

## SPATIAL EXTENT OF HUMAN-INTRUSION EFFECTS ON SUBALPINE BIRD DISTRIBUTIONS<sup>1</sup>

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**Abstract.** Low levels of human intrusion have become ubiquitous, yet the distance at which they affect bird distributions remains unclear. By testing for changes in bird abundance, we assessed whether low levels of intrusion altered bird distributions within and beyond intruded sites. In Wyoming subalpine forests, we experimentally implemented intrusions within circular 1.0-ha (113-m diameter) sites for 1–2 hr (Snowy Mountains, 1989–1993) or for 5 hr (Pole Mountain, 1991–1993) each week during 10 consecutive weeks of the breeding season. The intrusions did not displace birds during most years, with the following exceptions. Mean abundances for Mountain Chickadee (*Parus gambeli*) in the Snowy Mountains (1992) and at Pole Mountain (1993), and mean abundances for American Robin (*Turdus migratorius*) and Hermit Thrush (*Catharus guttatus*) in the Snowy Mountains (1989), were 46–57% lower within intruded sites than they were within control sites. Intrusion did not influence abundances outside of the 1.0-ha intruded sites. Minimum detectable effect sizes ( $R^2$ s for the intrusion effect) were 18–32%; effects of this magnitude and larger were detectable with a probability of 0.80. We would therefore have readily detected moderate and large abundance changes had they occurred. The spatial extent of intrusion effects on distributions was thus limited to the actual sites of intrusion, and the effects occurred infrequently. Knowledge about the distance at which low levels of intrusion do and do not alter bird distributions is essential for protecting intrusion-sensitive species and avoiding unnecessary restrictions on landscape use by the public.

**Key words:** bird disturbance, human intrusion, spatial distributions, subalpine forest, Wyoming.

### INTRODUCTION

Human intrusion is environmental disturbance caused by the mere presence of people. It does not involve habitat destruction, introduction of exotic species, pollution, or other negative consequences that often accompany human activities. Intrusion displaces birds from important breeding, feeding, and resting sites (Boyle and Samson 1985, Purdy et al. 1987, Knight and Gutzwiller 1995). Displacement generates gaps in resources for birds because species that are sensitive to intrusion cannot access resources at intruded sites even though the resources themselves remain intact (Burger 1988). Such gaps force birds to meet their needs elsewhere (Burger 1988), which may include less-preferred habitats (Erwin 1980, Boyle and Samson 1985, Burger 1986).

Gap formation in habitats (landscape perforation) is a common process that leads to habitat

fragmentation and landscape transformation (Forman 1995). Like gaps created in forested landscapes by logging, gaps in resource accessibility caused by intrusion may reduce the extent to which birds occupy (Burger et al. 1995) and move across landscapes (Forman 1995). Often, no obvious structural or floristic changes to vegetation result from intrusion. Consequently, gaps in resource accessibility and associated changes in bird distributions caused by this form of disturbance are not conspicuous. As human populations grow and the frequency and spatial scale of intrusion increase, it will become increasingly important to be able to detect this form of landscape transformation and to understand its effects on birds.

Intrusion in wildlands is often concentrated in small areas that collectively involve only a minor portion of the landscape. But even under these circumstances, a high degree of spatial and temporal overlap between intrusion and essential resources can influence avian demographic parameters (Safina and Burger 1983). A significant

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consequence of small, intrusion-induced gaps in breeding habitats, for example, is reduced sizes of breeding populations (Yalden 1992, Woehler et al. 1994). To understand better the potential for such impacts, it is important to determine the effects of localized intrusion on bird distributions.

By inducing flows of energy, matter, or organisms, environmental disturbances can have important ecological impacts beyond their sites of origin. Landscape areas affected by such flows are known as influence fields (Forman 1995), and their geographic extent can be substantial. Transported air and water pollutants, for example, can cause problems many kilometers away (Aber 1993, Cole et al. 1993), and vehicle noise from highways can repel birds that are more than 1 km away (Reijnen et al. 1995). Conceivably, intrusion may affect resource accessibility beyond the actual sites of disturbance. Intrusion-induced gaps in resource accessibility might therefore be appreciably larger than the areas in which intrusion occurs and, consequently, have more serious effects on bird distributions than would be expected from the size of intruded areas alone.

Low levels of intrusion have caused significant reductions in avian reproduction and survival (Götmark 1992, Knight and Gutzwiller 1995), but the effects of low-level intrusion on bird distributions remain unclear. Assumptions that low levels of intrusion have negligible distribution effects have not been substantiated. Furthermore, low levels of intrusion occur frequently in many habitats, even in protected areas, so they have the potential to affect many bird species (Gutzwiller et al. 1994). Accordingly, we determined whether repeated intrusion by one person for 1–5 hr week<sup>-1</sup> influenced bird distributions. These levels of intrusion are similar to those from anglers, hikers, backpackers, ecotourists, researchers, and others, but they are relatively low compared to levels associated with camping, mountain biking, and off-road-vehicle events (Gutzwiller et al. 1994). The species we studied were involved in one or more of the following activities: territory establishment and maintenance, mating, nesting, and feeding of nestlings or fledglings. Changes in bird distributions were inferred from bird-abundance data. We tested for distribution changes within and beyond intruded sites to provide information about the spatial extent to which low-level in-

trusion had effects. Land-use planners and conservation biologists can use this information to manage the spatial distribution of intrusion in such a way that intrusion-sensitive species are protected and human use of landscapes is not unnecessarily restricted.

## METHODS

### STUDY AREAS

Data were collected about 70 km WNW of Laramie, Wyoming (41°32'N, 106°20'W) in the Snowy Mountains. In May 1989, we randomly established 30 circular 1.0-ha (56.4-m radius) sites. Sites were an average of 0.7 km apart and were 0.4 km from a narrow dirt road that carried infrequent (0–2 vehicles hr<sup>-1</sup>), low-speed vehicular traffic. The same 30 1.0-ha sites were used during 1989–1993. We also collected data approximately 16 km SE of Laramie (41°15'N, 105°23'W) at Pole Mountain. We randomly established 20 circular 1.0-ha sites at Pole Mountain in 1991 and used these same 20 sites during 1991–1993. The sites were an average of 0.7 km apart and were 216–696 m from a narrow dirt road with infrequent (0–2 vehicles hr<sup>-1</sup>), low-speed vehicular traffic. In both study areas we used a permanent transect from the road to the site center to access each site. Elevations, dominant plant species, and weather data for both study areas are provided in Gutzwiller et al. (1997).

### INTRUSION TREATMENTS

During May 1989, we randomly assigned intrusion and control treatments to the 1.0-ha sites in the Snowy Mountains, with the restriction that adjacent sites did not receive the same treatment. Five sites received one intrusion treatment week<sup>-1</sup> (F1) within the inner 25% (S25) of the 1.0-ha site; five sites received two intrusion treatments week<sup>-1</sup> (F2) within the inner 25% of the 1.0-ha site; five sites received one intrusion treatment week<sup>-1</sup> throughout 100% (S100) of the 1.0-ha site; five sites received two intrusion treatments week<sup>-1</sup> throughout 100% of the 1.0-ha site; and 10 sites were assigned to be controls (no intrusion treatments). F1 treatments were implemented on Wednesdays and F2 treatments were administered on Mondays and Fridays so that treatments would not coincide with bird counts, which occurred on Tuesdays and Thursdays. Within intrusion frequency groups (F1 and F2), the initial order in which sites were treated

was assigned randomly. We rotated this order each new intrusion day so that each site was intruded an equal number of times during various times of day each study season. Intrusion treatments were initiated between 07:00 and 08:00 and completed by mid-afternoon. Except when lightning occurred, treatments were implemented under all weather conditions. The treatment schedule was identical during all 5 years and lasted 10 weeks from late May to early August.

An intrusion treatment was implemented by one person and was started at the marked perimeter of the 1.0-ha site. The person walked to the marked site center and then walked through the site in a radial pattern from the center to the perimeter and back again, shifting the path of movement approximately 40° after each return to the site center. Each single treatment lasted 1 hr, during which the specified area was covered twice; the investigator walked either halfway (for S25 sites) or all of the way (for S100 sites) to the perimeter of the 1.0-ha site. The number of steps required to cover these distances was determined separately by each investigator, which ensured that sites were disturbed only within specified boundaries. Within and among study seasons (years), two different persons implemented intrusion treatments, but the same (and only one) person administered treatments at a given 1.0-ha site during a study season.

No trails or other disruption of vegetation were evident during or after the experiments (Gutzwiller et al. 1994). During intrusion treatments, investigators did not try to conceal themselves, and clothing color was not restricted. Investigators faced and approached directly all birds detected near their radial lines of movement during intrusion treatments; investigators did not otherwise attempt to elicit responses from birds. As investigators implemented intrusion treatments, birds flushed from resting, feeding, singing, and nesting sites (Gutzwiller et al. 1997).

For Pole Mountain, all aspects of the intrusion treatments were identical to those for the Snowy Mountains, with the following exceptions. We randomly assigned intrusion and control treatments to the 1.0-ha sites in May 1991. Five sites received five intrusion treatments week<sup>-1</sup> within the inner 25% of the 1.0-ha site; five sites received five intrusion treatments week<sup>-1</sup> throughout 100% of the 1.0-ha site; and 10 sites were assigned to be controls (no intrusion treatment).

Treatments were implemented once each day from Monday through Friday during each week and were administered only during 1991–1993.

We recorded a few brief instances of human disturbance other than our treatments during the experiments, but bird data were not influenced by these incidents (Gutzwiller et al. 1994). In each study area each year, investigators spent on average approximately 700 person-hours at the experimental sites and in adjacent areas during daily periods when people typically traveled along the roads; we would therefore have easily detected people on or near our sites. Any disturbance that may have escaped our notice would have been equally likely to occur on intruded and control sites because the spatial distribution of site types was randomized initially. Thus, any disturbances that we did not detect were probably minor and inconsequential for our experiments (Gutzwiller et al. 1994).

#### BIRD SAMPLING

Before collecting bird data each year, investigators practiced determining from auditory and visual cues whether a bird was within or outside of a marked site with dimensions equal to those of our actual 1.0-ha study sites. Observers were accurate in distance determinations after practicing approximately 1 hr day<sup>-1</sup> for 2 weeks. All data for the present analysis were based on initial detections during 15-min unlimited-distance counts (Ralph et al. 1995) completed between 05:00 and 11:00. Investigators began recording the presence of birds inside and outside of the 1.0-ha site as soon as they reached the 1.0-ha perimeter (Hutto et al. 1986). This perimeter was clearly marked to help observers determine whether birds were inside or outside of the 1.0-ha site. Investigators continued to distinguish whether detected individuals were inside or outside of the 1.0-ha area as they proceeded past the perimeter toward the site center where they completed the 15-min count. Typically, about 14 min of the 15-min count were spent standing at the site center. Using the timing and location of auditory and visual cues, and considering possible unseen movements, observers recorded only those individuals they knew were distinct. Investigators sampled birds when wind speed was < 20 km hr<sup>-1</sup>, air temperature was > 0°C, and no rain was falling (Robbins 1981).

In the Snowy Mountains, half of the sites were sampled on Tuesdays and half on Thurs-

days each week during a 10-week period from late May to early August each year. In contrast to what was worn during intrusion treatments, investigators wore dark drab clothing so as not to repel or attract birds (Gutzwiller and Marcum 1993, 1997). The initial order in which sites were sampled was randomized, and this order was rotated each new sample day to eliminate time-of-day and seasonal biases. On each new sample day, each investigator sampled an equal number of control and intruded sites so that possible differences in investigator abilities would not generate biases in inferences about treatment effects. Within and among study seasons, two different persons conducted counts, but the same (and only one) person conducted counts at a given 1.0-ha site during a study season. The sampling schedule was identical during each of the 5 years of the Snowy Mountains experiment. We used the same techniques to sample Pole Mountain sites, except that all of the latter sites were sampled on Saturdays, three persons were involved, and each week we reversed the order in which we sampled sites.

The movement of investigators during intrusion treatments may have conditioned some birds on intruded sites to reduce vocalizations, to hide, or do both whenever they detected a person; the same individuals may thus have been induced to remain silent or hide when they detected an investigator during sampling. But field observations (Gutzwiller et al. 1994) and analyses (Riffell et al. 1996) indicated that, unlike intrusion treatments, sampling was not intrusive, and we detected birds on and around sites before, during, and after sampling (Gutzwiller et al. 1997). Dense habitat and no investigator noises or movements for approximately 14 min after the site center was reached probably accounted for this lack of sampling effect. We believe that biases stemming from sampling-induced reactions by individual birds that may have been sensitized during treatments were negligible, if present at all (Riffell et al. 1996, Gutzwiller et al. 1997).

All sites were sampled 10 times each year with the same technique, so any undetected sampling effect on bird behavior would have been balanced between control and treated sites and would not have biased the assessment of intrusion effects. If sampling-induced behavioral changes occurred on control sites but not on intruded sites, the actual differences in abundances

due to intrusion treatments alone would be larger than we detected, so the results reported here would be conservative. Analyses (Riffell et al. 1996) indicated, however, that such an effect did not occur. We therefore attributed differences in abundance between control and intruded sites to intrusion-induced displacement, not to temporary behavioral responses to our presence during sampling.

#### BIRD DETECTION DISTANCES

We measured the distance at which we could reliably detect birds from auditory cues so that we could draw inferences about the size of areas beyond the perimeter of the 1.0-ha sites in which intrusions affected abundances. In both study areas during 1991–1993, investigators paced off the distance between themselves and birds that were singing or calling. Only those birds that were stationary during this measurement, or whose positions at the beginning of the measurement were visible, were included in this data set. These observations were not collected during actual censuses or treatments, and all measurements were completed more than 0.5 km from the actual 1.0-ha study sites. Using meter-tape measurements from different terrains and habitats, investigators calculated the average number of their respective paces that was equivalent to 1 m; they used this number to convert their detection distances in paces to meters. The conditions under which investigators measured detection distances, including dark drab clothing, time of day and month, weather, habitat structure, and floristic composition, matched those prevalent during actual bird sampling at the study sites.

To avoid the problem of pseudoreplication, we took precautions to obtain only one measurement from the same individual. Each year in each study area, investigators randomly selected new  $1.6 \times 1.6$  km sections in which to measure detection distances, and no section was ever visited more than once. Within each section, parallel routes of travel were spaced about 300 m apart, and the same species was not studied twice in a row unless the sexes of the two individuals differed. Detection distances were measured for Mountain Chickadee (*Parus gambeli*), Red-breasted Nuthatch (*Sitta canadensis*), American Robin (*Turdus migratorius*), Hermit Thrush (*Catharus guttatus*), Ruby-crowned Kinglet (*Regulus calendula*), Yellow-rumped

Warbler (*Dendroica coronata*), Pine Siskin (*Carduelis pinus*), Green-tailed Towhee (*Pipilo chlorurus*), and Dark-eyed Junco (*Junco hyemalis*).

#### HABITAT FEATURES

If differences in habitat features were confounded with treatment groups, effects of intrusions and effects of habitat conditions on avian abundances would not be distinguishable. Furthermore, habitat features can influence avian abundance (Verner et al. 1986, Verner and Larson 1989) and detection (Waide and Narins 1988, Schieck 1997). To check for habitat differences between intruded and control sites, and to control for variation in bird abundance that might be associated with habitat conditions, we estimated a variety of habitat parameters (Gutzwiller et al. 1997). None of the variables differed significantly between control and intruded sites for either study area during any year (Gutzwiller et al. 1997), indicating that habitat features were not confounded with treatment groups. We therefore attributed between-group differences in avian abundance to intrusion treatments.

#### STATISTICAL ANALYSES

For each year, study area, location (inside or outside of the 1.0-ha site), and species separately, we used the 10 bird-counts at each site to compute a site mean for abundance. Our experimental unit was a site, not an individual observation of a bird. This approach precluded the problem of pseudoreplication that would have been incurred if we had treated individual observations of birds as independent. For the present analysis we were interested only in whether there was a general intrusion effect, so for each study area separately we categorized all disturbed sites into a single group called intruded sites. For both inside and outside of the 1.0-ha sites separately, we tested hypotheses that species' mean abundances differed between control and intruded sites.

For each combination of year, study area, location, and dependent variable (species' mean abundance) separately, we identified the habitat variable that was most significantly ( $P < 0.10$ ) correlated with the dependent variable and that enabled us to meet the assumptions of analysis of covariance (ANCOVA, Huitema 1980). By using only one covariate, we minimized the loss of degrees of freedom, maintained statistical

power, and avoided problems due to collinearity among covariates (Huitema 1980). When habitat variables were not significantly correlated with dependent variables, or when the equal-slopes assumption of ANCOVA could not be met, we analyzed unadjusted means. With BMDP 1V software (Dixon 1990), we computed group means, adjusted for covariates when appropriate, and used two-tailed *a priori* contrasts (Ott 1993). We used habitat variables as covariates in these analyses to control for variation in bird data associated with habitat conditions; this enabled us to obtain a more accurate assessment of intrusion effects. We report either adjusted means (df for contrast = 24 and 16 for the Snowy Mountains and Pole Mountain, respectively) or unadjusted means (df for contrast = 25 and 17 for the Snowy Mountains and Pole Mountain, respectively), depending upon which was used in each contrast. We used a binomial test (Zar 1996) to determine whether patterns in results differed from those expected by chance alone.

Analyses were conducted, and associated results were reported, only for those species that used 20 or more of the 30 Snowy Mountains sites during a given year, or that used 13 or more of the 20 Pole Mountain sites during a given year. We used these criteria to focus the analyses on species that were common enough for us to be able to detect reliably small differences in abundance. Although such species were present on many or all sites, substantial differences in abundance between control and intruded sites could still have been induced by the intrusions. Less common species were not abundant enough for valid quantitative analyses.

We did not use repeated-measures analysis of variance because it assumes that, during the course of an experiment, repeated measurements are made on the same individual experimental units. This would require us to assume that the composition of our experimental units, the physical sites and individual birds that used them, was the same among years. Relatively short life spans, shifts in territory ownership or food availability, and many other factors made it quite unlikely that most of the same individuals returned to the same sites each year. We therefore could not assume that our experimental units were the same entities during the 5-year and 3-year experiments. We did not combine all of the data into one set and conduct a single standard AN-

OVA because, due to possible site fidelity by some individual birds and few if any changes in the physical sites, we could not assume that our experimental units were sufficiently independent among years. Furthermore, neither test would have enabled us to assess abundance differences for both inside and outside of the 1.0-ha sites simultaneously. Using separate contrasts, 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*  $\alpha = 0.10$  instead of 0.05 for all analyses to improve statistical power (Westmoreland and Best 1985). To control Type I error, we used a sequential Bonferroni adjustment of  $\alpha$  for simultaneous inferences; the sequential method is superior to the standard Bonferroni adjustment when more than one hypothesis in a set is false (Holm 1979, Rice 1989). For each dependent variable, year, and study area separately, we tested a set of two simultaneous hypotheses. For example, for Mountain Chickadees in 1989 for the Snowy Mountains, we tested whether the mean abundance inside the 1.0-ha site differed between control and intruded sites, and whether the mean abundance outside of the 1.0-ha site differed between control and intruded sites. We considered each set to be a "family" (sensu Miller 1981) of hypotheses because (1) both hypotheses in a set concerned the same dependent variable, year, and study area, and hence were related to one another, and (2) we wanted to draw inferences about effects of intrusion on overall distributions inside and outside of the 1.0-ha sites.

To assess the ability of our analyses to detect significant intrusion effects, we calculated minimum detectable effect sizes (Thomas 1997) in terms of  $R^2$  values (Cohen 1977, 1988) for the intrusion effect. The  $R^2$  values were the smallest percentages of variation in the bird data associated with the intrusion effect that we could have detected as statistically significant. To calculate these effect sizes, we used  $\alpha = 0.05$  and 0.10 (the minimum and maximum values involved in the sequential Bonferroni adjustment of  $\alpha$ ),  $\beta = 0.20$  (statistical power = 0.80, Cohen 1988), and the sample sizes and number of habitat covariates (0 or 1) involved in the analyses.

The study areas were almost 90 km apart, so there may have been ecologically important differences between the areas that were not obvious. We did not compare the effects of intrusion

for 1–2 hr week<sup>-1</sup> (Snowy Mountains) to those for 5 hr week<sup>-1</sup> (Pole Mountain) because abundance differences due to intrusion frequency would not have been distinguishable from those due to differences in study areas. The projects in the two areas were originally designed, and are analyzed herein, as separate studies (Gutzwiller et al. 1997).

## RESULTS

### ABUNDANCES INSIDE OF THE 1.0-HA SITES

Mean abundance of Mountain Chickadee during 1992 was 46% lower inside of intruded sites than it was inside of control sites (Table 1). During 1989, mean abundances of American Robin and Hermit Thrush were, respectively, 57% and 48% lower inside of intruded sites than inside of control sites (Table 1). No other differences in the mean number of individuals were detected for species in the Snowy Mountains. For Pole Mountain, the only significant difference detected was for Mountain Chickadee in 1993; its mean abundance was 50% lower inside of intruded sites than inside of control sites (Table 2).

### ABUNDANCES OUTSIDE OF THE 1.0-HA SITES

For the Snowy Mountains, mean abundances of various species outside of the 1.0-ha sites did not differ significantly between control and intruded sites for any of the years (Table 1). For Pole Mountain, mean abundance for Yellow-rumped Warbler during 1993 was 71% higher outside of intruded sites than outside of control sites (Table 2). No other species at Pole Mountain exhibited significant differences in mean abundance during the 3-year period.

### NUMBER OF DETECTED EFFECTS

For all species, locations, years, and study areas combined, we conducted 84 statistical tests. The number of statistically significant differences was only five, which is less than the eight significant differences expected by chance alone at  $\alpha = 0.10$  ( $84 \times 0.10 = 8.4$ ), implying that the differences were spurious. However, there was a significant pattern in the differences; for all four differences inside of the 1.0-ha sites, control-site means were greater than intruded-site means. We found that the binomial probability of obtaining all four results in the same direction (control mean > intruded mean) by chance was 0.06, which is less than our  $\alpha$  level. A similar

TABLE 1. Summary statistics and results of contrasts for species' mean abundances inside (I) and outside (O) of 1.0-ha control and intruded sites in the Snowy Mountains (1989–1993).

Species/Year	Location	Mean $\pm$ SE <sup>a</sup>		<i>t</i>	df	<i>P</i>
		Control ( <i>n</i> = 10)	Intruded ( <i>n</i> = 20)			
<b>Mountain Chickadee</b>						
1989	I	0.57 $\pm$ 0.09	0.41 $\pm$ 0.07	1.38	24	0.18
	O	0.17 $\pm$ 0.05	0.19 $\pm$ 0.03	0.36	25	0.72
1990	I	0.33 $\pm$ 0.10	0.40 $\pm$ 0.07	0.57	24	0.58
	O	0.13 $\pm$ 0.05	0.23 $\pm$ 0.04	1.58	24	0.13
1991	I	0.29 $\pm$ 0.06	0.24 $\pm$ 0.04	0.64	24	0.53
	O	0.29 $\pm$ 0.08	0.32 $\pm$ 0.06	0.33	24	0.74
1992	I	0.61 $\pm$ 0.09	0.33 $\pm$ 0.07	2.45	24	0.02 <sup>b</sup>
	O	0.37 $\pm$ 0.06	0.43 $\pm$ 0.05	0.61	25	0.55
1993	I	0.27 $\pm$ 0.03	0.36 $\pm$ 0.05	1.20	25	0.24
	O	0.38 $\pm$ 0.04	0.35 $\pm$ 0.04	0.45	25	0.66
<b>American Robin</b>						
1989	I	0.54 $\pm$ 0.06	0.23 $\pm$ 0.05	3.94	24	0.001 <sup>b</sup>
	O	0.18 $\pm$ 0.05	0.21 $\pm$ 0.04	0.43	24	0.67
1990	I	0.21 $\pm$ 0.03	0.14 $\pm$ 0.02	1.89	24	0.07
	O	0.20 $\pm$ 0.05	0.19 $\pm$ 0.04	0.09	24	0.93
<b>Hermit Thrush</b>						
1989	I	0.29 $\pm$ 0.06	0.15 $\pm$ 0.03	2.31	25	0.03 <sup>b</sup>
	O	0.43 $\pm$ 0.09	0.47 $\pm$ 0.06	0.33	24	0.74
1991	I	0.19 $\pm$ 0.06	0.22 $\pm$ 0.04	0.37	24	0.72
	O	0.30 $\pm$ 0.05	0.35 $\pm$ 0.06	0.57	25	0.58
1992	I	0.10 $\pm$ 0.03	0.15 $\pm$ 0.03	1.01	25	0.32
	O	0.43 $\pm$ 0.08	0.44 $\pm$ 0.06	0.13	24	0.90
<b>Ruby-crowned Kinglet</b>						
1989	I	0.72 $\pm$ 0.14	0.46 $\pm$ 0.07	1.88	25	0.07
	O	0.52 $\pm$ 0.07	0.63 $\pm$ 0.05	1.32	24	0.20
1990	I	0.30 $\pm$ 0.09	0.23 $\pm$ 0.04	0.96	25	0.35
	O	0.47 $\pm$ 0.06	0.56 $\pm$ 0.04	1.33	24	0.20
1991	I	0.32 $\pm$ 0.08	0.37 $\pm$ 0.05	0.54	24	0.60
	O	0.46 $\pm$ 0.09	0.52 $\pm$ 0.07	0.53	24	0.60
1992	I	0.30 $\pm$ 0.09	0.30 $\pm$ 0.06	0.02	24	0.98
	O	0.55 $\pm$ 0.08	0.60 $\pm$ 0.06	0.42	24	0.68
1993	I	0.28 $\pm$ 0.06	0.26 $\pm$ 0.05	0.18	24	0.86
	O	0.41 $\pm$ 0.06	0.44 $\pm$ 0.05	0.35	24	0.73
<b>Yellow-rumped Warbler</b>						
1990	I	0.28 $\pm$ 0.04	0.20 $\pm$ 0.03	1.51	24	0.15
	O	0.28 $\pm$ 0.04	0.27 $\pm$ 0.03	0.33	24	0.74
1991	I	0.36 $\pm$ 0.08	0.31 $\pm$ 0.05	0.56	24	0.58
	O	0.14 $\pm$ 0.07	0.22 $\pm$ 0.03	1.06	25	0.30
1992	I	0.52 $\pm$ 0.07	0.41 $\pm$ 0.05	1.37	24	0.18
	O	0.25 $\pm$ 0.07	0.35 $\pm$ 0.05	1.18	24	0.25
1993	I	0.32 $\pm$ 0.05	0.30 $\pm$ 0.04	0.33	24	0.74
	O	0.14 $\pm$ 0.05	0.18 $\pm$ 0.03	0.68	25	0.51
<b>Pine Siskin</b>						
1992	I	0.36 $\pm$ 0.07	0.46 $\pm$ 0.06	1.06	25	0.30
	O	0.14 $\pm$ 0.04	0.19 $\pm$ 0.03	0.82	25	0.42
<b>Dark-eyed Junco</b>						
1989	I	0.64 $\pm$ 0.12	0.60 $\pm$ 0.07	0.35	25	0.73
	O	0.21 $\pm$ 0.05	0.28 $\pm$ 0.04	1.05	24	0.31
1990	I	0.26 $\pm$ 0.06	0.18 $\pm$ 0.04	1.02	24	0.32
	O	0.25 $\pm$ 0.05	0.31 $\pm$ 0.04	0.94	24	0.36
1991	I	0.59 $\pm$ 0.08	0.44 $\pm$ 0.07	1.25	25	0.23
	O	0.23 $\pm$ 0.08	0.35 $\pm$ 0.06	1.28	24	0.21
1992	I	0.78 $\pm$ 0.11	0.80 $\pm$ 0.08	0.13	24	0.90
	O	0.37 $\pm$ 0.04	0.48 $\pm$ 0.06	1.29	25	0.21
1993	I	0.43 $\pm$ 0.10	0.46 $\pm$ 0.04	0.28	25	0.78
	O	0.28 $\pm$ 0.06	0.28 $\pm$ 0.05	0.06	25	0.95

<sup>a</sup> Units are number of individuals detected per site per 15-min count.<sup>b</sup> *P* value is significant at a family-wide  $\alpha = 0.10$  after a sequential Bonferroni adjustment.

TABLE 2. Summary statistics and results of contrasts for species' mean abundances inside (I) and outside (O) of 1.0-ha control and intruded sites at Pole Mountain (1991–1993).

Species/Year	Location	Mean $\pm$ SE <sup>a</sup>		<i>t</i>	df	<i>P</i>
		Control ( <i>n</i> = 10)	Intruded ( <i>n</i> = 10)			
<b>Mountain Chickadee</b>						
1991	I	0.32 $\pm$ 0.06	0.27 $\pm$ 0.05	0.62	17	0.55
	O	0.24 $\pm$ 0.06	0.28 $\pm$ 0.04	0.53	17	0.60
1992	I	0.48 $\pm$ 0.09	0.35 $\pm$ 0.09	1.01	16	0.33
	O	0.25 $\pm$ 0.05	0.21 $\pm$ 0.08	0.43	17	0.67
1993	I	0.40 $\pm$ 0.06	0.20 $\pm$ 0.06	2.38	16	0.03 <sup>b</sup>
	O	0.29 $\pm$ 0.05	0.28 $\pm$ 0.06	0.12	17	0.91
<b>Red-breasted Nuthatch</b>						
1992	I	0.18 $\pm$ 0.06	0.22 $\pm$ 0.06	0.57	16	0.58
	O	0.44 $\pm$ 0.08	0.45 $\pm$ 0.09	0.08	17	0.94
<b>American Robin</b>						
1991	I	0.25 $\pm$ 0.05	0.31 $\pm$ 0.06	0.79	16	0.44
	O	0.12 $\pm$ 0.04	0.22 $\pm$ 0.04	1.50	16	0.15
1992	I	0.33 $\pm$ 0.08	0.26 $\pm$ 0.06	0.73	17	0.48
	O	0.25 $\pm$ 0.08	0.28 $\pm$ 0.08	0.24	16	0.81
1993	I	0.31 $\pm$ 0.06	0.27 $\pm$ 0.04	0.51	17	0.62
	O	0.28 $\pm$ 0.06	0.46 $\pm$ 0.06	1.93	16	0.07
<b>Ruby-crowned Kinglet</b>						
1991	I	0.46 $\pm$ 0.07	0.39 $\pm$ 0.07	0.74	16	0.47
	O	0.34 $\pm$ 0.05	0.27 $\pm$ 0.05	0.94	16	0.36
1992	I	0.28 $\pm$ 0.08	0.30 $\pm$ 0.08	0.18	17	0.86
	O	0.34 $\pm$ 0.11	0.35 $\pm$ 0.13	0.06	17	0.95
1993	I	0.36 $\pm$ 0.09	0.26 $\pm$ 0.09	0.79	17	0.44
	O	0.47 $\pm$ 0.08	0.58 $\pm$ 0.08	1.05	16	0.31
<b>Yellow-rumped Warbler</b>						
1991	I	0.38 $\pm$ 0.07	0.48 $\pm$ 0.07	1.04	16	0.31
	O	0.28 $\pm$ 0.04	0.18 $\pm$ 0.04	1.80	16	0.09
1992	I	0.58 $\pm$ 0.08	0.58 $\pm$ 0.10	0.00	17	1.00
	O	0.27 $\pm$ 0.08	0.25 $\pm$ 0.08	0.17	16	0.87
1993	I	0.60 $\pm$ 0.08	0.42 $\pm$ 0.08	1.54	16	0.14
	O	0.21 $\pm$ 0.04	0.36 $\pm$ 0.04	3.05	16	0.01 <sup>b</sup>
<b>Green-tailed Towhee</b>						
1993	I	0.28 $\pm$ 0.06	0.30 $\pm$ 0.06	0.17	16	0.87
	O	0.29 $\pm$ 0.06	0.35 $\pm$ 0.06	0.67	16	0.51
<b>Dark-eyed Junco</b>						
1991	I	0.60 $\pm$ 0.09	0.79 $\pm$ 0.09	1.61	16	0.13
	O	0.20 $\pm$ 0.04	0.14 $\pm$ 0.04	1.18	16	0.25
1992	I	0.76 $\pm$ 0.11	0.58 $\pm$ 0.08	1.34	17	0.20
	O	0.17 $\pm$ 0.07	0.30 $\pm$ 0.12	0.91	17	0.37
1993	I	0.68 $\pm$ 0.07	0.53 $\pm$ 0.07	1.54	16	0.14
	O	0.20 $\pm$ 0.05	0.34 $\pm$ 0.08	1.68	17	0.11

<sup>a</sup> Units are number of individuals detected per site per 15-min count.

<sup>b</sup> *P* value is significant at a family-wide  $\alpha = 0.10$  after a sequential Bonferroni adjustment.

analysis was not possible for outside of the 1.0-ha sites because only one contrast was significant. During most years in both study areas, the intrusions did not influence most species' abundances inside or outside of the disturbed sites. For a few years, however, intrusions displaced some Mountain Chickadees, American Robins,

and Hermit Thrushes from the 1.0-ha sites (Tables 1 and 2).

#### MINIMUM DETECTABLE EFFECT SIZES

For the Snowy Mountains analyses, the minimum detectable  $R^2$  values at  $\alpha = 0.05$  were 21.9% (0 covariates) and 22.5% (1 covariate),



TABLE 3. Summary statistics for distances (m) at which birds were aurally detected in the Snowy Mountains and at Pole Mountain (1991–1993).

Species	<i>n</i>	Mean $\pm$ SE	Range
Mountain Chickadee	23	148.9 $\pm$ 5.2	104–195
Red-breasted Nuthatch	10	132.3 $\pm$ 8.6	84–159
American Robin	22	144.3 $\pm$ 4.7	85–182
Hermit Thrush	2	155.0 $\pm$ 3.0	152–158
Ruby-crowned Kinglet	29	158.7 $\pm$ 6.2	90–230
Yellow-rumped Warbler	22	137.5 $\pm$ 6.4	62–176
Pine Siskin	6	114.3 $\pm$ 7.8	104–153
Green-tailed Towhee	18	151.7 $\pm$ 6.7	75–211
Dark-eyed Junco	39	162.6 $\pm$ 5.2	84–208
All individuals	171	149.8 $\pm$ 2.3	62–230

and at  $\alpha = 0.10$  were 18.1% (0 covariates) and 18.6% (1 covariate). For the Pole Mountain analyses, the minimum detectable  $R^2$  values at  $\alpha = 0.05$  were 30.4% (0 covariates) and 31.6% (1 covariate), and at  $\alpha = 0.10$  were 25.6% (0 covariates) and 26.7% (1 covariate). We would have detected  $R^2$  values of this magnitude and larger with a probability of 0.80.

#### DETECTION DISTANCES

All minimum and mean detection distances for individual species (Table 3) were longer than the 1.0-ha radius (56.4 m), so if these species had emitted songs or calls within the boundaries of the 1.0-ha sites, we would have readily detected them. The overall mean detection distance of 149.8 m (Table 3) is an estimate of the usual distance at which we could reliably detect auditory cues from common birds in the study areas. This mean distance is about 93 m (149.8 m – 56.4 m = 93.4 m) beyond the perimeter of a 1.0-ha circle. The mean detection distance and numerous detections outside of the 1.0-ha sites (Tables 1 and 2) indicate that our sampling method was effective for detecting birds beyond the 1.0-ha perimeter.

#### DISCUSSION

##### DETECTABLE EFFECT SIZES

Our analyses were capable of detecting with a high probability moderate and large differences ( $R^2 \geq 18\%$ ) in bird abundances between control and intruded sites. Small intrusion effects ( $R^2 < 18\%$ ) were not reliably detectable, so we cannot be confident that small effects were not induced. Consequently, our results represent a conservative estimate of the effects of intrusion on distributions. The effect-size results support our

finding that intrusions induced only a few large distribution changes.

##### ABUNDANCES INSIDE OF THE 1.0-HA SITES

During a few years, abundances of Mountain Chickadee, American Robin, and Hermit Thrush inside intruded sites were lower than those inside control sites, indicating that intrusion displaced individuals of these species from intruded areas. Through displacement, intrusions prevented normal access to habitats and associated resources. Hermit Thrushes and American Robins are ground foragers, but Mountain Chickadees typically are not (DeGraaf et al. 1991). Dark-eyed Juncos and Green-tailed Towhees usually forage on the ground (DeGraaf et al. 1991), but they were not displaced. Thus, the ground-foraging habit does not explain the sensitivity to intrusion we observed. Migratory status, nest type, and nest height also did not influence whether species' distributions were affected by intrusion (Riffell et al. 1996).

In human-dominated areas, Mountain Chickadees and American Robins are relatively easy to approach and do not seem to be hampered by people (K. J. Gutzwiller, pers. observ.). Perhaps frequent encounters with people in such environments enable these two species to learn to tolerate or habituate to intrusion. The significant effects we found for Mountain Chickadees and American Robins suggest that these behavioral mechanisms for coping with intrusion are less developed where these species encounter fewer people, such as our study areas. Examples of context-dependent responses to intrusion within the same bird species are numerous (Götmark et al. 1989, Burger et al. 1993, Knight and Temple 1995).

Bird sensitivity to intrusion can depend significantly on whether experiences during earlier interactions with humans were positive, negative, or neutral, and the history of these experiences is likely to differ among individuals (Gutzwiller et al. 1994). During a multi-year period such as in our study, mortality and other factors cause changes in population composition in terms of individuals. As a result, the sensitivity to intrusion for individuals of a species at a given site may vary considerably among years (Gutzwiller et al. 1994, 1998). It is plausible that Mountain Chickadees, American Robins, and Hermit Thrushes were displaced during some years but not others because of such annual variation.

Annual differences in environmental conditions (weather, vegetation, regional bird population sizes) probably do not account for the annual differences in intrusion effects that we observed for some species. For this to be possible, environmental effects would have had to reduce bird abundance for intruded sites significantly below that for control sites, and this differential reduction would have had to occur during some years but not others. Environmental effects on bird abundance would have been manifested at both site types because of the spatial proximity and interspersion of intruded and control sites. Therefore, significant between-group differences in bird abundance are not likely to have been induced by environmental or other extraneous factors. This reasoning applies to all years because we used the same experimental design each year. No significant differences in a variety of habitat features were evident between intruded and control sites during the experiments (Gutzwiller et al. 1997). Based on our experimental design and knowledge of field conditions at the sites, we have no reason to believe that annual differences in some species' responses to intrusion are attributable to environmental differences among years.

#### ABUNDANCES OUTSIDE OF THE 1.0-HA SITES

The single effect observed for outside of the 1.0-ha sites (Yellow-rumped Warbler, Table 2) was large, and we detected it after controlling for Type I error. But, because only this one effect was detected, we were unable to test for overall patterns in the results for outside of the 1.0-ha sites; this single result could be spurious. The intrusions did not otherwise generate effects on

distributions beyond intruded sites, perhaps because intruders did not walk through these off-site areas and therefore did not directly or sufficiently disrupt breeding-season activities.

Our data for detection distances indicate we could have determined off-site influences, had they occurred, out to 93 m beyond the perimeters of the intruded sites. The detection distances we recorded for birds were quite comparable in magnitude and variation to those recorded by others. For example, American Robins were studied by both us and Emlen and DeJong (1981), and the mean detection distances ( $\pm$  SD) for this species in the latter and present studies were  $150 \pm 21$  m and  $144 \pm 22$  m, respectively. Our calculations of detectable effect sizes support the conclusion that intrusion did not induce moderate or large effects outside of the intruded sites. An alternative explanation for the lack of off-site influences is that the intrusions had effects on bird distributions at distances farther than 149.8 m from the site centers, which was beyond the distance at which we could reliably detect auditory cues.

#### IMPLICATIONS

To develop effective management strategies, conservationists need information about the levels of intrusion that do and do not affect distributions. Most of our results are valuable in the latter regard, for we found only minimal evidence that intrusion affected bird distributions. For the habitats, time of year, and other conditions of our experiments, our results help define the spatial extent to which low levels of intrusion do not readily displace the study species. Knowing the distance at which intrusion does not alter distributions is essential for determining where human intrusion can be permitted in landscapes that support intrusion-sensitive birds.

We caution that the lack of effects reported herein may not apply to other species and systems because intrusion does readily displace other bird species from a variety of significant feeding and breeding habitats (Klein et al. 1995, Knight and Gutzwiller 1995, Rodgers and Smith 1995). Because our results were obtained at somewhat remote sites, they are probably more applicable for wilderness, refuges, and other protected areas where birds experience relatively low levels of intrusion than for areas with extensive human activity. Effects of intrusion on birds are highly species- and context-dependent

(Gutzwiller et al. 1994, 1998). Even within the present study, only three of nine species were influenced by intrusion, and they were not affected consistently each year or between study areas. Sometimes birds ameliorate or preclude the detrimental effects of intrusion by habituating to intrusion (Poole 1981, Vos et al. 1985, Knight et al. 1987). Thus, to determine what intrusion-control measures if any are warranted, conservationists should evaluate each potential intrusion problem separately.

For species that are sensitive to intrusion, we hypothesize that the value of a landscape is influenced in part by the degree to which intrusion coincides in place and time with essential avian resources. With a high degree of spatial and temporal overlap, sensitive species may not use a landscape at all, whereas with minimal overlap between intrusion and resources, a landscape may be used extensively. These relations can be tested with management experiments (Gutzwiller 1993) involving various habitats, avian taxa, and levels of intrusion. Conservationists need information about the spatial extent to which intrusion does and does not affect bird distributions to determine which parts of landscapes can remain accessible to various users without detrimentally affecting birds.

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