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DIETARY AND SEXUAL CORRELATES OF CAROTENOID PIGMENT EXPRESSION IN DOVE PLUMAGE

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Abstract. Carotenoid pigmentation in birds' plumage is considered an honest indicator of phenotypic quality, and thus a target of sexual selection. But carotenoids also fulfill essential physiological functions, and therefore, carotenoids should only appear in plumage if they are in excess of those needed physiologically. We explored the presence of carotenoid-based plumage coloration in columbids and its association with diet and sexual dichromatism using a comparative analysis. We found that carotenoid plumage pigmentation appeared three times independently in doves, and that these events were always associated with frugivorous feeding habits. This suggests that expression of carotenoid-based plumage color in granivorous species may be constrained by the scarcity of carotenoids in their diet. However, more than half of the frugivorous species lack carotenoid-pigmented plumage, indicating that rich dietary sources of these compounds are a necessary but not sufficient cause for their expression in plumage. Analyzing 12 pairs of sister taxa, we found that plumage dichromatism was neither associated with the amount of carotenoid pigment present in the plumage nor with the sexual dimorphism in carotenoid-pigmented plumage. Although the presence of carotenoid-based plumage coloration has been related to sexual selection in several taxa, we failed to show such an association in columbids.

Key words: carotenoid pigments, Columbidae, dichromatism, doves, plumage color, sexual selection.

Correlación de la Expresión de Pigmentos Carotenoides en el Plumaje de Palomas con la Dieta y la Selección Sexual

Resumen. Los pigmentos carotenoides en el plumaje de las aves son considerados indicadores honestos de la calidad fenotípica y, por lo tanto, objetos de selección sexual. Sin embargo, los carotenoides también cumplen funciones fisiológicas esenciales, por lo cual aquellos que se expresan en el plumaje deberían estar en exceso de los utilizados a nivel fisiológico. Exploramos la presencia de carotenoides en el plumaje de las palomas y su asociación con la dieta y el dicromatismo sexual usando un análisis comparativo. Encontramos que el plumaje carotenoide apareció tres veces independientemente en palomas, y que estos eventos estaban siempre asociados a frugivoría. Esto sugiere que la expresión de carotenoides en el plumaje de especies granívoras puede estar restringida por la escasez de estos pigmentos en la dieta. Sin embargo, más de la mitad de las especies frugívoras carecen de plumaje carotenoide, indicando que alimentos ricos en este compuesto son una causa necesaria pero no suficiente para su expresión en el plumaje. Analizando 12 pares de taxa hermanos, encontramos que el dicromatismo no estaba asociado ni a la cantidad de pigmentos carotenoides presentes en el plumaje ni al dimorfismo sexual de plumaje carotenoide. Aunque la presencia de plumaje carotenoide ha sido relacionada con la selección sexual en numerosos grupos, no encontramos una asociación similar en palomas.

INTRODUCTION

The family Columbidae comprises about 300 species of pigeons and doves (Baptista et al. 1997, Gibbs et al. 2001). They occupy habitats ranging from forests to deserts, and show markedly different feeding habits, from mainly granivorous to exclusively frugivorous. Plumage coloration is very diverse within this group. It can range from cryptic gray and brown, to brilliant blue, orange, and green. Sexual dichromatism is also very variable among species, with some species in which the sexes look alike, others in which there is a small brightness difference between the sexes, and others in which the sexes are strongly dichromatic (Baptista et al. 1997, Gibbs et al. 2001).

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Plumage coloration can be produced in two ways: by color pigments or by feather structure. There are three types of pigments, each of which produces certain colors by absorbing particular wavelengths of the light and transmitting the remaining wavelengths. Melanin pigments produce black, gray, brown, reddish brown, and dull-yellow colors; porphyrin pigments produce green, red, and brown; and carotenoid pigments bright red, orange, and yellow, as well as purples when bound to proteins (Fox 1976, Brush 1978, Olson and Owens 1998). Structural colors are produced by interference and scattering of light in keratin layers of the feathers. White, blue, green, and iridescent plumage colors are produced in this way (Fox 1976, Brush 1978, Proctor and Lynch 1993).

Carotenoid pigments are not synthesized by birds and must be obtained through the diet (Goodwin 1984). The expression of carotenoid-based plumage coloration is thus constrained by the availability of these compounds in food. Several studies have shown how carotenoid acquisition affects, to a greater or lesser extent, the expression of bright carotenoid plumage coloration (Slagsvold and Lifjeld 1985, Hill 1992, Linville and Breitwisch 1997). Captive columbids of the genus *Treron* failed to express their carotenoid-based green and yellow plumage color if the diet was unsuitable, showing gray and purplish colors instead (Goodwin 1983). But apart from acting as color pigments in the plumage, carotenoids fulfill essential physiological functions related to immunocompetence and detoxification (Lozano 1994, Møller et al. 2000). This means that to produce ornamental coloration, levels of circulating carotenoid pigments should be above what is needed physiologically (Hill 1999). Therefore, we expect to find carotenoid pigmentation only in lineages that have a high intake of carotenoids with their diet. Fruits are richer in carotenoids than seeds or grains, and thus, we expect to find carotenoid-based plumage color patches in frugivorous lineages rather than in nonfrugivorous ones.

Several studies suggest that carotenoid-based plumage coloration is costly to produce and may thus honestly indicate phenotypic quality (Andersson 1986, Hill 1990, Zuk 1992). Costs associated with carotenoid coloration of feathers are related to both the acquisition and utilization of carotenoids (Hill 2000). Acquisition costs include the time spent searching for carotenoid-rich food sources, whereas utilization costs include biochemical and physiological mechanisms like absorption, transformation, and exhibition of carotenoids (Hudon 1991, Olson and Owens 1998). Costly indicators of phenotypic quality are suitable characters for sexual selection to act on, since they give reliable information to prospective mates or competing conspecifics (Zahavi and Zahavi 1997). Supporting this view, Gray (1996) found that within North American passerine birds carotenoid-derived plumage coloration was positively correlated with sexual dichromatism (used as an indirect measure of sexual selection), whereas structural and melanin-derived coloration was not. More recently, Badyaev and Hill (2000) also showed that dichromatism correlated positively with sexual differences in carotenoid coloration in carduline finches. If carotenoid pigmentation is a sexually selected trait in columbids, we would expect to find a positive association between plumage dichromatism and the total amount or the dimorphism in carotenoid-pigmented plumage patches.

The aim of this study was to test the association of carotenoid-based plumage color with both diet and sexual dichromatism. As species cannot be treated as independent points of comparison because of their shared evolutionary history (Ridley 1983, 1989, Felsenstein 1985) we looked at the independent instances of evolution of carotenoid pigmentation and analyzed if these events were associated to frugivory or sexual dichromatism.

METHODS

Data on sexual dichromatism and presence of carotenoid-based plumage colors were taken from the literature (Goernitz and Rensch 1924, Frank 1939, Auber 1957, Dyck 1987, Baptista et al. 1997, Gibbs et al. 2001), as well as from direct observation of specimens deposited at the Museo Argentino de Ciencias Naturales ''Bernardino Rivadavia'' (Buenos Aires, Argentina), the Natural History Museum (Tring, UK), and the American Museum of Natural History (New York). Data on feeding habits were taken from Baker (1913), Goodwin (1983), Baptista et al. (1997), Steadman and Freifeld (1999), and Gibbs et al. (2001).

The presence of carotenoid pigments in the plumage was assessed spectrophotometrically. Feathers for the analysis were taken from spec-

imens of the Museo Argentino de Ciencias Naturales ''Bernardino Rivadavia.'' Different plumage patches showing a distinctive coloration were analyzed for several species, each of them represented by one individual. The number of feathers taken from each plumage patch differed according to their size, so as to obtain a minimal weight of 7 mg. Prior to pigment extraction, feathers were washed with methanol (feather color remained unaltered with the washes). After drying, feathers were cut into small pieces and ground in a mortar with methanol (1: 0.5 mg dried weight:mL methanol). The suspension was evaporated to dryness in a boiling water bath and the residue resuspended in the same initial volume of methanol. The extract was filtered and carotenoids were determined using a Hewlett Packard Vectra 286/12 spectrophotometer. Carotenoid pigments were considered to be present in the feathers if spectra showed distinctive absorption peaks in the 400–500 nm interval (Hudon and Brush 1992, Ryan et al. 1994). Feathers of three species of passerines known to possess carotenoid-based color (*Carduelis magellanica*, *Piranga olivacea*, and *Icterus galbula*; Gray 1996, Badyaev and Hill 2000) were used to control for the sensitivity of the method. To control for the absence of these absorption peaks in feathers colored structurally or by other pigments, we analyzed white, iridescent, and brown feathers of *Gallicolumba luzonica*.

Species were considered to be sexually dichromatic if males and females differed in their plumage coloration, and they were considered to be sexually monochromatic if no color differences were found between sexes or if they just differed in brightness. Carotenoid pigmentation was categorized as absent or present for each species (Appendix). Feeding habits were divided into two categories: granivorous, when the diet was composed mainly of seeds and grains; and frugivorous, when the diet was composed mainly of fruits, either taken directly from trees or shrubs, or after falling to the ground (Appendix).

STATISTICAL ANALYSES

To test the association of carotenoid-based plumage color with diet we used the contingent states test (Sillén-Tullberg 1993). This test examines whether a transition in one dependent character (carotenoid plumage) is associated with a certain state of another independent character (frugivory).

To perform the contingent states test two things are required: a completely resolved phylogeny, and an optimization of the characters of interest on the tree, so that character states are defined on all branches. We based our analysis on the phylogenetic relationship of 307 species proposed by Goodwin (1983) and on additional information of species relationships taken from Baptista et al. (1997), Johnson and Clayton (2000a, 2000b), and Johnson et al. (2001). The contingent states test is not sensitive to the topology of branches when character states do not vary. Thus, the way polytomies (points in the phylogeny with more than two simultaneously derived branches) were resolved did not affect the results of the analysis.

The optimization of characters was carried out using MacClade 3.0 software (Maddison and Maddison 1992). Absence of carotenoid pigmentation was ancestral within columbids, whereas the feeding habit was uncertain (Fig. 1). To make the analyses more conservative, branches with uncertain feeding habit were resolved maximizing frugivory. In total, we analyzed 613 ($2N - 1$) branches.

We asked the question whether carotenoid pigmentation is equally likely to appear under the two states of foraging habits, granivory and frugivory. We compared the number of branches showing no carotenoid pigmentation with the number of branches in which carotenoid colors appeared, for granivory and frugivory, separately (Table 1). The test was performed with a 2×2 contingency table under the null hypothesis that carotenoid pigmentation is equally likely to originate in frugivorous and granivorous lineages. We used a *G*-test with Yates correction for continuity ($\alpha = 0.05$).

To test the association of carotenoid plumage coloration with sexual dichromatism the independent (raw) contrast method (Felsenstein 1985) was used. We compared 12 sister taxa that differed in sexual dichromatism (a surrogate measure of sexual selection; Hamilton and Zuk 1982, Møller and Birkhead 1994, Owens and Hartley 1998), and looked for associations with the amount of carotenoid pigments present in the plumage and dichromatism due to carotenoid patches. We scored males and females separately for six body regions: head, mantle, wing coverts, breast, belly, and undertail coverts. For each region we scored the following: presence or absence of dichromatism (coded as 1 and 0, re-

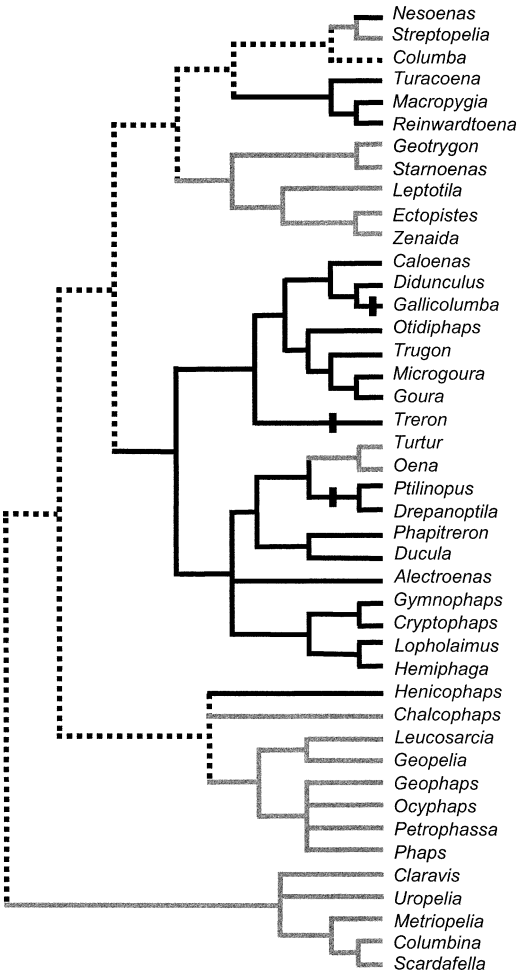

FIGURE 1. Phylogenetic tree for the Columbidae based on Goodwin (1983) and Johnson and Clayton (2000a). Branches show states for dietary habits (gray: granivory, black: frugivory, dotted: equivocal); vertical marks indicate acquisition of carotenoid-based plumage.

spectively), presence or absence of carotenoid-based color patches, and presence or absence of dichromatism due to carotenoid coloration. The presence of green plumage was categorized as 0 for *Ptilinopus* and *Treron*, because it is present in all species of these genera whereas they differ in other carotenoid-based colors. The final scores for total and carotenoid dichromatism ranged from 0 to 6, whereas the score for carotenoid coloration could range from 0 (if no carotenoid color patches were present in either sex) to 12 (if both sexes had carotenoid color patches in every region). Pairs of taxa used for this analysis and their scores are shown in Table 2. For the comparisons of sister clades with more than one species, average values were computed for each clade.

RESULTS

Spectrophotometric analyses of feathers confirmed earlier findings on the presence of carotenoid pigments in dove plumage (Goernitz and Rensch 1924, Frank 1939, Auber 1957, Dyck 1987), except for the green color in the genus *Ducula*. Carotenoid pigments show distinctive absorption peaks in the 400–500 nm interval of the spectrum (Fig. 2A), which are absent in spectra of carotenoid-lacking feathers (Fig. 2B). Carotenoids were present in the green feathers of the species analyzed for the genera *Treron* and *Ptilinopus*, but not in the green feathers of *Ducula poliocephala* (Fig. 2C). This latter result contradicts Frank's (1939) finding, which suggested that yellow carotenoids were present in the green plumage of *Ducula forsteni*, but agree with Dyck (1987), who did not find yellow carotenoids in the green plumage of *Ducula concinna*. Carotenoid pigments were also present in the yellow and orange plumage of *Treron* and *Ptilinopus*, and in the red and purple plumage patches of *Ptilinopus* and *Gallicolumba* (Fig. 2D).

TABLE 1. Distribution of transitions in carotenoid pigmentation on branches of the columbiform phylogeny (Fig. 1) reconstructed as having frugivorous or granivorous feeding habits.

	Frugivory	Granivory
Maintenance of no carotenoid pigmentation	261	197
Acquisition of carotenoid pigmentation	3	0
Maintenance of carotenoid pigmentation	152	0
Loss of carotenoid pigmentation	0	0

TABLE 2. Pairs of sister taxa (X-X′), differing in sexual dichromatism, used in an independent contrasts analysis of the relationship between dichromatism and carotenoid coloration in the Columbidae. For sister taxa including more than two species, average values of the clade with more than one species were used in the analysis. Presence or absence (coded as 1 and 0, respectively) of dichromatism and carotenoid-based color patches were scored for six body regions of each species: head, mantle, wing coverts, breast, belly, and undertail coverts. Final scores ranged from 0 (absent in every region) to 6 (present in all regions).

Taxon	Species	Total dichromatism	Male carotenoid coloration	Female carotenoid coloration	Carotenoid dichromatism
A	*Ptilinopus bernsteinii*	2	3	2	1
A′	*P. magnificus*	0	4	4	0
B	*Ptilinopus leclancheri*	2	1	1	0
B′	*P. subgularis*	0	2	2	0
C	*Ptilinopus victor*	6	6	2	4
C′	*P. layardi*	2	3	1	2
D	*Ptilinopus tannensis*	1	2	2	0
D′	*P. perlatus*	0	4	4	0
D′	*P. ornatus*	0	4	4	0
E	*Ptilinopus perousii*	5	6	3	3
E′	*P. superbus*	4	5	2	3
F	*Ptilinopus monacha*	2	4	3	1
F′	*P. coronulatus*	0	3	3	0
G	*Ptilinopus rivoli*	4	3	1	2
G	*P. solomonensis*	4	4	1	3
G′	*P. viridis*	0	2	2	0
G′	*P. eugeniae*	0	2	2	0
H	*Ptilinopus melanospila*	2	2	0	2
H′	*P. iozonus*	0	2	2	0
H′	*P. insolitus*	0	2	2	0
H′	*P. hyogaster*	0	2	2	0
H′	*P. granulifrons*	0	2	2	0
I	*Treron teysmannii*	2	1	1	0
I′	*T. floris*	0	1	1	0
I′	*T. psittacea*	0	1	1	0
J	*Treron griseicauda*	3	2	1	1
J′	*T. pompadora*	2	1	1	0
K	*Treron seimundi*	2	2	1	1
K′	*T. oxyura*	1	2	1	1
K′	*T. apicauda*	0	1	1	0
L	*Treron sphenura*	4	3	1	2
L′	*T. sieboldii*	2	2	1	1

Carotenoid-based plumage coloration occurred in about 80 of the 307 species of columbids included in the analysis (Appendix). This coloration appeared independently three times: (1) within the genus *Gallicolumba*; (2) in the genus *Treron*; and (3) in the clade *Ptilinopus* + *Drepanoptila* (Fig. 1).

Within the genus *Gallicolumba*, carotenoid colors are found in the clade including the *Gallicolumba luzonica* superspecies plus *G. rufigula* and *G. tristigmata*. In addition to the nominal form, the *G. luzonica* superspecies includes *G. criniger*, *G. platenae*, *G. menagei*, and *G. keayi*. They are globally known as ''bleeding heart doves'' because of the bright red patch in the middle of the breast. *G. rufigula* and *G. tristigmata* also exhibit a washed-yellow patch on the breast and an additional carotenoid patch on the forehead. The green plumage in the genera *Treron* and *Ptilinopus* is produced by a combination of melanin and yellow carotenoid pigments (Frank 1939, Auber 1957, Dyck 1987). In several species of the genus *Treron*, males also show orange carotenoid patches on the breast or belly, and sometimes on their crown or forehead, apart from the green coloration of the body. Carotenoid plumage patches in *Ptilinopus* species are very diverse; almost any body region may be pigmented with yellow, orange, purple, or bright red, but carotenoid patches on the crown, breast, belly, or undertail and wing coverts are particularly common.

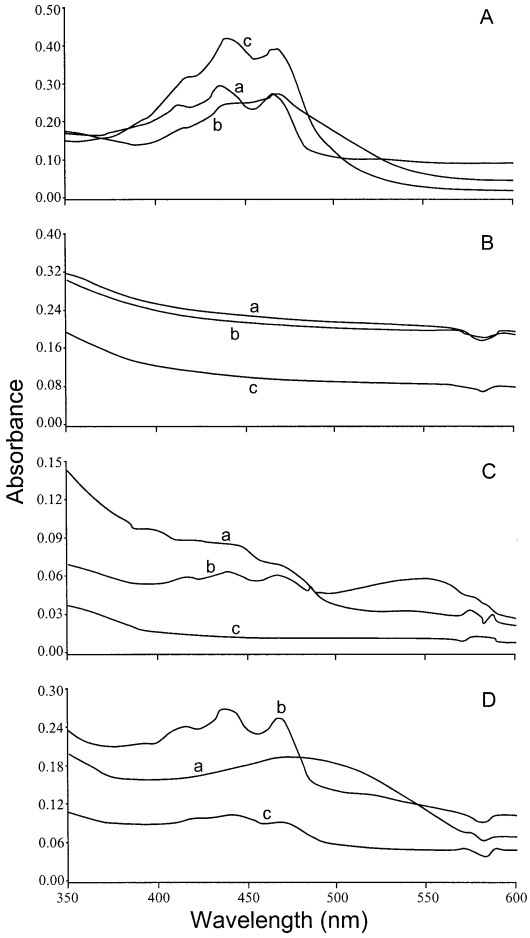

FIGURE 2. Spectra of pigment extractions of feathers belonging to various bird species. Absorbance peaks in the 400–500 nm interval indicate the presence of carotenoid pigment; where peaks are absent, the specified feather color is produced by feather structure or noncarotenoid pigment. (A) Carotenoid-pigmented feathers: a: *Carduelis magellanica* (yellow); b: *Piranga olivacea* (red); c: *Icterus galbula* (orange). (B) Carotenoid-lacking feathers: a: *Gallicolumba luzonica* (white); b: *Gallicolumba luzonica* (iridescent); c: *Gallicolumba luzonica* (brown). (C) Green feathers: a: *Treron phoenicoptera*, b: *Ptilinopus melanospila*, c: *Ducula poliocephala*. (D) Feathers from bright plumage patches: a: *Ptilinopus superbus* (purple), b: *Ptilinopus dupetithouarsii* (yellow), c: *Treron phoenicoptera* (yellow). Note that *y*-axis scales differ among graphs.

Carotenoid pigmentation always appeared in association with frugivory in doves (Fig. 1). However, the contingent states test showed that the association between characters was not statistically significant (Table 1, $G = 0.9$, $P > 0.1$). This result is a consequence of the low number of appearances of the trait. If the green plumage present in 20 species of the genus *Ducula* should prove to contain carotenoid pigments, optimization would yield six independent appearances of carotenoid plumage pigmentation, and its association with frugivory would be significant ($G = 4.4$, $P < 0.05$).

Comparisons among sister taxa did not show any association between dichromatism and carotenoid plumage coloration, neither when sexes were considered together nor separately (binomial tests: P [X $\geq$ 5] > 0.3, one tailed), which indicates that the species richer in carotenoid plumage are not always more dichromatic. In addition, no association was found between total dichromatism and carotenoid color dichromatism (binomial test P [X = 4] > 0.1, one tailed), indicating that an increase of dichromatism was not always due to carotenoid coloration.

DISCUSSION

Our study showed that carotenoid-based plumage coloration appeared at least three times in columbids, and that these events always occurred in frugivorous lineages. In contrast to Gray (1996) and Badyaev and Hill (2000), who found a positive relationship between carotenoid coloration and dichromatism in insectivorous and granivorous passerines, in which carotenoids are accessible but not superabundant in diet, we found that only frugivorous species show carotenoid pigmentation in columbids. This indicates that a more abundant source of carotenoids may be necessary for that coloration to evolve in dove plumage. Many granivorous dove species show bright-yellow or red orbital skins or beaks, but these color patches are much smaller than the ones displayed on plumage, suggesting that the expression of yellow, orange, or bright red colors in granivorous species' plumage may be constrained by the scarcity of carotenoids in their diet. Thus, it is possible that in columbids carotenoids can only be displayed if they are in excess of those needed physiologically and that the size or number of display patches increases in relation to the intake of carotenoids.

It is interesting to note that fewer than half of the frugivorous species show carotenoid plumage pigmentation. This indicates that the availability of carotenoids in diet is a necessary but not sufficient cause for the expression of that pigment in the plumage. Although the ultimate

cause for the display of carotenoid pigments in the plumage has not been directly assessed in our study, we tested the possibility that their expression is mediated by sexual selection, in which they act as an honest indicator of phenotypic quality. In order to honestly indicate phenotypic quality, carotenoids should be costly to obtain, absorb, transform, or allocate in feathers. Although carotenoids are abundant in the diet of frugivorous doves, signal honesty can still be preserved if their use as pigments implies physiological costs, such as absorption, assimilation, and chemical transformation, making carotenoid traits reflect the health of their bearers (Hill 2000). Nevertheless, we were not able to find any association between the degree of sexual dichromatism and either the amount of carotenoid pigmentation, or the dichromatism due to carotenoid coloration. It is possible that if carotenoids are superabundant in diet they are easy for individuals to express and therefore not useful as indicators of quality.

Still another possibility is that carotenoid pigmentation is sexually selected, but expressed in both sexes, either because of sexual selection on females (West-Eberhard 1983, Irwin 1994, Cunningham and Birkhead 1997) or because of genetic correlation after sexual selection on male plumage (Lande and Arnold 1985, Hill 1993). This would imply that sexual dichromatism is not an accurate indicator of sexual selection, and the actual presence of sexual selection can only be confirmed experimentally. Burley (1981) showed that in the Rock Dove (*Columba livia*) plumage coloration and pattern were selected by sexual preferences in both males and females. Although plumage colors of this sexually monomorphic species are not carotenoid based, the study shows that sexual selection on plumage coloration is present, but not associated with dichromatism. Thus, it is possible that in species that do not show sexual differences in plumage coloration, carotenoid pigments are still sexually selected.

A final possibility is that natural selection acts on plumage color and determines the patterns observed in doves. For example, predation risks and habitat effects on visual signal detectability could explain much of the variation in color observed. Martin and Badyaev (1996) found a negative correlation between nest predation and female (but not male) brightness in warblers and finches, and Burns (1998) also suggested that different predation pressures could explain the changes in female plumage in tanagers. However, dove species showing different dichromatism patterns have very similar nesting habits, and therefore similar predation risks (Martin and Badyaev 1996). This suggests that differences in plumage coloration may not be related to this factor. On the other hand, plumage colors can evolve to take advantage of the ambient spectrum of light for signaling purposes (Endler and Théry 1996), favoring the presence of bright, contrasting plumage patches (Marchetti 1993, Johnson and Lanyon 2000). Therefore, bright-yellow, orange, and red carotenoid plumage patches in doves may have evolved to increase conspicuousness in closed habitats (Bennett and Owens 2002), which would also explain why this trait is generally present in both sexes.

In conclusion, the patterns of carotenoid pigmentation in doves could not be attributed to sexual selection as determined using dichromatism. However, there may be many factors acting simultaneously on plumage coloration, making it difficult to find a strong association between variables.

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APPENDIX

Scientific names and character states for the 307 species of Columbidae included in an analysis of the association between carotenoid-pigmented plumage and diet. Absence of carotenoid pigmentation and presence of granivory = 0; carotenoid pigmentation and frugivory = 1. Missing data are indicated by ''?.''

Leptotila verreauxi (0, 0); *L. megalura* (0, 0); *L. ochraceiventris* (0, 0); *L. conoveri* (0, 0); *L. cassini* (0, 0); *L. rufaxilla* (0, 0); *L. wellsi* (0, 0); *L. plumbeiceps* (0, 0); *L. pallida* (0, 0); *L. jamaicensis* (0, 0); *L. battyi* (0, 0); *Geotrygon costaricensis* (0, 0); *G. lawrencii* (0, 0); *G. goldmani* (0, 0); *G. saphirina* (0, 0); *G. versicolor* (0, 0); *G. veraguensis* (0, 0); *G. frenata* (0, 0); *G. chrysia* (0, 0); *G. mystacea* (0, 0); *G. violacea* (0, 0); *G. montana* (0, 0); *G. linearis* (0, 0); *G. albifacies* (0, 0); *G. chiriquensis* (0, 0); *G. caniceps* (0, 0); *Starnoenas cyanocephala* (0, 0); *Zenaida aurita* (0, 0); *Z. galapagoensis* (0, 0); *Z. graysoni* (0, 0); *Z. macroura* (0, 0); *Z. auriculata* (0, 0); *Z. asiatica* (0, 0); *Z. meloda* (0, 0); *Ectopistes migratorius* (0, 0); *Metriopelia melanoptera* (0, 0); *M. ceciliae* (0, 0); *M. morenoi* (0, 0); *M. aymara* (0, 0); *Uropelia campestris* (0, 0); *Scardafella inca* (0, 0); *S. squammata* (0, 0); *Claravis mondetoura* (0, 0); *C. godefrida* (0, 0); *C. pretiosa* (0, 0); *Columbina cyanopis* (0, 0); *C. passerina* (0, 0); *C. minuta* (0, 0); *C. picui* (0, 0); *C. cruziana* (0, 0); *C. buckleyi* (0, 0); *C. talpacoti* (0, 0); *Columba livia* (0, 0); *C. rupestris* (0, 0); *C. leuconota* (0, 0); *C. guinea* (0, 0); *C. albitorques* (0, 0); *C. oenas* (0, 0); *C. eversmanni* (0, 0); *C. oliviae* (0, 0); *C. palumbus* (0, 0); *C. trocaz* (0, 1); *C. bollii* (0, 1); *C. unicincta* (0, 1); *C. junoniae* (0, 1); *C. arquatrix* (0, 1); *C. sjostedti* (0, 1); *C. thomensis* (0, 1); *C. pollenii* (0, 1); *C. hodgsonii* (0, 1); *C. albinucha* (0, 1); *C. pulchricollis* (0, 1); *C. elphinstonii* (0, 1); *C. torringtoni* (0, 1); *C. punicea* (0, 1); *C. argentina* (0, 1); *C. palumboides* (0, 1); *C. janthina* (0, 1); *C. vitiensis* (0, 1); *C. leucomela* (0, 1); *C. pallidiceps* (0, 1); *C. leucocephala* (0, 1); *C. squamosa* (0, 1); *C. speciosa* (0, 1); *C. picazuro* (0, 0); *C. corensis* (0, 1); *C. maculosa* (0, 0); *C. fasciata* (0, 1); *C. araucana* (0, 1); *C. caribaea* (0, 1); *C. cayennensis* (0, 1); *C. flavirostris* (0, 1); *C. inornata* (0, 1); *C. oenops* (0, 1); *C. plumbea* (0, 1); *C. subvinacea* (0, 1); *C. nigrirostris* (0, 1); *C. goodsoni* (0, 1); *C. delegorguei* (0, 1); *C. iriditorques* (0, 1); *C. malherbii* (0, 1); *C. jouyi* (0, ?); *C. versicolor* (0, ?); *C. larvata* (0, 0); *Nesoenas mayeri* (0, 1); *Streptopelia turtur* (0, 0); *S. lugens* (0, 0); *S. hypopyrrha* (0, 0); *S. orientalis* (0, 0); *S. bitorquata* (0, 0); *S. decaocto* (0, 0); *S. roseogrisea* (0, 0); *S. reichenowi* (0, 0); *S. decipiens* (0, 0); *S. semitorquata* (0, 0); *S. capicola* (0, 0); *S. vinacea* (0, 0); *S. tranquebarica* (0, 0); *S. picturata* (0, 0); *S. chinensis* (0, 0); *S. senegalensis* (0, 0); *Macropygia magna* (0, 1); *M. tenuirostris* (0, 1); *M. unchall* (0, 1); *M. amboinensis* (0, 1); *M. phasianella* (0, 1); *M. rufipennis* (0, 1); *M. nigrirostris* (0, 1); *M. mackinlayi* (0, 1); *M. ruficeps* (0, 1); *M. emiliana* (0, 1); *Reinwardtoena reinwardtii* (0, 1); *R. browni* (0, 1); *R. crassirostris* (0, 1); *Turacoena manadensis* (0, 1); *T. modesta* (0, 1); *Turtur chalcospilos* (0, 0); *T. abyssinicus* (0, 0); *T. afer* (0, 0); *T. tympanistria* (0, 0); *T. brehmeri* (0, 0); *Oena capensis* (0, 0); *Chalcophaps indica* (0, 0); *C. stephani* (0, 0); *Henicophaps foersteri* (0, 1); *H. albifrons* (0, 1); *Phaps chalcoptera* (0, 0); *P. elegans* (0, 0); *P. histrionica* (0, 0); *Ocyphaps lophotes* (0, 0); *Geophaps plumifera* (0, 0); *G. scripta* (0, 0); *G. smithii* (0, 0); *Petrophassa rufipennis* (0, 0); *P. albipennis* (0, 0); *Geopelia cuneata* (0, 0); *G. striata* (0, 0); *G. humeralis* (0, 0); *G. mauguei* (0, 0); *G. placida* (0, 0); *Leucosarcia melanoleuca* (0, 0); *Caloenas nicobarica* (0, 1); *Gallicolumba luzonica* (1, 1); *G. criniger* (1, 1); *G. platenae* (1, 1); *G. keayi* (1, 1); *G. menagei* (1, 1); *G. rufigula* (1, 1); *G. tristigmata* (1, 1); *G. jobiensis* (0, 1); *G. kubaryi* (0, 1); *G. erythroptera* (0, 1); *G. xanthonura* (0, 1); *G. stairi* (0, 1); *G. sanctaecrucis* (0, 1); *G. salamonis* (0, 1); *G. rubescens* (0, 1); *G. beccarii* (0, 1); *G. canifrons* (0, 1); *G. hoedtii* (0, 1); *Trugon terrestris* (0, 1); *Microgoura meeki* (0, ?); *Otidiphaps nobilis* (0, 1); *Goura cristata* (0, 1); *G. scheepmakeri* (0, 1); *G. victoria* (0, 1); *Didunculus strigirostris* (0, 1); *Phapitreron leucotis* (0, 1); *P. amethystina* (0, 1); *P. cinereiceps* (0, 1); *Treron fulvicollis* (1, 1); *T. olax* (1, 1); *T. vernans* (1, 1); *T. bicincta* (1, 1); *T. pompadora* (1, 1); *T. curvirostra* (1, 1); *T. griseicauda* (1, 1); *T. teysmannii* (1, 1); *T. floris* (1, 1); *T. psittacea* (1, 1); *T. capellei* (1, 1); *T. phoenicoptera* (1, 1); *T. waalia* (1, 1); *T. australis* (1, 1); *T. calva* (1, 1); *T. pembaensis* (1, 1); *T. sanctithomae* (1, 1); *T. apicauda* (1, 1); *T. oxyura* (1, 1); *T. seimundi* (1, 1); *T. sphenura* (1, 1); *T. sieboldii* (1, 1); *T. formosae* (1, 1); *Ptilinopus cinctus* (1, 1); *P. alligator* (1, 1); *P. dohertyi* (1, 1); *P. porphyreus* (1, 1); *P. marchei* (1, 1); *P. merrilli* (1, 1);

P. fischeri (1, 1); *P. occipitalis* (1, 1); *P. jambu* (1, 1); *P. bernsteinii* (1, 1); *P. magnificus* (1, 1); *P. leclancheri* (1, 1); *P. subgularis* (1, 1); *P. victor* (1, 1); *P. luteovirens* (1, 1); *P. layardi* (1, 1); *P. pulchellus* (1, 1); *P. coronulatus* (1, 1); *P. monacha* (1, 1); *P. eugeniae* (1, 1); *P. porphyraceus* (1, 1); *P. pelewensis* (1, 1); *P. greyii* (1, 1); *P. richardsii* (1, 1); *P. perousii* (1, 1); *P. rarotongensis* (1, 1); *P. roseicapilla* (1, 1); *P. regina* (1, 1); *P. purpuratus* (1, 1); *P. huttoni* (1, 1); *P. dupetithouarsii* (1, 1); *P. mercierii* (1, 1); *P. insularis* (1, 1); *P. ornatus* (1, 1); *P. perlatus* (1, 1); *P. tannensis* (1, 1); *P. aurantiifrons* (1, 1); *P. wallacii* (1, 1); *P. superbus* (1, 1); *P. rivoli* (1, 1); *P. solomonensis* (1, 1); *P. viridis* (1, 1); *P. melanospila* (1, 1); *P. nanus* (1, 1); *P. granulifrons* (1, 1); *P. hyogaster* (1, 1); *P. insolitus* (1, 1); *P. iozonus* (1, 1); *Drepanoptila holosericea* (1, 1); *Alectroenas madagascariensis* (0, 1); *A. sganzini* (0, 1); *A. pulcherrima* (0, 1); *Ducula poliocephala* (0, 1); *D. forsteni* (0, 1); *D. radiata* (0, 1); *D. mindorensis* (0, 1); *D. carola* (0, 1); *D. zoeae* (0, 1); *D. badia* (0, 1); *D. lacernulata* (0, 1); *D. cineracea* (0, 1); *D. rubricera* (0, 1); *D. myristicivora* (0, 1); *D. pacifica* (0, 1); *D. aurorae* (0, 1); *D. oceanica* (0, 1); *D. galeata* (0, 1); *D. rufigaster* (0, 1); *D. basilica* (0, 1); *D. finschii* (0, 1); *D. chalconota* (0, 1); *D. aenea* (0, 1); *D. perspicillata* (0, 1); *D. concinna* (0, 1); *D. pistrinaria* (0, 1); *D. whartoni* (0, 1); *D. rosacea* (0, 1); *D. pickeringii* (0, 1); *D. latrans* (0, 1); *D. brenchleyi* (0, 1); *D. bakeri* (0, 1); *D. goliath* (0, 1); *D. mullerii* (0, 1); *D. melanochroa* (0, 1); *D. pinon* (0, 1); *D. bicolor* (0, 1); *D. spilorrhoa* (0, 1); *D. luctuosa* (0, 1); *Lopholaimus antarcticus* (0, 1); *Hemiphaga novaeseelandiae* (0, 1); *Cryptophaps poecilorrhoa* (0, 1); *Gymnophaps albertisii* (0, 1); *G. mada* (0, 1); *G. solomonensis* (0, 1).