



Multiple ornaments correlate with aspects of condition and behaviour in female northern cardinals, *Cardinalis cardinalis*

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Male ornamentation in socially monogamous birds has been shown to provide information to potential mates on aspects of condition and behaviour. We studied female ornamentation in the socially monogamous, biparental northern cardinal to determine whether expressions of multiple ornaments correlate with aspects of female condition and behaviour. Expressions of the ornamental red-orange bill, red underwing feathers, head crest and blackish face mask were compared to several measures of condition, parental behaviour and intrasexual aggression. Red-orange bill colour of females was correlated with both body size and an index of body condition. Redness of the underwing feathers was correlated with body size, body condition, date of first nest produced and reproductive success. Face mask expression was correlated with both nestling feeding rate and level of intrasexual aggression. The length of head crest feathers did not correlate with any measured aspect of condition or behaviour. These results are consistent with the hypothesis that ornaments in female cardinals provide redundant information to prospective mates on aspects of female condition and behaviour.

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Studies of ornamentation have focused on male ornaments and their maintenance by sexual selection (Andersson 1994). A variety of studies on male ornaments has shown that they function in both aggressive competition and mate choice. Female ornaments are typically less extravagant than male ornaments and, thus, less studied. Lande (1980) modelled female ornament expression under the assumption that female ornaments are not sexually selected but are rather the unavoidable consequence of a genome shared by the sexes and strong selection on male ornamentation (the 'correlated response' hypothesis). He assumed that natural selection reduces female ornament expression, and this ongoing process of reduction explained common sexual dimorphism in ornamentation.

Amundsen's (2000) review of studies of female ornaments in birds supported the hypothesis that ornaments are maintained in females through sexual selection. Recent studies have shown that female ornaments are indicative of condition, that males assess female ornamentation, and that males prefer more ornamented females as mates (Hunt et al. 1999; Roulin 1999; Amundsen 2000; Amundsen &

Forsgren 2001; Berglund & Rosenqvist 2001a; Domb & Pagel 2001; Reichert et al. 2002; Romero-Pujante et al. 2002; Weiss 2002).

Although studies of ornamentation in males and females have focused on single conspicuous ornaments, many species possess multiple ornaments that are displayed by both sexes. Birds frequently display multiple ornaments, as well as a variety of ornament types (e.g. colourful plumage or skin, elongate or elaborate feathers, leg spurs). Studies of multiple ornaments have focused on males of promiscuous and polygynous avian species, because these groups include some of the most extravagantly ornamented species (Zuk et al. 1990, 1992; Ligon & Zwartjes 1995; Omland 1996; Andersson et al. 2002). Multiple ornaments in female birds have not been investigated.

Many socially monogamous, biparental birds also possess multiple ornaments, and expressions of male ornaments in these species correlate with aspects of condition and behaviour (Evans & Hatchwell 1992a, b; Marchetti 1998). It has been hypothesized that ornamentation in socially monogamous, biparental birds may also indicate parental care capabilities (Hoelzer 1989), and studies have shown that single ornaments in such species provide this information (Hill 1991; Sætre et al. 1995; Wiehn 1997; Linville et al. 1998; Voltura et al. 2002). Whether multiple ornaments in socially monogamous, biparental birds act together to provide information about parental care capabilities is not known.

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Several hypotheses that may explain the evolution of multiple ornaments have been presented. Originally presented to address male ornamentation, they are applicable to female ornamentation as well. Møller & Pomiankowski (1993) presented three hypotheses for the evolutionary maintenance of multiple ornaments by mate choice. Holland & Rice (1998) developed the chase-away model of sexual selection relevant to the question of multiple ornaments, focusing on sexual conflict as it influences ornament evolution. Alternatively, some ornaments of a multiple-ornament display may function solely in intrasexual interactions, although an individual's intrasexual status may affect its perceived attractiveness as a mate (Berglund et al. 1996). Finally, some ornamental characters may not function as indicators of condition but rather as amplifiers of other ornaments assessed during mate choice (Hasson 1989). Testing the various hypotheses for the evolutionary maintenance of multiple ornaments depends, to some degree, on determining both the relation between ornament expressions on the same individual and that between ornament expression and aspects of condition.

Northern cardinals are a socially monogamous, biparental species in which both sexes are multiply ornamented. Female cardinals possess four ornamental plumage characteristics: red underwing coverts (carotenoid-based coloration, K. McGraw, personal communication) that are displayed to males early in the breeding season (J. M. Jawor, R. Breitwisch, personal observation), reddish head crests, blackish face masks (melanin-based coloration) and red-orange bills. In female birds, carotenoid-based coloration has been shown to indicate condition (Burley et al. 1992) and parental behaviour (Linville et al. 1998), and to be preferred by males (Hill 1993). Melanin-based ornaments are indicative of aspects of condition and age and are used in mate choice (Amundsen et al. 1997; Tella et al. 1997; Otter & Ratcliffe 1999; Roulin 1999). Feather length ornaments are assessed during mate choice, are used in intrasexual interactions, and are indicative of condition (Jones & Hunter 1993, 1999; Møller 1993; Romero-Pujante et al. 2002). A previous study of female cardinal ornamentation focused on the red underwing coverts. Linville et al. (1998) found that underwing covert colour is indicative of the level of maternal care provided, in terms of nestling feeding. The signal content of other female cardinal ornaments has not been investigated.

We investigated the multiple ornaments of female cardinals to determine both the relation between ornament expressions on the same individual and that between ornament expression and measures of condition and behaviour. The first step in determining whether the multiple ornaments of females are sexually selected is to determine their signal content. The results of this research are relevant to both the sexual selection hypothesis for the evolution of female ornaments and several hypotheses for the evolution of multiple ornaments, especially in socially monogamous, biparental species.

METHODS

We conducted this study at Aullwood Audubon Center and Farm (39°52'N, 84°16'W), 15 km northwest of

Dayton, Ohio, U.S.A., during the breeding seasons of 3 years (2000–2002). We captured individuals with potter traps and mist nets during the early breeding season. Each bird was banded with a U.S. Fish and Wildlife Service numbered aluminium band and three coloured leg bands in unique combinations. Although some females remained on the study site for several years, each female contributed to this data set only once, during the first year of capture.

Ornament Measures

We recorded two plumage colour ornaments, a feather length ornament and bill colour for all birds. We measured the colour of carotenoid-based plumage ornaments using a Digital Swatchbook reflectance spectrophotometer (X-Rite, Inc., Grandville, Michigan, U.S.A.), which yielded reflected spectra of areas of plumage. Measurements of the underwing region of red coverts were taken. Spectral data were divided into three components: hue, saturation (chroma) and brightness. Variables were derived following Endler (1990) and as in Andersson et al. (2002). Briefly, we estimated hue as the wavelength at which reflectance was halfway between its minimum and maximum (designated as $\lambda(R50)$). We estimated saturation as the difference between two spectral segments, with the segment divider defined as $\lambda(R50)$. This difference was then divided by the total reflectance. We estimated brightness as the total reflectance between 400 and 700 nm. Ultraviolet (UV) reflectance was not considered because carotenoid-based plumage displays minimal reflectance in the UV part of the spectrum (Wolfenbarger 1999a; G. E. Hill, personal communication). Colour variables were then entered into a principal component analysis (PCA) to yield a single colour score (principal component 1) for plumage that was then used in all analyses. The first principal component explained 85% of the observed variation in female underwing plumage coloration. Hue and saturation components loaded positively, whereas brightness loaded negatively. These relationships were expected. As pigment concentration in plumage increases, hue shifts, and saturation increases at the expense of brightness (see Andersson et al. 2002). Individuals with a high colour score had redder, more saturated plumage that was not as bright as in individuals with a lower colour score.

We determined female face mask scores from standard photographs and ranked them from 1 (light grey mask barely extending from the bill) to 5 (black mask extending below the bill towards the neck and extending upward to the eyes). Face mask colour was not scored via the Digital Swatchbook due to the small size of many face masks in relation to the size of the measurement window of the spectrophotometer.

We measured crest length (mm) from the point of feather attachment to the end of the longest feathers. Female crest length was not related to structural size, measured as tarsus length ($r_{82} = 0.12$, $P = 0.24$). Therefore, we use crest length uncorrected for body size.

Bill colour score was determined by matching the bill to the most similar Munsell colour chip. We were unable to use the Digital Swatchbook to measure bill colour due

to the size and convexity of the bill relative to the size of the measurement window of the spectrophotometer. Because colour is a three-dimensional categorization, we converted Munsell scores to a one-dimensional ordinal continuum similar to that in [Burley & Coopersmith \(1987\)](#). We weighted colour brightness primary, with hue secondary and saturation tertiary, to prevent the possibility of a highly saturated pink outranking a darker, less saturated red-orange (as in [Linville et al. 1998](#)).

Researchers have found that avian ornament expression increases with age in some species. However, this is not the case with cardinals ([Jawor et al. 2003](#); J. M. Jawor & R. Breitwisch, unpublished data). Therefore, we did not assess age influence here.

Measures of Condition and Reproductive Success

We collected five measures of condition: mean growth of feathers during autumn moult, a body size measure (wing chord), an index of body condition, the date of nest initiation, and the number of nests produced during the breeding season. We determined mean feather growth during moult by locating and measuring 10 growth bars on the right outermost rectrix following the methods described in [Grubb \(1989\)](#). Individual nutritional status is reflected by the rate at which individuals complete moult ([Grubb 1989](#)). Additionally, [Grubb et al. \(1991\)](#) found that age and time of year can affect cardinal feather growth. We collected feathers only following the annual autumn moult. Although the females were of unknown age, there is no age effect on rate of feather growth for females in the autumn ([Grubb et al. 1991](#); T. C. Grubb, personal communication). Mean width of growth bars in feathers is not related to structural size, as measured by tarsus length ($r_{81} = -0.04$, $P = 0.69$). We determined the body condition index by linear regression of body weight on tarsus length, yielding a predicted body weight based on skeletal structural size ([Brown 1996](#)). Residuals of body weight were used as an index of body condition.

Cardinals are multibrooded, and nest searches began in mid-March of each year and continued until late August. We recorded the date of the first nest constructed, whether complete (lined and received eggs) or incomplete (nest base built, but no eggs laid). During late March and early April, inclement weather can delay egg laying in cardinals, and sometimes early nests do not receive eggs, but nest-building females show a readiness to breed. We recorded the number of nests that were completed (lined and received eggs) for each female on the study site. We recorded reproductive success of female cardinals as the number of fledged nests.

We did not use clutch size as a measure of condition because this population is heavily parasitized by brown-headed cowbirds, *Molothrus ater*. Female cowbirds sometimes remove a cardinal egg when they lay their own, and determining clutch size requires daily (and often more frequent) visits to nests during the egg-laying period ([Eckerle & Breitwisch 1997](#)). This, in turn, can lead to nest disturbance, which we hoped to avoid in this study. We used number of fledged nests in a season as our measure of reproductive success in preference to number of

fledglings, because heavy nest predation occurs in this population ([Filliater et al. 1994](#)) and there is no nestling starvation. Because nest predation led to complete loss of contents, reproductive success was primarily the consequence of the number of nests that avoided predation.

Female cardinals that are mated to more ornamented (redder upper breast plumage) males begin their first nest earlier in the breeding season than other females ([Wolfenbarger 1999b](#); [Jawor 2002](#)). Additionally, females mated to males with larger black face masks have fewer successfully fledged nests in a season ([Jawor 2002](#)). These patterns may be influenced by multiple factors, not the subject of this study. We did not consider male ornamentation in this study as a correlate of timing of a female's first nest or number of nests built or number of successfully fledged nests because not all males in pairs were captured. Controlling for male ornamentation would have reduced our sample sizes significantly. However, because cardinals in this population mate assortatively by multiple ornaments ([Jawor et al. 2003](#)) and because female ornament expression indicates aspects of condition (see [Results](#)), female ornamentation by itself may be a predictor of female readiness to nest.

Parental Care Behaviour

We determined nestling feeding rate as feedings per nestling per h during 1-h observation periods. Observations for each female occurred on 5 separate days of the 10-day nestling period, each between 0700 and 1300 hours. Because parents feed more frequently as nestlings age ([Filliater & Breitwisch 1997](#)), we controlled for nestling age by comparing each female's per nestling feeding rate on a given day to the mean rate of all other females whose nestlings were of the same age. This was done for each of the 5 days in a female's sample, and the summed departure from the summed mean yielded a standardized feeding score for each female (as in [Linville et al. 1998](#)). Because females in this population also may feed larger broods at lower rates on a per nestling basis ([Filliater & Breitwisch 1997](#)), we tested whether brood size (range 1–4 nestlings/brood) affected nestling provisioning rates and found that it did not (one-way analysis of variance, ANOVA: $F_{3,17} = 0.39$, $P = 0.67$).

Intrasexual Aggression

We also investigated whether female ornaments convey information about their behaviour towards conspecifics. Female cardinals can be very aggressive towards other females intruding into their territory (J. M. Jawor & R. Breitwisch, personal observation). We measured intrasexual aggression by recording the response of females towards a model female cardinal intruder at the nest early in incubation (2–5 days after clutch completion). We placed a model female cardinal at nest height 1 m from the nest of a focal female while the female was absent (i.e. between incubation bouts). We recorded the focal female's response to the 'intruder' upon discovery during a trial that lasted either 3 min or until the model was struck by

the female. Measures of aggression collected included the time until the model was struck (if a strike occurred), the number of strikes (some females struck the model repeatedly in less than 10 s), and the shortest distance to the model during the trial.

Statistical Analysis

Data were analysed using SAS 8.0 (SAS Institute 1999) for principal component analyses and SigmaStat Version 1.0 (1993) for Pearson linear correlations and backward stepwise linear regressions. We used Pearson linear correlations to compare expressions between ornaments on the same individual. In these correlations, we used ranks for bill colour scores because the scoring system was on an ordinal scale (see above). Significance of correlations was corrected by the sequential Bonferroni method (Rice 1989). For all nonsignificant test results, we determined the power of the test using the power tables of Cohen (1977) with $\alpha = 0.01$. The effect size used for power analyses was based on $r = 0.70$. At an r of 0.70, approximately half of the variance in one variable is associated with the other variable considered in the correlation (Snedecor & Cochran 1989). Backward stepwise linear regressions were conducted to assess the contributions of each ornament to predicting aspects of quality ($P \leq 0.05$ for inclusion). Sample sizes differed between statistical tests for several reasons. First, not all birds that were captured for ornament measures remained on the study site to breed. Second, not all birds resident on territories were captured. Finally, not all ornaments were measured on some individuals.

RESULTS

Ornament Expressions

We compared the expression of each of the four ornaments with the expressions of the other three. Although the correlations between bill colour and both plumage colour and crest length were the strongest, these relationships were not significant following sequential Bonferroni correction (Table 1). Thus, relative expressions of the ornaments on an individual female are neither similar nor inversely related to one another. The powers of these correlative tests were all greater than 0.99 (Cohen 1977, page 91).

Table 1. Pearson linear correlations between ornament expression of female cardinals

	Mask score		Crest length		Bill colour	
	r_{82}	P	r_{82}	P	r_{80}	P
Plumage colour	0.07	0.47	0.14	0.19	-0.26	0.01
Mask score			0.02	0.84	-0.06	0.56
Crest length					0.27	0.01

Sequential Bonferroni-corrected critical value for six correlations, $P = 0.0083$.

Individual Condition and Parental Behaviour

We entered the expressions of the four ornaments into backward stepwise linear regressions to determine their contributions to predicting components of condition (Table 2). Wing chord length and the body condition index were both positively predicted by underwing covert colour and bill colour. Date of first nest and reproductive success were both predicted by underwing covert colour. The negative t value associated with the date of first nest and underwing covert colour showed a positive association; redder females produced their first nests earlier in the breeding season. Last, nestling feeding rate was positively predicted by face mask score.

Intrasexual Aggression

We also entered the expressions of the four ornaments into backward stepwise linear regressions to determine their contributions to predicting components of aggression. Face mask score predicted the number of strikes delivered to the model (Table 2). Females with darker, more distinct face masks delivered more strikes than females with lighter, smaller face masks.

DISCUSSION

In this study, we investigated four ornaments of female northern cardinals. These ornaments included two carotenoid-based ornaments, a melanin-based ornament and a feather length ornament. Underwing plumage colour predicted three aspects of condition (body size, an index of body condition, and date of first nest) and seasonal reproductive success. Bill colour predicted body size and an index of body condition. Mask expression predicted levels of parental care and intrasexual aggression. There were no significant associations between ornament expressions. Therefore, the ‘strong’ version of Møller & Pomiankowski’s (1993) redundant signal hypothesis, which predicts that ornament expressions on the same individual reinforce an indication of the individual’s general condition, was not supported by our findings.

Lande’s (1980) correlated response hypothesis predicts that female ornaments are not indicative of condition. Our findings for three of four female cardinal ornaments (underwing plumage colour, bill colour and mask expression) did not support this hypothesis. Instead, they supported the sexual selection hypothesis. Additionally, underwing plumage colour and bill colour in females may influence male mate choice, as indicated by positive assortative mating in cardinals by both bill and plumage colour (Jawor et al. 2003). Crest length was not indicative of any aspect of condition or behaviour in females. This ornament, therefore, does fulfil one prediction of Lande’s hypothesis. However, crest length is not indicative of any aspect of condition in male cardinals either (Jawor 2002). Cardinals can differentially erect their head crest feathers during both agonistic and courtship interactions (Lemon 1968), suggesting a use for the crest in communication, perhaps to indicate motivational state. Because head crests are subject to both sexual and natural selection in other species of birds (Brown 1963; Jones & Hunter 1993;

Table 2. Backward stepwise linear regression analysis describing the predictive value of ornament expressions for measures of condition and behaviour

Measured trait	Predictive ornaments	R^2_{adj}	b	t	P	N
Wing chord length	Plumage colour	0.10	0.57	2.53	0.01	84
	Bill colour		0.30	2.83	0.006	81
Body condition	Plumage colour	0.08	0.89	2.77	0.007	84
	Bill colour		0.31	2.06	0.04	81
Date of first nest	Plumage colour	0.13	-4.51	-2.50	0.01	34
Nestling feeding rate	Mask score	0.16	0.77	2.31	0.03	23
Reproductive success	Plumage colour	0.23	0.34	3.43	0.001	36
Defence against female intruder	Mask score	0.13	0.24	2.09	0.05	22

Hagelin 2002), the possibility that the crest in cardinals is a Fisherian ornament remains open, and the testing of this hypothesis will require mate choice experiments. The finding that three of four ornaments in cardinals convey information about condition, whereas the fourth does not, suggests that, in females with multiple ornaments, some ornaments may be maintained by sexual selection, whereas others may simply be correlated responses.

Our tentative conclusion is that the multiple ornaments of female cardinals convey information to prospective mates and, perhaps, competing females about multiple aspects of condition and behaviour, although we recognize the importance of future experiments to the validation of this conclusion. Two ornaments, underwing plumage colour and bill colour, overlap in the measures of condition they indicate, and these ornaments may thus act as redundant signals (Møller & Pomiankowski 1993). These are also the same ornaments by which cardinals in this population mate assortatively (Jawor et al. 2003). Corresponding ornaments in male cardinals are best described as multiple messages (Møller & Pomiankowski 1993), with each ornament predicting a single aspect of condition (Jawor 2002). It is not apparent why different hypotheses would pertain to males versus females. One possibility is simply that additional aspects of condition not measured for males (e.g. endo- and ectoparasites, intrasexual aggression) may be indicated by multiple ornament expressions. If so, then male ornamentation, as in females, may be better explained by the redundant signal hypothesis.

The larger question concerning multiple ornaments is whether the redundant signal and multiple message hypotheses of Møller & Pomiankowski (1993) are mutually exclusive. It does appear that different types of ornaments may best reflect different aspects of condition. For example, carotenoid-based ornaments are more strongly affected by intestinal parasites (Hill & Brawner 1998; McGraw & Hill 2000), whereas melanin-based ornaments may reflect levels of ectoparasitism (Fitze & Richner 2002). However, during the production of ornaments, multiple factors simultaneously affect the expression of different ornament types. For example, food intake affects both carotenoid- and melanin-based ornaments (Hill & Montgomerie 1994; Veiga & Puerta 1996), and perhaps feather length ornaments (Grubb 1989). As sampled measures of condition increase, it becomes more likely that support for multiple messages will be transformed into support for redundant signals.

Males in many species have ornaments that females lack, and these ornaments are a focus of mate choice (Andersson 1994). In many other species, females display reduced expressions of male ornaments. In relatively few species, females have ornaments that males lack, and these ornaments are correlated with female condition (Amundsen & Forsgren 2001; Berglund & Rosenqvist 2001a, b; Domb & Pagel 2001; Reichert et al. 2002; Weiss 2002). Few studies have examined the ornaments of both sexes to determine the information about condition conveyed by ornamentation of each sex. In barn owls, *Tyto alba*, and bearded tits, *Panurus biarmicus*, as in cardinals, males and females share some ornaments, but the ornaments convey information about different aspects of condition in males and females (Roulin et al. 2000, 2001; Romero-Pujante et al. 2002). This suggests that, although ornaments in males and females are often similar in appearance, they may be selected to convey different information for each sex. In species where females have unique ornaments, these ornaments appear to have been selected to indicate reproductive quality (see Weiss 2002). We suggest that this same argument can be extended to any species in which an ornament is displayed by both sexes. That is, if female ornament expression is maintained by sexual selection acting on females, then such ornaments should provide information about female-specific reproductive capabilities (e.g. maternal effects), in addition to providing information about aspects of condition shared by the sexes (Møller 1993; Romero-Pujante et al. 2002).

We found that the substantial variation in the expression of the face mask of female cardinals was associated with the level of intrasexual aggression. Females with larger, darker masks were more aggressive to a model of a female intruder at the nest site. Anecdotally, we have observed female cardinals attack other females that have intruded on to their territories and approached their nests, indicating that females were responding normally to the model in our experiment. This aggression may be in response to the low incidence of intraspecific brood parasitism observed in this population (Linville 1997). In at least one other species of bird, female melanin-based ornamentation functions intrasexually. In dotterels, *Charadrius morinellus*, females with brighter melanin-based ornamental coloration are more aggressive than, and dominant to, females with duller coloration when competing for access to males (Owens et al. 1994). Although melanin-based ornaments can predict outcomes of intrasexual competition in males

(Badyaev & Hill 2000), it is unknown whether this is true for females. Additionally, intrasexual dominance status may be attractive to mates and thus influence mate choice (Berglund et al. 1996). In pipefish, *Syngnathus typhle*, dominant females are preferred as mates by males (Berglund & Rosenqvist 2001b). Future studies of dominance interactions between females will reveal whether female social status influences male mate choice.

We found that face mask expression in female cardinals indicates their level of parental care. Females with larger, darker face masks were better provisioners. In species with parental care, ornaments are predicted to convey information about the level or type of parental care provided (Hoelzer 1989), and our findings support this hypothesis for one female ornament. Paradoxically, females with larger and darker face masks were also more intrasexually aggressive towards the female model. In males of some species, more aggressive or dominant individuals are poorer parents (Qvarnström & Forsgren 1998), and this pattern may be influenced by testosterone titre in males (Ketterson & Nolan 1994). It is unknown whether female testosterone titre influences parental behaviour in a similar manner, but our results suggest that it may not.

In conclusion, our results are consistent with the hypothesis that three ornaments of female cardinals are maintained by sexual selection, although this conclusion requires verification in mate choice experiments. Our results show that multiple ornaments displayed by female cardinals may together provide information about several aspects of condition and behaviour to prospective mates. Finally, the fact that the sexes share ornaments does not mean that these ornaments provide information to prospective mates on the same aspects of condition.

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