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A PHYLOGENETIC PERSPECTIVE ON THE EVOLUTION OF SEXUAL DICHROMATISM IN TANAGERS (THRAUPIDAE): THE ROLE OF FEMALE VERSUS MALE PLUMAGE

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Abstract.—The evolution of sexual dichromatism in tanagers (family Thraupidae) was studied from a phylogenetic perspective using a molecular-based phylogeny. Mapping patterns of sexual dimorphism in plumage onto the phylogeny reveals that changes in female plumage occur more frequently than changes in male plumage. Possible explanations for this pattern include sexual selection acting on female plumage and natural selection for background matching. The results of this study and other recent phylogenetic and comparative studies suggest that factors affecting female plumage are important in shaping patterns of sexual dimorphism.

Key words.—Plumage color, sexual dichromatism, sexual dimorphism, sexual selection, tanager, Thraupidae.

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In many species males are often more brightly colored and have more elaborate secondary sexual characteristics than females. Many theories, which are not necessarily mutually exclusive of each other (Butcher and Rohwer 1989), have been proposed to explain such sexual dimorphism. Some of these include sexual selection (Darwin 1871; Sibley 1957; Selander 1972; Kirkpatrick et al. 1990), differential signaling of males and females to predators (Baker and Parker 1979; Götmark 1992, 1993), and selection for less conspicuous females (Wallace 1889; Beecher 1950; Skutch 1957). The most widely accepted of these theories argues that males are more brightly colored than females because of sexual selection (Darwin 1871). In birds, bright male plumage evolves either because it is preferred by females (intersexual selection) or males with bright plumage outcompete other males (intrasexual selection). Thus, in species where sexual selection is stronger (such as polygynous species), dimorphism is expected to be more pronounced (Darwin 1871; Payne 1984). Wallace (1889) disagreed with Darwin over the importance of sexual selection in shaping patterns of sexual dimorphism. Whereas Darwin emphasized the importance of sexual selection, Wallace felt that sexual dimorphism was more the result of natural selection for cryptically colored females. Wallace's ideas stemmed in part from his observations on bird coloration and nesting habits. Wallace (1889) noted that many species of birds that are monomorphic and have conspicuous plumage nest in cavities, while species that nest in the open have drably colored females.

Many studies have investigated what factors may contribute to maintaining sexual plumage dimorphism in birds, but few have actually been able to test different hypotheses about the evolutionary origins of dimorphism. Most studies of sexual dichromatism in birds involve field observations and experimental manipulations of individual species. These types of studies provide insight into the current functions of plumage dimorphism. Many have provided conclusive evidence that females prefer more conspicuously colored males or that more brightly plumaged males perform better in intrasexual competition (e.g., Smith 1972; Collias et al. 1979; Hill 1990; see review in Andersson 1994). Although studies such as these provide important information on what factors may maintain dichromatism, they do not provide information on the evolutionary origin of sexual dichromatism. Phylogenetic hypotheses provide the essential historical framework needed for addressing evolutionary patterns and processes (Brooks and McLennan 1991; Harvey and Pagel 1991). Mapping the evolutionary history of a trait onto a phylogeny (Maddison et al. 1984) can provide information about how the trait has changed throughout the history of a group. Thus, comparative phylogenetic studies and behavioral studies of individual species complement one another; comparative studies provide information on the origin of a trait and behavioral studies provide information on current function and maintenance of a trait.

A few studies have examined sexual dichromatism in birds within the context of a phylogeny. After controlling for phylogenetic effects, Höglund (1989) was unable to find a correlation between polygynous, lekking birds and sexual dimorphism in plumage (but see Oakes 1992). By tracing sexual dichromatism onto the phylogenies of two lineages of blackbirds, Björklund (1991) identified two cases where sexual dichromatism resulted from a loss of female brightness rather than a gain in male brightness. Irwin (1994) found that polygynous species of blackbirds were more often dimorphic in plumage than their nonpolygynous relatives. Contrary to expectations, however, this study also found that changes in female plumage were more common than modifications of male plumage. Thus, Irwin (1994) concluded that social selection on females has played a greater role in the evolution of plumage dichromatism than has sexual selection on males. Martin and Badyaev (1996) showed that predation at the nest site was correlated with female but not male plumage in two lineages of birds, wood warblers (Parulidae) and finches (Fringillidae). They found that female plumage was not as bright in those species that nested in areas with high predation. Two studies (Scott and Clutton-Brock 1989; Møller and Birkhead 1994) have shown a correlation between mating system and dichromatism when mating system is clearly de-

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fined (i.e., seasonal vs. life-long monogamy or considering extrapair paternity). Further studies are needed to help clarify factors affecting both male and female plumage that are important to the evolution of sexual dichromatism.

In this study, I examine the evolution of sexual dimorphism in plumage in tanagers (family Thraupidae) using recent phylogenies (Burns 1997) for this group. Tanagers are a large group of 242 species distributed mainly in South America and Central America. Although the bright and conspicuous plumage of species in this family is well known, many tanagers have more subtle, less obvious plumage coloration (Isler and Isler 1987). Roughly half (48%) of tanager species show marked sexual dimorphism in plumage. In all cases where species are dichromatic, males are more conspicuously colored than females. In contrast to differences in plumage, differences between males and females in overall body size are either absent or very small (Isler and Isler 1987). In general, tanagers show little variation in their breeding biology. Typically, tanagers build an open cup nest, eggs are incubated by the female, and both males and females feed nestlings. Species in this family are largely believed to be monogamous because polygyny has been observed only on a few occasions (Skutch 1989). Thus, if tanager species are largely monogamous and do not experience obvious differences in the intensity of sexual selection, it is intriguing that many species of tanagers are sexually dimorphic and many others are sexually monomorphic. Although monogamous birds can exhibit dichromatism as a result of sexual selection, they are not expected to have the degree of exaggeration of traits seen in many polygynous species (Kirkpatrick et al. 1990).

In this study, I first examine the pattern of evolution of sexual dichromatism within tanagers using the phylogeny of the group. Namely, I determine whether tanagers are derived from monomorphic or dimorphic taxa and the number of times sexual dimorphism in plumage has evolved within this lineage. I also determine the frequency of different kinds of changes in plumage dichromatism (e.g., how often do lineages in which both sexes have drably colored plumage evolve into dimorphic lineages with males more colorful than females?). Given this pattern of evolution of sexual dichromatism, I then evaluate different hypotheses that have been proposed to explain the evolution of sexual dichromatism.

METHODS

The phylogenies used in this study (Burns 1997) are based on 1045 base pairs of cytochrome *b* sequence data from representatives of 47 tanager genera. These trees were constructed using parsimony and several different weighting schemes. Trees were weighted by giving third-position transitions one-sixth the weight of other characters (TVW), using successive approximations with characters reweighted using the rescaled consistency index (SACI), and giving all characters equal weight (EQW). The TVW analysis resulted in six most-parsimonious trees, the EQW analysis resulted in two most-parsimonious trees, and the SACI analysis resulted in one tree. As a conservative test of the hypotheses being evaluated in this study, I used all nine of these trees to investigate the evolution of sexual dichromatism.

In this paper, I will follow Butcher and Rohwer (1989) and use the term "colorful" to refer to birds that are either distinctive or conspicuous against the habitat in which they are found. I will use the term "drab" to refer to individuals that are less conspicuous and distinctive within the context of their habitat. Within Thraupidae, some taxa are sexually dimorphic in plumage and some are monomorphic. In dimorphic taxa, males are always relatively more colorful than females. Additionally, there is variation among species and sexes in degree of colorfulness. Thus, five basic patterns of plumage morphism can be recognized within Thraupidae: (1) monomorphic, both sexes drab; (2) monomorphic, both sexes colorful; (3) dimorphic, male colorful and female drab; (4) dimorphic, both sexes drab; and (5) dimorphic, both sexes colorful.

Prior to knowledge of the phylogeny of Thraupidae, I categorized species of tanagers into one of the five categories of plumage listed above. Assessment of plumage colorfulness and sexual dichromatism was made with the help of museum specimens, experience with many species in the field, and the use of several references (primarily Isler and Isler 1987; but also Dunning 1982; Ridgely and Tudor 1989; Sick 1993). In total, museum specimens of approximately 61% of the species representing 71% of the genera were examined. Assignment of females into the categories drab and colorful was made in the context of all individuals being studied, not only in the context of the male of that particular species. In categorizing an individual as colorful or drab, I considered the habitat of the bird in question to be important. Birds classified as drab include individuals with brown, gray, dull yellow, and dull yellowish green plumage. Drab birds also include individuals with green or yellowish green plumage that would be considered bright except in the context of that species' dark forest or tropical canopy habitat (see Endler 1990). Birds classified as colorful include individuals with iridescent plumage, entirely black plumage, bold black-and-white patterns, carotenoid pigment colors (oranges, reds, yellows), and otherwise drab birds with bright color patches. The term "colorful" is somewhat misleading because entirely black birds and black and white patterned birds will be identified as colorful in this study.

Parsimonious reconstruction of ancestral character states (Maddison et al. 1984) as implemented in MacClade 3.0 (Maddison and Maddison 1992) was used to infer whether basal tanagers were dimorphic or monomorphic. Character-state reconstruction was also used to determine what types of transformations in plumage dimorphism occur. Specifically, I used character-state reconstruction to determine the number of times each of the possible transformations in plumage types occurred. Because I have categorized plumage into five different types, 20 possible transformations are possible (see Table 1 for a list of all possible transformations). Determining the ancestral condition in tanagers and the types of shifts that have taken place are essential to the discussion of the evolution of sexual dimorphism in plumage because they provide the necessary framework from which questions about the origin of dichromatism should be addressed. For example, we can only ask why males have evolved colorful plumage if the ancestral condition shows that males had drab plumage.

TABLE 1. Average number of transitions between different plumage types based on all equivocal reconstructions. Number of unambiguous changes and equivocal steps are given in parentheses. Topologies with identical reconstructions are merged into one column. *P* refers to the probability that the greater average number of changes in female plumage versus male plumage is observed by chance alone. Key to transition types: 1, monomorphic and drab; 2, monomorphic and colorful; 3, dimorphic with colorful male and drab female; 4, dimorphic with both sexes drab; 5, dimorphic with both sexes colorful.

		Phylogeny			
	Transition type	EQW 1 and 2	TVW 1, 2, 5, and 6	TVW 3 and 4	SACI
Change in female plumage, but not male plumage					
Change affects dimorphism					
	2 to 3	2.7 (1)	2.5 (1)	1.8 (0)	3.4 (1)
	3 to 2	6.1 (3)	5.7 (4)	6.2 (3)	5.8 (2)
Change does not affect dimorphism					
	3 to 5	6.7 (5)	7.3 (5)	7.6 (5)	5.7 (3)
	5 to 3	0.8 (0)	0 (0)	0 (0)	0.6 (0)
Change in male plumage, but not female plumage					
Change affects dimorphism					
	1 to 3	0.5 (0)	0.5 (0)	0.8 (0)	0.5 (0)
	3 to 1	4.4 (3)	3.7 (3)	4.2 (3)	3.8 (3)
Change does not affect dimorphism					
	3 to 4	2.8 (2)	3 (3)	3.3 (3)	3 (3)
	4 to 3	0 (0)	0 (0)	0 (0)	0 (0)
Changes in both sexes					
	1 to 2	1.5 (0)	2 (1)	2.3 (1)	0.9 (0)
	1 to 5	0.8 (0)	0.3 (0)	0.3 (0)	1.5 (1)
	2 to 1	7.4 (2)	7 (3)	6.3 (4)	7.7 (4)
	2 to 4	1.6 (0)	2 (1)	1.8 (1)	1.5 (1)
	4 to 2	0.3 (0)	0 (0)	0 (0)	0 (0)
	5 to 1	0.4 (0)	0.3 (0)	0.3 (0)	0 (0)
	4 to 5	0 (0)	0 (0)	0 (0)	0 (0)
	5 to 4	0 (0)	0 (0)	0 (0)	0 (0)
Neither sex changes brightness					
	1 to 4	0.7 (0)	0 (0)	0 (0)	0.5 (0)
	2 to 5	2.4 (1)	2.3 (1)	2.1 (1)	2.8 (1)
	4 to 1	0.3 (0)	0 (0)	0 (0)	0 (0)
	5 to 2	0.6 (0)	0.3 (0)	0.3 (0)	0.4 (0)
Equivocal changes		(21)	(15)	(16)	(20)
Total number of steps		38	37	37	39
P (changes in male versus female plumage)		0.076	0.047	0.076	0.047

RESULTS

Mapping the evolution of sexual dimorphism in plumage onto the cytochrome *b* phylogenies of Thraupidae (one tree shown in Fig. 1) reveals that tanagers are descended from an ancestor that was dimorphic in plumage with colorful males and drab females. All other plumage types subsequently evolved from this state. Therefore, many species of tanagers are dimorphic in plumage because dimorphism was retained from a more ancestral lineage. For other species, dimorphism originated more recently from monomorphic taxa that were derived themselves from dimorphic lineages.

Reconstructing changes between plumage categories reveals that there are several equally parsimonious, equivocal reconstructions on each of the phylogenies used in this study. Therefore, in addition to looking at the number of unambiguous transformations between each plumage type, I also looked at the mean number of each type of transformation when all equivocal reconstructions were averaged. Of the 20 specific types of plumage transformations possible (Table 1), two of the most common transitions that occur involve a change between two different types of dimorphism. Specifically, these transitions involve a change from dimorphic taxa in which males are colorful and females are drab to either dimorphic taxa in which both sexes are colorful (see Table 1: 3 to 5 transitions) or monomorphic taxa in which both sexes are colorful (3 to 2 transitions). In both cases, female plumage evolves from drab to colorful. Changes from monomorphic taxa with both sexes colorful to monomorphic taxa with both sexes drab (2 to 1 transitions) are also very common. However, in general, changes in which only males or only females change in plumage colorfulness are more common than changes in which both or neither sex changes in overall colorfulness (Table 1).

In all trees examined except the SACI tree, there is a greater number of unequivocal changes in female plumage than in male plumage. In the SACI tree, there is an equal number of unequivocal changes involving male and female plumage. When all possible equivocal changes are calculated, the average number of changes in female plumage is always higher than the average number of changes in male plumage in all trees. In fact, the average number of changes in female plumage is at least twice the average number of changes of male plumage. The probability that this pattern occurs by chance is low (binomial test: $P = 0.047$ for five of the trees; $P = 0.076$ for the remaining four trees; Table 1).

DISCUSSION

If sexual selection by female choice or male-male competition plays a critical role in the evolution of sexual di-

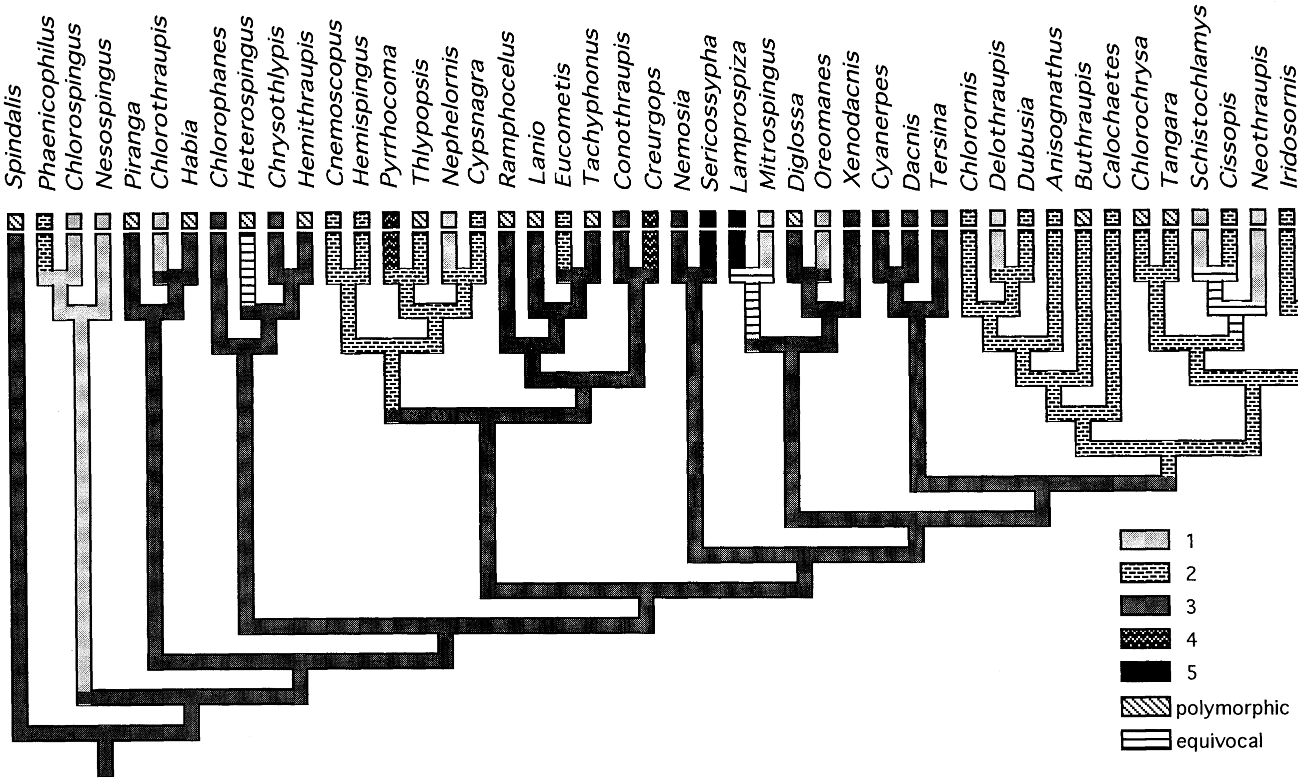

FIG. 1. Sexual dimorphism in plumage mapped onto one of the cytochrome b phylogenies of Thraupidae. Tree shown is one of the most-parsimonious reconstructions obtained when third position transitions were down-weighted relative to other characters (TVW tree 1). Key: 1, monomorphic and drab; 2, monomorphic and colorful; 3, dimorphic with colorful male and drab female; 4, dimorphic with both sexes drab; 5, dimorphic with both sexes colorful; polymorphic, more than one type of plumage dimorphism present; equivocal, character state assignment is uncertain.

chromatism in birds, it is interesting that tanagers show variation in degree of sexual dichromatism but have similar, monogamous mating systems. Other lineages of birds show similar contradictions in the observed pattern of sexual dichromatism versus what would be predicted if sexual selection has a strong influence on the evolution of plumage dichromatism. Like tanagers, many species of wood warblers (Parulidae) and finches (Fringillidae) are also apparently monogamous, but dimorphic in plumage. In hummingbirds (family Trochilidae), all species are polygynous, yet many species are monomorphic and female plumage can show considerable variability (Bleiweiss 1992). In addition, polygynous, lekking species are not more likely to be sexually dimorphic in plumage when the effects of phylogeny are controlled (Höglund 1989). Finally, in a study of European passerines, Møller (1986) found that polygynous species were not more often sexually dimorphic in plumage than monogamous species.

The pattern of evolution of different dichromatism types in tanagers (Fig. 1) suggests that what needs to be explained is not why males evolve colorful plumage, but why female plumage has changed so frequently. Two of the most common types of transitions in plumage on all of the trees investigated involve male plumage remaining the same, but female plumage increasing in colorfulness (3 to 5 and 3 to 2 transitions, see Table 1). The typical transition predicted by selection for colorful males (monomorphic taxa with both sexes drab evolving into dimorphic taxa with colorful male and drab female, 1 to 3 transitions) occurs only rarely. Thus, to understand the origin of patterns of sexual dichromatism among tanagers, we need to understand why females have evolved more colorful plumage in many species.

One possible explanation for the evolution of colorful female plumage is that the presence of such plumage is simply a correlated response to intense sexual selection for colorful male plumage (Lande and Arnold 1985, Hill 1993). That is, females may have colorful plumage because sexual selection for colorful ornaments in males is great, while selection against the same colorful ornaments in females is weak. However, Price and Birch (1996) showed that evolutionary changes between monomorphism and dimorphism are frequent in passerine birds and are unlikely to be constrained by an absence of genetic variation. The pattern of evolution of dimorphism types in tanagers is consistent with the results of Price and Birch (1996) and argues against female plumage evolving as a correlated response to factors affecting male plumage. If colorful female plumage evolves in concert with colorful male plumage, transitions in which both sexes increase in colorfulness should be common (i.e., 1 to 2, 1 to 5, and 4 to 5 transitions). However, these types of plumage transitions are infrequent in tanagers (Table 1). Thus, female plumage has changed independently of male plumage throughout the history of this group, and alternative explanations for the evolution of female plumage need to be considered.

Colorful female plumage could be the result of sexual selection acting on female plumage in the form of female-female competition or male choice. Social selection (West-Eberhard 1983) in the form of sexual selection on females has been demonstrated in several avian species (Cunningham and Birkhead 1997). Females with more conspicuous plumage than other females of the same species have been shown to be more aggressive in some species: pinyon jays (*Gymnorhinus cyanocephalus*, Johnson 1988), some hummingbirds (Bleiwess 1985, 1992), and in capuchinbirds (*Perissocephalus tricolor*, Trail 1990). Additionally, males have been shown experimentally to prefer brighter females in at least two species: pinyon jays (Johnson 1988) and house finches (*Carpodacus mexicanus*, Hill 1993). Irwin (1994) invoked social-selection arguments such as these to explain plumage evolution in blackbirds (Icteridae). Within blackbirds, Irwin (1994) found that changes in female plumage are more common than changes in male plumage across the phylogeny. Although the current study looked at patterns of change among a different lineage of birds, similar conclusions were reached. This suggests that a more general explanation for the evolution of plumage dimorphism should incorporate social-selection pressures on female plumage.

Alternatively, changes in female plumage in tanagers may be the result of different degrees of nest predation. Females that nest in areas exposed to predators may evolve less conspicuous plumage than species that nest in more concealed areas (Wallace 1889). In two lineages closely related to tanagers (Parulidae and Fringillidae), Martin and Badyaev (1996) identified such a relationship. When considering phylogenetic relationships of the species involved, Martin and Badyaev (1996) demonstrated a negative correlation between nest predation and female (but not male) plumage brightness. In addition to being closely related to Parulidae and Fringillidae, tanagers also share similar monogamous mating systems and similar degrees of male parental care. Tanager nests have been described in a variety of habitats, suggesting the variation in degree of exposure to predators needed for nest predation to influence plumage coloration. The ecological and evolutionary similarities of warblers, finches, and tanagers (together with the frequent changes in female plumage observed within tanagers) suggest that similar mechanisms may influence the evolution of plumage coloration in these three lineages.

Despite numerous studies investigating the evolution of sexual dimorphism in plumage, a comprehensive theory remains elusive. In reality, a mosaic of factors probably affect the evolution of sexual dichromatism as well as the evolution of monomorphic plumage. The prevailing view in the literature is that sexual selection for male plumage is the sole factor responsible for the evolution of sexual dimorphism. This viewpoint is so pervasive that sexual dimorphism is often assumed to represent degree of sexual selection (e.g., Hamilton and Zuk 1982; Møller and Birkhead 1994), and oftentimes simply the presence of sexual dimorphism is used as a proxy for sexual selection itself (e.g., Barraclough et al. 1995; McLain et al. 1995). The results of this study and other recent phylogenetic and comparative studies (Höglund 1989; Trail 1990; Björklund 1991; Irwin 1994; Martin and Badyaev 1996) suggest that sexual selection, as traditionally thought of as affecting only male plumage, may have a less important role in shaping patterns of sexual dimorphism in plumage than previously suggested. Other factors such as nest predation and sexual selection on female plumage need to be considered as well.

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LITERATURE CITED

ANDERSSON, M. 1994. Sexual selection. Princeton Univ. Press, Princeton, NJ.

BAKER, R. R., AND G. A. PARKER. 1979. The evolution of bird coloration. Philos. Trans. R. Soc. Lond. B Biol. Sci. 287:63–130.

BARRACLOUGH, T. G., P. H. HARVEY, AND S. NEE. 1995. Sexual selection and taxonomic diversity in passerine birds. Proc. R. Soc. Lond. B Biol. Sci. 259:211–215.

BEECHER, W. J. 1950. Convergent evolution in the American orioles. Wilson Bull. 62:51–86.

BJORKLUND, M. 1991. Coming of age in fringillid birds: heterochrony in the ontogeny of secondary sexual characters. J. Evol. Biol. 4:83–92.

BLEIWESS, R. 1985. Iridescent polychromatism in a female hummingbird: is it related to feeding strategies? Auk 102:701–713.

———. 1992. Widespread polychromatism in female sunangel hummingbirds (*Heliangelus*: Trochilidae). Biol. J. Linn. Soc. 45: 291–314.

BROOKS, D. R., AND D. H. MCLENNAN. 1991 Phylogeny, ecology, and behavior: a research program in comparative biology. Univ. of Chicago Press, Chicago.

BURNS, K. J. 1997. Molecular systematics of tanagers (Thraupinae): evolution and biogeography of a diverse radiation of Neotropical birds. Mol. Phylogenet. Evol. 8:334–348.

BUTCHER, G. S., AND S. ROHWER. 1989. The evolution of conspicuous and distinctive coloration for communication in birds. Curr. Ornithol. 6:51–107.

COLLIAS, E. C., N. E. COLLIAS, C. H. JACOBS, F. MCALARY, AND J. T. FUJIMOTO. 1979. Experimental evidence for facilitation of pair formation by bright color in weaverbirds. Condor 81:91–93.

CUNNINGHAM, E., AND T. BIRKHEAD. 1997. Female roles in perspective. Trends Ecol. Evol. 12:337–338.

DARWIN, C. 1871. The descent of man and selection in relation to sex. J. Murray, London.

DUNNING, J. S. 1982. South American land birds a photographic aid to identification. Harrowood Books, Newton Square, PA.

ENDLER, J. A. 1990. On the measurement and classification of colour in studies of animal colour patterns. Biol. J. Linn. Soc. 41:315–352.

GÖTMARK, F. 1992. Anti-predator effect of conspicuous plumage in a male bird. Anim. Behav. 44:51–55.

———. 1993. Conspicuous coloration in male birds: favoured by predation in some species, disfavoured in others. Proc. R. Soc. Lond. B Biol. Sci. 253:143–146.

HAMILTON, W. D., AND M. ZUK. 1982. Heritable true fitness and bright birds: a role for parasites? Science 218:384–386.

HARVEY, P. H., AND M. D. PAGEL. 1991. The comparative method in evolutionary biology. Oxford Univ. Press, Oxford.

HILL, G. E. 1990. Female house finches prefer colourful males: sexual selection for a condition-dependent trait. Anim. Behav. 40:563–572.

———. 1993. Male mate choice and the evolution of female coloration in the house finch. Evolution 47:1515–1525.

HÖGLUND, J. 1989. Size and plumage dimorphism in lek-breeding birds: a comparative analysis. Am. Nat. 134:72–87.

IRWIN, R. E. 1994. The evolution of plumage dichromatism in the New World blackbirds: social selection on female brightness? Am. Nat. 144:890–907.

ISLER, M. L., AND P. R. ISLER. 1987. The tanagers. Smithsonian Institution Press, Washington, DC.

JOHNSON, K. 1988. Sexual selection in pinyon jays. II. Male choice and female-female competition. Anim. Behav. 36:1048–1053.

KIRKPATRICK, M., T. PRICE, AND S. J. ARNOLD. 1990. The Darwin-Fisher theory of sexual selection in monogamous birds. Evolution 44:180–193.

LANDE, R., AND S. J. ARNOLD. 1985. Evolution of mating preference and sexual dimorphism. J. Theor. Biol. 117:651–664.

MCLAIN, D. K., M. P. MOULTON, AND T. P. REDFEARN. 1995. Sexual selection and the risk of extinction of introduced birds on oceanic islands. Oikos 74:27–34.

MADDISON, W. P., AND D. R. MADDISON. 1992. MacClade: analysis of phylogeny and character evolution. Ver. 3.0. Sinauer, Sunderland, MA.

MADDISON, W. P., M. J. DONOGHUE, AND D. R. MADDISON. 1984. Outgroup analysis and parsimony. Syst. Zool. 33:83–103.

MARTIN, T. E., AND A. V. BADYAEV. 1996. Sexual dichromatism in birds: importance of nest predation and nest location for females versus males. Evolution 50:2454–2460.

MØLLER, A. P. 1986. Mating systems among European passerines: a review. Ibis 128:234–250.

MØLLER, A. P., AND T. R. BIRKHEAD. 1994. The evolution of plumage brightness in birds is related to extrapair paternity. Evolution 48:1089–1100.

OAKES, E. J. 1992. Lekking and the evolution of sexual dimorphism in birds: Comparative approaches. Am. Nat. 140:665–684.

PAYNE, R. B. 1984. Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. Ornithological Monographs no. 33.

PRICE, T., AND G. L. BIRCH. 1996. Repeated evolution of sexual color dimorphism in passerine birds. Auk 113:842–848.

RIDGELY, R. S., AND G. TUDOR. 1989. Birds of South America. Vol. 1. The oscine passerines. Univ. of Texas Press, Austin, TX.

SCOTT, D. K., AND T. H. CLUTTON-BROCK. 1989. Mating systems, parasites and plumage dimorphism in waterfowl. Behav. Ecol. Sociobiol. 26:261–273.

SELANDER, R. K. 1972. Sexual selection and dimorphism in birds. Pp. 180–230 *in* B. Campbell, ed. Sexual selection and the descent of man 1871–1971. Aldine, Chicago.

SIBLEY, C. G. 1957. The evolution and taxonomic significance of sexual dimorphism and hybridization in birds. Condor 59:166–191.

SICK, H. 1993. Birds in Brazil. Princeton Univ. Press, NJ.

SKUTCH, A. F. 1957. Migratory and resident warblers in Central America. Pp. 275–285 *in* L. Griscom and A. Sprunt, eds. The warblers of America. Devin-Adair, New York.

———. 1989. Life of the tanager. Comstock, Ithaca, NY.

SMITH, D. G. 1972. The role of epaulets in the red-winged blackbird, *Agelius phoeniceus* social system. Behaviour 41:251–267.

TRAIL, P. W. 1990. Why should lek-breeders be monomorphic? Evolution 44:1837–1852.

WALLACE, A. R. 1889. Darwinism: an exposition of the theory of natural selection with some of its applications. Macmillan, London.

WEST-EBERHARD, M. J. 1983. Sexual selection, social competition and speciation. Q. Rev. Biol. 58:155–183.

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INTROGRESSIVE HYBRIDIZATION AND NONCONCORDANT EVOLUTIONARY HISTORY OF MATERNAL AND PATERNAL LINEAGES IN NORTH AMERICAN DEER

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Abstract.—Introgressive hybridization between mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) was studied using sequence analysis of the paternally inherited, Y-linked, Zfy gene. The distribution of Zfy genotypes indicate that male white-tailed deer disperse into the range of mule deer and successfully breed with mule deer does. In western Texas, F_1 hybrids are rare, but a relatively high proportion of backcross individuals was observed. Phylogenetic analysis of Zfy among white-tailed, mule, and black-tailed deer was consistent with traditional systematic placement of the latter two being sister-taxa, whereas previous mtDNA studies suggested mule and white-tailed deer were sister taxa.

Key words.—Deer, DNA, gene flow, hybridization, *Odocoileus*, paternal inheritance, Zfy, zinc finger.

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White-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and black-tailed deer (*O. hemionus*) are among the most broadly distributed and economically important species of wildlife in North America (Teer 1984). The two species are well distinguished by morphology, habitat-use patterns, behavior, and allozymes (Wishart 1980; Geist 1981;