Evolution, 50(6), 1996, pp. 2454–2460

SEXUAL DICHROMATISM IN BIRDS: IMPORTANCE OF NEST PREDATION AND NEST LOCATION FOR FEMALES VERSUS MALES

THOMAS E. MARTIN[1] AND ALEXANDER V. BADYAEV[2]
[1]*US National Biological Service, Montana Cooperative Wildlife Research Unit,*
University of Montana, Missoula, Montana 59812
E-mail: tmartin@selway.umt.edu
[2]*Department of Biological Sciences, University of Montana, Missoula, Montana 59812*
E-mail: abadyaev@selway.umt.edu

Abstract.—Examinations of variation in plumage dichromatism in birds have focused on male plumage brightness and largely neglected variation in female plumage brightness. Nest predation previously was concluded to constrain male brightness and thereby reduce dimorphism in ground-nesting birds based on an incorrect assumption that nest predation is greater for ground nests. Correlations of plumage brightness and dichromatism with nest predation have never been tested directly and we do so here with data for warblers (Parulinae) and finches (Carduelinae). We show that male plumage brightness varies among nest heights, but in a pattern that is not correlated with nest predation. Female plumage brightness also varies among nest heights, but in a pattern that differs from males, and one in which variation in female plumage brightness was negatively correlated with nest predation. These results suggest that nest predation may place greater constraints on female than male plumage brightness, at least in taxa where only females incubate eggs and brood young. These results also show that female plumage patterns vary at least partly independently of male patterns and emphasize the need to include consideration of both female and male plumage variation in tests of plumage dimorphism. Plumage dimorphism differs between ground and off-ground nesters as previously described and, if anything, the relationship between plumage dimorphism and nest predation was positive rather than negative as previously argued.

Key words.—Carduelinae, nest predation, Parulinae, sexual dichromatism, sexual dimorphism, sexual selection.

Received December 20, 1995. Accepted April 19, 1996.

Sexual dichromatism in birds is generally thought to arise from sexual selection favoring conspicuous coloration in males, although natural selection (e.g., predation) is thought to ultimately limit conspicuousness (Darwin 1871; Fisher 1930; Hingston 1933; Kodric-Brown and Brown 1984; Kirkpatrick et al. 1990; Promislow et al. 1992, 1994; Andersson 1994). Alternatively, bright coloration may be favored by predation because it advertises that a prey is unprofitable (Cott 1947; Baker and Parker 1979; Götmark 1992, 1993, 1995; but see Slagsvold et al. 1995). In both cases, studies of the evolution of dichromatism have focused largely on factors affecting variation in male coloration. Female coloration has been neglected because females are generally cryptic whereas male coloration is more variable (Irwin 1994). Greater crypsis in females is thought to be favored because bright colors potentially attract nest predators (Wallace 1889). Yet, variation in social competition or mate choice by males can favor variation in female brightness and influence dichromatism (e.g., Payne 1984; Trail 1990; Hill 1993; Irwin 1994). If nest predation constrains brightness (i.e., Wallace 1889; Baker and Parker 1979; Shutler and Weatherhead 1990; Johnson 1991), female brightness should vary with nest predation particularly in species where only the female incubates eggs and brood young. In contrast, male brightness may not vary as strongly with nest predation because of their reduced time at the nest. Thus, nest predation may cause variation in female brightness that can contribute to variation in sexual dichromatism independent of males.

More concealed nest sites are thought to allow more conspicuous coloration potentially because risk of nest predation is reduced (Wallace 1889; Baker and Parker 1979), but such arguments have been based largely on comparisons of hole-nesting birds with open nesters without directly testing relationships with nest predation. Similarly, nest predation has been argued to constrain male brightness and sexual dichromatism based on observations that dichromatism is reduced for ground-nesting birds compared to off-ground nesters and an assumption that nest predation is greater for ground-nesting birds (Shutler and Weatherhead 1990, Johnson 1991). Again, direct tests of relationships with nest predation are lacking and the assumption that ground-nesting birds have higher nest predation than off-ground nesters is not correct as a general rule (Martin 1993). Nest predation was less for ground nesters than off-ground nesters in general (Martin 1993, 1995) and given that plumage dimorphism is reduced for ground nesters (Shutler and Weatherhead 1990; Johnson 1991), sexual dichromatism may be *positively* correlated with nest predation rather than negatively correlated as long assumed. On the other hand, nest predation does not simply differ between ground and off-ground nests, but instead varies in a parabolic relationship with nest height; nest predation is greatest for shrub-nesting birds and less for ground and canopy nests (Martin 1993, 1995). If plumage brightness is influenced by nest predation, then brightness should also vary in a parabolic relationship with nest height, but in the opposite direction.

We examine the relative contribution of male versus female plumage brightness to plumage dichromatism and all three characteristics (female brightness, male brightness, sexual dichromatism) relative to variation in measured rates of nest predation and nest height. We examine these relationships for wood warblers (Parulinae) and finches (Carduelinae) because these two groups represent the largest groups with substantial nest height variation. These groups also are species where only females incubate eggs and brood young. In addition, warblers were the focus of earlier studies (Shutler and Weatherhead 1990).

METHODS

Plumage brightness was assessed by two persons, unaware of the questions being investigated, from illustrations of males and females in Clement et al. (1993) and National Geographical Society (1983). The overall brightness of each sex was scored on a scale from 1 to 6 (after Hamilton and Zuk 1982). Sexual dimorphism in plumage brightness was computed by subtracting the mean female score from the mean male score (e.g., Møller and Birkhead 1994). Mean interscorer values were used in analyses. There was a strong positive correlation between scorers for brightness scores (males: Spearman $r = 0.83$, $P < 0.0001$, females: Spearman $r = 0.62$, $P < 0.0001$). Mean scores are presented in Appendix.

Estimates of nesting failure due to predation were obtained from as many studies of warblers and finches as could be found in the literature and summarized in Appendix. References for data are provided in Martin (1995) and Cramp and Perrins (1994). Predation rates are reported on a per nest basis because of possible biases in determining causes of partial brood losses and because predation usually causes loss of the entire brood (Lack 1954; Nice 1957; Ricklefs 1969; Nilsson 1984; Møller 1989). Species were assigned to one of three general nest heights (ground, shrub, subcanopy/canopy). Nests were classified as ground nests if on the ground, shrub nests if off the ground but generally < 3 m high and as subcanopy/canopy nests if higher. Most species only used a single nest height, but some species were more variable and potentially added statistical noise to analyses. All percentage data were arcsine transformed for statistical analyses.

Data were first analyzed using nested analysis of variance (ANOVA), where nest height was nested within taxonomic family to examine differences in nest predation, plumage brightness, and dimorphism among nest heights. Post-hoc tests of differences among nest heights were conducted using Duncan's multiple range test.

Phylogenetic relationships potentially create a problem of statistical nonindependence among species (Felsenstein 1985; Grafen 1989; Harvey and Pagel 1991; Martins and Garland 1991). To control for possible phylogenetic effects, all data were analyzed using the independent contrast method of Felsenstein (1985) and incorporating the methods of Purvis and Garland (1993) for incompletely resolved phylogenies, based on the software described by Purvis and Rambaut (1995). This approach uses the full phylogenetic information at all taxonomic levels. The phylogenetic hypotheses are described in Martin (1995), Martin and Clobert (1996) and Badyaev (in review) and were constructed based on the most recent information available. We did not have consistent estimates of branch lengths because data came from studies using different methods. As a result, branch lengths were set as equal, reflecting a speciational model (see Garland et al. 1993), and also estimated using techniques described by Grafen (1989) and Pagel (1992). Analyses using these differing branch length estimates yielded equivalent results in terms of statistical significance, but examination of branch length diagnostics (see Garland et al. 1992) indicated that equal branch lengths were the most appropriate; absolute values of contrasts were not related ($P > 0.05$) to their standard deviations when branch lengths were set as equal. All relationships examined using independent contrasts were regressions where the regression line was forced through the origin (see Garland et al. 1992). Regression models were used on the phylogenetically transformed data (independent contrasts) to conduct analysis of variance (ANOVAs) or analysis of covariance (ANCOVAs). The main effect (nest height) was tested by creating $n - 1$ (= 2) dummy variables and these dummy variables were phylogenetically transformed. Statistical significance of nest height was tested by the cumulative change in sums of squares when these dummy variables were entered as a group (see Martin 1995; Martin and Clobert 1996). Post-hoc tests of differences were conducted using Duncan's multiple range test. Male plumage brightness generally varies more than female brightness and female and male brightness are thought to be genetically correlated (Lande 1980; Andersson 1994); indeed, male and female brightness were correlated (see results). As a result, male plumage brightness may constrain independent evolution in female brightness and such constraints were examined by using male brightness as a covariate to control its effects on variation in female plumage brightness. Finches and warblers showed the same relationships among nest heights and with nest predation for female, male, and dimorphism in plumage brightness. Thus, finches and warblers were pooled for all analyses presented here to increase statistical power.

RESULTS

When nest height was nested within taxonomic family, nest predation differed among nest heights ($F = 6.9$, $P = 0.003$, $n = 35$) in a parabolic relationship (Fig. 1A), where shrub nests had greater nest predation than both ground and canopy nests and canopy nests had greater nest predation than ground nests ($P < 0.05$, Duncan's test). When phylogenetic effects were controlled using independent contrasts, nest predation still differed among nest heights ($F = 14.7$, $P < 0.0001$, $n = 33$) in a parabolic relationship (Fig. 2A) where nest predation was greater for shrub nesters than ground and canopy nesters ($P < 0.05$, Duncan's test), but the latter two groups did not differ from each other ($P > 0.05$, Duncan's test).

Untransformed female plumage brightness differed among nest heights (nest height nested within taxonomic family ANOVA: $F = 10.6$, $P < 0.0001$, $n = 110$) in a parabolic relationship that was opposite that of nest predation; canopy nesters were brighter than ground or shrub nesters ($P < 0.05$, Duncan's test), but with the latter two barely not differing from each other ($P > 0.05$, Duncan's Test; Fig. 1B). Independent contrasts in female plumage brightness showed a similar parabolic difference among nest heights ($F = 6.6$, $P = 0.002$, $n = 91$; Fig. 2B); brightness of ground and shrub nesters was less than for canopy nesters ($P < 0.05$, Duncan's test), but the ground and shrub nesters did not differ from each other ($P > 0.05$, Duncan's test). When female brightness was controlled for male brightness, the residual variation in female brightness also differed parabolically among nest

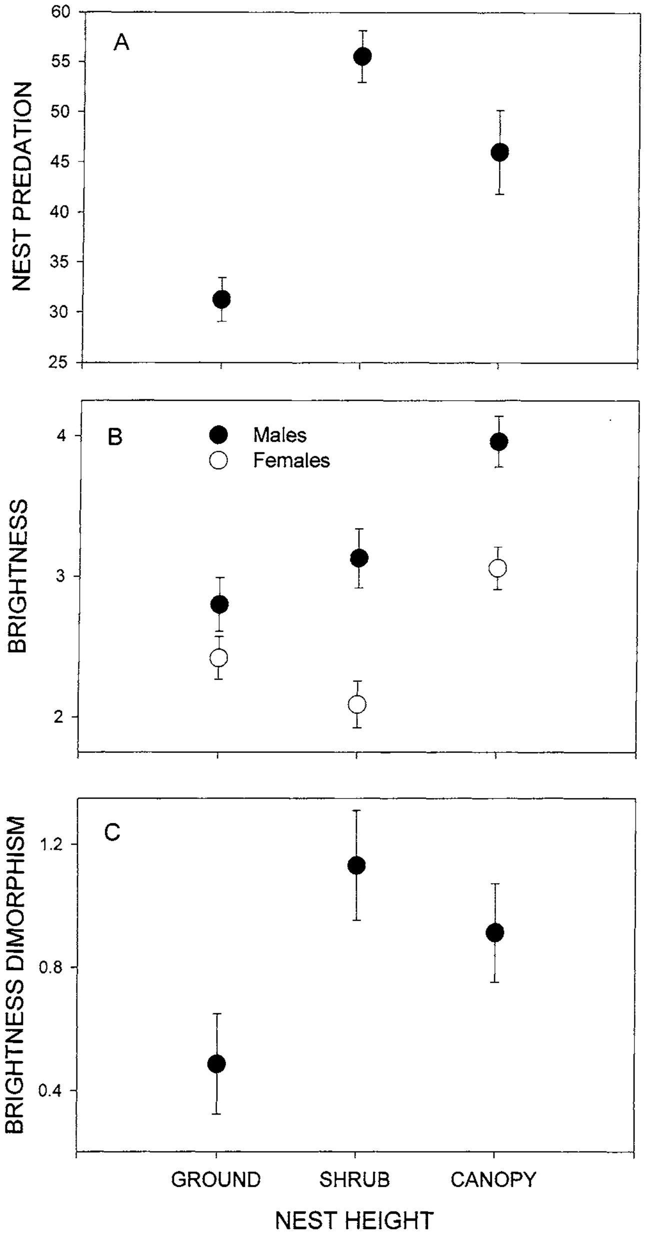

FIG. 1. Variation in means and one standard error for raw data among three nest heights for (A) nest predation (nest predation data were arcsine transformed for analyses, but raw data are shown to allow ease of interpretation) ($F = 6.9$, $P = 0.003$, $n = 35$); (B) male (solid circles) ($F = 9.5$, $P < 0.0001$, $n = 110$) and female (open circles) ($F = 10.6$, $P < 0.0001$, $n = 110$) brightness; and (C) dimorphism in brightness ($F = 3.8$, $P = 0.026$, $n = 110$).

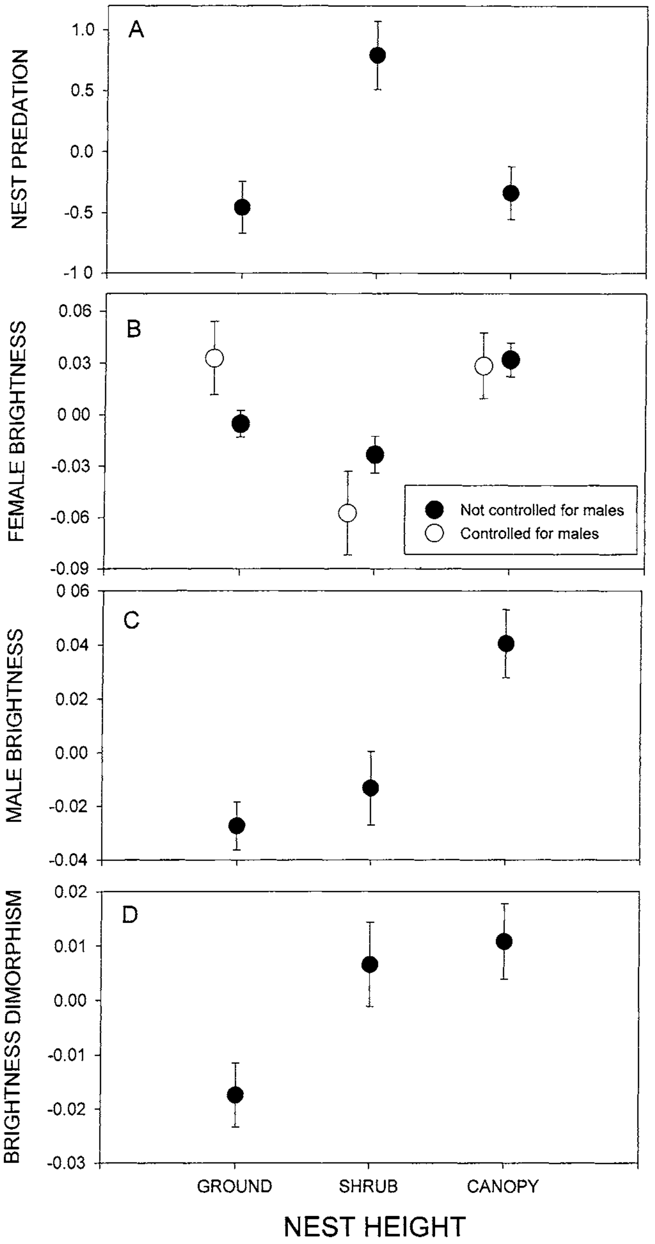

FIG. 2. Variation in means and one standard error for standardized independent contrasts (which control for possible phylogenetic effects) among three nest heights for (A) nest predation ($F = 14.7$, $P < 0.0001$, $n = 33$); (B) female brightness controlled ($F = 6.9$, $P = 0.0016$, $n = 91$) and not controlled for effects of male brightness ($F = 6.6$, $P = 0.002$, $n = 91$); (C) male brightness ($F = 9.0$, $P < 0.0001$, $n = 91$); and (D) dimorphism in plumage brightness ($F = 4.9$, $P = 0.008$, $n = 91$).

heights ($F = 6.9$, $P = 0.0016$) where ground and canopy nesters were brighter than shrub nesters ($P < 0.05$, Duncan's test), but ground and canopy nesters did not differ from each other ($P > 0.05$, Duncan's test). In all cases, the parabolas in female plumage brightness were opposite of nest predation, reflecting an inverse relationship between female brightness and nest predation ($r = -0.488$, $P = 0.004$, $n = 35$). This relationship was even stronger if possible constraints of male brightness on female brightness was examined through partial regression ($r_p = -0.51$, $P < 0.001$). Independent contrasts in female brightness and nest predation were not significantly correlated ($r = -0.241$, $P = 0.17$, $n = 33$), but when independent contrasts in female brightness were controlled for variation in independent contrasts in male brightness, the relationship was significant ($r_p = -0.329$, $P = 0.0575$; Fig. 3A).

Untransformed male plumage brightness differed among nest heights (nest height nested within taxonomic family ANOVA: $F = 9.5$, $P < 0.0001$, $n = 110$; Fig. 1B). Inde-

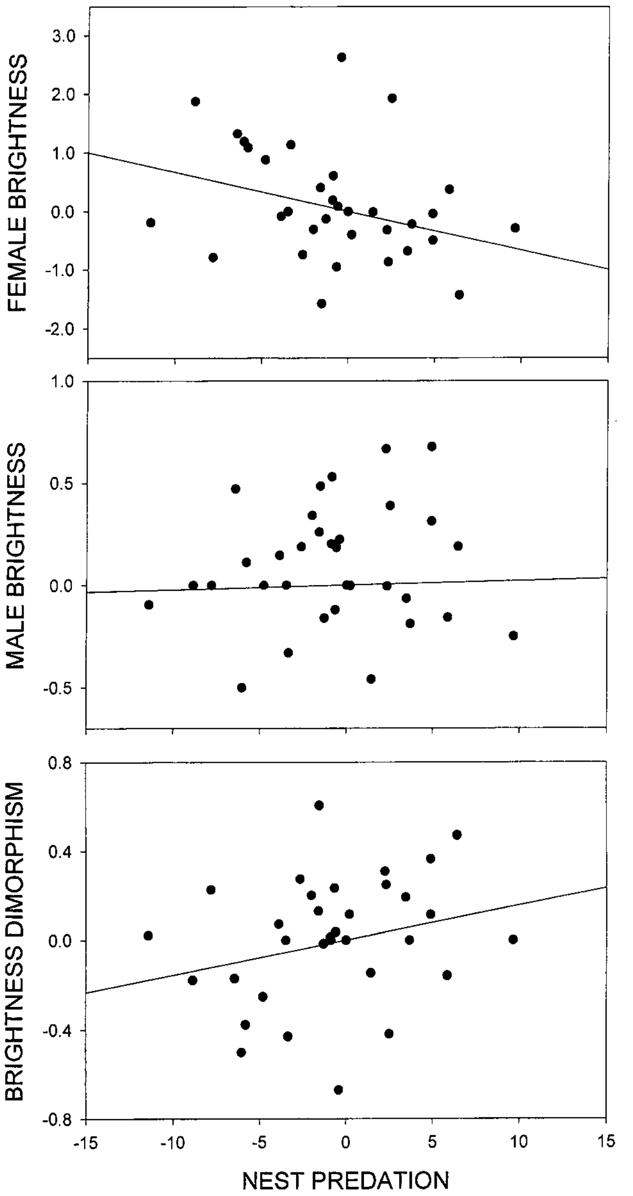

FIG. 3. Relationships between nest predation and (A) female brightness controlled for effects of male brightness) ($r_p = -0.329$, $P = 0.0575$, $n = 33$); (B) male brightness ($r = 0.03$, $P = 0.85$, $n = 33$); and (C) dimorphism in plumage brightness ($r = 0.26$, $P = 0.13$, $n = 33$). All values (plumage characters and nest predation) represent standardized independent contrasts (which control for possible phylogenetic effects) and the regression line is forced through the origin (see Methods).

pendent contrasts in male plumage brightness differed among nest heights ($F = 9.0$, $P < 0.0001$, $n = 91$; Fig. 2C), but not in a parabolic relationship like female plumage brightness or nest predation; male plumage brightness was greater ($P < 0.05$, Duncan's test) for canopy nesters than for shrub and ground nesters, but the latter two did not differ from each other ($P > 0.05$, Duncan's test). Male plumage brightness was not correlated with nest predation ($r = -0.176$, $P = 0.313$, $n = 35$) and the same was true when independent contrasts were used to control for phylogenetic effects ($r = 0.03$, $P = 0.85$, $n = 33$; Fig. 3B).

Dimorphism in plumage brightness differed among nest heights (nest height nested within taxonomic family ANOVA: $F = 3.8$, $P = 0.026$, $n = 110$; Fig. 1C). Independent contrasts in plumage brightness dimorphism (Fig. 2D) also differed among nest heights ($F = 4.9$, $P = 0.008$, $n = 91$). Dimorphism was less ($P < 0.05$, Duncan's test) in ground nesters than in shrub and canopy nesters, but the latter two groups did not differ from each other ($P > 0.05$, Duncan's test). Brightness dimorphism was positively correlated with nest predation ($r = 0.42$, $P = 0.012$, $n = 35$), but the relationship was not significant when independent contrasts were used to control for phylogenetic effects ($r = 0.26$, $P = 0.13$, $n = 33$; Fig. 3C).

Female plumage brightness was correlated with male brightness for raw data ($r = 0.707$, $P < 0.001$, $n = 110$) and for independent contrasts ($r = 0.606$, $P < 0.0001$, $n = 91$), but only about 35–49% of the variation in plumage brightness of one sex explained the other. This result taken together with the differing patterns for male versus female plumage brightness with nest height (Figs. 1B, 2B versus 2C) showed that female plumage patterns varied at least partly independently of male plumage patterns and influenced plumage brightness dimorphism differently.

DISCUSSION

Male plumage brightness is often emphasized in studies of plumage dichromatism because male brightness often varies more than female brightness. However, bright female plumage can be favored by various processes such as social competition or mate choice by males (e.g., Payne 1984; Trail 1990; Hill 1993; Irwin 1994). Such benefits to female brightness may be offset by constraints imposed by natural selection such as nest predation. Nest predation may be expected to exert particularly strong constraints on female plumage in taxa where females spend considerably more time at the nest than males, such as in warblers and finches where only the female incubates eggs and broods young. Female brightness was found in this study to vary among nest heights in a pattern inversely related to nest predation. Nest predation does not simply differ between ground and off-ground nesters as has been assumed in previous studies, but instead varies in a parabolic relationship with nest height (Figs. 1A, 2A). Plumage brightness patterns of females and males also vary in a more complex pattern than simply differing between ground and off-ground nesters (Fig. 1B, 2B, 2C). In addition, female plumage brightness patterns among nest heights differed from male plumage brightness patterns (Fig. 1B, 2B versus 2C). These differences between sexes supported a priori predictions that variation in nest predation is correlated with variation in female plumage brightness in taxa where only females incubate eggs and brood young. Variation in male plumage brightness was predicted to vary more weakly or not at all with nest predation, and in fact showed no hint of a relationship with nest predation (Fig. 3B). Instead, male plumage brightness increased monotonically with nest height (Fig. 1B, 2C).

The increase in male plumage brightness with nest height suggests that nest placement exerts some influence on male plumage brightness. Indeed, it is unlikely that the pattern with nest height reflects effect of some other factor such as foraging location because species within a nest height category vary strongly in foraging height. For example, warbler species that nest on the ground vary from ground to canopy in their foraging (Martin 1995). Johnson (1991) similarly concluded that nest location exerted a strong effect on plumage brightness. We identified three possible alternatives for the strong association of male brightness with nest height: (1) Less light is available for lower nests and reduces the significance of plumage brightness as a signal for mate choice, thereby favoring greater brightness at greater heights. This alternative is unlikely because other tests show that plumage brightness increases rather than decreases with greater darkness (Marchetti 1993). (2) Male coloration varies with extent of paternal care at the nest (Verner and Willson 1969; Baker and Parker 1979; Slagsvold et al. 1995) and nest height influences life history traits such as clutch size or fecundity (Martin 1988, 1995), which in turn can influence paternal care. Thus, male coloration may vary among nest heights related to the need for paternal care. (3) Males of species that nest on the ground or in shrubs often sing and forage higher than their nests and make long movements downward towards nests. Such long downward movements may make these males more vulnerable to predation or more conspicuous and attract attention of nest predators. Clearly, further tests of the possible causes of the strong association of male plumage brightness with nest height are needed.

Sexual dichromatism previously has been argued to vary inversely with nest predation based on observations that plumage dimorphism is reduced for ground-nesting birds and an invalid assumption that nest predation is reduced on the ground (i.e., Shutler and Weatherhead 1990; Johnson 1991). We showed however that sexual dichromatism was not significantly correlated with nest predation, and in fact showed a tendency to be positively correlated with nest predation, which is opposite the long-assumed negative relationship. However, the validity of this relationship is unclear as it disappeared when data were controlled for possible phylogenetic effects using independent contrasts. Ultimately, the strong difference in dimorphism between ground- and off-ground nesting birds results in part from a decrease in male brightness as previously argued (Shutler and Weatherhead 1990; Johnson 1991), but also is greatly facilitated by the increase in female brightness in ground-nesting birds related to their reduced risk of nest predation as compared to shrub nesters.

These results highlight the need for new and alternative perspectives when examining variation in avian plumage color patterns. The strong relationships of male plumage brightness and plumage dichromatism with nest height emphasize the need to consider new alternative causes of variation in coloration and dichromatism. More importantly, examinations of dichromatism need to extend focus beyond males alone and include consideration of possible causes of variation in female plumage (Trail 1990; Irwin 1994) and the roles of nest predation and nest placement.

ACKNOWLEDGMENTS

We thank P. Barber, C. Ghalambor, P. R. Martin, S. Osborn, and two anonymous reviewers for comments on the manuscript. We thank A. Rapone and W. B. Davison for scoring plumage brightness. TEM thanks the National Science Foundation (DEB-9407587, DEB-9527318) for research support.

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. Phil. Trans. R. Soc. B Biol. Sci. 287:63–130.

CLEMENT, P., A. HARRIS, AND J. DAVIS. 1993. Finches and sparrows: An identification guide. Princeton Univ. Press, Princeton, NJ.

COTT, J. B. 1947. The edibility of birds: Illustrated by five years' experiments and observations (1941–1946) on the food preferences of the hornet, cat and man; and considered with special reference to the theories of adaptive coloration. Proc. Zool. Soc. Lond. 116:371–524.

CRAMP, S., AND C. M. PERRINS, EDS. 1994. The birds of the western Palearctic. Vol. VIII. Oxford Univ. Press, Oxford.

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

FELENSTEIN, J. 1985. Phylogenies and comparative method. Am. Nat. 125:1–15.

FISHER, R. A. 1930. The genetical theory of natural selection. Dover, NY.

GARLAND, T., JR., P. H. HARVEY, AND A. R. IVES. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Syst. Biol. 41:18–32.

GARLAND, T., JR., A. W. DICKERMAN, C. M. JANIS, AND J. A. JONES. 1993. Phylogenetic analysis of covariance by computer simulation. Syst. Biol. 42:265–292.

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

———. 1993. Conspicuous coloration in male birds is favored by predation in some species and disfavored in others. Proc. R. Soc. Lond. B Biol. Sci. 253:143–146.

———. 1995. Black-and-white plumage in male pied flycatchers (*Ficedula hypoleuca*) reduces the risk of predation from sparrowhawks (*Accipiter nisus*) during the breeding season. Behav. Ecol. 6:22–26.

GRAFEN, A. 1989. The phylogenetic regression. Phil. Trans. R. Soc. Lond. B Biol. Sci. 326:119–157.

HAMILTON, W. D., AND M. ZUK. 1982. Heritable true fitness and bright birds: A role for parasites? Science 218:384–387.

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

HILL, G. E. 1993. Male mate choice and the evolution of female plumage coloration in the House Finch. Evolution 47:1515–1525.

HINGSTON, R. W. G. 1933. The meaning of animal color and adornment. Edward Arnold, London.

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

JOHNSON, S. G. 1991. Effects of predation, parasites, and phylogeny on the evolution of bright coloration in North American male passerines. Evol. Ecol. 5:52–62.

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

KODRIC-BROWN, A., AND J. H. BROWN. 1984. Truth in advertising: The kinds of traits favored by sexual selection. Am. Nat. 124: 309–323.

LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.

LANDE, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34:297–305.

MARCHETTI, K. 1993. Dark habitats and bright birds illustrate the role of the environment in species divergence. Nature 362:149–152.

MARTIN, T. E. 1988. Nest placement: implications for selected life-history traits, with special reference to clutch size. Am. Nat. 132:900–910.

———. 1993. Nest predation among vegetation layers and habitat types: Revising the dogmas. Am. Nat. 141:897–913.

———. 1995. Avian life history evolution in relation to nest sites, nest predation and food. Ecol. Monogr. 65:101–127.

MARTIN, T. E., AND J. CLOBERT. 1996. Nest predation and avian life history evolution in Europe versus North America: A possible role of humans? Am. Nat. 147:1028–1046.

MARTINS, E. P., AND T. GARLAND JR. 1991. Phylogenetic analyses of the correlated evolution of continuous characters: A simulation study. Evolution 45:534–557.

MØLLER, A. P. 1989. Parasites, predators and nest boxes: Facts and artefacts in nest box studies of birds? Oikos 56:421–423.

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

NATIONAL GEOGRAPHICAL SOCIETY. 1983. Field guide to the birds of North America. National Geographic Society, Washington, DC.

NICE, M. M. 1957. Nesting success in altricial birds. Auk 74:305–321.

NILSSON, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: The importance of nest predation and competition. Ornis Scand. 15:167–175.

PAGEL, M. D. 1992. A method for the analysis of comparative data. J. Theor. Biol. 156:431–442.

PAYNE, R. B. 1984. Sexual selection, lek an darena behavior, and sexual size dimorphism in birds. Ornithol. Monogr. 33:1–51.

PROMISLOW, D. E. L., R. D. MONTGOMERIE, AND T. E. MARTIN. 1992. Mortality costs of sexual dimorphism in birds. Proc. R. Soc. Lond. B Biol. Sci. 250:143–150.

———. 1994. Sexual selection and survival in North American waterfowl. Evolution 48:2045–2050.

PURVIS, A., AND T. GARLAND JR. 1993. Polytomies in comparative analyses of continuous characters. Syst. Biol. 42:569–575.

PURVIS, A., AND A. RAMBAUT. 1995. Comparative analysis by independent contrasts CAIC): An Apple Macintosh application for analysing comparative data. Computer Appl. Biosci. 11:247–251.

RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contrib. Zool. 9:1–48.

SHUTLER, D., AND P. J. WEATHERHEAD. 1990. Targets of sexual selection: song and plumage of wood warblers. Evolution 44: 1967–1977.

SLAGSVOLD, T., S. DALE, AND A. KRUSZEWICZ. 1995. Predation favors cryptic coloration in breeding male pied flycatchers. Anim. Behav. 50:1109–1121.

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

VERNER, J., AND M. F. WILLSON. 1969. Mating systems, sexual dimorphism and the role of male North American passerine birds in the nesting cycle. Ornithol. Monogr. 9:1–76.

WALLACE, A. R. 1889. Darwinism. Macmillan, London.

Corresponding Editor: M. Ryan

APPENDIX

Values used for analyses for female and male brightness (1, dullest; 6, brightest), brightness dimorphism (difference between female and male brightness), nest height (0, ground, 1, shrub, 2, subcanopy/canopy), and nest predation (percentage of nests lost to predators).

Species	Brightness			Nest height	Nest predation
	Female	Male	Dimorphism		
Callacanthis burtoni	2	3	1	2	
Cardellina rubrifrons	6	6	0	0	40.0
Carduelis ambigua	2	2	0	1	
Carduelis cannabina	2	2.5	0.5	1	65.0
Carduelis carduelis	4.5	4.5	0	2	
Carduelis chloris	2.5	2.5	0	1	61.6
Carduelis cucullata	3.5	6	2.5	2	
Carduelis flammea	2	3	1	1	46.5
Carduelis flavirostris	1.5	1.5	0	0	
Carduelis hornemanni	2.5	2.5	0	0	
Carduelis lawrencei	2.5	3	0.5	2	
Carduelis pinus	1.5	1.5	0	2	
Carduelis psaltria	2.5	3.5	1	2	
Carduelis sinica	2.5	2.5	0	2	
Carduelis spinoides	2.5	3	0.5	2	
Carduelis spinus	2.5	3	0.5	2	
Carduelis tristis	2.5	4	1.5	2	46.8
Carduelis xanthogastra	2.5	2.5	0	2	
Carpodacus cassinii	2	3	1	2	
Carpodacus erythrinus	1.5	3.5	2	1	70.0
Carpodacus mexicanus	1.5	2.5	1	2	45.8
Carpodacus pulcherrimus	1	2.5	1.5	1	
Carpodacus puniceus	1	2	1	0	
Carpodacus purpureus	2	3.5	1.5	2	
Carpodacus rhodochlamys	1	3.5	2.5	1	49.0
Carpodacus rhodochrous	1.5	3	1.5	2	
Carpodacus roseus	2	3.5	1.5	2	
Carpodacus rubicilla	1.5	4.5	3	0	
Carpodacus synoicus	1	2	1	0	
Carpodacus thura	1	2.5	1.5	1	
Coccothraustes coccothraustes	3.5	3.5	0	2	39.6
Coccothraustes vespertinus	2.5	4	1.5	2	
Dendroia caerulescens	2.5	4.5	2	1	32.0
Dendroica castanea	4.5	5.5	1	2	
Dendroica cerulea	3	5	2	2	
Dendroica coronata	2.5	3.5	1	2	37.9
Dendroica discolor	3.5	3.5	0	1	61.8
Dendroica fusca	4	6	2	2	
Dendroica kirtlandii	3.5	4	0.5	0	40.1
Dendroica petechia	3.5	4.5	1	2	34.2
Dendroica townsendi	5	5	0	2	
Eophona migratoria	2.5	2.5	0	2	
Eophona personata	3	3	0	2	
Geothlypis trichas	3	4	1	1	
Helmitheros vermivorus	2.5	2.5	0	0	21.4
Icteria virens	3	3	0	1	52.9
Leucosticte arctoa	1	2	1	0	
Leucosticte branti	2	2	0	0	
Leucosticte nemoricola	1.5	2	0.5	0	
Limnothlypis swainsonii	2	2	0	1	
Linurgus olivaceus	2	4	2	1	
Loxia curvirostra	1.5	4	2.5	2	74.3
Loxia leucoptera	2	3.5	1.5	2	
Loxia pytyopsittacus	1.5	3	1.5	2	
Loxia scotica	2	4	2	2	64.7
Mniotilta varia	2.5	2.5	0	0	26.3
Mycerobas carnipes	1	2	1	1	66.0
Mycerobas icterioides	2	5.5	3.5	2	
Mycerobas melanozanthos	2.5	3	0.5	2	
Oporornis formosus	3.5	4.5	1	0	30.0
Oporornis tolmiei	3	4	1	1	49.3
Parula americana	5	5	0	2	
Pinicola enucleator	3.5	3.5	1	2	41.9
Pyrrhula aurantiaca	2	3	1	2	
Pyrrhula pyrrhula	2	3.5	1.5	1	67.0
Rhodopechys githaginea	1	2.5	1.5	0	
Rhodopechys mongolica	1	2	1	0	
Rhodopechys obsoleta	2	2	0	1	61.7
Rhodopechys sanquinea	2	3	1	0	
Seiurus aurocapillus	3	3	0	0	24.5
Seiurus motacilla	3	3	0	0	
Seiurus noveboracensis	3	3	0	0	
Serinus alario	2	3.5	1.5	1	
Serinus albogularis	0.5	0.5	0	1	
Serinus ankoberensis	1	1	0	0	
Serinus atrogularis	1.5	1.5	0	2	
Serinus canaria	2	2.5	0.5	2	
Serinus canicollis	2	2.5	0.5	2	
Serinus capistratus	3	3	0	2	
Serinus citrinella	3	3	0	2	
Serinus citrinelloides	2.5	3	0.5	1	
Serinus citrinipectus	2	2	0	1	
Serinus dorsostriatus	3	3	0	2	
Serinus flaviventris	2	4	2	2	
Serinus gularis	1	1	0	2	
Serinus leucopterus	1	1	0	1	
Serinus leucopygius	1.5	1.5	0	2	
Serinus menachensis	1	1	0	0	
Serinus mennelli	2	2	0	2	
Serinus mozambicus	3	3.5	0.5	2	
Serinus nigriceps	3	3	0	1	
Serinus pusillus	3	3	0	1	48.0
Serinus scotops	2.5	2.5	0	2	
Serinus serinus	3	3.5	0.5	2	37.0
Serinus striolatus	2	2	0	2	
Serinus sulphuratus	2.5	3	0.5	2	
Serinus symonsi	1.5	2	0.5	1	
Serinus syriacus	2.5	2.5	0	1	
Serinus totta	2	2.5	0.5	0	
Serinus tristriatus	1	1	0	2	
Setophaga ruticilla	3	4.5	1.5	2	37.8
Uragus sibiricus	1.5	3.5	2	1	
Vermivora celata	1.5	2	0.5	0	33.3
Vermivora virginiae	3	3.5	0.5	0	30.8
Wilsonia citrina	4	6	2	1	47.0
Wilsonia pusilla	4	5	1	0	34.9