DOES MALE-LIKE COLORATION OF FEMALE HOODED WARBLERS INCREASE NEST PREDATION?[1]

BRIDGET J. STUTCHBURY

Department of Biology, York University, North York, Ontario M3J 1P3, Canada

JOAN S. HOWLETT
3662 Kinter Hill Rd., Edinboro, PA 16412

Abstract. We tested the hypothesis that male-like coloration of female birds increases the risk of nest predation in a sexually dimorphic songbird, the Hooded Warbler (*Wilsonia citrina*). Female Hooded Warblers vary greatly in the extent of the black hood, ranging from no black in yearlings to an almost complete black hood in some older females. However, the frequency of nest predation did not vary significantly with extent of male-like plumage during the egg stage, nestling stage, or over all nest stages. In addition, yearling females whose crown and throat was dyed black did not suffer a higher nest predation rate than unmanipulated and control yearlings. We found no evidence that breeding experience of yearling versus older females affects nest predation rate. In addition, yearling females did not tend to build more visually conspicuous nests. These results strongly suggest that predators did not use conspicuous plumage coloration as a cue for locating nests.

Key words: Sexual dimorphism; predation; coloration; Hooded Warbler; Wilsonia citrina.

INTRODUCTION

Ideas about the selective costs of conspicuous plumage coloration in birds are currently undergoing dramatic changes. Except for a minority of authors (Cott 1947, Baker and Parker 1979), bright coloration in birds has been widely assumed to increase the risk of predation on adults or their nests (e.g., Selander 1972, Procter-Gray and Holmes 1981, Butcher and Rohwer 1989, Kirkpatrick et al. 1990). However, recent field experiments with raptors have revealed that in several bird species brightly colored mounts are attacked less frequently by predators (Götmark 1992, 1993, 1994a, 1995; Götmark and Unger 1994), and that raptors are not more likely to capture brightly colored bird species (Baker and Bibby 1987). Furthermore, recent discoveries of poisonous birds (Dumbacher et al. 1992) have lent support to the hypothesis that in some species bright coloration could be an anti-predator adaptation via aposematic coloration (Baker and Parker 1979, Götmark 1994b). These recent studies have all focussed on the effects of conspicuous coloration on adult predation; in this study we test whether conspicuous plumage coloration increases the risk of nest predation.

The adaptive significance of cryptic female coloration in birds is an old and hotly debated issue in animal behavior, being a source of great disagreement between A. R. Wallace and C. Darwin, the co-founders of Natural Selection Theory (reviewed in Cronin 1991). Darwin (1871) believed that dull female coloration was a nonadaptive consequence of sex-limited inheritance. Wallace (1889) proposed the hypothesis that cryptic female coloration functions to reduce predation risk at the nest. Wallace's evidence included the observation that in many cavity-nesting species females are brightly colored, and males are more cryptic than females in species with sex role reversal. However, these results are also consistent with sexual selection theory.

Field tests of the nest predation hypothesis are rare, perhaps because extensive color variation among females within a sexually dimorphic species is uncommon. In this study, we test whether male-like coloration in female Hooded Warblers (*Wilsonia citrina*) increases the risk of predation on their nests. Hooded Warblers are ideal for such a study, because females vary naturally from having no male-like black hood to having an extensive black hood that almost resembles males (Lynch et al. 1985, Morton 1989, Stutchbury 1994, Stutchbury et al. 1994). We test two predictions of the nest predation hypothesis: (1) females with male-like coloration should suffer higher predation rates on their nests than more cryptic females, and (2) cryptic females that are

dyed black to resemble the most male-like fe-
males in the population should suffer higher pre-
dation rates than control females.

METHODS

This study was conducted from May–August
1991–1994 in northwestern Pennsylvania (41°N,
79°W). The study site was a 150 ha mixed hard-
wood forest. Each year, 35–40 breeding pairs of
adults were captured with mist nets and banded
with U.S. Fish and Wildlife bands and were in-
dividually color banded. We measured body
mass, flattened wing chord, and tarsus length for
all individuals. We also collected 30–100 μL of
blood from the brachial vein for use in DNA
fingerprinting (Stutchbury et al. 1994). All breed-
ing females were uniquely color banded. Terri-
tories of color banded males were mapped by
following singing individuals, and noting border
disputes.

We determined the degree of melanism for
each female using a scoring system similar to
Lynch et al. (1985), giving a score of 0–5 for
increasing amounts of black on the throat and
crown separately. The darkest females would
score 10. The darkest females are similar to males,
but have about 20% yellow feathering on the
throat (rather than being entirely black). Females
in their first breeding season ("second year" SY)
have little or no black (plumage score 0–3),
whereas virtually all older females have an in-
termediate (4–6) or extensive (7–10) amount of
black (Lynch et al. 1985; Evans Ogden and
Stutchbury 1994). After second year (ASY) fe-
males do not become darker with age (Morton
1989, Evans Ogden and Stutchbury 1994).

PREDATION RATES

Open cup nests are made of bark strips and fine
grasses with an outer wrapping of dead leaves on
the underside, and nests are placed 0.29–1.43 m
above the ground in a shrub (Evans Ogden and
Stutchbury 1994). Nests were located primarily
by following vocalizing females back to the nest
during nest building, egg-laying, and incubation.
Most nests were found by the incubation stage.
Visitation rates and degree of disturbance were
comparable for all nests. Nest contents were
checked every 4–5 days, nestling were banded,
and 30–75 μL of blood was sampled from most
nestlings at six days of age for use in DNA fin-
gerprinting. For about 50 nests in 1991–1993 we
monitored male feeding rates at nests using a

blind or video cameras (Evans Ogden 1994,
Stutchbury et al. 1994). In 1993, 30 nests were
used in a nest concealment experiment (Howlett
and Stutchbury, in review), and these experi-
mental nests were excluded from the analysis of
predation rates in this study.

We monitored a total of 154 nests from 1991–
1994. Females frequently renested or had second
broods on the same territory within a breeding
season. These nests were not used in our analysis
of female color because repeated nesting at-
tempts by the same female within a year may
not be independent due to variation among fe-
males in behavior or among territories in sus-
ceptibility to predation. The annual return rate
of banded females averaged 37% over all years,
but 68% ($n = 28$) of the returning females moved
to a different territory from where they had bred
previously. Therefore, we considered the first
nesting attempt per year per female ($n = 106$
nesting attempts) as independent events. The lack
of territory site fidelity in females was not related
to predation the year before; 9 of 14 females who
suffered nest predation moved, compared with
10 of 14 who did not suffer nest predation ($G =
0.16$, $P > 0.50$).

Nest predators common in the study site were
Blue Jays (*Cyanocitta cristata*), American Crows
(*Corvus brachyrhynchos*), eastern chipmunks
(*Tamias striatus*), red squirrels (*Tamiasciurus
hudsonicus*), raccoons (*Procyon lotor*), striped
skunks (*Mephitus mephitus*), weasels (*Mustela*
spp.), opossums (*Didelphis virginiana*) and black
rat snakes (*Elaphe obsoleta*).

PLUMAGE COLOR MANIPULATIONS

We conducted plumage color manipulation ex-
periments to separate the effects of female age
from plumage coloration. In each year we cap-
tured about half the females prior to egg-laying.
In 1991 and 1992 females with little or no black
hood (i.e., SY birds) were randomly assigned to
a control or experimental group. We dyed ex-
perimental females with Nyanzol dye (2 g in 50
ml solution of equal parts water and hydrogen
peroxide) so that they resembled the blackest
females in the population (plumage scores of 8–
10). This dye acts instantly, and does not affect
the structure of feathers or otherwise harm the
bird (Stutchbury 1991, Stutchbury et al. 1994).
Control birds were treated in exactly the same
way, except that water was applied to the feath-
ers. Total handling time was usually only 10–15
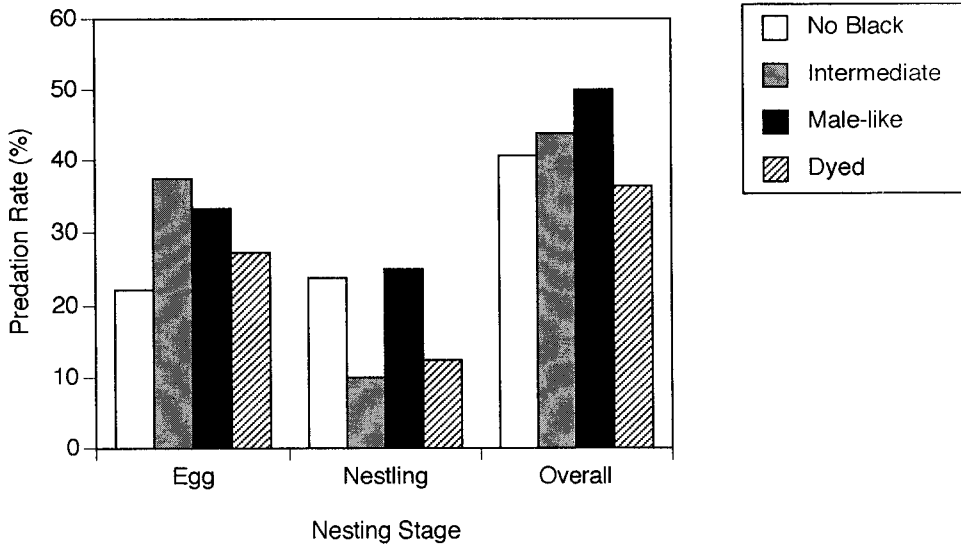min for the entire procedure.

FIGURE 1.   Frequency (%) distribution of predation on Hooded Warbler nests during egg and nestling stages, and overall. Nestling stage includes only those nests that escaped predation during incubation. Extent of female black hood given as no black (plumage score 0–3, $n = 27$), intermediate (4–6, $n = 32$), extensive (7–10, $n = 36$) and dyed (final appearance of 7–10, $n = 11$).

NEST SITE CHARACTERISTICS

Due to the possibility that age-specific choices of nesting sites could influence the risk of nest predation, we also characterized the microhabitat surrounding the nest. Only the first nesting attempt per year per female was used, and only nests in 1992–1993 were measured. First, the height of the nest above the ground, the depth of dead leaves hanging from the underside of the nest, and density of stems within a 1 m radius of the nest were measured (Howlett and Stutchbury, in review). Second, overall visibility of the nest was measured at three heights (ground, nest height, 1.5 m) parallel to the horizontal plane of the nest, using the methods of Holway (1991). The percentage of the nest that was visible (to the nearest 20%) from a distance of 1 m was recorded at each level, from each of eight points (45-degree compass intervals). In addition, the percentage of the nest visible from directly overhead at a height of 1.5 m was recorded. The overall visibility of the nest was calculated as an average of these nine scores.

RESULTS

PREDATION RATE

The predation rate for all nests (including renests) varied annually from 38.3% in 1991 ($n = 47$) to 44.4% in 1992 ($n = 63$) and 50% in 1993

($n = 24$) and 1994 ($n = 28$), but these differences were not statistically significant (G-test, $G = 0.95$, df $= 3$, $P > 0.50$). Sample sizes were relatively low in 1993 and 1994 due to the omission of nests used in other experiments unrelated to female coloration (Howlett and Stutchbury, in review). There was also no significant difference (G-test, $G = 0.74$, df $= 3$, $P > 0.50$) in predation rate at different times of the breeding season (15–31 May: 40.4% ($n = 52$); 1–15 June: 50% ($n = 28$); 16–30 June: 41.7% ($n = 36$); 1–31 July: 44.4% ($n = 18$)).

We did not systematically attempt to identify which predators were involved in nest predation. Video cameras used for monitoring parental behavior recorded single predation events by a Blue Jay, an eastern chipmunk, and a red squirrel.

EFFECTS OF FEMALE COLORATION

Over all four years, females with an extensive black hood did not have a significantly higher nest predation rate than females with intermediate or no black hood (Fig. 1) at the egg stage ($G = 1.72$, df $= 2$, $P > 0.20$), nestling stage ($G = 2.00$, $P > 0.20$) or overall ($G = 0.58$, $P > 0.50$). Furthermore, females who were dyed black prior to egg-laying did not suffer a significantly higher predation rate ($G < 0.50$, df $= 1$, $P > 0.40$) at any nest stage compared with females with no black hood.

TABLE 1. Pairwise comparison of nest predation for different colored females occupying the same territory ($n = 20$ territories) between years. Male-like coloration categorized as no black (0–3 plumage score), intermediate (4–6), and male-like (7–10, dyed). The occurrence or absence of predation was determined from the fate of the first nesting attempt for each female. Instances where the outcome was the same for both females (both or neither preyed upon) were lumped into a single category.

Plumage comparison	Nests preyed upon		
	Duller	Both/ neither	Brighter
No black/male-like	4	6	2
No black/intermediate	0	1	2
Intermediate/male-like	0	2	2

Some territories may be more susceptible to nest predation due to their proximity to the forest edge (e.g., Wilcove 1985) or differences in vegetation structure within the territory (Bowman and Harris 1980). Therefore, we used a pairwise comparison to determine if, on the same territory, nests of blacker females were more likely to be preyed on than those of more cryptic females. There was no significant tendency for blacker females to suffer more predation (Table 1; Sign test, $P > 0.20$).

EFFECTS OF AGE

All females that lack a black hood are second year (SY), so age and experience differs between hooded and non-hooded females. However, SY females did not have a significantly ($G = 0.57$, df = 1, $P > 0.40$) lower overall nest predation rate (39.5%; 15/38) than after second year (ASY) females (47.1%; 32/68). Since females usually do not return to the same territory between years, we could not test for age effects within the ASY age class.

AGE AND NEST SITE CHARACTERISTICS

The nests of Hooded Warblers vary considerably in visual conspicuousness due to differences in nest height (31–184 cm), depth of dead leaves hung under the nest (3–19 cm), density of stems near the nest (0.3–58 stems/m²), and overall visibility of the nest (10–78% visible). Age-specific differences in nest site selection and construction could potentially mask color-related differences in risk of predation. There was a tendency for SY females to place their nests lower to the ground

TABLE 2. Mean nest height, leaf depth, stem density within 1 m of the nest and overall nest visibility for SY ($n = 33$) and ASY ($n = 44$) female Hooded Warblers. Standard error given in parentheses.

	Female age	
	SY	ASY
Nest height (cm)	57.3 (4.06)	70.8 (5.52)
Leaf depth (cm)	7.7 (0.59)	6.8 (0.45)
Stems/m²	24.2 (2.68)	22.2 (2.20)
Visibility (%)	49.3 (2.49)	46.4 (2.06)

than ASY females (Table 2; Mann-Whitney U-test; $U = 550$, $0.05 < P < 0.10$), but there were no significant differences among age classes for leaf depth ($U = 628$, $P > 0.25$), stem density ($U = 463$, $P > 0.50$), or overall visibility of the nest ($U = 668$, $P > 0.50$).

DISCUSSION

Our study examined whether extensive female color variation has a significant effect on the risk of nest predation. We hypothesized that females with extensive black hoods would suffer a higher risk of nest predation, because this male-like plumage pattern is relatively conspicuous to predators. However, we found no relationship between natural female plumage variation and nest predation, nor higher nest predation on females experimentally dyed black. The null hypothesis that nest predation is not a significant source of selection on female coloration in Hooded Warblers seems likely.

We do not know the extent to which nest visitation by us affected predation patterns (Westmoreland and Best 1985, but see Martin and Roper 1988), and whether this could mask the effect of female color on nest predation. Overall predation rates (38–50%) were not unusually high for this population (Evans Ogden and Stutchbury 1994), and visitation rates were consistent with respect to female coloration. This suggests that our results indeed reflect natural patterns of predation.

Nest predators may not use female coloration as an important cue for several reasons. First, the assumption that sexual dimorphism results in differing conspicuousness to predators may not hold (Götmark 1992, 1993, 1994a, 1995). Conspicuousness to predators may vary with the color patterns of the background vegetation and the type of predators involved (Endler 1990,

1991). Second, predators may not use the conspicuous coloration of the parents to locate nests. Instead, olfactory, parental activity and auditory cues (e.g., nestling begging calls (Skutch 1949, Holway 1991, Reitsma et al. 1990, Perrins 1965) can be important. Also, several studies of avian and mammalian nest predators suggest that foraging search patterns are determined greatly by prior success in certain patches (Sugden and Beyersbergen 1986), foraging activity for other types of prey (Vickery et al. 1992) and spatial heterogeneity of the vegetation (Bowman and Harris 1980). Third, the conspicuousness of nests could influence predation more than conspicuousness of the female. However, we have shown elsewhere that nest conspicuousness in Hooded Warblers does not increase nest predation, even for nests where surrounding vegetation was experimentally removed (Howlett and Stutchbury, unpubl. ms.). The extent to which predators use bright plumage coloration as a cue for locating prey is therefore in question both for adult predation by raptors (Götmark 1992, 1993, 1994a, 1995) and nest predation (this study).

ACKNOWLEDGMENTS

LITERATURE CITED

BAKER, R. R., AND C. J. BIBBY. 1987. Merlin *Falco colombarius* predation and theories of the evolution of bird coloration. Ibis 129:259–263.

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

BOWMAN, G. B., AND L. D. HARRIS. 1980. Effect of spatial heterogeneity on ground-nest predation. J. Wildl. Manag. 44:806–813.

BUTCHER, G. S., AND S. ROHWER. 1989. The evolution of conspicuous and distinctive coloration for communication in birds. Current Ornithol. 6:51–108.

COTT, H. 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.

CRONIN, H. 1991. The ant and the peacock. Cambridge Univ. Press, Cambridge, U.K.

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

DUMBACHER, J. P., B. M. BEEHLER, T. F. SPANDE, H. M. GARRAFFO, AND J. W. DALY. 1992. Homobatrachotoxin in the genus *Pitohui*: chemical defense in birds? Science 258:799–801.

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

ENDLER, J. A. 1991. Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. Vision Res. 31: 587–608.

EVANS OGDEN, L. J. 1994. Cross-seasonal effects on the breeding strategy of the Hooded Warbler (*Wilsonia citrina*). M.Sc.thesis, York Univ., Ontario.

EVANS OGDEN, L. J., AND B. J. STUTCHBURY. 1994. Hooded Warbler. *In* A. Poole, P. Stettenheim, and F. Gill [eds.], The birds of North America, No. 110. The Academy of Natural Sciences, Philadelphia and The American Ornithologists' Union, Washington, DC.

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

GÖTMARK, F. 1993. Conspicuous coloration in male birds is favoured by predation in some species and disfavoured in others. Proc. R. Soc. Lond. B253: 143-146.

GÖTMARK, F. 1994a. Does a novel bright colour patch increase or decrease predation? Red wings reduce predation risk in European Blackbirds. Proc. R. Soc. Lond. B. 256:83–87.

GÖTMARK, F. 1994b. Are bright birds distasteful? A re-analysis of H. B. Cott's data on the edibility of birds. J. Avian Biol. 25:184–197.

GÖTMARK, F. 1995. Black-and-white plumage in male Pied Flycatchers (*Ficedula hypoleuca*) reduces the risk of predation from Sparrowhawks (*Accipter nisus*) during the breeding season. Behav. Ecol. 6: 22–26.

GÖTMARK, F., AND U. UNGER. 1994. Are conspicuous birds unprofitable prey? Field experiments with hawks and stuffed prey species. Auk 111:251–262.

HOLWAY, D. A. 1991. Nest-site selection and the importance of nest concealment in the Black-throated Blue warblers. Condor 93:575–581.

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

LYNCH, J. F., E. S. MORTON, AND M. E. VAN DER VOORT. 1985. Habitat segregation between the sexes of wintering Hooded Warblers (*Wilsonia citrina*). Auk 102:714–721.

MARTIN, T. E., AND J. R. ROPER. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. Condor 90:51–57.

MORTON, E. S. 1989. Female hooded warbler plumage does not become more male-like with age. Wilson Bull. 101:460–462.

PERRINS, C. M. 1965. Population fluctuations and clutch size in the Great Tit, *Parus major*. J. Anim. Ecol. 34:601–647.

PROCTER-GRAY, E., AND R. T. HOLMES. 1981. Adaptive significance of delayed attainment of plumage in male American Redstarts: tests of two hypotheses. Evolution 35:742–751.

REITSMA, L. R., R. T. HOLMES, AND T. W. SHERRY. 1990. Effects of removal of red squirrels, *Tamiasciurus hudsonicus,* and eastern chipmunks, *Tamias striatus,* on nest predation in a northern hardwood forest: an artificial nest experiment. Oikos 57:375–380.

SELANDER, R. K. 1972. Sexual selection and dimorphism in birds, p. 180–320. *In* B. G. Campbell [ed.], Sexual selection and the descent of man. Aldine, Chicago.

SKUTCH, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430–455.

STUTCHBURY, B. J. 1991. The adaptive significance of male subadult plumage in Purple Martins: plumage dyeing experiments. Behav. Ecol. Sociobiol. 29:297–306.

STUTCHBURY, B. J. 1994. Competition for winter territories in a Neotropical migrant: the role of age, sex and color. Auk 111:63–69.

STUTCHBURY, B. J., J. M. RHYMER, AND E. S. MORTON. 1994. Extra-pair paternity in Hooded Warblers. Behav. Ecol. 5:384–392.

SUGDEN, L. G., AND G. W. BEYERSBERGEN. 1986. Effect of density and concealment on American Crow predation of simulated duck nests. J. Wildl. Manag. 50:9–14.

VICKERY, P. D., M. L. HUNTER, JR., AND J. V. WELLS. 1992. Evidence of incidental nest predation and its effects on nests of threatened grassland birds. Oikos 63:281–288.

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

WESTMORELAND, D., AND L. B. BEST. 1985. The effect of disturbance on Mourning Dove nesting success. Auk 102:774–780.