

DOES HUMAN INTRUSION ALTER THE SEASONAL TIMING OF AVIAN SONG DURING BREEDING PERIODS?

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ABSTRACT.—The seasonal timing of male song during breeding affects the timing of territory establishment, mate attraction, pair formation, egg laying, and transmission of information about breeding songs to young. Thus, alteration of the seasonal timing of song may influence reproductive success and survivorship. Human intrusion has the potential to influence avian singing behavior. Accordingly, we determined whether repeated intrusion affected the seasonal timing of male song for three passerines (Ruby-crowned Kinglet [*Regulus calendula*], Yellow-rumped Warbler [*Dendroica coronata*], Dark-eyed Junco [*Junco hyemalis*]) in Wyoming forests. Intrusions involved one person walking through habitats for 1–2 h (Snowy Mountains, 1989–1993) or for 5 h (Pole Mountain, 1991–1993) each week for 10 consecutive weeks of each breeding season. For most comparisons, we did not detect a significant difference in the seasonal timing of singing activity between control and intruded sites. Two exceptions were: (1) the mean singing date for Ruby-crowned Kinglets was 11 days earlier on intruded sites than on control sites at Pole Mountain; and (2) the proportion of intruded sites with singing by Yellow-rumped Warblers (0.40) was smaller than that for control sites (1.00) during mid-June at Pole Mountain. Moderate and large differences in the timing of singing activity were detectable with a probability of 0.80, but small differences were not reliably detectable. Thus, our results are a conservative estimate of the effects of intrusion on the seasonal timing of song. Curtailment of singing on intruded sites may have reduced breeding activity and, consequently, the quality of those sites for producing young. Because intrusion-induced effects often are context-specific and can vary among individuals and species, and because our results are conservative, avian ecologists should continue to assess whether intrusion influences seasonal patterns of singing activity. Received 13 May 1996, accepted 12 September 1996.

AS HUMAN POPULATIONS grow in magnitude and geographic extent, their associated disturbances are becoming increasingly dominant forces in natural systems. Intrusion, the mere presence of people in the environment, is one form of human disturbance that has not received adequate study. Although intrusion often appears innocuous because of its inconsistent and inconspicuous consequences (Gutzwiller et al. 1994), mounting evidence indicates that intrusion can have insidious effects. In avian communities, human intrusion can displace individuals and reduce reproduction and survival (Boyle and Samson 1985, Knight and Gutz-

willer 1995). Almost invariably, these effects develop in the absence of habitat alteration or other detectable ecological changes. Levels of intrusion as low as 1 or 2 h per week during the breeding season can reduce the occurrence and weekly consistency of primary song (Gutzwiller et al. 1994).

Primary song carries far, is emitted by males in most species, and is important for securing territories, attracting mates, and maintaining pair bonds (Searcy and Andersson 1986, Radesäter et al. 1987, Welty and Baptista 1988, Kelsey 1989). In temperate regions, the seasonal timing of primary song occurs during a characteristic period for each species (Saunders 1947, 1948). Male singing stimulates female receptiveness and egg laying (Logan et al. 1990), and various species lay eggs during or immediately after the period of peak singing activity (Slagsvold 1977,

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Lampe and Espmark 1987, Catchpole and Slater 1995:94). Because human intrusion can influence singing behavior (Gutzwiller et al. 1994), it has the potential to influence the seasonal timing of primary song and, therefore, the timing of important breeding activities.

If most singing activity is restricted to early dates during the breeding season, e.g. due to intrusion-induced displacement or curtailment of singing, then males may not have sufficient time to establish territories, attract females, or form pair bonds. Even if sufficient singing occurs to stimulate egg laying at this time, unusually early breeders are sometimes not successful because of inclement weather (Perrins 1970, 1996). Song learning, its functional significance (Slater 1989), and ultimately reproductive success (O'Loughlen 1995) also may be affected adversely if young are not exposed adequately to song during the sensory phase, which for many species spans the weeks just after fledging (Böhner 1990, DeWolfe and Baptista 1995). It seems possible that human intrusion also could delay singing activity because males may not learn to tolerate or habituate to intruders for weeks, if they do so at all. As a consequence, eggs may be laid and fledglings may leave the nest later than normal. Late broods often have lower survivorship than do earlier broods, probably because of declining food supplies for young toward the end of the breeding season (Perrins 1965, 1970). Some species lay smaller clutches as the season progresses (Perrins 1970, Dalhaug et al. 1996), so a delay in the breeding season also could reduce the number of young initially produced.

The quality of habitats for producing young and subsequent breeders could be reduced if intrusion alters the seasonal timing of primary song. Human intrusion has become a ubiquitous form of disturbance (Gutzwiller et al. 1994), and ornithologists should assess its influence on habitat quality through its effects on the timing of breeding events. We experimentally determined whether repeated human intrusion during the breeding season influenced the seasonal timing of primary song for three passerines (Ruby-crowned Kinglet [*Regulus calendula*], Yellow-rumped Warbler [*Dendroica coronata*], Dark-eyed Junco [*Junco hyemalis*]). For each species, we tested the *a priori* hypothesis that dates of primary song at intruded sites differed from those at control sites where intrusions were not administered.

METHODS

Study areas and site establishment.—We conducted experiments in southeastern Wyoming in the Snowy Mountains and at Pole Mountain. The Snowy Mountains sites (41°32' N, 106°20' W) were about 70 km WNW of Laramie at elevations between 2,550 and 2,780 m. Mixed-conifer stands (limber pine [*Pinus flexilis*], Engelmann spruce [*Picea engelmannii*], and subalpine fir [*Abies lasiocarpa*]), pure stands of lodgepole pine (*Pinus contorta*), aspen groves (*Populus tremuloides*), clearcuts, meadows, and riparian habitats were dominant. Other common woody species included Oregon grape (*Mahonia repens*), alder (*Alnus incana*), snowberry (*Symphoricarpos oreophilus* var. *utahensis*), huckleberry (*Vaccinium scoparium*), kinnikinnick (*Arctostaphylos uva-ursi*), and sagebrush (*Artemisia* spp.; names from Dorn 1992).

We randomly established 30 circular 1.0-ha sites in stands across the study area during May 1989. We did not place sites in locations with either current or planned silvicultural or recreational activities. Sites averaged 0.7 km apart and were 0.4 km from the nearest used road. We accessed each site with a permanent transect from the road to the site center and marked the point at which the transect crossed the site perimeter as a reference for determining whether a singing bird was inside the circumference of the site. We also used this marker to determine where to begin and end disturbance treatments and for where to begin collection of singing data. The same 30 sites were used during 1989–1993. Weather data were obtained twice per week during the 10-week study season (late May to early August) each year at five permanent stations distributed equidistantly among the 30 sites. Mean maximum and minimum temperatures during the study season for the five-year period were $25.3 \pm \text{SD of } 4.9^\circ\text{C}$ and $-0.1 \pm 4.3^\circ\text{C}$. Mean daily precipitation during the study season for the five-year period was 1.7 ± 0.4 mm.

The Pole Mountain sites (41°15' N, 105°23' W) were approximately 16 km SE of Laramie at elevations between 2,500 and 2,690 m. The same tree and shrub species that were common in the Snowy Mountains were present. At Pole Mountain, however, lodgepole pine, limber pine, and sagebrush were much more prevalent, and subalpine fir and Engelmann spruce were uncommon. In 1991, we established and marked 20 sites at Pole Mountain with the same techniques and criteria used at the Snowy Mountains. We used the same 20 sites during 1991–1993. Both of our study areas are in the Medicine Bow National Forest, but the Pole Mountain area is not managed for timber and contained no clearcuts. Sites were 216 to 696 m from the nearest used road and were an average of 0.7 km apart. Two weather stations were established equidistantly among the 20 sites, and weather data were gathered twice each week during the 10-week study period from late May to early August each year.

Mean maximum and minimum temperatures during the study season for the three-year period were $23.9 \pm 5.8^\circ\text{C}$ and $2.7 \pm 4.6^\circ\text{C}$. Mean daily precipitation during the study season for the three-year period was 2.5 ± 0.5 mm.

Intrusion treatments.—For the Snowy Mountains sites, we randomly assigned all intrusion treatments to the 1.0-ha sites during May 1989, with the constraint that no two adjacent sites would receive identical treatments. Intrusion treatments involved two levels of spatial scale (the inner 25% [S25] or 100% [S100] of the site was disturbed), two levels of frequency (one [F1] or two [F2] intrusion treatments/week), and controls (no intrusion treatments). We replicated the five groups as follows: F1-S25 ($n = 5$); F1-S100 ($n = 5$); F2-S25 ($n = 5$); F2-S100 ($n = 5$); and Control ($n = 10$). In the present analysis, we were interested only in whether the intrusions in general were influential, so we placed all disturbed sites into a single group called intruded sites. F1 treatments were implemented on Wednesdays and F2 treatments were administered on Mondays and Fridays. Treatments did not coincide with collection of singing data, which occurred on Tuesdays and Thursdays. Within intrusion-frequency groups, we randomly assigned the initial order of treatments and then rotated this order on each new intrusion day so that each site was intruded an equal number of times during various times of day each season. Investigators started intrusion treatments between 0700 and 0800 MST and typically completed them by mid-afternoon. Intrusions were carried out under all weather conditions except when lightning occurred. The treatment schedule lasted 10 weeks from late May to early August and was the same during all five years.

A single intrusion treatment involved one person walking through the 1.0-ha site in a radial pattern from the center to the perimeter and back again; each treatment lasted 1 h, during which the specified area was covered twice. Investigators walked either halfway (for S25 plots) or all of the way (for S100 plots) to the perimeter of the 1.0-ha sites. To ensure that sites were disturbed only within specified boundaries, investigators determined before treatments began the number of their steps necessary to cover these distances. During treatments, investigators made no effort to conceal themselves, clothing color was not restricted, birds encountered were faced and approached directly at a normal walking pace, and investigators did not gesture or make noises to elicit bird responses. Birds flushed from resting, feeding, singing, and nesting habitats in response to investigator movements during treatments.

For the Pole Mountain sites, all intrusion treatments were randomly assigned to the 1.0-ha sites during May 1991, but no two adjacent sites received the same treatment. Intrusion treatments involved two levels of spatial scale (the inner 25% [S25] or 100% [S100] of the site was disturbed), one level of fre-

quency (five intrusion treatments/week [F5]), and controls (no intrusion treatments). The three groups were replicated as follows: F5-S25 ($n = 5$); F5-S100 ($n = 5$); and Control ($n = 10$). We grouped all intruded sites into a single group for analysis. Treatments were implemented once each day from Monday through Friday during each week. In all other respects, intrusion treatments at Pole Mountain were identical to those implemented in the Snowy Mountains.

Collection of singing data.—The species we studied sang primary songs frequently (5–12/min; Robbins et al. 1983, Gutzwiller pers. obs.), their songs were easily heard and readily distinguishable, they sang during various parts of our 10-week study season, and they were abundant in the study areas. These traits enabled us to obtain adequate data to characterize the timing of singing activity during the experiments. Other species encountered (see Riffell et al. 1996) did not exhibit all of these traits, so we did not include them in the our analyses.

Each year before bird data were collected, investigators practiced determining, by sound, whether a singing bird was within or beyond a marked site identical in dimensions to, but distinct from, our actual 1.0-ha study sites. Singing data for the present analysis originated from initial detections of individuals during 15-min point counts (Verner 1985) conducted between 0500 and 1100 MST. Only songs from individuals known to be distinct in time and space were recorded. Point counts were conducted when wind speed was less than 20 km/h, air temperature was greater than 0°C , and no more than a light drizzle was falling (Robbins 1981). Investigators conducting point counts wore dark drab clothing to avoid attracting or repelling birds (see Gutzwiller and Marcum 1993, 1997). During the first week of each season, all sites in the Snowy Mountains were first sampled within 50 h of one another, and all sites at Pole Mountain were first sampled on the same morning within a 5-h period. Half of the Snowy Mountains sites were sampled on Tuesdays and half were sampled on Thursdays each week during a 10-week period from late May to early August each year. To eliminate time-of-day and seasonal biases, we randomized the initial order in which Snowy Mountains sites were sampled and then rotated this order each sampling day. Each investigator also sampled an equal number of control and intruded sites to avoid introducing biases associated with investigator abilities. The sampling schedule was identical during each of the five years of the Snowy Mountains experiment. We used these same techniques to sample Pole Mountain sites, except that the latter sites were all sampled on Saturday each week, and the order in which sites were sampled was reversed each week.

It was clear from numerous observations that, unlike our treatments, point counts were not intrusive (Gutzwiller et al. 1994, Riffell et al. 1996). Upon detecting us, most individuals behaved as if we were

not present or did not pose a threat. In addition, each 15-min point count began when the investigator reached the perimeter of the 1.0-ha site (Hutto et al. 1986), which enabled us to record individuals that were singing at the site and that otherwise might have gone undetected because of their reactions to our approach to the site center. As a result of investigator movements during intrusion treatments, some individuals may have been conditioned to reduce their singing activity whenever they detected a person; such individuals thus may have been induced to remain silent upon the approach of an investigator during point counts. Our field observations indicated, however, that the counts were nonintrusive. We recorded singing at the site before birds would have detected us moving across it toward the center, and birds sang at the site before, during, and after point counts. We believe our data are accurate and that there were few if any biases originating from count-induced reactions by individuals that may have been sensitized during treatments (Riffell et al. 1996). Accordingly, we attributed changes in the seasonal timing of singing to intrusion-induced changes in singing behavior or species' distributions, not to temporary behavioral responses to our presence during point counts.

Collection of habitat data.—Variation in the seasonal timing of singing activity due to differences in habitat characteristics might have been confounded with treatment groups. To check for habitat differences between intruded and control sites, we estimated a variety of habitat parameters.

At the Snowy Mountains sites, habitat sampling occurred during mid-August in 1989, 1991, and 1993 after we completed intrusion treatments and point counts. We sampled habitat variables at two spatial scales for each site: the 1.0-ha site itself and a 7.1-ha area (diameter 300 m) centered on and including the 1.0-ha site (Gutzwiller et al. 1994, Riffell et al. 1996). The vegetative characteristics of the 1.0-ha site were sampled using four 52-m line transects radiating at right angles from the center to the perimeter of the site. We randomly selected the bearing for the first transect on each site. Four 3×10 -m plots were centered on each of the transects, and one such plot was placed within the following portions of each transect: 0–10 m, 14–24 m, 28–38 m, and 42–52 m. For each of the 16 plots, we recorded the presence of the following five types of coniferous and non-coniferous stems: (1) woody stem ≤ 0.5 m in height; (2) woody stem > 0.5 m and ≤ 2.5 m in height, excluding snags; (3) woody stem > 2.5 m in height and ≤ 15.2 cm dbh (diameter at breast height), excluding snags; (4) woody stem > 2.5 m in height and > 15.2 cm dbh, excluding snags; (5) free-standing snags ≥ 1.8 m in height and ≥ 10.2 cm dbh (adapted from Thomas 1979:60). Species were considered coniferous only if they were cone-bearing; deciduous species and evergreen species that do not bear cones were classified as non-

coniferous. The first 10 habitat components consisted of the coniferous and non-coniferous component frequencies; we calculated a frequency as the proportion of the 16 plots with a given stem type present. Mean number of different stem types per 30-m² sampling plot and the coefficient of variation for number of stem types per 30-m² sampling plot were measures of vertical and horizontal heterogeneity, respectively. At each site, the same transects and methods were used to sample habitat each year. These same techniques were used to obtain habitat data at the 1.0-ha scale for the Pole Mountain sites during mid-August 1991 and 1993.

For the 7.1-ha area, habitat coverages at the Snowy Mountains sites were determined from maps of stand types (U.S. Forest Service 1989). Maps were updated as necessary before we sampled habitats each year, and we used the same grid and methods each year. A circular grid with a map-scaled radius of 150 m, and composed of 200 points plotted on a sheet of clear acetate, was centered on the site center on the map. The percent cover of a particular stand type in the 7.1-ha area was the percentage of the 200 points that fell within the boundaries of that type on the map. Eleven different stand types were identified, but only five occurred frequently enough to be considered distinct variables. We measured percent cover for the following stand types: lodgepole pine, seedling/sapling; lodgepole pine, poletimber; lodgepole pine, sawtimber; riparian habitat; and non-forested openings. The number of different stand types (of the 11) that occurred within the 7.1-ha area also was recorded. We estimated elevation at the 1.0-ha site center from topographic maps. We used these same techniques to gather data at the 7.1-ha scale for the Pole Mountain sites, with the following exceptions: there were only three stand types that were encountered often enough to be considered distinct variables (lodgepole pine, poletimber; lodgepole pine, sawtimber; non-forested openings), and there were 13 stand types from which to determine number of stand types within the 7.1-ha area. We also measured the distance between each site and the nearest section of used road because this distance could not be standardized for all sites as in the Snowy Mountains area.

Statistical analyses.—Only data for individuals that sang within the 1.0-ha sites were used. Further, for a given combination of species, year, and study area, we only analyzed data for sites at which singing was recorded at least once during the 10-week study period. For each point count, we recorded the date on which each distinct individual sang. A number signifying the month and day of singing (actual song date; e.g. 7/31) would not have accurately represented the continuous ratio scale on which time is measured (Zar 1996:2). We therefore converted actual dates of singing to values of a ratio-scale variable that reflected the number of days between the date of singing and the date of the first point count for that site and year.

We hereafter refer to this variable as number of days. To estimate the seasonal timing of singing at a site for a given species and year, we calculated the mean number of days. Singing occurred on only a single sampling date for some sites, but most estimates of seasonal timing were based on an overall average of 3.1 song dates per species, site, and year (range of averages among species, years, and study areas = 2.0 to 5.0 song dates per site). To make use of all of the data collected, we used both single values and mean values of number of days (depending on which was available for a given site) in statistical analyses.

For each combination of species, year, and study area separately, our *a priori* null hypothesis was that the mean number of days did not differ between control and intruded sites; the associated alternative hypothesis was that group means differed. We used Student's *t*-test to assess between-group differences in means. When the assumption of equal variance was not clearly satisfied, we also conducted Welch's *t*-test (Ott 1993:269). For comparisons in which the assumption of normality was not clearly met, we applied the Mann-Whitney test (Ott 1993:279, Zar 1996:130) in addition to Student's *t*-test. The latter test always resulted in the same conclusions as did the Welch's *t* and Mann-Whitney tests, so we report results only for Student's *t*-test. Statistical tests were conducted with BMDP 3D software (Dixon 1990).

Some differences in the seasonal timing of singing during parts of the study season could have been obscured by analyzing mean number of days for the 10-week period as a whole. For example, if singing on control sites often occurred early and late during the 10-week period, and singing on intruded sites usually occurred during the middle of the period, our use of mean number of days for the 10-week period could have prevented us from detecting such differences. That is, with the entire 10-week period as the focus of analysis, values for mean number of days could have been quite similar for control and intruded sites, and differences between groups in the timing of singing activity during parts of the study season could have gone undetected.

To address this issue, we conducted comparisons to determine whether singing activity differed between control and intruded sites during each of the five two-week periods. Our *a priori* null hypothesis was that, during a given two-week period, the proportion of sites on which singing (one or more songs) occurred did not differ between the control and intruded groups; the alternative hypothesis was that these proportions differed. For each species, year, and study area combination, we tested these hypotheses for each of the five two-week periods separately. We used PROC FREQ (SAS Institute Inc. 1985) to conduct Fisher exact tests for differences in proportions (Zar 1996:540).

We did not use repeated measures analysis of variance (RMAOV) to analyze our data because conditions

necessary to ensure the validity and statistical power of this technique were not adequately met. An assumption of RMAOV is that the experimental unit on which repeated measurements are made is the same entity during the course of an experiment, implying in our case that the composition of our experimental units remained the same within and among breeding seasons. Our experimental unit consisted of the physical 1.0-ha site as well as the individual birds that sang on that site. Relatively short life spans in passerines, shifts in territory ownership or food availability, and many other changes can influence whether individuals remain at a site within a breeding season or return to a site during subsequent breeding seasons. Song dates within and among breeding periods would be expected to vary with the actual males that sang because males are likely to differ in many ways that could affect their singing behavior and reaction to human intrusion. We were not comfortable assuming that most of the same individuals were at the same 1-ha sites during one or more breeding seasons, or in general that our data were appropriate for RMAOV. Moreover, if observations are not true repeated measures, then the error variance in a RMAOV may not be reduced enough to compensate for the loss of error df that occurs in this design. In this situation, lower power may result by using a RMAOV than by using an analysis that does not assume repeated measures because the reduction in error df in the RMAOV leads to a larger critical value (Kirk 1995: 252–254). No untenable or questionable assumptions had to be made for the *t*-tests or Fisher exact tests that we used.

For all analyses we used an *a priori* $\alpha = 0.10$ (vs. 0.05) to improve statistical power (see Nichols et al. 1984, Westmoreland and Best 1985). To control for Type I error, we applied a sequential Bonferroni adjustment to α for simultaneous inferences (Rice 1989, Beal and Khamis 1991). Hypotheses for multiple years about number of days for a given species and study area (e.g. the five hypothesis tests for Dark-eyed Junco, Snowy Mountains, 1989–1993) were conceptually related because they dealt with the same species and study area. Each such set of related hypotheses was thus a "family" (sensu Miller 1981:34) of simultaneous hypotheses, and the α for each individual hypothesis in a family was adjusted so that the family-wide α was equal to the *a priori* level. The standard Bonferroni method accomplishes this but reduces statistical power when more than one null hypothesis in a group is actually false (Rice 1989). The sequential Bonferroni adjustment of α was devised to preclude this problem (Holm 1979).

Using the sequential method, we controlled family-wide α values at 0.10 first by ranking the *P* values for statistical tests for a given family from smallest to largest. Each *P* value was then compared to sequentially adjusted α levels. For analyses using *t*-tests, we had families of five (1989–1993, Snowy Mountains)

and three (1991–1993, Pole Mountain) hypotheses for each species. To be significant, the smallest P value within a family had to be $\leq \alpha/k$, where k equaled the number of hypotheses in a family. We examined the second smallest P value for significance only if the smallest P was significant. The second smallest P had to be $\leq \alpha/(k - 1)$ to be judged significant, and so on. If a P value did not meet the criterion for significance, then neither it nor any larger P value for that family of hypotheses was declared significant. We also applied this technique to the Fisher exact tests for differences in proportions of sites on which singing occurred; each set of five hypotheses (one hypothesis for each two-week period) for a given species, year, and study area was considered a family of hypotheses.

To assess the ability of the t -tests to detect actual between-group differences in mean number of days, we computed δ , the minimum detectable difference (Zar 1996:135). δ values were the smallest between-group differences in mean singing dates, in days, that our analyses would have been able to detect as statistically significant. For these calculations we used $\alpha = 0.02$ and 0.10 (the minimum and maximum levels involved in the sequential Bonferroni adjustment for the Snowy Mountains); $\alpha = 0.033$ and 0.10 (the minimum and maximum levels involved in the sequential Bonferroni adjustment for Pole Mountain); $\beta = 0.20$ (power = 0.80, Reed and Blaustein 1995); and the sample sizes and variances associated with the comparisons we made.

A literature review and consultation with statisticians (Beal and McDonald pers. comm.) indicated that a general estimator to compute detectable effect sizes for Fisher exact tests was not available, so we conducted simulations in FORTRAN to determine effect sizes. These effect sizes were the smallest between-group differences in the proportions of sites at which singing occurred that our analyses would have been able to detect as statistically significant. Our simulations assumed binomial distributions because a species either did or did not sing on a site; one binomial distribution was used for the control group and one was used for the intruded group. We used a trial-and-error method to find the smallest difference in proportions that could be detected 80% of the time at $\alpha = 0.02$ and at $\alpha = 0.10$ (the minimum and maximum levels possible for each family of hypotheses). We used 10,000 iterations per case for the final simulations to ensure confidence in the results. The ability of the Fisher exact test to detect a difference depends on (1) sample sizes, (2) the size of the true underlying difference in proportions, and (3) the location of this difference in the distribution of differences. Using our information about sample sizes and the distributional location of differences, we designed the simulations to take into account all three of these factors for each combination of two-week period, species, year, and study area separately.

We used ANOVA and BMDP 7D software (Dixon

1990) to test for differences in habitat features among treatment groups for each study area and year separately. For a few variables, the equal-variance assumption of ANOVA was not clearly met; in those cases we also computed both Welch and Brown-Forsythe F statistics, which are not based on the assumption of equal variances (Dixon 1990:192). Both of these latter statistics always resulted in the same conclusion as the standard F statistic.

Based on over 3,250 h of field observations, birds at our study sites were not influenced by human disturbances other than the experimental intrusions. Areas within several km of the Snowy Mountains sites were managed for timber and some recreational activity, whereas areas adjacent to the Pole Mountain sites were managed exclusively for recreation (i.e. no timber was harvested). The two regions thus experienced different levels and types of human activity. The study areas were almost 90 km apart, so there also may have been ecologically important differences between the areas that were not obvious. We did not compare effects of intrusion frequency (i.e. effects of 1–2 h/week in the Snowy Mountains vs. effects of 5 h/week at Pole Mountain) on singing because differences due to intrusion frequency would not have been distinguishable from effects due to differences in study areas. The projects in the two areas were originally designed and are analyzed herein as separate studies.

RESULTS

Mean singing dates.—For the Snowy Mountains, mean singing dates for the three species did not differ significantly between control and intruded sites during any of the years (Table 1). For Pole Mountain, only the comparison of mean singing dates for Ruby-crowned Kinglet in 1992 was significant, with the mean for intruded sites being 11 days earlier than that for control sites (Table 2). This difference in singing dates indicates that singing activity was curtailed considerably on intruded sites.

Singing activity during two-week periods.—For the Snowy Mountains, the proportions of control and intruded sites at which singing occurred did not differ significantly for any of the two-week periods (Table 3). For Pole Mountain, the proportions of control and intruded sites at which singing occurred did not differ significantly for most of the two-week periods. One exception involved Yellow-rumped Warblers during 1993, for which the proportion of intruded sites with singing during mid-June was 60% lower than that for control sites (Table 4).

Detectable effect sizes.—For t -tests, the minimum detectable differences in mean singing

TABLE 1. Summary statistics for singing dates on control and intruded sites in the Snowy Mountains (1989–1993), with *t* statistics for comparisons of mean dates.

Year	$\bar{x} \pm SE (n)^a$		<i>t</i>	<i>P</i>
	Control	Intruded		
Ruby-crowned Kinglet				
1989	6/15 ± 3.2 (10)	6/17 ± 2.0 (18)	0.54	0.596
1990	6/23 ± 2.9 (8)	6/16 ± 2.4 (16)	1.86	0.077
1991	6/23 ± 3.9 (9)	6/19 ± 1.5 (13)	0.92	0.371
1992	6/21 ± 4.1 (9)	6/13 ± 2.5 (15)	1.72	0.099
1993	6/20 ± 3.7 (8)	6/21 ± 3.3 (17)	0.27	0.790
Yellow-rumped Warbler				
1989	6/21 ± 3.6 (8)	6/13 ± 2.3 (13)	2.09	0.050
1990	6/22 ± 3.8 (9)	6/18 ± 3.1 (18)	0.88	0.390
1991	6/20 ± 4.6 (8)	6/22 ± 2.8 (14)	0.56	0.584
1992	6/18 ± 3.3 (10)	6/15 ± 2.4 (19)	0.74	0.467
1993	6/22 ± 3.6 (10)	6/21 ± 1.8 (18)	0.30	0.767
Dark-eyed Junco				
1989	7/10 ± 1.3 (6)	7/3 ± 3.7 (17)	1.14	0.268
1990	7/7 ± 2.3 (4)	6/28 ± 3.9 (5)	1.92	0.097
1991	6/30 ± 3.0 (8)	6/27 ± 3.4 (13)	0.64	0.528
1992	6/19 ± 2.5 (10)	6/21 ± 2.8 (20)	0.34	0.738
1993	7/1 ± 5.5 (7)	6/27 ± 3.1 (15)	0.71	0.485

^a Mean is average month/day of singing, SE units are days, and *n* = number of sites.

dates (δ) for the Snowy Mountains ranged from 9.2 to 21.4 days, with median values ranging between 10.3 and 19.0 days (Table 5). δ values for Pole Mountain ranged from 8.4 to 23.8 days, with median values ranging between 11.3 and 18.9 days (Table 5). Our analyses enabled us to detect differences this large and larger with an 80% probability. Differences in the seasonal timing of singing on the order of 10 to 20 days or larger therefore would have been readily de-

tected had they occurred, but smaller differences would not have been reliably detectable.

For Fisher exact tests, the minimum detectable differences in proportions of sites with singing activity for the Snowy Mountains ranged from 0.33 to 0.96, with median effect sizes ranging between 0.48 and 0.67 (Table 6). For Pole Mountain, effect sizes were generally larger, ranging between 0.46 and 0.90, with median values ranging between 0.53 and 0.82 (Ta-

TABLE 2. Summary statistics for singing dates on control and intruded sites at Pole Mountain (1991–1993), with *t* statistics for comparisons of mean dates.

Year	$\bar{x} \pm SE (n)^a$		<i>t</i>	<i>P</i>
	Control	Intruded		
Ruby-crowned Kinglet				
1991	6/22 ± 4.0 (9)	6/22 ± 1.9 (8)	0.07	0.942
1992	6/21 ± 3.6 (8)	6/10 ± 2.3 (8)	2.68	0.018 ^b
1993	6/17 ± 3.9 (10)	6/22 ± 6.4 (5)	0.68	0.509
Yellow-rumped Warbler				
1991	6/24 ± 3.9 (9)	6/22 ± 1.7 (9)	0.50	0.623
1992	6/17 ± 2.9 (10)	6/18 ± 1.3 (10)	0.25	0.807
1993	6/22 ± 2.5 (9)	6/19 ± 3.6 (10)	0.74	0.472
Dark-eyed Junco				
1991	6/28 ± 5.2 (8)	6/23 ± 2.7 (9)	0.82	0.424
1992	6/19 ± 3.0 (7)	6/26 ± 5.1 (9)	1.06	0.308
1993	6/22 ± 2.9 (10)	6/27 ± 5.2 (9)	0.83	0.418

^a Mean is average month/day of singing, SE units are days, and *n* = number of sites.

^b Difference is significant at a family-wide $\alpha = 0.10$ after a sequential Bonferroni adjustment.

TABLE 3. Proportions of control and intruded sites on which singing occurred during two-week periods from late May to early August in the Snowy Mountains (1989–1993), with Fisher exact test probabilities (P) for comparisons of proportions.

Year	n	Two-week period	Proportions		P
			Control	Intruded	
Ruby-crowned Kinglet					
1989	10, 18 ^a	1st	0.90	0.83	1.000
		2nd	0.80	0.72	1.000
		3rd	0.60	0.50	0.705
		4th	0.20	0.33	0.669
		5th	0.10	0.17	1.000
1990	8, 16	1st	0.38	0.63	0.390
		2nd	0.75	0.56	0.657
		3rd	0.75	0.31	0.082
		4th	0.38	0.31	1.000
		5th	0.13	0.00	0.333
1991	9, 13	1st	0.67	0.92	0.264
		2nd	0.67	1.00	0.055
		3rd	0.33	0.77	0.079
		4th	0.44	0.31	0.662
		5th	0.22	0.15	1.000
1992	9, 15	1st	0.78	0.73	1.000
		2nd	0.44	0.73	0.212
		3rd	0.67	0.47	0.423
		4th	0.33	0.13	0.326
		5th	0.22	0.20	1.000
1993	8, 17	1st	0.88	0.76	1.000
		2nd	0.75	0.59	0.661
		3rd	0.38	0.35	1.000
		4th	0.25	0.24	1.000
		5th	0.13	0.12	1.000
Yellow-rumped Warbler					
1989	8, 13	1st	0.63	0.85	0.325
		2nd	0.38	0.31	1.000
		3rd	0.75	0.31	0.080
		4th	0.38	0.08	0.253
		5th	0.00	0.00	— ^b
1990	9, 18	1st	0.44	0.61	0.448
		2nd	0.67	0.61	1.000
		3rd	0.67	0.22	0.039
		4th	0.56	0.28	0.219
		5th	0.00	0.00	—
1991	8, 14	1st	0.75	0.36	0.183
		2nd	0.63	0.79	0.624
		3rd	0.50	0.43	1.000
		4th	0.63	0.43	0.659
		5th	0.25	0.00	0.121
1992	10, 19	1st	0.40	0.58	0.450
		2nd	0.80	0.79	1.000
		3rd	0.70	0.53	0.449
		4th	0.40	0.32	0.698
		5th	0.00	0.05	1.000
1993	10, 18	1st	0.60	0.72	0.677
		2nd	0.70	0.61	0.703
		3rd	0.60	0.78	0.400
		4th	0.10	0.22	0.626
		5th	0.10	0.00	0.357
Dark-eyed Junco					
1989	6, 17	1st	0.17	0.12	1.000
		2nd	0.50	0.29	0.621

TABLE 3. Continued.

Year	n	Two-week period	Proportions		P
			Control	Intruded	
1990	4, 5	3rd	1.00	0.47	0.048
		4th	1.00	0.53	0.058
		5th	0.67	0.29	0.162
		1st	0.00	0.20	1.000
		2nd	0.50	0.40	1.000
		3rd	0.75	0.40	0.524
		4th	0.50	0.40	1.000
1991	8, 13	5th	0.25	0.00	0.444
		1st	0.25	0.38	0.656
		2nd	0.50	0.31	0.646
		3rd	0.50	0.46	1.000
		4th	0.63	0.54	1.000
1992	10, 20	5th	0.13	0.00	0.381
		1st	0.50	0.45	1.000
		2nd	0.70	0.55	0.694
		3rd	0.80	0.55	0.246
		4th	0.50	0.55	1.000
1993	7, 15	5th	0.10	0.05	1.000
		1st	0.57	0.60	1.000
		2nd	0.29	0.33	1.000
		3rd	0.43	0.40	1.000
		4th	0.43	0.53	1.000
		5th	0.29	0.13	0.565

^a Sample size for control, intruded sites.

^b No test was conducted because singing did not occur on any of the sites during the two-week period.

ble 6). Thus, only moderate or large differences in proportions were detectable 80% of the time.

Habitat features.—None of the habitat components differed significantly among treatment groups at the Snowy Mountains sites ($P_s = 0.167$ to 0.987) or at the Pole Mountain sites ($P_s = 0.135$ to 0.997). Habitat features were not confounded with treatment groups, so we attributed between-group differences in the seasonal timing of singing to the intrusion treatments.

DISCUSSION

Detectable effect sizes.—With a high probability, our analyses would have enabled us to detect large and medium-size differences in the seasonal timing of primary song, had they occurred. We were not able to detect small differences (less than about 10 days for mean singing dates, or less than about 0.35 for proportions of sites at which singing occurred) reliably; consequently, we cannot be confident that small differences did not occur. Many of the tests we conducted were not statistically significant because differences were either small or non-existent. Because the minimum detectable effect

TABLE 4. Proportions of control and intruded sites on which singing occurred during two-week periods from late May to early August at Pole Mountain (1991-1993), with Fisher exact test probabilities (P) for comparisons of proportions.

Year	n	Two-week period	Proportions		P
			Control	Intruded	
Ruby-crowned Kinglet					
1991	9, 8 ^a	1st	0.78	0.88	1.000
		2nd	0.44	0.75	0.335
		3rd	0.67	0.88	0.576
		4th	0.56	0.38	0.637
		5th	0.11	0.13	1.000
1992	8, 8	1st	0.63	0.88	0.569
		2nd	0.38	0.75	0.315
		3rd	0.63	0.25	0.315
		4th	0.38	0.00	0.200
		5th	0.13	0.00	1.000
1993	10, 5	1st	0.70	0.80	1.000
		2nd	0.60	0.80	0.600
		3rd	0.40	0.80	0.282
		4th	0.50	0.40	1.000
		5th	0.10	0.00	1.000
Yellow-rumped Warbler					
1991	9, 9	1st	0.67	0.67	1.000
		2nd	0.67	0.89	0.576
		3rd	0.56	1.00	0.082
		4th	0.44	0.44	1.000
		5th	0.00	0.11	1.000
1992	10, 10	1st	0.90	1.00	1.000
		2nd	0.70	0.80	1.000
		3rd	0.70	0.90	0.582
		4th	0.20	0.30	1.000
		5th	0.00	0.00	— ^b
1993	9, 10	1st	0.56	0.80	0.350
		2nd	1.00	0.40	0.011 ^c
		3rd	0.78	0.60	0.628
		4th	0.78	0.40	0.170
		5th	0.00	0.00	—
Dark-eyed Junco					
1991	8, 9	1st	0.50	0.56	1.000
		2nd	0.38	0.56	0.637
		3rd	0.75	0.78	1.000
		4th	0.38	0.56	0.637
		5th	0.13	0.00	0.471
1992	7, 9	1st	1.00	0.44	0.034
		2nd	0.57	0.44	1.000
		3rd	0.71	0.44	0.358
		4th	0.29	0.44	0.633
		5th	0.14	0.11	1.000
1993	10, 9	1st	0.40	0.33	1.000
		2nd	0.70	0.22	0.070
		3rd	0.80	0.56	0.350
		4th	0.50	0.78	0.350
		5th	0.20	0.00	0.474

^a Sample size for control, intruded sites.

^b No test was conducted because singing did not occur on any of the sites during the two-week period.

^c Difference is significant at a family-wide $\alpha = 0.10$ after a sequential Bonferroni adjustment.

TABLE 5. Minimum detectable effect sizes (δ), in days, for *t*-tests of differences in mean singing dates between control and intruded sites for the Snowy Mountains (1989-1993) and Pole Mountain (1991-1993).

Species	α	Median (range) for δ
Snowy Mountains		
Ruby-crowned Kinglet	0.020	13.4 (11.9-18.5)
	0.100	10.3 (9.2-14.2)
Yellow-rumped Warbler	0.020	14.2 (12.1-17.5)
	0.100	10.8 (9.3-13.5)
Dark-eyed Junco	0.020	19.0 (14.5-21.4)
	0.100	13.7 (11.2-16.4)
Pole Mountain		
Ruby-crowned Kinglet	0.033	16.2 (14.2-23.8)
	0.100	13.0 (11.4-19.0)
Yellow-rumped Warbler	0.033	14.0 (10.4-14.7)
	0.100	11.3 (8.4-11.9)
Dark-eyed Junco	0.033	18.9 (18.7-21.2)
	0.100	15.3 (15.1-17.0)

sizes were intermediate or large in magnitude, our results represent a conservative estimate of the effects of intrusion. The effect-size calculations support the conclusion that the intrusions typically did not induce moderate or large changes in the seasonal timing of primary song.

Mean singing dates.—Primary song by Ruby-crowned Kinglets at Pole Mountain in 1992 was an average of 11 days earlier on intruded sites than it was on control sites. Compared with males on control sites, those on intruded sites

TABLE 6. Minimum detectable effect sizes, in proportions, for Fisher exact probability tests of differences between proportions of control and intruded sites on which singing occurred in the Snowy Mountains (1989-1993) and at Pole Mountain (1991-1993).

Species	α	Median (range) for effect sizes
Snowy Mountains		
Ruby-crowned Kinglet	0.020	0.62 (0.53-0.74)
	0.100	0.48 (0.33-0.58)
Yellow-rumped Warbler	0.020	0.59 (0.48-0.77)
	0.100	0.50 (0.38-0.65)
Dark-eyed Junco	0.020	0.67 (0.49-0.96)
	0.100	0.55 (0.38-0.84)
Pole Mountain		
Ruby-crowned Kinglet	0.020	0.82 (0.70-0.84)
	0.100	0.67 (0.46-0.78)
Yellow-rumped Warbler	0.020	0.68 (0.64-0.79)
	0.100	0.53 (0.48-0.70)
Dark-eyed Junco	0.020	0.73 (0.63-0.90)
	0.100	0.57 (0.46-0.88)

sang mostly during the early part of the study season. The intrusions may have displaced individuals, caused them to sing less, or both. Because of the central role of primary song in avian breeding biology, we hypothesize that there would be fewer territories, nests, and young on intruded sites, and that the quality of such sites for producing subsequent breeders would be reduced.

Singing activity during two-week periods.—For the Snowy Mountains, no individual differences between proportions of control and intruded sites with singing were statistically significant, and most of the differences were small in magnitude. For Pole Mountain, the significant effect for Yellow-rumped Warbler in 1993 suggests that intrusion displaced individuals, altered their singing behavior, or both during the second two-week period (mid-June). Considering these effects, intruded sites during this time interval may have been less valuable than were control sites for producing viable young and individuals that learned their species-specific songs.

Implications.—Most of the differences observed were not statistically significant, implying intrusion had few important effects on the seasonal timing of primary song. But, depending on the ecological context, spatial scale, frequency and duration of intrusion, and the outcomes of an individual's prior experiences with human intruders, species and individuals are likely to react to intrusion in different ways (Gutzwiller 1991, 1993; Knight and Temple 1995). Responses to intrusion among species, within a species among years, and even within species during a single season are, consequently, often inconsistent (Gutzwiller et al. 1994, Knight and Temple 1995, Riffell et al. 1996). Based on the known functions of primary song, it is reasonable to expect a link between changes in the seasonal timing of primary song and reduced quality of sites for reproduction or song learning. For these reasons, and because our results are conservative, it would be prudent for avian ecologists to continue to examine intrusion as a potentially important form of disturbance. In this way, a more thorough understanding of the factors influencing avian breeding biology in human-dominated systems will develop. That our experiments induced few large effects is, in itself, an important result because it helps define the range of intrusion intensity that may influence the seasonal timing of primary song and related breeding events.

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