Paternity analysis reveals opposing selection pressures on crown coloration in the blue tit (*Parus caeruleus*)

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In socially monogamous species, extra-pair paternity can increase the variance in reproductive success and thereby the potential for sexual selection on male ornaments. We studied whether male secondary sexual ornaments are selected through within- and/or extra-pair reproductive success in the blue tit (*Parus caeruleus*). Male blue tits display a bright blue crown plumage, which reflects substantially in the ultraviolet (UV) and previously has been indicated to be an important sexual signal. We show that males with a more UV-shifted crown hue were less cuckolded, which probably resulted from female preference for more ornamented mates. By contrast, however, older males and males with a less UV-shifted hue sired more extra-pair young. This probably did not reflect direct female preference, since cuckolders were not less UV-ornamented than the males they cuckolded. Alternatively, a trade-off between UV ornamentation and other traits that enhance extra-pair success could explain this pattern. Our results might reflect two alternative male mating tactics, where more UV-ornamented males maximize within-pair success and less UV-ornamented males maximize extra-pair success. Since crown colour was selected in opposite directions by within-pair and extra-pair paternity, directional selection through extra-pair matings seemed weak, at least in this population and breeding season. Reduced intensity of sexual selection due to alternative mating tactics constitutes a potential mechanism maintaining additive genetic variance of male ornaments.

Keywords: extra-pair paternity; structural plumage coloration; sexual selection; *Parus caeruleus*

1. INTRODUCTION

Ornamental traits such as extravagant feathers and colourful plumage are widespread in birds. Usually, males are more ornamented than females, and this sexual dimorphism is associated with sexual selection (Darwin 1871; Andersson 1994). The potential for sexual selection to operate on a given trait is proportional to the variance in reproductive success (Arnold & Wade 1984) and extravagant ornamentation and sexual dimorphism are thus usually associated with polygynous mating systems (Darwin 1871). However, many monogamous species are sexually dichromatic despite an apparent lack of selection potential. Here, more ornamented males can increase their reproductive success by pairing with the most fecund females (Kirkpatrick *et al.* 1990) or through extra-pair matings (Trivers 1972). Genetic parentage analyses have shown that many socially monogamous species show a high incidence of extra-pair paternity (Petrie & Kempenaers 1998; Griffith *et al.* 2002), boosting the variance in male reproductive success (Møller & Ninni 1998).

Since comparative studies have found that sexual dimorphism in ornamentation correlates with the level of extra-pair paternity, it has been claimed that sexual selection through extra-pair matings is the main selective force behind the exaggeration of male ornaments in socially monogamous birds (Møller & Birkhead 1994; Owens &

Hartley 1998; but see Dunn *et al.* 2001). Given that male total fertilization success can increase by siring a larger proportion of the offspring in the own nest (within-pair success) and/or by siring more extra-pair offspring (extra-pair success), both components need to be assessed to evaluate the net effect of sexual selection on male ornamentation.

We studied how the expression of male plumage ornamentation relates to fertilization success in the blue tit (*Parus caeruleus*), a socially monogamous species in which extra-pair matings are known to increase the variance in male reproductive success (Kempenaers *et al.* 1992). Blue tits were traditionally considered to show only slight sexual dichromatism (Svensson 1992). Recently, however, the use of spectroradiometry has shown that the crown and other plumage regions differ substantially between males and females in the ultraviolet (UV, 300–400 nm). Males have brighter and more chromatic crown plumage with reflectance peaking deeper into the UV (Andersson *et al.* 1998; Hunt *et al.* 1998). Several lines of evidence suggest that crown coloration is under directional sexual selection by female choice. In indoor mate-choice experiments, females seemed to prefer males with brighter crowns (Hunt *et al.* 1998), and blue tits viewed through UV-blocking filters were less preferred than birds behind UV-transparent filters (Hunt *et al.* 1999). Free-living birds mate assortatively with respect to crown coloration (Andersson *et al.* 1998), and females produce more male offspring when paired to males with a highly UV-chromatic crown (Sheldon *et al.* 1999). Since these colourful

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males also survived better (Sheldon *et al.* 1999), females may perceive males with highly UV-reflectant crown plumage as high-quality mates. Males with high survival prospects achieve increased seasonal reproductive success by being less cuckolded and siring more extra-pair offspring (Kempenaers *et al.* 1997). These results suggest that male plumage colour could play an important role in female choice of social and extra-pair mates.

We investigated, by means of spectroradiometric colour measurement and microsatellite parentage analysis, whether within-pair and/or extra-pair success select for male UV crown ornamentation. We show that, despite increased variance in male reproductive success and significant effects of male ornamentation on both components of male fertilization success (within-pair and extra-pair paternity), the net directional selection on male UV crown colour is weak. Our results suggest that the effect of sexual selection on male ornamentation can be more complex than is usually assumed.

2. MATERIAL AND METHODS

(a) *Study site and general methods*

This study was carried out during March–June 2001, as part of a long-term research programme on the reproductive biology of a blue tit *Parus c. caeruleus* population. The study area of *ca.* 35 ha is located in Vienna, Austria (48°13′ N, 16°20′ E). It consists of a mixed deciduous woodland dominated by oak (*Quercus robur*), beech (*Fagus sylvatica*) and ash (*Fraxinus excelsior*) and contains approximately 220 nest-boxes.

We captured blue tits in nest-boxes, either in winter while they were roosting or in late spring during chick feeding. Unbanded birds were marked with a unique combination of plastic colour bands and a numbered metal ring. At capture, we measured tarsus length with a caliper to the nearest 0.05 mm, and body mass with an electronic balance to the nearest 0.1 g. Chick-feeding birds were sexed by the presence or absence of a brood patch and aged according to Svensson (1992) as juveniles (second-year birds) or adults (after second-year birds). A small (5–50 μl) blood sample was taken for parentage analysis and colour measurements were performed (see below).

Basic data on reproduction were obtained by regular nest-box checks starting during courtship and nest building (March–April) until fledging (May–June). Chicks were bled (5–25 μl) and banded 14 days after hatching. All unhatched eggs and dead chicks found in the nests were collected, and tissue samples were stored in 70% ethanol. As part of another project, 10 clutches were collected after 1 day of incubation; eggs were opened and embryos stored in ethanol.

(b) *Colour measurements*

Forty-nine males (25 juveniles and 24 adults) captured in the nest-box during chick feeding (days 8–9 after hatching) were colour measured. The reflectance of the crown was measured using a S-2000 spectroradiometer with a DH-2000-FHS deuterium-halogen light source (Ocean Optics, Eerbek, The Netherlands). We used a bifurcated fibre-optic probe on which a cylindrical plastic sheath was mounted to exclude ambient light and standardize measuring distance. The probe was held perpendicular to the feathers and measurements of five different and standardized spots (11.3 mm²) of the crown were made. Reflectance was calculated relative to a white standard (WS-2) with SPECTRAWIN 4.2 software (Top Sensor Systems). Raw spec-

tra were smoothed by a running average calculated on 10 nm intervals. We calculated colour coefficients from the smoothed spectra and averaged them for each individual. Three different coefficients (brightness, hue and chroma), describing the variation in spectral shape (Hailman 1977), were calculated for each spectrum. 'Brightness' (spectral intensity) was calculated as the average reflectance (R_{av}) in the 320–700 nm interval, which encompasses the entire visual sensitivity range of birds. 'Hue' (spectral location) was estimated as the wavelength of peak reflectance ($\lambda(R_{max})$), and 'chroma' (spectral purity) was calculated as $(R_{max}-R_{min})/R_{av}$, that is, the difference between peak and trough divided by brightness. Hue correlated with both chroma ($r = -0.43$, $p = 0.002$, $n = 49$) and brightness ($r = 0.37$, $p = 0.01$, $n = 49$), but the latter two were not correlated ($r = 0.01$, $p = 0.5$, $n = 49$).

(c) *Paternity analysis*

We used eight polymorphic microsatellite markers *Pca3*, *7*, *8* and *9* (Dawson *et al.* 2000), *Pocc1* and *6* (Bensch *et al.* 1996), *Phtr3* (Fridolfsson *et al.* 1997) and *PK11* (S. M. Tanner, H. Richner and D. Schuenperli, unpublished data; EMBL accession no.: AF041465) to determine the paternity of 574 offspring (nestlings and unhatched eggs) in 51 broods. We followed a standard PCR protocol using *ca.* 20 ng of genomic DNA, 0.25 U of *Taq* DNA polymerase (Promega) and 1.5 mM MgCl₂. The PCR profiles had the following annealing temperatures: 53 °C (*Pca8*, *Phtr3*) 55 °C (*Pca3*), 56 °C (*Pocc1*), 57 °C (*Pca9*, *Pocc6*) and 60 °C (*Pca7*, *PK11*). Amplified fragments were resolved on an ABI Prism 310 Genetic Analyser (Applied Biosystems).

The combined probability of exclusion (Jamieson 1994) for the marker set was greater than 0.999. Paternity was excluded if two or more loci showed mismatches between putative fathers and offspring. In 485 cases, there was no ($n = 475$), or one, mismatch ($n = 10$) with the social father. For these offspring, the average probability of false inclusion (Jeffreys *et al.* 1992) was $9.4 \times 10^{-5} \pm 3.5 \times 10^{-4}$ s.d. (range of 1.9×10^{-9}–4.8×10^{-3}). We therefore conclude that they were sired by the social male and that the single mismatches were due to mutations. The remaining 89 offspring showed two or more mismatches with the putative father and were thus sired by extra-pair males. For 66 of the extra-pair offspring, an alternative male matched the paternal genotype completely. One offspring showed a single mismatch with a putative extra-pair sire and since the same male was the unequivocal sire of another offspring in the same nest, we assigned both offspring to this male. The average probability of false inclusion was $8.2 \times 10^{-5} \pm 3.8 \times 10^{-4}$ s.d. (range of 1.6×10^{-9}–3.1×10^{-3}) for the 67 assigned extra-pair offspring.

(d) *Statistical analysis*

Male total fertilization success can increase by avoiding cuckoldry in the own nest (within-pair success) and/or by cuckolding other males (extra-pair success). Response variables to estimate within-pair success were: whether a male was cuckolded or not, the proportion of sired offspring in its nest and the number of cuckolding males siring young in its nest. The corresponding response variables for extra-pair success were: whether a male sired extra-pair young or not, the number of extra-pair young it sired and the number of males it cuckolded. Initially, univariate tests were performed to assess the relationship between male colour variables and within- and extra-pair paternity success. Parametric tests were used if the response variable was normally distributed, otherwise the non-parametric equivalent was used.

Table 1. Comparison of crown colour for (*a*) males that did and did not lose within-pair paternity in their nests (*n* = 47), and (*b*) males that did and did not gain extra-pair paternity (*n* = 49).
(Shown are means ± s.e.)

	(*a*) lost within-pair paternity				(*b*) gained extra-pair paternity			
	no (*n* = 16)	yes (*n* = 31)	*t*	*p*	no (*n* = 32)	yes (*n* = 17)	*t*	*p*
hue	381.2 ± 3.4	393.1 ± 2.6	−2.70	0.01	387.8 ± 2.6	392.1 ± 3.6	−0.94	0.35
brightness	0.23 ± 0.01	0.25 ± 0.01	−1.19	0.24	0.24 ± 0.01	0.26 ± 0.01	−1.18	0.24
chroma	1.02 ± 0.03	0.99 ± 0.02	0.88	0.38	0.99 ± 0.02	1.01 ± 0.04	−0.34	0.73

Table 2. Correlations between crown colour and male within-pair, extra-pair and total fertilization success.
(Shown are Pearson (*r*) or Spearman rank (*r*$_s$) correlation coefficients.)

	within-pair success (*n* = 47)		extra-pair success (*n* = 49)		total success (*n* = 47)
	% sired young	no. of cuckolders	no. of extra-pair young	no. of cuckolded males	no. of sired offspring
hue	$r_s = -0.33$, $p = 0.023$	$r_s = 0.40$, $p = 0.006$	$r_s = 0.18$, $p = 0.20$	$r_s = 0.14$, $p = 0.32$	$r = 0.18$, $p = 0.22$
brightness	$r_s = -0.15$, $p = 0.33$	$r_s = 0.20$, $p = 0.18$	$r_s = 0.19$, $p = 0.19$	$r_s = 0.20$, $p = 0.16$	$r = 0.09$, $p = 0.53$
chroma	$r_s = 0.12$, $p = 0.42$	$r_s = -0.20$, $p = 0.17$	$r_s = 0.01$, $p = 0.92$	$r_s = -0.02$, $p = 0.91$	$r = 0.07$, $p = 0.65$

All tests were two-tailed. In addition to simple correlations, we constructed multiple regression models to investigate the effect of colour variation on male mating success. Since male age and morphometrics can affect paternity (Kempenaers *et al.* 1992, 1997), and given that crown colour also differs between adults and juveniles (Andersson *et al.* 1998; authors' unpublished data), we included these variables together with the three colour variables in Generalized Linear Models. The full models were reduced by sequentially excluding the variables that did not explain a significant part of the deviance. Variables with $p < 0.1$ were included in the final model. All excluded variables were included, one by one, in the final model to confirm that they did not explain a significant part of the variation. Reported statistics and probabilities correspond to the variables when included in the final model. For more details on individual models see table 3. All analyses were performed with SPSS 11.0 and GENSTAT 6.0.

3. RESULTS

(a) *Patterns of within-pair and extra-pair paternity*

Thirty-three out of 51 nests (65%) contained at least one extra-pair young. The number of extra-pair young in a nest varied from 0 to 8 (0–73% of the clutch), and extra-pair offspring accounted for 15% of all typed eggs and young (*n* = 574). In most cases (24 out of 33) only one male sired all extra-pair offspring, while in seven nests two extra-pair fathers were present, and in two cases three males cuckolded the same male. For 67 out of the 89 extra-pair offspring (75%) we could assign the father. All except two extra-pair males were birds found breeding in 2001; two males that were caught during winter and probably bred at the boundary of the study area also sired extra-pair offspring. Within-pair paternity and extra-pair

paternity success were independent. Males that lost paternity in their own nest were neither more nor less likely to sire extra-pair young in other nests ($\chi_1^2 = 0.69$, $p = 0.41$, *n* = 47), and the proportion of young sired in the nest was not correlated with the number of extra-pair young sired by a given male (Spearman rank correlation, $r_s = -0.08$, $p = 0.57$, *n* = 47). The opportunity for sexual selection (I_s = variance in male reproductive success divided by the square of mean success; Arnold & Wade 1984) was 3.5 times higher for male actual fertilization success ($I_s = 0.123$) than expected for male apparent success ($I_s = 0.035$). Extra-pair success was assessed for all 49 colour measured males, while nest predation before blood sampling reduced our sample for within-pair and total success to 47 males.

(b) *Male coloration and within-pair success*

Males that were cuckolded had a more long-wave shifted hue (table 1) than those that achieved full paternity, but they did not differ in the other two colour variables. Similarly, males with a more long-wave hue sired a lower proportion of eggs in their own nest and were cuckolded by more males (table 2; figure 1*a*). The number of cuckolding males and the proportion of lost paternity were highly positively correlated (Spearman rank correlation, $r_s = 0.88$, $p < 0.001$, *n* = 47), even when only nests with extra-pair young were considered (Spearman rank correlation, $r_s = 0.54$, $p = 0.002$, *n* = 31).

Multiple logistic regression analysis, including the three colour variables, male age and morphometrics, confirm crown hue as the only significant predictor of the likelihood of losing paternity (table 3). Thus, males with long-wave shifted hue were more likely to be cuckolded.

Table 3. Generalized Linear Models (GLMs) for male within-pair, extra-pair and total fertilization success.
(Final models after sequentially dropping non-significant variables are depicted in bold. Statistics and probabilities of excluded variables are based on one-by-one inclusion in the final models.)

| | within-pair paternity success | | | | extra-pair paternity success | | | | | |
| | likelihood of losing within-pair paternity[a] | | proportion of sired young[b] | | likelihood of gaining extra-pair paternity[a] | | number of extra-pair young[c] | | total fertilization success[d] | |
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	t	p
age	0.00	0.947	0.72	0.400	**6.97**	**0.008**	**21.07**	**< 0.001**	**2.92**	**0.005**
hue	**6.81**	**0.009**	**3.88**	**0.055**	2.93	0.087	**9.11**	**0.004**	**2.01**	**0.05**
brightness	0.13	0.721	0.32	0.576	0.01	0.939	0.19	0.665	−0.78	0.438
chroma	0.05	0.828	0.52	0.474	0.89	0.345	0.94	0.338	1.16	0.252
tarsus length	0.04	0.836	0.65	0.425	0.86	0.352	0.05	0.830	−0.46	0.643
body mass	0.02	0.900	0.07	0.786	0.00	0.965	0.27	0.604	−0.88	0.384
final model	**6.81**	**0.009**	**3.88**	**0.055**	**3.96**	**0.019**	**12.88**	**< 0.001**	**5.15[e]**	**0.01**
d.f.	1		1		2		2		2	

[a] Binary logistic regression.
[b] GLM with binomial error distribution and logit link, binomial denominator = no. of typed offspring.
[c] GLM with Poisson error distribution and logarithm link.
[d] GLM with normal error distribution and identity link.
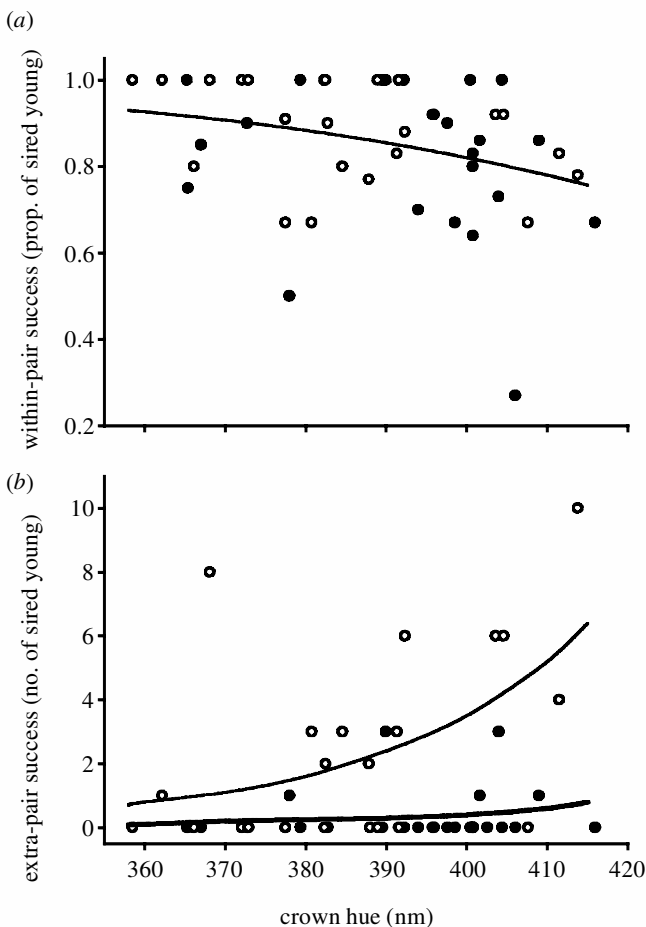[e] *F*-statistic.

(a)

(b)

Figure 1. Male crown hue correlates with (a) within-pair and (b) extra-pair paternity. Filled circles represent juvenile and open circles adult males. Trend lines are as predicted by Generalized Linear Models in table 3. In (b) the bold line corresponds to juvenile and the thin line to adult males.

Accordingly, these males had a higher proportion of extra-pair young in their nests, but this effect was weaker ($p = 0.055$; table 3).

(c) Male coloration and extra-pair success

Males that gained extra-pair paternity did not differ significantly in coloration from males that did not sire extra-pair offspring (table 1). Additionally, in the univariate analyses no colour variable correlated with the number of extra-pair young sired by a given male, nor with the number of nests a male cuckolded (table 2). Multiple regression models indicate that male age was the main determinant of extra-pair success (table 3). However, when age effects were accounted for, crown hue also predicted a significant part of the variation in extra-pair paternity (table 3; figure 1b); males with less UV-shifted crown hue were more likely to gain extra-pair paternity ($p = 0.087$) and sired significantly more extra-pair young ($p = 0.004$). Although this last effect seemed more pronounced in adults (figure 1b), the interaction term was not significant (age × hue, $\chi_1^2 = 0.18$, $p = 0.67$). In conclusion, older males and males with a less UV-shifted crown hue sired more extra-pair young.

(d) Pairwise comparisons between cuckolder and cuckolded males

Neither colour nor morphometric variables differed between cuckolded and cuckolder (paired *t*-test, all $p > 0.14$, $n = 26$). However, cuckolders were usually older than the males they cuckolded (Wilcoxon signed rank test, $Z = −2.50$, $p = 0.012$, $n = 26$). In four cases, males reciprocally exchanged paternity; excluding these cases did not change the conclusions (colour and morphometrics: paired *t*-test, all $p > 0.10$; age: Wilcoxon signed rank test, $Z = −2.88$, $p = 0.004$, $n = 18$).

(e) *Total fertilization success and male coloration*

The total number of eggs a male sired did not correlate with crown colour (table 2). In the multiple regression, including the three colour variables, morphometrics and age (table 3), age was the main predictor of total success, while there was a trend for males with more long-wave shifted hue to sire more offspring. Thus, older males, and to a lesser extent males with less UV-shifted crown hue, achieved greater seasonal fertilization success.

4. DISCUSSION

Crown colour of male blue tits correlated with both components of male seasonal reproductive success: within- and extra-pair paternity. Out of the three variables we used to describe crown colour, only hue was related to fertilization success. Hue, or spectral location, describes the spectral position of peak reflectance (Andersson *et al.* 1998). An increasingly UV-shifted reflectance peak is a likely form of exaggeration of a UV colour signal (Andersson 1999; Keyser & Hill 1999, 2000). Hence, we assume that males with a more UV-shifted crown plumage (hereafter 'more UV' males) display a more extreme ornament than males with a less UV-shifted hue (hereafter 'less UV' males).

Previous studies highlighted the importance of brightness (Hunt *et al.* 1998) and chroma (Sheldon *et al.* 1999) as sexually selected signals in blue tits. We found these two variables to be uncorrelated with fertilization success. However, since hue correlates with brightness as well as chroma, it is apparent that the colour variables are not independent. This is also evident in the study by Sheldon *et al.* (1999) where both chroma and hue correlated with the proportion of male offspring in the brood, although only chroma predicted overwinter survival. Interestingly, in blue tit nestlings the chroma of the UV/blue tail feathers is strongly condition dependent, while hue, although also influenced by condition, seems to be mainly genetically determined (Johnsen *et al.* 2003), suggesting that these two components could be signalling different aspects of quality.

'More UV' males achieved higher within-pair fertilization success independent of age: they were less likely to be cuckolded, sired a larger proportion of their broods (figure 1*a*), and lost paternity to fewer extra-pair males. More elaborate ornaments are usually produced by higher-quality males, and such males should therefore be preferred by females (Andersson 1994). Accordingly, higher within-pair fertilization success of more ornamented males has been shown in many bird species (for a recent review see Griffith *et al.* 2002). In the blue tit, crown UV reflectance has been related to survival (Sheldon *et al.* 1999), and males with higher survival suffered less from cuckoldry (Kempenaers *et al.* 1997). Thus, female blue tits can use male crown coloration to assess the quality of their mate, and our observation that females were more faithful to males with more UV-shifted crown reflectance supports this idea. Alternatively, 'more UV' males might be better at protecting paternity or could have ejaculates that better outcompete the sperm of extra-pair males, but our data do not support this. Although the association between paternity assurance behaviours (like mate guarding) and coloration in the blue tit is unknown,

mate guarding seems to be ineffective at preventing cuckoldry in this species (Kempenaers *et al.* 1995). Likewise, if colourful males have more competitive sperm we would also expect them to sire more extra-pair young, which was not the case (see below).

Extra-pair success was mainly determined by male age (figure 1*b*): older (adult) males were more likely to gain extra-pair paternity and sired a greater number of extra-pair offspring. Since most (72%) of the identified extra-pair fathers were adult birds, cuckolders were usually older than the males they cuckolded. Higher extra-pair fertilization success of older males has been observed before in blue tits (Kempenaers *et al.* 1997), and in several other bird species (Griffith *et al.* 2002). This might be due to older males being more experienced and skilled in sexual display or in the pursuit of extra-pair copulations (Johnsen *et al.* 2001), but it is usually considered a result of direct female preference for older males because of their proven survival ability (Brooks & Kemp 2001). Females can use the more developed ornaments of older males to assess their age. Therefore, since adult blue tits are on average more colourful than juveniles (Örnborg 2002; authors' unpublished data), we might expect that UV ornamentation is one cue by which females assess male age. However, this is not the case: the adults that were most successful at siring extra-pair offspring were those that most strongly resembled juveniles (figure 1*b*).

The (unexpectedly) higher extra-pair success of less UV-ornamented males (figure 1*b*) is difficult to explain but very interesting. Several studies have failed to find a relationship between secondary sexual traits and extra-pair paternity (Hill *et al.* 1994; Cordero *et al.* 1999; Johnsen *et al.* 2001), but to our knowledge this is the first evidence of a negative correlation between ornament expression and extra-pair success to date. This is, however, unlikely to be due to active female choice for 'less UV' males as extra-pair mates. If females would indeed seek less ornamented males as extra-pair partners, we would expect cuckolders to be less UV-shifted than the males they cuckold, which was not the case.

A negative correlation between male UV ornamentation and extra-pair success can arise if crown coloration correlates negatively with other male characteristics that increase their extra-pair success. We showed that less ornamented birds are at higher risk of being cuckolded, and since mate guarding appears ineffective in blue tits (Kempenaers *et al.* 1995), an alternative tactic would be to increase the effort in pursuing extra-pair copulations. 'Less UV' males might thus devote more time and resources to intruding on other territories, or invest more in other sexual displays, such as song. Song is a sexually selected trait in the blue tit (Kempenaers *et al.* 1997; Poesel *et al.* 2001), but there are no published data on the relationship between coloration and song in this species. However, a recent comparative analysis found that elaboration of plumage ornamentation was negatively related to song complexity in cardueline finches, suggesting a trade-off between the expression of different sexual traits (Badyaev *et al.* 2002). That trade-offs between multiple sexual ornaments can operate intraspecifically has recently been shown for tail length and carotenoid coloration in a widowbird (Andersson *et al.* 2002). In blue tits, a similar trade-off between UV ornamentation and some other

trait(s) that enhance(s) male extra-pair success may set the stage for a conditional mating strategy with two alternative tactics (Gross 1996): either invest in crown UV ornamentation and thereby reduce the likelihood of losing paternity, or invest primarily in traits or behaviours that increase extra-pair copulation success, perhaps at the expense of crown coloration. Depending on their phenotypes, individual males should adopt the tactic that maximizes individual fitness, either through within-pair or extra-pair paternity. Detailed behavioural observations and experiments are needed to test this idea.

Irrespective of the explanation, the observation that the same male ornamental trait correlates in opposite directions with the two components of male fertilization success has important implications. Earlier studies have found that more ornamented males achieve either higher within-pair success (Johnsen *et al.* 2001), or higher extra-pair success (Sundberg & Dixon 1996; Yezerinac & Weatherhead 1997; Thusius *et al.* 2001), or both (Saino *et al.* 1997; Sheldon & Ellegren 1999), but to our knowledge this study is the first indication that these two components of male fertilization success exert selection on the same trait in opposite directions. Our results point to the critical importance of estimating both components of male fertilization success to evaluate the effect of sexual selection through extra-pair matings on male ornaments. Conclusions on directional selection on male ornament exaggeration based on studies relying only on within-pair paternity (e.g. Møller & Ninni 1998) should thus be treated with caution.

In summary, we have shown that sexual selection, acting through within-pair and extra-pair paternity, has the potential to shape the evolution of male crown coloration in the blue tit. Since these two selective forces almost cancel each other out (table 3), net directional selection on male UV ornamentation seems weak. However, our study did not assess potential selective forces other than fertilization success. For example, more UV-ornamented males might have an advantage in male–male competition and therefore settle on the best territories, have higher initial pairing success or pair with higher-quality females producing better quality offspring, or show higher survival. Future studies should address these issues to get a more complete understanding how crown UV colour is selected in the blue tit. Meanwhile, our results suggest that the effect of sexual selection on male ornaments through extra-pair matings can be more intricate than is usually assumed (Møller & Birkhead 1994; Møller & Ninni 1998). The existence of alternative male mating tactics linked to ornament expression can reduce the intensity of directional selection on a given trait, and this could help maintain additive genetic variance of sexually selected ornaments.

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