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Redness as a measure of the production cost of ornamental coloration

GEOFFREY E. HILL

Department of Zoology and Wildlife Science and Alabama Agricultural Experiment Station, 331 Funchess Hall, Auburn University, Auburn, AL 36849-5414, USA

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Understanding the relative costs of different forms of ornamental displays is fundamental to research on the evolution of such traits. For traits such as elongated tails, assessing the degree of exaggeration is straight-forward: bigger is more exaggerated and more costly. In contrast, assignment of such a hierarchical ranking of costliness and exaggeration to color displays has not been possible. In this paper, I consider whether red carotenoid displays represent a more energetically costly form of ornamentation than yellow or orange carotenoid displays. Several lines of evidence support the idea that red carotenoid pigmentation is particularly costly. Red carotenoid pigments are less abundant than yellow pigments in the diet of virtually all vertebrates. Although many vertebrates can convert some yellow carotenes and xanthophylls to red pigments, all species appear to be restricted in the types of metabolic conversions of which they are capable as well as by the costs of such conversions. In virtually all avian taxa with carotenoid-based coloration, when females and juvenile males show plumage hue that is different than that of adult males, their plumage is less red (more orange or yellow). Finally, in a comparative study of cardueline finches, there was a significant positive relationship between the degree of sexual dichromatism and the redness of male plumage, suggesting that red is a particularly costly color display. The finding that red is a more costly color display than yellow or orange has important implications for comparative studies of the evolution of ornamental plumage.

KEY WORDS: sexual selection; ornaments; carotenoids; plumage color; sexual dichromatism; cardueline finches.

INTRODUCTION

Since Darwin, evolutionary biologists have been intrigued by morphological and behavioral features of animals that appear to be ornamental; that is, traits that seem to enhance an animal's ability to attract or procure mates rather than to increase its survival or fecundity. In studies of ornaments in vertebrates, research has centered on four broad groups of traits, accessory morphological features (combs, wattles, spurs, antlers, etc. that seem completely unnecessary outside sexual competition), morphological features of exaggerated size (elongated tails or increased body size), behavioral displays (song, dance, flight displays, etc.), and color displays. The latter group comprises some of the gaudiest displays in nature, but even though ornamental coloration has been the focus of intense study in birds and fish (e.g. BUTCHER & ROHWER 1989, KODRIC-BROWN 1990), it remains among the least understood of display traits.

In many ways, morphological display traits such as elongated tails lend themselves to study. In most cases, such traits can be relatively easily measured and manipulated (e.g., ANDERSSON 1982a, MØLLER 1988, EVANS & HATCHWELL 1992), and there is little argument that traits become more costly as they increase in size (ANDERSSON 1982b, KODRIC-BROWN & BROWN 1984, BASOLO 1990), although more complex traits such as deer antlers and peacocks' tails can present problems. In contrast, color displays are much more difficult to quantify (ENDLER 1990), and the color equivalent of a long tail is not always obvious. Generally, increasing brightness is equated to more costly and exaggerated color display (KODRIC-BROWN 1985, ENDLER 1990, HILL 1990), but "brightness" is not always easy to define. Within a hue, brighter colors are generally considered those with greater color saturation (intensity). When the comparison spans different color hues (e.g. yellow versus orange versus red, or blue versus green), however, defining brightness and estimating the cost of color display becomes much more difficult.

In a study of House Finches (*Carpodacus mexicanus*), a species in which males vary continuously in ornamental coloration from yellow through orange to red, I judged red plumage to represent a more exaggerated and costly form of color display than orange plumage which, in turn, I judged to be more exaggerated and costly than yellow (HILL 1990). At first, this assessment was largely subjective; to my eye, red males were the brightest. Years of data gathering have enabled me to support this contention empirically. On a diet of plain seeds, captive male House Finches grow pale yellow feathers (HILL 1992). Males only grow red feathers in captivity if their diet is supplemented with red pigments (HILL 1992, 1993a). Color intensity and hue are highly correlated in male House Finches: one rarely encounters a washed-out red male or an intensely plumaged yellow male (HILL 1990, 1992, 1993a). The plumage of males tends to get redder between their first and subsequent breeding seasons (HILL 1992), just as the tails of swallows get longer and the antlers of deer get larger as these animals age (CLUTTON-BROCK et al. 1982, MØLLER 1988). In the wild, the redness of male plumage is correlated to feather growth rate, a measure of nutritional condition (HILL & MONTGOMERIE 1994). Most importantly, female House Finches from a number of populations show a strong preference to pair with the reddest male available to them (HILL 1990, 1991, 1994a), and there is a significant positive correlation between male feeding rate at the nest and the redness of their plumage (HILL 1991). So, in the House Finch, there is now good evidence that red is a more exaggerated and costly form of color display than orange or yellow.

My work with House Finches led to the obvious question: is it a general feature of integumentary pigmentation of animals that red displays represent a more costly form of ornamentation than orange or yellow displays? In vertebrates, bright red (here meaning scarlet or crimson) integumentary displays can result from three mechanisms: (1) the circulation of the blood near the surface of a body region that lacks fur, feathers, or scales, (2) carotenoid-based pigments deposited in integumentary structures (FOX & VERVERS 1960), and (3) the red pigment turacin, found only in touracos (Cuculiformes Muscophagidae). No other sources of scarlet red coloration are known in vertebrates (FOX & VERVERS 1960). Melanin pigments produce "red" hair in humans and other mammals and the rust and tawny coloration in birds, but melanins cannot produce the scarlet red coloration that is the focus of this paper (FOX & VERVERS 1960, BRUSH 1978). No mammals are known to have carotenoid-based integumentary displays (GOODWIN 1984), but carotenoids account for most of the bright red, orange, and yellow displays of birds (including House Finches), fish, amphibians, and invertebrates (FOX & VERVERS 1960, BRUSH 1978, GOODWIN 1984). Unlike melanin pigments, turacin, and hemoglobin, carotenoid pigments cannot be synthesized by animals; they must be ingested either directly or indirectly from plants (GOODWIN 1984). Because their expression depends on dietary intake of pigments, carotenoid-based displays are among the best examples of condition-dependent ornaments that reflect individual quality (KODRIC-BROWN 1985, 1989; HILL 1990, 1991). In this paper I focus exclusively on carotenoid-based color displays.

To test the idea that red carotenoid displays are more costly to produce and hence represent a more exaggerated ornamental display than yellow or orange carotenoid displays, I will first address whether there is empirical support for the assumption that, relative to yellow or orange pigments, red carotenoid pigments are scarce in food and expensive to manufacture from yellow precursors. Second, I will look at variation in expression of plumage redness among adult male, adult female, and juvenile cardueline finches. Finally, I will present a comparative analysis looking at how the evolution of red carotenoid display compares to the evolution of sexual dichromatism among cardueline finches.

DISTRIBUTION OF CAROTENOIDS IN THE WILD

Abundance of red versus yellow

Carotenoids are lipid-soluble, unsaturated C-40 hydrocarbons. They are the most widespread and abundant natural pigments in plants (GOODWIN 1976, 1980; GROSS 1987). The particular colors of the various carotenoid pigments result from the large number of unsaturated carbon bonds in the molecules as well as the number and placement of keto and hydroxy functional groups (VERVERS 1982). Carotenes, the simplest carotenoids composed solely of hydrocarbons, produce yellow to yellow-green or yellow-orange coloration in the structures that contain them. Xanthophylls are the oxygenated derivatives of carotenes and, depending on the type and position of their functional groups, they produce yellow, orange, red, and rarely violet coloration in the structures that contain them (Fox & Ververs 1960, Goodwin 1976).

What little data exist on the distribution of carotenoids in the wild suggests that in nearly all parts of all plants, yellow pigments are the most abundant carotenoids and that red and orange xanthophylls are substantially less common (Goodwin 1984, Gross 1987, Goodwin & Britton 1988). Carotenoids occur in remarkably uniform distribution in all green tissue of higher plants (Goodwin 1976, Goodwin & Britton 1988), and all of the primary carotenoid pigments of green plant tissue are yellow, yellow-orange, or yellow-green in color.

While the distribution of carotenoids is best known for the green tissue of plants, relatively few vertebrate species rely on such tissue as a primary food source. Far more animals showing carotenoid-based integumentary displays rely on fruits, seeds, or other non-photosynthetic plant parts or on animal tissue for nutrition (Martin et al. 1951). Although these non-photosynthetic food sources contain a greater diversity of carotenoid pigments than green plant tissue, including in some cases more red xanthophylls, yellow carotenoid pigments appear to be far more abundant than red carotenoids in a wide range of foods. For instance, seeds generally contain relatively few carotenoid pigments, and what few pigments are present are almost all yellow carotenes and xanthophylls (Brockmann & Völker 1934, Goodwin 1973, Brush & Power 1976). The variety and relative abundances of carotenoids in fruits and vegetables is highly variable (Gross 1987, Goodwin & Britton 1988), and some fruits contain some red xanthophylls. Never-the-less, yellow carotenoid pigments (β-carotene, lutein, α-carotene) are still by far (generally by an order of magnitude or more) the most abundant carotenoids in a large sample of fruits and vegetables (Gross 1987, Mangels et al. 1993).

Arthropods provide the most likely vertebrate food source for relatively large quantities of red xanthophylls. Some insects accumulate carotenoids such as β-carotene from their diet and oxidize carotenes into brightly colored xanthophylls. For most insects, though, yellow carotenoids, particularly β-carotene and lutein, are the most abundant pigments (Goodwin 1984). Similarly, some crustaceans produce large quantities of red pigments, particularly astaxanthin (Goodwin 1984), but very few species have more red than yellow carotenoid pigments in their tissues (Fox & Ververs 1960, Goodwin 1984). In sum, unless a vertebrate has found a very specialized source of red carotenoid pigments such as certain arthropods, it almost certainly ingests far more yellow than red pigment.

Metabolic costs of carotenoid conversions

The literature suggests that yellow carotenoid pigments are more accessible than red carotenoid pigments in the diets of most vertebrates. However, although animals cannot manufacture their own carotenoid pigments, they can modify the structure, and hence the color, of those carotenoid pigments that they ingest (Goodwin 1984, Davies 1985, Schiedt et al. 1985, Brush 1990, Hencken 1992). If animals could freely convert various types of carotenoids and no costs were involved in the modification of carotenoid molecules, then the distribution of red versus yellow carotenoid pigments in the wild would be irrelevant: animals would simply change yellow carotenoids to red as needed. The available data, however, indicate that animals are very restricted in the sort of carotenoid modifications of which they are capable, that carotenoid metabolism is an energetically costly process, and that animals use dietary carotenoids without modification as integumentary pigments whenever possible (GOODWIN 1984, BRUSH 1990).

The process by which carotenoids go from food in the gut to pigments of the integument involves four main stages: absorption, transport, metabolism, and deposition (BRUSH 1978). At each stage, animals are selective about which carotenoids are utilized (see examples below), and such specificity suggests that costs and constraints are involved in the processing of carotenoids. If all carotenoids were equally useful as integumentary pigments or pigment precursors, then there would be no need for specificity; animals would simply use all ingested carotenoids indiscriminately. The fact that animals have evolved complex mechanisms to be discriminating in their use of carotenoids suggests that not all carotenoids are equally useful to all vertebrates.

For instance, carotenoids are absorbed through the lining of the gastrointestinal tract along with their lipid solvents (LUCAS & STETTENHEIM 1972), but not all carotenoids are taken up with the same affinity. More than four decades ago, WEIS & BISBEY (1947) showed that, in chickens, xanthophylls are absorbed from the diet more readily than carotenes (see also TYCZKOWSKI & HAMILTON 1986). Similar selectivity of carotenoid use has been observed in goldfish (*Carassius auratus*; studies summarized in GOODWIN 1984). Such selective uptake of carotenoids would not be predicted if animals could freely interconvert between different carotenoid.

A primary reason for such specificity in carotenoid uptake is that there are constraints on the sort of metabolic conversions of carotenoids of which vertebrates are capable. For instance, no animals are able to convert between α- and β-carotenes (the two most common classes of carotenes) and their xanthophyll derivatives (FOX & HOPKINS 1966, LEE 1966, WILLIAMS et al. 1967). Thus, for those vertebrates whose enzyme systems are geared to one class of carotenoids (presumably out of the need for efficiency), other classes of carotenoids are unusable as integumentary pigments. In general, vertebrates are very adept at discriminating (in a physiological sense) between carotenoids that they use as integumentary pigments and pigments that they do not use. An example concerns the African Oriole (*Oriolus auratus*). Lutein, which is the primary pigment of African Oriole plumage, is absorbed efficiently from food, while β-carotene, which serves as neither pigment or pigment precursor, is not absorbed (THOMMEN 1971). The use of only a fraction of available carotenoid as integumentary pigments by most vertebrates raises the cost of display of the red end products of carotenoid conversions.

The best example of the range as well as the limits of carotenoid conversions of which some vertebrates are capable is the work by Fox and co-workers on various species of flamingos (*Phoenicopterus* sp.). FOX & MCBETH (1970) and FOX et al. (1970) fed flamingos carotenoid-deficient diets for several weeks, until the levels of carotenoids in the flamingos' blood were very low. The diets of the flamingos were then supplemented with a variety of carotenoids. All the carotenoids that were assimilated from the diet (i.e., those that were either stored unchanged or metabolized) by flamingos were plumage pigments or precursors for plumage pigments (FOX 1962, FOX & HOPKINS 1966); those that were not assimilated were neither pigments nor precursors. Again, such selective uptake and conversion suggests that birds are limited in the type of carotenoid metabolism of which they are capable, and that birds maximize their intake of carotenoids that can serve as integumentary pigments.

Another important conclusion from the work of FOX et al. is that ingestion of one unit of a yellow metabolic precursor does not yield one unit of a red end-product. Metabolic conversion of, for example, (yellow) β-carotene to (red) astaxanthin involves approximately four steps, each of which is far less than 100% efficient in using substrate (FOX & HOPKINS 1966, FOX et al. 1967). The end result is that 1 unit of yellow precursor yields only a small fraction of that amount of red end product. If access to carotenoid pigments is limited (see HILL 1993a, 1994b; HUDON 1994) and especially if animals must expend time and energy in searching for carotenoid pigments (HILL 1993a), then both physiological constraints that reduce the types of carotenoids that can be used as integumentary pigments and inherent inefficiencies in metabolic conversion of those carotenoids that are suitable add to the cost of red ornamentation.

There are also direct energetic costs of converting yellow carotenes and xanthophylls to red end products. Modifications of the structure of carotenoids require enzymes (BRUSH 1990) that have to be manufactured using protein and energy (LEHNINGER 1975) and the carotenoid conversions themselves require energy (BRITTON 1976). If relatively large quantities of carotenoids are needed to produce an ornamental display, as is probably the case in many species (FOX 1962; THOMMEN 1971; SLAGSVOLD & LIFJELD 1985; HILL 1992, 1993a), the energetic costs of such metabolism may be substantial. This general argument is also supported by a basic observation: virtually all animals with carotenoid displays show a greater affinity for integumentary pigments in the diet than for pigment precursors, and most animals deposit integumentary pigments directly when they are available (GOODWIN 1984). For instance, when American Flamingos (*Phoenicopterus ruber*) were fed large quantities of β-carotene, a potential precursor of most red integumentary pigments displayed by the species, quantities of β-carotene appeared in the feces (FOX et al. 1969). In contrast, when the flamingos were fed large quantities of the red astaxanthin, a carotenoid that can serve directly as an integumentary pigment, none was detected in the feces (FOX & MCBETH 1970). And, as noted above, carotenoids that served as neither pigments nor precursors were not absorbed (FOX et al. 1970). Thus, the bird's physiological response to the various dietary carotenoids suggests that red end products are more valuable than yellow precursors.

To my knowledge, only one study provides direct evidence of a cost of carotenoid conversion. SCHERESCHEWSKY (1929) observed that male Bullfinches (*Pyrrhula pyrrhula*) produced brighter red plumage on a high-quality diet versus a low-quality diet, even when access to yellow xanthophylls and carotenes was the same. Thus, birds subjected to fewer energetic constraints are able to convert more precursor into integumentary pigment and achieve a brighter plumage. More studies of this sort are needed.

In sum, many vertebrate species show the capability to convert yellow carotenes and xanthophylls to red xanthophylls. However, only specific yellow pigments are used as precursors for such conversions, inherent inefficiencies in the conversion systems require large quantities of yellow precursors to produce modest quantities of red end product, and the process of carotenoid conversion appears to be energetically costly. Thus the physiological literature supports the idea that the greater abundance of yellow compared to red carotenoid pigments in almost all food sources makes red display more costly than yellow display.

PATTERNS OF AGE, SEX, AND SEASON

Methods

One of the best ways to assess the relative costs of an ornamental trait is to look at expression of the trait in adult females and juveniles relative to adult males. Juveniles almost invariably show reduced expression of ornamental traits relative to adult males and, with rare exceptions that are generally associated with polyandrous mating systems, females show equal or reduced ornamentation relative to adult males. For example, relative to adult males, juveniles and females typically show reduced horns, antlers, wattles, song production, etc. (ANDERSSON 1994).

If red carotenoid pigmentation is an inherently more costly display than orange or yellow carotenoid pigmentation, then I predicted that in cases in which hue varies among age/sex classes, juveniles and females will show reduced plumage redness. I tested this prediction among species of cardueline finches by comparing the hue of carotenoid-based plumage coloration of adult males, females, and juveniles. Cardueline finches (subfamily Carduelinae, family Fringillidae) are a monophyletic group of passerines with about 133 species, 103 of which show carotenoid-based plumage coloration (LONNBERG 1938, BRUSH & POWER 1976, GOODWIN 1984) that varies across species from yellow to red. All 133 species of cardueline finches are illustrated in (CLEMENT et al. 1993), with female plumages shown for all species (except monomorphic species) and juvenile plumage shown for 67 species. I used these illustrations to tally the direction of change in brightness and hue of plumage coloration between adult males in breeding plumage, adult females in breeding plumage and young birds in juvenile plumage. When the hue of carotenoid-based color did not vary among the age/sex classes, I scored adult males relative to both females and juveniles as having brighter, drabber, or the same plumage brightness. When hue varied between adult males and females or juveniles, I scored adult males as having redder, less red, or the same plumage hue. Species lacking carotenoid-based coloration were excluded from analysis.

Results

In 15 species, adult males are redder than females; in 80 species adult males and females show similar plumage hue but males are brighter; in seven species in which adult males are yellow, the sexes show similar plumage hue and similar plumage brightness; and, in one species in which adult males are red, the sexes show similar plumage hue and similar plumage brightness. Juvenile plumage was illustrated for 67 species. In 10 species adult males are redder than juveniles; in 55 species in which adult males are yellow, adult males and juveniles show similar plumage hue but adult males are brighter; and, in two species in which adult males are yellow, the adult males and juveniles show similar plumage hue and similar plumage brightness. In no cases were females or juveniles brighter than adult males and in all cases in which hue varied among age and sex classes, males had the reddest plumage.

COMPARATIVE TEST WITH CARDUELINE FINCHES

Methods

The cardueline finches are an excellent group to use in a comparative analysis addressing the cost of carotenoid displays of different colors. All cardueline finches share a similar socially-monogamous mating system (AUSTIN 1968, NEWTON 1972). In all species, females alone build nests and incubate eggs, but females depend on their mates to provide food during incubation and to feed young after they have hatched (NEWTON 1972, HARRISON 1975). The variance in male reproductive success among species of cardueline finches is unknown, but the similarity in mating systems across species suggests that males of all species are subject to similar sexual selection (PAYNE 1984). This similarity in mating systems reduces the number of confounding variables in a comparative study of the evolution of male ornamental coloration.

Virtually all cardueline finches are sexually dichromatic, with males displaying brighter carotenoid-based coloration than females. The degree of dichromatism varies among species, however, and this variation is largely a function of the amount of ornamentation displayed by females (as opposed to a loss of coloration by males). In some species, females show no detectable ornamental coloration; in most species they show some ornamental coloration but less than males; and, in a few species, females are as brightly colored as males.

In at least two species of cardueline finches, the ornamental carotenoid pigmentation of males is used by females in choosing mates (HILL 1990, 1991, 1994a; JOHNSON et al. 1993). The function of female ornamental plumage in cardueline finches is unclear, but in at least one species, female plumage coloration appears to play a role in male mate choice (HILL 1993b). Assuming that expression of female ornamental coloration is a function of a balance between the mating advantages of displaying the trait and the costs of producing the trait (WEBSTER 1992, HILL 1993b), I predicted that across species the degree of female ornamentation, as measured by degree of sexual dichromatism, should correlate with the cost of producing the ornament. In other words, if ornamental plumage becomes more costly to produce as it becomes redder, then dichromatism should increase as male plumage gets redder. I also predicted that if red is a particularly costly color to display then there should be a negative correlation between the redness of male plumage and the extent of plumage with carotenoid-based pigmentation. Finally, many cardueline finches display ornamental black plumage in addition to ornamental plumage pigmented with carotenoids (NEWTON 1972, CLEMENT et al. 1993). The costs of melanin pigmentation are unknown, but I made the general prediction that if red pigmentation is particularly costly, then the redness of male plumage should be negatively correlated with non-carotenoid ornaments such as black plumage. The logic behind this last prediction is that effort expended in production of one type of ornament will decrease energy available for the production of other ornament types.

To test these predictions, I analyzed data on hue of carotenoid-based plumage coloration and degree of sexual dichromatism of cardueline finches. I conducted this study in two manners. The first analysis included all 133 cardueline finches, and plumage characteristics were scored from paintings of the birds in CLEMENT et al. (1993). This analysis had the advantage of being comprehensive, including all extant taxa in the clade, and hence generating a large sample for comparison. Unfortunately, phylogenetic information exists for only a subset of the cardueline finches, so no correction for phylogenetic effects could be made (see below). The second analysis of plumage color and sexual dichromatism included only the 13 North American taxa. This analysis had the disadvantage of sampling only a small subset of all cardueline finches and generating a small sample for comparison, but photographs of males and females of the 13 species are available for scoring plumage coloration and there is a published hypothesis of the phylogenetic relationships of these species (see below).

For both analyses, male plumage hue and degree of dichromatism were scored by observers who had not been informed of the hypothesis being tested. To score finches for the first analysis, four biologists used plates in CLEMENT et al. (1993). For images of the birds in the second analysis, 10 scorers used primarily photographs from FARRAND (1983) and BULL & FARRAND (1977). For the few species not adequately covered in these guides, scorers referred to plates in NATIONAL GEOGRAPHIC SOCIETY (1983). For each species, male plumage hue was scored by comparing the brightest (most intensely pigmented) portion of the male's plumage to plates in KORNERUP & WANSHER (1983). Hue was recorded as page number (see HILL 1992, HILL et al. 1994 for details of quantifying plumage hue). Dichromatism was recorded as the estimated percent difference in carotenoid plumage pigmentation between males and females (profile view of perched birds, wings folded), so that completely dimorphic species scored 100 and monomorphic species scored 0. For each species, scorers also estimated percent of the entire male plumage (profile view of perched birds, wings folded) with carotenoid pigmentation and with black pigmentation. There was good agreement among scorers in all characteristics that were measured (r > 0.90 between all observers for color scores and r > 0.77 between all observers for percent dimorphism, carotenoid coloration, and percent black coloration) and I used the mean of four scores in the first analysis and the mean of 10 scores in the second analysis.

Comparative studies can be confounded by the non-independence of points: some birds will show a similar relationship between color and dimorphism not because of a similar response to selection, but because they share a common ancestral condition (HARVEY & PAGEL 1991, BROOKS & MCLENNAN 1991). To control for such phylogenetic effects, I used the Comparative Analysis by Independent Contrasts (C.A.I.C.) computer package (PURVIS 1991). In this approach, rather than comparing between endpoints on an evolutionary tree, one compares the degree of change in traits between nodes (hypothetical ancestors) and daughter taxa (HARVEY & PAGEL 1991). The condition of the variables at nodes is estimated from a weighted average of the condition of the daughter taxa. The number of comparisons in the analysis is set by number of independent contrasts (nodes with daughter taxa).

Comparative contrasts analysis requires a well-resolved phylogeny for the taxa being studied, preferably with branch lengths. There is no published phylogeny for the entire cardueline finch clade, so no correction for phylogenetic effects could be made in the first analysis. To correct for phylogeny in the second analysis, I used a phenogram for 13 North Ameri-

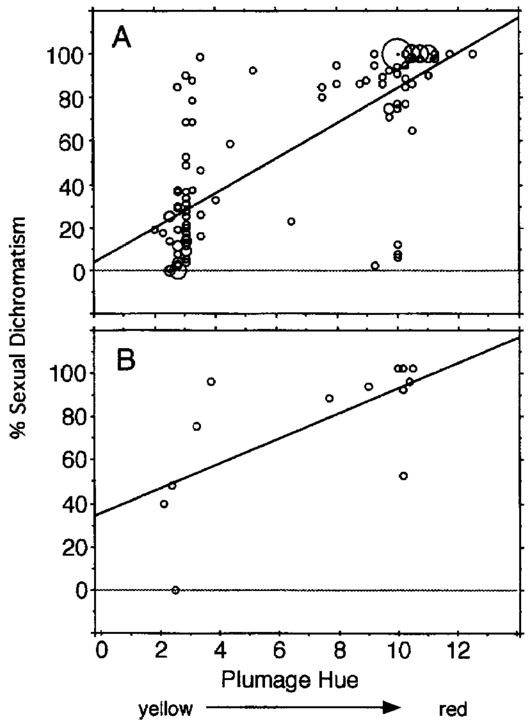

Fig. 1. — Relationship between the hue of male carotenoid pigmentation and the degree of sexual dichromatism of carotenoid ornamentation for (A) 103 cardueline finch species with carotenoid-based plumage coloration and (B) the 13 species of North American cardueline finches used in the comparative contrasts analysis. Point size is proportional to the number of overlapping observations.

Table 1.
Values for plumage characteristics of cardueline finches used in comparative analyses [1].

Species	Plumage hue [2]	% sexual dimorphism [3]	% carotenoid pigmentation [4]	% black [5]
Carpodacus cassini	10.0	1.0	20.5	0.2
Carpodacus purpureus	10.2	1.0	41.5	1.0
Carpodacus mexicanus	10.5	1.0	13.5	0.2
Loxia curvirostra	7.7	0.87	69.5	25.5
Loxia leucoptera	10.2	0.91	60.0	23.5
Carduelis flammeus	10.2	0.51	21.5	6.1
Carduelis pinus	2.5	0.10	9.7	8.9
Carduelis psaltria	2.4	0.47	43.5	58.0
Carduelis lawrencei	3.2	0.74	32.0	14.0
Carduelis tristis	2.1	0.38	67.5	32.0
Leucosticte arcotoa	10.4	0.94	31.5	6.2
Pinicola enucleator	9.0	0.92	72.0	11.5
Coccothraustes vespertinus	3.7	0.95	71.0	21.0

[1] All values are the means of 10 scorers. [2] Plume hues from KORNERUP & WANSCHER (1983): 2-3 = yellow, 6-7 = orange, 10-11 = red. [3] Percent sexual dichromatism of carotenoid ornamentation. [4] Per cent of plumage with carotenoid pigmentation (wings folded). [5] Percent of plumage with black pigmentation (wings folded).

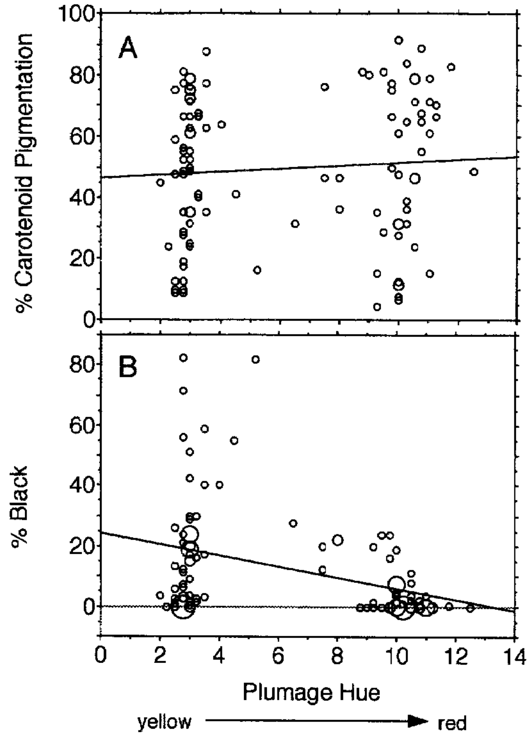

Fig. 2. — Relationship between hue of male carotenoid pigmentation and the proportion of plumage with (A) carotenoid pigmentation or (B) black pigmentation for 103 cardueline finch species with carotenoid-based plumage coloration. Point size is proportional to the number of overlapping observations.

can cardueline finch taxa (Martin & Johnson 1986). If one assumes that the rate of molecular evolution among these lineages has been similar, this phenogram can be used as a hypothesis of phylogenetic relatedness. Because all of the taxa in the study share a similar monogamous mating system (see above) with the same generation time and grossly similar population sizes, the molecular clock assumption seems reasonable. Moreover, the phenogram published by Sibley & Ahlquist (1990) based on an independent molecular data set corroborates that of Martin & Johnson (1986), although the Sibley & Ahlquist tree contains only six cardueline finches. In my analysis of color and dichromatism, I used Martin & Johnson's phenogram as a phylogeny except that (1) I removed subspecies from my analysis (including the Hoary Redpoll, *Carduelis hormemanni*, which is considered by many ornithologists to be a subspecies of the Common Redpoll; Troy 1985, Seutin et al. 1992), and (2) I removed the European Goldfinch (*Carduelis carduelis*), since all other taxa are North American (Table 1). For branch lengths I used genetic distances from fig. 2 in Martin & Johnson (1986).

For the contrast analysis all variables were log transformed (Purvis 1991). Tests of significance of the relationships between variables are based on least-squares regression of contrast scores with the regression forced through the origin (Purvis 1991).

Results

When I performed simple correlational analysis with no correction for phylogeny, I found a significant positive relationship between plumage hue and dichromatism for all cardueline finches (r_s = 0.78, n = 103, P = 0.0001; Fig. 1) and for the subset of North American taxa (r_s = 0.70, n = 13, P = 0.02; Fig. 1). In other words, species with redder males tended to be more sexually dichromatic. I found a significant negative relationship between plumage hue and amount of black in the plumage for all cardueline finches (r = – 0.36, n = 103, P = 0.0002; Fig. 2) and for the subset of North American taxa (r_s = – 0.71, n = 13, P = 0.01; Fig. 2). The relationship between plumage hue and extent of carotenoid pigmentation was not statistically significant either when all taxa were considered (r_s = – 0.18, n = 103, P = 0.06;

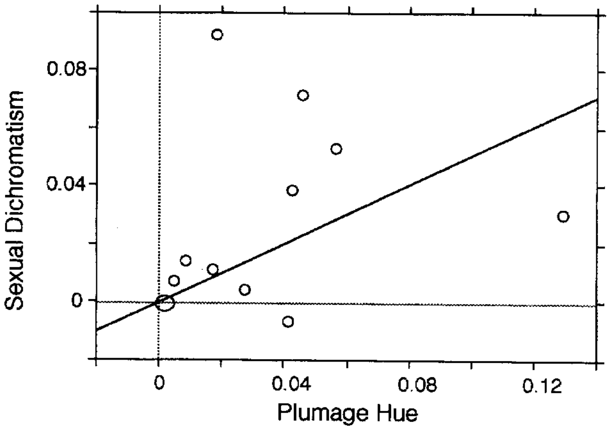

Fig. 3. — Relationship between the hue of male carotenoid pigmentation and the degree of sexual dichromatism of carotenoid ornamentation for 13 species of North American cardueline finches. Each point is an independent contrast score (see text). The regression line was forced through the origin (Harvey & Pagel 1991). Point size is proportional to the number of overlapping observations.

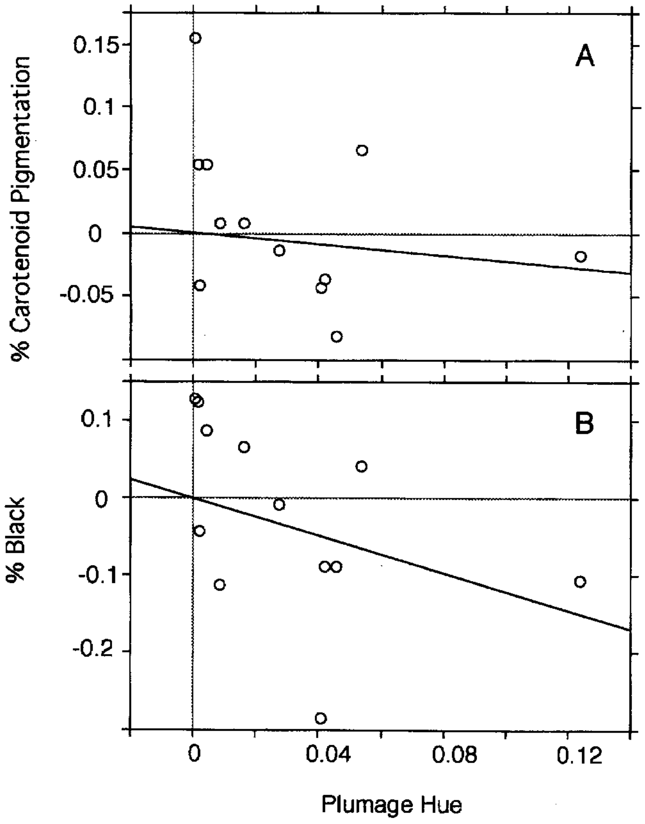

Fig. 4. — Relationship between the hue of male carotenoid pigmentation and the proportion of plumage with (A) carotenoid pigmentation or (B) black pigmentation for 13 species of North American cardueline finches. Each point is an independent contrast score (see text). The regression line was forced through the origin (Harvey & Pagel 1991).

Fig. 2) or when only North American taxa were considered (r_s = – 0.31, n = 13, *P* = 0.28; Fig. 2).

Using contrast scores to control for phylogenetic effects, I found a significant positive relationship between plumage redness and degree of dichromatism (r = 0.60, n = 12, *P* = 0.03; Fig. 3). I failed to find a significant relationship between redness and percent of plumage with either carotenoid pigmentation (r = – 0.22, n = 12, *P* = 0.60; Fig. 4) or black coloration (r = – 0.14, n = 12, *P* = 0.11; Fig. 4).

DISCUSSION

As I have used it in this paper, "trait exaggeration" refers to how far trait expression deviates from that expected under natural selection. If one is considering condition-dependent traits such as the elongated tails of swallows or carotenoid-based coloration, exaggeration is synonymous with costliness (KODRIC-BROWN 1985, HILL 1994a). Tails become more costly to produce as they get longer and colors become more costly to produce as they get more intense. Thus, demonstrating that color displays also become more exaggerated as they become redder entailed that I demonstrate that red is more energetically costly to produce than yellow or orange carotenoid displays.

The evidence presented in this paper supports the idea that red carotenoid pigmentation is a more energetically costly display than orange or yellow. Red carotenoid pigments are certainly less abundant in the diet of virtually all vertebrates than yellow pigments. Although many vertebrates can convert some yellow carotenes and xanthophylls to red pigments, animals appear to be limited by the types of conversions of which they are capable as well as by the costs of the conversions. More detailed study is needed, however, on the energetic costs of pigment modification. Thus, strictly from the standpoint of resource abundance and the cost of acquisition, red carotenoid displays are inherently more costly than yellow displays for most organisms.

Further evidence for the cost of red carotenoid displays comes from examining the pattern of color displays among cardueline finches. In species with ornaments for which a hierarchy of costs relative to trait expression is obvious (bigger = more exaggerated: antlers, horns, or elongated tails), sexually mature males in breeding condition invariably have larger ornaments than females or juvenile males (ANDERSSON 1994). I found this same pattern with respect to red color display in cardueline finches: sexually mature males invariably displayed redder plumage than females or juveniles. In other words, whenever age/sex classes varied in plumage hue, adult males had redder plumage. This same analysis could have been conducted on any number of avian taxa with the same result. I chose cardueline finches because the entire group is well-illustrated (CLEMENT et al. 1993), and red coloration is known to be carotenoid-based in this group. Of the hundreds of species of birds with bright red coloration, I know of only one non-polyandrous species in which females have redder plumage than males, the Eclectus Parrot (*Eclectus roratus*). Moreover, most cardueline finches show little seasonal variation in plumage coloration so no seasonal comparisons could be made. In many other groups of birds, however, males grow very differently colored breeding and non-breeding plumages and invariably, the color change from breeding to non-breeding is to drabber and less red. There are several species in which juveniles have redder plumage than adult males (e.g. many species in family Picidae) but these may represent cases in which juvenile plumage redness is under selection as a signal in parent-offspring communication (LYON et al. 1994). In sum, differences in plumage hue among age/sex classes of birds as well as seasonal changes in plumage coloration are as predicted if red is a more costly color display than orange or yellow.

The second pattern of carotenoid-based color displays that supports the hypothesis that red is a particularly costly display is a significant positive relationship across species of cardueline finches between the degree of sexual dichromatism and the redness of male plumage. This relationship was significant whether it included all cardueline finches with no correction for phylogenetic effects or it included only a small subset of finches with a correction for phylogeny. While numerous causal explanations can be applied to any correlational relationship, one explanation for the observed pattern of redness and dichromatism is that as the costs of ornamental display rise, selection against expression of the trait in females increases and leads to increased sexual dichromatism. This explanation will become more convincing if the same pattern of increased dichromatism with increased plumage redness is found in other taxa. As more phylogenies for bird groups become available, more comparative tests of this sort should be possible.

It is important to note that condition-dependent traits such as red coloration can be costly in two very different ways: they can be costly to produce or they can be costly to maintain. These two types of cost impact individuals at different life stages and they are not mutually exclusive. In this discussion of trait exaggeration, I refer only to the cost of production (finding, ingesting, and processing carotenoid pigments). Maintenance costs related to ornament display are generally synonymous with predation risk (PROMISLOW et al. 1993) and different colors (particularly iridescent versus carotenoid displays) are known to incur a different predation risk in fish (ENDLER 1978, 1983). However, while there is evidence that structural versus carotenoid-based displays might differ in visibility to predators, there is no evidence that various carotenoid-based color displays (yellow, orange, red) evoke different predation risk (see GÖTMARK 1992, 1995 for evidence that brighter plumage coloration might actually deter avian predators in some species). In a study of House Finches (HILL 1991), males with brighter plumage had higher over-winter survival, but brighter males were also the males in better physiological condition (HILL & MONTGOMERIE 1994). House Finches along with many other species of cardueline finches grow buffy edges to their brightly colored feathers that are worn off before courtship and mating begin (HILL 1993c, CLEMENT et al. 1993), which suggests that colorful plumage does entail some maintenance cost. Moreover, it has been suggested that, unlike red coloration, yellow coloration (SLAGSVOLD & LIFJELD 1985) or yellow coloration associated with black (COTT 1940, HAILMAN 1977) may function primarily in crypsis. Thus, there is mixed evidence to support the hypothesis that some carotenoid displays entail a greater maintenance cost than others. Given the available evidence, production costs that are directly related to carotenoid availability seem more important than maintenance costs in influencing the evolution of carotenoid displays (HILL 1993a), but this is a topic that warrants further study.

While there was a clear relationship between plumage redness and sexual dichromatism among cardueline finches, the hypothesis that there is a tradeoff between redness and the extent of carotenoid displays was not supported: the negative relationship between plumage hue and extent of carotenoid pigmentation was weak and not significant regardless of whether I controlled for phylogeny. However, the manner in which animals distribute energy across a suite of alternative ornamental traits is poorly understood (MØLLER & POMIANKOWSKI 1993, HILL 1994c), so failure to support this prediction provides only weak evidence against the hypothesis that red is a costly display trait. Moreover, I found some support for the hypothesis that there is a tradeoff between expression of carotenoid and non-carotenoid ornaments: there was a highly significant negative correlation between the hue of carotenoid-based coloration and the extent of black in the plumage when all cardueline finches were considered. However, I could not control for phylogenetic effects in this analysis. The relationship between black ornamentation and red ornamentation did not hold after I controlled for phylogeny, but the sample size was very small. Additional testing with larger sample size might yield different results. This possible tradeoff between different classes of ornaments is intriguing and warrants further study. Alternative hypotheses, such as yellow associated with black resulting in disruptive crypsis (COTT 1940) could also be explored with a larger data set.

If the conclusions drawn in this paper are correct and red is a more exaggerated color display than yellow, it has important implications for comparative studies. To date, all comparative studies focusing on male plumage brightness have used a subjective categorical brightness score that relies entirely on the impressions of the scorer to determine what sort of color display is more or less exaggerated (HAMILTON & ZUK 1982, READ 1988, READ & HARVEY 1989, PROMISLOW et al. 1993). By this method, a male American Goldfinch might be scored as having a more exaggerated color display than a male Red Crossbill or vice versa depending on the impact that the illustrations of the birds have on the scorer. If one accepts a hierarchy of carotenoid-based color displays (red > orange > yellow) then there is an a priori justification for weighting red displays higher than orange and orange higher than yellow (and hence the Red Crossbill above the American Goldfinch). If this weighting of color displays provides a better approximation of the true costs of the color displays, then it should remove some of the noise from previous comparative studies of color displays and make some patterns clearer.

This is the first attempt to test the idea that some color displays are more energetically costly (i.e. are more exaggerated) than other color displays. In this paper I focused on carotenoid-based yellow, orange, and red displays because this is one of the most widespread and best-understood classes of color display in birds and fish. Also, because of my observations of House Finches, I had an a priori reason to believe that carotenoid-based color displays varied in cost. It is possible that particular hues in other suites of color displays that are not carotenoid-based might also exact different costs. For instance, a quick look at North American passerines shows that bright blue structural colors are more common than bright violet or green structural colors. Almost nothing is known, however, about the proximate controls and hence cost of color displays that are not carotenoid-based. It will be interesting to see in future research if carotenoids are unique in having a hierarchy of costs associated with various color displays or if this is a common feature to many color systems.

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