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Regulation of integumentary colour and plasma carotenoids in American Kestrels consistent with sexual selection theory

J. J. NEGRO,* G. R. BORTOLOTTI,†§ J. L. TELLA,* K. J. FERNIE‡ and D. M. BIRD‡

**Consejo Superior de Investigaciones Científicas, Estación Biológica de Doñana, 41013 Sevilla, Spain, †Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada S7N 5E2, and ‡Avian Science and Conservation Centre, Macdonald College, McGill University, Ste-Anne-de-Bellevue, Quebec, Canada H9X 3V9*

Summary

1. Sexually selected traits are expected to vary seasonally, with the maximal expression of the character being evident during mate choice; however, the mechanisms controlling or regulating such traits are generally poorly known.
2. Carotenoid pigments responsible for bright red or yellow coloration in the feathers, skin or other integumentary structures of birds are generally believed to vary seasonally because of diet.
3. Variation in carotenoid-dependent skin colour between winter and spring (mating season) was investigated, as was variation in plasma carotenoids across the breeding season in captive American Kestrels, *Falco sparverius*, fed a uniform diet.
4. Kestrels were more brightly coloured in the mating period than in winter, and plasma carotenoid concentrations declined from the time of mating to the rearing of young.
5. Although carotenoid levels were highly sexually dimorphic during mating and laying, males and both breeding and non-breeding females all had similar levels by the incubation period, and the pattern of variation over time suggests rheostatic regulation.
6. These results suggest kestrels may have the ability to regulate (rather than merely control) their colour physiologically, the variation in colour and carotenoids is consistent with that expected of a sexually selected trait, and the loss of colour after breeding may suggest a trade-off between the show and health functions of carotenoids.

Key-words: Falco sparverius, honest signalling, regulation

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Introduction

Charles Darwin (1871) proposed the theory of sexual selection, whereby the choice of mates by females could result in the evolution of elaborate secondary sex traits. Various patterns in nature suggested sexual selection to Darwin. He proposed that when morphological characters were sexually dimorphic, developed in males only at sexual maturity, and appeared during the breeding season, then such traits functioned to enhance a male's chance of reproducing (see Andersson 1994). While recent research has contributed considerably to the development of sexual selection theory, empirical studies of physiological mechanisms responsible for the expression and development of the selected traits have lagged behind (see Cronin 1991; Andersson 1994).

The evolution of bright coloration in male birds has been a frequent, albeit controversial, topic since Darwin's time (Cronin 1991). Of particular recent interest has been the role of carotenoid pigments in sexual selection. These compounds are responsible for most bright reds and yellows in vertebrates (Brush 1990), but they also are important physiological modulators and so have a range of health-related functions (Lozano 1994; Rock, Jacob & Bowen 1996). A number of studies of birds (Zuk *et al.* 1990; Hill & Montgomerie 1994; Hudon 1994; Dufva & Allander 1995; Sundberg 1995) and fish (Milinski & Bakker 1990; Houde & Torio 1992) have shown links between carotenoid-based coloration and physical condition, or associated phenomena (e.g. parasite infection). The most thoroughly investigated avian species, from both the perspective of proximate and ultimate control of colour, is undoubtedly the House Finch (*Carpodacus mexicanus*) (Brush & Power

§To whom reprint requests should be addressed.

1976; Hill 1990, 1991, 1992, 1995). The feather coats of male finches have substantially more red than those of females. The extent of red feathering appears to be condition-dependent, and is used by females to identify a high-quality mate (Hill 1990, 1991). Coloration in finches signals quality because carotenoids are thought to be limited in the environment, and so only birds that are superior foragers or are in good condition can be brightly coloured (Hill 1991; Hill & Montgomerie 1994; see also Endler 1980).

Hill (1995) also proposed that the seasonal pattern of plasma hues (and hence presumably carotenoid levels themselves) was consistent with the hypothesis that plumage colour was sexually selected. The mechanism for such seasonal variation was again linked to diet. There was indirect evidence that finches consumed more carotenoid-rich foods during the period of moult than at other times of the year (Hill 1995). The importance of dietary intake of carotenoids to coloration at some level is unquestionable, because these compounds cannot be synthesized *de novo* in birds (Brush 1990; Hill 1996). However, it is equally clear that ingestion of these pigments alone may not be responsible for all variation in brightness (Hudon 1994), including two of three patterns that led Darwin to his theory, i.e. age- and gender-dependent coloration (Bortolotti *et al.* 1996).

In this paper we explore the third of Darwin's observed patterns – seasonal variation. We provide novel evidence for a programmed, physiological regulation of coloration and plasma carotenoids that is consistent with the seasonal pattern expected of sexually selected traits. Instead of plumage, however, we use the colour of the exposed integument, the cere, lores and tarsi, of the American Kestrel (*Falco sparverius*), a small falcon. The lores and ceres are conspicuous structures that vary from a dull yellow to a bright red-orange depending on the amount of carotenoids (Bortolotti *et al.* 1996). Although most researchers have focused their efforts on plumage, there are several advantages to studying skin colour. The colour of feathers is only indicative of conditions at the time that they were grown. Furthermore, the period of moult often does not coincide with when mates are chosen, or when investigators capture their subjects for evaluation. Factors such as the wear, bleaching and structural properties of feathers can make it difficult to assess plumage colour properly. In contrast, the colour of skin or other 'fleshy' parts, such as wattles or combs, may be a reflection of more recent physiological events and hence have the potential to be an indicator of the current physical condition of the individual (Burley, Price & Zann 1992; Lozano 1994; Owens & Short 1995; Bortolotti *et al.* 1996).

Methods

This study was carried out in 1994 and 1995 at the Avian Science and Conservation Centre of McGill University, Canada. A colony of captive kestrels has been maintained there since 1974 (Bird 1982), and at the time of study consisted of about 400 individuals. During autumn and winter (September–March), kestrels were housed communally in unheated, indoor pens of 25–35 individuals segregated by sex. In April, some individuals were paired up by the investigators in smaller breeding pens, while the remainder stayed in the communal pens, still segregated by sex. The breeding pens were cardboard boxes 1 m x 1 m x 2 m, with solid walls but an open plastic mesh roof for light, a nest box and rope perch. All birds were exposed to natural photoperiod.

Of particular importance to this study of carotenoid-based coloration is that all kestrels had been maintained exclusively on day-old cockerels (*Gallus gallus domesticus*) for at least 3 years prior to this investigation (see also Bortolotti *et al.* 1996). Cockerels appear to be a carotenoid-rich diet as poultry are given carotenoid-supplemented feed (Marusich & Bauernfeind 1981). We have previously shown that variation in plasma carotenoids during the mating period (April) was not attributable to diet, parasites or androgen levels (Bortolotti *et al.* 1996).

The within-individual variation in integumentary colour was evaluated using a sample of 75 males and 49 females in late November 1994, April 1995 and early December 1995. Entire pens of birds were sampled to avoid any potential bias of selecting individuals within a pen. During each sampling time, the colours of the unfeathered ceres, lores and tarsi were scored by G.R.B. by comparing the bird with a six-option colour chart derived from paint samples (Bortolotti *et al.* 1996). The extremes (6 = pale yellow, 1 = red-orange) were identified based on G.R.B.'s extensive experience, and we considered birds to be increasing in brightness as the amount of orange increased (see also Bortolotti *et al.* 1996; Hill 1996). Typically, brightly coloured birds were bright for all three characters. A total colour score per individual was derived by summing the scores of the three body parts. These colour scores were previously demonstrated to correlate well with the concentration of plasma carotenoids in April (Bortolotti *et al.* 1996).

Plasma carotenoid analyses were conducted four times during the breeding season in 1995. A total of 121 male and 82 female kestrels was sampled in April, which included those individuals scored for integumentary colour. The subsequent samples were taken in late-May during egg-laying (after the third of four or five eggs in a clutch), in mid-June during incubation, and in mid-July during the nestling period for both members of 28 breeding pairs. In mid-June we also sampled 11 non-breeding females from the communal pens.

For the quantification of carotenoids ≈ 0·45 ml of blood was extracted from the jugular or brachial veins using a heparinized syringe. The blood was centrifuged to separate the plasma, which was frozen immediately until subsequent analyses (about one month after

sampling). The methodology of Bortolotti *et al.* (1996) was followed to quantify plasma carotenoids. Some 0·1 ml of plasma was diluted with acetone (1:10), mixed well, and the flocculant protein was precipitated by centrifuging the sample at 1500 g for 10 min. The supernatant was examined in a Beckman Du-70 spectrophotometer (Beckman Instruments Inc., Mississauga, Ontario, Canada) and the optical density of the carotenoid peak at 476 nm was determined. Carotenoid concentration was estimated as $\mu g\ ml^{-1}$ of plasma, using a standard curve of lutein (alpha-carotene-3,3´-diol, Sigma-Alorich Canada Ltd, Oakville, Ontario, Canada).

Our sample is primarily longitudinal in that the same individuals were sampled repeatedly. The results may thus be more reliably interpreted as physiological processes occurring within individuals, than perhaps artefacts of differential survival or sampling of a population. Because we have previously demonstrated that gender and age have pronounced effects on colour and carotenoids of these kestrels (Bortolotti *et al.* 1996), males and females were examined separately, as were juveniles (hatched in 1994) and adults (all older birds).

Results

COLOUR

A distinct seasonal pattern of coloration was apparent (Fig. 1). For both age classes of males (Friedman's ANOVAs, adults: $\chi^2 = 113{\cdot}54$, df = 2, $n = 62$, $P < 0{\cdot}0001$; yearlings: $\chi^2 = 24{\cdot}13$, df = 2, $n = 13$, $P < 0{\cdot}0001$) and females (Friedman's ANOVAs, adults: $\chi^2 = 90{\cdot}43$, df = 2, $n = 36$, $P < 0{\cdot}0001$; yearlings: $\chi^2 = 23{\cdot}24$, df = 2, $n = 13$, $P < 0{\cdot}0001$) colour scores differed significantly among the three sampling periods. Birds were relatively dull in winter (November and December) and bright in the mating season in spring (April).

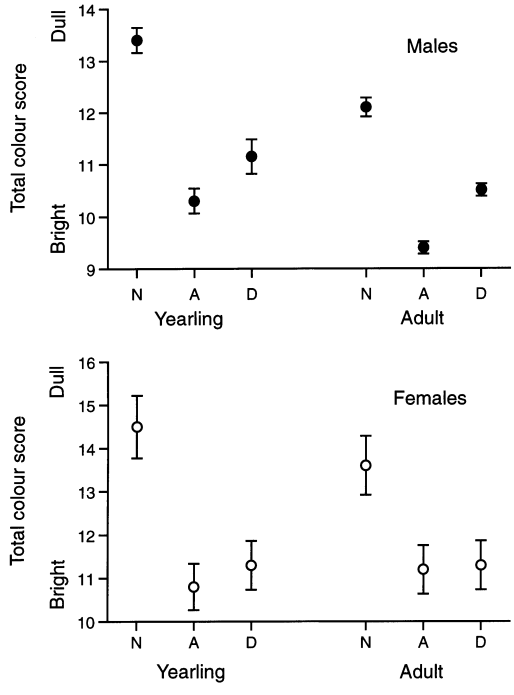

Fig. 1. Mean ± SE of total colour scores (cere plus lores plus tarsi) for 13 yearling and 62 adult male, and 13 yearling and 36 adult female, American Kestrels in November 1994 (N), April 1995 (A) and December 1995 (D).

PLASMA CAROTENOIDS

There was a limited number of individuals sampled in all four periods of the breeding season, largely because some of the birds used for breeding were not bled in April. We therefore present results for birds sampled in all periods, and for a larger sample of birds including those bled from laying onwards. The figures show all available data. For adult males, plasma carotenoid levels decreased steadily from the mating period to the nestling stage (repeated measures ANOVA, $F = 50{\cdot}60$, df = 3,51, $P < 0{\cdot}0001$, Fig. 2). Similarly, the decline from laying to the nestling period was significant (repeated measures ANOVA, $F = 24{\cdot}79$, df = 2,52, $P < 0{\cdot}0001$). The carotenoids of adult females also varied significantly among the four periods (repeated measures ANOVA, $F = 53{\cdot}83$, df = 3,30, $P < 0{\cdot}0001$), and from the laying to nestling periods (repeated measures ANOVA, $F = 41{\cdot}95$, df = 2,40, $P < 0{\cdot}0001$); however, concentrations decreased more abruptly than for males between mating and laying, increased to some degree in incubation and finally decreased during the nestling period (Fig. 2). Yearlings were excluded from the above statistical treatments because of the small sample sizes, but their trends mimic those of adults (Fig. 2).

The pattern of change over time differed somewhat between males and females (Fig. 2), undoubtedly because carotenoids were deposited in eggs (see Discussion). In addition, the absolute differences in carotenoids between the sexes also varied among periods in that males had significantly higher concentrations during both mating (*t*-test for unequal variances, $t = 2{\cdot}54$, df = 137·3, $P = 0{\cdot}012$) and laying (*t*-test for unequal variances, $t = 7{\cdot}28$, df = 24·7, $P < 0{\cdot}001$), but not during the incubation (*t*-test equal variances, $t = 1{\cdot}28$, df = 38, $P = 0{\cdot}208$) or nestling periods (*t*-test for unequal variances, $t = 1{\cdot}53$, df = 29·2, $P = 0{\cdot}138$).

Plasma carotenoid levels were also determined for 11 non-breeding, adult females sampled at the same time that breeding females were incubating. There was no significant difference in mean carotenoid concentrations between non-breeders ($x = 10{\cdot}47$, SE = 1·58, $n = 11$) and breeders ($x = 9{\cdot}37$, SE = 0·70, $n = 18$) (*t*-test, $t = -0{\cdot}73$, df = 27, $P = 0{\cdot}474$).

Discussion

Our longitudinal sample of kestrels under controlled conditions has provided insight into both mechanisms and functions of coloration. Kestrels were more

brightly coloured in April, the mating season, than during winter (Fig. 1). The obvious annual differences in colour, i.e. between winters (Fig. 1) cannot be explained completely. Birds were brighter in the second winter, in part because they were a year older (there are age effects on colour, Bortolotti *et al.* 1996). It is plausible that environmental influences, other than diet, may also account for some of these results, as well as potential biases in subjectively assessing colour (although only one person scored all birds). It was not known if there was a corresponding annual difference in carotenoids in winter; however, circulating levels of carotenoids did decrease rapidly after the mating season (Fig. 2). The exceptional decline of carotenoids in females during laying was presumably the result of depositing pigments in the eggs. Such a pathway is well known, for carotenoids have been used extensively by the poultry industry to manipulate yolk colour (Fletcher 1992).

Trends over time, particularly across the breeding season, have also been noted in the redness (believed to be carotenoid-dependent) of the bills of Zebra Finches (*Taenopygia guttata*) (Burley *et al.* 1992). The bills of female finches were dull during laying, increased in colour during incubation, and then became dull again when the birds reared young. Male Zebra Finches showed a steady decline in colour over the breeding season (Burley *et al.* 1992). These patterns for males and females parallel our findings for the carotenoids of kestrels (Fig. 2). Given that access to carotenoids did not vary over time for either finches or kestrels, these results suggest a programmed rheostasis (Mrosovsky 1990). In other words, there was a sliding set point for optimal carotenoid concentration. An analogous situation is the programmed pattern of decline in mass of incubating, female Jungle Fowl (*Gallus gallus*): despite the availability of food, body mass declines in a temporally predictable manner (Mrosovsky & Sherry 1980). The key observation for kestrels is that after the low concentration during laying, carotenoid levels of females increased; however, they did not rise to prelaying (i.e. mating) levels. The carotenoid concentrations of females during incubation were substantially lower than those in the mating period and, more importantly, they were indistinguishable from concentrations of either males or non-breeding females. All birds appeared to follow a 'schedule' of decline over time independent of starting levels (e.g. compare adult and yearling trends), and directed towards a common target level during incubation.

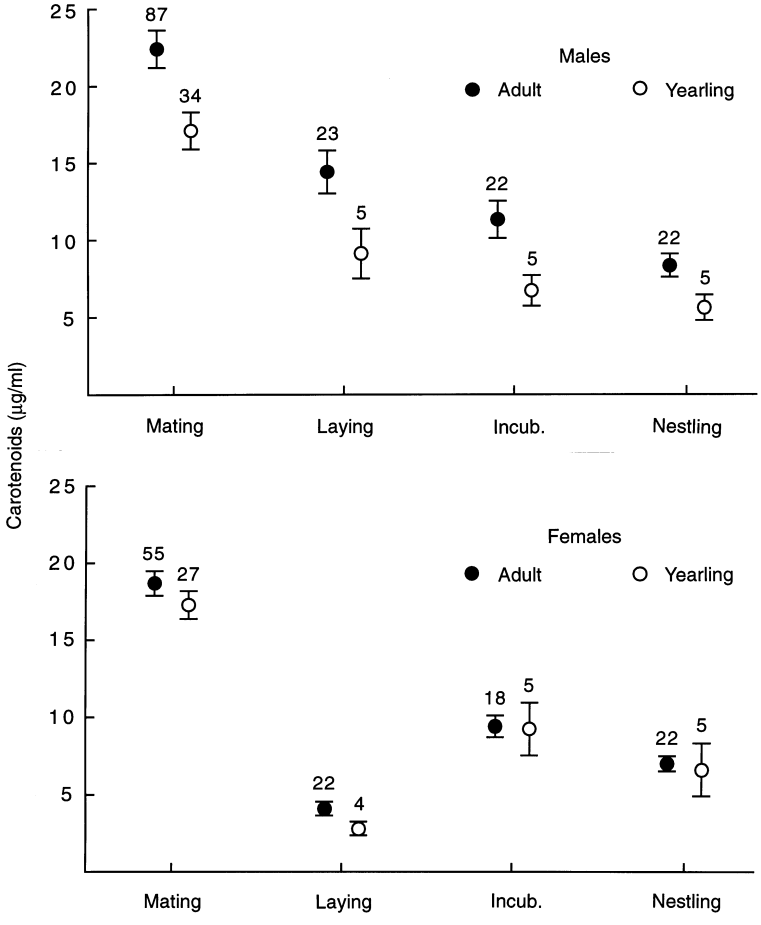

Fig. 2. Mean ± SE of concentrations of plasma carotenoids during the mating (April), laying (May), incubation (June) and nestling (July) periods for male and female American Kestrels. Numbers above bars represent sample sizes.

Seasonal patterns in carotenoids and colour in birds have been reported elsewhere, but dietary effects have been invoked to explain them (Slagsvold & Lifjeld 1985; Hill 1995). Even in the extensive literature on humans, seasonal trends in carotenoids have been assumed to be a product of the seasonal nature of markets or dietary preference (e.g. Olmedilla *et al.* 1994). The first study to examine the association between human food consumption and plasma carotenoids found seasonal patterns in carotenoids independent of diet (Scott *et al.* 1996). The confirmation of any new source of variation in colour implies that there may be a need to re-evaluate existing literature, and that future studies must be designed to consider the possibility of such effects. We echo Sullivan's (1990) concerns that temporal variability in the attributes important in mate choice must be considered, and we extend that advice to any investigation of the physiological activity of carotenoids regardless of interest in evolutionary questions. Similarly, manipulation of dietary constituents, such as is common in the poultry industry (Fletcher 1992) and in zoo management (Brush 1981), must also be done with the understanding that optimal formulae for achieving pigmentation might be seasonally dependent.

While vertebrates can exercise some degree of *control* over carotenoid concentrations by varying their diet, they cannot *regulate* them in that manner. Regulation, as implied by our data, suggests a more sophisticated physiology. The actual mechanisms that may control or regulate carotenoids in birds are still largely a matter of speculation (Brush 1990). Some

endocrine effects on coloration are known (Tewary & Farner 1973; Brush 1990; Owens & Short 1995), but it is clear that other factors must also be involved **(**Burley *et al.* 1992; Bortolotti *et al.* 1996). Although mechanisms are poorly known and apparently variable among species, studies of Zebra Finches (Burley *et al.* 1992), House Finches (Hill 1995) and kestrels (this study) all imply that ultimately, patterns of coloration are a product of sexual selection; birds are consistently at their brightest during the most important time for mating. However, the question remains, why is seasonal variation exhibited at all? Especially for birds such as kestrels given diets with adequate quantities of carotenoids, why should colour not be maintained throughout the year? Is there a cost to being brightly coloured?

We believe that the physiological regulation of carotenoids is consistent with honest-signalling models of sexual selection; elaborate traits are costly for the bearer to produce or maintain (see Andersson 1994; Johnstone 1995; Hill 1996). Therefore, it is predicted that individuals should reduce the cost of these characters when they no longer function in mate choice. Many birds have dull plumages, bills or integument after the breeding season (e.g. see field guides, Burley *et al.* 1992; Fig. 1). In the House Finch, the cost of producing red feathers may include the finding and ingestion of carotenoid-rich foods, or the energetics of processing the pigments (Hill 1996). Neither seems relevant to kestrels. Carotenoids were always available to our kestrels, and colour appears to be related to the quantity of carotenoids in the bloodstream rather than the product of metabolic conversion (Bortolotti *et al.* 1996). In addition, while the direction of colour change (Fig. 1) may be consistent with an energetic stress hypothesis (Hill 1996), the trend for carotenoids over the breeding season (Fig. 2), i.e. as ambient temperatures increase, is opposite to that which would be predicted.

Changes in colour, as observed here, may suggest that there may be trade-offs between the 'show' functions and the 'health' functions of carotenoids. Given the abundant evidence for the importance of carotenoids as physiological modulators, maintaining colour beyond the time when it is needed for mate choice may be at the expense of physiological processes unrelated to epigamic functions. Unfortunately, carotenoids are a diverse array of compounds and their physiology is poorly known in birds and other vertebrates. Whether there is competition for carotenoids among multiple functions, whether pigments used in colour could later be mobilized from the skin to other organs, and the degree to which carotenoids might be facultatively channelled for different purposes contingent on an individual's need, are just a few of many exciting questions for future study (see also Lozano 1994; Gray 1996).

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