Mate choice, male quality, and carotenoid-based plumage coloration

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Carotenoid pigments produce ornamental red, orange, and yellow coloration in plumage. They are unique among pigments used to colour feathers in that they cannot be manufactured by birds and must be ingested. Expression of carotenoid-based plumage coloration has been proposed to serve as an honest signal of male quality that is used by females in choosing mates. I review the evidence that females use carotenoid-based plumage coloration in mate choice. I then consider how carotenoid-based plumage coloration might serve as a signal of male quality, and I review the evidence that either access to carotenoids (acquisition) or use of acquired carotenoids (utilization) affects expression of carotenoid-based plumage coloration. Finally, I review the evidence that females receive either good genes or resource benefits through their choice of a males with bright, carotenoid-based plumage coloration.

INTRODUCTION

One of the most widespread and striking forms of ornamental display of plumage is the red, orange, and yellow coloration produced by carotenoid pigments deposited in feathers. Carotenoids are unique among pigments used to colour feathers in that birds are incapable of synthesizing carotenoid pigments from basic biological precursors (Goodwin 1984). For a bird to use carotenoid pigments to colour feathers, it must ingest the carotenoids. In many, perhaps most, species of birds that have carotenoid-based plumage coloration, however, carotenoid pigments can be structurally modified (e.g. yellow carotenes converted to red xanthophylls) once they are ingested (Brush 1990a, Goodwin 1984). Thus, the process by which a bird acquires its plumage coloration is complex, involving both behaviour and physiological mechanisms.

For students of sexual selection, two questions have dominated studies related to carotenoid-based plumage pigmentation: is ornamental plumage coloration of males used by females to choose mates and does ornamental coloration signal male quality? In this paper I will review evidence suggesting that female birds use carotenoid-based plumage coloration to choose mates and that expression of carotenoid-based plumage by males is a reliable signal of individual condition. I will also consider the benefits to females of choosing as a mate a well-coloured, high-quality male. Birds also use carotenoid pigments to colour non-feathered integumentary structures such as legs, eyes, and combs. While the focus of this review will remain on plumage coloration, important and insightful studies of soft-part coloration will also be discussed. The role of ornamental coloration in intrasexual aggressive encounters is the topic of another paper in this symposium (Senar 1998) and will not be discussed in this review.

CAROTENOID-BASED COLORATION AS A CRITERION IN FEMALE MATE CHOICE

Pioneering work.

The earliest studies testing basic function of plumage coloration, including carotenoid-based coloration, focused on the effect of removing the ornamental coloration entirely. Smith (1972) and Peek (1972) both blackened the red epaulets of Red-winged Blackbirds (*Agelaius phoeniceus*) and demonstrated that this carotenoid-based colour display was important in territorial defense. Peek (1972) but not Smith (1972) also found weak evidence that males with blackened epaulets had more difficulty in attracting females than normally coloured males, but neither study constituted a very convincing test of female choice for males with red coloration.

A more convincing test of female mate choice based on presence of carotenoid-based plumage coloration was a study of captive Village Weaverbirds (*Ploceus cucullatus*)(Collias et al. 1979). Over three years, seven adult males either had their yellow underwings blackened or left yellow. These treatments were rotated among males so each individual served as both a blackened and yellow male in different years. Blackened males were significantly less successful in attracting females than sham-manipulated, yellow-winged males. These colour-removal experiments constituted the first tests of female mate preference relative to carotenoid-based coloration of males and provided the first experimental evidence that females birds do respond to carotenoid-based plumage coloration in choosing a mate. Presence/absence experiments, however, tell one nothing about female choice relative to natural variation among males in expression of the ornament. Such studies would have to come from a different type of manipulation experiment.

Mate preference in relation to variation in carotenoid-based plumage coloration.

The first studies of female choice relative to natural variation in expression of plumage coloration focused on melanin-based coloration (e.g. (Lifjeld and Slagsvold 1988, Møller 1988, Røskaft and Jarvi 1983) or on age-specific variation in plumage expression (delayed plumage maturation)(e.g., (Payne 1982, Price 1984, Procter-Gray and Holmes 1981). Eckert and Weatherhead (1987) looked at reproductive effects of variation in the size (but not hue or intensity) of red epaulets of Red-winged Blackbirds. They found that epaulet size was positively correlated with nest defense, but they were unable to show that female used epaulet size in choosing mates.

Female mate choice relative to natural variation in the coloration (i.e., hue, intensity, and tone) of carotenoid-based plumage pigmentation was first tested in the House Finch (*Carpodacus mexicanus*) (Hill 1990, Hill 1991), a species in which males display highly variable ornamental plumage (Hill 1993, Michener and Michener 1931). First, it was observed that, among wild finches, males that paired with females had redder and more intensely pigmented ornamental coloration than males that did not pair (Hill 1990, Hill 1991, Hill et al. in press). These observations were followed by experiments in which either hair dyes or diet treatments during moult were used to manipulate the coloration of males. Both wild and captive female House Finches were given a choice of males that varied in plumage redness and brightness, and females consistently showed a mating preference for the reddest and most brightly coloured male available to them (Hill 1990, Hill 1991, Hill 1994a). Experimental studies of mate choice and carotenoid-based male coloration have subsequently been conducted with American Goldfinches, *Carduelis tristis*, (Johnson et al. 1993), Yellowhammers, *Emberiza citrinella*, (Sundberg 1995a), and Linnets, *Carduelis cannabina* (Drachman 1997). In all studies females showed a significant preference for males with maximum carotenoid-based coloration. Wolfenbarger (1996) also found a significant negative relationship between male plumage redness and first egg date in Northern Cardinals (*Cardinalis cardinalis*) suggesting that redder males were preferred as mates. The only published study of which I am aware in which carotenoid-based plumage coloration was studied and found not to be used in female choice is Bjorklund’s (1990) study of the Common Rosefinch (*Carpodacus erythrinus*). However, variation in expression of carotenoid-based plumage coloration was scored only as “bright” or “dull” and only five birds were used in the comparsison.

Feathers are not the only integumentary structures in which carotenoids pigments are deposited and displayed in an ornamental fashion. The legs, bills, eyes, and fleshy structures such as combs and wattles of birds often have carotenoid-based coloration, and it has been shown in some species that females use the coloration of these structures in choosing mates. Perhaps the most convincing study of female preference for bright, carotenoid-based leg coloration came not from direct manipulations of leg colour, but from a series of studies on the effect of leg-band colour on female mate choice in the Zebra Finch (*Taeniopygia guttata*). The carotenoid-based leg colour of male Zebra Finches ranges from pale orange to bright orange-red (Burley et al. 1992), and female Zebra Finches show a strong preference for red bands over orange, blue, or green bands (Burley et al. 1982). Female Zebra Finches even adjust the sex ratio of offspring in response to male band colour (Burley 1981). The most straight-forward interpretation of these studies is that red leg bands accentuate natural leg colour and females respond as they would to redder carotenoid display. By painting the bills of Zebra Finches, Burley and Coopersmith (1987), were also able to show female mate preference for males with the reddest bills (but see Collins (1994)). Similarly, female Red Jungle Fowl (*Gallus gallus*) prefer as mates males with the most intense carotenoid-based coloration of the eye and comb (Zuk et al. 1995, Zuk et al. 1990).

1.3. Paternity and coloration.

One form of female choice that is difficult to measure directly is choice of extra-pair sexual partners. This form of mate choice can be studied indirectly, however, by determining the paternity of offspring (Birkhead and Møller 1992). In a study of House Finches, Hill et al. (1994b) found that drably pigmented males were no more likely to be cuckolded than brightly pigmented males. Whether or not brightly coloured males gained paternity through extra-pair copulations, however, could not be determined in this analysis (Hill et al. 1994b). Similarly, in Yellowhammers, drably coloured males were no more likely to be cuckolded than brightly coloured males, but males that gained paternity through cuckoldry were brightly coloured (Sundberg and Dixon 1996). In contrast, Linville and Breitswich (GET PERMISSION FROM RANDY) found that male Northern Cardinals (*Cardinalis cardinalis*) that gained paternity through extra-pair copulations were no brighter on average than males that had no such paternity gain and that bright males were cuckolded more than drab males. In Zebra Finches, males with red leg bands (simulating bright carotenoid pigmentation) gained more paternity through extra-pair fertilizations and were cuckolded less than males banded with green bands (Burley et al. 1994, Burley et al. 1996).

An association between extra-pair copulations and non-carotenoid plumage coloration has also been found in several species. In Yellow Warblers, *Dendroica petechia* , males with more melanin-based breast streaking gained more extra-pair fertilizations than males with less breast streaking (Yezerinac and Weatherhead 1997). In the Pied Flycatcher (*Ficedula hypoleuca*), however, males with darker melanin coloration were actually cuckolded more than males with drabber melanin coloration (Lifjeld et al. 1987). In a comparative analysis, Møller and Birkhead (1994) found higher rates of extra-pair copulation in species with brightly coloured plumage compared to species with drab plumage. Clearly, more studies of paternity and carotenoid-based plumage coloration are needed to properly test the role of carotenoid-based plumage coloration in female choice of extra-pair partners.

MALE QUALITY

Determinants of colour expression.

Mate choice studies provide convincing evidence that in at least some species of birds females prefer to mate with males with the most intense or reddest integumentary carotenoid display. These observations evoke the question: what do females gain by choosing to mate with redder or more brightly coloured males? To answer this question we have to consider the sort of environmental factors that might affect expression of carotenoid-based plumage coloration.

Carotenoid pigments must ultimately be derived from the diet (Goodwin 1984). The process by which carotenoids go from potential food sources to pigments in a bird's feathers is complex and not very thoroughly studied (Brush 1978, Brush 1990a, Goodwin 1984). For simplicity, however, one can think of the process that determines individual expression of carotenoid pigmentation as having two distinct phases: acquisition and utilization. "Acquisition" refers to the accruement of carotenoids from the environment into the gut. It includes all behaviours and structures that facilitate obtaining carotenoids. "Utilization" refers to the manner in which acquired carotenoids are used. It includes the physiological mechanisms by which the body moves carotenoids from the gut to the growing feather and by which ingested carotenoids are structurally modified before being deposited in feathers. There has been on-going debate over the relative importance of acquisition versus utilization in determining expression of carotenoid pigmentation (Bortolotti et al. 1996, Hill 1992, Hill 1994b, Hudon 1994, Thompson et al. 1997), so it is instructive to consider each of these phases separately.

Carotenoid acquisition.

What is the evidence that acquisition affects plumage coloration? Zoo biologists have long known that diet affects expression of carotenoid-based plumage coloration (Bruning 1971, Delacour 1928, Wackernagel 1959). A series of experiments on various species of cardueline finches (family Fringillidae) in Germany (Brockmann and Völker 1934, Völker 1934, Völker 1938, Völker 1962) and with captive flamingos (*Phoenicopterus* ssp.) (Fox and McBeth 1970, Fox et al. 1970, Fox et al. 1967, Fox et al. 1969) showed clearly that altering dietary access to carotenoid pigments could alter plumage coloration. In some studies, however, cage size and physiological condition were also invoked as more important than dietary carotenoids in determining plumage coloration (see Hudon (1994) for a review).

More recently, the extent to which dietary access to carotenoid pigments can determine coloration has been demonstrated in a series of experiments on male House Finches (Brush and Power 1976, Hill 1992, Hill 1993). In these experiments, the amount and type of carotenoids in the diet was varied among groups of males during their annual moult. Within a treatment in which access to dietary carotenoids was held constant, males converged on a very similar appearance regardless of their pre-treatment coloration (Brush and Power 1976, Hill 1992, Hill 1993). Moreover, the full range of natural variation in plumage coloration of male finches could be induced even within a single individual (across different moults) simply by manipulating dietary intake of carotenoid pigments (Hill 1992, Hill 1993). More controlled feeding experiments are needed on other species of birds with carotenoid-based plumage coloration, but clearly altering dietary access to carotenoid pigments during moult can alter expression of carotenoid-based plumage coloration.

These feeding experiments were conducted in artificial aviary environments that might have affected birds' abilities to pigment feathers (Hudon 1994). Is there evidence from wild birds that carotenoid access might alter plumage coloration? The best study of carotenoid access affecting plumage coloration in wild birds was conducted on nestling and adult Great Tits, *Parus major* (Partali et al. 1987, Slagsvold and Lifjeld 1985). Adult and nestling Great Tits living in deciduous forest had access to greater quantities of β-carotene, lutein, and zaxanthin and grew brighter, yellower plumage than did tits living in nearby coniferous forest (Partali et al. 1987, Slagsvold and Lifjeld 1985). These studies remain the best evidence that dietary access to carotenoid pigments can be the basis for variation in expression of plumage coloration within a wild population of birds.

More indirect evidence that the diets of wild birds can affect plumage coloration comes from a study using growth bars as a measure of nutritional condition. Wild House Finches grew tail feathers significantly more slowly than captive male House Finches that had access to unlimited food (Hill and Montgomerie 1994) supporting the assertion that feather growth rate can be used as a measure of nutritional condition at the time of moult (Grubb and Cimprich 1990, Grubb 1989, Grubb 1991). Furthermore, plumage redness of male House Finches was significantly positively associated with the rate at which tail feathers were grown, suggesting that males that grow redder plumage are in better nutritional condition presumably with greater access to carotenoid pigments (Hill and Montgomerie 1994).

Another line of evidence that diet affects expression of carotenoid-based plumage coloration in wild birds comes from observations of variation in the plasma coloration of House Finches across seasons and between age and sex groups. Plasma coloration changes in hue from yellow through orange to reddish-orange as the concentration of circulating carotenoid pigments increases (Hill 1995, Hill et al. 1994a). Hill et al. (1994a) found a significant positive relationship between the redness of growing feathers and plasma redness among males (Hill et al. 1994a), demonstrating that differences among males that will result in variation in plumage coloration occur before carotenoids reach the growing feather (Hill et al. 1994a). Moreover, young males had less red plasma on average than older males (Hill et al. 1994a), and plasma was much redder during fall moult (the only time when circulating carotenoid pigments can affect plumage coloration) than during non-moult periods (Hill 1995). Based on diet samples from Beal (1907), it was also shown that increases in plasma redness coincide with a shift from carotenoid-deficient diet of seed to a carotenoid-rich diet of fruit (Hill 1995). These studies suggest that differential access to dietary carotenoids affects levels of circulating carotenoids and plumage colour. It remains possible, however, that differences in circulating carotenoid levels are altered independent of dietary access to carotenoid pigments by parasites (see section 2.3) or by some form of individual self-regulation (Bortolotti et al. 1996)(see section 2.5).

Further evidence that access to dietary carotenoid pigments affects expression of plumage coloration comes from observations of temporal and geographic variation in mean plumage coloration of populations associated with changes in environmental condition and carotenoid availability. House Finches of the subspecies *C. m. frontalis* are native to the Pacific Coast of the U.S. and Northern Mexico (Moore 1939). Over the last one hundred years *frontalis* House Finches have also been introduced to the Hawaiian Islands and to eastern North America (Hill 1993). On the Hawaiian Islands, House Finches showed a dramatic loss of ornamental coloration, with virtually all males displaying orange or yellow rather than red coloration (Grinnell 1912, Hill 1993, Hirai 1975). So dramatic was this loss of coloration, that Grinnell (1912) proposed that the population had mutated into a new species -- *Carpodacus mutans*. Hill (1993) quantitatively documented the substantial geographic variation in mean male plumage coloration among populations in California, Hawaii, and eastern North America, showing that even between populations of finches separated by only 12 km, the mean coloration of males varied substantially.

To test whether geographic variation in plumage coloration resulted from geographic variation in carotenoid acquisition or in the utilization of carotenoids, males from bright and drab populations in Hawaii, California, and Michigan were captured and held in outdoor aviaries in which their dietary access to carotenoids could be controlled during fall moult (Hill 1993). When males from these populations had access to the same quantity of carotenoid pigments, virtually all variation in expression of ornamental coloration disappeared -- e.g. on a high-carotenoid diet, males from the drab Hawaiian population grew red plumage that was identical to the red plumage grown by males from brightly coloured populations (Hill 1993). This experiment demonstrated that all male House Finches from all populations have the capacity to express maximum ornamental coloration if given sufficient dietary carotenoids. Thus, it appears that geographic variation in mean male plumage coloration is a result of variation in access to dietary carotenoid pigments in different geographic locations. It is possible, however, that an environmental stressor such as a parasite varies geographically and is causing the variation in plumage coloration.

Local variation in expression of carotenoid-based plumage coloration has been noted in other species. For instance, extreme variation in carotenoid-based plumage coloration among upland and lowland populations of the Tristan Bunting (*Neospiza acunhae*) separated by only a few km on Inaccessible Island may reflect differential access to carotenoid pigments (Ryan et al. 1994). Diet analyses or feeding experiments are needed to rule out other factors, such as a parasite restricted to a particular elevation, that may have caused this local variation in expression of plumage coloration.

Temporal variation in carotenoid availability at a single location has also been linked to change in carotenoid-based plumage coloration. A dominant and carotenoid-rich food in the diet of Northern Cardinals in Ohio during moult is grapes (*Vitis* spp.)(Linville and Breitwisch 1997). Following a year of extreme cold that caused drastic reduction in availability of grapes, male Northern Cardinals were significantly less red than they had been following years of normal grape production (Linville and Breitwisch 1997).

Perhaps the clearest case of diet altering the expression of carotenoid-based plumage coloration in wild birds involves the coloured band on the tip of the tail of the Cedar Waxwing (*Bombycilla cedrorum*). This band is typically yellow. Beginning in the early 1960's, individuals with orange bands on their tails began to be observed in the northeastern U.S. (Hudon and Brush 1989, Mulvihill et al. 1992, Witmer 1996). The coloured tail band of waxwings is a result of carotenoid pigments, and the change from yellow to orange was the result of a new red carotenoid, rhodoxanthin, being used by birds to pigment their feathers (Hudon and Brush 1989). Rhodoxanthin is found in the berries of Morrow's honeysuckle (*Lonicera morrowii*) (Brush 1990b) the introduction of which to the northeastern U.S. coincided with the appearance of orange tails in waxwings (Mulvihill et al. 1992). Feeding experiments confirmed that on a diet of Morrow's honeysuckle, waxwings grow orange tail tips (Witmer 1996). In a similar example, orange coloration recently began to appear in the typically yellow plumage of some Bananaquits (*Coereba flaveola*). This change was linked to the deposition of a novel red carotenoid presumably found in a food to which some birds had recently gained access (Hudon et al. 1996).

Taken together, these studies suggests that dietary access to carotenoid pigments is at least partly responsible for variation in carotenoid-based plumage coloration. Controlling carotenoid access among captive birds can clearly impact their expression of carotenoid-based plumage coloration. One direct test of plumage coloration and environmental carotenoids and several more indirect studies suggest that carotenoid access also affects the colour expression of wild birds. It cannot be emphasized too strongly, however, that demonstration of a role for carotenoid access in expression of plumage coloration does not diminish the potential for carotenoid utilization to also affect expression of plumage coloration.

Carotenoid utilization.

Does utilization of ingested carotenoids affect ornamental coloration? If carotenoid pigmentation is a sexually selected trait within a species, then all males of that species should possess the appropriate physiological mechanisms for maximum ornament expression (i.e., these traits should be fixed in the population)(Hill 1994c). Variation in utilization, therefore, should arise from environmental perturbations that disrupt normal pigmentation mechanisms. The most obvious environmental stressors that might affect how ingested carotenoids are expressed are parasites. Hamilton and Zuk (1982) originally proposed that ornamental plumage coloration might have evolved as a signal of parasite resistance. The potential explanatory power of this hypothesis has been widely appreciated, and tests of this hypothesis relative to carotenoid-based plumage coloration have been undertaken.

Several studies have looked at blood haematozoa in relation to carotenoid-based plumage coloration. In the Yellowhammer, a significant positive correlation was found between the brightness of carotenoid-based plumage display and degree of infection by *Haemoproteus coatneyi* (Sundberg 1995b). In other studies, however, no relationship has been found between infection by haematozoa and carotenoid-based plumage coloration (various wood warblers, (Weatherhead et al. 1991); Common Redpoll, *Carduelis flammea*, (Seutin 1994); House Finch (Hill et al. unpubl data); Northern Cardinal [GET PERMISSION FROM RANDY] or carotenoid-based bill coloration (Burley 1981). Blood-born parasites, however, may generally not be appropriate for testing the Hamilton-Zuk Hypothesis because of extreme temporal and geographic variation in infection levels as well as the lack of demonstration of a mechanism by which these parasites could directly affect expression of plumage coloration (see Yezerinac (1995)). Dufva and Allander (1995) found a significant positive relationship between number of heterophyls (one type of white blood cell) and the brightness of yellow, carotenoid-based plumage coloration in the Great Tit. They argued that this relationship supported the idea that more brightly plumaged males had superior immune systems and greater resistant to parasite infection (Dufva and Allander 1995).

The most extensive studies on the effect of parasites on expression of carotenoid-based plumage coloration have been conducted on House Finches. In a study of wild House Finches in California, significant negative correlations were found between male plumage coloration and infection by both avian pox (a virus) and feather mites (*Proctophyllodes* sp.): birds that grew redder plumage had fewer parasites during moult (Thompson et al. 1997). Infection experiments with captive House Finches demonstrated that infection during moult by either coccidia (genus *Isospora*) and the bacterium *Mycoplasma gallicepticum* inhibited expression of carotenoid-based plumage coloration in males (Brawner 1997). Male American Goldfinches infected with *Isospora* also grew paler yellow feathers than males that were not infected (Olson 1996). Coccidians are known to inhibit carotenoid absorption from the gut in poultry (Allen 1987, Allen 1992, Augustine and Ruff 1983, Ruff et al. 1974, Tyczkowski et al. 1991), so there is an obvious mechanism for the disruption of carotenoid utilization by coccidia. Interestingly, melanin-based feather coloration of House Finches was not affected by parasite infection (Hill and Brawner 1998). Moreover, the number of feather mites increased on male House Finches infected with coccidia but remained unchanged on control birds (Brawner 1997). This association between coccidial infection and mite abundance, along with the lack of a mechanism for mites to effect plumage coloration, suggests that the correlation found by Thompson et al. (1997) between feather mites and plumage coloration may have actually been a correlated effect of coccidial infection on plumage coloration.

Overall, the Hamilton-Zuk Hypothesis (Hamilton and Zuk 1982) as applied to plumage coloration in general and carotenoid-based coloration in particular remains controversial and incompletely tested almost twenty years after it was first proposed. The few studies listed above have demonstrated that some parasites can reduce expression of carotenoid-based ornamental coloration. The heritability of resistance to parasites that depress expression of carotenoid pigmentation, which is a critical assumption of the Hamilton-Zuk Hypothesis, remains to be tested in any species of bird (although Møller (1990) demonstrated heritable resistance to parasites that affect the length of ornamental tail feathers).

The immunocompetence hypothesis and carotenoid pigmentation.

One mechanism that has been proposed for insuring the honesty of ornamental traits is a trade off between the enhancement of ornamental traits through the presence of testosterone and the suppression of the immune system induced by testosterone (Folstad and Karter 1992, Ligon et al. 1990). According to the immunocompetence hypothesis, only males in superior condition will be able to both remain healthy and raise their testosterone to a level necessary for maximum ornament expression (Folstad and Karter 1992). For plumage ornaments, including carotenoid-based coloration, it is difficult to see how an immunocompetence mechanism could work. Moult, and hence development of plumage ornaments, is either unaffected by testosterone or occurs when testosterone is at an annual low (Owens and Short 1995). However, Tewary and Farner (1973) found that castrated House Finches grew feathers lacking carotenoid pigmentation, suggesting that testosterone may play some role in carotenoid-based colour display. Stoehr and Hill (unpubl data) found that male House Finches that had their circulating testosterone levels artificially elevated until just prior to moult (House Finches would not moult until testosterone levels were dropped) grew very drab carotenoid-based plumage. Clearly more research on the role of testosterone and other hormones on control of carotenoid-based plumage coloration is needed.

Energetic constraints

If most species of birds modify the carotenoids that they ingest prior to deposition (Brush 1978, Brush 1990a) and carotenoid metabolism is costly (Hill 1996), there may be energetic constraints on expression of carotenoid-based plumage coloration. To my knowledge, this idea has only been tested once. Schereschewsky (1929) maintained two groups of captive Bullfinches (*Pyrrhula pyrhula*), a species with extensive carotenoid-based coloration. Both groups had the same access to carotenoid pigments, but one group was restricted in its caloric intake while the other group was not. The nutritionally-stressed group grew drabber plumage than the group fed ad lib. No recent study of this sort has been conducted on birds, but it was demonstrated experimentally that male three-spined sticklebacks (*Gasterosteus aculeatus*) produce brighter carotenoid coloration on a high-quality than on a low-quality diet with the same carotenoid content (Frischknecht 1993). Moreover, in Zebra Finches, males maintained on the same diet but subjected to variable stress in the form of crowding and agnostic interaction varied in bill coloration according to physical condition (Burley et al. 1992). More work testing the effects of energetic constraints independent of carotenoid access is needed.

CAROTENOID-BASED INTEGUMENTARY COLORATION INDEPENDENT OF CONDITION

Wallace (1889) originally proposed that the bright coloration of skin and feathers of birds might simply be deposits of unwanted or harmful biological products (ideas reviewed in Cronin (1991)). Furthermore, Wallace (1889) proposed that the brightness of colour display would correlate with vigor since vigorous males would have more active metabolisms and deposit more pigments. This idea received little serious attention, but recent studies on captive American Kestrels (*Falco sparverius*) have generated new interest in the idea. American Kestrels have bright yellow legs that derive their coloration from carotenoid pigments. Bortolotti et al. (1996) and Negro et al. (1998) looked at leg coloration and the quantity of circulating carotenoid pigments relative to parasites, androgens, sex, age, and season. They found that despite the fact that levels of dietary pigments were held constant and the birds were unparasitized, males were brighter than females, older birds were brighter than younger birds, and breeding birds were brighter than non-breeding birds. Androgens seemed to have no effect on coloration (Bortolotti et al. 1996). Bortolotti et al. (1996) and Negro et al. (1998) suggested that kestrels may self-regulate their expression of carotenoid pigments (i.e., exert rheostatic control). Unfortunately, there is no evidence that leg coloration in kestrels is a sexually selected trait, and it is questionable whether the observations from American Kestrels can be extrapolated to carotenoid-based ornaments that are the focus of female mate choice. Nevertheless, the studies on American Kestrels make the valid point that non-adaptive hypotheses need consideration.

A SIGNAL OF GOOD GENES OR GOOD PHENOTYPE?

A major controversy concerning the evolution and function of honest signals of quality is whether females choosing well-ornamented males gain indirect genetic benefits for offspring or direct resource benefits. No study has convincingly demonstrated that female gain genetic benefits by choosing brightly coloured males. In studies that have shown that parasites affect expression of carotenoid-based plumage coloration (see above), no experiments have been conducted to test whether resistance to the parasite is heritable and hence whether females may acquire genes for disease resistance in offspring by choosing highly ornamented males. If one assumes that females gain no direct benefit from extra-pair males, then the observation that female Yellowhammer choose brightly coloured males as extra-pair mates suggests that female may be choosing for good genes. Moreover, the fact that female Zebra Finches chose males with bright red bills and legs as extra-pair mates and shifted the sex ratio of broods to male-biased when the young were fathered by brightly coloured males also suggests that females may gain genetic benefits by choosing well-pigmented males. Neither of these studies, however, was able to rule out possibility of subtle direct benefits for females.

The evidence for resource benefits resulting from choice of red males has been much more clearly demonstrated, at least for some species of birds. Because carotenoid pigmentation is ultimately tied to accruement of carotenoid resources from the environment, it seems logical that carotenoid pigments might serve as honest signals of foraging, and hence provisioning, ability (Endler 1980, Endler 1983, Hill 1990). In the House Finch (Hill 1991) and Northern Cardinal (Linville et al. 1998), males with brighter or redder carotenoid pigmentation tended to provide more food to mates or offspring than did drabber males. However, in the Linnet (Drachman 1997), Yellowhammer (Sundberg and Larsson 1994), and Zebra Finch (Burley 1988) drabber males fed at nests more than brighter males. Moreover, both positive and negative associations have also been found between feeding rate and expression of non-carotenoid plumage coloration (Grant and Grant 1987, Palokangas et al. 1994, Studd and Robertson 1985). No satisfactory explanation has been proposed for these variable relationships between plumage coloration and feeding rate. Thus, while the question of what benefits females gain by choosing a highly pigmented male lies at the heart of most studies on carotenoid-based plumage coloration, no general answer to this question is yet possible. Clearly, the testing of the good genes and good parent hypotheses relative to careteniod-based plumage coloration is an area of research in which much more work is needed.

CONCLUSIONS

Expression of carotenoid-based plumage coloration and bill, leg, and eye pigmentation is highly variable in many species of birds. In the relatively few species that have been studied, this variation is related to dietary access to carotenoid pigments or to degree of parasite infection (but see Bortolotti et al. (1996)). This sort of condition-dependent expression makes carotenoid-based coloration exactly the sort of ornamental trait that is predicted to be used by females to choose high-quality males. In species that have been tested, females show a preference to mate with males that have maximum carotenoid display. To date, however, despite the fact that carotenoid-based plumage coloration is found in the majority of avian families, all experimental studies of female mate choice relative to natural variation in plumage coloration have been conducted within two families of passerine birds (Fringillidae and Emberizidae). A more diverse range of avian taxa needs to be studied before broad generalization can be made.

There is substantial evidence from observations of both captive and wild birds that access to carotenoid pigments can affect expression of plumage coloration. However, the overall contribution of carotenoid acquisition to variation in plumage coloration among wild birds remain controversial. Parasites can depress expression of carotenoid-based plumage coloration; the effects of energy constraints, stress, or hormones on expression of carotenoid-based plumage coloration remain virtually unknown. Studies of both captive and wild birds in which carotenoid pigments are tracked from food to feathers using modern molecular techniques (as was done once over twenty years ago) are needed to fill major gaps in our understanding of the proximate control of carotenoid pigmentation.

Finally, the benefits to a female of choosing a well-pigmented male remain poorly understood. Carotenoid pigmentation as a signal of foraging ability and hence male parental ability has been demonstrated in some species and remains a popular explanation for female choice of males with extreme expression of carotenoid display. However, in more than half the species studied to date, carotenoid pigmentation has been inversely related to parental care. Several studies have suggested that females may gain genetic benefits for offspring by choosing well-pigmented males, but this remains to be demonstrated convincingly in any species.

Our understanding of the role of carotenoid-based pigmentation in female mate choice and proximate factors that control expression of carotenoid pigmentation has increased dramatically over the last decade. Nevertheless, some of the most basic questions related to sexual selection and carotenoid displays remain to be answered.

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