching in colour the bright orange-scarlet male breeding plumage on mating behaviour and mating success. The position of the red ring served as marker for the year of capture.

Blood samples of adult birds were obtained by puncturing with a sterile 25-gauge needle the brachial vein where it crosses the elbow on the underside of the wing after cleaning the area with ethanol. In total, 20–60 µl of blood was collected with a heparinized microcapillary tube before the bleeding spontaneously stopped making no further treatment of the birds necessary. The blood sample was transferred into in a sterile 1.5-ml microfuge tube containing about 0.7 ml of the non-lytic buffer PBS (phosphate-buffered saline: 3 mM KCl, 8 mM Na_2HPO_4, 2 mM KH_2PO_4, 0.14 M NaCl, 6 mM EDTA, 0.2 % sodium azide), and the tubes were inverted several times to bring the cells into suspension. About 6–8 h after blood collection, the cells had settled at the bottom of the tube and we removed the supernatant, replaced it with 500 µl of fresh PBS solution, and resuspended the cells by inverting the tubes several times. After the cells had settled again we repeated this rinsing procedure once more and then stored the blood samples in the refrigerator at 4 °C. Nestlings were leg banded when about 10 days old, that is about 2–3 days before they left the nest. On that occasion, blood samples were collected using the method described above. In the first study season (1993/1994) we marked 87% of all fledglings from the colony and collected blood samples from them; in the remaining three seasons, we marked and took blood samples from all fledglings.

Genetic analysis

DNA extraction and assessment of DNA concentration, purity and condition

After adding 40 µl 10% sodium dodecyl sulphate (SDS) and 30 µl proteinase K (10 mg/ml), we incubated the blood samples at 58 °C overnight in a waterbath. Following five extraction steps (two with phenol, two with 25:24 :1 phenol:chloroform: isoamyl alcohol, and one with 24:1 chloroform:isoamyl alcohol), we dialysed the final aqueous phase overnight against TNE_2 (10 mM Tris, pH 8.0, 10 mM NaCl, 2 mM EDTA). Extracted DNA samples were then stored at 4 °C in the refrigerator in screw-cap microfuge tubes until further processing. We determined the concentrations of the extracted DNA by examining UV absorbance with a spectrophotometer (Hitachi U-1100) at a wavelength of 260 nm. Concentration estimates for our samples ranged from 0.1 to 0.8 µg DNA/µl, resulting in yields of extracted DNA of about 50–500 µg DNA per sample. DNA purity was assessed by determining the ratio of absorbances at 260 and 280 nm. Most of our samples showed ratios close to 1.8, indicating high purity of the isolated DNA. To check whether it had undergone degradation, we electrophoresed 2 µg DNA of most of the samples collected during the first two breeding seasons for 2 h at 80 V in an 0.8% agarose gel. We then stained the gel with ethidium bromide and photographed it under UV light. Even for DNA extracted from blood samples that had been stored for more than 2 years, the photographs showed only one clear band of intact, high-molecular-weight DNA without any signs of smear indicating degradation. Since these results showed that our storage and extraction procedures conserved the samples reliably, we dispensed with this step for the samples in the remaining two seasons.

DNA digestion and Southern blotting

We digested 5 µg DNA from each sample with a fivefold excess of the four-cutter restriction endonuclease *Hae*III or its isoschizomer *Bsu*RI for 4 h at 37 °C in a waterbath. After adding 8 µl of Blue Juice II (0.25% bromophenol blue, 0.25% xylene cyanol, 15% ficoll) we loaded each sample on a 0.8% agarose gel (20 × 25 cm) and ran the electrophoresis in a recirculating 1 × TBE buffer (89 mM Tris, 89 mM boric acid, 2 mM EDTA, pH 8.0) at 20 V for 65 h. We checked the quality of the digestion by staining the gel with ethidium bromide and examining it under UV illumination. Following denaturation of the DNA by two washes in 0.5 M NaOH/1.5 M NaCl, and neutralization by two washes in 3 M NaCl/0.5 M Tris, pH 7.4, we transferred the DNA fragments to a positively charged nylon membrane (Boehringer Mannheim) by vacuum blotting (Vacu-Aid, Hybaid) for 1.5 h in 10 × SSC (3 M NaCl, 0.3 M sodium citrate). We fixed the DNA fragments to the membrane by baking in an oven at 120 °C for 0.5 h and stored it in blotting-paper envelopes.

Hybridization and signal detection

We determined parentage in the red bishop by non-radioactive multilocus DNA fingerprinting using the digoxigenin-labelled oligonucleotide probe $(GGAT)_4$ in combination with the DIG Luminescent Detection Kit from Boehringer Mannheim. We first washed the membranes briefly in 5 × SSC, then placed them in rotisserie bottles containing 50 ml of pre-hybridization solution (5 × SSC, 0.1% N-lauroylsarcosine, 0.02% SDS, 1% blocking reagent; membranes were separated by nylon mesh sheets), and let them rotate in a hybridization oven at 38 °C. After 2 h we discarded the pre-hybridization solution and replaced it with 50 ml of fresh pre-hybridization solution, to which we added 500 pmol of the digoxigenin-labelled oligonucleotide probe $(GGAT)_4$. Hybridization was then carried out by incubating the membranes for 6 h in the

hybridization oven at 38 °C. Following two washes in 2 × SSC/0.1% SDS for 5 min each, two washes in 0.5 × SSC/0.1% SDS for 15 min each, and one wash in washing buffer (100 mM maleic acid, pH 7.5, 150 mM NaCl, 0.3% Tween 20), the membranes were treated for 1 h at room temperature with blocking solution (100 mM maleic acid, pH 7.5, 150 mM NaCl, 1% blocking agent) to prevent non-specific binding of antibody to the membranes. Then the membranes were incubated for 30 min in antibody solution (5 µl Anti-Digoxigenin-AP, 750 units/ml, diluted in 50 ml blocking solution). After two washes in washing buffer for 15 min each, the membranes were equilibrated in detection buffer (100 mM Tris, 100 mM NaCl, pH 9.5) and incubated in a CSPD solution (diluted 1:100 in detection buffer) for 5 min. The membranes were then wrapped in plastic foil, incubated for 15 min in an oven at 37 °C, and exposed to Lumi-Film (Boehringer Mannheim) for 90 min for initial exposure and subsequently for 12 h to produce a final image of the position of the bands labelled on the membrane. An example of a DNA fingerprint with three families showing different numbers of extra-pair young (EPY) is shown in Fig. 1.

Paternity analysis

Using the oligonucleotide probe $(GGAT)_4$, we scored 10.6 ± 2.4 (mean ± SD) bands per individual in the range of 4–23 kb (following the procedures described in Westneat 1990). Gels were constructed in such a way that no more than three lanes lay between nestlings and their putative parents, to minimize possible scoring errors which could result from large distances between lanes under comparison (Piper and Parker Rabenold 1992). We determined the descent of a total of 432 nestlings from 187 broods using both the number of novel bands (i.e. bands scored in the fingerprint of a nestling that were not present in either of its putative parents' fingerprints) and the bandsharing rate, which was calculated as $2N_{AB}/(N_A + N_B)$, where N_A and N_B are the number of bands in individuals A and B, and N_{AB} is the number of bands shared by both individuals (Wetton et al. 1987).

Figure 2 shows the distribution of novel bands in fingerprints of 177 nestlings, for which both putative parents were observed. Assuming that mutations occurred randomly across loci, we fitted a Poisson distribution (sum-of-least-squares method) to the data and calculated the Poisson probabilities for the occurrence of one or more novel bands. The probability for the occurrence of one novel band was 0.241, indicating that a single novel band can easily be explained by mutation alone and, therefore, that nestlings with none or only one novel band are likely to be the genetic descendant of both putative parents. The Poisson probability for two novel bands was 0.041 and for three or more novel bands it was 0.005. Based on these probabilities, we concluded that nestlings with two or more novel bands were not the descendants of either the putative father or mother or both the putative parents and thus the result of either extra-pair fertilizations or intraspecific brood parasitism. The mean occurrence of novel bands per nestling that could be explained by spontaneous mutations was 0.20 (29 novel bands/145 unexcluded nestlings) and the mutation rate per locus per generation could then be calculated as 0.019 [29 novel bands/(145 unexcluded nestlings × 10.59 scorable bands per nestling)].

In a next step we calculated the bandsharing rates for 138 nestlings with less than two novel bands with each of their parents to obtain a distribution of bandsharing rates for first-order relatives. The remaining 7 nestlings with less than two novel bands were excluded from this analysis, because they shared all but one band with one putative parent. The very low bandsharing rate with the other putative parent did not allow us to conclude unambiguously whether or not the other parent was the genetic sire. Therefore, these nestlings were not included in the sample defining the distribution of bandsharing rates between first-order relatives. Figure 3a shows the distribution obtained for the presumed first-order relatives in comparison to the distribution of bandsharing rates of presumably unrelated adults (the one case of a bandsharing rate of 0.417 lying well within the distribution for first-order relatives may possibly represent two adults that were full siblings). The average bandsharing rate between unrelated adults was 0.088 ± 0.079 (mean ± SD; $n = 149$), and the average bandsharing rate between first-order relatives was 0.51 ± 0.117 ($n = 276$). After confirming that the distribution of bandsharing rates between first-order relatives was not significantly different from a normal distribution (Kolmogorov-Smirnov test, $z = 0.856$, $P = 0.457$), we calculated the lower 95% confidence limit of the bandsharing rates between nestlings and their genetic parents as 0.51 minus 1.96 standard deviations resulting in a value of 0.281, and set this bandsharing rate as a threshold for the exclusion of subjects as potential parents. Calculations of the lower limit of the bandsharing rates among first-order relatives might be confounded by non-independence of the data used, particularly if many similarity measures involve the same individual (e.g. a very successful territorial male). If this individual shows several bands that are either very common or very rare in the population, this will lead to unusually high or low similarities with all other members of the population, thereby influencing the calculation of the lower limit of bandsharing (Lynch 1990). To test whether our calculation of the lower limit of the bandsharing rates among first-order relatives was affected by the repeated use of some territorial males, we calculated the similarities of first-order relatives using every male and female only once (selected at random). The resulting average bandsharing rate was 0.507 ± 0.118 ($n = 89$), almost identical to the bandsharing rate obtained when using all possible similarity measures

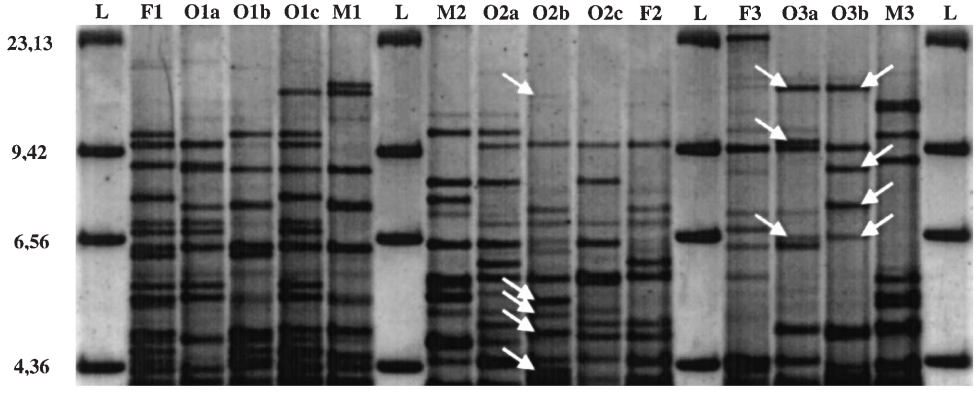

Fig. 1 Example of a DNA fingerprint showing three families with different numbers of extra-pair young (*M* male, *F* female, *O* offspring, *L* ladder). The numbers to the left indicate fragment size of the ladder in kilobases. *White arrows* indicate novel bands. Family 1: all offspring (*O1a–c*) are genetic descendants of both their social parents (*M1* and *F1*). Family 2: two of the three offspring (*O2a*, *O2c*) are genetic descendants of both their social parents (*M2* and *F2*), while the third offspring (*O2b*) is an extra-pair young. Family 3: both offspring (*O3a*, *O3b*) are extra-pair young

(see above). This indicates that our calculations were not biased by the repeated use of some individuals.

Assuming all alleles have equal frequencies, the mean allele frequency q can be derived from $x = 2q - q^2$, where x is the mean proportion of bands shared by non-relatives (Jeffreys et al. 1985);

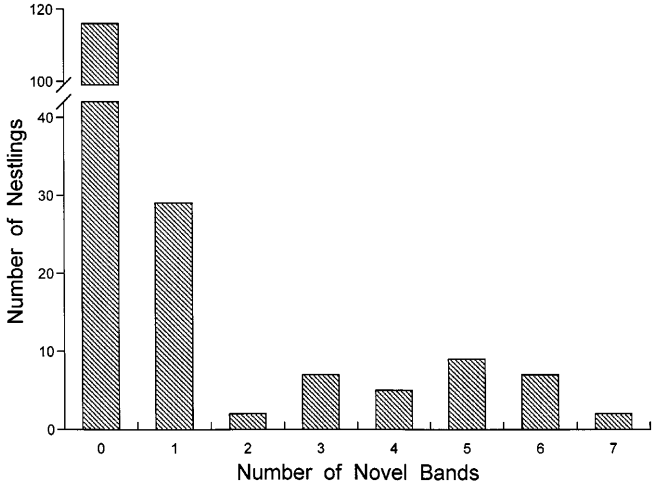

Fig. 2 Frequency distribution of the number of novel bands scored in fingerprints of 177 nestlings for which both social parents were individually known

hence $q = 0.045$. The proportion of paternal-specific bands can then be calculated as $(1 + q - q^2)/(2 - q) = 0.534$ (Jeffreys et al. 1985) and, given that the mean number of bands scored per individual n was 10.6 (see above), the mean expected number of paternal-specific bands in an offsprings' fingerprint p is 5.655. The mean probability of assigning an unrelated male as father can then be calculated as $x^p = 1.07 \times 10^{-6}$. Therefore, it is highly unlikely that we made any false inclusions of a non-father.

For 168 out of the 177 nestlings for which both putative parents were known, both the criteria 'number of novel bands' and 'bandsharing rate' were consistent in determining genetic parentage. All 32 nestlings with two or more novel bands also showed a bandsharing rate below the threshold of 0.281 with at least one putative parent. In 28 of those cases, the low bandsharing rate was found between the nestling and the putative father, indicating that these 28 nestlings were not sired by the territory holder. In three cases, the nestlings had bandsharing rates below 0.281 with both putative parents and were probably the result of conspecific brood parasitism. One nestling had a bandsharing rate of 0.59 with the putative father and a bandsharing rate of 0.125 with the putative mother, and this was interpreted as a special case of conspecific brood parasitism in which the egg of a parasitic female was fertilized by the territorial male. Of the 145 cases in which the nestlings had no or a single novel band, 136 nestlings had bandsharing rates above the threshold of 0.281 with both putative parents, confirming the hypothesis that they were the genetic descendants of both their social parents. In the 9 remaining cases, the two criteria – number of novel bands and bandsharing rate – led to different conclusions about genetic parentage. All 9 nestlings shared a high proportion of their bands with one of their putative parents, and they had a very low bandsharing rate with the other. The probability that a male

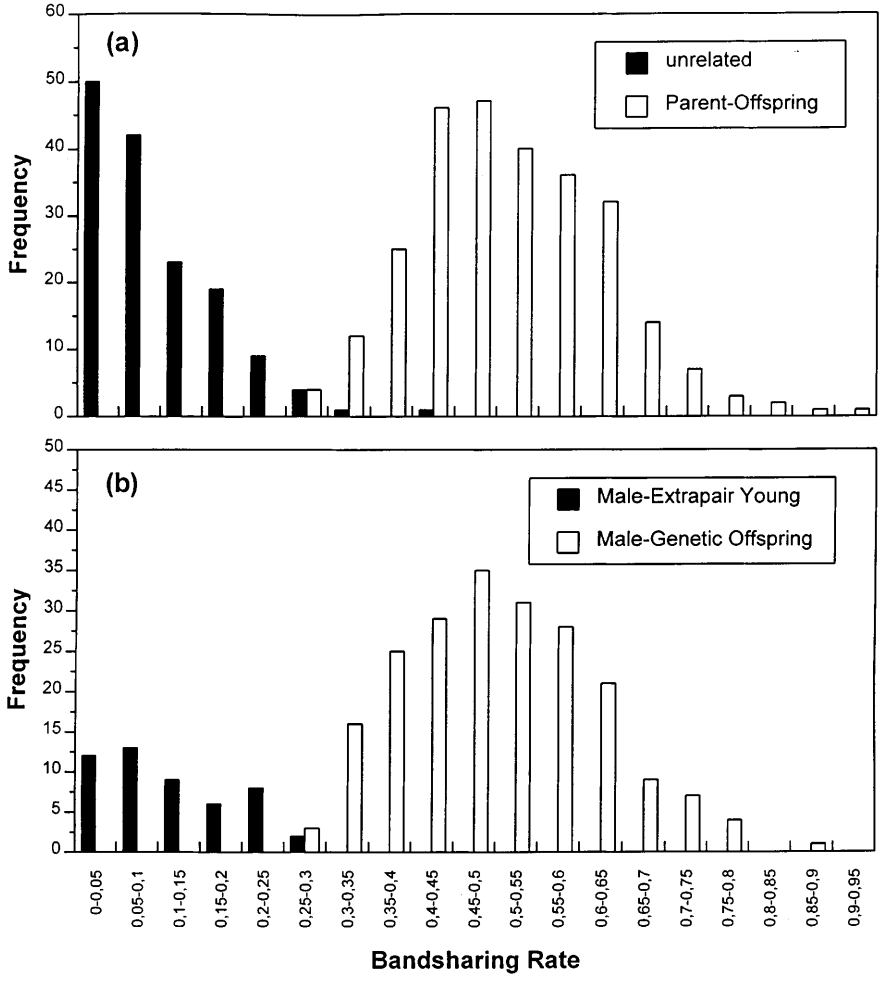

Fig. 3a,b Frequency distributions of bandsharing rates. **a** Bandsharing rates between parents and their genetic offspring (*white bars*) and between presumably unrelated adults (*black bars*). **b** Bandsharing rates between males and their genetic offspring (*white bars*) and between males and excluded offspring (*black bars*) for cases where the social mother was not individually known

that is not the genetic father of a nestling will have a single non-maternal band found in the nestling's fingerprint is equal to the bandsharing rate between unrelated individuals (=0.088). We decided these cases on the basis of the estimated rate of mutations per locus per generation. Consider a nestling that shared all but one band with its putative mother. If the nestling is also a genetic descendant of the putative father, it should share the remaining band with him unless this band was subject to mutation. Since the mutation rate per locus and generation (that is, the probability of a mutation of the band in question) found in this study was only 0.019 (see above), we concluded that the putative father is likely to be the genetic father if he shares the band with the nestling, even if the resulting bandsharing rate lies below the threshold for parental exclusion of 0.281. If, on the other hand, the putative father does not share the remaining band with the nestling, and the band is scored as a novel band, we concluded that the nestling is likely to be an EPY.

Paternity of the 255 nestlings, for which we were unable to catch the social mother and were thus unable to obtain a blood sample from her, was decided on the basis of bandsharing rate between the nestling and the putative father alone, using the threshold value of 0.281 as criterion for assigning paternity. The distribution of bandsharing rates between these nestlings and their putative fathers is shown in Figure 3b, and the observed bimodality closely reflects that of bandsharing rates between first-order relatives on the one hand and between unrelated adults on the other hand shown in Figure 3a.

Statistical analysis

All data analysis was performed using the software package SPSS/PC (SPSS Inc.). All *P*-values given are two-tailed unless stated otherwise.

Results

During the 4 study years, a total of 670 breeding attempts were recorded in 1254 nests built by breeding males of the colony. The results presented here were obtained by studying the reproductive success of a total of 84 breeding males over four breeding seasons. Since on average 43% of the males were observed in consecutive breeding seasons, the data from different years were analysed separately to avoid a mixture of independent and related samples in the statistical analysis (within each year, data from different males represent independent data points).

Frequency of young sired by territory holders

We determined genetic parentage for a total of 432 nestlings from 187 broods to estimate the frequency of young that were not descendants of the owner of the territory that contained the nest from which they fledged. According to the criteria for excluding paternity outlined above, 76 nestlings (17.6%) were EPY (i.e. young not sired by the territory owner), and 57 (30.5%) of all broods that were investigated contained at least one EPY. Measuring a male's reproductive success in terms of number of eggs or young found in nests on his territory could lead to erroneous conclusions, if EPYs are common and there is no close correlation between the number of young in the nest and the number of genetic offspring. In the red bishop, however, the number of 10-day-old nestlings in a male's territory and the number of nestlings in his territory that were found to be his genetic offspring were positively correlated in three of the four study seasons (Spearman rank-correlation coefficients r_s ranged from 0.87 to 0.94, all $P < 0.001$). The positive but non-significant correlation (Spearman rank correlation coefficient $r_s = 0.49$, $P = 0.184$) in the first season was probably the result of genetically analysing fewer nestlings than in the other seasons. If only a small number of young are analysed per territory owner, a larger amount of variation is due to sampling error. In the three breeding seasons 1994/1995, 1995/1996, and 1996/1997, the percentage of young that were EPY was not related to the number of 10-day-old young in a male's territory. Only in the first breeding season, 1993/1994, in which few males were studied, was there a correlation between the percentage of young that were EPY and the number of 10-day-old young in a male's territory, which was just significant (Spearman rank correlation coefficient $r_s = 0.67$, $P = 0.05$, $n = 9$). In none of the four breeding seasons was the percentage of young that were EPY significantly correlated with the number of young that hatched in a male's territory (Spearman rank correlation coefficient, all $P > 0.05$). Therefore, the number of nestlings in a male's territory or the number of eggs can be considered as useful measures of the reproductive success of a male red bishop on that territory. This conclusion is further supported by the fact that the standardized variance (variance/mean^2) in male reproductive success obtained on the territory was on average only 21.9% higher (14.1% in 1993/1994, 12.3% in 1994/1995, 42.3% in 1995/1996, and 18.9% in 1996/1997) when based on realized success (number of genetically sired offspring on the territory) as compared to apparent success (number of fledglings on the territory). Whenever we refer to male reproductive success in the remaining parts of the Results section, we mean the component of male reproductive success that is acquired on the territory.

Variation in male reproductive success

We measured four different variables representing male reproductive success: (1) the number of nests on a male's territory that are accepted by females, (2) the number of eggs laid in the nests on a male's territory, (3) the number of hatchlings in the nests on a male's territory and (4) the number of nestlings in the nests on a male's territory that reached the age of 10 days. All four measures representing male reproductive success showed highly significant correlations with each other in all four study seasons (Spearman rank correlation coefficients r_s ranged from 0.58 to 0.99; all $P < 0.002$). There was high variation among males regarding the measures of reproductive success in all four study seasons (Table 1).

Table 1 Variation in different measurements of male reproductive success in the four study seasons

	Breeding season	Median	Interquartile	Range	Standardized variance (variance/mean^2)
Number of nests accepted	1993/1994	5.5	1.25–8.0	0–13	0.575
	1994/1995	5.0	2.0–8.75	0–12	0.505
	1995/1996	3.0	1.0–4.0	0–7	0.553
	1996/1997	5.0	1.0–8.0	0–18	0.61
Number of eggs laid	1993/1994	16.0	3.5–26.75	0–39	0.598
	1994/1995	14.5	5.25–24.0	0–36	0.509
	1995/1996	8.0	2.0–12.0	0–19	0.529
	1996/1997	15.0	4.0–25.25	0–54	0.568
Number of hatchlings	1993/1994	8.5	1.25–14.25	0–24	0.743
	1994/1995	8.5	3.0–15.0	0–27	0.655
	1995/1996	2.0	0.0–5.0	0–8	1.252
	1996/1997	10.0	3.0–15.25	0–30	0.594
Number of 10-day-old nestlings	1993/1994	2.0	0.0–6.0	0–11	1.455
	1994/1995	5.0	2.0–8.75	0–18	0.779
	1995/1996	0.0	0.0–3.0	0–5	1.737
	1996/1997	4.0	0.0–9.5	0–14	0.816

Male reproductive success was considerably skewed, with half of the males accounting for 76.7–83.1% of all accepted nests, 77.2–84.0% of all eggs, 81.7–93.6% of all hatchlings, and 85.4–100% of all 10-day-old nestlings in the four different seasons. Table 1 also shows the standardized variance (variance/mean^2) in male reproductive success, which can be considered as the upper limit of the strength of directional selection (Wade and Arnold 1980; Arnold and Wade 1984), for each of the four study seasons.

Determinants of male reproductive success

Since male red bishops varied considerably in their reproductive success, we explored the factors that may lead to these differences. Table 2 shows Spearman rank correlation coefficients between the four different measures of male reproductive success and several male traits. The correlations between male reproductive success and the four morphological measures were mostly far from significant; only wing length in the season 1993/1994 and tarsus length in the season 1995/1996 showed significant positive correlations with two of the four measures of male reproductive success (Table 2). There was no significant correlation between the four morphological measures and the number of nests built in a breeding season (Spearman rank correlation coefficients ranged from −0.24 to 0.27, *P*-values ranged from 0.19 to 0.95). Only the number of nests that a male built on his territory was strongly and consistently related to male reproductive success. This is apparent in the Fig. 4 scatter diagrams of both the number of nests accepted by females (Figure 4a) and the number of 10-day-old nestlings in the territory (Figure 4b) for the four study years in relation to the number of nests built by the males.

The number of nests a male built on his territory can be partitioned into two factors: (1) the number of weeks a male held a territory, and (2) the nest-building performance of this male, measured as the average number of nests built per week on the territory. We used these two factors as independent variables to predict male mating success in a multiple-regression analysis. The results show that both factors combined explain most of the variation in male reproductive success (Table 3). The partial correlation coefficients also given in Table 3 reveal that both factors exhibit a strong positive influence on male reproductive success independently from each other.

To investigate if there were male characteristics other than number of weeks with territory and nest-building performance that influence reproductive success, we calculated the residuals from the multiple-regression analysis of number of weeks with territory and nest-building performance on the different measures of male reproductive success given in Table 3. We then looked for correlations of these residuals of the individual males between different years. Significant correlations would be expected if the reproductive success of individual males was consistently below or above the regression lines in different years, indicating that there were factors other than number of weeks with territory and nest-building performance that influence reproductive success. However, none of the correlations were significant (Spearman rank correlation coefficients r_s ranged from −0.38 to 0.31; *P*-values ranged from 0.217 to 0.733). Therefore, and because of the high coefficients of determination (see Table 3), we conclude that the number of weeks a male held a territory and his nest-building performance were the main determinants of his reproductive success, even if we cannot entirely rule out the possibility that females also used other mate choice cues that varied from year to year for individual males.

Reproductive success in relation to male quality

Males could obviously enhance their reproductive success by holding a territory as long as possible and by

Table 2 Spearman correlation coefficients between four different measures of male reproductive success and five male traits for the four study seasons

	Breeding season	Number of nests built	Wing length	Tarsus length	Culmen length	Weight
Number of nests accepted	1993/1994	0.89***	0.44*	0.10	−0.26	0.11
	1994/1995	0.88***	0.31	0.06	0.22	0.30
	1995/1996	0.72***	0.12	0.43*	0.01	0.28
	1996/1997	0.89***	−0.18	0.28	0.30	0.39
Number of eggs laid	1993/1994	0.89***	0.47*	0.10	−0.39	0.12
	1994/1995	0.90***	0.31	0.03	0.14	0.31
	1995/1996	0.72***	0.10	0.45*	0.00	0.28
	1996/1997	0.88***	−0.18	0.24	0.30	0.36
Number of hatchlings	1993/1994	0.86***	0.32	0.12	−0.55	0.05
	1994/1995	0.81***	0.30	0.01	0.26	0.31
	1995/1996	0.76***	0.25	0.05	−0.16	−0.13
	1996/1997	0.75***	−0.16	0.21	0.36	0.35
Number of 10-day-old nestlings	1993/1994	0.49*	0.23	0.00	−0.26	0.14
	1994/1995	0.83***	0.24	0.00	0.25	0.31
	1995/1996	0.50**	0.23	−0.15	0.02	0.00
	1996/1997	0.65***	−0.19	0.12	0.08	0.05

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

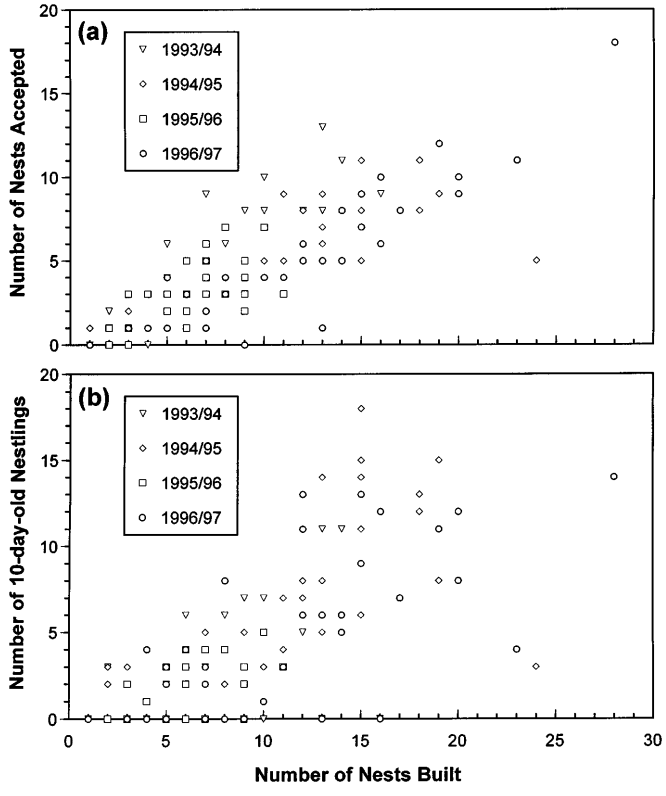

Fig. 4a,b Correlations between the number of nests built by a male and two measures of male reproductive success in the four study seasons. **a** Correlation between the number of nests built and the number of nests on a male's territory that were accepted by females. **b** Correlation between the number of nests built and the number of 10-day-old nestlings on a male's territory

building many nests. Yet, there was considerable variation between males in terms of the number of built nests, the number of weeks with a territory and the nest-building performance (see Table 4). The breeding season of the red bishop is very long, lasting from 5 to 6 months, and a preliminary analysis of male time budgets revealed that during the morning hours in which most of the activity takes place, males spent 70–90% of their time within their territories (N. Geberzahn and T.W.P. Friedl, unpublished data). Consequently, only 10–30% of their time is available for foraging outside the territory. Territorial defence, courtship behaviour and nest-building behaviour taken together accounted for 25–68% of the time on the territory (N. Geberzahn and T.W.P. Friedl, unpublished data), indicating that holding a territory requires a considerable amount of energetically demanding activity. Therefore, we conclude that the variation between males in the number of nests built, the number of weeks with a territory and the nest-building performance are probably due to differences in male condition and quality, because only males in good condition or of high quality should be able to establish and defend a territory over a long period of time. To test this hypothesis further, we compared the number of nests built, the number of weeks with a territory and the nest-building performance between males that did and did not establish a territory in the following breeding season (Fig. 5). The results show that males that did establish a territory in the following season built more nests and held a territory for a longer period of time than males that did not establish a territory in the following season. For nest-building performance, however, there were no significant differences between these two groups (Figure 5c).

It could be argued that this result is explained by the fact that birds are more likely to return to a particular breeding site if they have been successful previously and to move elsewhere if they have been unsuccessful. For two reasons we think that our results reflect differences in male condition and quality independently of whether males follow such a 'win/stay–lose/shift' decision rule. First, establishing and holding a territory for a long period of time in itself reflects good condition and high

Table 3 Multiple-regression analysis with the four different measures of male reproductive success as dependent variables and the number of weeks a male held a territory (weeks with territory, WWT) and the nest-building performance (NBP) as independent variables

	Breeding season	Regression equation	Coefficient of determination	*df*	*F*	Partial correlation coefficient with WWT, controlling for NBP	Partial correlation coefficient with NBP, controlling for WWT
Number of nests accepted	1993/1994	0.59WWT + 4.08NBP − 3.86	0.856	23	62.26***	0.91***	0.69***
	1994/1995	0.44WWT + 2.25NBP − 2.57	0.806	35	68.67***	0.89***	0.32
	1995/1996	0.37WWT + 3.63NBP − 2.75	0.534	30	16.03***	0.66***	0.42*
	1996/1997	0.67WWT + 4.82NBP − 7.58	0.779	33	54.67***	0.88***	0.57***
Number of eggs laid	1993/1994	1.92WWT + 12.22NBP − 12.43	0.863	23	66.35***	0.92***	0.68***
	1994/1995	1.29WWT + 7.61NBP − 8.26	0.818	35	74.24***	0.90***	0.37*
	1995/1996	0.87WWT + 11.37NBP − 7.6	0.545	30	16.75***	0.63***	0.50**
	1996/1997	2.04WWT + 14.04NBP − 21.77	0.779	33	54.66***	0.88***	0.55***
Number of hatchlings	1993/1994	1.03WWT + 7.52NBP − 7.48	0.759	23	33.0***	0.85***	0.60**
	1994/1995	0.84WWT + 2.99NBP − 4.67	0.707	35	39.77***	0.84***	0.18
	1995/1996	0.38WWT + 7.65NBP − 5.63	0.533	30	15.99***	0.55**	0.58***
	1996/1997	1.19WWT + 7.02NBP − 10.87	0.679	33	32.74***	0.82***	0.40*
Number of 10-day-old nestlings	1993/1994	0.3WWT + 3.17NBP − 2.35	0.323	23	5.02*	0.51*	0.36
	1994/1995	0.52WWT + 3.65NBP − 3.98	0.587	35	23.47***	0.75***	0.25
	1995/1996	0.26WWT + 1.37NBP − 1.89	0.322	30	6.64**	0.53**	0.17
	1996/1997	0.61WWT + 1.96NBP − 3.57	0.497	33	15.3***	0.69***	0.16

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

Table 4 Variation in the three male traits that were found to affect male reproductive success in the four study seasons

	Breeding season	Median	Interquartile	Range
Number of nests built	1993/1994	6.0	3.0–10.0	1–16
	1994/1995	11.0	3.5–15.0	1–24
	1995/1996	6.0	3.0–8.0	2–11
	1996/1997	12.0	6.75–15.25	1–28
Number of weeks with territory	1993/1994	10.0	6.0–17.75	3–19
	1994/1995	15.0	6.5–20.75	2–24
	1995/1996	8.0	6.0–13.0	4–13
	1996/1997	11.0	4.75–17.25	2–19
Nest building performance	1993/1994	0.58	0.44–0.74	0.17–2.0
	1994/1995	0.69	0.54–0.83	0.25–1.5
	1995/1996	0.6	0.5–0.82	0.33–1.0
	1996/1997	1.1	0.89–1.31	0.5–2.0

quality (see above), independently of how the males perform in the following season. Second, we performed another analysis by comparing males that established a territory in the following breeding season and males that did not but were seen at the breeding site (as revealed by direct observation), thus excluding males that have died or moved to another site. Since this reduced the sample size of males that did not establish a territory in the following season considerably, we were unable to conduct the comparison on a seasonal basis. Instead, we pooled the data over the four seasons and converted the variables number of nests built, number of weeks with a territory and nest-building performance to Z-scores to correct for differences between years. Males that did establish a territory in the following season built significantly more nests (Mann-Whitney *U*-test; $n = 68$, $P = 0.027$) and held a territory for a significantly longer period of time (Mann-Whitney *U*-test; $n = 68$, $P = 0.006$) than males that did not establish a territory in the following season but were present at the breeding site, while there were no significant differences with regard to nest-building performance (Mann-Whitney *U*-test; $n = 68$, $P = 0.947$).

If the number of nests built and the number of weeks with a territory reflect male quality, one would expect these variables to be consistent across years for individual males. We therefore calculated the correlation coefficients between the number of nests built by individual males in two successive seasons as well as between the number of weeks individual males held a territory in two successive seasons. Both correlations between the breeding seasons 1993/1994 and 1994/1995 were highly significant ($n = 12$; number of nests built: $r_s = 0{,}87$, $P < 0.001$; number of weeks with territory: $r_s = 0.81$, $P < 0.001$), as expected under the genetic-quality hypothesis. However, all correlations involving the breeding season 1995/1996, which was characterized by unusually low breeding activity (see Table 1), were non-significant.

Discussion

Variation in male reproductive success and frequency of EPY

The amount of variation in male reproductive success is generally considered an indicator of the intensity of

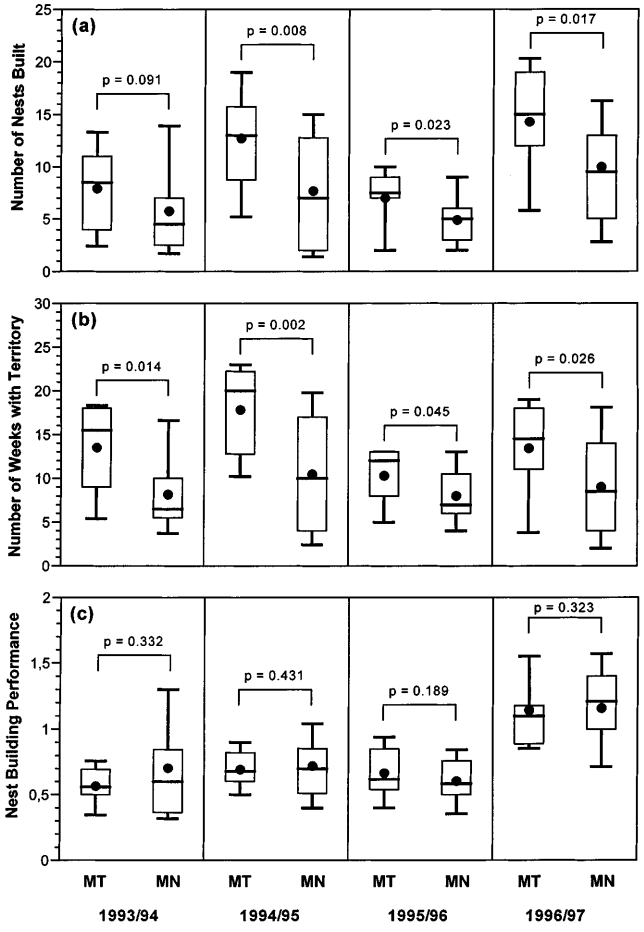

Fig. 5a–c Comparison of three male traits related to male reproductive success between males that established a territory in the following season (males with territory, *MT*) and males that did not do so (males with no territory, *MN*). *Box plots* show medians, interquartiles, 10% and 90% percentiles, and means (*black circles*). Two-tailed *P*-values refer to comparisons using the Mann-Whitney *U*-test. **a** Comparison of the number of nests built by the males. **b** Comparison of the number of weeks the males held a territory. **c** Comparison of male nest-building performance (average number of nests built per week)

sexual selection (e.g. Wade and Arnold 1980; Arnold and Wade 1984; Andersson 1994; Höglund and Alatalo 1995). The standardized or relative variance (variance/mean^2) in mating success among males has proven to be a useful tool in estimating the upper limit of the strength of directional sexual selection (Wade and Arnold 1980; Arnold and Wade 1984) and has therefore been termed the 'opportunity for sexual selection'. Even if it cannot be used to quantify the strength of selection of particular traits, it reflects the potential for sexual selection in a species and can therefore help to decide whether a species is suitable to study different aspects of sexual selection in more detail. The high relative variance of mate mating success in the red bishop (see Table 1) indicates a high potential for sexual selection, making the red bishop a very interesting subject for studies on sexual selection and evolution of male and female mating behaviour.

The occurrence of extra-pair fertilizations in birds, which can account for up to 65% of all nestlings (e.g. Birkhead and Møller 1992; Westneat and Sherman 1997) is an important factor that can greatly affect the amount of variation in male reproductive success (e.g. Webster et al. 1995). Using a meta-analytic approach to assess the available literature on paternity studies in birds, Møller and Ninni (1998) found that the relative variance in realized male reproductive success acquired on the territory (as revealed by allozyme and molecular techniques) was on average 4.6 times higher than the variance in apparent male reproductive success. This indicates the importance of paternity testing for studies on sexual selection in general and for studies on factors affecting male reproductive success in particular. In this study, we determined paternity and realized male reproductive success acquired on the territory in a colony of red bishops. However, it has to be kept in mind that we could not measure male reproductive success obtained outside the territory (i.e. EPY sired on other male's territories) and that the inclusion of these young would probably increase the variation in male reproductive success and modify the correlations found between male behavioral performance and male reproductive success.

Nest number, nest characteristics, and nest-building performance as factors influencing male reproductive success in birds

Several bird studies have identified traits correlated to male reproductive success (for a review, see Andersson 1994). Among the characters selected are territory size and quality, song rate, song repertoire size, certain plumage characteristics, arrival dates, and courtship display rates. There are, however, only a few studies that have demonstrated an effect of nest characteristics or nest number on male mating success. In the penduline tit (*Remiz penduliinus*), males build elaborate nests to attract females, which seem to use nest size as a cue for mate choice. Large nests were characterized by better thermal insulation, which in turn led to increased fledging success (Hoi et al. 1994, 1996). Studying breeding behaviour of the village weaver (*Ploceus cucullatus*) in a large outdoor aviary, Collias and Victoria (1978) found that females prefer fresh green nests over old brown ones. However, this preference was probably due to the fact that males advertised fresh nests significantly more often than old nests, since nest colour alone has been shown to be of minor importance for female nest choice decisions (Collias and Victoria 1978; Jacobs et al. 1978). In the same study, Collias and Victoria (1978) found a significant positive correlation between the number of nests built by a male and the number of nests accepted, similar to the results we obtained in our study on the red bishop both in the field (see results) and in the laboratory (R. Petri, G.M. Klump, T.W.P. Friedl, unpublished data). Results of another study on red bishop reproductive behaviour that were

recently reported as a conference abstract also suggest that the only correlate of male mating success in the red bishop is the number of nests built by the territorial males (Goddard et al. 1998). Similar results were obtained for the yellow-shouldered widowbird, *E. macrourus* (Savalli 1994). Nest number has also been shown to affect female mate choice in wrens, *Troglodytes troglodytes* (Evans and Burn 1996). They found that males that built more nests had a higher mating success than males with fewer nests. A multiple-regression analysis revealed that male age, but no other morphological character, affects the number of nests built, with males building more nests per season as they get older (Evans 1997). However, the results of an additional analysis of covariance led Evans (1997) to the conclusion that in the wren, the number of nests built reflects male condition rather than age and thus can be considered as a signal for male quality.

We found no difference in nest-building performance between males that indicated their superior quality by establishing a territory in the following season and those that did not. This was quite unexpected because nest-building performance exerts strong positive effects on male mating success. Furthermore, there was no correlation of nest-building performance of individual males between different years (Spearman rank correlation coefficients ranged from 0.02 to 0.27, *P*-values from 0.392 to 0.96), indicating that there were no consistent differences between males. One explanation could be the relationship of nest-building performance to age. Collias and Collias (1984) have shown that nest-building ability is poor in young village weaver (*P. cucullatus*) males and that they have to practise before they can build nests properly. This is certainly also true for the red bishop, because the nests built by 1-year-old males were most often untidy, misshapen, and unfinished (personal observation). Even if nests built by 2-year-old males in their first breeding season could not be distinguished from nests built by older and more experienced males (personal observation), a 2-year-old male might take longer to construct a proper nest. Unfortunately, our current database on nest-building performance of males of known age is too small to address this question. In the wren (*T. troglodytes*), where male nest number determines mating success in a way similar to red bishops (Evans and Burn 1996), older males build more nests (Evans 1997). Older males seem to achieve this by starting nest building earlier in the breeding season and building nests for a longer period of time than young males, rather than by building faster (Evans 1997). In the penduline tit (*R. pendulinus*), Schleicher et al. (1996) found a significant repeatability in size of nests built by individual males within a season; however, they neither present data on the repeatability in size of nests built by individual males between seasons nor on repeatability of nest-building rates.

Male quality

Many studies have demonstrated that breeding and rearing offspring is associated with reduced survival of parents (for a review, see Clutton-Brock 1991). A detailed analysis of energetic costs of nest building in several bird species revealed that the energy spent for nest building exceeded the basal metabolic rate by a factor of 1.5–4.9 and equalled the energy spent for the production of 0.5–2.7 complete clutches (Dolnik 1991) demonstrating that nest building requires a considerable amount of energy. Furthermore, data on time budgets obtained for territorial red bishop males in the colony indicated that holding a territory requires a considerable effort (see Results). Therefore, one would expect that males building many nests and holding a territory for a long time in one season would have a lower probability of establishing a territory in the following season than males that hold a territory for a shorter period of time. In our study, however, we found that males that established a territory in the following season held their territory for a longer period of time and built more nests than males that did not establish a territory in the following season (see Results and Fig. 5). That is, males that showed a superior performance in one season by building more nests and holding a territory for longer than other males, also demonstrated a high performance in the following season by establishing a territory, itself an indicator of male competitive ability. This suggests that the number of nests built and the number of weeks a male held a territory may reflect male condition and quality, and thus that successful males are of higher quality than unsuccessful males. The quality differences between males might be caused by environmental and non-additive genetic factors contributing to male condition and quality or they might represent inherent genetic differences between the males.

Do red bishop females choose their mates?

We have shown that measures indicating the condition and quality of male red bishops, i.e. the number of nests built and the number of weeks with a territory, are also correlated with male mating success, as would be expected if females preferentially choose high-quality males. Some studies have indeed demonstrated that female choice is based on male characteristics that seem to indicate male quality (e.g. Von Schantz et al. 1989). By choosing high-quality males, females might gain direct benefits through better paternal care (e.g. Norris 1990; Hill 1991) as well as indirect, genetic benefits in the form of genetically superior offspring (e.g. Houtman 1992; Norris 1993; Petrie 1994; Hasselquist et al. 1996). Red bishop males provide no parental care or food within the territories. Territory quality seems to be very similar between males, since all territories were located in rather uniformly structured reedbeds or bullrush stands around a circular water body. Therefore, potential material benefits of female mate choice seem to be low. However, if females choose males with many nests, they would choose males in good condition and of high quality. This could have implications for females, e.g. in terms of less

courtship disruption and harassment by other males (because high-quality males might be less subject to territory intrusions than low-quality males). Furthermore, if the quality differences are based on inherent genetic differences between males, females choosing males with many nests might gain indirect benefits in terms of high-quality offspring.

The question is whether red bishop females exert any mate choice at all. The linearity of the correlations between the number of nests built by red bishop males and the number of nests accepted by females (see Fig. 4) indicates that male mating success is directly proportional to the number of nests built, and that males that build many nests do not have a disproportionally high number of nests accepted. This mating pattern may represent either random female settlement or result from females choosing the males with the highest available number of empty nests (i.e. according to an ideal free distribution; Fretwell and Lucas 1970). Indeed, a detailed analysis of female settlement rules provided little evidence for active female mate choice, the data rather suggesting random female settlement (Friedl 1998; T.W.P. Friedl and G.M. Klump, unpublished data). This might explain the observed direct proportionality of male mating success to the number of nests built.

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