DOES REPEATED HUMAN INTRUSION ALTER USE OF WILDLAND SITES BY RED SQUIRRELS? MULTIYEAR EXPERIMENTAL EVIDENCE

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Intrusion by humans into wildlife habitat during recreational activities has become a worldwide conservation concern. Low levels of intrusion, which occur frequently in many wildlands, could influence use of sites by red squirrels (*Tamiasciurus hudsonicus*) and have important ramifications for conservation. Red squirrels can influence forest composition and regeneration by feeding on conifer buds, seeds, and vascular tissues, and they prey on avian nests. Attraction of red squirrels could increase the risk of these activities, whereas displacement of red squirrels may exacerbate demographic problems for small populations of red squirrels in isolated habitats. We implemented experimental intrusions during 10 consecutive weeks of the red squirrel breeding season, 1 or 2 times/week (1990–1993) in 1 area and 5 times/week (1991–1993) in another area in Wyoming. Each intrusion lasted 1 h and involved 1 person. Abundance of red squirrels at intruded sites did not differ significantly from that at control sites during either experiment. However, experiments should be conducted to examine longer-term effects and effects of higher levels of intrusion because alteration of distributions of red squirrels may affect forest conditions and demographics or fitness of birds and red squirrels.

Key words: attraction, conservation, displacement, human disturbance, predation, *Tamiasciurus hudsonicus*, wildlands, Wyoming

The mere presence of humans in animal habitat has become a common disturbance in many wildlands, including some that are protected and remote (Woehler et al. 1994). Wildlands, such as wilderness and national forests, are large natural environments that have relatively few roads, trails, or facilities and that are distant from large populations of humans (Gutzwiller and Cole 2005). Recreationists use some wildlands intensively, although use typically varies across space and through time. Intrusion associated with wildland recreation is a worldwide conservation concern because it can adversely affect animal physiology, behavior, distributions, reproduction, and survival (Carney and Sydeman 1999; Knight and Gutzwiller 1995); participation in many wildland recreational activities is expected to increase (Blumstein et al. 2005; Gutzwiller and Cole 2005); and wildlands are important harbors of biodiversity (DellaSala et al. 1996; Grumbine 1991).

Most research on how animals respond to recreational disturbance has focused on birds or large and medium-size mammals. Little is known about the effects of human intrusion on small mammals (Joslin and Youmans 1999). We are not aware of any studies that have assessed the influence of wildland recreational disturbance on local habitat use by red squirrels (*Tamiasciurus hudsonicus*), yet such effects could have important ramifications for forest ecology and avian and red squirrel conservation.

Red squirrels can have important effects on forest composition and regeneration by feeding on conifer buds, phloem, and cambium; by caching and eating conifer seeds; and by dispersing mycorrhizal fungi that are important for the health and survival of conifers (Maser et al. 1978; Steele 1998). Red squirrels also are a major cause of avian nest failure in North American coniferous forests (Darveau et al. 1997; Sieving and Willson 1998; Tewksbury et al. 1998), where rates of avian nest predation are associated positively with local abundance of red squirrels (Martin and Joron 2003; Willson et al. 2003). If human intrusion attracted red squirrels to an area, the likelihood of these effects at such sites would increase. Intrusion could conceivably increase use of local wildland sites by red squirrels in several ways. For example, some animals associate food with the presence of recreationists (Knight and Temple 1995). Some predators learn to locate unattended bird nests by watching adults flush in response to

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human disturbance (Joslin and Youmans 1999; Knight and Cole 1995). Also, because recreational disturbance can displace birds of prey (Joslin and Youmans 1999), which are important predators of red squirrels (Steele 1998), intrusion by humans may result in sites with lower predation risk for red squirrels.

If intrusion results in displacement of red squirrels, use of local sites by squirrels and thus the likelihood of their impacts on forests and avian nests would decrease in the intruded areas. If habitat patches are isolated and squirrel populations therein are small, intrusion-induced displacement also may exacerbate the genetic and demographic problems that often plague small populations. Underlying causes of intrusion-induced displacement of animals in wildlands include their perception of human intruders as potential predators, and the negative fitness consequences of reduced feeding, territory maintenance, and breeding caused by abnormal vigilance toward and avoidance of intruders (Knight and Gutzwiller 1995, and references therein). Such factors have the potential to cause displacement of red squirrels as well.

Relatively low levels of intrusion often occur repeatedly for weeks or months in many natural areas (Gutzwiller et al. 1994, 2002). Consequently, slight levels of intrusion have the potential to affect local distributions of species. We assessed whether low levels of repeated human intrusion can alter use of local wildland sites by red squirrels. Our study involved red squirrel habitat in montane forests. Understanding effects of intrusion on red squirrels in this vegetation type is important because montane forest occurs in many natural areas in the western United States that are popular with wildland recreationists.

One might argue that low-level intrusion is probably inconsequential to the use of local sites by red squirrels because such intrusion typically does not physically alter foods or habitats, it does not cause direct mortality of red squirrels, and, by virtue of their arboreal habits, red squirrels are often vertically separated from disturbances associated with ground-level intrusions. However, assumptions that low levels of intrusion do not affect use of wildland sites by red squirrels have not been substantiated with research. The frequency of high levels of intrusion may enable red squirrels to habituate to the disturbance, whereas low-level intrusion may not occur frequently enough to elicit this adaptive response. Relatively low levels of human disturbance are known to have important impacts on other mammals (Joslin and Youmans 1999).

We studied the influence of 1 person walking through forested sites for 1–2 h/week or 5 h/week during 10 consecutive weeks. These levels of disturbance are similar to those from individual hikers, backpackers, anglers, ecotourists, wildlife viewers, and photographers in private and public wildlands. The levels of intrusion we examined were substantially lower than those from more intensive wildland disturbances such as nature tours, group camping, motorized-vehicle activities, and mountain-bike events (Gutzwiller et al. 2002).

We conducted multiyear experiments during the breeding season of red squirrels in 2 different study areas. Using relative abundance of squirrels as an index of site use, we tested the

a priori hypothesis that repeated human intrusion by 1 person can alter use of local wildland sites by red squirrels.

MATERIALS AND METHODS

Study areas and experimental sites.—We conducted 2 experiments in different parts of the Medicine Bow National Forest in southeastern Wyoming (Gutzwiller and Anderson 1999). All research was approved by the Baylor University Institutional Animal Care and Use Committee and met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). Red squirrel habitat occurred throughout both study areas. In 1989, we initiated a 5-year experiment in the Snowy Mountains (41°32′N, 106°20′W) and randomly established 30 circular 1-ha sites. In 1991, we initiated a 3-year experiment at Pole Mountain (41°15′N, 105°23′W), where we randomly positioned 20 circular 1-ha sites. In both experiments, we used the same sites during all years. Gutzwiller et al. (1997) and Gutzwiller and Anderson (1999) provided details about weather, elevations, and coniferous and mixed-forest plant species common in the study areas. Average territory sizes for red squirrels in Wyoming are 0.28–0.48 ha (Steele 1998). The 1-ha study sites therefore had the potential to encompass entire territories or parts of adjoining territories.

Intrusion treatments.—At the beginning of the 1st year of each experiment, we randomly assigned intrusion and control treatments to sites. We applied these original treatments to the same sites throughout the course of both experiments. In the Snowy Mountains, 5 sites received 1 intrusion/week (F1) within the inner 25% of the 1-ha site; 5 sites received 1 intrusion/week throughout 100% of the 1-ha site; 5 sites received 2 intrusions/week (F2) within the inner 25% of the 1-ha site; 5 sites received 2 intrusions/week throughout 100% of the 1-ha site; and 10 control sites did not receive experimental intrusions. F1 intrusions were administered on Wednesdays and F2 intrusions were implemented on Mondays and Fridays. Each year, treated sites were intruded for 10 consecutive weeks between late May and early August, a period that lies within the range of dates for breeding activity by red squirrels in montane forest in the study region (Dolbeer 1973).

An intrusion was applied by 1 technician, and it began when that person reached the perimeter of the 1-ha site. The technician proceeded to the center of the site, and then walked from the center toward the perimeter and back again in a radial pattern (path of movement shifted about 40° after each return to the site center) so that the assigned area was covered twice in a 1-h period. Intrusions began in early morning and were completed by midafternoon. Technicians did not make noises or otherwise try to elicit responses from red squirrels.

At Pole Mountain, the protocol for intrusion treatments was the same as that in the Snowy Mountains, with a few exceptions. Five sites received 5 intrusions/week within the inner 25% of the 1-ha site; 5 sites received 5 intrusions/week throughout 100% of the 1-ha site; and 10 control sites did not receive experimental intrusions. Intrusions were administered once each day from Monday through Friday each week.

Gutzwiller and Anderson (1999) described weather conditions during treatments, the number of technicians who applied treatments, the colors of clothing worn by technicians during treatments, and the lack of treatment-induced vegetation changes. The treatment schedule was the same during all years of both experiments, and extraneous human disturbances were rare, brief, and inconsequential for our inferences (Gutzwiller and Anderson 1999).

Sampling of red squirrels.—In summer, red squirrels move and vocalize frequently, especially during morning hours (Steele 1998). Consequently, the relative abundance of red squirrels is commonly and effectively estimated with point-count methods used for counting birds (Bayne and Hobson 2000; Tewksbury et al. 1998; Willson et al. 2003). Each year for 10 consecutive weeks between late May and early August, a 15-min point count was conducted between 0600 and 1200 h at each site each week (Gutzwiller and Anderson 1999). A count began when a technician reached the perimeter of the 1-ha site, it continued as the person walked toward the center of the site, and it ended at the center of the site, where the technician stood during approximately 14 min of the count. During each count, technicians recorded the number of red squirrels detected inside the 1-ha perimeter.

The counts provided a reasonable index of site use. Based on measurements within our study areas, the average maximum distance at which technicians could hear vocalizing red squirrels was 136 m (range = 86–252 m, n = 8 different squirrels—K. J. Gutzwiller, in litt.); even the minimum distance exceeded the 56.4-m radius of the 1-ha site. The 1st minute of the count protocol enabled detections that may not have been possible later from the center of the site. Visual detections of foraging movements and conspecific chases were common. Considering territorial vocalizations and chasing behavior of red squirrels (Steele 1998), our sampling was capable of detecting primarily dominant adults and possibly subordinate adults.

Technicians sampled one-half of the Snowy Mountains sites on Tuesdays and one-half on Thursdays, and they sampled all Pole Mountain sites on Saturdays. Red squirrels were not counted during 1989 in the Snowy Mountains experiment, but they were counted during all subsequent years in both study areas. The sampling schedule was the same during all years of both experiments.

Gutzwiller and Anderson (1999) described the colors of clothing worn by technicians to reduce detection of technicians by squirrels, the timing of counts used to avoid time-of-day and seasonal biases, methods to record squirrels before entering the 1-ha site and to avoid double counting, and the number of technicians involved in sampling. For reasons detailed previously (Gutzwiller and Anderson 1999), it is highly unlikely that red squirrels were conditioned by treatments to alter their movements or vocalizations when they detected technicians during counts, and any unknown effects of counts on behavior of red squirrels would not have biased the outcomes of the experiments because such effects would have been balanced between control and treated sites.

Habitat variables.—If habitat conditions were confounded with treatment groups, it would not be possible to infer that intrusion treatments caused between-group differences in use of wildland sites by red squirrels. We measured habitat variables within a circular 1-ha area (radius = 56.4 m) and within a circular 7.1-ha area (radius = 150 m) surrounding each site center, and analyses indicated that numerous habitat conditions were not confounded with control and intruded groups (Gutzwiller et al. 1997). Further, for reasons explained by Gutzwiller et al. (2002), it was highly improbable that pretreatment habitat conditions biased the between-group comparisons of abundance of red squirrels.

Statistical analyses.—Use of local wildland sites by red squirrels was inferred from estimates of relative abundance. For a given site and year, we estimated the relative abundance of red squirrels as the mean of the 10 weekly counts. A site was the unit of analysis; this approach precluded pseudoreplication problems that would have been incurred had we used a count as the unit of analysis. We used SAS version 9 (SAS Institute Inc., Cary, North Carolina) for all statistical tests.

Originally, the 2 multiyear experiments considered a total of 4 a priori orthogonal contrasts: the spatial extent of intrusion (inner 25% versus 100% of 1-ha site), the frequency of intrusion (1 versus 2/week for Snowy Mountains), an interaction effect involving extent and frequency, and a general intrusion effect (control sites versus all intruded sites as a group). For the present study, we were only interested in testing the contrast for a general intrusion effect. Before testing this contrast, we used analysis of variance (ANOVA) to assess whether it was appropriate to combine data on abundance of red squirrels from all intruded sites into 1 group for intruded sites.

To test the hypothesis that repeated intrusion altered use of local sites by red squirrels, we tested for differences in mean abundance of red squirrels between control and intruded sites. We used 2-tailed Welch *t*-tests (Zar 1999) to test for differences in mean abundance for each combination of year and study area separately. Conditions detailed in earlier work (Gutzwiller and Anderson 1999; Gutzwiller et al. 1997) indicated it was not appropriate to use repeated-measures ANOVA or combine data for all years and conduct a single standard ANOVA. By applying a Welch *t*-test for each year separately, no untenable or questionable assumptions about repeated measures were necessary, and we precluded pseudoreplication among years.

Most detections of red squirrels were based on vocalizations. If intrusion affected vocalization rates of red squirrels, the effects of intrusions on abundance would be difficult to discern. For each site and year, we computed vocalization rate as the proportion of all (aural plus visual) detections of red squirrels that were aural detections. We used ANOVA to assess whether mean vocalization rates differed among groups of intruded sites and therefore whether it was appropriate to combine all intruded sites into 1 group to test for a general intrusion effect on vocalization rate. We used Welch *t*-tests to test for this general effect.

To reduce the chance of committing type II errors, we used an a priori alpha of 0.10 (instead of 0.05) for statistical tests
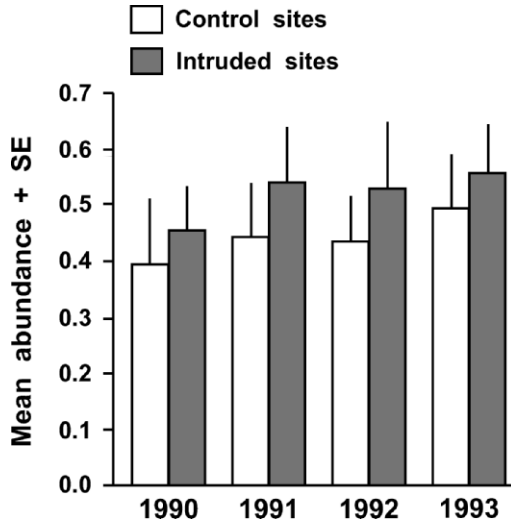
F<small>IG</small>. 1.—Mean abundance of red squirrels (*Tamiasciurus hudsonicus*) + *SE* (squirrels count^{-1} site^{-1}) on control sites ($n =$ 10) and intruded sites ($n = 20$) in the Snowy Mountains, Wyoming, 1990–1993.

(Gutzwiller et al. 1994; Nichols et al. 1984). To control type I errors, we applied a standard Bonferroni correction to alpha. We made this correction across years within a study area for sets of ANOVAs and sets of Welch *t*-tests.

Statisticians recommend using confidence intervals (*CI*s) to interpret the biological meaning of research results, including results that are not statistically significant (Gerard et al. 1998; Hoenig and Heisey 2001). To gain understanding of the biological significance of our abundance results, for each year and study area separately, we computed 90% *CI*s for between-group differences in mean abundance of red squirrels (equation 8.18 in Zar [1999]). We considered between-group differences that were large (≥50% of their respective control-site means) to be biologically important.

We did not compare results of different intrusion frequencies (1–2/week in the Snowy Mountains versus 5/week at Pole Mountain) because the 2 study areas were approximately 90 km apart and differed ecologically (Gutzwiller et al. 1997). Differences in abundance of red squirrels caused by differences in intrusion frequency could not have been distinguished from those due to differences (known and unknown) between study areas. The 2 studies were originally designed as separate experiments and were analyzed as such in the present paper.

RESULTS

Mean vocalization rates.—Vocalization rates differed between groups of intruded sites only during 1991 ($F = 4.38$, *d.f.* = 3, 13, $P = 0.025$) in the Snowy Mountains (remaining ANOVAs for the Snowy Mountains: $F = 0.10–2.35$, *d.f.* = 3, 13–16, $P = 0.117–0.959$; ANOVAs for Pole Mountain: $F = 0.33–2.12$, *d.f.* = 1, 6, $P = 0.196–0.586$). Pairwise comparisons using Student's *t*-tests indicated that this difference occurred because the mean for sites that received 1 intrusion/week throughout 100% of the 1-ha site (F1E100)

was significantly lower ($P = 0.006–0.026$) than the means for the other 3 groups. With these sites included, neither the control versus intruded comparison for 1991 nor those for other years in either study area were significant (Welch $t = -0.96–1.46$, *d.f.* = 8.0–22.1, $P = 0.178–0.928$). When we deleted the 1991 F1E100 sites, the ANOVA was no longer significant ($F = 0.25$, *d.f.* = 2, 10, $P = 0.786$), and the control versus intruded comparison remained nonsignificant (Welch $t = -1.33$, *d.f.* = 10.8, $P = 0.212$). Because inclusion of the F1E100 sites did not change the conclusion about the control versus intruded comparison, it was reasonable to combine vocalization data from all intruded sites into 1 group of intruded sites for this comparison. After we deleted the 1991 F1E100 sites, the ANOVA and Welch *t*-test results for abundance remained nonsignificant (see below). Thus, effects of intrusion on vocalization rates during 1991 did not translate to a significant general effect of intrusion on vocalization rate, to a significant difference in abundance among groups of intruded sites, or to a significant general effect of intrusion on abundance. In brief, our inferences about the effects of intrusion on mean abundance were not confounded with effects of intrusion on vocalization rates.

Mean abundances.—The relative abundance of red squirrels did not differ among the 4 groups of intruded sites during any year in the Snowy Mountains ($F = 0.36–0.63$, *d.f.* = 3, 16, $P = 0.605–0.785$); after we deleted F1E100 sites for 1991, the ANOVA remained nonsignificant ($F = 0.67$, *d.f.* = 2, 12, $P = 0.529$). Abundances also did not differ between the 2 groups of intruded sites during any year at Pole Mountain ($F = 0.02–0.93$, *d.f.* = 1, 8, $P = 0.364–0.899$). Therefore, it was reasonable to combine data from the different groups of intruded sites into 1 group of intruded sites for the control versus intruded contrast.

In the Snowy Mountains, mean abundances at intruded sites were higher than those at control sites by 15%, 22%, 22%, and 12% during 1990, 1991, 1992, and 1993, respectively (Fig. 1), but none of the differences was statistically significant (Table 1). The control versus intruded comparison remained nonsignificant after we deleted the 1991 F1E100 sites from the analysis (Welch $t = -0.73$, *d.f.* = 22.5, $P = 0.472$). At Pole Mountain, mean abundances at intruded sites were lower than those at control sites by 31%, 17%, and 40% during 1991, 1992, and 1993, respectively (Fig. 2), but none of these differences was statistically significant (Table 1).

Most of the values within the 90% *CI*s for between-group differences in mean abundance of red squirrels (Table 2) were near 0.0 squirrels count^{-1} site^{-1} or were <50% of the control-site means (Figs. 1 and 2), implying the intrusion effects on use of local sites by red squirrels were usually not biologically significant. However, differences ranging from −0.195 to −0.341 squirrels count^{-1} site^{-1} near the lower *CI* endpoints for the Snowy Mountains were 50–79% of their respective control-site means, and differences ranging from 0.210 to 0.336 squirrels count^{-1} site^{-1} near the upper *CI* endpoints for Pole Mountain were 50–80% of their respective control-site means (Table 2), indicating that the intrusions had the potential to generate biologically important effects.

TABLE 1.—Results of 2-tailed Welch *t*-tests for differences in the mean number of red squirrels (squirrels count^{-1} site^{-1}) that used control and intruded sites in southeastern Wyoming, 1990–1993.

Year	Snowy Mountains[a]			Pole Mountain[b]		
	t[c]	*d.f.*	*P*	*t*	*d.f.*	*P*
1990	−0.43	16.9	0.673			
1991	−0.69	23.8	0.497	1.59	17.4	0.129
1992	−0.66	28	0.517	0.65	17.8	0.524
1993	−0.47	23	0.646	1.78	17.7	0.092[d]

[a] For all tests, $n = 10$ control sites, $n = 20$ intruded sites.

[b] For all tests, $n = 10$ control sites, $n = 10$ intruded sites.

[c] Negative *t*-statistics indicate that the mean number of red squirrels for intruded sites was larger than that for control sites.

[d] This *P*-value was not statistically significant after a Bonferroni adjustment of $\alpha = 0.10$.

DISCUSSION

Intrusion effects.—Relatively low frequencies of repeated intrusion by 1 person did not significantly increase local use of wildland sites by red squirrels as measured by their abundance. Because use of sites by red squirrels did not increase appreciably at intruded sites, it is unlikely that the impacts of red squirrels on forest ecology or songbird nests were increased substantially at intruded sites. Slight levels of intrusion did not significantly reduce abundance of red squirrels, indicating that the intrusions did not displace red squirrels from local wildland sites. Consequently, potential impacts of displacement on red squirrels, such as exacerbation of genetic and demographic problems for small populations, lower overwinter survival for individuals without territories (Larsen and Boutin 1994), and higher predation of young that travel off of their natal territory (Larsen and Boutin 1994), were not likely.

Biological significance of results.—The lack of statistical significance for the lower abundances on intruded sites at Pole Mountain during 1991 and 1993 may have been an artifact of small sample sizes. At least for these 2 years at Pole Mountain, the attained significance of the *t*-tests may fail to reflect the true effects of intrusion on use of local sites by red squirrels.

The *CI*s indicated that the intrusions did not cause extreme effects (changes >80% of control-site means) on abundances of red squirrels. However, the *CI*s also revealed that effects that one might reasonably consider to be biologically important (changes = 50–80% of control-site means) were possible. For our data, differences of this magnitude involved on average 2 or 3 squirrels/site over a 10-week period each year. Gain or loss of this number of squirrels on a 1-ha site each year for 3–4 years translates to changes in site use that may be important in several ways. In the context of attraction (Snowy Mountains; Table 2), changes in abundance of this magnitude may appreciably affect predation on buds, cones, and avian nests because 1 squirrel can prey on many of these items during a 10-week period. In the context of displacement (Pole Mountain; Table 2), adult red squirrels without territories and young red squirrels that travel off of natal territories can experience higher mortality (Larsen and Boutin 1994).
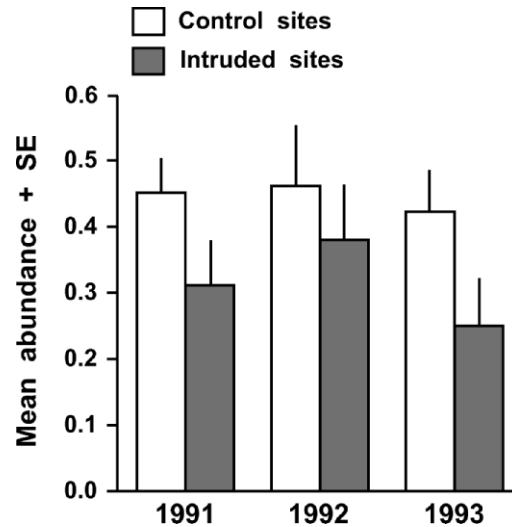

FIG. 2.—Mean abundance of red squirrels (*Tamiasciurus hudsonicus*) + *SE* (squirrels count^{-1} site^{-1}) on control sites ($n = 10$) and intruded sites ($n = 10$) at Pole Mountain, Wyoming, 1991–1993.

Synthesis and conservation implications.—The bulk of our evidence supports the conclusion that the relatively slight levels of intrusion we studied did not typically have biologically large effects on use of local wildland sites by red squirrels. Therefore, under the circumstances of our studies, and until information to the contrary becomes available, these levels of intrusion may be acceptable in wildlands during most years. This conclusion applies to use of local sites, but we cannot infer on the basis of the present study whether it holds for other important aspects of the biology of red squirrels such as reproduction and survival.

For example, the decision by an animal to avoid human disturbance by leaving a disturbed site depends in part on the availability of other suitable locations, and animals that do not have access to acceptable habitat near disturbed sites may remain at disturbed sites, despite potentially detrimental

TABLE 2.—Ninety percent confidence intervals (*CI*s) and biologically important estimates for between-group differences in the mean number of red squirrels (squirrels count^{-1} site^{-1}) that used control and intruded sites in southeastern Wyoming, 1990–1993.[a]

	Lower confidence limit	Between-group difference	Upper confidence limit	Biologically important estimates[b]
Snowy Mountains				
1990	−0.304	−0.060	0.184	−0.195 − −0.304
1991	−0.331	−0.095	0.141	−0.220 − −0.331
1992	−0.341	−0.095	0.151	−0.215 − −0.341
1993	−0.281	−0.060	0.161	−0.245 − −0.281
Pole Mountain				
1991	−0.013	0.140	0.293	0.225−0.293
1992	−0.134	0.080	0.294	0.230−0.294
1993	0.004	0.170	0.336	0.210−0.336

[a] Negative values indicate that the mean number of red squirrels for intruded sites was larger than that for control sites.

[b] Between-group differences within the *CI* that were ≥50% of the control-site mean (Figs. 1 and 2).

consequences for reproduction and survival (Gill et al. 2001). Red squirrels are territorial throughout the year (Steele 1998), so alternative nearby habitat may not always be accessible for red squirrels. If animals have no place to go, they may not exhibit strong avoidance of human disturbance even when costs to reproduction or survival are substantial (Gill et al. 2001). In short, lack of displacement, which was apparent in the present study, may belie impacts on fitness (e.g., Müllner et al. 2004).

In situations where the number of people, and the duration and frequency of intrusion, are higher than those with which we experimented, effects of intrusion on use of local wildland sites by red squirrels may be significant. Depending on numerous environmental conditions and prior experience with humans, tolerance to human disturbance can vary considerably among individuals of a species and between locations (Knight and Gutzwiller 1995). For these reasons, further assessment of the effects of repeated intrusion on use of local wildland sites by red squirrels is warranted.

Recreational disturbance of wildlands should be regulated only when it is likely to cause important impacts. Otherwise, public support for natural areas may decline, and necessary restrictions on use may become difficult to enforce. With these concerns in mind, it is important to document levels of intrusion that do not significantly alter use of local wildland sites by red squirrels. Both kinds of information—impacts and lack thereof—are required to define the continuum of conditions in which intrusion causes problems. Knowledge of this continuum for red squirrels will help conservationists manage recreational use of wildlands in a manner that protects this species without alienating wildland recreationists.

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