EFFECTS OF HUMAN INTRUSION ON SONG OCCURRENCE AND SINGING CONSISTENCY IN SUBALPINE BIRDS

Kevin J. Gutzwiller,[1,2] Richard T. Wiedenmann,[1,4]
Krista L. Clements,[1,5] and Stanley H. Anderson[3]

[1]*Department of Biology, and* [2]*Department of Environmental Studies, Baylor University,
Waco, Texas 76798, USA; and*
[3]*Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming,
Laramie, Wyoming 82071, USA*

ABSTRACT.—In 1989, 1990, and 1991, we conducted experiments on 30 circular 1.0-ha sites to assess whether human intrusions during a 10-week period influenced the occurrence and consistency of primary song in breeding subalpine birds. Using only those weekly censuses during which a species was present at a site, we computed song occurrence as the percentage of censuses during which a species sang, and we calculated singing consistency as the maximum number of consecutive censuses during which a species sang. An intrusion bout involved one person who walked through a site for 1 or 2 h. We used *a priori* contrasts, involving habitat covariates when appropriate, to assess differences in song occurrence and singing consistency between control and intruded sites and between sites at which the inner 25% of the site was disturbed (S25) and those at which 100% of the site was disturbed (S100). Singing by a number of species did not appear to be influenced by intrusion. For several species, however, song occurrence and singing consistency were higher on control sites than on intruded sites, indicating intrusion reduced singing activity. Song occurrence was higher on S100 relative to S25 sites as well. This latter pattern may have emerged because all of the individuals using the S100 sites were able to observe us during repeated intrusions and discern that we were not predators, whereas most of the individuals using the S25 sites likely did not have this opportunity. Thus, some of the individuals using S25 sites may have reduced their singing to avoid detection by us. Because song is essential in territory defense, mate acquisition, and in other reproductive activities, levels of intrusion that alter normal singing behavior have the potential to lower the reproductive fitness of males that are sensitive to this form of disturbance. *Received 16 October 1992, accepted 28 January 1993.*

PRIMARY SONG is loud and far-reaching, occurring most often during the early breeding season and less frequently while young are being raised (Welty and Baptista 1988:224). Two important functions linked to primary song in breeding males are territory defense and mate attraction (Krebs 1977, Eriksson and Wallin 1986, McDonald 1989). Indirect evidence for the territorial function includes observations that most singing occurs during periods of territory establishment and maintenance and is restricted to defended areas (Falls 1988, Welty and Baptista 1988:227, 252). In addition, males countersing with conspecific males on adjoining territories (Wasserman 1977a), and they can be induced to sing with auditory playbacks that simulate territorial intrusion (Falls 1981, 1988). The territory-defense role has been demonstrated experimentally through the surgical muting of males (Peek 1972a, Smith 1979, McDonald 1989), the tranquilizing of males (Peek 1972b), and the use of recorded playbacks (Krebs 1977, Falls 1988). The mate-attraction function of song has been corroborated with observations that singing activity is higher in males before they pair with females than after pairing (Wasserman 1977b). Experimental removal of females from pairs caused significantly higher singing rates by associated males (Wasserman 1977b, Krebs et al. 1981, Cuthill and Hindmarsh 1985). Moreover, males that were surgically muted were unable to attract females (e.g. McDonald 1989), even when such males possessed territories in good habitat and unmated females were present in the area (Peek 1972a).

Because singing is important in territory defense and mate attraction, human disturbance that alters singing behavior may influence a

---

[4] Present address: John E. Conner Museum, Texas A&M University-Kingsville, Box 2172, Station 1, Kingsville, Texas 78363, USA.

[5] Present address: 1306 Fox Street, Bossier City, Louisiana 71112, USA.

bird's reproductive performance. Major distur-bances such as habitat destruction frequently displace birds, whereas slight disturbances that do not influence habitat structure may cause only behavior modifications, including reduced or inconsistent singing. One form of human disturbance with this potential is intrusion—the mere presence of people in the environment (apart from associated habitat alterations, noise, pollution, etc.). Intrusion is known to cause im-portant reproductive declines in various species (e.g. Tremblay and Ellison 1979, Safina and Bur-ger 1983, Westmoreland and Best 1985), but the possible impacts of intrusion on singing be-havior have not been assessed. The levels of intrusion that are likely to alter singing behav-ior, but not displace individuals, could be quite subtle.

Slight levels of intrusion, such as one person walking through an area several times each week, occur in vast amounts of habitat. Parks, forests, military reservations, refuges, wilder-ness areas, and many other public and private holdings are the key sources and sinks for birds. At least some level of human intrusion occurs in all such areas. Human intrusion, which often does not lead to structural or floristic changes in vegetation or other environmental altera-tions, is an inconspicuous but pervasive form of environmental disturbance (Purdy et al. 1987: 21). Because of its ubiquity in time and space, intrusion has the potential to influence the singing behavior (hence, reproductive success) of many species and individuals. Our objective was to determine whether slight but repeated intrusions influenced the occurrence or consis-tency of primary song in subalpine birds.

METHODS

Study area.—We worked on the Brush Creek District of the Medicine Bow National Forest about 70 km WNW of Laramie, Wyoming (41°32′N, 106°20′W; Wie-denmann 1991). The habitat was a mosaic of mixed-conifer stands, pure stands of lodgepole pine (*Pinus contorta*), riparian areas, meadows, and clearcuts. The dominant plants in the study area were lodgepole pine, limber pine (*P. flexilis*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), aspen (*Populus tremuloides*), Rocky Mountain juniper (*Junip-erus scopulorum*), mountain alder (*Alnus incana*), west-ern red birch (*Betula occidentalis*), birchleaf mountain mahogany (*Cercocarpus montanus*), chokecherry (*Pru-nus virginiana*), silver sagebrush (*Artemisia cana*), mountain big sagebrush (*A. tridentata*), snowbrush

(*Ceanothus velutinus*), kinnikinnick (*Arctostaphylos uva-ursi*), Oregon grape (*Mahonia repens*), whortleberry (*Vaccinium scoparium*), western snowberry (*Symphori-carpos occidentalis*), and pricky rose (*Rosa acicularis*; names from Nelson 1984). Elevations ranged between 2,550 and 2,780 m.

In May 1989 we randomly established 30 circular 1.0-ha (113-m diameter) sites in remote stands across 15 km of our study area. Locations with current or planned silvicultural or recreational activities during the breeding season were avoided. The centers of neighboring sites were an average of 0.66 km (range 0.3–4.0 km) apart, and site centers were 0.4 km from the nearest used road. Each site was reached by walk-ing a permanently marked transect from the road to the site center. For each site we marked the point at which the transect crossed the 1.0-ha perimeter. This point (56.4 m from center) served as a reference for determining: whether a bird was inside the circum-ference of the site; where to begin and end treatment bouts; and where to begin censuses (see below). The same 30 sites were used during 1989, 1990, and 1991. At five permanent sampling points spaced equidis-tantly among the 30 sites, weather data were recorded twice per week during the 10-week study period each year. The three-year means for minimum and maxi-mum air temperatures and precipitation were 1.0 ± SD of 4.6°C, 26.5 ± 4.9°C, and 1.6 ± 2.7 mm per day, respectively.

Intrusion treatments.—Before intrusions were car-ried out in 1989, treatments were assigned randomly to individual sites with the restriction that no two adjacent sites could receive identical treatments. The treatments assigned in 1989 were also implemented on the same sites during 1990 and 1991. Two levels of intrusion frequency (one intrusion/week [F1], two intrusions/week [F2]) and two levels of intrusion scale (inner 25% of 1.0-ha site [S25], 100% of 1.0-ha site [S100]) were administered during a 10-week period from late May to early August each year. The treat-ment groups (and replicates) were: F1&S25 ($n = 5$); F1&S100 ($n = 5$); F2&S25 ($n = 5$); F2&S100 ($n = 5$); controls (no intrusions; $n = 10$). A single bout of in-trusion involved one person walking through the habitat on a site for a 1.0-h period beginning when the person reached the perimeter of the site. The researcher moved from the site's perimeter to its cen-ter, and then proceeded to walk back and forth ra-dially between the center and the edge of the circular area corresponding to the intruded area for that site (radius = 28.2 m for S25 sites and 56.4 m for S100 sites). Prior to treatments each year, individual re-searchers measured the number of comfortable steps they needed to travel the specific radii; this ensured that the intrusions occurred only within the specified spatial scales. Intrusions were implemented at a pace that enabled investigators to cover the area to be dis-turbed twice during the 1.0-h period. Each bout ended with the researcher on the transect at the perimeter

of the site. The radial intrusion pattern was shifted frequently so that trails were not created; researchers were also careful not to disturb live or dead plant materials or rocks as they walked across sites.

In relation to other types of human intrusion, such as repeated wildlife viewing by parties of ecotourists, off-road-vehicle events, and campground activities, the disturbances we administered were slight. We did not alter the structure or floristic composition of the vegetation. Virtually no herbaceous material was present for us to trample, and our protocol ensured that we did not create trails or disturb shrubs, saplings, or down material. At the end of our study, our sites looked the same as adjacent forest in all perceptible respects. We did not generate noise from radios, conversation, motorized vehicles, or other means. Some forms of intrusion (e.g. boating, beach activities, off-road events in deserts) can harm habitat, nests, young, and adults directly and permanently by mechanical means (Boyle and Samson 1985). Our treatments clearly differed from these more drastic types of intrusion. The levels of disturbance we administered are analogous to those caused by anglers, hikers, backpackers, picnickers, nature viewers, wildlife photographers, and researchers.

During disturbance bouts, researchers wore clothing of various colors and made no attempt to conceal themselves. They faced and approached directly any birds detected during intrusion (see Burger and Gochfeld 1981, Knight and Temple 1986a). This enabled the researchers to have a fixed protocol for administering the treatments; such direct approaches also are similar to disturbances from bird watchers, nature viewers, photographers, researchers, and others who seek out and approach their subjects (Boyle and Samson 1985). An investigator's approach typically caused individuals to cease vocalizations and to flush from song perches, nests, and resting and feeding sites. F1 intrusions were implemented only on Wednesdays; F2 intrusions were carried out each week only on Mondays and Fridays. This regular schedule prevented the treatments from being confounded with different disturbance periodicities. Within disturbance frequency groups (F1, F2), the initial order in which sites were disturbed was assigned randomly. This order was then rotated each new disturbance day (for F1 and F2 sites separately) so that each site was disturbed an equal number of times during various times of day each year.

Intrusion bouts began between 0700 and 0800 MST and continued from one site to the next through early or midafternoon. Intrusions were administered under all weather conditions except when lightning threatened investigator safety. In such situations researchers left the site, waited on the nearest used road until the danger passed, and then returned the same day to complete the scheduled intrusions at that site and at any remaining sites. To avoid confounding treatment effects with responses to individual intruders

(see Knight and Temple 1986a) each year, each of two investigators disturbed 10 sites that included essentially one-half of the sites in each of the four groups of intruded sites. Intrusions were implemented in the same way and with the same schedule during all three years of the experiment.

Each year, we recorded one-time instances of another person who had traversed some of our treated sites on foot or with a three-wheel off-road vehicle. Only one or two of our treated sites were involved each year. An examination of bird-census data before and after these events indicated no detectable impacts of these added intrusions. These additional disturbances, which probably lasted less than 2 or 3 min each, were quite brief compared to the 10 and 20 h of intrusion administered each year on the F1 and F2 sites, respectively. Furthermore, the chance that another person might inadvertently traverse one of our sites was equal among treatment groups because the spatial distribution of site types was randomized initially. For these reasons, the few additional disturbances are likely to be inconsequential for this experiment. Each year during the 10-week period, approximately 620 person-hours were spent at the 30 sites and on the roads near our sites. Thus, the presence of still other people on or near our sites is not likely to have escaped our notice.

Bird censuses.—Prior to data collection, observers flagged the distance of 56.4 m (radius of a 1.0-ha site) in different directions from a practice point to gain experience in assessing whether an individual was within this distance based on aural and visual cues. During the actual fieldwork, the point at which the site perimeter intersected the entrance transect (56.4 m from the site center) also was flagged to provide a reference point for distance judgments. All individuals detected by sight, calls, or songs, and known to be distinct in time and space within the 1.0-ha site, were recorded by species during weekly 15-min fixed-radius (56.4 m) point counts (Verner 1985:284) over the 10-week period each year. Point counts began when the observer reached the perimeter of the site so that any individuals flushed or temporarily silenced by the observer's approach to the site center would be recorded (Hutto et al. 1986). The researcher moved quietly to the center of the site where the 15-min count was completed. We did not census when wind speed was more than 20 km per hour (Robbins 1981), air temperature was less than 0°C, or more than a light drizzle fell. Occasionally during the three-year period, unacceptable weather conditions (e.g. air temperature <0°C at 0500) caused us to delay counts so that some were completed during 1000–1100, but the vast majority of point counts were conducted from 0500–1000. When delays were necessary, investigators waited on the nearest used road, not on the site itself.

To avoid observer bias each year, each of two researchers censused 15 sites that included essentially

one-half of the sites in each of the five treatment groups. For a given observer each year, the order in which the 15 sites were censused was randomized and then rotated each new week so that each site was censused an equal number of times during various parts of the morning each year. Time-of-day effects (e.g. air temperature, wind speed) on bird activity (hence, census results), thus, were balanced among treatment groups and the potential for confounding was precluded. Because sites were remote and point counts were restricted to morning hours, only one-half of the 30 sites were censused on Tuesdays; the remaining sites were censused on Thursdays the same week. Censuses were completed one, three, or six days after intrusions and these elapsed times were balanced between S25 and S100 sites. Each observer censused both control and intruded sites on each census day. Observers wore dark, drab clothing during censuses. The same census methods and schedule were used during all three years.

Based on field observations, the censuses themselves were nonintrusive. Birds frequently flew, perched, or fed within 1 to 2 m of researchers, apparently unaware of (or unperturbed by) the motionless observer. Further, birds singing on the site were recorded as soon as we reached the site perimeter; thus, such individuals were included in our data even if they temporarily stopped singing after detecting our movement to the center of the site. On both treated and control sites, birds sang during investigators' approaches to sites, during censuses, and after observers left sites, indicating few, if any, census-induced changes in singing behavior. If birds curtailed singing in response to intruders moving throughout the site during treatments, the same individuals might have been induced to remain silent upon detecting an observer during a census. But the censuses were nonintrusive and our technique enabled us to record singing activity on the entire site before we moved across it toward its center. Thus, we believe the data are accurate and that biases originating from census-induced behavior, if present, are negligible. We reasoned that any differences in singing behavior that might emerge among treatment groups would be sustained effects caused by the repeated intrusions we administered, not brief responses to observer presence during censuses.

Habitat measurements.—The chances of encountering various bird species depend in part on the vegetation structure and floristic composition of an area (e.g. Verner and Larson 1989 and references therein). Vegetation characteristics also can influence an observer's ability to detect birds by sound (Richards 1981, Waide and Narins 1988) and sight. Therefore, we estimated habitat parameters on each site for use as covariates in our analyses of intrusion effects. Habitat data were collected in mid-August after intrusions and censuses were completed. All sites were sampled in 1989. For our 1990 analyses, we used the 1989 hab-

itat data because the vegetation parameters we estimated had not changed appreciably since August 1989. One exception was a situation in which old slash from a site had been bulldozed to another location. Because the understory and ground-cover vegetation on part of our 1.0-ha site was changed from 1989, we resampled this site in 1990 and used the updated habitat data in our 1990 analyses. In 1991, all sites were sampled again.

Habitat data were collected for each site on two scales: the 1.0-ha site, and a 7.1-ha area (radius = 150 m) centered on the 1.0-ha site center. For the first scale, we used a random bearing to establish a transect from the center to the edge of the site. Three other transects were then positioned at 90°, 180°, and 270° from the first. The same bearings were used to set up sampling plots at the respective sites during all three years. Each transect was 52 m long; four 3×10 m plots were centered on the transect and extended along each transect from 0–10 m, 14–24 m, 28–38 m, and 42–52 m. For each of the 16 plots on a site, we recorded the presence of 10 habitat components. The 10 components sampled were coniferous and nonconiferous forms of five classes: (1) woody stems ≤ 0.5 m in height; (2) woody stems >0.5 m but ≤ 2.5 m in height, excluding snags; (3) woody stems >2.5 m in height and ≤ 15.2 cm diameter at breast height (dbh), excluding snags; (4) woody stems >2.5 m in height and >15.2 cm dbh, excluding snags; and (5) free-standing snags ≥ 1.8 m in height and ≥ 10.2 cm dbh (see Thomas 1979: 60, Wiedenmann 1991:21). With these data we computed each site's component frequencies, the mean number of components per 30-m² plot, and a coefficient of variation for the number of components per 30-m² plot. The elevation at each site's center was obtained from a topographic map.

For the second scale of data collection, we estimated the areal coverages of habitat types within the 7.1-ha circle. Data were obtained from maps of stand types (e.g. lodgepole pine, riparian) and dbh classes (e.g. poletimber, sawtimber; U.S. Forest Service 1989). We centered a clear-acetate circular grid containing 200 points, and having a radius of 150 m drawn to the scale of the map, over each site center plotted on the map. The percent cover of a habitat type in the 7.1-ha area was computed as the proportion of the 200 points that fell within the boundaries of that habitat type on the map. The habitat maps were updated in 1989 prior to data collection; no corrections were needed in 1990, and only minor updates for two sites were necessary in 1991. We estimated the coverage of five habitat types: lodgepole pine, sapling/seeding; lodgepole pine, poletimber; lodgepole pine, sawtimber; riparian areas; and nonforested areas (meadows, clearcuts; U.S. Forest Service 1989). Other habitat types (e.g. spruce-fir, aspen) occurred too infrequently to be considered as distinct variables, but we included them in our estimate of the number of habitat types present within the 7.1-ha area.

Statistical analyses.—For each habitat variable, we used one-way analysis of variance (ANOVA; Dixon 1988; BMDP7D) to determine whether habitat features were confounded with (differed among) treatment groups. Before the analyses, habitat variables recorded as percentages were transformed with an arcsine transformation (Zar 1984).

We defined song occurrence at a site as the number of censuses during which an individual species sang, divided by the number of censuses during which that species was detected on the site. Singing consistency at a site was calculated as the maximum number of consecutive censuses during which an individual species sang, out of the number of censuses it was detected on the site. A species was considered present if either a male or female was detected by sight or sound during a census; we worked during the breeding season and reasoned that, if a female was detected on a site, a male was probably present as well. Data for censuses during which a species was not detected (neither heard nor seen) were not used in the present analyses because the intrusions may have caused that species to vacate the site. This approach ensured that we would address only the effects of intrusion on song occurrence and singing consistency and that these results would be distinguished from other effects such as displacement. Examination of the immediate and cumulative effects of intrusion on spatial distributions is beyond the scope of the present analysis, but K.J.G. will address these topics elsewhere. Prior to analyses, song-occurrence values (percentages) were transformed using an arcsine transformation and singing-consistency data (counts) were transformed with a square-root transformation (Zar 1984:241, eq. 14.8).

For each species, we identified the habitat variable that was most highly correlated (separately) with the transformed values for song occurrence and singing consistency. The single most significant ($P < 0.05$) habitat variable that also enabled us to meet the assumptions of analysis of covariance (ANCOVA; Huitema 1980:98–122) was used. By using only one covariate we minimized the loss of degrees of freedom (thereby maintaining statistical power) and avoided problems due to collinearity among covariates (Huitema 1980:161). When habitat variables were not significantly correlated with song occurrence or singing consistency, or when the assumptions of ANCOVA could not be met, we analyzed unadjusted means. The group means, adjusted for covariates when appropriate, were generated with BMDP1V programs (Dixon 1988) and used in two-tailed *a priori* contrasts (Ott 1988:437–440; R. S. Cochran pers. comm.).

We constructed the contrasts to test whether there were significant differences in song occurrence or singing consistency between control and intruded sites and between S25 and S100 sites. Thus, we used contrasts to test for the main effect of intrusion scale, which is an effect one would test for in a conventional

ANOVA or ANCOVA. However, our contrast approach also enabled us to compare control and treated sites, which is not an effect that is tested for simultaneously in an ANOVA or ANCOVA. These two contrasts were not *a posteriori* contrasts, for which an experimentwise error rate is specified to limit the collective Type I error rate. We formulated the contrasts before the data were collected.

We did not test for intrusion frequency effects or intrusion frequency-and-scale interaction effects. On average, censuses for F1 sites occurred about 3.5 days after we administered treatments, whereas censuses for F2 sites were completed about 2 days after disturbances. Time and personnel constraints prevented us from avoiding this difference. Under these circumstances, effects of intrusion frequency cannot be distinguished clearly from effects of differences in the timing of censuses relative to treatments. Consequently, we did not test for frequency or frequency-and-scale interaction effects. Because control and intruded sites were censused the same day, and S25 and S100 sites were censused on average both 2 and 3.5 days after intrusions, the control-versus-intruded and S25-versus-S100 comparisons were not affected by the association between intrusion frequency and time between treatments and censuses. Earlier results about frequency and frequency-and-scale interaction effects on singing behavior (Wiedenmann 1991) are, strictly speaking, not interpretable, but inferences about control-versus-intruded and S25-versus-S100 comparisons in Wiedenmann (1991) are sound.

Approximately 65 species of birds breed in our study area, but only about 35 of these sing. Of these 35, we considered only those species that sang or used our sites frequently enough for us to study their singing behavior quantitatively. We used the control-versus-intruded and S25-versus-S100 contrasts for species that sang commonly and that were present on at least 20 sites, including at least two sites in each treatment group. Within some species the number of sites differed slightly among intruded groups, but contrast orthogonality was not affected appreciably because we used the method of unweighted means to construct the contrasts (Bancroft 1968:35; R. S. Cochran pers. comm.). For each species that did not sing frequently, that was not on at least 20 sites, or both, we used a two-tailed Fisher exact test (Zar 1984:390–395) to test *a priori* null hypotheses that the proportion of sites on which singing occurred did not differ between treatment groups. For singing consistency, we used a two-tailed Mann-Whitney test (Zar 1984:139–141) to test *a priori* null hypotheses that singing consistency did not differ between treatment groups. We applied this latter technique for species that sang sporadically, that were not common in our study area, or both. We used $\alpha = 0.10$ for contrasts of singing behavior. All of the habitat analyses and contrasts for singing behavior were completed each year separately. To assess whether patterns in the results differed

TABLE 1.   Contrasts of song occurrence for 1989 and 1991, with $\bar{x} \pm$ SE [n] and contrast statistics for arcsine-transformed data.

Species	Contrast[a]	t	df	P
	1989			
Ruby-crowned Kinglet	Control (1.51 ± 0.06 [10]) vs. intruded (1.28 ± 0.10 [19])	2.00	24	0.058
Ruby-crowned Kinglet	S25 (1.07 ± 0.17 [9]) vs. S100 (1.46 ± 0.07 [10])	2.77	24	0.011
	1991			
Hermit Thrush	Control (1.54 ± 0.23 [6]) vs. intruded (0.99 ± 0.14 [17])	2.12	17	0.049
Pine Siskin	S25 (0.20 ± 0.13 [8]) vs. S100 (0.71 ± 0.21 [6])	2.17	15	0.048

[a] Control = no intrusion; intruded = all intruded sites as a group. S25 = inner 25% of 1.0-ha site intruded; S100 = 100% of 1.0-ha site intruded.

from those expected by chance alone, we used two-group (1 df) chi-square tests with $\alpha = 0.10$. We calculated a corrected chi square (Zar 1984:48) to preclude the bias that is possible with one degree of freedom.

We used different levels of α depending on the topic being addressed. Being able to detect substantial differences in habitat conditions among treatment groups was essential, but being able to detect very slight differences was less critical, so we used $\alpha = 0.05$. To identify optimal covariates we used $\alpha = 0.05$ because we wanted a covariate that was associated with a substantial amount of the variation in the dependent variable. If we had used $\alpha = 0.10$ for this aspect of the work, we would have used up a degree of freedom (for the covariate) for less gain (relative to using $\alpha = 0.05$) in variance reduction. The reason is that attained significance levels are highly and negatively correlated with the strength of the relation between a dependent variable and a covariate; typically, the stronger the relation, the better the reduction in variance. This was a strategy to enhance statistical power for the contrasts of singing behavior (dependent variable), and it depended on gaining more power (by reducing variance in the singing behavior variables) than what would be lost by using a degree of freedom (for the covariate). Singing behavior was the central theme of our work, and we wanted to be able to detect both large and small effects. To maintain the ability to detect slight differences due to treatments and subtle patterns in the results (i.e. maintain statistical power), we used $\alpha = 0.10$. In ecological settings, it is not unusual to use $\alpha = 0.10$ to maintain or increase statistical power (e.g. Coon et al. 1981, Hensler and Nichols 1981, Nichols et al. 1984, Westmoreland and Best 1985). In short, we used α levels that were consistent with our objectives for particular analyses.

RESULTS

Habitat features.—None of the 19 habitat variables differed among treatment groups ($P = 0.22$–0.98) during any of the three years. Thus, hab-

itat conditions were not confounded with treatment combinations.

Song occurrence.—Contrasts of song occurrence revealed treatment effects for some species during 1989 and 1991, but not during 1990 (Table 1). To our knowledge, nothing unusual occurred on our sites or in our study area in 1990. Based on contrasts, we did not detect treatment effects on song occurrence for: Hermit Thrush (*Catharus guttatus*), Yellow-rumped Warbler (*Dendroica coronata*), Mountain Chickadee (*Parus gambeli*), or Dark-eyed Junco (*Junco hyemalis*) during 1989; Yellow-rumped Warbler, Dark-eyed Junco, American Robin (*Turdus migratorius*), Ruby-crowned Kinglet (*Regulus calendula*), or Mountain Chickadee during 1990; and Yellow-rumped Warbler, Dark-eyed Junco, Mountain Chickadee, or Ruby-crowned Kinglet during 1991.

Fisher exact tests indicated that during 1989 the proportion of control sites at which singing occurred was higher than that for intruded sites for American Robins (0.44 vs. 0.11; $P = 0.064$) and Red-breasted Nuthatches (*Sitta canadensis*; 0.50 vs. 0.00; $P = 0.077$). The control-versus-intruded comparison was made for the Brown Creeper (*Certhia americana*), Pine Siskin (*Carduelis pinus*), Cassin's Finch (*Carpodacus cassinii*), and Western Tanager (*Piranga ludoviciana*) as well, but no differences were found. Sample sizes also were adequate to conduct S25-versus-S100 comparisons for the American Robin, Red-breasted Nuthatch, and Pine Siskin in 1989, but treatment effects were not evident. For the Hermit Thrush, Warbling Vireo (*Vireo gilvus*), Pine Siskin, Brown Creeper, and Red-breasted Nuthatch in 1990, Fisher exact tests were conducted, but we did not detect any intrusion effects. For 1991, the S25-versus-S100 comparison involving the Warbling Vireo, American Robin, Brown Creeper, and Mountain Bluebird (*Sialia curru-*

TABLE 2. Contrasts of singing consistency for 1989 and 1990, with $\bar{x} \pm$ SE [n] and contrast statistics for square-root transformed data.

Species	Contrast[a]	t	df	P
	1989			
Mountain Chickadee	Control (2.36 ± 0.23 [10]) vs. intruded (1.82 ± 0.17 [18])	1.86	22	0.080
Ruby-crowned Kinglet	Control (4.38 ± 0.28 [10]) vs. intruded (3.76 ± 0.21 [19])	1.86	23	0.079
Hermit Thrush	Control (2.97 ± 0.41 [9]) vs. intruded (2.22 ± 0.19 [14])	1.92	18	0.098
Yellow-rumped Warbler	Control (3.33 ± 0.25 [8]) vs. intruded (2.54 ± 0.18 [17])	2.50	19	0.022
	1990			
Yellow-rumped Warbler	Control (3.63 ± 0.20 [9]) vs. intruded (2.96 ± 0.15 [18])	2.75	21	0.013

[a] Groups defined as under Table 1.

coides), and the control-versus-intruded comparison involving the Dusky Flycatcher (*Empidonax oberholseri*) and Red-breasted Nuthatch, were implemented with Fisher exact tests. Song occurrence for these species was not influenced significantly. Overall, the intrusions did not consistently influence song occurrence for any single species during the three-year period.

Using the untransformed data for song occurrence, we computed percent differences associated with declines as $100(\bar{x}_I - \bar{x}_C)/\bar{x}_C$, and as $100(\bar{x}_{S100} - \bar{x}_{S25})/\bar{x}_{S25}$. In 1989, song occurrence was lower on intruded sites than on control sites by 8% for Ruby-crowned Kinglets, 75% for American Robins, and 100% for Red-breasted Nuthatches; for 1991 a 30% difference developed for Hermit Thrushes. In 1989, song occurrence was lower on S25 sites by 22% for Ruby-crowned Kinglets and by 91% for Pine Siskins.

Singing consistency.—For 1989 and 1990, the contrasts of singing consistency demonstrated intrusion effects for several species (Table 2). We are not aware of anything that occurred in 1991 that was unusual. Based on contrasts, we did not detect treatment influences on singing consistency for: Dark-eyed Junco during 1989; Dark-eyed Junco, American Robin, Ruby-crowned Kinglet, or Mountain Chickadee during 1990; and Hermit Thrush, Yellow-rumped Warbler, Ruby-crowned Kinglet, Mountain Chickadee, Pine Siskin, or Dark-eyed Junco during 1991.

Mann-Whitney tests indicated that, in 1989, Cassin's Finch sang more consistently on control sites ($\bar{x} = 1.75 \pm$ SE of 0.25 consecutive weeks) than on intruded sites (0.80 ± 0.20 consecutive weeks; Mann-Whitney $U' = 18.0$, $P = 0.100$). For 1989, the control-versus-intruded comparison was also completed for the American Robin, Pine Siskin, Western Tanager, Red-breasted Nuthatch, and Brown Creeper, and the

S25-versus-S100 comparison was made for the American Robin; no intrusion influences were found. For 1990, the S25-versus-S100 comparison for the Pine Siskin and the control-versus-intruded comparisons for the Hermit Thrush, Warbling Vireo, and Brown Creeper were implemented with Mann-Whitney tests, but intrusion effects on singing consistency were not evident. We conducted Mann-Whitney tests for the 1991 control-versus-intruded comparisons involving the Warbling Vireo, American Robin, Brown Creeper, and Mountain Bluebird, as well as the S25-versus-S100 comparisons for the American Robin and Brown Creeper. Our treatments did not affect these species' singing consistency. Only one species, the Yellow-rumped Warbler, exhibited the same effect during consecutive years; its singing consistency was higher on control sites than on intruded sites during both 1989 and 1990.

Based on the untransformed data for singing consistency, we calculated percent differences associated with declines. Singing consistency on intruded sites in 1989 was lower than that for control sites by 57% for Mountain Chickadees, 29% for Ruby-crowned Kinglets, 55% for Hermit Thrushes, 50% for Yellow-rumped Warblers, and 54% for Cassin's Finch; in 1990 it was lower by 39% for Yellow-rumped Warblers.

Number of detected effects.—We completed 111 statistical tests for all comparisons, dependent variables, species, and years combined. Of these, 12 (10.8%) were significant at $P \leq 0.10$, which is only slightly greater than the 10% expected by chance alone. The directions of significant differences, however, were highly consistent within a comparison type (control-versus-intruded, S25-versus-S100), between dependent variables (song occurrence, singing consistency), among species, and among years (see Tables 1 and 2, and significant results above). Specif-

ically, control means that were significantly different from intruded means were always larger, and S25 means that differed significantly from S100 means were always smaller. These patterns hold even though different dependent variables, different statistical techniques, different species, and different years were involved. If chance effects were important, one would expect approximately one-half of the differences to be in the opposite direction (i.e. $\bar{x}_I > \bar{x}_C$ and $\bar{x}_{S25} > \bar{x}_{S100}$) among dependent variables, species, and years. We rejected the null hypothesis that, for the significant effects, the differences between groups occurred in both directions with equal frequency ($X^2 = 10.08$, df $= 1$, $P = 0.002$). Thus, the results are not consistent with simple chance-effect outcomes. More plausibly, the results indicate that only a few of the species we studied were sensitive to low levels of intrusion.

One could argue that species that exhibit low song occurrence would likely exhibit low singing consistency as well, regardless of the actual effect of intrusion on singing consistency. That is, one might expect comparable effects such that $\bar{x}_C > \bar{x}_I$ (or $\bar{x}_{S100} > \bar{x}_{S25}$) for both song occurrence and singing consistency within a species and year. One interpretation of such effects might be that the information in the two variables is not distinct. We rejected the null hypothesis that comparable effects and noncomparable effects occurred with equal frequency as would be expected by chance alone ($X^2 = 5.82$, df $= 1$, $P = 0.018$). Among the significant results (Tables 1 and 2, and results above), only the control-versus-intruded comparison for Ruby-crowned Kinglets exhibited a comparable effect. These results are the opposite of what one would predict if song occurrence and singing consistency were simply related numerically. In this study, song occurrence and singing consistency evidently provide information about distinct aspects of singing behavior.

DISCUSSION

The disturbances we administered can influence song occurrence and singing consistency for some species. Responses to intrusions were sustained into the census days, when singing activity was recorded. That such changes occurred is surprising given the low levels of intrusion involved. Some bird species habituate to repeated intrusion, with varied consequences. For example, compared to individuals

that are disturbed only occasionally, frequently disturbed individuals of some species vocalize more aggressively, have higher body masses, or tend to remain in place while an intruder approaches (e.g. Cairns 1980, Parsons and Burger 1982). Song occurrence was higher on S100 sites than on S25 sites for Ruby-crowned Kinglets in 1989 and for Pine Siskins in 1991. One might expect song occurrence on S100 sites to be lower, not higher, than that on S25 sites, but this assumes these species do not habituate to or learn to tolerate the S100 level of intrusion.

One possible explanation for this scale pattern is that some of the individuals that used the outer 75% of the S25 sites were not able to observe us often enough to discern that we were not potential predators; therefore, they may have reduced their singing to avoid attracting our attention. In contrast, all of the individuals using the S100 sites were able to observe us because we walked through all of the area of each S100 site. Thus, song occurrence for these two species may have been higher on S100 sites because the individuals that used these sites were able to determine from our repeated presence during treatments that we were not predators and that our presence and activities were benign. The higher song occurrence at S100 sites does not appear to reflect an aggressive response to human intruders, as may be elicited from species that defend their territories against people (e.g. Welty and Baptista 1988:253), or that may be induced by familiar intruders (see Knight and Temple 1986a, c). In such situations, one would expect song occurrence and singing consistency to be higher on intruded sites than on control sites; our experiments established the reverse of this pattern.

Within species and among years, responses to intrusion were not consistent. Numerous studies during the last few decades collectively demonstrate that the effects of intrusion on birds can be very context specific (Gutzwiller 1993). Different responses within a species at the same sites during consecutive years are conceivable because population composition in terms of individuals changes continually, particularly for smaller short-lived species. Disparate responses to human intrusion are not rare among individuals of the same species (see Knight et al. 1987, Götmark et al. 1989, Kenney and Knight 1992) because of differences in prior experiences with people (Fraser et al. 1985, Knight and Temple 1986b).

For the control-versus-intruded comparison,

seven results had P levels > 0.05 and ≤ 0.10, but each contributed to the unmistakable pattern exhibited by all 10 control-versus-intruded effects: higher singing activity on control sites. When we examined the untransformed data for song occurrence and singing consistency and the percent differences associated with declines, we found that most of the influences on singing behavior were substantial. Such impacts may influence the reproductive fitness of males that are sensitive to intrusion by hampering territory defense, mate attraction, and other reproductive functions of primary song (see Arcese 1987, Radesäter et al. 1987). Reduced singing activity would require males to rely more heavily on physical deterrents (chasing, fighting) to maintain territories, and these behaviors are typically quite time-consuming and energetically expensive (see Gill and Wolf 1975, Ewald and Carpenter 1978, Carlson and Moreno 1992). Consistent or regular singing on the temporal scale of minutes may help females locate males, advertise a male's singleness, and reduce territorial intrusions by conspecifics (Beletsky 1989). It is reasonable to expect regular singing on the scale of days and weeks to confer similar advantages. Thus, the disruption of consistent singing, not just song occurrence, may also have important biological ramifications.

In our experiments, the singing behavior of some species was altered by low levels of intrusion. Because song is an integral part of reproduction, it is reasonable to hypothesize that such disturbances will lead to reduced breeding success. However, the connection between altered singing behavior and reduced breeding success has not been established. We caution that additional experiments must be conducted to determine whether there is an actual causal link between intrusion-induced changes in singing behavior and lower reproductive success.

ACKNOWLEDGMENTS

LITERATURE CITED

ARCESE, P. 1987. Age, intrusion pressure and defence against floaters by territorial male Song Sparrows. Anim. Behav. 35:773–784.

BANCROFT, T. A. 1968. Topics in intermediate statistical methods, vol. 1. Iowa State Univ. Press, Ames.

BELETSKY, L. D. 1989. Communication and the cadence of birdsong. Am. Midl. Nat. 122:298–306.

BOYLE, S. A., AND F. B. SAMSON. 1985. Effects of nonconsumptive recreation on wildlife: A review. Wildl. Soc. Bull. 13:110–116.

BURGER, J., AND M. GOCHFELD. 1981. Discrimination of the threat of direct versus tangential approach to the nest by incubating Herring and Great Black-backed gulls. J. Comp. Physiol. Psych. 95:676–684.

CAIRNS, D. 1980. Nesting density, habitat structure and human disturbance as factors in Black Guillemot reproduction. Wilson Bull. 92:352–361.

CARLSON, A., AND J. MORENO. 1992. Cost of short flights in the Willow Tit measured with doubly-labeled water. Auk 109:389–393.

COON, R. A., J. D. NICHOLS, AND H. F. PERCIVAL. 1981. Importance of structural stability to success of Mourning Dove nests. Auk 98:389–391.

CUTHILL, I., AND A. HINDMARSH. 1985. Increase in Starling song activity with removal of mate. Anim. Behav. 33:326–335.

DIXON, W. J. (CHIEF ED.). 1988. BMDP statistical software manual. Univ. California Press, Berkeley.

ERIKSSON, D., AND L. WALLIN. 1986. Male bird song attracts females—A field experiment. Behav. Ecol. Sociobiol. 19:297–299.

EWALD, P. W., AND F. L. CARPENTER. 1978. Territorial responses to energy manipulations in the Anna Hummingbird. Oecologia 31:277–292.

FALLS, J. B. 1981. Mapping territories with playback: An accurate census method for songbirds. Stud. Avian Biol. 6:86–91.

FALLS, J. B. 1988. Does song deter territorial intrusion in White-throated Sparrows (Zonotrichia albicollis)? Can. J. Zool. 66:206–211.

FRASER, J. D., L. D. FRENZEL, AND J. E. MATHISEN. 1985. The impact of human activities on breeding Bald Eagles in north-central Minnesota. J. Wildl. Manage. 49:585–592.

GILL, F. B., AND L. L. WOLF. 1975. Economics of feeding territoriality in the Golden-winged Sunbird. Ecology 56:333–345.

GÖTMARK, F., R. NEERGAARD, AND M. ÅHLUND. 1989. Nesting ecology and management of the Arctic Loon in Sweden. J. Wildl. Manage. 53:1025–1031.

GUTZWILLER, K. J. 1993. Serial management experi-

ments: An adaptive approach to reduce recreational impacts on wildlife. Trans. N. Am. Wildl. Nat. Resour. Conf. 58:528–536.

HENSLER, G. L., AND J. D. NICHOLS. 1981. The Mayfield method of estimating nesting success: A model, estimators and simulation results. Wilson Bull. 93:42–53.

HUITEMA, B. E. 1980. The analysis of covariance and alternatives. John Wiley and Sons, New York.

HUTTO, R. L., S. M. PLETSCHET, AND P. HENDRICKS. 1986. A fixed-radius point count method for nonbreeding and breeding season use. Auk 103: 593–602.

KENNEY, S. P., AND R. L. KNIGHT. 1992. Flight distances of Black-billed Magpies in different regimes of human density and persecution. Condor 94:545–547.

KNIGHT, R. L., D. J. GROUT, AND S. A. TEMPLE. 1987. Nest-defense behavior of the American Crow in urban and rural areas. Condor 89:175–177.

KNIGHT, R. L., AND S. A. TEMPLE. 1986a. Methodological problems in studies of avian nest defence. Anim. Behav. 34:561–566.

KNIGHT, R. L., AND S. A. TEMPLE. 1986b. Why does intensity of avian nest defense increase during the nesting cycle? Auk 103:318–327.

KNIGHT, R. L., AND S. A. TEMPLE. 1986c. Nest defence in the American Goldfinch. Anim. Behav. 34:887–897.

KREBS, J. R. 1977. Song and territory in the Great Tit, *Parus major*. Pages 47–62 *in* Evolutionary ecology (B. Stonehouse and C. M. Perrins, Eds.). Macmillan, London.

KREBS, J. R., M. AVERY, AND R. J. COWIE. 1981. Effect of removal of mate on the singing behavior of Great Tits. Anim. Behav. 29:635–637.

MCDONALD, M. V. 1989. Function of song in Scott's Seaside Sparrow, *Ammodramus maritimus peninsulae*. Anim. Behav. 38:468–485.

NELSON, B. E. 1984. Vascular plants of the Medicine Bow Range, 4th ed. Jelm Mountain Press, Laramie, Wyoming.

NICHOLS, J. D., H. F. PERCIVAL, R. A. COON, M. J. CONROY, G. L. HENSLER, AND J. E. HINES. 1984. Observer visitation frequency and success of Mourning Dove nests: A field experiment. Auk 101:398–402.

OTT, L. 1988. An introduction to statistical methods and data analysis, 3rd ed. PWS-KENT Publishing Company, Boston, Massachusetts.

PARSONS, K. C., AND J. BURGER. 1982. Human disturbance and nestling behavior in Black-crowned Night Herons. Condor 84:184–187.

PEEK, F. W. 1972a. An experimental study of the territorial function of vocal and visual display in the male Red-winged Blackbird (*Agelaius phoeniceus*). Anim. Behav. 20:112–118.

PEEK, F. W. 1972b. The effect of tranquilization upon territory maintenance in the male Red-winged Blackbird (*Agelaius phoeniceus*). Anim. Behav. 20: 119–122.

PURDY, K. G., G. R. GOFF, D. J. DECKER, G. A. POMERANTZ, AND N. A. CONNELLY. 1987. A guide to managing human activity on national wildlife refuges. U.S. Fish and Wildl. Serv., Office of Information Transfer, Fort Collins, Colorado.

RADESÄTER, T., S. JAKOBSSON, N. ANDBJER, A. BYLIN, AND K. NYSTRÖM. 1987. Song rate and pair formation in the Willow Warbler, *Phylloscopus trochilus*. Anim. Behav. 35:1645–1651.

RICHARDS, D. G. 1981. Environmental acoustics and censuses of singing birds. Stud. Avian Biol. 6:297–300.

ROBBINS, C. S. 1981. Bird activity levels related to weather. Stud. Avian Biol. 6:301–310.

SAFINA, C., AND J. BURGER. 1983. Effects of human disturbance on reproductive success in the Black Skimmer. Condor 85:164–171.

SMITH, D. G. 1979. Male singing ability and territorial integrity in Red-winged Blackbirds (*Agelaius phoeniceus*). Behaviour 68:191–206.

THOMAS, J. W. (TECH. ED.). 1979. Wildlife habitats in managed forests: The Blue Mountains of Oregon and Washington. U.S. Dep. Agriculture Forest Service Agricultural Handbook No. 553.

TREMBLAY, J., AND L. N. ELLISON. 1979. Effects of human disturbance on breeding of Black-crowned Night Herons. Auk 96:364–369.

U.S. FOREST SERVICE. 1989. Standard specifications: Stage II inventory. U.S. Dep. Agriculture Forest Service, Rocky Mountain Region, Denver, Colorado.

VERNER, J. 1985. Assessment of counting techniques. Curr. Ornithol. 2:247–302.

VERNER, J., AND T. A. LARSON. 1989. Richness of breeding bird species in mixed-conifer forests of the Sierra Nevada, California. Auk 106:447–463.

WAIDE, R. B., AND P. M. NARINS. 1988. Tropical forest bird counts and the effect of sound attenuation. Auk 105:296–302.

WASSERMAN, F. E. 1977a. Intraspecific acoustical interference in the White-throated Sparrow (*Zonotrichia albicollis*). Anim. Behav. 25:949–952.

WASSERMAN, F. E. 1977b. Mate attraction function of song in the White-throated Sparrow. Condor 79:125–127.

WELTY, J. C., AND L. BAPTISTA. 1988. The life of birds, 4th ed. Saunders College Publishing, New York.

WESTMORELAND, D., AND L. B. BEST. 1985. The effect of disturbance on Mourning Dove nesting success. Auk 102:774–780.

WIEDENMANN, R. T. 1991. Effects of repeated human intrusion on singing behavior in subalpine breeding birds. M.S. thesis, Baylor Univ., Waco, Texas.

ZAR, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall, Englewood Cliffs, New Jersey.