BREEDING BEHAVIOR OF EVENING GROSBEAKS[1]

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Abstract. From 1983–1987 we studied the breeding behavior of Evening Grosbeaks (*Coccothraustes vespertinus*) living in the Front Range of the Rocky Mountains of Colorado. These birds were typically monogamous; at only one of 64 nests (1.6%) was polygyny documented. Reproductive behaviors performed by adult males and females were first analyzed across all mating seasons and then with respect to five consecutive nest stages (build/egg laying, incubate, brood, brood/fledge, fledge) and the outcome (success or failure) of individual nests. Adult males and females contributed unequally to the ten most frequently observed behaviors; half were performed almost exclusively by one or the other sex. Males typically fed and protected their mates and what we presumed to be their young; whereas females usually built the nest, incubated, brooded, and also fed their young. Feeding, soft calling from the perch, and fecal removal were performed relatively equally by adult males and females. The success or failure of nests was not associated with patterns of parental behavior. Our results indicate that Evening Grosbeaks formed a partnership in which they divided the effort involved in nest preparation and raising the young at the high altitude where this population was observed.

Key words: Breeding biology; reproductive behavior; parental investment; monogamy; Rocky Mountain National Park; Evening Grosbeaks; Coccothraustes vespertinus.

INTRODUCTION

Evening Grosbeaks (*Coccothraustes vespertinus*; hereafter called grosbeaks) are common inhabitants of coniferous forests throughout the western United States. Early studies were limited to general anecdotal descriptions (Speirs 1968), observations of flocking and feeding at artificial feeding stations (Shaub 1963; Balph 1976, 1977; Balph and Lindahl 1978, Balph and Balph 1979), and the assessment of grosbeaks' impact on spruce budworm (*Choristoneura fumiferana* [Clem.]) populations (Blais and Parks 1964, Takekawa et al. 1982, Langelier 1983). Our research has examined grosbeak special organization, aggression, and dominance relationships (Bekoff and Scott 1989) and ecological influences on nest site selection (Bekoff et al. 1987) and nest success (Bekoff et al. 1989). We found grosbeaks to be nonterritorial, seasonally gregarious flockers, that behave similarly to other finches (Newton 1972), especially during nonbreeding seasons when they live in large groups. For example, in our study areas, flocks of 30–100 grosbeaks often were seen

outside of the breeding season (September–April) at elevations ranging from 1,500–2,700 m, but during the mating season birds were generally less social and moved to higher elevations.

In order to formulate a more comprehensive picture of the social ecology of a species, its reproductive habits must also be examined. Such a study entails analyzing the behaviors that are used during different stages of breeding and identifying the proximate and evolutionary factors that might be responsible for observed mating patterns. Until the 1970s, most research on avian mating systems concentrated on species-typical patterns of reproductive behavior (Verner and Willson 1966, 1969; Lack 1968). However, more recently there has been a shift of emphasis toward gaining a better understanding of individual variations in mating behavior, behavioral adaptations associated with reproducing in varying habitats, and environmental factors that may influence the evolution of mating patterns (Oring 1982).

The purpose of this study was to describe the breeding behavior of adult male and female grosbeaks living in the Front Range of the Rocky Mountains of Colorado, analyze sex differences in nest building and care-giving activities, and speculate which behavioral patterns were most likely to be influenced by environmental factors.

We also wanted to discern if reproductive behavior of grosbeaks is similar to that of other avian taxa in which monogamy has either been exclusively or most commonly observed (Verner and Willson 1969, Wittenberger and Tilson 1980, Oring 1982, Welty 1982). Since previous work showed that ecological factors could be used to predict nest success or failure (Bekoff et al. 1989), we also determined if patterns of reproductive behavior could be used to discriminate between successful and unsuccessful nests.

METHODS

Examination of grosbeak breeding behavior began in April 1983. Due to grosbeaks' high mobility (Bekoff and Scott 1989), only six banded individuals were found in the two study sites where we found concentrations of nesting grosbeaks (see Bekoff and Scott 1989 for details concerning trapping, handling, and banding; USFWS federal permit 21627). Therefore, most of our data are from observations of unbanded birds. We found two separate locations that contained breeding pairs. One was in Rocky Mountain National Park (Estes Park, Colorado; 60 km northwest of Boulder; elevation 2,530 m) and the other just west of Nederland, Colorado (33 km southwest of Boulder; 2,420 m elevation; see Bekoff et al. 1987 for descriptions of the study areas). Systematic searches for grosbeak nesting activity were conducted in river and perennial creek drainages throughout the study areas from late April through June in each of five years (1983–1987).

Sixty four nests were watched daily for 60–80 consecutive min during the two time periods (05:00–11:30 and 17:00–20:30; ambient temperatures ranged between 15–22°C) when the highest concentration of observable grosbeak activity occurred. These time periods were chosen after observations made during four consecutive 24-hr watches indicated that 98% (57/58 instances) of grosbeak activity that we could see (or hear) occurred during these times.

Observations were made using 20 × 45 spotting scopes or 10 × 25 binoculars. Data were written or spoken into a tape recorder for later transcription. Grosbeak vocalizations were recorded using a Sony F-26s cardioid dynamic microphone mounted on a Sony PBR-3300 parabolic reflector. Tape speed was 19 cm/sec.

BEHAVIOR OF REPRODUCTIVE ADULTS AND YOUNG GROSBEAKS

Eighteen different behaviors were observed during courtship and nesting, with 10 actions accounting for 96% of the total frequency ($n =$ 4,254) with which all behaviors were seen. Vocalizations (calls, soft calls, trills, and soft trills) were categorized according to sound quality and the location at which they were performed relative to the nest. Although some behavioral patterns were actually composite actions, each was recorded as only one of the eighteen different behaviors. For example, begging typically included a postural component, wing flutter, and vocalization, all of which were necessary for an activity to be classified as a bout of begging.

The ten main behavioral patterns were: 1) *feeding* (FEED); 2) *begging* (BEG): adult females, nestlings, and fledglings stretched their neck upward, gaped, fluttered their wings (see below), and emitted a vocalization consisting of one fundamental and two harmonics with a frequency range of 2.0–7.0 hKz; 3) *carrying nest material* (CNM); 4) *building nest* (BN); 5) *removing fecal matter* (FR); 6) *calling from a perch* (CP): (the perch was fewer than 3.5 m from the nest tree) calls refer to single- or double–note vocalizations with ascending frequency from 2.0–5.0 kHz leading quickly into descending frequency from 5.0–2.0 kHz with no harmonics; 7) *soft calling from a perch* (SCP): soft calls consist of an ascending fundamental of 2.0 kHz with two harmonics, ranging from 2.0–7.0 kHz (perch was less than 3.5 m from the nest tree); 8) *calling from nest* (CN): see 6 for description of calls; 9) *calling from nest tree* (CNT): see 6 for description of calls; and 10) *soft trilling from nest* (STN): soft trill consists of two notes, each with one harmonic ranging from 5.0–8.0 kHz. The soft trill and trill (see below) are structurally similar but differ in use. Soft trills are usually heard during feeding and preening, whereas trills seem to be used as contact vocalizations.

Eight other behavioral patterns that were not statistically analyzed because of the low frequency with which each was observed (less than 2% n) were: *wing droop* ($n = 37$): wings are held close to the body and lowered while the tail is cocked upwards; performed by males and females during courtship and nest building; *wing flutter* ($n = 84$): wings are outstretched and fluttered at a rapid cadence; adult females flutter

their wings during courtship and begging, and nestlings and fledglings flutter their wings when begging; *courtship dance* ($n = 1$): during precopulatory behavior, an adult male bent his head backwards, swivelled his body back and forth, and successively fluttered and drooped with wings in close proximity to his mate; *headfluff* ($n = 3$): head feathers are raised to varying degrees, often in conjunction with wing flutter (especially during male courtship); headfluff is also observed during agonistic encounters; *copulation* ($n = 12$): the male performs a wing flutter while facing the female, the female moves in front of the male and executes a wing flutter with her back to the male, and the male then mounts the female; copulation occurs for approximately 3–5 sec after which the male dismounts while still fluttering his wings; *bill touch* ($n = 10$): mated pairs touch beaks with no food exchange; *practice flight* ($n = 16$); and *trilling from nest* ($n = 21$): trills consist of one fundamental with a frequency range from 2.5–5.0 kHz and one harmonic with a frequency range from 5.5–7.0 kHz.

TIME BUDGET ANALYSES

The amount of time a female spent on or away from the nest was recorded for each observation period. The following three measures were used in time budget analyses: 1) total time within an observation period that females spent on the nest (TOTFON); 2) the time that females spent on their nest during *each* visit (FON); and 3) the time females spent off their nest each time they departed (FOFF).

We also calculated the frequency with which males visited their nests (MVN). Frequency rather than mean time is reported here because males usually spent less than 2 min at their nest.

NEST STAGES

Nest stages were assigned on the basis of adult male and female behavior. At first, we climbed trees in order to observe the number of eggs and to assign hatching dates; however, this practice was discontinued because of nest failure immediately after these efforts. Nests were otherwise inaccessible so other attempts at direct verification were unsuccessful. Mean duration of each nest stage was quantified only from nests with complete data. *Building/egg laying* was assigned as a stage as soon as an individual was observed

carrying nest material or seen arranging material in a tree where a nest subsequently was used by a grosbeak pair. The *building/egg laying* stage was only quantified when the entire building process could be observed. *Building/egg laying* was characterized by short (<3 min) frequent visits to the nest. Egg laying was assumed to be completed at the onset of incubation. The *incubation* stage began as soon as a female was observed sitting on the nest for more than five consecutive minutes. *Incubation* was characterized by a female sitting on the nest for longer periods of time (usually 10–50 min). Mean incubation time calculated from periods of known length was 26.6 ± 24.7 min. During incubation females left the nest unattended only for short periods of time ($\bar{x} = 2.4 \pm 3.4$ min), but when they were gone males usually remained near the nest tree. *Brooding* began as soon as the adult male or adult female left the nest for short (3–5 min) excursions and returned with food. On most occasions nestlings were fed by the returning adult. Nestlings were usually big enough to be observed two or four days after feeding by adults began, and nestlings could be observed throughout brooding. *Brooding* ended as soon as one nestling fledged. Because nestlings did not fledge simultaneously, we labeled a stage *"brood/fledge"* to indicate the period when a female was still brooding some nestlings after other young had fledged; her behavior was not a result of a second or double clutch. The *brood/fledge* stage did not occur at all nests. The *fledgling* stage began after all known nestlings had fledged and lasted as long as the fledglings were being fed by at least one parent.

Nests also were classified as being successful or unsuccessful. *Successful* nests were those that resulted in at least one known fledgling, whereas *unsuccessful* nests were those that failed during building, incubation, or brooding. Nest failure and abandonment were obvious; adult birds did not return to the nest and no grosbeaks were subsequently observed in the area.

STATISTICAL ANALYSES

The number of nests found each year was different, consequently the total frequencies of behavioral patterns observed also varied among years. However, because mean rates of performance of behavioral patterns (in terms of bouts per number of nests observed each year) and time budgets did not vary in pair-wise comparisons

between years or between nests, data from all years and nests were combined.

SPSS statistical programs (Nie et al. 1975) were used for univariate and multivariate analyses. Means ± standard deviations (SD) are reported. Behaviors were analyzed only for nests at which the duration of observed nest stages could be determined. Behavioral patterns were recorded as individual "bouts" when there was a clear transition between different activities; they were analyzed with respect to the age and sex (adult male, adult female, nestling, or fledgling) of the bird that performed (or initiated) them and where appropriate, the age and sex of recipients. Chisquare analyses were used to test for differences in the frequency distributions of each reproductive behavior across all years and of patterns of behavior initiated and received by different individuals. Kruskal-Wallis analyses of variance were used to determine if there were differences among nest stages in terms of 1) the mean frequencies of occurrence of the ten main behavioral patterns and 2) the variables described in time budgets (TOTFON, FON, FOFF). For these analyses we assumed that there was independence among the different nests and also among sequential nest stages for the same nest in a given year because of the extensive time intervals over which data were collected (see Hejl et al. 1990).

Successful and unsuccessful nests were compared using Mann Whitney-U tests with respect to 1) the mean frequencies of occurrence of each of the ten main behavioral patterns, 2) the variables described in the time budgets (TOTFON, FON, FOFF), and 3) the mean frequencies of male visits to the nest (MVN). Stepwise logistic regression (Kachigan 1986) was used to examine the possibility that a single behavior, or combination of behaviors, could be used to discriminate between successful and unsuccessful nests.

RESULTS

The mean duration (days ± SD) of each nesting stage was: build/egg laying = 6.3 ± 4.4; incubating = 13.4 ± 4.0; brooding = 14.1 ± 4; and brood/fledge = 2.4 ± 1.2 Grosbeaks arrived in their breeding areas during mid-to-late May as a mated pair. Observations in both study areas began in April and there was no grosbeak activity until pairs arrived. Almost immediately, pairs began nest building; there was no indication that they attempted to establish territories. The first nest we observed was on 18 May 1985, however,

most nests were begun in late May or early June. Sixty-four nests were found. Most were found during building ($n = 36$; 56%) and incubation ($n = 22$; 34%). Two nests were reused for second clutches and none were used in subsequent breeding seasons. We assumed that the two grosbeaks observed feeding their young were their parents; no third birds were observed. Sixty-three of 64 (98.4%) mated pairs were assumed to be monogamous based on behavioral observations (see below).

During courtship, adult males and females were secretive. Neither sex perched conspicuously and after an individual was observed, following it usually did not result in our finding a nest. Vocalizations occurred sporadically and did not permit us to localize pairs near their nest. The most commonly observed behaviors during courtship period were wing flutter, calls from perch, and wing droop (Table 1). Other behaviors observed during courtship were begging, feeding, bill-touching, head-fluffing, soft-calling from a perch, and calling from the nest tree.

When courtship behaviors were observed at the nesting sites, the male and female appeared already to have formed a pair bond. The one courtship dance we observed occurred just prior to copulation. Wing flutter performed by the adult female occurred most frequently during courtship in response to a male's wing droop. Wing flutters performed by adult females during incubation appeared to be a form of food-soliciting and were most often seen in conjunction with begging. Wing flutter performed by an adult appears to be a "socio-infantile" behavioral pattern (Wickler 1968) commonly observed in feeding, greeting, and submissive behavior.

Nest construction was performed almost solely by females (141/151; 93.4%). Males helped minimally by occasionally carrying nest material to the nest (13/201; 6.5%). All four types of vocalizations (calls, soft calls, trills, soft trills) were heard during building. Lone females were extremely secretive during egg-laying. In fact, when females were observed during nest construction and egg-laying, they were accompanied by a male either at the nest site or while flying in and out of the nest tree.

During incubation, males often foraged within sight of the nest tree, but they also were observed flying long distances (up to 1,000 m) during a foraging excursion. Females exclusively incubated eggs, while males typically fed their mate

TABLE 1. Frequencies of reproductive behaviors observed during courtship and different nest stages at 64 evening grosbeak nests.

Behavior	Courtship	Build/egg laying	Incubation	Brood	Fledgling	Brood/ fledge	Total
			Stage				
Courtship dance	100	—	—	—	—	—	1
Bill touch	100	—	—	—	—	—	10
Head fluff	100	—	—	—	—	—	3
Wing flutter	37	8	26	16	11	2	84
Wing droop	62	22	13	—	3	—	37
Copulation	17	50	33	—	—	—	12
Begging	1	1	54	25	8	11	449
Feeding	—	—	11	75	6	7	1,415
Carry nest material	—	84	16	—	—	—	201
Build nest	0	81	18	1	—	—	151
Soft calls from perch	6	8	35	20	20	11	224
Calls from perch	5	7	63	20	2	3	680
Calls from nest	—	11	70	10	7	2	369
Calls from nest tree	3	17	56	11	3	10	213
Trills from nest	—	9.5	38	9.5	—	43	21
Soft trills from nest	—	16	60	12	7	5	243
Fecal removal	—	—	—	93	—	7	125
Practice flight	—	—	—	38	6	56	16
Total	129	506	1,529	1,592	242	256	4,254

by regurgitation. After feeding their mate, males then perched nearby, presumably defending the nest tree. Calls from a perch, the nest, or the nest tree, were most commonly heard during incubation. These calls appear to be location and/or defense calls (Ritchison 1980); we found that the frequency of these calls increased during nest stages in which eggs or nestlings were present. Both nestlings and fledglings were capable of producing vocalizations which sounded similar to adult vocalizations. However, young birds only vocalized when their presumed parents were observed near their nest tree.

Fledglings were observed in the nesting area for two to five days after leaving their nest. Their plumage was dull gray (similar to that of adult females) and they were well-camouflaged in the habitat surrounding the nest. Most nestlings fledged by late July. Fledglings were fed by both adults at feeding stations in lower elevations throughout August and the first three weeks of September (Bekoff and Scott 1989). During the brood/fledge stage, one to two fledglings were often observed near the nest tree; they perched quietly within 20 m of the nest tree and vocalized only when adults were nearby. Nestlings begged and trilled more than did fledglings.

Frequencies of occurrence of the 18 behaviors (n = 4,254) observed during courtship and throughout nesting are presented in Table 1. Feeding occurred most often, with the next most common behaviors being vocalizations from a perch, vocalizations from the nest, and begging. The frequency of occurrence of each behavioral pattern varied throughout the breeding season (Kruskal-Wallis analysis of variance, in all cases $P < 0.0001$). For example, during building/egg laying 57% of all observed behaviors involved carrying nest material or nest building. The behaviors most commonly observed during incubation were: calls from perch (28%); calls from nest (17%); and begging (16%). Feeding occurred most during brooding (67%) with calls from perch being the next most common behavior (9%). During the fledgling stage, feeding was again the most common behavior (36%), with soft calls from a perch (19%) and begging (15%) the next most commonly observed activities. The most commonly observed behaviors performed during brood/fledge were: feeding (37%); begging (18%); calls from nest tree (8%); and calls from a perch (7%).

Adult males and females contributed unequally to the ten main reproductive behaviors (Fig. 1; x^2 = 1,022.79, df = 9, P = 0.0001). Half of these behaviors were performed almost exclusively by one or the other sex. The behaviors performed relatively equally by adult males and
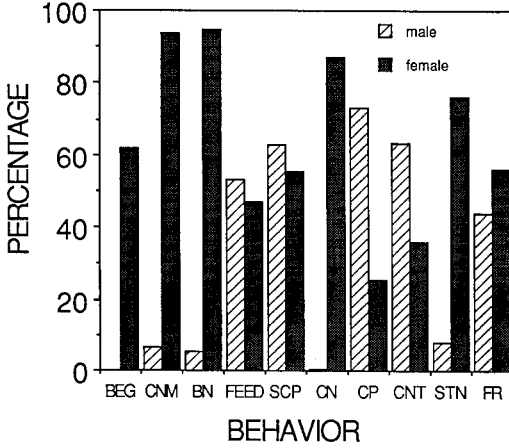
FIGURE 1.   Percentages of behavioral patterns performed by adult males and females for all nest stages combined. BEG, begging; CNM, carrying nest material; BN, build nest; FEED, feeding; SCP, soft calling from perch; CN, calling from nest; CP calling from a perch; CNT, calling from nest tree; STN, soft trilling from nest; and FR, fecal removal.
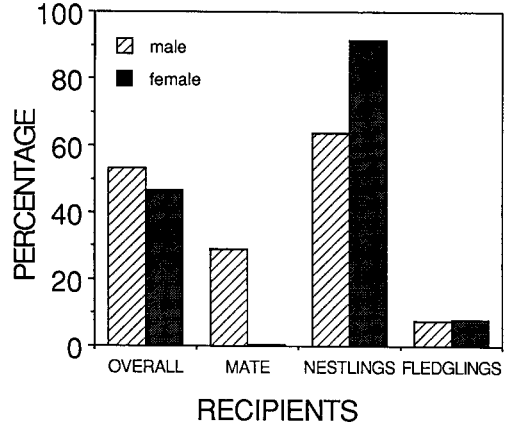

FIGURE 2.   Percentage of feeding bouts initiated by adult males (cross-hatched bars) and adult females (solid bars) and the recipients of food delivered by each, for all nest stages combined.

females were soft calls from perch, feeding, and fecal removal. However, feeding was nonrandomly distributed among recipients (Fig. 2; $\chi^2 = 230.33$, df $= 3$, $P = 0.0001$). Females fed nestlings more than males did; both adults fed fledglings equally and only males fed their mates. Mean values for females' time spent on and away from the nest, and the frequency with which males' visited nests, also varied throughout the nesting stages (Table 2).

Patterns of change in the relative percentages of behaviors performed by adult males, adult females, nestlings, and fledglings during: a) building/egg laying, b) incubating, c) brooding, d) fledgling, and e) brood/fledge are presented in Figure 3. When both nestlings and fledglings were present at the nest site (brood/fledge), the percentages of behaviors performed by adult males, females, nestlings, and fledglings were different from the patterns observed during either brooding or fledging. During the brood/fledge stage, nestlings begged more than fledglings (34/46 [74%]) and soft trilled from the nest more than fledglings (9/12 [75%]). Neither nestlings nor fledglings called from the nest tree. Calls and soft calls from fledglings in perches were rare ($n = 6$). The most common vocalization by fledglings was soft call from a perch ($n = 38$).

There were no differences in the mean fre-

quencies with which adult males or adult females performed the ten main reproductive behaviors when comparing successful with unsuccessful nests. Furthermore, stepwise logistic regression showed that no behavioral patterns were useful for discriminating between successful or unsuccessful nests ($P > 0.05$); only 69% ($n = 44$) of all nests were correctly classified. For both successful and unsuccessful nests, the number of nestlings ranged from 1 to 4. The mean number of nestlings for successful ($n = 35$) and unsuccessful ($n = 29$) nests was 2.9 (SD $= 0.98$) and 3.2 (SD $= 1.0$), respectively ($P > 0.05$).

DISCUSSION

BEHAVIORAL CHANGES AND PARENTAL INVESTMENT DURING BREEDING

The present study demonstrated that the behavior of adult grosbeaks changed at the beginning of, and throughout, the breeding season. At the onset of the breeding season we observed a shift in grosbeak social organization from one characterized by gregarious flocking to one characterized by smaller groups, pairs, and singletons (Bekoff and Scott 1989). This shift in social organization may be grosbeaks' response to an increase in food availability. Since food appears to be more abundant and more evenly distributed during the breeding season when compared to other times of the year (Bekoff et al. 1989), grosbeaks may not benefit from group foraging while

TABLE 2. Time budgets for mean time (± standard deviation) engaged in three activities during each of four nesting stages. The three activities were: (1) the total number of minutes females spent on their nest in each stage during 60 min watches (TOTFON), (2) the number of minutes per hour females spent on their nest during each visit (FON), and (3) the number of minutes per hour females spent off their nest each time they departed (FOFF). The frequency per hour with which males visited their nests (MVN) is also presented in this table. The column labeled "Mean Frequency" indicates the mean frequency of occurrence of each activity performed during a 60-min observation period for all stages combined.

| Variable | Stage | | | | |
	Build/egg laying	Incubation	Brood	Brood/Fledge	Mean frequency
TOTFON[A]	15.0	50.0	28.0	4.3	36.0
$n = 1,285$	(±11.3)	(±27.0)	(±21.8)	(±1.8)	(±27.1)
FON[A]	2.4	26.6	10.6	1.3	15.0
$n = 2,568$	(±3.4)	(±24.7)	(±14.8)	(±14.3)	(±20.2)
FOFF[A]	6.2	10.1	11.6	15.3	10.9
$n = 2,362$	(±9.2)	(±10.7)	(±9.7)	(±14.3)	(±11.2)
MVN[A]	8.2	3.6	5.7	3.1	4.0
$n = 1,071$	(±8.4)	(±6.7)	(±10.3)	(±1.6)	(±5.7)

[A] Kruskal-Wallis analysis of variance, comparing means for each nest stage for each variable; $P < 0.00001$.

breeding (Bekoff and Scott 1989). While individuals living in large flocks may be at an advantage both with respect to the detection of predators and the protection that a group confers, it also may be that by foraging independently or in pairs or small groups, individuals reduce the likelihood of attracting predators.

Although we refer to the behavioral patterns that we observed during nest building and care-giving as "parental investment," we do not know that these actions actually "increase the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring" (Trivers 1972, p. 139). Under natural conditions it is common for researchers to be unable to assess either the outcome of different rearing strategies with respect to offspring survival or if care provided to young is really costly to care-givers (Byers and Bekoff 1990). Reliable comparative measures of "parental investment" also are difficult to come by (e.g., Cash and Johnson 1990, Gori 1990).

Our assessments of parental investment reflect the amount of time spent performing specific activities or the frequency with which different behavioral patterns were initiated during the breeding season. Sex differences indicated that male and female grosbeaks formed a partnership that resulted in each parent providing a different type of care to each other and to their young. Some other passerines have been shown to have similar partnerships in which adult males and adult females contribute about equally to care-giving (Sullivan 1990).

BEHAVIOR AS A FACTOR IN NESTING SUCCESS

There was little variation in the behavior of adults attending successful nests or nests that failed before fledglings emerged. Successful and unsuccessful nests could not be differentiated using behavioral data. However, in a previous study specific habitat characteristics were predictably associated with the success or failure of grosbeak nests (Bekoff et al. 1989). The ecological features that were associated with successful nests appeared to be important in reducing predation by terrestrial and aerial predators and also facilitated thermoregulation of the nest's occupants. Thus, our data indicate that the initial location of the nest site influences the eventual outcome of the nest more than does the behavior of either member of the mated pair after the nest site is established.

The dominance rank of a male also might influence nest placement, but we were unable to assess this possibility. Hill (1988) found that dominant male Black-headed Grosbeaks (*Pheucticus melanocephalus*) tended to occupy more heterogeneous habitat which contained fewer Steller's Jays (*Cyanocitta stelleri*), the most common predator of Black-headed Grosbeak nests. Time and energy expended during interspecific aggression also may be reduced by 1) placing
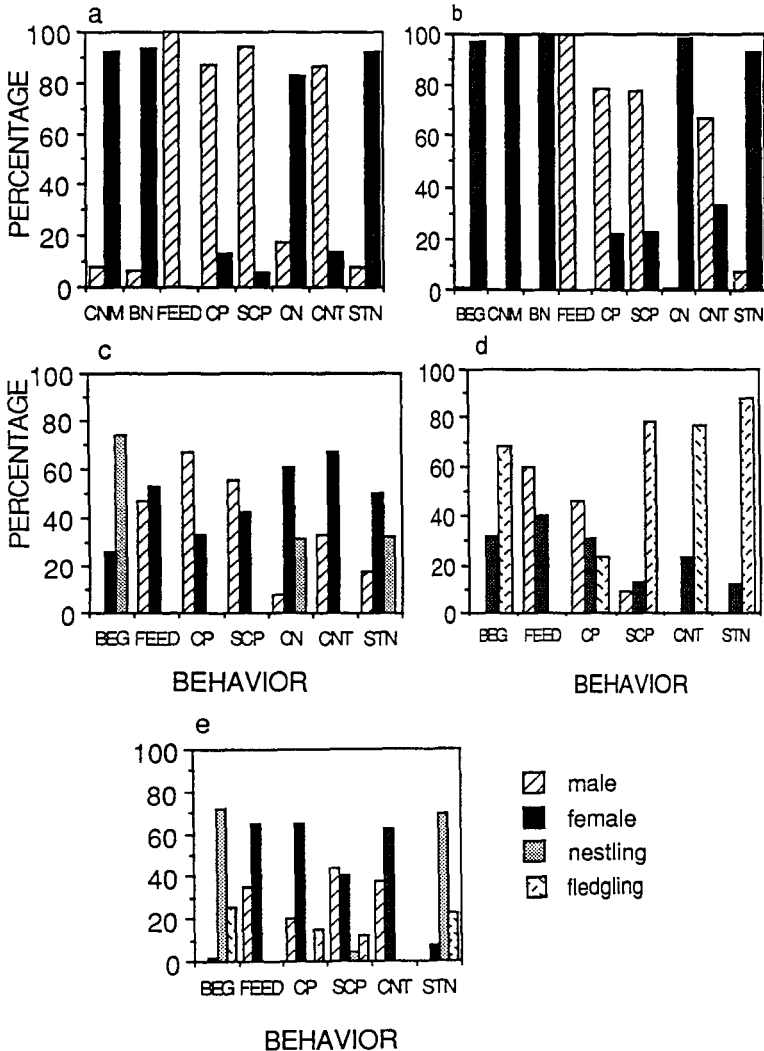
FIGURE 3.   Relative frequencies with which adult males, adult females, nestlings, and fledglings performed behaviors during (a) building/egg laying, (b) incubation, (c) brooding, (d) fledgling, and (e) brood/fledge stages. CNM, carrying nest material; BN, building nest; BEG, begging; FEED, feeding; CP, calling from a perch; SCP, soft calling from a perch; CN, carrying nest material; STN, soft trilling from nest; and CNT, calling from nest tree.

nests away from areas inhabited by nonpredatory competitors, a situation that we did not encounter on our study area, or by 2) establishing nest sites and feeding in areas where nonpredatory noncompetitors live. Interspecific aggressive interactions rarely were observed between grosbeaks and similarly-sized nonpredatory noncompetitors in the same area (Black-headed Grosbeaks; Robins, *Turdus migratorius*). Smaller noncompeting nonpredatory species such as Pine Siskins (*Carduelis pinus*), Mountain Chick-

adees (*Parus gambeli*), Golden-crowned Kinglets (*Regulus satrapa*), and Green-tailed or Rufous-sided Towhees (*Pipilo chlorurus* and *P. erythrophthalmus*) were not chased from the nest or nearby trees.

REPRODUCTIVE LIFE HISTORY STRATEGIES AND MATING PATTERNS

Life history strategies, including reproductive behavioral patterns and associated mating systems, evolve as a result of complex interactions

between animals and their environment (Partridge and Harvey 1988). We speculate that grosbeaks are adapted behaviorally to breed in habitats that often have severe weather and short growing seasons because they: 1) devoted little or no time to prenesting activities compared to the time spent performing other reproductive behaviors, 2) did not establish breeding territories, 3) spent only a short time building nests, and 4) produced fledglings that only remain in the breeding area for a short period of time. White-crowned Sparrows (*Zonotrichia leucophrys*) living at high latitudes also show similar behavioral patterns when compared to conspecifics nesting at lower latitudes and in warmer climates (Morton 1976).

Birds nesting at higher latitudes typically tend to produce larger clutches than those nesting at lower latitudes and in warmer climates where the breeding season is longer (Van Tyne and Berger 1971). Mean clutch size in this study was three, which is smaller than the average that is typically reported for other passerines (Austin 1968). However, no comparative data exist for grosbeaks breeding at different altitudes or latitudes. Lastly, grosbeaks only produced one brood per season, which is common for birds breeding at higher altitudes (Hubbard 1978, Carey 1988).

Life history analyses that entail characterizing a species' "mating system" (see Emlen and Oring 1977, p. 222) also are confronted with difficult problems, especially of definition (Emlen and Oring 1977, Harrington et al. 1982, Dewsbury 1987). Gathering unequivocal evidence of mating patterns also is problematic (Kleiman 1977, Wittenberger and Tilson 1980). For example, Dewsbury (1987) discussed the diversity of definitions of monogamous mating systems by using the following criteria: 1) exclusivity of mating; 2) joint parental care; and 3) association. He concluded that none of these three criteria alone is sufficient for inferring monogamy. However, a combination of two or more of these criteria results in a more reliable assignment of monogamy as the observed mating system.

We infer that grosbeaks are typically monogamous based on our observations of joint parental care and patterns of association between an adult male and an adult female during the breeding season. We assumed that the male associated with the female during and after nest building began was both the father of her offspring and her mate throughout the season, based on the following criteria: 1) constant attendance by males

was seen only during the build/egg laying stage and may be a way in which males "insured their paternity" (Gowaty 1983, Fitch and Shugart 1984, Gowaty and Plissner 1987); 2) there were very few instances of male-male aggression near the nest after the nest was completed; 3) even when two males were seen near the nest, only one of them was tolerated by the female and the other male would usually leave the nest tree; and 4) the male fed the female and defended the nest tree during incubation and contributed to rearing young throughout all nest stages.

In many vertebrates, monogamy is thought to evolve in response to specific environmental and social conditions (Kleiman 1977, Wittenberger and Tilson 1980). Although we did not directly test Wittenberger and Tilson's (1980, pp. 199–200) hypotheses, our data support two of five of their suggestions. First, male grosbeaks contributed substantially to all nests and most behaviors performed by the mated pair were displayed exclusively by one parent or the other. Second, because there were no cases where females raised young without adult male assistance, it seems as if participation by males in reproductive efforts is necessary but not sufficient. Thus our data suggest that "male parental care is both non-shareable and indispensable to female reproductive success" (Wittenberger and Tilson 1980, p. 199). However, comparative data are needed for nests at which males are absent to substantiate this claim and this information is presently unavailable. Furthermore, in this nonterritorial species, males defended access to individual females. "[D]efending exclusive access to a single female" (Wittenberger and Tilson, 1980, p. 200) is also seen in other monogamous finches (Newton 1972, Ricklefs 1977, Wittenberger and Tilson 1980).

The one instance of polygynous behavior observed during this study (Fee and Bekoff 1986) indicates that although grosbeaks are usually monogamous, there may be some flexibility in their mating habits. Other studies also indicate that passerines are not locked into a rigid monogamous mating system. However, polygyny has only been documented in approximately 36 passerine species (Ford 1983; see also Fitch and Shugart 1984, Gowaty 1987).

Our data also indicate that adult grosbeaks show male-biased sex ratios throughout breeding and nonbreeding seasons (Bekoff and Scott 1989). However, Balph and Balph (1976) observed female-biased sex ratios in winter flocks observed

at feeding stations in Utah. In general, monogamous birds have been characterized as showing higher female than male parental investment (sensu Trivers 1972), a conclusion that stems from observations of adult sex ratios favoring males (Trivers 1972, Breitwisch 1989). However, Breitwisch (1989) showed that skewed sex ratios favoring adult males may not necessarily be a result of higher female parental investment, and also that skewed sex ratios biased toward adult males do not invariably favor the evolution or adoption of monogamy in all environments. Further, Murray (1984) and Lamprecht (1987) suggested that resource quality and availability, and protection of nests, mates, and young, are probably more influential in shaping mating systems than are biased sex ratios.

In summary, our analyses show that although adult males and females appear to play different reproductive roles during various parts of the breeding season, they both contribute to building nests and care-giving throughout the breeding season. Grosbeak parents, who are typically monogamously bonded, continually divided the work of nest preparation and raising their young. For example, we found that males typically fed and protected their mate and their young, whereas females primarily built the nest, incubated, brooded, and also fed their young.

ACKNOWLEDGMENTS

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