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VERTICAL DISTRIBUTIONS OF BREEDING-SEASON BIRDS: IS HUMAN INTRUSION INFLUENTIAL?

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ABSTRACT.—Human intrusion has become a widespread and chronic disturbance for birds in many wildlands. Because bird species often seek refuge, feed, and nest only in certain vegetation strata, intrusion-induced changes in vertical distributions could reduce access to such strata, increase interspecific competition, heighten energetic expenditures, and reduce nesting success. In Wyoming subalpine forests during the breeding seasons of 1989–1993, we studied the effects of intrusion on vertical distributions of Mountain Chickadees (*Parus gambeli*), Ruby-crowned Kinglets (*Regulus calendula*), Yellow-rumped Warblers (*Dendroica coronata*), and Dark-eyed Juncos (*Junco hyemalis*). Intrusion by one person for 1–2 h/week, similar in intensity to intrusion from some wildland recreationists and ecotourists, did not appreciably affect distributions of any of the species in three vegetation strata above the ground: less than 0.5 m, 0.5–3.0 m, more than 3.0 m. Although human disturbance has caused an increase in the height at which bird species in various habitats nest and roost, we found little evidence that intrusion altered vertical distributions of four passerines that nest, forage, sing, and seek refuge in subalpine forest. The minimal effects we observed indicate that the species we studied were able to tolerate low levels of intrusion. Studies of intrusion levels that do and do not affect vertical distributions are necessary to define the range of intrusion intensity that is influential. *Received 12 Jan. 1998, accepted 25 June 1998.*

Many bird species use specific vertical strata for nesting, feeding, and shelter (Dunlavy 1935, Colquhoun and Morley 1943, Preston and Norris 1947, MacArthur 1958, Cody 1985, Martin 1988). Vertical stratification is believed to partition resources and thereby reduce competition among coexisting species (Anderson et al. 1979). One factor that might alter vertical stratification is human intrusion. Intrusion is a pervasive and chronic disturbance that occurs even in protected habitats (Anderson and Keith 1980, Burger and Gochfeld 1991, Gutzwiller et al. 1994), and its effects on birds can include significantly lower reproduction and survival, displacement from crucial habitats, and abnormally high amounts of vigilance that reduce time for other essential activities (Boyle and Samson 1985, Burger and Gochfeld 1991, Knight and Gutzwiller 1995). For some bird species, human disturbance can also cause birds to increase nest height above the ground (Stoner 1937, Preston and Norris 1947, Anderson and Keith 1980, Knight and Fitzner 1985, Datta and Pal 1993).

One would expect a species' characteristic vertical location during breeding periods to reflect energetic efficiency of movements to nests, food sources, and shelter. Short flights between foraging substrates can cost more than 20× the energy used while resting (Goldstein 1990), so repeated flights to vertical strata that are atypical for a species could be maladaptive (Dhindsa et al. 1989). Disruption of vertical distributions may thus have significant impacts on competitive relations among species, energy budgets, and hence fitness.

As an initial assessment of whether intrusion could cause such changes, we tested for intrusion effects on vertical distributions. Because low levels of intrusion in wildlands are more ubiquitous than are intense levels of intrusion, low levels have the potential to affect more individuals and species (Gutzwiller et al. 1994). Therefore, we examined whether low levels of intrusion (1–2 h/week) caused sustained effects on vertical distributions of birds in three vegetation strata above the ground: less than 0.5 m (stratum 1), 0.5–3.0 m (stratum 2), more than 3.0 m (stratum 3). Our ob-

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jective was to determine whether intrusion would displace birds from strata 1 and 2, where disturbance from a walking intruder is most intense, into stratum 3.

METHODS

Study area.—Data were collected approximately 70 km WNW of Laramie, Wyoming (41° 32′ N, 106° 20′ W) in the Snowy Mountains. Plant communities, elevations, and weather conditions are described in Gutzwiller and coworkers (1997). In May 1989, we randomly established 30 circular 1.0-ha (113-m diameter) sites for the 5-year study. Sites were 0.4 km from the nearest used road and were an average of 0.7 km apart.

Intrusion treatments.—We randomly assigned intrusion treatments to the 1.0-ha sites during May 1989; the same assignments were used during all 5 years. Treatments involved two levels of frequency [one (F1) or two (F2) intrusion treatments/week], two levels of spatial scale [the inner 25% (S25) or 100% (S100) of the site was intruded], and controls (no intrusion treatments). The five groups were replicated as follows: F1-S25 (n = 5); F1-S100 (n = 5); F2-S25 (n = 5); F2-S100 (n = 5); Control (n = 10). In the present analysis, we were only interested in whether the intrusions in general were influential, so we grouped all disturbed sites into a single group called intruded sites. F1 treatments were implemented on Wednesdays and F2 treatments were administered on Mondays and Fridays so treatments would not coincide with bird sampling, which occurred on Tuesdays and Thursdays.

Each year for 10 weeks between late May and early August, each treated site was intruded an equal number of times during various times of day between 07:00–15:00 MST. A single intrusion treatment involved one person walking through the site in a radial pattern, beginning when the person reached the marked perimeter of the 1.0-ha site. Movements were made from the site center (marked) to the perimeter and back again; directions of movement were shifted approximately 40° after each return to the center, and the specified area was covered twice during a 1-h period. Additional details about intrusion treatments are in Gutzwiller and coworkers (1997).

Bird sampling.—Data for the present analysis were gathered with the sampling techniques described by Riffell and coworkers (1996) and Gutzwiller and coworkers (1997). When investigators reached the marked 1.0-ha perimeter, they began recording the vertical position (stratum 1, 2, or 3) of birds inside the 1.0-ha site. They continued to record these data as they proceeded toward the site center where they completed the 15-min count. When a bird was heard but not seen, investigators could not always clearly ascertain its vertical location; the present analysis involves only birds for which the vertical stratum was known. Half of the sites were sampled on Tuesdays and half on Thursdays each week. Daily timing, weather conditions, and randomization for sampling are described elsewhere (Gutzwiller et al. 1997).

Habitat features.—If differences in habitat features were confounded with treatment groups, effects of intrusion on vertical distributions would not be distinguishable from those caused by habitat conditions. We measured a variety of habitat variables and found that none differed between control and intruded sites during any year (details in Gutzwiller et al. 1997), indicating that habitat features were not confounded with treatment groups.

Statistical analyses.—For each year, site, and stratum separately, we computed the total number of individuals detected for four species that occurred on at least 19 of the 30 sites: Mountain Chickadee (*Parus gambeli*), Ruby-crowned Kinglet (*Regulus calendula*), Yellow-rumped Warbler (*Dendroica coronata*), Dark-eyed Junco (*Junco hyemalis*). These four species were sufficiently abundant to allow us to detect differences in vertical distributions. To avoid the problem of pseudoreplication that would have been incurred if we had treated individual observations of birds as independent, our experimental unit was a site. Because intrusion may have displaced birds from an entire site, those sites that did not have detections for a species within any of the three strata for a given year were not used in analyses for that species and year. This approach reduced the possibility that changes in vertical distributions would be confounded in our analyses with displacement effects.

The normality assumption of Student's t-test and Welch's t-test was not always tenable. Consequently, for each species, year, and stratum separately, we used Mann-Whitney U statistics (Zar 1996) from BMDP 3D software (1990 release, VAX mainframe, Dixon 1990) to test the following *a priori* 1-tailed research hypotheses: for strata 1 and 2, number of birds detected on control sites is greater than that on intruded sites; for stratum 3, number of birds detected on control sites is less than that for intruded sites. As recommended by Zar (1996), U' was used to test the hypotheses for strata 1 and 2, and U was used to test the hypothesis for stratum 3. We reported group means because in most cases the mean was the best descriptor of central tendency. We did not use repeated measures ANOVA for the reasons given by Gutzwiller and coworkers (1997). We did not combine all of the data into one set and conduct a single standard ANOVA because possible site fidelity by individual birds and small changes in the physical sites made it inappropriate to assume that our experimental units were sufficiently independent among years. Using separate Mann-Whitney tests, we did not have to make any untenable or questionable assumptions and there was no pseudoreplication within or among years.

We used an *a priori* α = 0.10 instead of 0.05 for all analyses to improve statistical power (Westmoreland and Best 1985). To control for Type I error, we used a sequential Bonferroni adjustment of α for simultaneous inferences (Holm 1979, Rice 1989). For each species and year, we tested a set of three simultaneous hypotheses, one for each of the three strata. We considered each set to be a "family" (Miller 1981)

TABLE 1. Mean number of individuals for four species on control sites at three vertical strata, 1989–1993. Each value is a 5-year mean of the number of individuals per vertical meter of stratal height span (0.5 m for stratum 1; 2.5 m for stratum 2; 12 m for stratum 3).

Species	Vertical stratum (m) <0.5	 0.5–3.0	 >3.0
Mountain Chickadee	0.4	4.5	1.8
Ruby-crowned Kinglet	0.4	1.8	2.4
Yellow-rumped Warbler	0.0	1.6	1.9
Dark-eyed Junco	17.6	8.6	1.5

of hypotheses. The sequential α levels for significance within a family were 0.033, 0.05 and 0.10.

We determined whether our sampling method provided data on vertical habitat use that were consistent with the strata the species are known to use during the breeding season in the absence of repeated intrusion. Control-site data for the four species were used for this analysis. For each species, year, and stratum separately, we tallied the total number of individuals. Because the three strata had different vertical extents, the number of individuals recorded for the three strata were not directly comparable. To determine relative concentrations of individuals among the strata, we computed the total number of individuals for a given species, year, and stratum on a per meter basis, dividing stratum 1 totals by 0.5 m (0.5 − 0.0 m = 0.5 m), stratum 2 totals by 2.5 m (3.0 − 0.5 m = 2.5 m), and stratum 3 totals by 12 m. The latter span of height reflected the possibility that the highest nests were 15 m above the ground (15 − 3 m = 12 m), the approximate height of nest substrates in the canopy at our sites. For each species and stratum, we calculated a 5-year mean for the number of individuals/m; we compared the resulting vertical distributions with those expected based on published heights for foraging and nesting.

A general estimator to calculate minimum detectable effect sizes for Mann-Whitney tests is not available. Consequently, we programmed simulations with FORTRAN to determine effect sizes, which were the smallest between-group differences in the number of individuals that we could have detected as statistically significant. For each species, year, and stratum, we used an iterative trial-and-error method to find the smallest difference in number of individuals that led to a significant U value 80% of the time at $\alpha = 0.033$ and at $\alpha = 0.10$ (the minimum and maximum α levels possible for each family of hypotheses). We simulated scores from distributions that mimicked observed sample distributions. Once the underlying distributions were established, scores were randomly drawn from them and the Mann-Whitney U was calculated. We repeated this step 10,000 times and computed the percentage of these iterations in which the null hypothesis was rejected.

RESULTS

Assessment of vertical sampling.—During the 5-year period, species were detected on control sites to varying extents in the three strata (Table 1).

Vertical distributions.—Most tests indicated no differences in number of individuals between control and intruded sites (Tables 2–5). The only statistically significant effect oc-

TABLE 2. Summary statistics and results of Mann-Whitney tests for number of Mountain Chickadees on control and intruded sites at three vertical strata.

Year	Vertical stratum (m)	Mean ± SE (n) Control	 Intruded	U', U[a]	P
1989	<0.5	0.00 ± 0.00 (10)	0.00 ± 0.00 (15)	—[b]	—[b]
	0.5–3.0	2.90 ± 0.91 (10)	1.53 ± 0.38 (15)	91.5	0.191
	>3.0	1.30 ± 0.21 (10)	2.07 ± 0.52 (15)	89.0	0.231
1990	<0.5	0.00 ± 0.00 (6)	0.00 ± 0.00 (18)	—	—
	0.5–3.0	0.33 ± 0.33 (6)	0.06 ± 0.06 (18)	60.5	0.349
	>3.0	2.83 ± 0.91 (6)	3.61 ± 0.53 (18)	68.0	0.189
1991	<0.5	0.00 ± 0.00 (8)	0.00 ± 0.00 (16)	—	—
	0.5–3.0	0.38 ± 0.26 (8)	0.25 ± 0.11 (16)	66.0	0.464
	>3.0	2.75 ± 0.75 (8)	2.56 ± 0.29 (16)	63.5	0.524
1992	<0.5	0.10 ± 0.10 (10)	0.00 ± 0.00 (17)	93.5	0.347
	0.5–3.0	1.20 ± 0.59 (10)	0.88 ± 0.23 (17)	83.5	0.539
	>3.0	4.00 ± 1.18 (10)	2.94 ± 0.42 (17)	82.0	0.568
1993	<0.5	0.00 ± 0.00 (10)	0.00 ± 0.00 (20)	—	—
	0.5–3.0	1.00 ± 0.26 (10)	1.15 ± 0.21 (20)	93.5	0.619
	>3.0	1.70 ± 0.26 (10)	2.40 ± 0.45 (20)	111.5	0.317

[a] U' = Mann-Whitney statistic for strata 1 and 2; U = statistic for stratum 3.

[b] — indicates no individuals were detected on either control or intruded sites, so a statistical test was not conducted.

TABLE 3. Summary statistics and results of Mann-Whitney tests for number of Ruby-crowned Kinglets on control and intruded sites at three vertical strata.

Year	Vertical stratum (m)	Mean ± SE (*n*)		U', U[a]	*P*
		Control	Intruded		
1989	<0.5	0.11 ± 0.11 (9)	0.05 ± 0.05 (19)	90.5	0.414
	0.5–3.0	0.89 ± 0.48 (9)	0.42 ± 0.16 (19)	94.0	0.350
	>3.0	5.67 ± 1.22 (9)	3.63 ± 0.58 (19)	60.0	0.897
1990	<0.5	0.00 ± 0.00 (6)	0.00 ± 0.00 (15)	—[b]	—[b]
	0.5–3.0	0.17 ± 0.17 (6)	0.40 ± 0.13 (15)	34.5	0.799
	>3.0	3.17 ± 0.60 (6)	2.00 ± 0.35 (15)	23.0	0.960
1991	<0.5	0.00 ± 0.00 (9)	0.00 ± 0.00 (15)	—	—
	0.5–3.0	0.22 ± 0.15 (9)	0.47 ± 0.19 (15)	58.0	0.721
	>3.0	3.33 ± 0.62 (9)	4.13 ± 0.57 (15)	84.0	0.174
1992	<0.5	0.00 ± 0.00 (9)	0.00 ± 0.00 (17)	—	—
	0.5–3.0	0.78 ± 0.36 (9)	0.65 ± 0.31 (17)	85.0	0.336
	>3.0	2.33 ± 0.75 (9)	2.65 ± 0.45 (17)	91.5	0.221
1993	<0.5	0.00 ± 0.00 (8)	0.00 ± 0.00 (18)	—	—
	0.5–3.0	0.50 ± 0.27 (8)	0.56 ± 0.18 (18)	70.0	0.554
	>3.0	2.75 ± 0.73 (8)	2.39 ± 0.47 (18)	62.5	0.707

[a] U' = Mann-Whitney statistic for strata 1 and 2; U = statistic for stratum 3.

[b] — indicates no individuals were detected on either control or intruded sites, so a statistical test was not conducted.

curred during 1990 for Dark-eyed Juncos, which were more abundant in stratum 1 on control sites than they were in this stratum on intruded sites (Table 5).

Effect sizes.—Minimum detectable effect sizes were an average of 1.05–2.11 times (α = 0.033) and 0.84–1.71 times (α = 0.10) the magnitude of control-site means of the original data (Table 6). Differences in number of individuals of these magnitudes and larger would have been detectable with a probability of 0.80; smaller differences were detectable with less reliability.

DISCUSSION

Assessment of vertical sampling.—The midpoint of the usual nest-height range for Mountain Chickadees is 3.2 m above the ground (Terres 1980) and, for much of their food, Mountain Chickadees glean insects from fo-

TABLE 4. Summary statistics and results of Mann-Whitney tests for number of Yellow-rumped Warblers on control and intruded sites at three vertical strata.

Year	Vertical stratum (m)	Mean ± SE (*n*)		U', U[a]	*P*
		Control	Intruded		
1989	<0.5	0.00 ± 0.00 (7)	0.14 ± 0.10 (14)	42.0	0.708
	0.5–3.0	0.29 ± 0.18 (7)	0.21 ± 0.11 (14)	52.5	0.414
	>3.0	2.00 ± 0.49 (7)	1.64 ± 0.29 (14)	40.0	0.756
1990	<0.5	0.00 ± 0.00 (8)	0.00 ± 0.00 (13)	—[b]	—[b]
	0.5–3.0	0.13 ± 0.13 (8)	0.46 ± 0.22 (13)	41.5	0.783
	>3.0	1.88 ± 0.44 (8)	1.85 ± 0.25 (13)	54.0	0.458
1991	<0.5	0.00 ± 0.00 (10)	0.00 ± 0.00 (15)	—	—
	0.5–3.0	0.30 ± 0.15 (10)	0.60 ± 0.25 (15)	68.0	0.656
	>3.0	2.90 ± 0.60 (10)	3.20 ± 0.49 (15)	82.5	0.352
1992	<0.5	0.00 ± 0.00 (10)	0.00 ± 0.00 (19)	—	—
	0.5–3.0	0.60 ± 0.34 (10)	0.89 ± 0.27 (19)	80.0	0.758
	>3.0	3.70 ± 0.96 (10)	3.53 ± 0.61 (19)	95.5	0.500
1993	<0.5	0.00 ± 0.00 (10)	0.00 ± 0.00 (18)	—	—
	0.5–3.0	0.80 ± 0.29 (10)	1.28 ± 0.31 (18)	73.5	0.789
	>3.0	1.90 ± 0.28 (10)	2.17 ± 0.34 (18)	95.5	0.407

[a] U' = Mann-Whitney statistic for strata 1 and 2; U = statistic for stratum 3.

[b] — indicates no individuals were detected on either control or intruded sites, so a statistical test was not conducted.

TABLE 5. Summary statistics and results of Mann-Whitney tests for number of Dark-eyed Juncos on control and intruded sites at three vertical strata.

Year	Vertical stratum (m)	Mean ± SE (n)		U', U[a]	P
		Control	Intruded		
1989	<0.5	1.00 ± 0.55 (9)	2.06 ± 0.49 (17)	47.5	0.943
	0.5–3.0	4.00 ± 1.07 (9)	1.76 ± 0.43 (17)	110.0	0.037
	>3.0	0.67 ± 0.29 (9)	0.65 ± 0.23 (17)	74.0	0.563
1990	<0.5	0.67 ± 0.21 (6)	0.08 ± 0.08 (13)	62.0	0.023[b]
	0.5–3.0	0.67 ± 0.21 (6)	1.00 ± 0.28 (13)	33.0	0.711
	>3.0	1.67 ± 0.67 (6)	1.23 ± 0.30 (13)	33.5	0.696
1991	<0.5	0.70 ± 0.34 (10)	0.94 ± 0.35 (18)	85.0	0.602
	0.5–3.0	1.60 ± 0.60 (10)	1.83 ± 0.51 (18)	84.0	0.620
	>3.0	3.00 ± 0.37 (10)	2.89 ± 0.44 (18)	76.5	0.746
1992	<0.5	1.00 ± 0.60 (10)	0.95 ± 0.35 (20)	98.5	0.534
	0.5–3.0	2.90 ± 0.62 (10)	4.30 ± 0.82 (20)	80.0	0.813
	>3.0	3.50 ± 0.79 (10)	2.30 ± 0.36 (20)	70.0	0.909
1993	<0.5	1.40 ± 0.76 (10)	1.60 ± 0.29 (20)	70.0	0.909
	0.5–3.0	2.20 ± 0.59 (10)	1.70 ± 0.33 (20)	115.0	0.265
	>3.0	0.70 ± 0.34 (10)	1.10 ± 0.20 (20)	127.5	0.120

[a] U' = Mann-Whitney statistic for strata 1 and 2; U = statistic for stratum 3.

[b] P value was significant at a family-wide $\alpha = 0.10$ after a sequential Bonferroni adjustment.

liage (DeGraaf et al. 1991). Most foliage at the study sites was associated with saplings and trees of aspen (*Populus* spp.) and conifers and occurred in strata 2 and 3. Nests are typically near the boundary of strata 2 and 3, so movements near the nest within strata 2 and 3 would be common. Most Mountain Chickadees were detected in strata 2 and 3, which is consistent with their breeding-season habitat use.

The midpoint of the typical nest height range for Ruby-crowned Kinglets is 15.6 m (Terres 1980). One common component of their nests is rootlets, which are obtained at ground level. This species typically gleans or hawks insects and spiders (DeGraaf et al. 1991) at the tips of branches, around twigs, and occasionally in vegetation near the ground (Terres 1980). Because its nest is high and it tends to search upper layers of foliage for food, one would expect to detect most Ruby-crowned Kinglets in stratum 3, fewer in stratum 2, and the fewest in stratum 1. This is the pattern we observed.

Yellow-rumped Warblers have a range midpoint of 8.1 m for nest height (Terres 1980). They usually glean and flycatch from vegetation layers that are high above the ground (Curson et al. 1994), but individuals may fly vertically from bushes to flycatch (Terres 1980). Yellow-rumped Warblers often vocalize from the tops of pines and firs (Terres 1980). Given this information, one would expect few if any individuals to occur in stratum 1, more to occur in stratum 2, and most to occur in stratum 3. Our results are consistent with these expectations.

Typically, Dark-eyed Juncos nest on or near the ground and forage for seeds and insects at or near ground level (Terres 1980, Farrand 1983, DeGraaf et al. 1991). Consistent with these generalizations, we detected most Dark-eyed Juncos within stratum 1, fewer in stratum 2, and fewest in stratum 3.

Our observations on control sites were in close accord with the breeding season habitat use and foraging behaviors of these four species. These results indicate that the method we used to record vertical locations accurately reflected distributions and therefore provided ecologically relevant data. Evidently, practicing before collecting data and using only those observations about which an investigator was confident effectively controlled errors in height estimation. The consistency between our observations on control sites and species' typical vertical distributions also supports previous evidence (Gutzwiller et al. 1994, Riffell et al. 1996) that the sampling technique itself was not intrusive.

Effect sizes.—Minimum detectable effect sizes indicated that we can be confident with

TABLE 6. Summary statistics for minimum detectable effect sizes for Mann-Whitney tests. Table entries are for all years and strata combined and are in terms of multiples of the magnitude of control-site means for the original data; individual effect sizes were divided by their associated control-site means before summary statistics were computed.

Species	Mean (range)	
	$\alpha = 0.033$	$\alpha = 0.100$
Mountain Chickadee	2.11 (0.91–5.40)	1.71 (0.83–4.30)
Ruby-crowned Kinglet	1.86 (0.57–4.91)	1.48 (0.49–4.00)
Yellow-rumped Warbler	1.18 (0.61–2.21)	0.97 (0.55–1.76)
Dark-eyed Junco	1.05 (0.77–1.34)	0.84 (0.61–1.00)

a probability of 0.80 that few large changes in the vertical distributions of birds were caused by the intrusions we administered. Only large differences were likely to be detected, however, so the single significant effect reported here should be regarded as a conservative estimate of the effects of intrusion on vertical distributions.

Vertical distributions.—Several biological reasons are plausible for the lack of change in vertical distributions. First, bird sampling at all sites occurred an average of 2.0–3.5 days after treatments, and it is possible that changes induced during treatments did not last long enough to be detected during subsequent sampling. Second, individuals that were displaced from their characteristic strata may have been replaced by other territory seeking conspecifics not yet exposed to the intrusion treatments. Third, individuals chased from their typical vegetation layers may have had their undefended nests preyed upon (see Boyle and Samson 1985); one consequence might have been site abandonment by these individuals and subsequent occupation by conspecifics that up to that time had been off site without territories. Fourth, unfavorable physical conditions (Adams 1941, Dhindsa et al. 1989), the number of existing territories, and interspecific competition may have prevented lower-strata species from using stratum 3. Nest type and migratory status did not seem to influence these species' sensitivities to intrusion (Riffell et al. 1996).

Human disturbance can cause birds to nest or roost higher above the ground than normal (Preston and Norris 1947, Anderson and Keith 1980, Knight and Fitzner 1985, Datta and Pal 1993). Higher nests can be more susceptible to wind damage (Knight and Fitzner 1985), may expose eggs and nestlings to winds and low temperatures, and may force adults to expend more energy to feed nestlings (Dhindsa et al. 1989). Because of less favorable physical conditions (Adams 1941), higher strata may not be energetically advantageous for foraging or refuges. For these reasons, it would be valuable to know the level of intrusion that would cause changes in vertical distributions. The levels of intrusion we experimented with were evidently too low to induce substantial or sustained effects, but higher levels of intrusion might be influential. A series of experiments involving a range of intrusion intensities would help identify threshold levels of intrusion. The absence of effects found in the present study helps define the level of intrusion that is not influential, at least for the species and conditions we studied.

We tested for intrusion effects on vertical distributions associated with all typical breeding season behaviors combined. Although this general approach was valuable, detections from some behaviors (e.g., singing) may have masked intrusion effects on strata used during other behaviors (e.g., foraging). For a more thorough assessment, experiments involving all behaviors combined and specific behaviors separately are needed. Serial experiments (Gutzwiller 1993) with various avian taxa, vegetation types, and intrusion intensities should be used to clarify whether vertical distributions are usually affected and, in turn, whether such changes reduce avian fecundity or survival.

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