Red plumage and its association with reproductive success in red-capped robins

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Red plumage is produced mainly by deposition of carotenoid pigments into the feathers and is assumed to be costly. Recent studies suggest red plumage may be a condition-dependent, sexually selected signal. To date, few studies have explored the relationship between carotenoid-based plumage colour and genetic (realised) reproductive success. This is despite the rarity of genetic monogamy among avian mating systems. We studied this relationship in the red-capped robin (*Petroica goodenovii*) across two breeding seasons, using spectrophotometric techniques to score colour and molecular markers to assign paternity. Males with the highest within-pair reproductive success during the first season moulted into the most colourful plumage at the conclusion of that season. We found no such correlations when using putative measures of reproductive success, underlining the importance of unambiguous paternity assignment. However, males that moulted into the most colourful plumage did not go on to attain highest reproductive success during the subsequent breeding season (while displaying this plumage). Instead, variation in male reproductive success was explained by male body condition and age. These results suggest that the information value of male plumage colour is unpredictable.

Introduction

Red, orange and yellow plumage is often produced by the deposition of carotenoid pigments into the feathers. Expression of such plumage depends, in part, on ingestion of these carotenoid pigments because birds cannot produce them *de novo* (Fox 1979, Brush 1981, Goodwin 1984, Olson & Owens 1998). The acquisition and subsequent deposition of carotenoids into the plumage is assumed to be costly, because carotenoids are often limited in availability and may be energetically costly to metabolise. Red plumage, in particular, is probably the most costly carotenoid-based plumage to produce (Hill 1996, Olson & Owens 2005). Additionally, because carotenoids are implicated to be important for immune function (Bendich 1993, Lozano 1994, von Schantz *et al.* 1999), individuals might face a trade-off with respect to carotenoid allocation: they may use carotenoids to enhance immune function or they can be deposited into ornamental patches (Lozano 1994). If so, then only high-quality individuals should be able to invest in the most colourful carotenoid-based ornaments and still have enough carotenoids or metabolic

energy left-over to maintain healthy immune function. Thus, carotenoid-based plumage ornaments (and in particular red ornaments) are promising candidates for reliable sexual signals (Olson & Owens 1998).

Several studies have shown that the expression of red plumage can be condition-dependent (Hill & Brawner 1998, Hill 2000, McGraw & Hill 2000), and in three species the most colourful individuals also appear to enjoy reproductive benefits (house finch *Carpodacus mexicanus*: Hill 1990, McGraw *et al*. 2001; northern cardinal *Cardinalis cardinalis*: Wolfenbarger 1999; red-collared widowbird *Euplectes ardens*: Pryke *et al*. 2001a, Pryke 2003). Other studies have found no relationship between the expression of red plumage and reproductive success (Weatherhead & Boag 1995, Dale 2000, Wiebe & Bortolotti 2002).

Most previous studies of carotenoid-based plumage expression measured male reproductive success using putative measures (such as number of fledglings produced within a male's territory). Estimation of reproductive success by such measures may be inappropriate in some cases, given that extra-pair fertilisations (EPFs) are so common in birds (Birkhead & Møller 1992, Griffith *et al*. 2002). This problem has been routinely addressed by employing molecular markers to resolve paternity in relation to plumage ornament expression (e.g. Yezerinac & Weatherhead 1997, Johnsen *et al*. 1998, 2001). However, although carotenoid-based plumage is widespread among avian taxa, very few studies to date have actually examined its influence on genetic reproductive success (cf. Hill *et al*. 1994, Weatherhead & Boag 1995, Sundberg & Dixon 1996).

Here, we use objective techniques to examine the relationship between expression of red plumage colour and reproductive success in the sexually dichromatic red-capped robin (*Petroica goodenovii*). We examine whether the expression of red plumage colour in males was related to reproductive success in the previous or subsequent breeding season. Spectrophotometric measures of male plumage colour were collected once in 2001 (following the annual moult and in between the two breeding seasons studied). If red plumage is a signal of quality, then we predict

that: (1) males with high reproductive success in the 2000/2001 breeding season should moult into the most colourful plumage at the conclusion of that season, and (2) males moulting into the most colourful plumage should go on to have highest reproductive success in the subsequent 2001/2002 season (while displaying this colourful plumage). We also evaluated other phenotypic correlates of male reproductive success. Furthermore, to investigate whether the sexes paired or mated according to quality-related traits, we examined the relationship between breeding success and phenotypic traits in females, and associations between paired males and females in the degree of trait expression.

Methods

Species

Red-capped robins are sexually dichromatic. Adult males (> 1 year old) possess black and white plumage with red forehead and breast patches. This red plumage consists primarily of two red keto-carotenoid pigments, canthaxanthin and adonirubin (High Performance Liquid Chromatography analysis; S. Andersson pers. comm.). In contrast, adult females (> 1 year old) are buff-grey, with rufous forehead caps that contain the same carotenoid pigments, but in smaller quantities (S. Andersson pers. comm.).

Each sex has delayed plumage maturation. Yearling males (in their first year, $n = 26$) resemble adult females but moult into bright plumage at the end of their first breeding season. All females banded as nestlings that recruited into the study area lacked rufous forehead caps as yearlings ($n = 6$). We assumed that other females lacking forehead caps that were recruited into the study area were also yearlings ($n = 16$).

Bird capture and measurement

The study was conducted over two breeding seasons (approximately August to February of 2000/2001 and 2001/2002) at Terrick Terrick National Park, in northern Victoria, Australia. Individuals ($n = 158$) were caught with mist-nets

and banded with a numbered metal band and a unique combination of colour rings to permit individual identification. We measured the length of both tarsi and the head-bill length with callipers to 0.01 mm, and the length of the right wing with a ruler to 0.5 mm. The length and width of the red forehead and breast patches of adult males were measured with callipers to 0.01 mm. The length of adult female forehead caps was measured to 0.01 mm. For females, plumage colour was subjectively classified by DKD as either pale brown, brown or rufous-red. The body mass of each bird was measured to 0.1 g with a spring balance. A small blood sample (approximately 70 μl) was taken by brachial venipuncture and stored in ~95% ethanol for subsequent paternity analysis.

Red-capped robins moult annually in February, directly following the breeding season (pers. obs.). Following convention, we assume that plumage colour changes only at moult because deposition of carotenoid pigments into the feathers can only occur when feathers are replaced. Thus, plumage colour should remain unchanged between moults with the possible exception of minor changes caused by feather abrasion, soiling or pigment degradation over the season (*see* McGraw & Hill 2004). At the onset of the 2001/2002 breeding season, between mid-May and July (breeding season begins in August; Dowling 2003), reflectance spectra of the red cap and breast were measured once for 35 adult males using a S2000 spectrometer, PX-2 pulse xenon light source, a fibre-optic reflectance probe and OOIBase32 software (Ocean Optics, Inc., Dunedin, USA). Four scans were taken from four separate but central areas of the cap and breast patch of each male. Reflectance spectra between 300 and 700 nm were measured relative to white Spectralon (Labsphere Inc.) and dark references against which the spectrophotometer was calibrated between measurements of each new plumage patch.

Reflectance spectra were separated into three objective colour components: brightness (spectral intensity), hue (spectral location or colour: referred to as 'redness'), and chroma (spectral purity or saturation). Brightness was calculated as $R_{300-700}$, the sum of reflectances from 300 to 700 nm. Hue was calculated as λ_{R50}, the wave-

length halfway between the minimum (R_{min}) and maximum (R_{max}) reflectance. Chroma was calculated by dividing the reflectance of the red wavelengths of the spectrum by the total reflectance between 300 and 700 nm: $R_{450-700}/R_{300-700}$. Brightness and chroma measurements were calculated for each of the four scans taken per plumage patch (repeatabilities: breast brightness $r_i = 0.35$, $F_{34,105} = 3.258$, $p < 0.001$, cap brightness $r_i = 0.58$, $F_{35,108} = 6.587$, $p < 0.001$, breast chroma $r_i = 0.33$, $F_{34,105} = 2.927$, $p < 0.001$, cap chroma $r_i = 0.56$, $F_{35,108} = 4.358$, $p < 0.001$) and then averaged. Raw spectra were averaged for each patch per individual and hue measures were calculated from these averaged spectra.

Nesting

The nesting success and breeding behaviour of robins was monitored during the 2000/2001 ($n = 50$ pairs) and 2001/2002 ($n = 60$ pairs) breeding seasons. Each territory was visited at least once every three days to determine locations of colour-banded individuals, and to monitor nesting activity and nest fates. Nestlings ($n = 240$) were banded with a metal band and a unique combination of colour-bands, usually between five and eight days after hatching. A small blood sample (about 50 μl) was taken by brachial venipuncture and stored in ~95% ethanol for parentage analysis.

Once fledged, colour-banded juveniles were monitored every three to five days in their natal territories until evicted by their parents. At this stage, parents stopped feeding and began to actively chase away begging fledglings. If juveniles disappeared from their natal territories within two weeks of fledging (before they could forage independently), we assumed they had died. Juveniles that disappeared following parental aggression three or four weeks after fledging, and when they were no longer dependent on their parents to feed, were assumed to have reached nutritional independence and dispersed.

Microsatellite analysis and paternity assignment

DNA was extracted from blood samples using a

salting-out procedure (Bruford *et al*. 1992). All individuals were genotyped at six loci (*Pgm1–4*, *Escmu6*, *Pocc6*) to determine paternity, using procedures outlined in Dowling *et al*. (2003). The number of alleles per loci ranged from 3 to 48 (mean = 14.8) and observed heterozygosity from 0.08 to 0.91 (mean = 0.51) for 158 sampled adults. The general exclusion probability for 158 genotyped adults was 0.9885.

Two methods were used to assign paternity: exclusion and a likelihood-based approach (Marshall *et al*. 1998). Firstly, putative paternal genotypes were identified by subtracting maternal alleles from the genotype of each nestling, and then this putative genotype was compared to that of the social father. In cases where the social male mismatched the nestling at one or more loci, the nestling was initially assumed to be extra-pair, and a database containing the genotypes of potential fathers in the population was searched to identify whether any other males possessed all the paternal alleles in the offspring. To confirm that exclusion accurately identified the genetic sires, a likelihood-based approach was used to assign paternity, which accounts for possible genotyping errors and mutations. The natural logarithm of the likelihood ratio is called the LOD score (Marshall *et al*. 1998). The simulation program in CERVUS 2.0 was used to estimate the required critical difference in LOD scores between the first and second most likely candidate parent for assignment at a 95% (strict) and 80% (relaxed) confidence level. Nestling genotypes were compared to genotypes of all potential fathers in the population, using LOD scores and a 80% confidence level to rank the likelihood of a given male being the genetic father and assign paternity. Using the above approach, we identified 53 extra-pair fertilisations (of which sires were confirmed for 42).

Data analyses

Estimating body condition

Three measures of body size (mean tarsus length, right wing length and head-bill length) were entered as variables in a Principal Components Analysis (PCA). Separate analyses were con-

ducted for each sex because all three size variables differ between the sexes (Dowling 2003). In both analyses, the first principal component (PC1) was positively correlated with all three size measures and it accounted for 52% of variance in males and 44% in females. Thus, following convention (Pimental 1979), PC1 was used as the index of body size.

An index of body condition was calculated separately for each sex as the residuals of linear mixed model regressions of body mass (g) on size (PC1). Male mass varies with time of day (Dowling 2003). Thus, time of day was included as a fixed effect in the male body condition model. Individual identity was included as a random effect to account for individuals that were measured in both breeding seasons. This analysis was conducted using JMP 5 (2002). There has been recent contention regarding the use of mass-size residuals (Green 2001, Schulte-Hostedde *et al*. 2005) and therefore the residuals were carefully examined to validate they were adequate indices of relative mass (Dowling & Mulder 2006). In brief, certain key assumptions (*see* Green 2001, Schulte-Hostedde *et al*. 2005) were fulfilled. Among these, we confirmed that the relationship between mass and size was linear (using LOWESS smoothing on the scatterplots of body mass and PC1), and that the residuals were also unrelated to PC1 scores.

Male reproductive success

Generalised linear models (GLMs) and generalised linear mixed models (GLMMs, *see* below) were used to examine correlates of male reproductive success. The total reproductive success of a male is the sum of within- and extra-pair paternities. While it is possible to measure a male's total within-pair paternity confidently, it was not possible to determine a male's total extra-pair success. This is because our study site was surrounded by other breeding territories that we did not monitor, and some males within our study site are likely to have gained paternity in territories outside of the study site. For this reason, here we examine only total within-pair reproductive success per male, which is the number of offspring produced by a male's social partner for

which he was the genetic sire (weighted by total number of offspring genotyped from that male's territory, using a binomial denominator in the analysis). To compare realised reproductive success with a putative measure, we also measured putative reproductive success for each male as the total number of fledglings raised in his territory that reached independence (regardless of paternity source).

We used three different sets of models for each measure of male reproductive success. This was necessary because although most variables were collected throughout two breeding seasons, plumage colour was measured only in May–July 2001. The first set of models examined relationships between male reproductive success during the 2000/2001 breeding season and plumage components following moult at the conclusion of this season (patch lengths and spectral components of plumage). These models examined whether males with high reproductive success in 2000/2001 moulted into more colourful plumage at the post-season moult. The second set of models examined the relationship between the same male plumage properties and reproductive success in 2001/2002 (the breeding season following moult).

In both sets of models, we also included male body condition as a covariate in the full model to control for this variable. Also, some of the six components of plumage colour were inter-correlated (Table 1), with either positive or negative correlations. Such negative correlations between colour components are expected in pigment colours because absorptance (i.e. pigment concentration) increases chroma at the expense of brightness, and also shifts hue (Pryke *et al.* 2001b; S. Andersson pers. com.). Breast chroma

was omitted from subsequent statistical analyses to reduce the potential for multicollinearity because it was strongly correlated with breast hue ($r^2 > 0.5$).

In the third set of models, we examined the relationship between male reproductive success in both seasons and a number of other variables measured in both seasons (male age: yearling or adult, age of mate: yearling or adult, paternal cap and breast patch lengths, maternal cap length, paternal and maternal body size and condition) to determine other potential correlates of male reproductive success.

We then examined the relationships between male body condition (both in 2000/2001 and then 2001/2002) and male plumage components.

Female traits, reproductive success and pairing

We examined the relationship between four female traits (adult female cap length, female age: yearling or adult, female body condition and size) and three indices of reproductive success: (1) the date at which a female initiated her first nesting attempt of the season, (2) the total number of offspring successfully raised to independence, and (3) whether the female engaged in EPFs. To determine whether females paired with males according to phenotypic traits, we also included the following attributes of her social partner: age, cap length, breast patch length, body condition and size. We compared the four female traits with the red plumage of their social male partners in another set of models because the colour data were only available during 2001/2002.

Table 1. Pearson correlation matrix of the six plumage colour components ($n = 35$). Correlation coefficients between the same colour component of different patches (eg. cap hue *vs.* breast hue) are set in boldface. Significant correlations ($p < 0.05$) are indicated with asterisks.

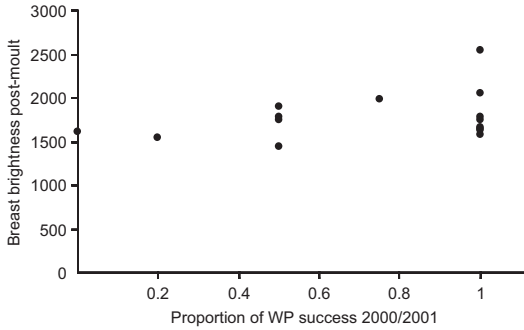|	Breast brightness	Breast hue	Breast chroma	Cap bright	Cap hue
Breast hue	−0.622*				
Breast chroma	−0.682*	0.838*			
Cap brightness	**0.219**	0.064	0.010		
Cap hue	0.245	**−0.023**	−0.079	−0.155	
Cap chroma	−0.520*	0.300	**0.305**	−0.401	0.179

Fig. 1. The proportion of fertilisations each male gained from nestlings hatched in nests on his own territory in the 2000/2001 breeding season, and the subsequent brightness of his breast patch following moult. WP = within-pair success, calculated by dividing the number of offspring sired by a male on his own breeding territory by the total number of offspring genotyped in nests on that territory. Note the GLM algorithm uses weighted proportions, with the number of within-pair fertilisations as the response variable and the total number of offspring genotyped from a given male's territory as the binomial total.

Generalised Linear Models (GLMs) and Generalised Linear Mixed Models (GLMMs)

In all models, the response variable followed either a normal, binomial or Poisson distribution and was analysed in GLMMs or GLMs with normal (identity link), binomial (logit link) or Poisson (logarithm link) error variances. GLMMs were used for analyses containing data from both breeding seasons, to account for individuals present during both seasons. In these cases, individual identity was included as a random effect. All other variables were included as fixed effects.

Full models were reduced by sequentially excluding non-significant interactions and main effects from the model. Models were confirmed by re-including excluded variables, one at a time, into the final model to check they did not explain a significant part of the variance. When the response variable was binary, the dispersion parameter was fixed at 1. For other analyses with binomial or Poisson error variances, dispersion parameters were initially estimated. There were no cases of substantial overdispersion. In cases of under-dispersion, the analysis was repeated with the dispersion parameter fixed at 1. Statistical significance of fixed effects was assessed using Wald statistics compared to a χ^2 distribu-

tion. We did not employ Bonferroni corrections, for reasons outlined in Nakagawa (2004).

GLMs were used for analyses containing spectral colour components because these data were collected in only one season. Full models were reduced sequentially by excluding variables that did not explain a significant part of the deviance. Models were confirmed by re-including excluded variables, one at a time, into the final model to check they did not explain a significant part of the deviance. For simplification, and reasons of space limitation, only variables with $p < 0.1$ are presented in the results. GLMMs and GLMs were conducted using GenStat 6.0 (2002).

Results

Genetic mating system and paternity

Of 227 genotyped offspring, there were two cases where offspring alleles did not match those of their social mothers at one of the typed loci (once with *Pgm 1* and once with *Escmu6*). It was assumed these were mutations or typing errors because all other loci matched the nestling to the social mother.

Twenty three per cent of offspring were sired by extra-pair fathers, and 37% of broods contained at least one extra-pair offspring. Extra-pair sires were typically males in neighbouring territories (23 extra-pair sires were direct neighbours, 15 sires resided two territories from the offspring, three sires were three territories distant and one sire was four territories distant).

Male reproductive success and plumage colour

Males with high within-pair reproductive success in the 2000/2001 breeding season moulted into more colourful plumage (brighter caps and breast patches, higher carotenoid-saturation of cap and higher breast hue) after the post-breeding moult at the conclusion of that season (Fig. 1 and Table 2). Males in high body condition in 2000/2001 tended to moult into brighter (GLM, $t = 1.89$, $n = 20$, $p = 0.076$) and more carotenoid-saturated caps ($t = 1.80$, $n = 20$, $p = 0.09$) at
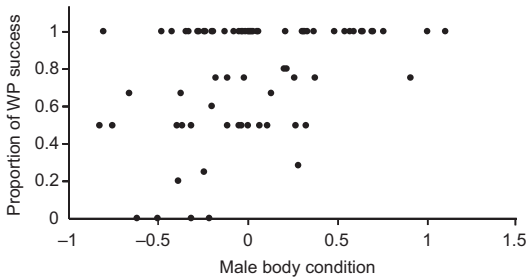
Fig. 2. The proportion of fertilisations each male gained from nestlings hatched in nests on his own territory (Proportion WP success) and the associated body condition of that male. Data are pooled for both seasons.

Fig. 3. Cap lengths (mm) of adult females and the corresponding date each female initiated her first nesting attempt of the season.

the conclusion of that season. Finally, putative reproductive success in 2000/2001 was unrelated to all plumage components post-moult.

There were no relationships between male plumage colour, measured in May/June 2001, and reproductive success (within-pair or putative) in the subsequent 2001/2002 season, nor between plumage colour and body condition in 2001/2002.

Correlates of male reproductive success

Combining data from both seasons, males in higher body condition had higher within-pair success than those in lower condition (GLMM: binomial error, $n = 76$, Wald = 8.15, $p = 0.004$, Fig. 2). Males body condition was repeatable between seasons, with males in high condition in 2000/2001 also generally in high condition in the 2001/2002 season ($r = 0.49$, $n = 22$, $p = 0.007$). Older males (> 1 year, in adult plumage) started nesting earlier in the season (GLMM: normal error, $n = 88$, Wald = –21.49, $p < 0.001$), gained EPFs more often (GLMM: binomial error, $n = 88$, Wald = 4.53, $p = 0.033$) and sired more offspring that reached independence than yearling males in female-like plumage (GLMM: Poisson error, $n = 88$, Wald = 4.78, $p = 0.029$).

Female traits and reproductive success

Female cap length was positively related to our categorical cap colour index ($F_{2,43} = 4.04$, $p = 0.025$). We used cap length as a proxy for
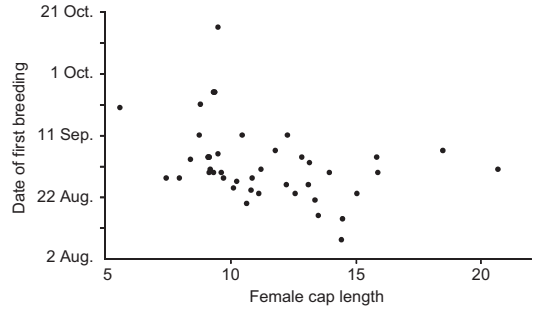
female cap ornamentation because it was the more objective measure (female cap colour was measured without reflectance spectrometry).

Adult females started breeding earlier in the season (GLMM: normal error, Wald = –4.94, $n = 86$, $p = 0.026$), produced more offspring that reached independence (GLM: Poisson error, $t = 0.207$, $n = 86$, $p = 0.039$) and tended to engage in more EPFs than yearlings (GLMM: Poisson error, $n = 76$, Wald = 3.79, $p = 0.052$). Among adult females, those with longer forehead caps initiated their first nesting attempts of the breeding season earlier than those with smaller caps (GLMM: normal error, $n = 52$, Wald = –5.10, $p = 0.024$, Fig. 3).

Pairing according to quality-related traits

Individuals paired assortatively with respect to age, with yearlings more often pairing with year-

Table 2. Relationship between male within-pair reproductive success in 2000/2001 and plumage colour following moult. Model has binomial error distribution and logit link. Response variable = number of within-pair fertilisations, binomial total = total number of nestlings genotyped in that male's nests; $n = 20$, dispersion fixed at 1.

	GLM estimate	SE	t	p
Constant	–485	205		
Breast brightness	0.01049	0.00360	2.91	0.004
Breast hue	0.684	0.315	2.17	0.030
Cap chroma	59.1	26.8	2.21	0.027
Cap brightness	0.00584	0.00281	2.08	0.038

lings and adults with adults (GLMM: binomial error, $n = 83$, Wald = 8.13, $p = 0.004$). Females with longer caps paired with males with shorter (GLMM: normal error, Wald = –9.52, $n = 18$, $p = 0.002$), but more carotenoid-saturated caps (Wald = 5.02, $n = 18$, $p = 0.025$). Larger females paired with males with redder caps (higher cap hue) than did smaller females (Wald = 7.35, $n = 21$, $p = 0.007$). Table 3 summarises all correlations involving male plumage colour.

Discussion

Males with highest within-pair reproductive success in the 2000/2001 breeding season moulted into the most colourful plumage at the post-season moult (2001). Strikingly, male within-pair success in 2000/2001 was positively and consistently related to almost all measures of male ornamental colour (cap and breast brightness, cap length and chroma, breast hue and patch length) at the subsequent 2001 moult. Additionally, males in high body condition in 2000/2001 tended to moult into more colourful caps at the subsequent 2001 moult. Males in high body condition during the 2000/2001 breeding season remained in high condition for the subsequent 2001/2002 season. Combined, these results would suggest that plumage attributes in red-capped robins may convey some quality-related signal content. For instance, it is possible that the highest quality males were able to invest most in reproduction, while still possessing relatively larger reserves than less successful males to invest in colourful plumage at moult. Yet, if so, then it is predicted that the highest-quality individuals should consistently express the most colourful plumage and enjoy the highest repro-ductive success across seasons. However, male reproductive success in the breeding season after the 2001 moult did not correlate with any measures of plumage ornamentation. Furthermore, we found no unambiguous female preference for expected plumage attributes. For instance, high-quality females (those that began breeding earlier and subsequently produced more offspring reaching independence; Dowling 2003) had longer forehead caps and paired with males that had shorter, but more carotenoid-saturated caps, while larger females paired to males with redder caps. Also, we found no evidence that females pairing with highly-ornamented males gained numeric reproductive benefits because male colour attributes were unrelated to the number of offspring surviving to independence in his territory during the 2001/2002 season. We may have failed to detect a relationship between plumage colour and reproductive success in 2001/2002 because the relationship was swamped by stochastic effects. For instance, nest predation rates within this population were high (particularly in 2001/2002) and variable (Dowling 2003), and may have masked any effect of plumage colour on reproductive success in 2001/2002.

Previous studies examining the relationship between the expression of red plumage in males and reproductive success have produced conflicting results. The house finch provides perhaps the most comprehensive example of red, carotenoid-based plumage correlated with high reproductive success in males. Hill (1991) found that colourful males had a higher probability of pairing. Among paired males, redder individuals paired with females that initiated nesting earlier (Hill *et al.* 1999), and produced more fledglings (McGraw *et al.* 2001). EPFs occur in this species (8% of offspring in a Michigan population), but

Table 3. Summary of relationships involving male plumage colour components. ++ = significant positive relationship ($p < 0.05$), + = positive relationship ($p < 0.1$).

Colour component in 2001/2002	Previous reproductive success (2000/2001)	Male condition	Pair formation	Reproductive success (2001/2002)]
Breast brightness	++			
Breast hue	++			
Cap brightness	++	+		
Cap chroma	++	+	++	
Cap hue			++	

colourful males were not cuckolded less than duller males (Hill *et al*. 1994). Wolfenbarger (1999) also found a similar relationship in northern cardinals to the above example, and Pryke *et al*. (2001a, 2001b, 2002) revealed that collar colouration in red-collared widowbirds is probably maintained through intra- rather than inter-sexual selection. In contrast, studies of a number of other species have failed to find relationships between expression of red plumage and reproductive success (Weatherhead & Boag 1995, Dale 2000, Wiebe & Bortolotti 2002). Among possible explanations for the lack of the expected relationships in these studies, Weatherhead and Boag (1995), who studied red-winged blackbirds (*Agelaius phoeniceus*), suggested that they had either failed to measure the plumage trait correctly or that the trait, having evolved via sexual selection, was no longer subject to directional selection. Wiebe and Bortolotti (2002) found no relationship between plumage colour and reproductive success in the northern flicker (*Colaptes auratus*) in a hybrid zone. This is perhaps unsurprising considering that males in the hybrid population that they studied were of intermediate plumage colour when compared with males from the parental populations. Thus, the variation in plumage colour they observed was unlike that of most populations of flickers. Finally, Dale (2000) found no relationships between plumage colour and reproductive success in male red-billed queleas (*Quelea quelea*), and suggested that red plumage colour in this species may be a signal of individual identity rather than a condition-dependent trait.

With the exception of a couple of studies (Hill *et al*. 1994, Weatherhead & Boag 1995), most studies to examine the functional significance of red plumage colouration have measured putative rather than genetic (realised) reproductive success. This omission is potentially worrying because EPFs occur in most bird species, including those with bi-parental care (Birkhead & Møller 1992). The EPF rate in red-capped robins was 23%, and EPF rates may reach 80% in some birds (Mulder *et al*. 1994, Hughes *et al*. 2003). When we analysed our data using putative measures of reproductive success as the response variable (i.e. total fledglings surviving to independence in a male's territory), there were no

relationships between male reproductive success in 2000/2001 and plumage colour post-moult, or between reproductive success in 2001/2002 and plumage colour in the same season. Clearly, putative measures of reproductive success may be misleading indices of true reproductive success in red-capped robins, and potentially in other species.

Although males possessing colourful plumage did not produce more offspring in 2001/2002, other variables did correlate with male reproductive success. Over both years of the study, males in higher body condition had higher within-pair reproductive success than those in lower condition. Thus, it appears that the within-pair success of a male is partly determined by his body condition, with females mating extra-pair more often when their social mate is in poor condition. When mating extra-pair, the sire was determined by three factors: male age (generally yearling males did not gain EPFs), proximity of the extra-pair male (extra-pair sires were often territory neighbours) and genetic diversity (extra-pair males were more heterozygous than their within-pair counterparts; Dowling & Mulder 2006). Although we can only speculate as to why males in high condition procured a greater share of within-pair paternity, one likely explanation is that mate-guarding is an energetically costly activity and that males in high condition are better able to guard their mates from prospective extra-pair sires. In support of this, Komdeur (2001) experimentally demonstrated that male Seychelles warblers (*Acrocephalus sechellensis*) that were induced to reduce mate-guarding spent more time foraging and gained higher body condition than control males.

Male age was also an important contributor to reproductive success, with adult males (in colourful plumage) commencing breeding earlier in the season, gaining more EPFs and producing more fledglings (that reached independence) in their territories than yearling males. An increase in reproductive success with male age is a common pattern among passerines (eg. Wetton *et al*. 1995, Johnsen *et al*. 2001, Geslin *et al*. 2004). In red-capped robins, yearling males tend to be in poorer body condition than adult males (Dowling & Mulder 2006). Combined with the lack of prior breeding experience within this age

class, it is unsurprising that yearling males have lower reproductive success than adults.

In conclusion, expression of red plumage in male robins was related to their reproductive success during the previous breeding season, and thus may effectively convey some quality-related signal content. However, this did not result in the most colourful males producing more offspring in the subsequent season. Instead, male body condition and age were important in determining male reproductive success. The information content of male plumage colour was therefore inconsistent and females, if choosing, presumably benefit from basing their choice of mates on multiple cues.

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