Breeding strategy and morphological characters in an urban population of blackbirds, *Turdus merula*

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Pairing patterns in monogamous birds are thought to be the consequence of mutual mate choice by males and females for characters linked to individual quality in the opposite sex. Although this may result in assortative pairing for a single character, there may be no simple match between male and female phenotype if the traits linked to individual quality are sex specific. For instance, in several passerine species, females tend to select males on the basis of territory quality or characters that may reflect health or vigour, whereas males benefit from pairing with females in good condition that breed early because early breeding increases reproductive success. We investigated pairing patterns in an urban population of the sexually dimorphic European blackbird in relation to bill colour in males and body condition in females, over a 3-year period. Females breeding early were in significantly better condition than those breeding late. The number of breeding attempts per season was significantly positively correlated with female condition, while the number of fledglings reared by a female in a breeding season was positively correlated with the number of breeding attempts, independently of female condition. Bill colour varied in males and was related to body weight, although not to condition. Female condition was correlated with male bill colour within pairs, with males showing more orange bills being paired to females in better condition. We discuss the observed pairing pattern in relation to individual or territory quality and to the constraints and costs associated with reproduction in each sex.

Pairing is rarely, if ever, random in natural populations (Bateson 1983). In monogamous bird species, adaptive mutual mate choice by males and females is expected to result in assortative pairing for characters linked to individual quality (Andersson 1994). Evidence for assortative pairing in monogamous birds has been presented for characters such as age (Reid 1988; Cézilly et al. 1997), colour morph (O'Donald 1983; Cooke et al. 1995), body or morphological trait size (Boag & Grant 1978; Cooke et al. 1995) and ornaments (Jones & Hunter 1993). However, pairing between individuals according to quality may not always result in positive assortative pairing for a single character, particularly if the constraints and costs associated with reproduction differ between the sexes. This is likely to be the case in monogamous bird species

showing a marked sexual dimorphism. In such species females may select males on the basis of territory quality (Jennions & Petrie 1997) or sexually dimorphic characters that may reflect health and vigour (Zahavi 1975; Hamilton & Zuk 1982; Hill 1991). However, it is difficult to infer pairing processes from a knowledge of pairing patterns, because different processes can lead to similar patterns (Burley 1983; Cézilly et al. 1997).

In passerines, female quality, male ornamentation and territory size and quality may combine in determining pairing patterns and reproductive success. In particular, females in good condition should be able to pair and breed earlier and thus to select the best males or settle on the best territories. Males would benefit from early pairing with females in good condition since early breeding is often associated with higher reproductive success in birds (Darwin 1871; Price et al. 1988). In studies conducted over several years and populations, Hill et al. (1994, 1999) reported that redder male house finches, *Carpodacus mexicanus*, were paired with females that initiated nesting earlier. In addition, Wolfenbarger (1999) showed that redder male northern cardinals, *Cardinalis cardinalis*, a

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dimorphic monogamous passerine, obtained territories of higher quality, paired with earlier breeding females, and experienced increased reproductive success independently of territory quality. However, the relative influences of male and female quality on overall breeding success often remain unclear (see Rintamäki et al. 1998; Wolfenbarger 1999).

We examined pairing patterns in relation to the morphological characteristics of males and females in an urban population of European blackbirds. This socially monogamous species (Snow 1958; Desrochers & Magrath 1996) shows a marked sexual dimorphism. Plumage is entirely black in males, whereas it is brownish in females. In addition, both bill and eye ring are bright yellow to orange in males and some interindividual variation in the intensity of bill colour can be observed within natural populations. Females have brown to dark brown bills, with dull yellow areas in some individuals. However, despite previous studies on pairing in blackbirds (Snow 1958; Edwards 1983; Desrochers & Magrath 1993, 1996), little is known about the importance of bill colour in female mate choice. We therefore examined the relationship between male bill colour and female body condition within pairs over three consecutive breeding seasons.

METHODS

We conducted the study over 3 successive years, from 1997 to 1999, in a 5.5-ha urban park (Jardin de l'Arquebuse) in Dijon (Burgundy, eastern France). Blackbirds were trapped with mist nets from January to July. All captured birds were ringed with one aluminium ring (with authorization from the Ministère de l'Environnement and the Museum National d'Histoire Naturelle-CRBPO) and a unique combination of colour plastic rings. Breeding pairs were monitored each day during each breeding season from February to July. Once pairs had formed we found nests by following females that were carrying nesting material and by weekly systematic searches for nests in bushes, hedges and trees in the park. One male and one female observed together on several occasions with a clear association between them (for example, female following the male, male and female being aggressive to intruders) were considered a pair if at least one full nest was built.

We inspected nests every 2 days for eggs and nestlings. After each inspection, we checked whether females returned to the nest and resumed their incubating or brooding activities. There was no evidence that females abandoned their nest after nest inspection at any stage in the breeding cycle.

To standardize for the stage in the breeding cycle, only individuals and breeding pairs that were ringed and measured early in the breeding season (February–March) were considered in the analyses. Some breeding pairs and individuals were observed over two or three breeding seasons. To avoid pseudoreplication, pairs or individuals that were observed over several years were randomly assigned to one breeding season only. Thus, 28, 13 and 25 males, and 41, 25 and 29 females, were considered for

1997, 1998 and 1999, respectively. These birds corresponded to the sample analysed for body condition measurement. Only some of those individuals were later identified as breeding birds in the study area. Therefore, only 30 breeding pairs (10, 11 and 9 for 1997, 1998 and 1999, respectively) were considered in subsequent analyses. Among the 11 pairs considered in 1998, only the female was ringed and measured in four pairs; for these females we used their measurements only to test relationships between female body condition and breeding success. For each breeding pair, we recorded (1) the first clutch initiation date, (2) the number of breeding attempts in the season (a breeding attempt implied that at least one egg was laid), (3) the number of successful breeding attempts (attempts with at least one fledgling), and (4) the breeding success (number of fledglings produced per breeding season). In further analyses, date of initiation of first clutch, number of breeding attempts and breeding success were standardized to a mean of 0 and a standard deviation of 1. Standardization eliminated possible annual variations in the variables measured.

Morphological and Colour Measurements

We measured right and left tarsus length with callipers to the nearest 0.02 mm, and body weight with a balance with a precision of 0.1 g. For males, we estimated bill colour uniformity by the presence or absence of dark or brown spots on the bill. Thus, the bill was considered as 'spotted' or 'unspotted'. We assigned 0 to individuals with a spotted bill and 1 to individuals with an unspotted bill. Bill colour was assessed with a coloration index derived from the Yolk Colour Fan (Roche, Neuilly-sur-Seine, France), and thus could range from 1 (pale yellow) to 15 (orange). The selected colours have been characterized by tristimulus values of the CIE—1931-standard colorimetric system.

From an independent sample of 46 males captured in different habitats in the area of Dijon, we compared this coloration index with an objective measure of bill coloration by using a quantum spectroradiometer (Endler 1990; Endler & Théry 1996). This instrument (Ocean Optics, Dunedin, Florida, U.S.A.) records the light intensity at each wavelength from 300 to 800 nm. Ultraviolet wavelengths (320–400 nm) were included because birds are known to see in this region of the spectrum (Hunt et al. 1997). Hue, chroma and brightness were then computed, between 320 and 700 nm, using the segment method of Endler (1990). Chroma is a measure of the 'purity' or 'saturation' of a colour (Endler 1990). Bills were measured on one area of 2×3 mm for each side of the superior mandible. As a chroma measure, we used the mean of the two sides. Coloration index showed a highly significant and positive relationship with chroma measurement (Spearman rank correlation: $r_S=0.471$, $N=46$, $P=0.003$; Fig. 1), but not with hue measurement (Spearman rank correlation: $r_S=0.022$, $N=46$, $P=0.881$). In further analyses, bill colour index was standardized to a mean of 0 and a standard deviation of 1.

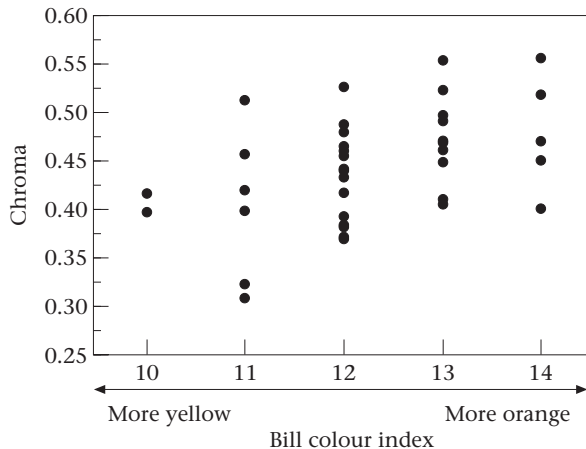Because only a few males were measured in each of the 3 years, we assessed changes in bill colour between years

Figure 1. Relationship between bill colour index (attributed by comparison with the Yolk Colour Fan Roche) and chroma measured with a quantum spectroradiometer (Ocean Optics), for 46 male blackbirds.

by comparing measurements obtained from pairs of successive years (1997 versus 1998, or 1998 versus 1999). Individuals measured over the 3 years were randomly allocated to one pair of years for the analysis.

Body Condition

Individual body condition corresponded to the residuals obtained from a linear regression between log(mean tarsus length) and log(body weight) (Cézilly et al. 1995; Kotiaho 1999). An ANCOVA did not detect any year effect (females: difference between slopes: $F_{2,89}=0.057$, $P=0.940$; difference between intercepts: $F_{2,91}=0.589$, $P=0.573$; males: difference between slopes: $F_{2,61}=1.171$, $P=0.317$; difference between intercepts: $F_{2,63}=1.481$, $P=0.235$). Thus, samples were pooled for each sex over the 3 years before calculation of individual body condition.

For the 30 breeding pairs considered, bill coloration was characterized for 26 males whereas body weight was measured for only 21 of them. Thus, sample sizes differ between statistical treatments.

All statistical tests are two tailed.

RESULTS

First clutch initiation date was measured for 27 of 30 pairs, and three breeding pairs built one nest but did not lay eggs. Ten pairs had at least one successful breeding attempt.

Temporal Variation of Bill Coloration and Uniformity

No significant relationship was observed between the date of measurement of bill coloration in paired males and the value of the estimated colour index (Spearman rank correlation: $r_S=-0.239$, $N=26$, $P=0.231$).
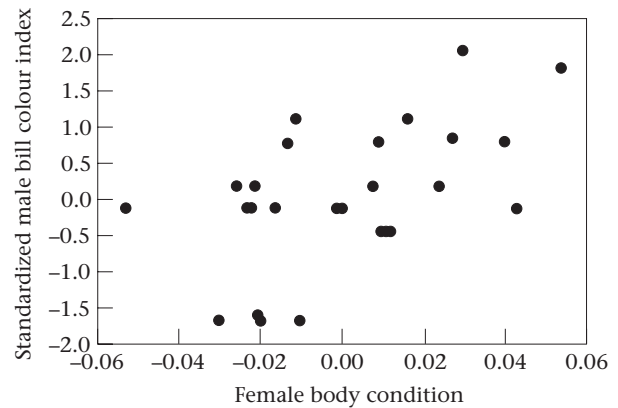

Figure 2. Relationship between female body condition and the bill colour index of their mates.

No interannual variation was observed in bill colour index between 2 consecutive years (1997–1998: 3 individuals; 1998–1999: 9 individuals; Wilcoxon signed-ranks test on pooled data: $T=41$, $N=12$ (with 2 ties), $P=0.193$). In addition, bill uniformity did not change significantly between 2 consecutive years (sign test: $N=12$, $P>0.999$).

Morphological Characteristics of Males

The body condition of males was not significantly correlated with bill colour index (Kendall rank correlation: $\tau=0.228$, $N=21$, $P=0.149$), and did not differ between males with spotted ($N=3$) and unspotted ($N=18$) bills (permutation test for independent samples: $P=0.599$). Bill colour index was, however, significantly correlated with male body weight, larger males having more orange bills (Kendall rank correlation: $\tau=0.354$, $N=21$, $P=0.025$), and did not differ between males with spotted ($N=3$) and unspotted ($N=23$) bills (permutation test for independent samples: $P=0.966$).

Morphological Characteristics and Pairing

Body condition of females was not significantly correlated with the body condition (Kendall rank correlation: $\tau=0.078$, $N=21$, $P=0.622$), or the body weight (Kendall rank correlation: $\tau=0.265$, $N=21$, $P=0.093$) of their mates. Similarly, body condition did not differ between females mated with males with unspotted ($N=23$) and spotted ($N=3$) bills (permutation test for independent samples: $P=0.857$). However, the body condition of females was significantly correlated with the bill colour index of their mates, females in better condition being mated to males with more orange bills (Kendall rank correlation: $\tau=0.327$, $N=26$, $P=0.019$; Fig. 2). Female body condition was still correlated with the bill colour index of their mates when male body weight was kept constant (Kendall partial rank-order correlation: $\tau=0.334$, $N=21$, $P=0.034$), but not with the body weight of their mates when male bill colour index was kept constant (Kendall partial rank-order correlation: $\tau=0.148$, $N=21$, $P=0.349$).
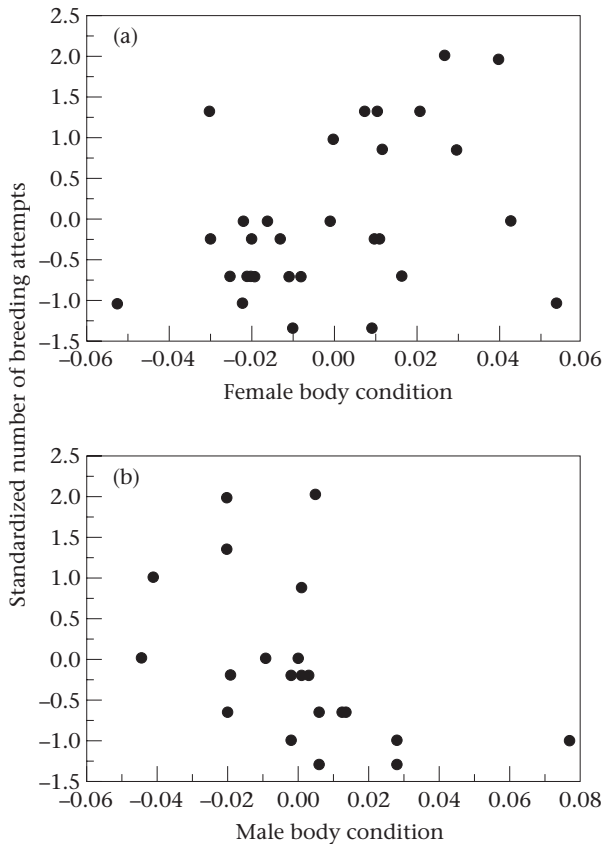
Figure 3. Relationship between (a) female and (b) male body condition and their standardized number of breeding attempts observed throughout the breeding season.

Morphological Characteristics and Breeding

Number of breeding attempts (Fig. 3a) and date of initiation of first clutch were both significantly correlated with female body condition (Kendall rank correlation: $\tau=0.278$, $N=30$, $P=0.031$, and $\tau=-0.336$, $N=27$, $P=0.014$, respectively), while the number of breeding attempts was correlated with first clutch initiation date (Kendall rank correlation: $\tau=-0.298$, $N=27$, $P=0.029$). Females in good condition started reproduction earlier and initiated more breeding attempts than those in poor condition. In addition, the number of breeding attempts was still correlated with female body condition when the first clutch initiation date was kept constant (Kendall partial rank-order correlation coefficient $\tau=0.508$, $N=27$, $P=0.003$). The proportion of successful attempts was not correlated with female body condition (Kendall rank correlation: $\tau=-0.022$, $N=27$, $P=0.869$), whereas the number of successful attempts was significantly correlated with the total number of breeding attempts (Kendall rank correlation: $\tau=0.365$, $N=27$, $P=0.048$).

Females that had more successful breeding attempts produced significantly more fledglings per breeding season (Kendall rank correlation: $\tau=0.507$, $N=10$, $P=0.041$), although the body condition of females that undertook successful attempts was not correlated with either fledgling number per breeding season (Kendall

rank correlation: $\tau=0.076$, $N=10$, $P=0.761$), or fledgling number per breeding attempt (Kendall rank correlation: $\tau=-0.027$, $N=10$, $P=0.914$).

Bill colour index in males was not significantly correlated with first clutch initiation date (Kendall rank correlation: $\tau=-0.098$, $N=23$, $P=0.524$) or the number of breeding attempts (Kendall rank correlation: $\tau=0.082$, $N=26$, $P=0.564$), or with fledgling number (Kendall rank correlation: $\tau=0.023$, $N=23$, $P=0.879$). However, male body condition was significantly negatively correlated with the number of breeding attempts (Kendall rank correlation: $\tau=-0.479$, $N=21$, $P=0.002$; Fig. 3b), males in better condition having fewer attempts, but not with first clutch initiation date (Kendall rank correlation: $\tau=0.147$, $N=18$, $P=0.394$) or breeding success (Kendall rank correlation: $\tau=0.182$, $N=21$, $P=0.277$). In addition, male body condition was still correlated with the number of breeding attempts when female body condition was kept constant (Kendall partial rank order correlation coefficient $\tau=-0.566$, $N=21$, $P=0.005$), and female body condition was still correlated with the number of breeding attempts when male body condition was kept constant (Kendall partial rank order correlation coefficient $\tau=0.516$, $N=21$, $P=0.009$).

DISCUSSION

Our results show the importance of female body condition in the reproductive strategy of urban blackbirds, despite the lack of a direct relationship between this female characteristic and fledgling number per breeding attempt. Females in better condition initiated reproduction earlier and had more breeding attempts than females in poorer condition. Furthermore, the number of young fledged in the breeding season was positively related to the number of breeding attempts. This is not surprising, because the energetic cost of reproduction, in particular egg laying and incubation, is high for females (Trivers 1972; Nur 1984; Martin 1987). Female body condition is directly or indirectly associated with fecundity or breeding success in several bird species such as the house martin, *Delichon urbica* (Bryant 1988), or the common tern, *Sterna hirundo* (Wendeln 1997). Thus, the observed reproductive strategy of urban blackbird pairs appears to be based on the addition of reproductive attempts during the breeding season. Such a strategy maximizes the probability of a successful attempt, and may be expected under high predation pressure (Slagsvold 1984; Milonoff 1989; Martin & Li 1992) as observed in this study, where about 50% of nests failed from predation (B. Faivre, unpublished data). In consequence, males paired with females in good condition experienced indirect benefits in terms of breeding success.

One surprising finding was the negative correlation between male body condition and number of breeding attempts. We have no clear interpretation of this result. One possibility is that males in poor condition have clutches that are more often predated, although we have no evidence of this from our field observations.

An important result of our study is that female blackbirds that bred early were in better condition than

late-breeding ones, and were more likely to be paired with males with more orange bills. A similar pattern was reported in the house finch with redder males being paired with early-breeding females (Hill et al. 1994, 1999). This observed pairing pattern is open to alternative explanations. First, females could prefer and choose males with more orange bills, with females in better condition being the first to choose. Female preference may be linked to direct or indirect benefits (Searcy 1982; Hill 1991; Andersson 1994; Gray 1996; Møller & Thornhill 1998). Orange bill colour of male blackbirds is dependent on carotenoids (F. Belleville-Nabet, personal communication), which cannot be synthesized by birds and are therefore only available from the diet. Hence, males with bright bills may signal their ability to provide good-quality food to the nestlings. Bright bills may also signal resistance to parasites (cf. Hamilton & Zuk 1982). Møller et al. (in press) have recently reported that male blackbirds with bright bills have smaller spleens, indicating better health. In addition, Hatchwell et al. (in press) have also observed a strong tendency of bill colour to be related to blood parasite load in male blackbirds. These studies thus provide some evidence that bill colour may be a signal of male quality in terms of immunocompetence. If immunocompetence has some degree of heritability, females that choose to pair with brightly coloured males may also obtain good genes for their offspring.

Despite a significant correlation between bill colour index and body weight in males, we did not observe assortative pairing with respect to body condition. The association initially detected between female body condition and male body weight was clearly nonsignificant when male bill colour index was kept constant. Some studies have suggested that colour provides a better estimate of individual quality than morphological traits based on size and weight. Johnson & Marzluff (1990) reported that preferred pinyon jay, *Gymnorhinus cyanocephalus*, males were more brightly coloured, but not necessarily larger. In addition, Wolfenbarger (1999) did not observe any correlation between plumage coloration and body size measurements within male northern cardinals, although redder individuals were paired with early-breeding females. Futhermore, in some bird species, variation in colour between males may depend on age, which may also influence female choice (see Andersson 1994; Sundberg & Dixon 1996) and therefore be a confounding factor. Our observations detected no significant changes in bill colour of males measured in 2 successive years. However, the small size of the samples, and the short time scale of our study relative to the blackbird's life span, may be insufficient to test a change in bill coloration with age and a long-term study will probably provide important results on this point.

Alternatively, the observed pairing pattern may arise from intrasexual competition for territories (see Snow 1958; Davies 1992): males with more orange bills could defend better territories, and females in good condition may settle on better territories. Thus, the positive association between females in good condition and males having more orange bills may reflect choice of a territory rather than female preference for a particular male trait

(see Desrochers & Magrath 1996). In this case, different processes could explain a relationship between bill coloration and territory quality: bill colour of males may (1) reflect quality of resources obtained from territories, or (2) be an advertising signal in male–male competition, and males with more orange bills may be dominant during territory acquisition. Røskaft & Rohwer (1987) have reported a similar process in males of red-winged blackbirds, *Agelaius phoeniceus*, where large red epaulettes are perceived as a threat by other males.

Although our results suggest that bill colour of males plays a role in mate choice or territory acquistion in blackbirds, direct evidence is lacking. Future research should thus evaluate the preference of females for males in the field or in a controlled environment, using mounted skins or artificial models (e.g. Enstrom 1993; Jones & Hunter 1993), and the relationship between territory quality and bill colour should also be elucidated.

A related perspective concerns the relationship between male quality, as evaluated through immunocompetence, bill colour and testosterone level. Owens & Short (1995) have suggested that bill coloration may be more appropriate than plumage coloration to test hypotheses about sexual selection and resistance to parasites. Given the potential implication of carotenoid pigments in the elaboration of immune defences (Lozano 1994; Olson & Owens 1998), blackbirds may be a particularly appropriate model to test current hypotheses on sexually dimorphic traits and immunocompetence.

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