

AGE, PLUMAGE BRIGHTNESS, TERRITORY QUALITY, AND REPRODUCTIVE SUCCESS IN THE BLACK-HEADED GROSBEAK¹

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Abstract. I studied a color-banded population of Black-headed Grosbeaks (*Pheucticus melanocephalus*) in the Sandia Mountains of central New Mexico to investigate the relationship between the age and plumage brightness of territorial males and the quality of their breeding habitat. In three seasons of fieldwork, I found that the breeding territories defended by males varied in vegetation structure and hence in the abundance of Scrub Jays (*Aphe- locoma coerulescens*) and Steller's Jays (*Cyanocitta stelleri*), the primary nest predators of grosbeaks. Age appeared to be the primary correlate of male territory quality. Males 3 years and older defended areas with heterogeneous vegetation and low density of jays and, consequently, had high reproductive success; yearling and 2-year-old males occupied more densely vegetated areas with higher jay activity and had lower reproductive success. Independent of age, there was also a tendency for brightly plumaged males to occupy more heterogeneous habitat with lower jay activity than duller males. This age-and-plumage-structured settlement pattern is apparently maintained between years by the shifting of males into more preferred habitat as they become older. These observations are consistent with the hypothesis that habitat saturation, resulting in limited opportunities for recruitment into the breeding population, may have been an important factor in the evolution of delayed plumage maturation in this species.

Key words: Territory quality; age; plumage brightness; nest predation; Black-headed Grosbeak; Scrub Jay; Steller's Jay; delayed plumage maturation; New Mexico.

INTRODUCTION

Males of many avian species defend territories during the breeding season that contain resources both limited in supply and critical to successful reproduction (Brown 1969, Fretwell and Lucas 1970). In species that are seasonal migrants, returning males usually reoccupy their former territories (Greenwood and Harvey 1982), but if suitable nesting habitat is limited, young and previously unsuccessful males will compete for the available spaces (Brown 1969). Males that are unable to successfully defend a territory are forced to leave the breeding habitat or become non-breeding floaters with limited opportunity for successful reproduction (Brown 1969, Smith 1978, Arcese 1987).

Within suitable breeding habitat, crucial resources are seldom evenly distributed, so the quality of male territories varies (Fretwell and Lucas 1970, Pleszczynska 1978). Moreover, be-

cause the quality of breeding habitat that a male defends largely determines its reproductive success, either through the provisioning of more young (Högstedt 1980) or the attraction of more females that produce more young (Searcy 1979, Lenington 1980, Wittenberger 1980, Askemo 1984) or both (Pleszczynska 1978, Pleszczynska and Hansell 1980), males compete for territories of high quality. Thus, when breeding habitat is saturated, males vie for territories on two levels: first for possession of any territory and then for possession of a territory of high quality (Brown 1969).

The manner in which breeding habitat is partitioned among individual males is poorly understood. Fretwell and Lucas (1970) predicted that dominant males would occupy preferred or high quality territories, but few studies have sought to quantify the attributes that make a male dominant and enable it to gain and hold preferred breeding habitat (but see Petrie 1984, Eckert and Weatherhead 1987). To address these questions I monitored a color-banded population of a monogamous passerine species, the Black-headed Grosbeak (*Pheucticus melanocephalus*).

Black-headed Grosbeaks are common sum-

¹ Received 16 July 1987. Final acceptance February 1988.

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mer residents throughout forested regions of western North America. Male and female Black-headed Grosbeaks are highly dichromatic and slightly dimorphic in size, males being the larger and more brightly colored sex (Hill 1987, 1988). In their first breeding season, male grosbeaks are sexually mature and capable of breeding (Hill 1988), but they do not attain a fully-adult alternate plumage until their second spring (Hill 1987, 1988). The extent to which individual males delay plumage maturation is highly variable, however, with some yearling males attaining an almost complete definitive alternate plumage and resembling adult males, while others retain most of their first basic plumage and more closely resemble females (Hill 1987, 1988). In addition, the definitive alternate plumages of individual adult males vary substantially in brightness (Hill 1988).

The manner in which breeding habitat is partitioned among males, particularly of different age classes, bears directly on theories of delayed plumage maturation (Rohwer et al. 1980, Rohwer 1983, Lyon and Montgomerie 1986). Two principal hypotheses have been proposed to explain the function of subadult plumage in male passerines: (1) young males sport a subadult plumage to mimic females and use their deceptive appearance to gain an advantage in acquiring territories (female-mimicry hypothesis; Rohwer et al. 1980); or, (2) yearling males display a relatively dull breeding plumage to avoid aggression from older males and to reduce their risk of predation (cryptic hypothesis; Procter-Gray and Holmes 1981, Selander 1972). A critical assumption of both of these hypotheses is that yearling males are disadvantaged in their first reproductive season because older, more experienced males monopolize females or breeding habitat. However, within the cryptic hypothesis dull subadult plumage has been proposed to function in two manners. Lyon and Montgomerie (1986) suggested that subadult plumage could serve as a reliable signal of subordinance if females choose males on the basis of plumage coloration rather than territory quality; therefore, delayed plumage maturation should be found in species in which males defend simple nesting territories that do not vary in quality. Alternatively, subadult plumage may function primarily as a signal of fighting ability in intrasexual aggressive encounters and should occur when males compete for limited resources (Procter-Gray and

Holmes 1981). Thus, an understanding of territoriality in species that display delayed plumage maturation can aid in evaluating hypotheses for the evolution of subadult plumage.

Black-headed Grosbeaks are a good subject for investigating questions related to territoriality because males vigorously defend fairly discrete territories, which are re-established at the beginning of each breeding season. Also, the distinctive subadult plumage of yearling male grosbeaks is useful in determining the age classes of males and makes grosbeaks good subjects for testing models of delayed plumage maturation (Hill 1988). My goals in this study were to investigate how male Black-headed Grosbeaks partition breeding habitat by (1) quantifying the resources that are defended by territorial males, (2) measuring the extent to which territories vary in characteristics that affect reproductive output (i.e., quality), and (3) identifying the attributes of a male grosbeak that are correlated with the type of habitat that it can defend. In addition, I used observations on grosbeak territoriality to evaluate models for the evolution of delayed plumage maturation.

METHODS

I collected data on breeding Black-headed Grosbeaks from late April through early August 1984 to 1986 in the Sandia Mountains of central New Mexico (elevation 2,100 m) about 16 km east of Albuquerque. The 15-ha study area was centered in a narrow moist valley, bounded to the north and south by dry hillsides. The central and eastern sections of the valley supported a patchwork of different vegetation types including areas with large deciduous trees, predominantly willow (*Salix* sp.), Fremont cottonwood (*Populus fremontii*), white poplar (*P. alba*), Lombardy poplar (*P. nigra*), and Chinese elm (*Ulmus parvifolia*), with either no understory or small dense patches of willow (*Salix* sp.). Interspersed among these groves of large trees were small fields and patches of dense shrubby vegetation (Fig. 1). In contrast, the western section of the valley supported a more uniform low dense growth of Gambel oak (*Quercus gambelii*), willow (*Salix* sp.), Russian olive (*Elaeagnus angustifolia*), and common juniper (*Juniperus communis*). The hillside to the south supported a dense band of Gambel oak at its base with pinyon (*Pinus edulis*)-juniper woodland above. The north hillside supported only pinyon-juniper woodland (Fig. 1).

I color-banded and determined the age and sex (see Hill 1987 for details) of all resident male and most resident female Black-headed Grosbeaks. I scored the plumage of individual grosbeaks by ranking the appearance of 16 feathered regions on a 4-point scale. The scale for most of these 16 regions measured the intensity of rust coloration on various parts of the bird and the degree of contrast between the dark and light patches on the wings and tail. Zero was assigned to the most feminine expression of a region, 3 to the most masculine expression, 1 or 2 to intermediate expressions. The sixteen scores obtained from each bird were then summed to give a plumage brightness index with a range of 0 to 48 (see Hill 1987 for details).

For the purpose of analysis I recognized three age classes of males: (1) males 3 years old or older, which were breeding in adult plumage for at least the second season (hereafter, old adult males), (2) 2-year-old males, which were breeding in adult plumage for the first season (hereafter, young adult males), and (3) yearling males in subadult plumage. I delineated the territories of males by plotting on a map a male's position each time I observed it singing or acting agonistically toward another male. I connected the outermost of these points to form an estimate of the size and position of that male's territory (maximum territory estimate; Odum and Kuenzler 1955).

In 1986, I also monitored a population of Black-headed Grosbeaks along the Rio Grande north of Albuquerque, about 25 km from the Sandia Mountain study area. I was able to band only a few birds in this population and I could class males only as adult or subadult, so I will use observations from this population primarily for comparison to the Sandia Mountain site.

For a monogamous species like the Black-headed Grosbeak, the quality of a breeding territory can be measured in terms of the reproductive success of the birds that occupy it. Habitat in which pairs fledge a relatively large number of young on average is judged to be of higher quality than habitat in which pairs fledge fewer young on average (assuming that the pairs being compared are equivalent in other respects such as age, experience, and vigor). I used this definition to recognize high and low quality habitat and then looked for features (resources) that varied among habitats and correlated with reproductive success.

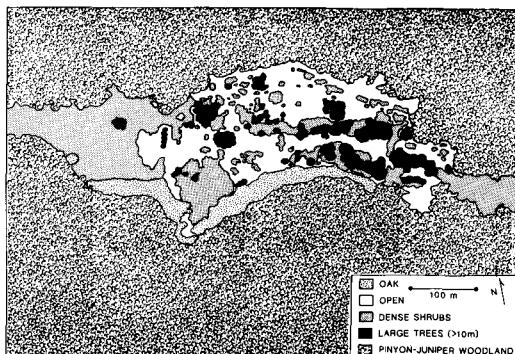


FIGURE 1. Vegetation structure of the Sandia Mountain study site.

To quantify the gross vegetation structure within a male's territory, I superimposed the boundaries of male territories on an aerial photo of the study area and used a planimeter to measure the area within each territory covered by (1) open meadows, (2) large trees (>10 m), and (3) all other woody vegetation (pinyon-juniper, oak, willow, etc.), which I lumped as dense vegetation. Open areas smaller than 10 m^2 were lumped with the woody vegetation that surrounded them. In analyzing the vegetation structure of the territories of males of different ages, I pooled data between years, but because males often returned to the same territory between years, some samples were not independent. Consequently, I used data from repeat males only in the first year of their occurrence in which their age was known. If a male shifted territories (with no overlap) between years, I used both territories in my analysis.

I checked nests every other day using a mirror attached to a pole and recorded the number of eggs or nestlings present. I estimated the reproductive success of a male grosbeak by whether it fledged young from its nest. Throughout the paper when I refer to the reproductive success of males within an age class or in a particular habitat, I will mean the percent of nests in that group that fledged young.

I assumed that nests had been robbed by Scrub Jays (*Aphelocoma coerulescens*) or Steller's Jays (*Cyanocitta stelleri*) in cases in which the contents were removed but the nest, including the lining, was undamaged. I witnessed the theft of grosbeak eggs by jays on only one occasion, but there was strong circumstantial evidence that jays were responsible for robbing most or all grosbeak

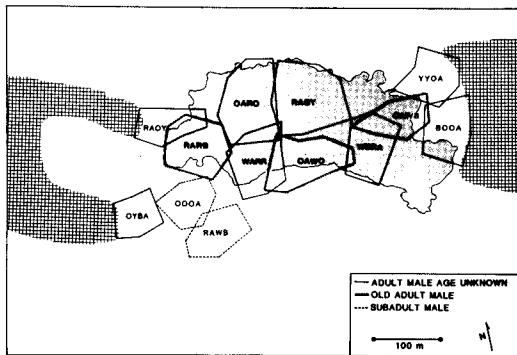


FIGURE 2. The spatial arrangement of the territories of male Black-headed Grosbeaks at the Sandia Mountain study area in 1984. The cross-hatched region was occupied by grosbeaks but not carefully monitored, and the shaded area denotes heterogeneous vegetation (see Fig. 1). Males are identified by band codes.

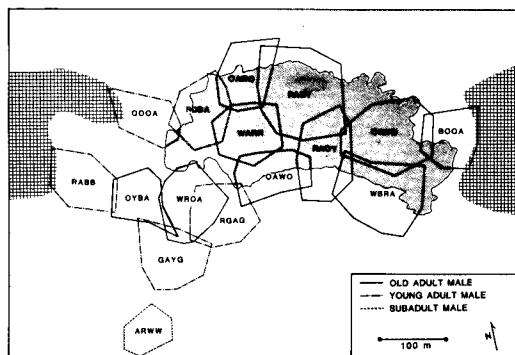


FIGURE 3. The spatial arrangement of the territories of male Black-headed Grosbeaks at the Sandia Mountain study area in 1985. The cross-hatched region was occupied by grosbeaks but not carefully monitored, and the shaded area denotes heterogeneous vegetation (see Fig. 1). Males are identified by band codes.

nests. Both species of jays are relentless nest predators of all cup-nesting species in the area (Bent 1946; pers. observ.; J. D. Ligon, pers. comm.), where they are the only common nest predator (pers. observ.). Furthermore, seven dummy nests containing soft clay eggs anchored by 5-cm strings were set out around the study area in June 1987, and in five of these nests jays attempted to remove the eggs within a few hours to 8 days. In two of the above cases Scrub Jays were witnessed robbing the dummy nest; in the remaining cases, bill impressions implicated jays.

To monitor the time that grosbeaks spent sitting on nests and to estimate the activity of Scrub and Steller's jays around nests, I conducted 40-min nest watches. I estimated jay activity by recording the number of seconds that jays spent within 10 m of the nest during the 40-min observation period, averaged over three or more observations conducted at least 24 hr apart. I recorded jay activity at all nests that I located in 1985 and 1986 but only at four nests in 1984. In calculating time spent incubating, I used only observations that recorded entire individual attendance periods between exchanges.

Most of my data sets were small, contained categorical variables, and consisted of values that were not normally distributed. For this reason I made statistical comparisons using nonparametric tests following Siegel (1956). I used data pooled between years for all comparisons, but I excluded data from repeat males in comparisons where such data posed problems with independence of samples.

RESULTS

SETTLEMENT PATTERN

Male Black-headed Grosbeaks displayed a conspicuous age-related settlement pattern. Of the 13 males in my study area in 1984, I knew the age class of only five—the two breeding subadults and three old adult males that had been banded on the study area as adult males in 1983. The three old adult males settled largely in the heterogeneous habitat, and the two territorial subadult males settled in the low dense vegetation of the western section of the valley, peripheral to the cluster of adult male territories (Figs. 1 and 2).

This pattern of habitat segregation by age class was clearer in 1985 and 1986, when I had marked males returning and could thus sort all males into specific age groups. Yearling males continued to hold peripheral territories in structurally simple habitat; old adult males, with few exceptions, occupied territories in the most heterogeneous habitat with the greatest vertical vegetation structure in the central and eastern sections of the valley; and young adult males generally settled between subadult and old adult males in areas with intermediate vegetation structure and density (Figs. 1, 3, and 4).

VEGETATION STRUCTURE

A comparison of the gross vegetation structure of the territories of the three age classes of males confirmed that they settled in structurally different habitats. Yearling-male territories had a

greater proportion of dense woody vegetation and a lower proportion of large trees than the territories of either young or old adult males; the territories of young adult males were intermediate to the territories of yearling and old adult males in both features ($P < 0.02$ for comparisons of both vegetation features, Kruskal-Wallis one-way ANOVA; $n = 5, 11, 11$ for males age 1, 2, 3+ years). The territories of yearling males also had significantly less open area than those of old adult males ($P < 0.01$, Mann-Whitney U -test; $n = 5, 11$, respectively), but the territories of young adult males did not differ significantly from the territories of either yearling or old adult males in the proportion of open area ($P > 0.10$ for both comparisons, Mann-Whitney U -test; same n as above).

Despite the differences in vegetation structure among grosbeak territories, there was no obvious difference in the abundance of food or the availability of nest sites among territories. No grosbeak nestlings starved; all nest losses were due to predators or, in a few cases, nest desertion or storms. Moreover, grosbeaks nested in open cups of grass and twigs, which they constructed in at least seven species of tree or shrub that were abundant everywhere on the study site. There were, however, obvious differences in predator abundance among territories.

JAY ACTIVITY AND REPRODUCTIVE SUCCESS

The abundance of Scrub and Steller's jays was directly related to vegetation structure. Jays appeared to prefer to stay in the low, dense vegetation of the western valley and the oak and pinyon-juniper woodlands of the north and south hillsides and to avoid the more open, heterogeneous habitat of the central and eastern valley. The habitat preference of jays was reflected in the amount of time that jays spent around nests in these various regions. For the purpose of comparison, I divided nests into those in heterogeneous habitat in the central and eastern valley and those in the vegetation of surrounding habitats (i.e., those that fell inside the shaded region of Figs. 2 to 4 vs. those that fell outside). The jay activity around nests in heterogeneous vegetation (median = 0.0 sec, $n = 10$) was significantly lower than the jay activity around nests in areas with denser vegetation (median = 50.6 sec, $n = 19$; $P < 0.001$, Mann-Whitney U -test). Moreover, the increase in jay activity away from

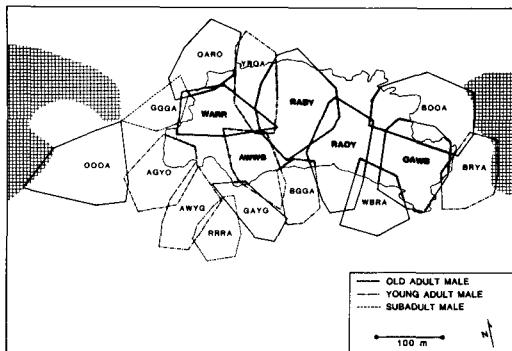


FIGURE 4. The spatial arrangement of the territories of male Black-headed Grosbeaks at the Sandia Mountain study area in 1986. The cross-hatched region was occupied by grosbeaks but not carefully monitored, and the shaded area denotes heterogeneous vegetation (see Fig. 1). Males are identified by band codes.

the heterogeneous habitat had a direct negative impact on the nesting success of grosbeaks. Only 12% (2/17) of nests in the heterogeneous habitat were lost to predators while 67% (12/18) of nests in denser habitat were robbed ($P = 0.001$, Fisher's exact probability test). There were no significant differences in the height of nests placed in dense vs. heterogeneous habitats ($P > 0.19$, Mann-Whitney U -test).

To more directly test whether jay activity around nests has an effect on reproductive success, I compared the success of nests in areas with different levels of jay activity. I arbitrarily divided the data into three categories (by dividing the data into three approximately equal parts) based on measured levels of jay activity: (1) no jay activity (hereafter, low jay activity; nine nests); (2) an average of 0.5 to 51.0 sec of jay activity (hereafter, moderate jay activity; 10 nests); and (3) an average of 52.0 to 350.0 sec of jay activity (hereafter, high jay activity; 10 nests). Reproductive success of pairs nesting in areas with low jay activity (8/9, 89%) was higher than the success of pairs in areas with moderate jay activity (6/10, 60%) which, in turn, was higher than the success of pairs nesting in areas with high jay activity (2/10, 20%; $\chi^2 = 20.3$, $df = 2$, $P < 0.001$, extension of the median test). The habitat-age associations that I described previously also resulted in significant differences in the amount of jay activity in the territories of male grosbeaks of different ages. Median jay activity around the nests of subadult males in the densest vegetation was 175 sec; around young adult male nests in

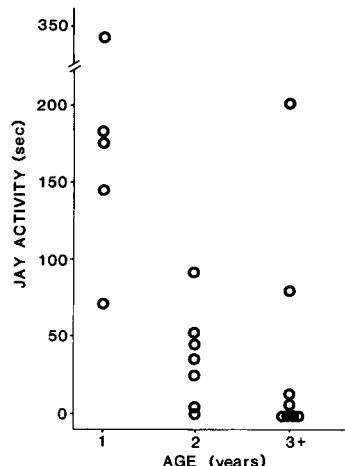


FIGURE 5. Amount of time spent by jays within 10 m of the nests of male Black-headed Grosbeaks in relation to the age of the grosbeaks.

intermediate habitat it was 34 sec; and around the nests of adult males (excluding repeat males) in the most open habitat it was 4 sec ($H = 8.0$, $df = 2$, $P < 0.012$, Kruskal-Wallis one-way ANOVA; Fig. 5).

AGE EFFECTS

The overall reproductive success (excluding failed first attempts when the pair renested), again measured as the proportion of nests that fledged young, was higher for old adult males (79%) than for young adult males (50%), and both were higher than that for subadult males (20%; $\chi^2 = 6.4$, $df = 2$, $P < 0.05$, extension of the median test; Table 1). To see if differences in reproductive success are attributable to differences in habitat occupied by grosbeaks of different ages and not to an age effect such as inexperience at nest defense, I compared the success of pairs within an age class nesting in areas with different jay activity. Old adult males nested successfully 100% (8/8) of the time in areas with low jay activity, 60% (3/5) of

the time in areas with moderate jay activity, and 33% (1/3) of the time in areas with high jay activity. The only young adult male that nested in an area with low jay activity failed, while 60% (3/5) of young adult males that nested in areas with moderate jay activity were successful and none (0/2) were successful in areas with the highest jay activity. The samples are small, but the trends are as predicted (lower reproductive success in areas with higher jay activity) with the exception of the reproductive failure of the single young adult male that settled in an area with low jay activity.

Because all subadult males nested in dense habitat with high jay activity, I could not make between-habitat comparisons within this age group. However, other evidence supports the assertion that yearling males are as capable as adult males at fledging young given favorable conditions. Subadult males were as attentive at nests as adult males, spending about as much time sitting on eggs ($\bar{x} = 1,526$ sec, $SD = 537$, $n = 13$) as either adult males ($\bar{x} = 1,949$ sec, $SD = 930$, $n = 19$) or females ($\bar{x} = 1,761$, $SD = 725$ sec, $n = 13$; $P > 0.11$ for all comparisons, t -test; Table 1). The two yearling male grosbeaks (one at the Sandia study area and another at the second study area along the Rio Grande) whose nests were not taken by predators fledged all the young in their nests (Hill 1988). And, when failures due to predation are discounted, the three age classes of males fledged about the same number of young per year (Table 1).

At the Rio Grande study site in 1986, yearling males settled together, away from clusters of adult male territories (Hill 1988). The vegetation of the area that yearlings occupied was structurally different from that occupied by adult males, with significantly fewer small trees ($P < 0.001$, Mann-Whitney U -test). Moreover, at the Rio Grande site yearling males had a higher rate of nest predation and fledged young from a lower propor-

TABLE 1. Reproductive parameters of three age classes of male Black-headed Grosbeaks.

Age (years)	Reproductive success*	Median jay activity (sec/40 min)	Mean† time on nest \pm SD	Mean clutch size \pm SD	Mean‡ no. young fledged \pm SD
1	1/5 (20%)	175	1,526 \pm 573	3.0 \pm 0.63	4.0
2	3/6 (50%)	34	{ 1,949 \pm 930	3.1 \pm 0.83	3.0 \pm 0.82
3+	11/14 (79%)	4		2.9 \pm 0.83	2.9 \pm 0.78

* Proportion of nests that fledged young, excluding failed first attempts.

† Time between nest exchanges.

‡ Excludes failed nesting attempts.

tion of nests than adult males (11/12, 92% and 1/3, 33% successful, respectively).

PLUMAGE EFFECTS

Superimposed on this age-structured settlement pattern was a tendency for males with the brightest plumage to occupy the central and eastern portion of the valley in heterogeneous vegetation where the jay activity was low, while duller males tended to occupy denser areas with higher jay activity. Part of this pattern obviously results from the presence of territorial subadult males, which were in all cases duller than adult males (Hill 1987, 1988) and invariably settled in the peripheral sites with very high jay activity. But even when subadult males are ignored, there was a significant negative correlation between the activity of jays around a male's nest and its plumage score ($r_s = -0.53, n = 16, P < 0.05$, Spearman's rank correlation coefficient; Fig. 6). I also looked for a relationship between size and territory quality, but there was no correlation between either the wing length or weight of a male and the activity of jays around its nest ($r_s = -0.048, n = 17$ and $r_s = -0.097, n = 16$, respectively).

SURVIVORSHIP AND TERRITORY SHIFTS

Adult male Black-headed Grosbeaks display low annual mortality for a small migratory passerine (Lack 1954, Ricklefs 1973). I estimated that the annual survivorship of adult male grosbeaks was 77% based on the number of adult territorial males that returned from one year to the next. Returning males were generally faithful to their territory sites between years. Of the 21 territorial males that returned between 1984 to 1985 and 1985 to 1986 (including six that returned between both 1984 to 1985 and 1985 to 1986), 18 settled on essentially the same territory that they had defended in the previous year; three shifted one to three territory spaces (Figs. 2, 3, and 4). One shift involved a bird that had defended a territory in the previous year as a subadult; the other two involved adults. All males that relocated moved toward the preferred habitat of the central and eastern valley, either from areas with high jay activity to areas with moderate jay activity (OOOA 1984 to 1985; GAYG 1985 to 1986; Figs. 2, 3, and 4) or from areas with moderate jay activity to areas with very low jay activity (RAOY 1984 to 1985; Figs. 2 and 3).

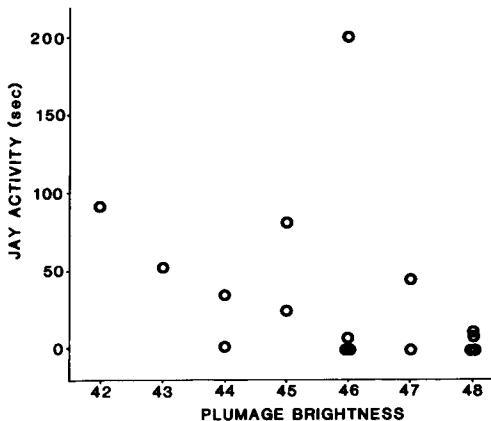


FIGURE 6. Amount of time spent by jays within 10 m of the nests of adult male Black-headed Grosbeaks in relation to their plumage brightness. Higher plumage scores indicate brighter plumage (see Hill 1987).

DISCUSSION

For breeding Black-headed Grosbeaks in the Sandia Mountains the prevalence of avian nest predators appears to be the key determinant of nesting success. Grosbeaks that nest in territories with low activity of Scrub and Steller's jays are more than four times more likely to fledge young than grosbeaks that nest in territories with high jay activity. Not surprisingly, male Black-headed Grosbeaks appear to respond to a gradient in jay density by competing for territories with the lowest activity of jays.

I found that male age is the attribute that correlates most strongly with the type of breeding habitat that a male can successfully defend. As subadults in their first breeding season, male grosbeaks either forsake breeding (ca. 70 to 90%; Hill 1988) or defend territories in poor habitat with the highest jay activity and low probability of successful reproduction. By their second breeding season, males are in adult plumage, and all defend territories that generally range in quality from moderate to poor in which they have a fairly good chance of successful reproduction. Finally, by their third year males are breeding in habitat of good or at least moderate quality with a high probability of reproductive success. At the Rio Grande study site, grosbeaks displayed a similar age-related settlement pattern (Hill 1988) suggesting that this may be a typical pattern for breeding populations of Black-headed Grosbeaks.

Adult male Black-headed Grosbeaks arrived

and established territories in a flurry of activity lasting only a few days in late April and early May. The first subadult males arrived 12 to 17 days after the first adult males, by which time the adult males had firmly established their territory boundaries and were breeding (Hill 1988). Thus, subadult males had virtually no choice in territory placement, being almost entirely constrained by territorial adult males. In both years that I had marked males returning, young adult males arrived on my study site first, followed 1 to 5 days later by old adult males. Young adult males sang widely over the study area during the first few days following their arrival, not settling into well-defined territories until after the arrival of most or all adult males. Apparently, some age-related factor such as site dominance or experience allows old adult males to reclaim their previous territories.

In other studies of breeding birds, age has been commonly implicated as an important factor in determining the quality of habitat that a male can defend (Dhondt and Huble 1968, Best 1977, Baeyens 1981, Askenmo 1984, Reese and Kadlec 1985). Most studies have compared only yearling and older males, but Dhondt and Huble (1968) found that both territory size and quality continue to increase through the fourth breeding season of male Great Tits (*Parus major*). Thus, for at least some relatively small, short-lived passerines, including the Black-headed Grosbeak, the quality of territory that a male occupies as well as its reproductive success continues to increase after its second year.

Although it is often clear that young males occupy different habitat than older males and have lower reproductive success, the two are not necessarily causally linked. The poor success of young birds may be due to age effects such as poor foraging ability (Orians 1969) or ineffective nest defense rather than poor breeding habitat. This is apparently not the case with Black-headed Grosbeaks. Within an age class, males generally did better in higher quality territories with low jay activity, and the reproductive success of all age classes was about the same within a habitat.

Although age explains most of the pattern of territory placement by male Black-headed Grosbeaks, the brightness of a male's plumage also plays some role in the type of habitat that it can defend. Only subadult males with bright plumage hold territories; duller individuals remain float-

ers (Hill 1988). In addition, I found a correlation between the plumage coloration of adult males and the type of habitat that they defended. Although all adult males apparently hold a territory and attract a mate (Hill 1988), adult males with bright plumage tended to defend habitat with fewer nest predators than adult males with relatively dull plumage. The plumage of adult males does not brighten with age after the acquisition of a definitive alternate plumage in their second spring (Hill 1987), so the correlation between territory quality (jay activity) and plumage brightness is not directly age-related. Apparently, a combination of age and plumage brightness determines the type of habitat that a male can defend and, ultimately, its reproductive output.

Several studies have found that yearling males with a dull subadult plumage have lower reproductive success or less success at establishing a territory than more brightly plumaged adult males (Samson 1976, Labedz 1984, Lanyon and Thompson 1986). Others have noted that brightly plumaged subadult males have higher reproductive success than dully plumaged subadult males (Ralph and Pearson 1971, Rohwer and Niles 1979, Payne 1982, Price 1984, Hill 1988). Relatively few studies have considered plumage variation within adult males, although it is clear that the adult males of many passerine species display substantial variation in either plumage pattern or pigmentation (Rappole 1983) and that plumage variation can be associated with a male's breeding status (Rohwer 1982). When plumage variation has been related to male reproductive status, a positive association has often been found (but see Alatalo et al. 1984). For instance, Edwards (1982) noted a striking relationship between territory placement and quality and the amount of black on the face, neck, and breast of the Greater Golden Plover (*Pluvialis apricaria*). Similarly, Studd and Robertson (1985a) found that male Yellow Warblers (*Dendroica petechia*) with extensive chestnut streaking on their breast were dominant to individuals with less streaking and defended breeding territories of higher quality.

The correlation between age and plumage brightness and the placement of territories by male Black-headed Grosbeaks appears to be maintained by progressive shifts, between years, of individual males first into the breeding population in marginal habitat and then, as they gain experience, toward preferred habitat. Møller

(1982) proposed a similar "flow" of territorial male Magpies from territories of low quality to territories of higher quality as they age, and Beletsky and Orians (1987) found that male Red-winged Blackbirds shift territories between years when they have the opportunity to move to a territory of higher quality in their immediate neighborhood. Although my data on territory shifts are limited, the correlation between plumage brightness and territory quality seems likely to be the result of dull males being less successful than brighter males at shifting into the most preferred habitat as they mature.

My observation that Black-headed Grosbeaks defend discrete breeding territories that contain critical and limited resources (nest sites with few predators) contradicts a key prediction of the hypothesis that subadult plumage serves as a reliable indicator of male status because plumage coloration is the principal criterion for female mate choice. This hypothesis predicts that in species with delayed plumage maturation, males will defend only simple nesting territories with little variation in territory quality (Lyon and Montgomerie 1986). Resource defense and the saturation of preferred breeding habitat by adult males is consistent with predictions of the female-mimicry hypothesis (Rohwer et al. 1980), but other data make this an unlikely explanation for subadult plumage in Black-headed Grosbeaks (Hill 1988).

My observations of grosbeak territoriality are also consistent with a critical assumption of the hypothesis that the subadult plumage of yearling male grosbeaks is part of a strategy of reduced reproductive effort, adopted in response to the saturation of breeding habitat by adult males (Procter-Gray and Holmes 1981, Studd and Robertson 1985b). Yearling male grosbeaks are faced with severe competition with experienced adult males for limited breeding territories. Even 2-year-old males breeding in adult plumage seem to be unable to acquire preferred habitat and enjoy only moderate reproductive success. Under such conditions, assuming a bright plumage would likely not increase a yearling male's chances of acquiring a territory in habitat of better quality. However, a bright plumage could, through increased risk of injury from adult males (Lyon and Montgomerie 1986) or increased risk of predation (Procter-Gray and Holmes 1981), decrease an individual's probability of surviving to the next spring or reduce its competitiveness in

future breeding seasons. Faced with such a situation, yearling males probably do well to accept limited first-year reproduction and adopt a strategy that maximizes their probability of surviving to their second and subsequent breeding seasons in which their chances for successful reproduction are much higher.

ACKNOWLEDGMENTS

This project would not have been possible without the help of J. David and Sandy Ligon, who allowed me to work on their property and provided logistical support throughout this study. I am also indebted to John Wiens and J. David Ligon for their encouragement and support through all phases of this project. Michael Lombardi kindly performed the dummy nest experiments in 1987, and Todd Haagenstad and John Baumann assisted with the fieldwork in 1985. Robert Payne, Lyle Gibbs, J. David Ligon, and two anonymous reviewers read versions of this manuscript and provided many useful comments. This project was generously supported by an E. Alexander Bergstrom Award from the Northeastern Bird-Banding Association, a Paul A. Stewart Award from the Wilson Ornithological Society, a Frank M. Chapman Research Grant from the American Museum of Natural History, a grant-in-aid of research from Sigma Xi, The Scientific Research Society, a research grant from the Western Bird-Banding Association, and the Graduate Student Association and the Department of Biology at the University of New Mexico.

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