REPEATED HUMAN INTRUSION AND THE POTENTIAL FOR NEST PREDATION BY GRAY JAYS

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Abstract: Through attraction of avian nest predators, human activity near nests is known to cause lower nesting success or nest failure in some species. This is a significant conservation issue because many wildlands are subjected to repeated intrusion by recreationists, ecotourists, and other user groups during avian breeding seasons. Yet, wildlife scientists still have limited knowledge about the extent to which repeated human intrusion attracts avian nest predators. We studied this topic in subalpine forest in Wyoming, USA, and experimented with the gray jay (*Perisoreus canadensis*), a nest predator that is known to approach recreationists. During 1989–1993, we implemented intrusions within 20 circular 1-ha (113-m-diam) sites for 1 or 2 hr each week during a 10-week period when potential passerine prey were breeding. Simultaneously, 10 circular 1-ha control sites did not receive experimental intrusions. The average number of gray jays on intruded sites was higher than that on control sites by 156% (1989), 225% (1990), 59% (1991), 13% (1992), and 29% (1993). The probability of gray jay recurrence on intruded sites was higher than that on control sites by 125% (1989), 300% (1990), 20% (1991), 33% (1992), and 20% (1993). By increasing the number and recurrence of gray jays, relatively low levels of repeated intrusion can increase the potential for nest predation by gray jays. We caution that additional work is necessary to assess whether attraction of gray jays actually leads to increased nest predation. Knowledge of when intrusion does and does not attract gray jays is important because information about both events is necessary to define the levels and circumstances of intrusion that are influential. Wildlife managers can use knowledge about intrusion-induced attraction of avian nest predators to help decide whether or how recreational activity in wildlands should be managed.

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Human intrusion is a widespread form of disturbance that involves the simple presence of people in the environment (Gutzwiller et al. 1994). In many wildlands, even in some protected and remote locations, birds are subjected to intrusion by recreationists, ecotourists, and other user groups (Boyle and Samson 1985, Woehler et al. 1994). Some birds experience repeated intrusion over the course of weeks or months, and it occurs in habitats and during periods that are crucial for reproduction and survival (Burger 1986, Burger and Gochfeld 1991, Burger et al. 1995). The impacts that intrusion can have on bird behavior, distributions, reproduction, and survival have become increasingly apparent during recent years (Knight and Gutzwiller 1995). Yet, conservationists still have rather limited knowledge about the extent to which repeated human intrusion attracts avian nest predators.

This is an important issue because repeated human intrusion is common in many natural areas (Purdy et al. 1987), and intrusion-induced attraction of avian nest predators can seriously exacerbate predation on eggs and nestlings (Kury and Gochfeld 1975, Anderson and Keith 1980, Strang 1980). Investigator presence near nests can induce significant impacts on nest success through predation by larids or corvids (Götmark 1992). These effects have been documented most frequently for colony-nesting birds and waterfowl that nest in relatively open habitats, but they also have been reported for non-colonial species that nest in dense vegetation, such as the willow warbler (*Phylloscopus trochilus*; Tiainen 1983) and mourning dove (*Zenaida macroura*; Westmoreland and Best 1985). Such impacts also may be caused by other types of human intrusion (e.g., wildlife viewing and photography, ecotourism) whose frequency, duration, and proximity to nests are comparable to those of nest-investigator disturbance (Gutzwiller 1995).

It is not known whether human intrusion that occurs repeatedly over weeks or months displaces or attracts avian nest predators. If repeated intrusion increases the number of individual predators that visit a site, the potential for predation would be higher there than it would be in comparable areas with fewer predator individuals. The potential for

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predation also would be higher if intrusion increases the probability of predator recurrence in an area.

We studied whether the number of predators and predator recurrence were influenced by repeated intrusion in subalpine forest. This vegetation type supports many potential prey species (DeGraaf et al. 1991), and it occurs in numerous parks, national forests, and other natural areas in the Rocky Mountain region of the western United States, which is used extensively by outdoor recreationists and ecotourists during avian breeding periods (Youmans 1999).

We assessed whether human intrusions attracted gray jays. This is an appropriate species for analysis of whether repeated intrusion from recreationists can heighten the potential for predation in subalpine forests because it preys on eggs and nestlings (Ouellet 1970, Strickland and Ouellet 1993), it preys on species that breed in Rocky Mountain subalpine forests (Ouellet 1970, Kingery and Kingery 1995), and, unlike other avian nest predators, gray jays often are attracted to recreationists (DeGraaf et al. 1991). It has long been known that gray jays will watch and follow people, but we are not aware of any study of whether this predator is attracted by repeated intrusion.

In many natural areas, relatively low levels of repeated human intrusion are more common than are high levels of intrusion (Gutzwiller et al. 1994), so we assessed whether low levels of intrusion attracted gray jays. Specifically, we examined the effects of 1 or 2 hr of intrusion by 1 person each week for 10 weeks during the breeding seasons of potential prey species. In intensity and frequency, our intrusions were comparable to the relatively low levels of intrusion generated by solitary hikers, anglers, backpackers, wildlife photographers, and ecotourists. The intrusion levels we studied were lower than those associated with more disruptive activities such as group camping and nature tours, mountain bike competitions, and off-road vehicle events (Gutzwiller and Anderson 1999).

As a first step in assessing whether human intrusion can increase the potential for nest predation by gray jays, we tested the following hypotheses: repeated intrusion can increase the average number of gray jays that visit a site, and repeated intrusion can increase the probability of gray jay recurrence at a site.

STUDY AREA

We collected data approximately 70 km WNW of Laramie, Wyoming, USA (41°32′N, 106°20′W) in subalpine forests of the Snowy Mountains. Elevations, dominant plant species, and weather data for the study area are presented in Gutzwiller et al. (1997). Common potential prey species whose nests were accessible to gray jays were the American robin (*Turdus migratorius*), hermit thrush (*Catharus guttatus*), ruby-crowned kinglet (*Regulus calendula*), yellow-rumped warbler (*Dendroica coronata*), and dark-eyed junco (*Junco hyemalis*).

METHODS

Establishment of Experimental Sites

We randomly established 30 circular 1-ha (56.4-m-radius) sites during May 1989. Sites were an average of 0.7 km apart and were 0.4 km from a narrow dirt road that carried infrequent (0–2 vehicles/hr), low-speed vehicular traffic. The same 30 sites were used during 1989–1993. We used a permanent transect from the road to the site center to access each site.

Intrusion Treatments

During May 1989, we randomly assigned intrusion and control treatments to the 30 1-ha sites; during the entire study, each site received the same treatment that it was originally assigned during May 1989. Five sites received 1 intrusion treatment/week (F1) within the inner 25% (S25) of the 1-ha site; 5 sites received 2 intrusion treatments/week (F2) within the inner 25% of the 1-ha site; 5 sites received 1 intrusion treatment/week throughout 100% (S100) of the 1-ha site; 5 sites received 2 intrusion treatments/week throughout 100% of the 1-ha site; and 10 control sites did not receive any intrusion treatments.

F1 treatments were implemented on Wednesdays, and F2 treatments were administered on Mondays and Fridays so that treatments would not coincide with gray jay sampling, which occurred on Tuesdays and Thursdays. Within intrusion-frequency groups (F1 and F2), the initial order in which sites were treated was assigned randomly. We rotated this order each new intrusion day so that each site was intruded an equal number of times during various times of day each study season. Intrusion treatments were initiated between 0800 and 0900 hr and completed by mid-afternoon. The treatment schedule was identical during all 5 years and lasted 10 weeks from late May to early August.

An intrusion treatment was implemented by 1 person and was started at the marked perimeter of the 1-ha site. The person walked to the marked site center and then walked through the site in a

radial pattern from the center to the perimeter and back again, shifting the path of movement approximately 40° after each return to the site center. Each single treatment lasted 1 hr, during which the specified area was covered twice. During intrusion treatments, technicians did not try to conceal themselves, and clothing color was not restricted. Technicians faced and directly approached all gray jays detected near their radial lines of movement during intrusion treatments. Technicians did not otherwise attempt to elicit responses from gray jays. Except for occasional slight noises caused by movements through vegetation, technicians did not make any noises during treatments. Details about weather conditions during treatments, the number of technicians who implemented treatments, and the absence of treatment-induced vegetation changes are provided in Gutzwiller and Anderson (1999).

During the experiments, we recorded a few brief instances (probably lasting <2–3 min) of human disturbance other than our treatments on 1 or 2 of the treated sites. The duration of these disturbances was negligible compared to the 10 or 20 hr of intrusion administered each year on F1 and F2 sites, respectively, and bird data were not influenced by these events (Gutzwiller et al. 1994). Each year, technicians spent about 620 person-hr at the experimental sites and in adjacent areas during daily periods when people typically traveled along the roads; we would therefore have easily detected people on or near our sites. Thus, any disturbances that we did not detect were probably minor and inconsequential for our experiments (Gutzwiller et al. 1994).

Gray Jay Sampling

All data for our analysis were based on initial detections of gray jays during 15-min unlimited-distance counts (Ralph et al. 1995) completed between 0600 and 1200 hr. Technicians began recording the presence of gray jays inside and outside the 1-ha site as soon as they reached the marked 1-ha perimeter. Technicians continued to record data as they proceeded quietly and directly toward the site center where they completed the 15-min count. Typically, about 14 min of the 15-min count were spent standing at the site center. Using the timing and location of auditory and visual cues, and considering possible unseen movements, technicians recorded only those individuals they knew were distinct. Weather conditions during sampling and the number of technicians involved in sampling were the same as those reported previously for related studies (Gutzwiller and Anderson 1999).

Half of the sites were sampled on Tuesdays and half on Thursdays each week during a 10-week period from late May to early August each year. On each sampling day, each technician sampled an equal number of control and intruded sites so that possible differences in technician abilities, weather conditions, or other factors would not generate biases in inferences about treatment effects. The initial order in which sites were sampled was randomized, and this order was rotated each new sample day to preclude time-of-day and seasonal biases. Technicians wore dark drab clothing so as not to repel or attract birds (Gutzwiller and Marcum 1997). The sampling schedule and protocol were identical during each of the 5 years of the experiment. The technicians were not aware of the hypotheses we tested.

Habitat Features

Vegetation features can influence distributions of corvids and other avian nest predators (Miller et al. 1998, Sieving and Willson 1998). If differences in habitat features were confounded with treatment groups, effects of intrusions on gray jay numbers and probability of recurrence would not be distinguishable from those caused by habitat conditions. We measured 19 habitat variables at 2 spatial scales and found that none of the variables differed significantly between control and intruded sites during the 5-year period (details in Gutzwiller et al. 1997), indicating that habitat conditions were not confounded with treatment groups. Consequently, we considered intrusion treatments to be the cause of between-group differences in gray jay numbers and probability of recurrence.

Statistical Analyses

Response Variables and Experimental Unit.—For each year separately, we used the 10 unlimited-distance bird counts at each site to compute a site average for the number of gray jays, and to determine whether gray jays recurred on a site. Gray jays recurred at a site during a given year if at least 1 gray jay was detected on ≥2 weekly counts, otherwise recurrence did not occur. The experimental unit was a site, not an individual observation of a bird.

Hypotheses and Significance Level.—Our gray jay research was part of a broader project designed to test a priori orthogonal contrasts for various species. For the present analysis, however, we

were interested in testing only the orthogonal contrast for the general intrusion effect, which involved comparing a response variable between control sites (n = 10) and all intruded sites collectively (n = 20). Analysis of variance (ANOVA) indicated that mean number of gray jays did not differ among the 4 groups of intruded sites during any year ($F_{3, 16}$ = 0.37–1.68, P = 0.211–0.773), and contingency χ^2 analyses indicated that the proportion of sites with recurrence did not differ among the 4 groups during any year (likelihood ratio χ^2 = 1.73–4.06, df = 3, P = 0.255–0.631). We tested the following 1-tailed hypotheses: the average number of gray jays was higher on intruded sites than it was on control sites, and the probability of recurrence of gray jays was higher on intruded sites than it was on control sites.

These 2 hypotheses constituted a "family" (sensu Miller 1981:34) of simultaneous hypotheses because both response variables addressed gray jay reactions to intrusion. We tested this family of hypotheses for each year separately. We used an a priori family-wide α of 0.10 to reduce the chance of Type II errors (Westmoreland and Best 1985, Thompson and Schwalbach 1995), and within each family of hypotheses, we applied the sequential Bonferroni technique (Rice 1989) to control Type I errors.

Average Number of Gray Jays.—We tested for between-group differences in average number of gray jays with Student's t-test. To meet this test's assumptions of normality and equal variances (Ott 1993:268), we applied a $\log_{10}$ (Y+1) transformation (Zar 1999:275) to the data. If the equal-variance assumption was not met after applying this transformation, we tested for differences using Welch's t-test, which does not assume equal variances (Ott 1993:269). For average number of gray jays, the t and associated P-values reported below are based on transformed data, but the values of summary statistics we supply are for untransformed data. For reasons explained previously (Gutzwiller et al. 1997, Gutzwiller and Anderson 1999), we did not use repeated-measures ANOVA or combine data across years and conduct a single standard ANOVA. Using a separate t-test for each year, we did not have to make any untenable or questionable assumptions, and no pseudoreplication occurred within or among years.

Probability of Recurrence.—We tested for between-group differences in the probability of gray jay recurrence using the χ^2 statistic for −2 Log L from logistic regression (Hosmer and Lemeshow 1989:15–17; SAS Institute 1989:1075, 1089). For each logistic regression analysis, the response variable for a site was coded as either a 1 (recurrence occurred) or 0 (recurrence did not occur); the explanatory variable was treatment and each site was coded as either a 1 (intruded) or 0 (control). In logistic regression, aberrantly large standard errors (SE) for regression coefficients signal important numerical problems (Hosmer and Lemeshow 1989:126); the SE of coefficients for our analyses were not large, indicating no numerical problems occurred in our study.

Among-site Relations.—Strickland and Ouellet (1993) estimated internest distances for gray jays to be about 0.9 km (Quebec) and 1.3 km (Ontario), and they cited other approximate internest distances of 0.6 km (Alberta) and 1.0 km (interior Alaska). If one assumes that gray jay nests lie at the center of adjoining territories whose shapes are roughly hexagonal, as Strickland and Ouellet (1993) did to estimate internest distances, the simple average of these 4 distances, which rounds to 1 km, can be used as a general estimate of the diameter of gray jay territories. Our experimental sites averaged 0.7 km apart, so more than 1 of them could have occurred within a 1-km diameter (0.5-km radius) territory. It is therefore possible that the number of gray jays at a given experimental site may have been positively or negatively associated with that at other experimental sites within a territory.

To determine whether such relations were influential in our study, we tested—for each year separately—whether the average number of gray jays and the probability of recurrence on a given experimental site (focal site) were associated significantly (a priori α = 0.10) with average number of gray jays on the nearest experimental site within 0.5 km (NEAR), and the collective average number of gray jays on the set of non-focal experimental sites within 0.5 km (SET). The test statistic for average number of gray jays was Spearman's rank correlation coefficient, and the test statistic for the probability of recurrence was the χ^2 statistic for −2 Log L.

When significant relations with NEAR and SET were detected, we used least-squares regression (for average number of gray jays) and logistic regression (for probability of recurrence) to control analytically for these associations and assess whether our conclusions about intrusion effects were the same as those obtained without controlling for NEAR and SET. All assumptions for Spearman's rank correlation (Zar 1999:395), least-squares regression (Ott 1993:525), and logis-

tic regression (Hosmer and Lemeshow 1989:7–9) were met.

Timing of Gray Jay Detections.—Gray jay sampling occurred 1, 3, or 6 days after human-intrusion treatments each week. Our project was not designed to assess whether gray jay attraction varied with time since intrusion. However, for those years during which significant attraction was evident, knowledge of how long after treatments gray jays were detected at intruded sites would be valuable in judging whether the effects of intrusion lasted beyond the intrusion events themselves. We estimated the average number of days after intrusions each week that gray jays were detected on intruded sites by calculating a weighted average of the number of 1-, 3-, and 6-day (elapsed-time) counts during which at least 1 gray jay was detected.

RESULTS

Average Number of Gray Jays.—The average number of gray jays on intruded sites was higher than that on control sites during all 5 years (Fig. 1), but the percent differences in these averages (156% [1989], 225% [1990], 59% [1991], 13% [1992], and 29% [1993]) generally decreased during the 5-year period. Intrusion effects were significant during the first 2 years but not during the last 3 years (Table 1). For those years with significant intrusion effects, the average number of gray jays (for all 10 weeks of each study season combined) per control site and per intruded site, respectively, was 0.90 and 2.30 (1989), and 0.60 and 1.95 (1990). Therefore, relative to control sites, the average number of additional gray jays per site on intruded sites was 1.40 (1989) and 1.35 (1990).

Probability of Recurrence.—For all 5 years, the probability of recurrence on intruded sites was higher than that on control sites (Fig. 2). However, the percent differences in these probabilities (125% [1989], 300% [1990], 20% [1991], 33% [1992], 20% [1993]) reflected a general decline in intrusion effect. Paralleling this trend, the probability of recurrence on control and intruded sites differed significantly during 1989 and 1990 but not during the last 3 years (Table 1).

Table 1. Results of 1-tailed statistical tests for differences between control sites (n = 10) and intruded sites (n = 20) in average number of gray jays and probability of recurrence, Snowy Mountains, Wyoming, USA, 1989–1993.

	Average number of gray jays			Probability of recurrence	
Year	t[a]	df[b]	P	χ^2[c]	P
1989	−2.35	26.7	0.013*	1.90	0.084*
1990	−3.24	27.1	0.002*	3.23	0.036*
1991	−1.57	28	0.063	0.27	0.302
1992	−0.54	15.4	0.297	1.32	0.125
1993	−0.96	28	0.173	0.27	0.302

[a] Negative t-statistics indicate that the average number of gray jays for intruded sites was larger than that for control sites.
[b] Non-integer df are reported for Welch's t-test.
[c] df = 1 for all tests.
* P was significant after a sequential Bonferroni adjustment of the family-wide α (0.10).

Among-site Relations.—No negative associations between the average number of gray jays at focal experimental sites and NEAR or SET emerged, but we did detect positive associations between average number of gray jays and NEAR for 1989, 1991, and 1992, and SET for 1992. Similarly, no negative associations occurred between the probability of recurrence at focal experimental sites and NEAR or SET, but we found positive associations with NEAR for 1989, 1991, and 1992, and with SET for 1991 and 1992. When we controlled

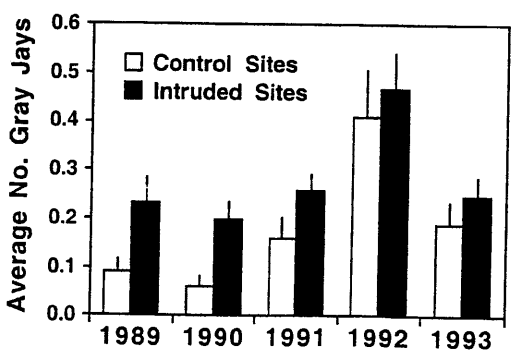

Fig. 1. Average number of gray jays (individuals per count per site; + SE) on control sites (n = 10) and intruded sites (n = 20) in the Snowy Mountains, Wyoming, USA, 1989–1993.

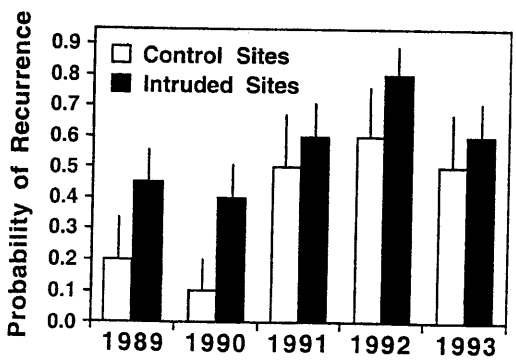

Fig. 2. Probability of gray jay recurrence (+ SE) on control sites (n = 10) and intruded sites (n = 20) in the Snowy Mountains, Wyoming, USA, 1989–1993.

for these relations via regression, we found that our conclusions about intrusion effects were the same as those based on the initial t and χ^2 statistics (i.e., the results without controlling for NEAR and SET), indicating that the among-site relations in number of gray jays did not influence the outcome of our experiments.

Timing of Gray Jay Detections.—During the 2 years for which we found significant intrusion effects, gray jays were detected on intruded sites an average of 2.9 days (1989) and 2.8 days (1990) after intrusions were administered.

DISCUSSION

Intrusion Effects

The higher gray jay numbers and probability of recurrence on intruded sites during 1989 and 1990 indicate that gray jays were attracted during these years by the experimental intrusions. These differences were associated with detections of gray jays on intruded sites that occurred an average of almost 3 days after the intrusions, indicating that the attraction effect of intrusion lasted beyond the intrusion events themselves.

It is reasonable to expect that the potential for avian nest predation at a site depends in part on the number of predators that are attracted and the extent to which they recur. If repeated human intrusion attracts gray jays to sites, periods during which predators are present are lengthened, and opportunities for nest detection and predation increase accordingly. These opportunities may be purely incidental to gray jay attraction; that is, one need not assume that gray jays follow recreationists in anticipation of finding nests or young that recreationists might view, photograph, or inadvertently disturb.

The significant differences in gray jay numbers between control and intruded sites were not large in terms of the absolute number of individuals per site. We hypothesize, however, that such differences may be biologically important because the average differences were evident for 10-week periods during 2 consecutive passerine breeding seasons; a single gray jay can prey upon multiple nests; nest predation by another corvid (common raven [*Corvus corax*]) has been shown to be substantially higher than what would be expected from its relative density (Andrén 1992); and there is potential for gray jay attraction to occur over a large geographic area because repeated human intrusion occurs in many Rocky Mountain subalpine forests.

Explanations for Intrusion Effects

Several explanations for the attraction patterns we observed seem possible, but we consider the following explanation to be more plausible than those described in other paragraphs of this section. Attraction may have declined during the study (Figs. 1, 2) because, during successive years of unrewarded approaches to experimental intruders, the proportion of gray jays living on and around our study sites that became disinterested in the intruders increased.

One could argue that the attraction effects we observed occurred because, during 1989 and 1990 but not during 1991–1993, more intruded sites occurred within or near gray jay territories than did control sites. However, we randomly established the experimental sites, and we randomly assigned treatments to sites. Consequently, control and intruded sites were dispersed randomly with respect to environmental conditions that would be important to territory establishment. This point is supported by our finding that various habitat conditions at different spatial scales did not differ significantly between control and intruded sites during the 5-year study (see Habitat Features). Thus, it is unlikely that our results were caused by nonrandom (between-group) differences in the spatial arrangement of experimental sites and gray jay territories.

Gray jays could have been rewarded with food by persons not involved in our study prior to traversing our study sites. Such experiences would reinforce attraction, and this behavior may have been temporarily elicited anew by the mere sight of technicians during sampling periods. For this to be a reasonable explanation for the results we found, such events would have had to occur many times and primarily on intruded sites. Yet, both control and intruded sites were sampled each sampling day of each week, control and intruded sites were sampled the same number of times each year, and technicians did not reinforce attraction behavior during sampling (or at any other time) at any site. Because many vegetation conditions on control and intruded sites did not differ (see Habitat Features), technicians also were probably equally visible during counts on control and intruded sites. Our study sites were rarely used by persons other than the technicians (see Intrusion Treatments). Our study area and adjacent locales were equally accessible to people during all 5 years, but the attraction response was strong during only the first 2 years. Therefore, it is difficult to believe that attraction to technicians

during sampling, induced by food rewards from others in or near our study area, caused the patterns we observed.

Perhaps between-group differences in gray jay numbers prior to the experiments are responsible for our results. Gray jay numbers probably are determined largely by habitat features and associated conditions. Mean number of gray jays was significantly correlated with an average of about 4 habitat variables per year (r_S = –0.601 to 0.307, df = 28, P < 0.001–0.099). But there were no between-group differences in these and other variables (see Habitat Features), and each year, there would have been negligible (if any) change in these variables between the time we measured them and the time prior to our experiments. Furthermore, between-group differences in conditions not represented by or not correlated with the habitat features we studied were improbable before and during experiments because we randomly selected the study sites and randomly assigned treatments to the sites. The effectiveness of this randomization was confirmed by the absence of significant between-group differences in the habitat features we studied. Thus, significant between-group differences in the number of gray jays prior to the experiments were unlikely.

The movement of technicians during intrusion treatments may have conditioned some gray jays on intruded sites to behave a certain way (e.g., increase or decrease vocalizations, move toward or away from humans) whenever they detected a person. The same individuals may thus have been induced to behave similarly when they detected a technician during sampling. Such a "training" effect could have influenced gray jay detectability on intruded sites and consequently the outcome of our analyses. These potential problems were unlikely for 2 reasons. First, analyses indicated that sampling did not generate differences among treatment groups in gray jay vocalization rates (Riffell et al. 1996). Second, no training could have occurred because technicians did not feed or otherwise directly reinforce attraction behavior on or around experimental sites during intrusion treatments, sampling periods, or any other times.

Our observations indicate that the counts themselves were not influential (Gutzwiller and Anderson 1999). Dense vegetation, direct and quiet movement toward the site center, technicians' dark drab clothing, and no technician noises or movements for approximately 14 min after the site center was reached probably account for this lack of sampling effect. We believe that biases stemming from sampling-induced reactions by individual birds that may have been sensitized during treatments were negligible, if present at all (Riffell et al. 1996, Gutzwiller et al. 1997). In addition, all sites were sampled 10 times each year with the same technique, so any undetected sampling effect on bird behavior would have been balanced between control and treated sites and would not have biased the assessment of intrusion effects.

Potential and Actual Predation

It is important to distinguish between predation risk and actual nest predation. We did not study the effects of gray jay attraction on nest predation, and we emphasize that additional research is necessary to determine whether higher numbers and recurrence of gray jays actually result in higher rates of nest predation.

MANAGEMENT IMPLICATIONS

The gray jay has been widely identified as a passerine nest predator (e.g., Bent 1964, Ouellet 1970, Kingery and Kingery 1995, Sieving and Willson 1998, Rangen et al. 2001). Strickland and Ouellet (1993:4) indicated that gray jay predation on eggs and nestlings is common, and even juvenile gray jays are capable of predatory behavior (Barnard 1996). These various observations, coupled with our finding that repeated intrusion can attract gray jays, indicate that management-based analyses of gray jay responses to intrusion are warranted. We recommend that serial management experiments (Gutzwiller 1993) be conducted to determine whether intrusion by wildland recreationists induces actual nest predation by gray jays.

Because the degree of gray jay attraction at intruded sites varied among years (Figs. 1, 2; Table 1), results for any 1 or 2 years of our study did not represent what occurred during the 5-year period. Thus, studies lasting only 1 or 2 years may not accurately characterize longer-term effects of intrusion on gray jay attraction (compare Wiens 1981). Management decisions sometimes must be formulated from 1- or 2-year field studies, but we recommend on the basis of our results that, whenever feasible, conservationists conduct management experiments that span longer periods of time. Data on when intrusion does and does not attract gray jays, such as those we have reported here, are important because information about both events is necessary to define the levels and circumstances of intrusion that are influential. Long-term experimental studies of recreational impacts are likely to pro-

vide the most defensible data for establishing management policies (Gutzwiller 1993).

Avian responses to intruders often vary among locations, years (as during our study), and individuals within a population, as well as with such factors as time of year, vegetation conditions, and prior experiences with humans (Knight and Gutzwiller 1995). Thus, even within a species, it is not safe to assume that intrusion effects (or lack thereof) for 1 set of conditions will necessarily apply to another set of conditions. It would not be wise, for example, to consider our results and assume for another area that after 2 consecutive years of repeated intrusion, few or no effects on gray jay attraction will occur. Before devising and implementing policies that would limit human use of subalpine forests in the Rocky Mountain region, managers should determine whether gray jay attraction generates a nest-predation problem for their particular set of circumstances.

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LITERATURE CITED

ANDERSON, D. W., AND J. O. KEITH. 1980. The human influence on seabird nesting success: conservation implications. Biological Conservation 18:65–80.

ANDRÉN, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology 73:794–804.

BARNARD, W. H. 1996. Juvenile gray jay preys upon magnolia warbler. Journal of Field Ornithology 67:252–253.

BENT, A. C. 1964. Life histories of North American jays, crows, and titmice. Volume 1. Dover Publications, New York, USA.

BOYLE, S. A., AND F. B. SAMSON. 1985. Effects of nonconsumptive recreation on wildlife: a review. Wildlife Society Bulletin 13:110–116.

BURGER, J. 1986. The effect of human activity on shorebirds in two coastal bays in northeastern United States. Environmental Conservation 13:123–130.

———, AND M. GOCHFELD. 1991. Human distance and birds: tolerance and response distances of resident and migrant species in India. Environmental Conservation 18:158–165.

———, ———, AND L. J. NILES. 1995. Ecotourism and birds in coastal New Jersey: contrasting responses of birds, tourists, and managers. Environmental Conservation 22:56–65.

DEGRAAF, R. M., V. E. SCOTT, R. H. HAMRE, L. ERNST, AND S. H. ANDERSON. 1991. Forest and rangeland birds of the United States: natural history and habitat use. Agriculture Handbook 688. U.S. Forest Service, Washington, D.C., USA.

GÖTMARK, F. 1992. The effects of investigator disturbance on nesting birds. Current Ornithology 9:63–104.

GUTZWILLER, K. J. 1993. Serial management experiments: an adaptive approach to reduce recreational impacts on wildlife. Transactions of the North American Wildlife and Natural Resources Conference 58:528–536.

———. 1995. Recreational disturbance and wildlife communities. Pages 169–181 *in* R. L. Knight and K. J. Gutzwiller, editors. Wildlife and recreationists: coexistence through management and research. Island Press, Washington, D.C., USA.

———, AND S. H. ANDERSON. 1999. Spatial extent of human-intrusion effects on subalpine bird distributions. Condor 101:378–389.

———, E. A. KROESE, S. H. ANDERSON, AND C. A. WILKINS. 1997. Does human intrusion alter the seasonal timing of avian song during breeding periods? Auk 114:55–65.

———, AND H. A. MARCUM. 1997. Bird reactions to observer clothing color: implications for distance-sampling techniques. Journal of Wildlife Management 61:935–947.

———, R. T. WIEDENMANN, K. L. CLEMENTS, AND S. H. ANDERSON. 1994. Effects of human intrusion on song occurrence and singing consistency in subalpine birds. Auk 111:28–37.

HOSMER, D. W., AND S. LEMESHOW. 1989. Applied logistic regression. John Wiley & Sons, New York, USA.

KINGERY, H. E., AND U. C. KINGERY. 1995. Gray jay as predator on Cassin's finch nestlings. Colorado Field Ornithologists' Journal 29:17.

KNIGHT, R. L., AND K. J. GUTZWILLER, editors. 1995. Wildlife and recreationists: coexistence through management and research. Island Press, Washington, D.C., USA.

KURY, C. R., AND M. GOCHFELD. 1975. Human interference and gull predation in cormorant colonies. Biological Conservation 8:23–34.

MILLER, R. G., JR. 1981. Simultaneous statistical inference. Second edition. Springer-Verlag, New York, USA.

MILLER, S. G., R. L. KNIGHT, AND C. K. MILLER. 1998. Influence of recreational trails on breeding bird communities. Ecological Applications 8:162–169.

OTT, R. L. 1993. An introduction to statistical methods and data analysis. Fourth edition. Wadsworth, Belmont, California, USA.

OUELLET, H. 1970. Further observations on the food and predatory habits of the gray jay. Canadian Journal of Zoology 48:327–330.

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 Wildlife Service, Office of Information Transfer, Fort Collins, Colorado, USA.

RALPH, C. J., J. R. SAUER, AND S. DROEGE, technical editors. 1995. Monitoring bird populations by point counts. U.S. Forest Service General Technical Report PSW-GTR-149. Albany, California, USA.

RANGEN, S. A., R. G. CLARK, AND K. A. HOBSON. 2001. Predator responses to similarity and dispersion of artificial nest sites: implications for the structure of boreal forest songbird communities. Auk 118:105–115.

RICE, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

RIFFELL, S. K., K. J. GUTZWILLER, AND S. H. ANDERSON. 1996. Does repeated human intrusion cause cumulative declines in avian richness and abundance? Ecological Applications 6:492–505.

SAS INSTITUTE. 1989. SAS/STAT user's guide. Version 6 edition. SAS Institute, Cary, North Carolina, USA.

SIEVING, K. E., AND M. F. WILLSON. 1998. Nest predation and avian species diversity in northwestern forest understory. Ecology 79:2391–2402.

STRANG, C. A. 1980. Incidence of avian predators near people searching for waterfowl nests. Journal of Wildlife Management 44:220–222.

STRICKLAND, D., AND H. OUELLET. 1993. Gray jay (*Perisoreus canadensis*). The birds of North America, number 40. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and The American Ornithologists' Union, Washington, D.C., USA.

THOMPSON, F. R., AND M. J. SCHWALBACH. 1995. Analysis of sample size, counting time, and plot size from an avian point count survey on Hoosier National Forest, Indiana. Pages 45–48 *in* C. J. Ralph, J. R. Sauer, and S. Droege, technical editors. Monitoring bird populations by point counts. U.S. Forest Service General Technical Report PSW-GTR-149. Albany, California, USA.

TIAINEN, J. 1983. Dynamics of a local population of the willow warbler *Phylloscopus trochilus* in southern Finland. Ornis Scandinavica 14:1–15.

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

WIENS, J. A. 1981. Single-sample surveys of communities: are the revealed patterns real? American Naturalist 117:90–98.

WOEHLER, E. J., R. L. PENNY, S. M. CREET, AND H. R. BURTON. 1994. Impacts of human visitors on breeding success and long-term population trends in Adélie penguins at Casey, Antarctica. Polar Biology 14:269–274.

YOUMANS, H. 1999. Project overview. Pages 1.1–1.18 *in* G. Joslin and H. Youmans, coordinators. Effects of recreation on Rocky Mountain wildlife: a review for Montana. Montana Chapter of The Wildlife Society, Helena, USA.

ZAR, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.

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