NONRANDOM NEST-SITE SELECTION IN EVENING GROSBEAKS[1]

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Abstract. Nest-site selection was studied in Evening Grosbeaks (*Coccothraustes vespertinus*) living in two areas (Eldora and Wild Basin) of the Front Range of the Rocky Mountains of Colorado. One hundred and twenty-nine original variables were reduced to compare nesting (NS; *n* = 49) and nonnesting control (NNS; *n* = 10) sites using multivariate and univariate statistics. Overall, four of the five variables best discriminating between NS and NNS were measures of habitat density (deciduous stem intersect, deciduous canopy cover) or shrub dispersion (large clumps, irregular matrix). Although there were distinct differences between the two NS with respect to shrub dispersion, canopy cover, and the relative proportion of major vegetation, NS were more open than NNS within the same area. In both Eldora and Wild Basin, grosbeaks showed a preference for ponderosa pines (*Pinus ponderosa*) in which to build high camouflaged nests, close to the main tree trunk, predominantly with southern or northern exposures. We suggest that these nest locations provide (1) high visibility for detection of potential predators, (2) the opportunity for grosbeaks to see their nests from a distance, (3) easy access for departure and arrival, (4) aid in thermoregulation, and (5) protection from wind and rain and increased nest stability.

Key words: Evening Grosbeaks; Coccothraustes vespertinus; nest-site selection; breeding biology; vegetation analyses; habitat analyses; Colorado Rocky Mountains.

INTRODUCTION

Evening Grosbeaks (*Coccothraustes vespertinus*) are typically nonterritorial, highly social birds, that live in large groups (Alexander 1943, Shaub 1963, Blais and Parks 1964, Verner et al. 1980, Langelier 1983). The size and age and sex composition of flocks vary seasonally (Bekoff and Scott, unpubl. data); individuals move freely in and out of groups throughout the year. Because they are gregarious and visible while flocking, grosbeaks are ideal subjects for studying social behavior and behavioral ecology. However, very little detailed research has been done on this species (Speirs 1968; Balph 1976, 1977; Balph and Balph 1976; Balph and Balph 1979; Balph and Lindahl 1978; Langelier 1983; Fee and Bekoff 1986).

In the Front Range of the Rocky Mountains of Colorado, the breeding season of grosbeaks extends from late May through mid-July. For 3 to 4 weeks prior to this time, large flocks are rarely observed; pair-bonding occurs within small groups of about four to 10 birds. Nest building is usually synchronized with the start of deciduous foliage. Although it has been assumed that Evening Grosbeaks typically are exclusively mo-

nogamous (Verner and Willson 1966, Lack 1968, Speirs 1968, Terres 1980), a case of "incidental" polygyny has been observed (Fee and Bekoff 1986). Females exclusively incubate eggs, while males forage and provide most of the female's diet. Females occasionally leave the nest for short periods to forage nearby. During brooding, both adults forage and feed the young. Consequently, nestlings may be left alone for varying periods of time.

The purpose of this study was to analyze how environmental variables influenced nest-site selection. Although adults and young (after fledging) grosbeaks are easy to observe once they are discovered, nests are very difficult to find (Willard 1910, Alexander 1943, Parks and Parks 1963, Speirs 1968, Langelier 1983). Thus, there are few data about nesting habits in this species. We have taken a detailed quantitative approach to determine how single factors and combinations of these variables played a role in grosbeaks' choice of nest sites (Hildén 1965, Noon 1981, Downing 1986).

METHODS

STUDY AREAS

Nest sites were sampled during the 1983 to 1986 breeding seasons. Two major breeding areas were located, one outside the town of Eldora (30 km

west of Boulder; valley floor elevation = 2,695 m) and the other in the Wild Basin region of Rocky Mountain National Park (60 km northwest of Boulder; valley floor elevation = 2,530 m). Wild Basin is about 32 km (aerial distance) from Eldora in the Middle Saint Vrain River drainage. Extensive riparian habitat, mainly dense willows (*Salix* spp.), extends from approximately 7 to 366 m on either side of the stream. The valley varies from about 150 to 610 m in width. Steep ridges on either side rise from approximately 2,540 to 2,680 m. In Eldora, the more sparsely vegetated riparian habitat extends from about 1 to 5 m on either side of the South Fork of Middle Boulder Creek. Valley floor width ranges between 75 and 300 m and steep ridges rise from about 2,700 to 3,000 m.

Both nesting areas are in the Upper Montane Forest Climax Region (Marr 1967) and consist of U-shaped glacial valleys with their upper ends bounded by steep-walled cirques (Chronic and Chronic 1972). Major trees include Douglas firs (*Pseudotsuga menziesii*), ponderosa pines (*Pinus ponderosa*), lodgepole pines (*Pinus contorta*), and aspens (*Populus tremuloides*). North-facing slopes are dominated by Douglas firs, especially on steep slopes with rocky soil. Ponderosa pines are more abundant in finer deep soil on the valley floors. Other major plants in the study areas include subalpine firs (*Abies lasiocarpa*), limber pines (*Pinus flexilis*), Engelmann spruce (*Picea engelmanii*), willows, honeysuckles (*Lonicera* spp.), currants (*Ribes* spp.), mountain ash (*Sorbus americana*), Rocky Mountain maples (*Acer glabrum*), and cow parsnip (*Heracleum sphondylium*). Western spruce budworms (*Choristoneura occidentalis* Freeman) and aspen leaf-rollers (*Choristonerua conflictana*) were abundant in each area, both of which are preyed upon by grosbeaks.

SAMPLING METHODS

Twenty-one nesting sites in Eldora and 29 in Wild Basin were sampled. Nest sites were selected for analysis after incubation began. Five control plots which were within the birds' home ranges, but where no grosbeak nests were observed, were also chosen in each area by pacing in various directions from a central location; number of steps and direction were determined from a random number table. All distances were taken with a tape measure and heights were estimated using a range finder. Sampling methods

developed by James and Shugart (1970) and Noon (1981) were used but modified where necessary to suit regional vegetation. General habitat variables were measured in a 0.04-ha (diameter = 22.6 m) circle and quantitatively analyzed (see Noon 1981). These variables and details about vegetation sampling are included in Appendix 1. Specific measures used in various comparisons are presented in Appendix 2.

STATISTICAL METHODS AND DATA REDUCTION

Where appropriate, pair-wise analyses of percentage data were performed using the z statistic (Bruning and Kintz 1977; see Table 1, footnote A). In all other cases, SPSS programs (Nie et al. 1975) were used. Stepwise discriminant function analysis (DFA) showed which combinations of habitat variables best distinguished between nesting and nonnesting sites in (1) Eldora, (2) Wild Basin, and (3) Eldora and Wild Basin combined. With one exception (data reduction; see below), $P < 0.05$ was used for determining statistical significance.

The large number of variables entered into the DFA was reduced to avoid the possibility that results would be due solely to chance variation in the sample. Small data sets also were combined. Jurs (1986) pointed out that unless the number of cases in the analysis is several times larger than the number of variables, chance variation may play a major role in the separation between groups (see also Morrison 1984).

The following procedures were used to reduce the variable set (Appendix 2):

(1) Mean values for each variable for nesting and nonnesting sites were tested for significant differences using Mann-Whitney U-tests (Hull and Nie 1981), where U was transformed into a normally distributed z statistic for $n > 30$. A less rigorous standard of $P < 0.10$ was used to insure that the number of variables that might be important in discriminating between groups was maximized. Variables that did not differ significantly in mean value were discarded (see also Dunn and Braun 1986, p. 230).

(2) The second and third most dominant shrub and ground cover species were removed because of infrequent occurrence or absence.

(3) Mean values for north, south, east, and west deciduous stem intersects (DECIDSTI) were used instead of values for each compass direction. Mean values also were used for distance to the

TABLE 1.   Percentage of occurrence (n in parentheses) of predominant trees at nesting (NS) and nonnesting (NNS; control) sites in Eldora and Wild Basin. Rare species (<1.0% occurrence) were excluded. Percentage of nests (%NESTS) built in these trees also is presented. PP = ponderosa pine, DF = Douglas fir, ASP = aspen, LPP = lodgepole pine, SAF = subalpine fir, and ES = Engelmann spruce.

	Species					
	PP	DF	ASP	LPP	SAF	ES
Eldora NS	7.9 (64)	20.6 (167)	61.4 (497)	5.4 (44)	0	4.5 (36)[A,B]
%NESTS	42.9 (9)	28.6 (6)	0	14.3 (3)	0	14.3 (3)[G]
Wild Basin						
NS	27.4 (196)	30.3 (217)	14.7 (105)	24.8 (177)	0	2.8 (20)[C,F]
%NESTS	64.3 (18)	14.3 (4)	0	21.4 (6)	0	0[H]
Eldora NNS	0	0	61 (249)	0	25.7 (105)	13 (53)[D]
Wild Basin						
NNS	30 (48)	30 (48)	30 (48)	8.1 (13)	0	0[E]

[A] Critical values of z for pair-wise comparisons of percentages are listed in Table 2 (footnote B). Pair-wise analyses were run after determining that the distribution of data was heterogeneous, using Snedecor's (1956, p. 227ff) x^2 test for the homogeneity of three or more percentages (also see Sokal and Rohlf 1969, p. 608). Comparisons not included here are either statistically similar ($P > 0.05$) or are for relative differences smaller or greater than those for which significant z scores were calculated. x^2 values for the comparison of the relative percentages of different trees among NS and NNS are (df = 3, $P \ll 0.001$ in all cases): PP: 221.0; DF: 143.6; ASP: 409.3; LPP: 220.5; SAF: 457.7; ES: 76.21.
[B] Eldora NS ($n = 809$, $x^2 = 1,497.7$, df = 5, $P \ll 0.001$): ASP > DF ($z = 16.65$); DF > PP ($z = 6.37$).
[C] Wild Basin NS ($n = 715$, $x^2 = 409.6$, df = 5, $P \ll 0.001$): LPP > ASP ($z = 5.03$).
[D] Eldora NS vs. NNS ($n = 408$, $x^2 = 826.2$, df = 5, $P \ll 0.001$): > PP ($z = 5.61$), DF ($z = 10.42$), and LPP ($z = 4.60$); < SAF ($z = 14.80$) and ES ($z = 4.94$).
[E] Wild Basin NS vs. NNS ($n = 160$, $x^2 = 142.3$, df = 5, $P \ll 0.001$): < ASP and PP ($z = 4.61$).
[F] Wild Basin NS vs. Eldora NS: > PP ($z = 9.75$), DF ($z = 4.33$), and LPP ($z = 9.66$); < ASP ($z = 18.05$).
[G] % nests ($n = 21$) built in tree species in Eldora ($x^2 = 20.34$, df = 5, $P < 0.005$): PP > LPP and ES ($z = 2.05$).
[H] % nests ($n = 28$) built in tree species in Wild Basin ($x^2 = 61.4$, df = 5, $P \ll 0.001$): PP > DF ($z = 3.03$) and LPP ($z = 3.25$).

nearest tree (TRDIST), diameter at breast height (DBH), distance to the nearest log (LOGDIST), and diameter (DIALOG) and length (LENLOG) of the largest log.

(4) Nine DBH size classes (Appendix 1) were collapsed into two classes, 3–38 cm and >38 cm, because of too few measures in some ranges.

Separate stepwise analyses were performed for habitat variables so that nesting and control sites could be compared (Appendix 2). Stepwise selection criteria entered variables in an attempt to maximize the Mahalonobis distance (D^2) between the two groups. Variables from the reduced list were entered into the analysis if their partial multivariate F ratio was ≥0.15.

RESULTS

NESTING SITES COMPARED TO NONNESTING AREAS

Critical values and significance levels for the z statistic computed for pair-wise comparisons of percentages are presented in Table 2 (footnote B). For other analyses, the value of the statistic and its significance are provided in the text. Means ± standard deviations also are presented.

A single discriminant function consisting of five variables (Table 2) correctly separated 91.5% (54) of all nesting ($n = 49$) and control ($n = 10$) areas. The percentage of plots that would be ex-

pected a priori to be correctly classified is 71.8%, [$(49/59)^2 + (10/59)^2$] × 100, which is significantly less than our calculated value of 91.5% ($z = 2.64$). Deciduous stem intersect (DECIDSTI) and shrub dispersion of large clumps (SHDISPLG) best discriminated between nesting and nonnesting sites. Nesting areas had a lower mean number of deciduous stem intersects, a lower mean percentage of deciduous canopy cover (DECIDCANCVR), and a smaller mean diameter of the largest log (DIALOG). The percentage of sites with large deciduous clumps or irregular matrix (SHDISPIM) was significantly smaller for nesting sites than for nonnesting areas (Table 2).

The relative frequency of occurrence of different trees also varied among nesting and nonnesting sites (Table 1). For example, when compared to Eldora control sites, nesting areas there contained (1) relatively more ponderosa pines, Douglas firs, and lodgepole pines, (2) about the same relative proportion of aspens, and (3) fewer subalpine firs, and Engelmann spruce. In Wild Basin, nesting areas contained about the same relative proportion of ponderosa pines, Douglas firs, and Engelmann spruce as did nonnesting sites, but the latter had more aspens and fewer lodgepole pines. Neither nesting nor nonnesting areas in Wild Basin contained subalpine firs.

TABLE 2.   Significant discriminating variables and their discriminant function coefficients (DFC) in order of decreasing value for nesting ($n = 49$) and nonnesting ($n = 10$) sites in Eldora and Wild Basin. Fifty-four of the 59 sites (91.5%) were correctly classified as being either nesting or nonnesting areas. Mean values (standard deviations in parentheses) are provided for deciduous stem intersect (DECIDSTI), deciduous canopy cover (DECIDCANCVR), and mean diameter of largest log (DIALOG) as are the percentages of sites with large clumps (SHDISPLG) or irregular matrix (SHDISPIM). The canonical correlation, $r = +0.75$, $x^2 = 45.63$, df = 5, $P < 0.00001$.

Variable	DFC	Nesting sites	Nonnesting sites
Deciduous stem intersect	0.94811	0.90 stems (1.8)	8.18 (10.0)[A]
Shrub dispersion, large clumps	0.83626	6.1%	40%[B,C]
Shrub dispersion, irregular matrix	0.58170	20.4%	50%[D]
Deciduous canopy cover	−0.51367	7.14% (13.8)	15.5% (19.1)[E]
Diameter of largest log	0.44429	6.95 cm (8.4)	13.75 (10.0)[F]

[A] $z = 2.87$, $P = 0.004$.
[B] Critical values of z for pair-wise analyses of percentages (see text) are: 1.96 ($P < 0.05$), 2.58 ($P < 0.01$), and 3.30 ($P < 0.001$).
[C] Nesting sites < nonnesting sites, $z = 3.03$.
[D] Nesting sites < nonnesting sites, $z = 1.96$.
[E] $z = 2.03$, $P = 0.042$.
[F] $z = 2.40$, $P = 0.016$.

None of the variables separating nesting areas and nonnesting sites in Eldora were important in Wild Basin. Nesting areas in both locations were more open than nonnesting sites. Although Eldora nesting sites had a greater mean percentage ($z = 3.87$, $P = 0.0001$) of deciduous canopy cover (DECIDCANCVR: $\bar{x} = 15.23\% \pm 17.99$; coefficient of variation, CV = 118%) than did nesting areas in Wild Basin ($\bar{x} = 1.07 \pm 3.15$; CV = 294%), there was a large amount of variability (CVs > 100%) in each area. Mean DECIDCANCVR was greater in the control areas in each location (Eldora: $\bar{x} = 25.00 \pm 22.90$; Wild Basin: $\bar{x} = 6.00 \pm 8.22$), but the difference was significant only in Wild Basin ($z = 2.47$, $P = 0.014$).

Nesting areas in Wild Basin contained no large clumps (SHDISPLG; 40% of nonnesting sites contained large clumps: $z = 3.46$), had no instances of forbs as ground cover (GRNDCVRFO; 40% of nonnesting areas contained forbs: $z = 3.46$) and fewer occurrences of irregular matrix (SHDISPIM; $n = 6$, 21.4%; nonnesting areas: $n = 3$, 60%: $z = 2.46$). Ninety-seven percent (32/33) of all nesting and nonnesting sites were correctly classified; the a priori probability of correct classification = 0.74 ($z = 2.45$).

In Eldora, all nesting and nonnesting areas were classified correctly; the a priori probability of correct classification = 0.69 ($z = 3.07$). Nesting sites when compared to nonnesting areas had shorter downed logs (LENLOG; $\bar{x} = 1.48$ m $\pm$ 1.8; nonnesting areas: $\bar{x} = 6.8$ m ± 2.7; $z = 3.27$, $P = 0.001$), a larger percentage of plots with small clumps (SHDISPSM; $n = 11$, 52.4%; nonnesting areas: $n = 0$: $z = 2.13$), and more 3 to 38 cm

Douglas firs (FDOUGFIR; $\bar{x} = 7.71 \pm 10.2$; nonnesting areas; $n = 0$; $z = 2.40$, $P = 0.017$). As in Wild Basin, nonnesting areas were characterized by the presence of large clumps or irregular matrices.

NEST-SITE CHARACTERISTICS

A comparison of Eldora and Wild Basin nesting areas showed that overall shrub dispersion and percentage of deciduous canopy cover best separated the two sites. All nesting sites in Eldora contained shrubs, whereas significantly fewer (75%; $z = 2.48$) of the nesting areas in Wild Basin had shrubs.

With respect to major vegetation (Table 1), there was a positive but nonsignificant rank-order correlation ($r_s = 0.66$, df = 4, $P > 0.05$) for the relative proportion of the most predominant trees in the nesting areas in both locations. There was a significantly greater proportion of aspens in Eldora than in Wild Basin, whereas in Wild Basin there was a larger proportion of ponderosa pines, Douglas firs, and lodgepole pines. Engelmann spruce occurred in about the same relative proportion in both areas and subalpine firs were not found in the nesting areas in either location. Among Eldora nest sites, there was a greater relative percentage of aspens than Douglas firs and more Douglas firs than ponderosa pines. Ponderosa pines, Douglas firs, and lodgepole pines occurred in about the same relative proportion among nest sites in Wild Basin.

NEST LOCATIONS

In Eldora, the same percentage of nest trees was located on flat ground (33.3%) and on moderate

(38.1%) and steep slopes (28.6%), whereas in Wild Basin, a significantly higher percentage of nest trees ($z = 3.74$) was located on flat ground (75.0%) than on moderate (14.3%) or steep slopes (10.7%). In neither locale was there a significant correlation between the relative abundance of a tree species and the percentage of nests that were built in that tree. In Eldora and Wild Basin, grosbeaks built the majority of their nests in either ponderosa pines or Douglas firs (Table 1). The percentage of nests built in ponderosa pines and Douglas firs in Eldora was statistically equal. In Wild Basin, relatively more nests were built in ponderosa pines than in Douglas firs or lodgepole pines, but the percentage of nests built in Douglas firs or lodgepole pines did not differ. No nests were built in aspens or subalpine firs in either area.

In Eldora, 36.8% of nests were built on the south side of the nest tree and 21.1% faced north. However, there were no significant differences among the relative percentages of nests that were built in any compass direction. In Wild Basin, a significantly greater percentage of nests (48.6%) was built on the south side of nest trees than in any other compass direction ($z = 2.72$; 20.9% faced north). Nests were located significantly farther ($z = 2.42$, $P = 0.016$) from water in Eldora ($\bar{x} = 78.59$ m $\pm$ 95.90, CV = 122%) than in Wild Basin ($\bar{x} = 43.65$ m $\pm$ 63.34, CV = 145%), but there was considerable variability in these measures in both areas.

Nests were built a mean distance of 1.5 m (± 1.00) from the tree trunk (NESTTREETRNK) at an average height (NESTHT) of 9.7 m (± 5.6). Mean NESTTREETRNK (Eldora: 1.54 m $\pm$ 0.39; Wild Basin: 1.40 m $\pm$ 0.63) and NESTHT (Eldora: 8.31 m $\pm$ 5.04; Wild Basin: 10.8 m $\pm$ 5.85) were the same in both areas. Mean NESTHT was also the same in nest trees located on flat ground or on moderate or steep slopes. Mean height of the nest tree (NESTTREEHT) was less in Eldora than in Wild Basin (Eldora: 12.7 m $\pm$ 6.5; Wild Basin: 16.5 m $\pm$ 7.2; $z = 2.09$, $P = 0.037$), whereas mean maximum canopy height (CANHTMAX) did not differ (Eldora: 16.1 m $\pm$ 7.3; Wild Basin: 17.2 m $\pm$ 7.5). In both areas, mean NESTHT was about 65% of mean NESTREEHT.

DISCUSSION

Our results show that Evening Grosbeaks living in two different habitats did not randomly choose trees in which to build nests. Questions dealing with nest-site selection (Head 1904, Titus and Mosher 1981, Clark et al. 1983, Burger and Gochfeld 1985, Finch 1985, Marks 1986, Parker 1986, Santana et al. 1986, Snyder et al. 1986, Speiser and Bosakowski 1987) were viewed as a subset of more general queries concerned with habitat selection (Lack 1933, 1937; Thorpe 1945; Hildén 1965; Wiens 1969; Orians 1971; Partridge 1978; Cody 1981; Rice et al. 1983; Pulliam and Caraco 1984; Menkens and Anderson 1987). Once they are settled into a general area where they feel "comfortable" (Lack 1937, Orians 1971), animals appear to assess their surroundings in a hierarchical fashion in which habitat must be found suitable and reinforcing (Darlington 1975) at larger scales before assessment occurs at the next lower level (Speiser and Bosakowski 1987; B. Noon, pers. comm.). There is a sequence of finer and finer choices (microhabitat selection, Walsberg 1985) of available space in which each successive array of environmental stimuli contains some, but not all, of the previous habitat features (Hildén 1965).

Generally, it has been assumed that the initial gross-scale selection of habitat by Evening Grosbeaks is based on prey productivity, especially high spruce budworm density (Blais and Parks 1964, Erskine 1977 cited in Langelier 1983, Torgersen and Campbell 1982, Langelier 1983, Takekawa et al. 1982, Takekawa and Garton 1984). Both of our study sites were infested with spruce budworm. In each area grosbeaks chose a general location in which to settle before the larval stage of spruce budworm, suggesting that they may be selecting the site based on past experience (tradition, Newton 1973, p. 228) or on obvious budworm damage (J. Takekawa, pers. comm.). Langelier (1983) suggested that because Evening Grosbeaks are nonterritorial flockers that move about regularly (Willard 1910; Alexander 1943; Shaub 1963; Newton 1973; Bekoff and Scott, unpubl. data), it is more likely that food and not habitat structure or competition is the main driving force in the initial selection of an area in which to live (see also Speirs 1968 and Verner et al. 1980).

A COMPARISON OF NESTING SITES AND NONNESTING AREAS

Overall, four of the five variables best discriminating between nesting and nonnesting areas were indicators of *habitat density* (deciduous stem intersect, deciduous canopy cover) or *shrub dispersion* (large clumps and irregular matrix). All

measures showed vegetation on nesting sites to be less dense and more dispersed than that on nonnesting areas. Thus, we characterized nesting areas as being more *open* than nonnesting sites. Openness may be an important variable in initial choice of nesting habitat. Evening Grosbeaks living in Idaho, Washington, Oregon, and Montana also prefer open areas and avoid dense deciduous stands (Langelier 1983).

There is a number of reasons that grosbeaks might choose to build high nests in open habitat. Such nests permit high visibility of their surroundings which would be important for detecting predators such as Red-tailed Hawks (*Buteo jamaicensis*) and Common Ravens (*Corvus corax*) that may harass the incubating female or feed on eggs, altricial nestlings, or young individuals. On two occasions, a Great-horned Owl (*Bubo virginianus*) was detected and then mobbed by a group of about eight grosbeaks before it got close to a nest. Other birds also appear to build nests that facilitate the detection of potential predators (Balda and Bateman 1972, Clark et al. 1983, Burger and Gochfeld 1985, Finch 1985, Page et al. 1985, Belles-Isles and Picman 1986, Marks 1986, Santana et al. 1986). Of course, it is important to point out that open nests are also more easily detected by predators. However, grosbeak nests are well-camouflaged (see below).

Open habitat may also allow the nest to be seen from a distance; during incubation adult grosbeaks can be away from their nest for as long as 50 to 60 min (Bekoff and Scott, unpubl. data; J. Takekawa, pers. comm.). Nests positioned in an open area also allow easier access for departures and arrivals (Titus and Mosher 1981, Burger and Gochfeld 1985, Santana et al. 1986, Menkens and Anderson 1987, Speiser and Bosakowski 1987). Grosbeaks usually depart rapidly from their nest but approach them cautiously, stopping nearby before flying on to them. Cautious approach may reduce the likelihood of the birds being followed to their nest.

Temperature regulation also plays a role in nest-site selection (Ricklefs and Hainsworth 1969, Balda and Bateman 1972, Clark et al. 1983, Burger and Gochfeld 1985, Finch 1985, Walsberg 1985). Grosbeak nests allow sunlight and ultraviolet radiation to penetrate them, aiding in thermoregulation at the high altitudes where these birds nest and temperatures fluctuate greatly. Rapid heat gain (Ricklefs and Hainsworth 1969, Finch 1985) also could be facilitated by placing nests in an open area; overexposure or over-heating do not seem to be problematic. The high percentage of grosbeak nests built on the south and north sides of nest trees may aid in thermoregulation by protecting nests from prevailing winds that blow strongly from the west in both study areas. The placement of nests close to the main tree trunk also would shelter them from wind and rain and increase their stability.

A COMPARISON OF NESTING AREAS AND THE CHOICE OF NEST TREES

Nesting sites in Eldora and Wild Basin showed marked variations in vegetation. In Wild Basin, where there is a much broader valley floor than in Eldora, shrubs are more dispersed and there is a significantly lower percentage of deciduous canopy cover (DECIDCANCVR). In this respect, Wild Basin is more open than Eldora. More nests were built in trees on flat terrain than in trees on slopes in Wild Basin. In Eldora, where houses occupy flat ground, the same percentage of nests was built in trees on flat and sloping terrain.

Habitat differences did not influence the placement of nests in trees; mean distance from the trunk of the nest tree, absolute nest height regardless of ground slope, and nest height expressed as a percentage of nest tree height were the same in both areas. Mean nest height recorded in this study is about the same as that reported elsewhere (Willard 1910; Jensen 1930; DeGroot 1934a, 1934b; Speirs 1968; Langelier 1983). In Eldora, where houses were built close to streams, nest trees were located significantly farther from water than in Wild Basin.

An important question in the analysis of nest site selection centers on whether or not animals are actually choosing specific trees in which to build nests. It is possible that birds simply are nesting in whatever tree species are disproportionately abundant (Reese and Kadlec 1985). However, they may be choosing a specific tree species in which to build a nest regardless of its overall availability.

Our data show that grosbeaks were making specific choices of nest trees in Eldora and Wild Basin. In both areas, the highest percentage of nests was built in ponderosa pines, the long needles of which may help to camouflage and to protect nests. In Eldora, ponderosa pines occurred very infrequently compared to aspens, in which no nests were built, and Douglas firs, in which a smaller (though statistically similar) percentage of nests was constructed. In Wild Basin,

ponderosa pines, Douglas firs, and lodgepole pines comprised about the same relative proportion of major vegetation; however, 64.3% of nests were built in ponderosa pines. Thus, in both areas, grosbeaks appeared to be choosing ponderosa pines as the preferred nest tree.

Although we do not yet have sufficient data comparing successful and unsuccessful grosbeak nests, it is likely that the differential success of nests influences the evolution of species-typical patterns of nest placement (Rosenzweig 1985, Belles-Isles and Picman 1986; but see Verbeek 1981). However, because criteria of success vary according to the time at which it is measured (egg laying, hatching, fledging, attaining independence by young individuals), factors other than nest placement may also influence reproductive output. Of course, all grosbeaks did not always choose what we determined to be the best area in which to nest. Grosbeaks' and other birds' brains can probably process only a limited amount of information simultaneously and successively and combine this input with information gathered in the past (see Klopfer 1963 and Klopfer and Ganzhorn 1985 for discussions of how early experience influences habitat selection). They also are limited in their ability to anticipate the future consequences of their choices. Thus, although selection may influence the evolution of general species-typical patterns of nest-site selection, variability (individual behavioral plasticity) due to individual judgement and a little bit of luck (anonymous referee) probably play some role in the successful selection of a nesting area in variable environments (Rosenzweig 1985).

In summary, our quantitative analysis of nest site selection in Evening Grosbeaks allowed us to identify those factors that influenced where nests were built. Grosbeaks, like many other avian species regardless of whether they are tree or ground nesters and irrespective of the habitat in which they live, appear to choose specific trees or areas in which to build nests. Generally nest sites are selected to provide high visibility, protection from predators, easy access, aid in thermoregulation, and/or shelter from various climatic elements.

ACKNOWLEDGMENTS

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APPENDIX 1. Descriptions of general habitat variables and vegetation sampling methods.[A]

Mnemonic	Description
DBH	Diameter at breast height (cm) of all saplings and standing trees; following Noon (1981), nine size classes were initially compiled (3–8, 9–15, 16–23, 24–38, 39–53, 54–69, 70–84, 85–102, and >102), but not all were used in the final analysis (see text).
DECIDSTI	Shrub density at breast height; determined by counting the number of woody stems <3 cm DBH contacting outstretched arms while walking along north–south and east–west transect lines; Noon (1981) presents the formula for calculating number of stems/hectare using this technique.
CANCOV or GRDCOV	Canopy or ground cover expressed as a percentage of total cover; determined by walking each transect and recording the presence or absence of vegetation using an ocular tube; GRDCOV refers to plants <1 m tall.
DISP	Plant dispersion index (see Emlen 1956).
CANHT or CANHTMAX	Canopy height or maximum canopy height (m).
TRDIST or LOGDIST	Tree or log distance; using nest tree as the center of the plot, distance to the nearest tree (m) and its DBH were measured as was the distance to, and DBH and length of, the largest log; Noon (1981) refers to these measures as indices of tree and log dispersion.
GRNDCOV	Ground cover ranked in order of most common to least common life forms (grasses, sedges, forbs, seedlings, litter, slash, logs) or habitat features (rocks, bare ground; see Noon 1981).
SHSP	Shrubs ranked in order of most common to least common species.
DISTWATER	Distance (m) to nearest water source from the nest tree; measurements were taken from United States Geological Survey (USGS) topographical maps and Colorado Public Service (CPS) aerial photographs.
DISTNEST	Distance (m) to the nearest Evening Grosbeak nest occupied during that breeding season; hand-measured or estimated from USGS or CPS maps.
NESTTREEHT	Estimated height of nest tree (m) using range finder.
NESTTREESP	Nest tree species.
NESTTREEDBH	Nest tree diameter at breast height (cm).
NESTTREETRNK	Distance (m) from nest to tree trunk.
COMPDIRNEST	Compass direction of nest.
NESTHT	Nest height (m).

[A] The list of original variables is available from the senior author. Vegetation samples to determine density and dispersion were analyzed using the point-quarter technique. The nest tree was designated "center" and from this point four quadrants were generated from 11.3 m transects along compass cardinal directions. Shrub frequencies were determined in each quadrant by counting the number within 0.5 m of each other but > 1 m from another shrub. Two to five shrubs fulfilling these criteria comprised a *clump*. If at least one clump occurred in each quadrant it was defined as a *small clump matrix*. More than five shrubs in a clump and a minimum of one clump per quadrant comprised a *large clump matrix*. When inconsistency within the four quadrants existed, we called the area an *irregular matrix*; when at least four shrubs in each quadrant were spaced fairly equally, we used the term *regular matrix*.

For descriptive measures of ground cover, the term small clump was used to designate quadrants where there were distinct areas of cover about 0.5 m in diameter, with little to no ground cover between them and at least one clump per quadrant. Large clumps were determined as above with ground cover about 1 m in diameter. An even matrix was defined by ground cover with equal spacing in more than half of each quadrant, whereas the term irregular matrix was used to refer to random or sparse ground cover.

APPENDIX 2. Specific variables included in final discriminant function analysis (see text for discussion of data reduction methods). Differences between means for nest sites and control areas for all variables were first tested using Mann-Whitney U-tests. The variables in this list were retained for inclusion in the final analysis if $P < 0.10$ (to maximize the number of variables retained). WB = comparison of Wild Basin nest sites to Wild Basin control areas; ELD = comparison of Eldora nest sites to Eldora control areas; WB/ELD = comparison of all nest sites to all control areas.

Mnemonic	Description	Comparison
DECIDCANCVR	Deciduous canopy cover	WB; ELD; WB/ELD
WILLOW	Frequency of 3- to 8-cm willows	WB; ELD; WB/ELD
DBH	Diameter (cm) at breast height of nearest trees	WB; ELD; WB/ELD
DECIDSTI	Deciduous stem intersect	WB; WB/ELD
SHDISPLG	Shrub dispersion, large clumps	WB; WB/ELD
SHDISPIM	Shrub dispersion, irregular matrix	WB; WB/ELD
FLIMBER	Frequency of 3- to 38-cm limber pine	WB; ELD
GRNDCVRFO	Dominant ground cover, forbs	WB
DOMSHASPEN	Dominant shrub, aspens	WB
CANHTMIN	Minimum canopy height (m)	ELD; WB/ELD
LOGDIST	Mean distance (m) to largest log within quadrant	ELD; WB/ELD
DIALOG	Mean diameter (m) of largest log within quadrant	ELD; WB/ELD
LENLOG	Mean length (m) of largest log within quadrant	ELD; WB/ELD
FENGEL	Frequency of 38- to 102-cm Engelmann spruce	ELD; WB/ELD
FENGEL1	Frequency of 3- to 38-cm Engelmann spruce	ELD; WB/ELD
SHDISPSM	Shrub dispersion, small clumps	ELD; WB/ELD
GRNDSLLOG	Dominant ground cover, slash and logs	ELD
DOMSHJUN	Dominant shrub, juniper	ELD
FPON	Frequency of 3- to 38-cm ponderosa pine	ELD
FDOUGFIR	Frequency of 3- to 38-cm Douglas fir	ELD
CONSTEM	Coniferous stem intersect	WB/ELD