THE FUNCTION OF DELAYED PLUMAGE MATURATION IN MALE BLACK-HEADED GROSBEAKS

GEOFFREY E. HILL[1]

Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131 USA

ABSTRACT.—I used data from two breeding populations of Black-headed Grosbeaks (*Pheucticus melanocephalus*) in central New Mexico to test alternative hypotheses regarding the function of delayed plumage maturation in male passerines. Yearling male grosbeaks displayed a wide range of subadult plumage types, but most individuals were intermediate in appearance between adult males and females. Subadult male grosbeaks arrived on the study sites about 2 weeks after adult males, with no tendency for individuals with brighter or duller plumage to arrive first. Only a few of the most brightly plumaged subadult males defended territories and attracted females; most were nonterritorial floaters. All territories of subadult males were positioned outside clusters of adult male territories with few total neighbors. When I removed adult males from their territories, the territories remained empty. These results are not consistent with predictions of the female-mimicry hypothesis, but they are in accord with those of the cryptic hypothesis. *Received 1 June 1987, accepted 13 October 1987.*

MALES of many of North America's most brightly plumaged passerine species retain a portion of their first basic plumage as part of their first breeding plumage, giving them a relatively femalelike appearance. The evolutionary significance of such delayed plumage maturation has been the subject of speculation since Lack (1954, 1968) first proposed what Rohwer et al. (1983) termed the "cryptic hypothesis." Lack, and later Selander (1965, 1972), suggested that males have low reproductive success if they attempt to breed in their first year. To minimize potential losses, yearling males forego breeding and sport a cryptic plumage that minimizes their risk of predation and frequency of intrasexual aggressive encounters. In this way males increase the probability of reaching their second breeding season, when they have a much greater opportunity for successful reproduction.

The realization that subadult males of many species are sexually mature and often breed (Ficken and Ficken 1967, Samson 1976, Rohwer and Niles 1979, Payne 1982, Flood 1984, Lanyon and Thompson 1986) prompted Procter-Gray and Holmes (1981) to modify the cryptic hypothesis. Rather than delayed sexual maturation and no first-year reproduction, they proposed a reduced reproductive effort in first-year males that included a delay in plumage maturation. Under this modified cryptic hypothesis, subadult males are opportunists, exploiting relatively low-cost (and low-benefit) reproductive opportunities when they arise. Studd and Robertson (1985) formalized this hypothesis in a threshold model that predicted the combinations of first-year survivorship, adult survivorship, yearling reproductive potential, and adult reproductive potential that will lead to the evolution of delayed plumage maturation. Recently, Lyon and Montgomerie (1986) proposed that the primary role of subadult plumage was to signal subordinance and reduce aggression from adult males. Although potentially an important

observation, this hypothesis can be subsumed within the cryptic hypothesis as an alternative mechanism by which subadult plumage reduces the cost of first-year reproduction, so I will not treat it as a distinct hypothesis. Throughout this paper, I consider the Procter-Gray and Holmes/Studd and Robertson views to represent the cryptic hypothesis.

Rohwer (1978) and Rohwer et al. (1980) challenged the cryptic hypothesis with the female-mimicry hypothesis. They suggested that the femalelike plumage of first-year males is actually mimetic. By appearing to be females, first-year males gain access to and familiarity with the territories of adult males. Assuming that site dominance is established rapidly (Krebs 1982), this residency in an area makes yearling males more competitive with experienced males when they attempt to establish their own territories. Yearling males with a relatively bright plumage gain no advantage through deception and are disadvantaged in competition with adult males, but they do well in competition with other subadult males. Thus, according to the female-mimicry hypothesis, yearling males may adopt two alternative reproductive tactics that, unlike the strategy proposed in the cryptic hypothesis, maximize immediate reproductive success rather than minimize the risk of mortality.

A third hypothesis is that delayed plumage maturation is an adaptation to the winter rather than the breeding environment (the winter-adaptation hypothesis; Rohwer et al. 1983, Rohwer 1986). This idea warrants further testing, but the paucity of existing data and the focus of this study on the breeding grounds necessitate that I ignore it here.

In contrast to the winter-adaptation hypothesis, a substantial amount of effort has been devoted to addressing the female-mimicry and cryptic hypotheses, but neither hypothesis has been adequately falsified nor strongly supported (for a review see Studd and Robertson 1985, Lyon and Montgomerie 1986). The problem lies partly in the lack of rigor in attempts to test the theory (Rohwer 1983) and in the fact that the hypotheses are not mutually exclusive (Rohwer et al. 1980, Flood 1984, Lyon and Montgomerie 1986). For instance, a yearling male could display subadult plumage primarily to enhance first-year reproduction through female mimicry, while at the same time benefiting from a lower risk of predation because of the increased plumage crypticity.

I monitored two breeding populations of a sexually dichromatic passerine, the Black-headed Grosbeak (*Pheucticus melanocephalus*). My objectives were to quantify the effects of subadult plumage on the biology of yearling male grosbeaks, particularly with regard to reproduction, and to perform tests of predictions of the cryptic hypothesis and female-mimicry hypothesis. I tested eight specific predictions, five generated by the female-mimicry hypothesis and three by the cryptic hypothesis (Table 1). I will treat the underlying assumptions of each prediction in detail below. Based on the relation of the data to the predictions, I assessed the validity of the cryptic and female-mimicry hypotheses.

METHODS

I conducted the study in central New Mexico on the eastern slope of the Sandia Mountains (elevation 2,100 m) 16 km east of Albuquerque in 1984–1986 and along the west bank of the Rio Grande (elevation 1,550 m) 10 km north of Albuquerque in 1986 (see Hill 1988 for a description of the study sites). I color-marked all resident males and most females in all 3 yr at the Sandia Mountain study area but only a few birds at the Rio Grande site in 1986. I also weighed, determined the age and sex (Hill 1987), scored the plumage, and measured tail length, flattened wing cord, and tarsus length of grosbeaks that I captured. (Occasionally, birds escaped before they could be measured, and I did not weigh or measure the tarsus length of birds in 1984. This accounts for the discrepancies within Table 2 and between Table 2 and Fig. 1.)

I scored plumage by quantifying the brightness of 16 feathered regions that differed consistently between females and adult males. For each region I developed a scale of 0–3 in which 0 was assigned to the dullest/most femalelike expression of that plumage region, 3 was assigned to the brightest/most adult-male-like expression, and 1 and 2 were assigned to intermediate expressions (see Hill 1987 for details). The scores of the 16 regions were then added, yielding a plumage index with a range of 0 to 48.

To test for size differences between age-sex classes of grosbeaks, I performed paired comparisons of morphological measurements between adult males, subadult males, and females using a two-way Student's *t*-test. There was no year effect in these morphological data ($P > 0.10$ for all comparisons), so data from all 3 yr were pooled for comparisons. I also made paired comparisons of plumage scores between these age classes using a Wilcoxon's rank-sum test. I found no year effect within an age class ($P > 0.10$ for all comparisons), so I made the plumage comparisons using data pooled for all years.

At the Sandia Mountain study site I delineated male

territories by plotting on a map a male's position each time it was seen singing or acting agonistically toward another male. Delineation of adult male territories was completed within 7–10 days of the arrival of the first adult male. Once I was confident that I had adequately sampled a male's singing domain, I connected the outermost of the display points to form a polygon that I used to estimate the position of that male's territory. At the Rio Grande study site I mapped territories less precisely by censusing singing males over several days and outlining approximate territory positions. Using territory maps, I compared the number of total neighbors and the number of subadult neighbors for both subadult and adult males at the Rio Grande site and the Sandia Mountain site (pooled 1984–1986) with a Mann-Whitney U-test.

I removed 1 territorial male in both 1985 and 1986 from the Sandia Mountain study area and 3 males from the Rio Grande study area in 1986. An additional territorial adult male abandoned its territory on the Sandia Mountain site in 1984. I performed all removals within 6 days of the arrival of the first yearling males on the respective study area, 14–18 days after the first adult male had been seen. I monitored vacant territories daily for activity of potential replacement males.

RESULTS

I captured 549 Black-headed Grosbeaks at the Sandia Mountain study site. Most of these birds resided outside of the study area, but I included them in my analysis of morphological characteristics and plumage scores to increase the sample size. As expected, female grosbeaks generally had low plumage indices, with a range of 0–19 (median = 5.0, n = 235). Adult male indices were high, with a range of 39–48 (median = 46.0, n = 210; Fig. 1). Subadult males generally had intermediate plumage scores and were more variable than either adult males or females; scores ranged from 14 to 42 (median = 26.0, n = 106; Fig. 1). Each age-sex class differed significantly from others in plumage score ($P < 0.001$).

There was considerable size overlap among the three age-sex classes of grosbeaks (Table 2). Adult male grosbeaks had significantly longer wings, tails, and tarsi than females and significantly longer wings and tails than subadult males, but females weighed more than either age class of males. Although the differences were not always significant, subadult males were smaller than adult males in all categories (Table 2).

In all years and at both sites, adult males arrived approximately 2 weeks before subadult

TABLE 1. Testable predictions of the female-mimicry hypothesis and the cryptic hypothesis. Asterisks indicate mutually exclusive predictions.

Predictions of the female-mimicry hypothesis

1. Femalelike subadult males arrive on the breeding grounds before brightly plumaged subadult males and before adult males have firmly established territory boundaries.
2. Subadult males are either adult-male-like or femalelike; few intermediates are expected.
3. Yearling males settle both among and peripheral to the territories of adult males.
4. Femalelike subadult males settle with mostly adult male neighbors; adult-male-like subadult males settle with mostly other subadult males as neighbors.
5. Territory vacancies among adult males are filled by femalelike subadult males.*

Predictions of the cryptic hypothesis

6. Subadult males settle peripheral to the territories of adult males.
7. Very few or no subadult males breed; those that do breed are the most brightly plumaged subadult males.
8. Territory vacancies among adult males either remain vacant or are filled by the most brightly plumaged subadult males.*

males; females arrived within a few days of adult males. All territorial adult males settled within 1 week of the arrival of the first adult male in late April or early May. In all cases there was at least 1 week between the arrival and settlement of the latest adult males and the first yearling males. In 2 yr at the Sandia Mountain site, I found no correlation between the date a subadult male arrived (was first captured) and the brightness of its plumage (1984: $r^2 = 0.05$, $n = 42$, $P > 0.16$; 1985: $r^2 = 0.03$, $n = 22$, $P > 0.48$). There was also no significant correlation between arrival date and wing length (1984: $r^2 = 0.05$, $n = 40$, $P > 0.20$; 1985: $r^2 = 0.13$, $n = 18$, $P > 0.09$) or arrival date and mass (1985: $r^2 = 0.01$, $n = 18$, $P > 0.62$) of subadult males.

Adult males began to sing and establish territories within 1–2 days of arriving. By the time subadult males arrived, adult males had firmly established their territories and were breeding. These adult territories generally filled the open riparian areas of the Sandia Mountain study area. Only dry or densely vegetated areas remained unoccupied. At the Rio Grande study area adult males occupied areas with both large cottonwoods and a thick understory, leaving subadult males only areas with little under-
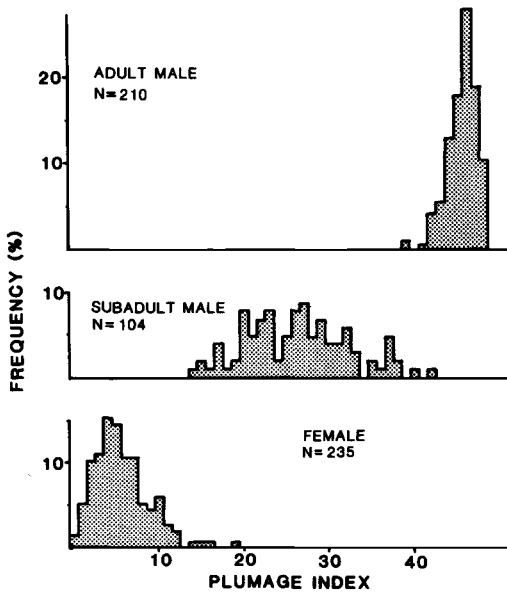
Fig. 1. Plumage index scores of Black-headed Grosbeaks.

story. Between 11 and 15 adult males and 1 or 2 subadult males established territories on the Sandia Mountain study area (Fig. 2), and 41 adult males and 7 subadult males established territories on the Rio Grande study area (Fig. 3).

Of 12 subadult males that established territories and attempted to breed, 11 had plumage scores greater than the median score of all subadult males ($P < 0.003$, binomial test); the plumage score of the remaining male was equal to the median. These breeding subadult males represented only a small proportion of subadult

males that resided on the study areas. As is the case with Red-winged Blackbirds (*Agelaius phoeniceus*; Payne 1979) and probably many other passerine species, nonterritorial subadult males are difficult to census because they are very wide-ranging. I estimated the number of resident subadult males on the Sandia Mountain study site as the number of subadult males either captured or resighted at least three different times over a period of at least 2 weeks. "Resident" is a rather ambiguous term when applied to a floating population of males. I used the term to identify nonterritorial yearling males that spent a significant portion of the breeding period in the vicinity of the study area. Using this definition, 8 of the 42 males banded in 1984, 6 of the 22 banded in 1985, and 7 of the 25 banded in 1986 were resident on the Sandia Mountain study area. I observed many nonterritorial subadult males on the Rio Grande study area as well, but few birds were banded and I could not estimate the population of nonbreeding resident subadult males there.

All territorial subadult males defended territories away from the main cluster of adult male territories (Figs. 2 and 3). Subadult males had significantly fewer total neighbors than did adult males in all 3 yr ($P < 0.004$). The same pattern held for territorial subadult males in the Rio Grande study area ($P < 0.04$) where subadult males also had significantly more subadult neighbors than adult males ($P < 0.04$). At no time did a subadult male display on areas held by adult males for more than a brief period. At the Rio Grande site I observed no subadult males in the northern half of the study area,

TABLE 2. Size comparison of age-sex classes of Black-headed Grosbeaks.

Character	Sex	Age[a]	n	$\bar{x}$	SD	Comparison[b]
Wing length	F	AHY	193	103.31	2.45	AHY-ASY***
(mm)	M	ASY	181	106.59	2.33	ASY-SY***
	M	SY	83	103.48	2.49	AHY-SY[NS]
Tail length	F	AHY	193	78.34	2.68	AHY-ASY***
(mm)	M	ASY	180	79.62	2.45	ASY-SY***
	M	SY	83	77.41	2.59	AHY-SY**
Mass (g)	F	AHY	156	48.18	4.80	AHY-ASY***
	M	ASY	151	46.05	3.34	ASY-SY*
	M	SY	56	44.32	4.98	AHY-SY***
Tarsus	F	AHY	116	21.01	0.84	AHY-ASY**
(mm)	M	ASY	126	21.46	1.32	ASY-SY[NS]
	M	SY	47	21.34	0.38	AHY-SY[NS]

[a] AHY = after hatching year, SY = second year, ASY = after second year.
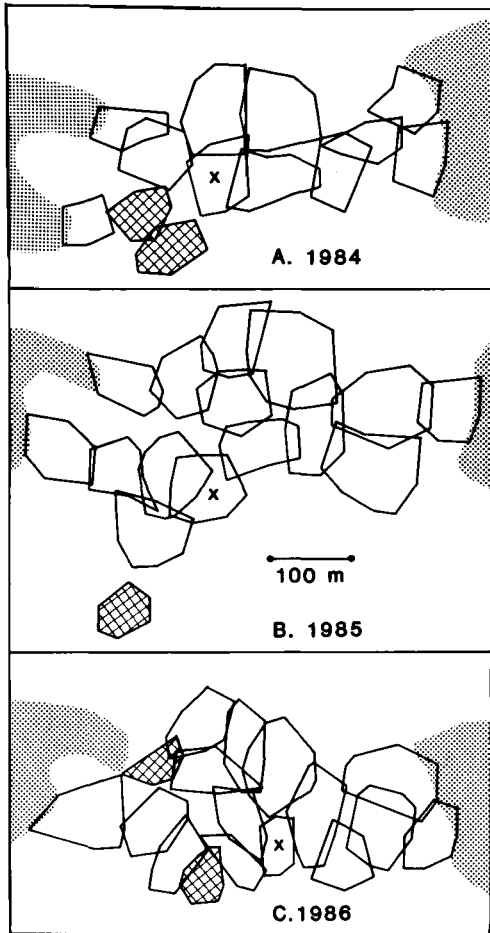[b] * $P = 0.05$, ** $P = 0.01$, *** $P = 0.001$, NS = not significant.

Fig. 2. Spatial arrangement of male Black-headed Grosbeak territories in the Sandia Mountains, New Mexico, in 1984–1986. Territories of subadult males are shaded, territories from which males were removed or that was deserted by the resident male are marked with an ×, and border areas occupied by Black-headed Grosbeaks but outside the study area are stippled.
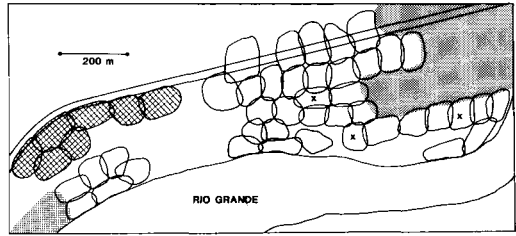

Fig. 3. Spatial arrangement of male Black-headed Grosbeak territories along the Rio Grande, New Mexico, in 1986. Territories of subadult males are shaded, territories from which males were removed are marked with an ×, and border areas occupied by Black-headed Grosbeaks but outside the study area are stippled.

where adult male territories were concentrated (Fig. 3), until late in the season after adult males had ceased to defend boundaries, despite the fact that subadult males were numerous 300 m to the south. At both study sites, when nonterritorial subadult males sang it was generally in the vicinity of territorial subadult males or in some unoccupied locality.

All territory vacancies (Figs. 2 and 3) remained empty, despite the fact that I created vacancies just as subadult males arrived on the study site and just before the settlement of those

subadult males that attempted to breed. In most cases adult males made only brief, peripheral encroachments into the vacant area. That these territories actually remained empty was exemplified by an observation at the removal territory at the Sandia Mountain site in 1986. A captive male, held 4 weeks, was released in Albuquerque at 0530, 16 km from its former territory. By noon that day the male was singing on its territory. I was on the study area for the entire morning and noted no agonistic interactions, so I presume that the male simply reoccupied its still-vacant territory.

Subadult male grosbeaks initiated nests later than adult males (Hill 1988), but too few subadult males bred for the differences to be significant statistically. Nesting success varied substantially among years and sites (Table 3). Except for 1985 at the Sandia Mountain site, subadult males had lower nesting success than did adult males in all years and at both sites, with a significant difference in the pooled data ($P < 0.02$, Fisher's exact test). No chicks starved in any of the nests I monitored, and there were no instances of partial brood loss (excluding unhatched eggs). Nearly all failed nests at the Sandia Mountain site were lost to nest predators, primarily Scrub Jays (*Aphelocoma coerulescens*) and Steller's Jays (*Cyanocitta stelleri*; Hill 1988).

TESTS OF PREDICTIONS (Table 1)

Prediction 1.—The female-mimicry hypothesis proposes that subadult males that resemble females use their deceptive appearance to gain access to adult male territories, thereby enhancing their ability to carve out their own territories in high-quality habitat (Rohwer et al.

TABLE 3. Nesting success of Black-headed Grosbeak pairs.

	Age of male	Success-ful	Failed	Total
Sandia Mountain study area				
1984	Adult	5	3	8
	Subadult	0	2	2
1985	Adult	8	2	10
	Subadult	1	0	1
1986	Adult	6	5	11
	Subadult	0	2	2
Rio Grande study area				
1986	Adult	11	1	12
	Subadult	1	2	3
Pooled	Adult	30	11	41
	Subadult	2	6	8

1980, Rohwer 1983). Femalelike subadult males are predicted to arrive on the breeding grounds relatively early, before adult males have rigidly established their territory boundaries, which gives them the opportunity to slip in among adult males. Brightly plumaged yearling males, on the other hand, are expected to do well in competition with other subadult males and poorly in competition with adult males. Brightly plumaged yearling males are expected to arrive relatively late, after adult males have settled, to avoid direct competition with adult males. The cryptic hypothesis makes no strong prediction regarding the arrival sequence, but it predicts a relatively late arrival by all subadult males so they can avoid direct competition with adult males.

Rohwer et al. (1980) generated a different prediction from the female-mimicry hypothesis regarding the arrival sequence for subadult males, but I believe their assumptions in making this prediction are invalid for Black-headed Grosbeaks. My prediction and that made by Rohwer et al. agree that successful female mimics must arrive after adult males have settled but before territories are rigidly delineated. We disagree on the presumed optimal strategy for brightly plumaged subadult males under the female-mimicry hypothesis. Rohwer et al. assumed that brightly plumaged subadult males could compete succcessfully with adult males if they arrived early and settled among adult males. Brightly plumaged subadult males that arrive after adult males have settled are assumed to have missed potential breeding opportunities.

In contrast, I argue that even the most brightly plumaged subadult male cannot compete effectively with adult males, so the best strategy for these adult-male-like subadult males is to delay arriving on the breeding grounds until adult males have firmly established territories. Brightly plumaged subadult males may then settle in the remaining habitat without the threat of direct conflict with adult males.

The lack of correlation between arrival date and plumage brightness and the late arrival of all subadult males is inconsistent with either prediction under the female-mimicry hypothesis. The most convincing falsification is that in all years and at both sites, no femalelike subadult males (or any subadult males for that matter) were yet present by the time all resident adult males had arrived, established territory boundaries, and paired with females. Although not strongly supported, the cryptic hypothesis is at least in accord with these observations.

Prediction 2.—Under the female-mimicry hypothesis, yearling males gain an advantage either in interactions with adult males by appearing to be females (sporting a dull plumage) or in conflicts with other yearlings by having a bright plumage. Yearlings with intermediate plumages are at a disadvantage in competition with both adult males and yearling males. The female-mimicry hypothesis thus predicts a bimodal distribution of yearling male plumage types such that most individuals should be either very bright or very dull. Yearling males with intermediate plumages are expected to be relatively rare (prediction 2 of Rohwer et al. 1980: 421). The cryptic hypothesis makes no specific prediction about the frequency of plumage types. Thus, the observed distribution (Fig. 1), in which yearling males with intermediate plumage predominate and individuals with very bright or very dull plumage are rare, is not in agreement with the prediction of the female-mimicry hypothesis. The observed distribution is neutral with repect to the cryptic hypothesis.

Predictions 3 and 6.—Given the two strategies for reproduction by yearling males proposed by the female-mimicry hypothesis, subadult males are predicted to establish territories both among adult males in high-quality habitat, with mostly adult males as neighbors, and peripheral to adult males in marginal habitat, with mostly other subadult males as neighbors. Conversely, the cryptic hypothesis predicts that, regardless of plumage type, subadult males are competitively

inferior to adult males. Thus, if subadult males breed at all, the cryptic hypothesis proposes that they will settle away from adult males with other subadult males as their neighbors.

The observation that yearling male grosbeaks settled peripherally to clusters of adult male territories (Figs. 2 and 3) is in accord with predictions of the cryptic hypothesis, but, because no subadult males settled among adult males, it partially falsifies the female-mimicry hypothesis.

Predictions 4 and 7.—Superimposed on the settlement pattern predicted by the female-mimicry hypothesis (Prediction 3) is the prediction that subadult males that settle among adult males will be femalelike, whereas those that settle peripherally to adult males will be bright. The cryptic hypothesis predicts that bright subadult males will settle peripherally to (in less preferred habitat than) adult males, but that femalelike subadult males will not breed. Predictions of the cryptic hypothesis are based on the assumption that bright plumage carries higher costs, realized in terms of increased mortality, than does dull (cryptic) plumage. At the same time, bright plumage has the benefit of increasing the competitive ability or attractiveness of the bearer, or both. Consequently, brightly plumaged males have a lower probability for future reproduction relative to dully plumaged males but an increased opportunity for immediate reproduction, so they are expected to invest more in first-year reproduction. As with Predictions 3 and 6, my observation that only brightly plumaged subadult males bred supports predictions of the cryptic hypothesis, but, because no "female mimics" bred, it is not consistent with the female-mimicry hypothesis.

Predictions 5 and 8.—When adult territory vacancies occur, such as when an adult male dies after establishing a territory and no adult males without territories are in the vicinity, the female-mimicry hypothesis predicts that the vacancy will be filled by a femalelike subadult male. According to the female-mimicry hypothesis, femalelike yearling males use their deceptive appearance to gain access to adult male territories, thus establishing site dominance (Rohwer et al. 1980, Rohwer 1983). This presumably makes femalelike subadult males more competitive than brightly plumaged subadult males in claiming such vacancies. The cryptic hypothesis predicts the opposite. Given the higher probability of mortality and greater

competitive abilities of brightly plumaged yearling males, they are expected to outcompete dully plumaged subadult males in any circumstance, including the acquisition of vacated territories. If the competitive abilities of even the most brightly plumaged yearling male are still much less than those of adult males, then no subadult is expected to fill the vacancy because no subadult male could handle the aggressive arena that the vacated territory presents.

The failure of subadult males to fill vacant territories of adult males contradicts a key prediction of the female-mimicry hypothesis. In contrast, it is in accord with predictions of the cryptic hypothesis.

DISCUSSION

When fitted to the predictions (Table 1), studies of other North American passerines also fail to support the female-mimicry hypothesis. Subadult male Painted Buntings (*Passerina ciris*; Lanyon and Thompson 1986), American Redstarts (*Setophaga ruticilla*; Ficken and Ficken 1967, Sherry 1979), Red-winged Blackbirds (Orians 1961, Greenwood 1985), and Tricolored Blackbirds (*Agelaius tricolor*; Orians 1961) defend territories that are peripheral to the territories of adult males. Moreover, subadult males of these species appear to settle in inferior habitat relative to that occupied by adult males. For instance, the territories of subadult male redstarts have a relatively high proportion of coniferous vegetation and high density of Least Flycatchers (*Empidonax minimus*), a competitively dominant species (Sherry 1979), making them less suitable for breeding than the territories of adult males (Sherry and Holmes 1985, Sherry pers. comm.). Like the settlement pattern observed in grosbeaks, these results are not consistent with Predictions 3 and 4 of the female-mimicry hypothesis (Table 1). A removal experiment conducted on Red-winged Blackbirds (Orians 1961) also verifies my findings. Despite the presence of a large floating population of yearling males, vacated adult territories were not occupied by subadult males until several groups of adult replacement males had been removed and few adult males remained on the marsh. There was no rapid replacement of the original removals by site-dominant subadult males, as would have been expected under the female-mimicry hypothesis. This result corroborates my falsification of Prediction 5 (Table 1).

Other studies also support my findings involving plumage variability. In both Indigo Buntings (*Passerina cyanea*; Payne 1982) and Pied Flycatchers (*Ficedula hypoleuca*; Alatalo et al. 1984) no correlation existed between the arrival date of subadult males and their plumage type, supporting the falsification of Prediction 1 (Table 1). Finally, in no species in which yearling males display subadult plumage is there a bimodal distribution of subadult male appearances (see Rohwer et al. 1980: 404–405). Subadult males of the 31 species of dichromatic North American passerines that display delayed plumage maturation are either all femalelike, all adult-male-like, or predominantly intermediate. Again, this supports my finding and falsifies Prediction 2 (Table 1). (The bimodal distribution of subadult plumages noted by Lyon and Montgomerie [1986] is an artifact of using the mean plumage scores of species. It reflects the tendency for individuals of many species to be mostly adult-male-like or femalelike and does not represent bimodality within species.)

In contrast to the female-mimicry hypothesis, my observations are consistent with the cryptic hypothesis. For the cryptic hypothesis to be applicable, there must be intense competition among males for females or the resources needed to attract females, and yearling males must be sufficiently disadvantaged in such competition that their best strategy is to reduce their reproductive effort and maximize their probability of surviving or their future reproductive status. Yearling male grosbeaks are smaller than adult males and lack their experience, so if intermale competition were keen, it would not be surprising to find that subadults fared poorly. Black-headed Grosbeaks are strictly monogamous, however (Weston 1947, Ritchison 1983, this study), a situation that is generally believed to result in low intrasexual competition (Payne 1984). Indeed, in the population I studied, access to females did not appear to limit male reproduction. No male grosbeak successfully defended a territory without attracting a female. Moreover, the operational sex ratio of males to females at the Sandia Mountain study area over 2 yr was skewed in favor of females (0.71:1.00, $n = 250$; Hill 1986), and some females probably resided on the study area without pairing with a male. Particularly compelling evidence for this latter point is my observation of a resident female killing an intruding female, apparently over access to a territorial male (Hill 1986).

In contrast to this apparent surplus of females, a combination of moderate fecundity and high annual adult male survivorship appears to result in a severe limitation of territory space for male grosbeaks. My data on life-history characteristics of Black-headed Grosbeaks are limited, and for this reason they must be applied cautiously. Nevertheless, I think they can provide insight into the potential value of subadult plumage for yearling male grosbeaks. Adult male survivorship at the Sandia Mountain site was relatively high in both 1985 (82%) and 1986 (65%). Moreover, grosbeak pairs fledged an average of 1.3 young in 1984 and 2.7 young in 1985. As a result few adult territories were vacated between years, and these vacancies were filled by males that had been resident subadult males in the previous year (Hill 1988), leaving virtually no site of suitable quality on which inexperienced yearling males could breed. Thus, as predicted by Brown (1969), a combination of high survivorship and moderate fecundity apparently has resulted in a surplus of both sexes in the breeding season. This means that for subadult male grosbeaks the only unoccupied sites for a territory are in habitat with little vertical vegetation structure and high potential nest predation, where the probability of successful reproduction is low (Hill 1988). Under such conditions of low probability for first-year reproductive success and a relatively long expected individual lifespan, a strategy of reduced reproductive effort, including late arrival on the breeding grounds and delayed maturation of plumage that increases survival probability, would be favored (Studd and Robertson 1985).

Because the cryptic hypothesis fits with my own and other's observations, it is tempting to embrace the idea strictly on the basis of corroborative evidence. As has been the case with other studies of delayed plumage maturation, however, corroborative evidence can be misleading. Unlike the female-mimicry hypothesis, none of the predictions that I tested was central to the cryptic hypothesis. To test this hypothesis rigorously, reliable data on the survivorship and lifetime reproductive success of subadult males of different plumage types and first-year reproductive status are required (Studd and Robertson 1985). Because Black-headed Grosbeaks migrate annually and can easily dis-

perse widely, I could not reliably estimate mortality figures for yearling males. Thus, the critical test of the cryptic hypothesis remains to be conducted.

LITERATURE CITED

ALATALO, R. V., A. LUNDBERG, & K. STAHLBRANDT. 1984. Female mate choice in the Pied Flycatcher *Ficedula hypoleuca*. Behav. Ecol. Sociobiol. 14: 253–261.

BROWN, J. L. 1969. Territorial behavior and population regulation in birds: a review and re-evaluation. Wilson Bull. 81: 293–329.

FICKEN, M. S., & R. W. FICKEN. 1967. Age-specific differences in the breeding behavior and ecology of the American Redstart. Wilson Bull. 79: 188–199.

FLOOD, N. J. 1984. Adaptive significance of delayed plumage maturation in male Northern Orioles. Evolution 38: 267–279.

GREENWOOD, H. 1985. Sexual selection and delayed plumage maturation of the subadult male cohort of the Red-winged Blackbird (*Agelaius phoeniceus*). Ph.D. dissertation, Montreal, McGill Univ.

HILL, G. E.. 1986. Severe aggression between female Black-headed Grosbeaks. Wilson Bull. 98: 486–488.

———. 1987. Aging and sexing Black-headed Grosbeaks in alternate plumage. J. Field Ornithol. 58: 311–317.

———. 1988. Age, plumage brightness, territory quality, and reproductive success in the Black-headed Grosbeak. Condor in press.

KREBS, J. R. 1982. Territorial defense in the Great Tit (*Parus major*): do residents always win? Behav. Ecol. Sociobiol. 11: 185–194.

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

———. 1968. Ecological adaptations for breeding birds. London, Methuen.

LANYON, S. M., & C. F. THOMPSON. 1986. Site fidelity and habitat quality as determinants of settlement pattern in male Painted Buntings. Condor 88: 206–210.

LYON, B. E., & R. D. MONTGOMERIE. 1986. Delayed plumage maturation in passerine birds: reliable signaling by subordinate males? Evolution 40: 605–615.

ORIANS, G. H. 1961. The ecology of blackbird (*Agelaius*) social systems. Ecol. Monogr. 31: 285–312.

PAYNE, R. B. 1979. Sexual selection and intersexual differences in variance of breeding success. Am. Nat. 114: 447–466.

———. 1982. Ecological consequences of song matching: breeding success and intraspecific song mimicry in Indigo Buntings. Ecology 63: 401–411.

———. 1984. Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. Ornithol. Monogr. No. 33.

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

RITCHISON, G. 1983. Breeding biology of the Black-headed Grosbeak in northern Utah. West. Birds 14: 159–167.

ROHWER, S. 1978. Passerine subadult plumages and the deceptive acquisition of resources: test of a critical assumption. Condor 80: 173–179.

———. 1983. Testing the female mimicry hypothesis of delayed plumage maturation: a comment on Procter-Gray and Holmes. Evolution 37: 421–423.

———. 1986. A previously unknown plumage of first-year Indigo Buntings and theories of delayed plumage maturation. Auk 103: 281–292.

———, S. D. FRETWELL, & D. M. NILES. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. Am. Nat. 115: 400–437.

———, W. P. KLEIN JR., & S. HEARD. 1983. Delayed plumage maturation and the presumed prealternate molt in American Redstarts. Wilson Bull. 95: 199–208.

———, & D. M. NILES. 1979. The subadult plumage of male Purple Martins: variability, female mimicry and recent evolution. Z. Tierpsychol. 51: 282–300.

SAMSON, F. B. 1976. Pterylosis and molt in Cassin's Finch. Condor 78: 505–511.

SELANDER, R. K. 1965. On mating systems and sexual selection. Am. Nat. 99: 129–141.

———. 1972. Sexual selection and dimorphism in birds. Pp. 180–230 *in* Sexual selection and the descent of man (B. G. Campbell, Ed.). Chicago, Aldine.

SHERRY, T. W. 1979. Competitive interactions and adaptive strategies of American Redstarts and Least Flycatchers in a northern hardwood forest. Auk 96: 265–283.

———, & R. T. HOLMES. 1985. Dispersion patterns and habitat responses of birds in northern hardwood forests. Pp. 283–309 *in* Habitat selection in birds (M. L. Cody, Ed.). London, Academic Press.

STUDD, M. V., & R. J. ROBERTSON. 1985. Life span, competition, and delayed plumage maturation in male passerines: the breeding threshold hypothesis. Am. Nat. 126: 101–115.

WESTON, J. G., JR. 1947. Breeding behavior of the Black-headed Grosbeak. Condor 49: 54–73.