Effects of Tourists on Behavior and Demography of Olympic Marmots

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Abstract: *If changes in animal behavior resulting from direct human disturbance negatively affect the persistence of a given species or population, then these behavioral changes must necessarily lead to reduced demographic performance. We tested for the effects of human disturbance on Olympic marmots (*Marmota olympus*), a large ground-dwelling squirrel that has disappeared from several areas where recreation levels are high. We assessed the degree to which antipredator and foraging behavior and demographic rates (survival and reproduction) differed between sites with high recreation levels (high use) and those with little or no recreation (low use). Compared with the marmots at low-use sites, marmots at high-use sites displayed significantly reduced responses to human approach, which could be construed as successful accommodation of disturbance or as a decrease in predator awareness. The marmots at high-use sites also looked up more often while foraging, which suggests an increased wariness. Marmots at both types of sites had comparable reproductive and survival rates and were in similar body condition. Until now, the supposition that marmots can adjust their behavior to avoid negative demographic consequences when confronted with heavy tourism has been based on potentially ambiguous behavioral data. Our results support this hypothesis in the case of Olympic marmots and demonstrate the importance of considering demographic data when evaluating the impacts of recreation on animal populations.*

Keywords: habituation, human disturbance, *Marmota olympus*, national parks, Olympic marmot, tourism effects

Efectos del Turismo sobre el Comportamiento de *Marmota olympus*

Resumen: *Si los cambios en el comportamiento animal resultantes de la perturbación humana directa afectan negativamente la persistencia de una especie o población determinada, entonces estos cambios conductuales necesariamente deben llevar a una reducción en el funcionamiento demográfico. Probamos los efectos de la perturbación humana sobre* Marmota olympus*, una ardilla terrestre que ha desaparecido de varias áreas con niveles altos de recreación. Evaluamos el grado en que difirieron el comportamiento antidepredador y de forrajeo y las tasas demográficas (supervivencia y reproducción) entre sitios con niveles altos de recreación (uso alto) y sitios con poca o ninguna recreación (uso bajo). En comparación con marmotas en sitios de uso bajo, las marmotas en sitios de uso alto desplegaron respuestas significativamente reducidas a la proximidad humana, lo cual pudiera interpretarse como acomodo exitoso a la perturbación o como una disminución en la percepción de depredadores. Las marmotas en sitios de uso alto miraban hacia arriba más frecuentemente cuando forrajeaban, lo que sugiere una mayor percepción. Las marmotas en ambos tipos de sitio tuvieron tasas reproductivas y de supervivencia comparables y fueron similares en condiciones corporales. Hasta ahora, la suposición de que las marmotas pueden ajustar su comportamiento para evitar consecuencias demográficas negativas cuando confrontan turismo intenso se ha basado en datos conductuales potencialmente ambiguos. Nuestros resultados soportan esta hipótesis en el caso de* M. olympus *y*

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demuestran la importancia de considerar datos demográficos cuando se evalúan los impactos de actividades recreativas sobre poblaciones animales.

Palabras Clave: acostumbramiento, efectos del turismo, *Marmota olympus*, parques nacionales, perturbación humana

Introduction

Hiking, wildlife observation, and other nonconsumptive outdoor recreation can have considerable influence on the behavior and distribution of wild animals (e.g., Klein et al. 1996; Constantine et al. 2004; Finney et al. 2005). Changes in behavior and distribution have the potential to translate into fitness costs. Nevertheless, the demographic effects of avoidance or habituation behavior are not always obvious, and truly informed management can occur only if the impacts of recreation on a population's vital rates are known (Gill et al. 2001). Unfortunately, such demographic data are often lacking; thus, management recommendations are made based solely on behavior and distribution changes (e.g., Klein et al. 1996; Papouchis et al. 2001; King & Heinen 2004), leaving the potential for unnecessary (and unpopular) restrictions on recreation if impacts are overestimated.

Alternatively, the true cost of disturbance may be underestimated, particularly in species that manifest few overt responses to human disturbance. Species with limited ability to move away from disturbance could suffer a high demographic cost and so be particularly vulnerable (Gill et al. 2001). Similarly, one life stage or age class may be affected negatively by disturbance, whereas another may be unaffected or appear to habituate. In one of the few studies that has explored demographic costs of disturbance, Müllner et al. (2004) found that adult Hoatzins (*Opisthocomus hoatzin*) habituate to regular tourism but that similarly exposed juvenile birds exhibited increased hormonal stress responses, reduced body mass, and ultimately, lower survival than those at undisturbed sites. Other apparently habituated animals display altered hormonal and behavioral responses to simulated (and possibly real) threatening situations. Magellanic Penguins (*Spheniscus magellanicus*) habituate only after a few visits, but highly disturbed birds have a reduced capacity to secrete corticosterone—the long-term effects of these physiological changes are unknown (Walker et al. 2006). Finally, even where habituation does not result in physiological or behavioral changes, tolerance is unlikely to be absolute (Frid & Dill 2002). Animals continue to flee from some tourists and expend time and energy monitoring those outside the flight zone. Without demographic data, the true costs of these responses cannot be evaluated.

The impact of human disturbance on alpine-dwelling members of the genus *Marmota* is a concern because recreation in their habitats has increased. These large ground-dwelling squirrels inhabit alpine and subalpine meadow throughout the northern hemisphere (Armitage 2003). Their narrow habitat requirements and dependence on a complex burrow system prevent them from moving away from an area if conditions deteriorate. Similarly, they cannot temporally avoid tourists because they are diurnal and must forage extensively during the short alpine summer—when tourism is highest. Most marmot species have been hunted (Armitage 2003), sometimes intensively, for millennia and thus would be expected to respond to humans as a threat (Frid & Dill 2002).

The Olympic marmot (*Marmota olympus*) is endemic to subalpine meadows on the Olympic Peninsula in Washington State (U.S.A.). Their habitat lies almost entirely within Olympic National Park, where they are viewed by thousands of park visitors. In the last 15 years Olympic marmots have declined or disappeared completely from several locations that had been continuously occupied for at least 40 years (S.C.G., M.L.T, and L.S.M., unpublished data). Human activity levels are high in some of these areas. It is unknown whether the locations of the known declines are related to recreation or are an artifact of historic sampling effort.

Most evaluations of the impacts of nonconsumptive recreation on fossorial sciurid rodents (prairie dogs [*Cynomys* spp.], ground-squirrels [*Spermophilus* spp.], and marmots) have been limited to examining warning and flight responses of animals that frequently encounter hikers relative to those that do not. Alpine marmots (*M. marmota*) inhabiting popular hiking areas and prairie dogs (*C. ludovicianus*) in urban parks both exhibit reduced flight distance in response to predictable human actions (Neuhaus & Mainini 1998; Louis & Le Berre 2000; Magle et al. 2005), although with repeated direct approaches, prairie dogs increase their reaction distance (Magle et al. 2005). It has been postulated that the increased tolerance to close human approach indicates that marmots can adjust their behavior to accommodate human presence, avoiding demographic costs (Neuhaus & Mainini 1998; Louis & Le Berre 2000).

Conversely, reduced flight distance may be synonymous with generally reduced wariness (Blumstein et al. 2001), and it is unknown whether habituation is accompanied by physiological changes in stress response as seen in other species (Walker et al. 2006). Mainini et al. (1993) found that habituated marmots react more strongly to a hiker with a dog than to one without, suggesting that

the predator response is present, but no comparison was made with undisturbed animals, so it remains unclear whether the response of regularly disturbed marmots is dampened. Others have investigated space use and burrow distribution within the home range (Franceschina-Zimmerli & Ingold 1996; Semenov et al. 2002) and time budgets (Louis & Le Berre 2002) when human disturbance is high. Nevertheless, these studies were unreplicated and did not investigate demographic responses to tourism. Several sciurid species are listed as threatened or endangered by state, provincial, or federal governments (e.g., Vancouver Island marmot [*M. vancouverensis*]; Mexican prairie dog [*C. mexicanus*]), and these animals are often found in recreation areas.

We used recreation level at different marmot colonies as a treatment in a natural experiment to assess whether visitors are having a negative impact on extant Olympic marmot colonies. We first determined the degree to which multiple antipredator and foraging behaviors of Olympic marmots differ between heavily visited and relatively unvisited sites. Because the importance of observed behavioral differences were not immediately obvious, we then used existing data to determine whether survival and reproductive rates were lower at the heavily visited sites.

Methods

Study Area

Olympic marmots inhabit scattered meadows above 1400 m throughout Olympic National Park (ONP) and surrounding Olympic National Forest. Over 3 million people visit ONP annually, with June–August being the most popular months (National Park Service 2005). Three roads allow summer access into the high country. Hiking and backpacking occur throughout ONP but high-country use is the heaviest near these roads. Marmots currently inhabit meadows adjacent to, and even bisected by, the Obstruction Point Road. Until recently marmots also occupied meadows surrounding a large parking lot on Hurricane Ridge.

Behavioral-Observation Sites

Behavioral experiments and observations were made on 1 or 2 days in 2004 at each of seven heavily visited sites (high use) and six undisturbed (low use) sites (Table 1). For the purpose of this study, a site is a meadow occupied by one family group or interacting family groups of marmots. Randomly assigning sites to receive different levels of tourist pressure was not possible. Instead, we minimized the confounding effects of other factors by observing behavior at multiple sites for each visitation level. We selected behavioral sites so that we could compare naïve marmots with those that were heavily exposed to humans.

We chose seven high-use sites from among those with the greatest levels of human visitation among extant marmot colonies. These seven sites represented a range of human activity types (car, hiker, or campsite) and geographic distribution. Marmot colonies at these sites were bisected by or adjacent to a heavily used trail, road, or designated high-use campsite. As a coarse index of human use, we counted hikers and cars (collectively, tourists) during a single morning or in both the morning and afternoon at each site. One or more hiker groups or cars were seen at each of the seven high-use sites during the morning (0700–1300 hours; Table 1). Cars or hikers appeared to be visible to a focal marmot for an average of 27 minutes (7.7%) of the 6-hour period (Fig. 1). At three of the high-use behavioral sites, cars and hikers were also counted in

Table 1. Descriptions of study sites used for behavioral observations of Olympic marmots in 2004.

Site	*UTM coordinates (easting, northing)*[a]	*Marmots trapped?*	*Activity budget date*	*No. marmots*[b]	*Tourist infrastructure*	*No. tourist groups*[c]
High use						
Eagle Point	469116, 5309321	yes	15 July	3	road	13 cars
Bogacheil Peak	442170, 5306070	no	18 August	3	trail	6 groups
Marmot Flats	470150, 5307814	yes	30 June	5	road	13 cars
Obstruction Point	471435, 5307188	yes	20 July	7	parking lot & trailhead	8 cars
Gladys Lake	473040, 5302750	no	10 July	5	trail & campsite	4 groups
Moose Lake	473680, 5303315	no	12 July	2	trail & campsite	2 groups
Elk Mountain	473753, 5307904	no	29 July	3	trail	3 groups
Low use						
Heart Lake	446200, 5306981	no	20 August	6	none	0
Happy Lake	448680, 5318100	no	23 July	5	none	0
Swimming Bear Lake	446500, 5307000	no	12 July	10	none	0
Constance Pass North	486830, 5291150	no	5 August	5	none	0
Dodger Point	462000, 5302400	no	26 July	3	none	0
Swimming Hole	473230, 5305100	no	8 July	4	none	0

[a] *Universal transverse mercator coordinates, NAD 83 datum, zone 10.*
[b] *Marmots age ≥ 1 year old seen at the site during behavioral observations.*
[c] *Groups of hikers or tourist cars seen during the morning activity period (0700–1300 hours).*

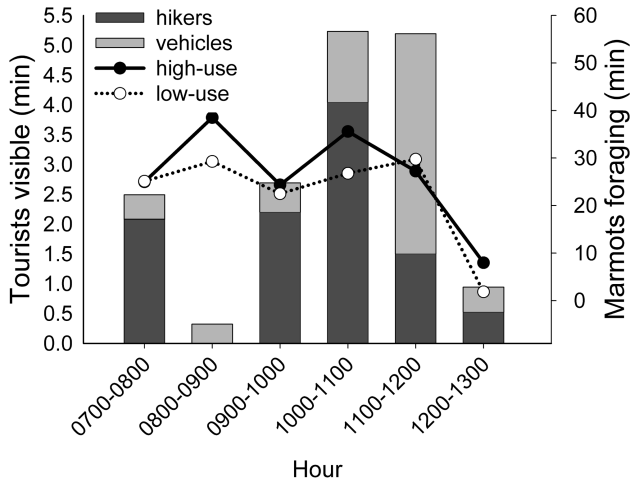

Figure 1. Average time (minutes) that hikers and vehicles were visible to focal Olympic marmots at seven sites with high tourist levels (high use) during each hour of morning observation periods and the average time spent foraging by focal marmots at seven high-use sites and six low-use sites. No tourists were seen at the low-use sites during the morning observation periods.

the afternoon (1300–2000 hours) and appeared to be visible to the marmots for an average of 64 minutes, or 15.3% of that 7-hour period. This is consistent with our impression that human disturbance is greater in the afternoon. Since 2002 we have conducted trapping and radiotelemetry work at three high-use sites (Eagle Point, Marmot Flats, and Obstruction Point). We always conducted behavioral observations at least 5 days after any trapping operations to avoid aftereffects of our activities.

The six low-use sites were generally >100 m from any trail, road, or campsite and not visible from areas regularly used by tourists. These sites were identified in the course of extensive ground surveys in 2002 and 2003 (S.C.G., M.L.T., and L.S.M., unpublished data) but were not visited in 2004 prior to the behavioral observations. We did not see any humans at the low-use behavioral sites during our observations.

Demographic Sites

We used data (collected in 2002–2005 as part of a separate study) from marked marmots at 11 sites to compare reproductive rates, survival, and body condition among marmots at sites that had heavy human traffic (high use; $n = 7$; Table 2) in the form of hikers, cars, or both and at sites that were largely undisturbed (low use, $n = 4$). We conducted trapping and telemetry operations several days each year at each of these sites. These activities may have influenced the marmots' behavior, but it is not possible to gather detailed demographic data without disturbing the animals. To confirm that the effect of our disturbance was minimal, we compared behavioral data from three of the four low-use demographic sites (Royal Basin, Pumpkin Seed Lake, and Jon's Basin) with data from low-use behavioral sites. Not all demographic sites were studied in all years. Marmots did not persist at Hurricane-Elwha Junction after June 2003, and we added sites in 2003. We did not include data from several colonies that had intermediate levels of disturbance.

Behavioral Observations

We conducted observations at the 13 behavioral sites in clear or partly cloudy weather between late June and late August 2003 (Table 1). Observations at both high- and low-use sites were distributed similarly throughout summer ($n = 13$; Mann-Whitney $U = 15.5$; $p = 0.431$). Likewise, sites had similar numbers of marmots ≥1 year old (infants appear above ground in late July) present at the time of sampling ($n = 13$; $U = 12.5$; $p = 0.212$). Through the use of multiple sites of each type, we attempted to minimize the effects of site-specific conditions such as topography or recent predation events on marmot behavior. The same observer (T.V.) made all observations and experiments except those at Swimming Bear Lake, which were done by an observer trained by T.V. The distance between the observer and the focal marmot was never <50 m and usually >100 m.

LOOKING-UP AND FLIGHT BEHAVIOR

The vigilance behavior during foraging, as measured by the frequency (number of looks), average duration (average look), and total time the animal devoted to looking up (total time looking), was observed for two or three adult (≥2 years old) animals per site generally following the methods of Blumstein et al. (2001). Specifically, once a focal animal had been foraging for several minutes, we noted, on a handheld tape recorder, each time the marmot looked up and then back down during a 2.5-minute period. The first 0.5 minutes of tape were not used in the analyses to reduce biases associated with the timing of initiation of the observation period. For comparison with low-use sites, observations at high-use sites were made when no tourists were present. Easily recognized marmots (distinctive molt pattern) were chosen for observation to avoid using the same animal twice. In each case the number of other marmots (foraging group size) apparently visible to the focal animal during the observations was noted because vigilance may be affected by group size (Blumstein 1996; Blumstein et al. 2004). One person (T.V.) transcribed all tapes and used a stopwatch used to measure time between each word *up* and *down*.

We evaluated the relative sensitivity of marmots to a potential predator by measuring how close a human, walking at a constant pace across the slope directly toward a foraging marmot, could get to the animal before it ran to a burrow (flight distance) and subsequently went below ground (ground distance) and by measuring how long the

Table 2. Sites used for demographic analysis of the effects of tourism on Olympic marmots.

Site	*UTM coordinates (easting, northing)*	*Tourist infrastructure*	*Years of study*	*No. marmots with transmitters*	*No. 15-day transmitter periods*	*Females (litters)*
High use						
Eagle Point	469116, 5309321	road	2002–2005	7	107	4 (3)
Marmot Flats	470150, 5307814	road	2002–2005	13	170	11 (7)
Obstruction Point	471435, 5307188	parking lot & trailhead	2002–2005	5	96	11 (5)
Wolf Creek[a]	461722, 5313233	trail	2002–2005	2	19	0 (0)
Hurricane-Elwha Junction	460352, 5315334	trail junction	2002–2003	2	7	0 (0)
Pull-Out	469523, 5308374	scenic overlook (road)	2003–2005	3	18	2 (1)
Zenith	460768, 5315211	trail end & overlook	2002–2005	1	27	1 (1)
Total high use				33	337	29 (17)
Low use						
Royal Basin	483700, 5296750	none[b]	2003–2005	16	241	27 (7)
Lower Ridgely	460857, 5314961	none[c]	2002–2005	0	0	0 (0)
Pumpkin Seed Lake	471514, 5306428	abandoned trail[d]	2003–2005	7	66	4 (4)
Jon's Basin	460157, 5315559	none[e]	2002–2005	5	77	5 (0)
Total low use				28	384	36 (11)

[a] *Females were present at Wolf Creek in all years but were not considered because there was no male present.*
[b] *There is a trail in Royal Basin on the far side of the valley (>200 m) from the marmot meadow. We have only once in 3 years seen a hiker on or near the meadow itself, which is very steep and separated from the trail by a marsh.*
[c] *Lower Ridgely is isolated from hikers, but the female was not included in the analysis of reproductive output because she occasionally traveled to an area where she would have encountered visitors. The infants from a litter in 2004 never traveled into the tourist area and were used in the infant-survival calculations.*
[d] *Of the low-use sites, Pumpkin Seed Lake had the most tourist pressure—we estimated that one or two groups of hikers visit this site in a typical week and on two occasions, campers were seen on our arrival in the morning (S.C.G., personal observation), although camping was banned in this area.*
[e] *There is a trail along the rim of Jon's Basin from which hikers sometimes look down, but we never saw a hiker descend into the basin, which is extremely steep and rocky.*

marmot remained in the burrow after the human moved away (exit delay). The distance of the marmot (distance to burrow) from its burrow at the start of the experiment was also recorded because this distance can influence flight distance (Bonenfont & Kramer 1994). All distances were measured with a laser range finder. Three marmots on each site were tested, with ≥30 minutes between the culmination of the experiment on one animal and the beginning of the experiment on the next. We conducted all flushing experiments after collection of observational data.

ACTIVITY BUDGET

To assess the amount of time marmots devoted to foraging and vigilance, we compiled a morning activity budget for one adult marmot at each of the 13 sites. We watched the first readily identifiable marmot from its initial emergence in the morning until it reentered its burrow and remained there for at least 1 hour after 1200 hours. In no case did a marmot fail to remain in the burrow for at least 1 hour in the early afternoon. We restricted our observations to the morning activity period because heavy rain or extreme heat in the afternoon frequently caused the marmots to remain inactive for several hours (Barash 1973; Melcher et al. 1990).

We continuously monitored the behavior of the focal animal, recording the time that a change in activity occurred. For analysis, activities were classified as below ground; foraging (including brief instances of looking up, ≤10 seconds); vigilance (any instance of looking up > 10 seconds, typically while sitting or lying at the burrow entrance or on a rock); traveling; and other (social, grooming, and other activity). A sixth activity (lying down without looking around) was measured but not considered because it averaged <1% of marmots' morning activity. When a marmot at a visited site went below ground, we noted whether the animal appeared to be fleeing a human or whether it did so of its own volition.

Demographic Observations

TRAPPING AND IMPLANTATION OF RADIO TRANSMITTERS

As part of an ongoing study, all marmots at the 11 demographic sites had been marked and monitored since 2002 or 2003, and a subset had radio-transmitter implants (Table 2). We generally followed trapping and handling procedures outlined in Bryant (1996), with two exceptions: we used xylazine in addition to ketamine to sedate the marmots and we attached one or two small (<1 cm) pieces of colored wire to each ear tag to facilitate recognition of individuals without recapture. Most subsequent recaptures were identified, weighed, and released.

We surgically implanted 40-g radio transmitters in the peritoneal cavity of 62 marmots ≥1 year old, following

published surgical methods (Van Vuren 1989; Bryant & Page 2005). Intraperitoneal transmitters have been widely used in studies of marmots with no detectable reduction in survival or reproduction (Van Vuren 1989; Bryant & Page 2005; Griffin et al. unpublished data). We never trapped or resighted a marmot with a failed transmitter, but we did replace five transmitters as they neared the end of the expected battery life.

SURVIVAL AND REPRODUCTION

We confirmed the status (alive or dead) of marmots with radio implants at least twice per month during the active season, except during September 2002 and May 2003, when status was checked only once per month. We found two transmitters beneath the snow outside the burrows in May 2003—these animals were presumed to have died prior to initiating hibernation in September 2002.

We used two measures of reproductive success: weaning success and litter size. Weaning success was defined as the proportion of adult females present in late June that weaned litters (infants appearing above ground), determined by observing females and their primary burrows several times per week during mid-July through August. Litter size was determined by observing the litter on several occasions within 10 days of emergence, a period when infants remain close to the natal burrow and are easily counted. Whenever possible, we trapped and marked the infants to facilitate counting. Females at Obstruction Point and Marmot Flats in 2002 and Royal Basin in 2003, 2004, and 2005 were checked only once every 10–14 days. In some cases the mobility of infants when we discovered them suggested that they had been above ground for more than a week. We excluded these litters from the analysis of litter size because it was possible that some infants had already been lost to predation.

We determined apparent survival for each juvenile from initial tagging in the year of its birth until the following spring, when it was considered a yearling, based on whether the animal was trapped or resighted (ear-tag numbers read with binoculars or spotting scope) in May or June. In addition to intensive spring trapping and regular observation, we conducted scheduled "resighting" sessions at each site in late June, attempting to positively identify all marmots present on each of 3 days. Our estimated detection probabilities approach 1.0 over the 3 days, and no yearling that we failed to detect prior to 1 July was later trapped or resighted (S.C.G., M.L.T. & L.S.M., unpublished data).

Statistical Analyses

BEHAVIORAL DATA

We used a multivariate analysis of variance (MANOVA; SPSS version 12.0) to examine the effect of visitation on the suite of six looking-up and flight-response behaviors. Prior to fitting the MANOVA, we used correlations and general linear models to determine whether distance to burrow influenced flight distance and whether foraging group size influenced any of the three looking-up responses. We found no significant relationships, so we did not include distance to burrow or foraging group size in the MANOVA. We used the z scores (to standardize the disparate units and scales) of the log-transformed variables as the dependent variables in the MANOVA, with level of visitation as a fixed factor. After establishing overall model significance, the effect of visitation on the individual response variables was examined.

In addition to the MANOVA, we used discriminate function analysis (DFA) to evaluate whether the marmots at the low-use demographic sites behaved similarly to those at the low-use behavioral sites. We used a stepwise entry procedure (discriminate: Wilks, p to enter ≤ 0.15) to develop a function that best discriminated between marmots at the high- and low-use sites based on the looking-up and flushing data from the 13 behavioral sites.

We used the resulting classification function, built using data from the behavioral sites, to assign marmots from the low-use demographic sites to either the high- or low-use categories, based on their looking-up and flushing responses. We did not, however, collect all response variables on every marmot at the demographic sites. In these cases the mean value of the cases used to build the model was substituted for the missing value. The use of mean values rather than actual data is not ideal for DFA; it results in conservative discriminate function scores that are closer to the cut point than they might be otherwise. Nevertheless, the direction of the deviation from the cut point and the resulting group classification was determined by the variables that were measured on each animal.

Finally, we conducted a second MANOVA to determine whether the overall pattern of activity of marmots varied at the high- and low-use sites. We converted the time each marmot devoted to each of the five activities to a proportion of the total time available to that individual. To reduce heterogeneity of the variances and increase residual normality, we transformed data to the arc-sine square root. Because vigilance was strongly correlated with "other activities" ($r = -0.72$, $p = 0.01$) and with being below ground ($r = -0.69$, $p = 0.01$) and we were interested primarily in vigilance behavior, "below ground" and "other" were not included in the MANOVA. Thus, vigilance, foraging, traveling, and total time (time from the marmot's first appearance until the afternoon move to the burrow) were used as the response variables with visitation as a factor.

DEMOGRAPHIC DATA

The potential effect of human disturbance on the body mass of 117 marmots $\geq$1 year old was evaluated at

high- and low-use sites in a mixed linear model. Our sample of infants was too small and unbalanced to include them in this analysis. We initially fit a model that included visitation as a fixed effect, Julian date as a covariate, and six age-sex classes (yearling, 2-year-old male, 2-year-old female, adult male, adult nonreproductive female, and reproductive female). Because we had multiple measurements per animal (range = 1-10, median = 2), we included the individual marmot as a random effect nested within site. After examining the residuals, we added an interaction term, Julian date $*$ class, which allowed for different age classes to gain weight at different rates across the summer, and a quadratic term, Julian date^2 to account for a tendency for animals to gain weight most rapidly at the beginning of the summer. Parameters were estimated with restricted maximum likelihood.

We used known-fate models in program Mark (White & Burnham 1999) to compare survival of radio-implanted marmots at high- and low-use sites (Table 2). We developed a set of a priori models for bimonthly survival during the active period (approximately 1 May–1 October). No radio-tagged marmot died during hibernation, so we set survival during that period equal to 1. These models potentially included sex, age, and visitation as individual covariates. Because it was also biologically reasonable that pulses of mortality occurred during particular times of year (Bryant & Page 2005), some models included one parameter for September survival, applied to all marmots, that was estimated separately from May–August survival. We also estimated a separate parameter that allowed adult female survival to differ from the rest of the population in June, a period when females are potentially under increased stress during pregnancy and lactation.

Our interest lay in testing the hypothesis that visitation reduces marmot survival, rather than estimating parameters or selecting models. Thus, we used AIC_c values to identify the most parsimonious model that included the visitation effect (Burnham & Anderson 2002) and then performed a likelihood ratio test on nested models with and without visitation to test for an effect of this parameter (Wolfinger 1993; Cooch & White 2006). This approach allowed us to identify the most likely model structure of our candidate set and obtain a significance level for the factor of interest, namely visitation, given that model structure.

Weaning success and apparent infant survival for the two visitation groups were compared with chi-square tests, and litter size was compared with a two-sample t test. Because reproductive and infant survival data from low-use sites were relatively sparse, we also made qualitative comparisons of rates from high-use sites with those measured for Olympic marmots during a period of relative stability (1967–1969; Barash 1973) and two other North American species for which long-term data are available (*M. flaviventris*, Schwartz et al. 1998; *M. vancouverensis*, Bryant 2005).

Results

Looking-Up and Flight Behavior

Marmots exhibited clear differences in looking-up and flight behavior between the visited and unvisited sites (Fig. 2). The MANOVA indicated an overall effect of visitation ($F^6_{31} = 3.36$, $p = 0.01$), with significant univariate differences observed in five of the six behaviors. During the 2-minute foraging bouts, marmots at high-use sites looked up more often than marmots at low-use sites ($p = 0.03$) and, ultimately, devoted a greater amount of time to looking up ($p = 0.02$). The duration of each look up was essentially the same at high- and low-use sites ($p = 0.85$). Marmots at high-use sites allowed humans to approach to a distance of less than half that tolerated by marmots at remote sites before fleeing to ($p = 0.01$) and then entering ($p = 0.03$) the burrow. Once the human withdrew, the marmots at the high-use sites typically remained in their burrows less than a minute, whereas marmots at the unvisited sites took several minutes to reemerge ($p < 0.01$).

The DFA stepwise procedure identified number of looks and exit delay as the two variables most useful in discriminating between marmots at low- and high-use behavioral sites. The resulting function significantly discriminated between groups (Wilks' lambda = 0.62; $\chi^2_2 = 16.89$; $p < 0.01$) and correctly assigned group membership to 71% of the 38 marmots used to build the model. When applied to the marmots from the low-use demographic sites, this same function assigned 70% (7 of 10) animals to the low-use category, confirming that marmots at these sites retained behavioral traits of the most naïve marmots, despite disturbance related to our trapping and telemetry work.

Activity Budget

In contrast to the differences observed in the flushing and vigilance behavior of visited and unvisited marmots, the overall pattern of marmot daily activity did not differ as a function of visitation ($F^4_8 = 1.44$, $p = 0.31$), and visitation did not affect any of the individual activities (all $p > 0.05$; Fig. 3). Nevertheless, there was a tendency for marmots at high-use sites to spend more time in "other activities" ($p = 0.07$). This difference arose because several marmots at high-use sites spent considerable time (in one case 72 minutes) in activities related to humans, such as licking roads or places where campers had urinated. Qualitatively, there did not appear to be any tendency for the timing of foraging activity to vary between low- and high-use sites as a function of the timing of tourist activity (Fig. 1). Only once during the activity budget observations did a marmot enter a burrow in response to a tourist.

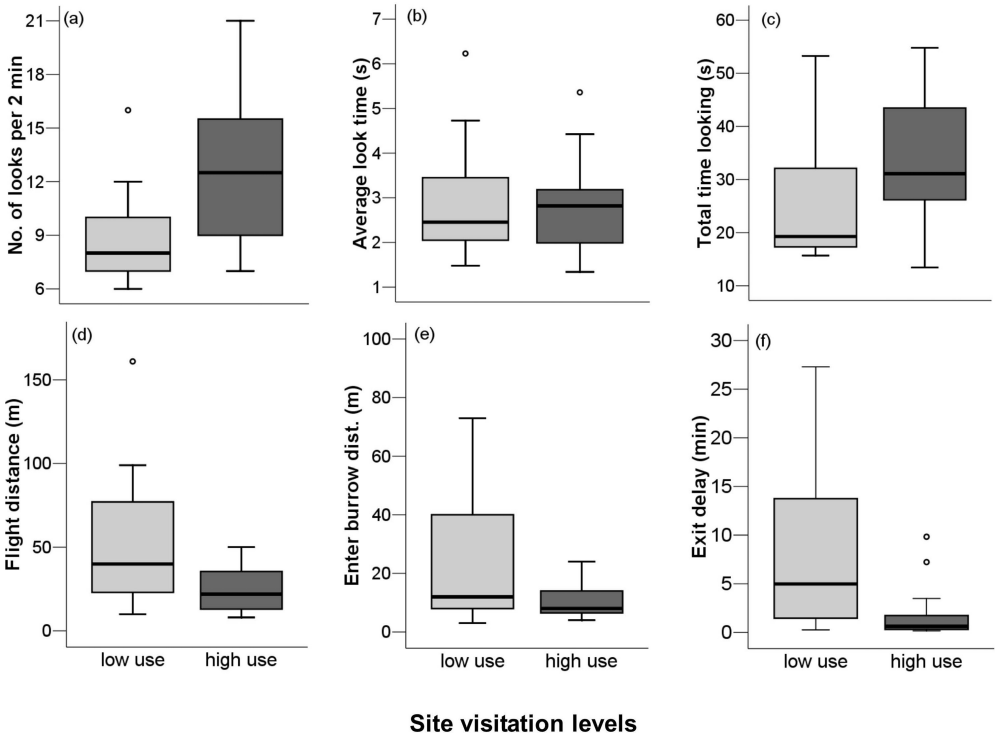

*Figure 2. Medians (horizontal line), 25th and 75th percentiles (bottom and top, respectively, of bars), 5th and 95th percentiles (bottom and top whiskers respectively), and outliers (circles) of the untransformed behavioral observations collected on Olympic marmots at sites with high levels of tourist use (*n *= 18 marmots) and low levels of tourist use (*n *= 20). Data shown are for (a) number of times a marmot looked up per 2-minute observation period, (b) average duration of each look, (c) total time spent looking up per 2-minute observation period, (d) distance at which marmots fled to their burrow in response to an approaching human, (e) distance between an approaching human and marmots that prompted marmots to enter their burrows, and (f) time the marmots remained in their burrows after the human withdrew.*

Condition, Survival, and Reproduction

Current levels of tourism did not appear to affect Olympic marmot body condition or demographic rates. The mixed model analysis on 334 mass measurements from 117 marmots ≥1 year old indicated that tourism levels did not influence marmot body condition at our sites. The visitation parameter was not statistically significant ($p = 0.67$), and the estimated marginal difference of 0.035 kg between marmots at low- and high-visitation sites was <1% of the body mass of a breeding female and smaller than the precision of our measurements.

Out of 62 marmots with surgically implanted radio transmitters, 15 mortalities were confirmed by recovery of the radio transmitter, and 11 marmots disappeared at the same time we lost the signal. The patterns of signal losses were generally inconsistent with transmitter failure or animals moving off the study area (S.C.G., M.L.T., and L.S.M., unpublished data); it is probable that most or all of these animals were killed. Nevertheless, we conducted survival analyses on two data sets. In the first data set, we treated 9 of these 11 animals as having died during the period in which we first were unable to locate the radio; removed from the data set 1 of the 11 marmots because its signal was never heard following the surgery; and assumed that the final marmot, which carried a very old transmitter for which a signal was lost in late September,

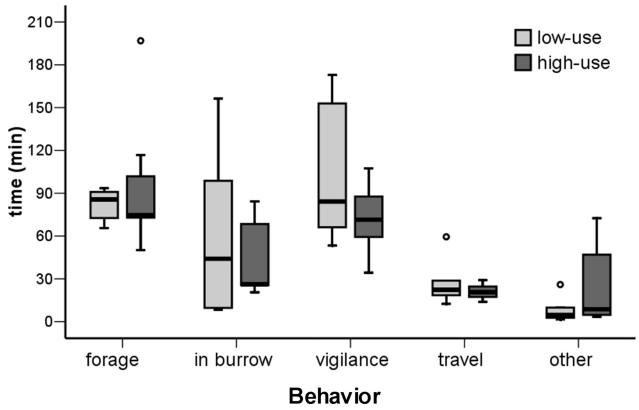

Figure 3. Time devoted by Olympic marmots from low-use and high-use tourist sites to each of six behaviors (described in the text) during the course of the morning on which the marmots were observed.

had successfully hibernated with a failed radio. In the second data set, we assumed that the missing transmitters had failed or the animals had left the study area, and we removed them from the data set beginning in the time-period in which they disappeared (i.e., they were right censored). Regardless of the treatment of the missing marmots, visitation did not affect survival rates. Of our candidate model set, a model that included parameters for September and adult females in June had the most support based on AIC_c values. The likelihood-ratio test indicated that inclusion of the visitation parameter did not significantly improve model fit regardless of whether the missing marmots were assumed dead ($\chi^2_1 = 0.37$, $p = 0.54$) or were censored ($\chi^2_1 = 0.85$, $p = 0.36$).

Similarly, infant survival was not depressed at any of our sites. At high-use site 55% (22 of 40) of tagged infants were resighted or trapped the following spring; 50% (10 of 20) of tagged infants at low-use sites were similarly identified in the spring. These proportions are statistically indistinguishable ($\chi^2_1 = 0.01$; $p = 0.93$) and similar to those measured in Olympic marmots during a period of population stability and other marmot species (Barash 1973; Schwartz et al. 1998; A.A. Bryant, personal communication).

Neither weaning success nor litter size was lower at the high-use sites than at the low-use sites. Weaning success was determined for a total of 29 and 36 adult females at high- and low-use sites respectively. A greater proportion of females produced litters at the high-use sites (59%) than at low-use sites (31%, $\chi^2_1 = 4.08$; $p = 0.04$), a difference largely driven by low reproduction at Royal Basin (Table 2), where a very high density of marmots may have resulted in reproductive suppression (Wasser & Barash 1983; Blumstein & Armitage 1998; Hacklander et al. 2003). Litter size was similar across visitation levels ($t = 0.62$; $p = 0.55$), averaging 3.75 at the low-use sites and 3.46 at high-use sites. Both weaning success and litter size were similar to those seen in other marmot species (Fig. 4).

Discussion

If changes in animal behavior resulting from direct human disturbance negatively affect the persistence of a given species or population, these changes must necessarily lead to reduced demographic performance (Gill et al. 2001). Our results indicate that Olympic marmots frequently exposed to hikers and vehicular traffic exhibit reduced sensitivity to humans, as manifested by shorter flight distances and decreased hiding time following disturbance, and that these marmots also look up more frequently while foraging. Nevertheless, analysis of existing demographic data showed that these behavioral changes were not associated with decreased survival, reproduction, or body condition.

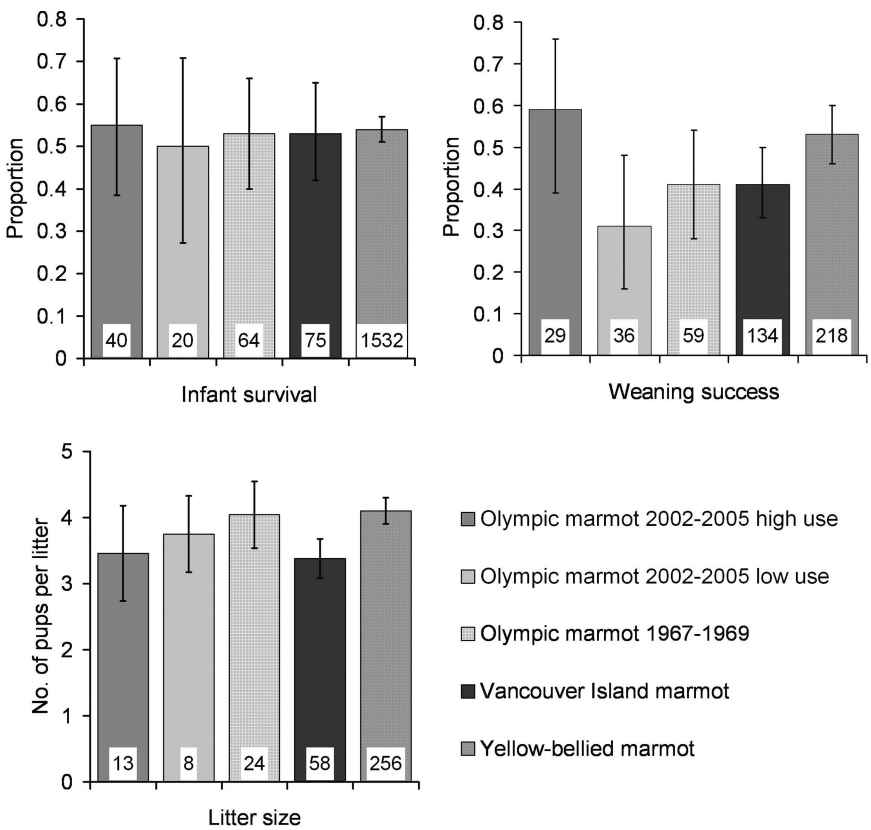

Figure 4. Mean reproductive rates and infant apparent survival rates (weaning to spring) of Olympic marmots at sites with high and low levels of tourism (this study), Olympic marmots in the 1960s (Barash 1973), Vancouver Island marmots (weaning success and litter size, Bryant 2005; infant survival, A. Bryant, personal communication), and yellow-bellied marmots in Colorado (Schwartz et al. 1998). Error bars represent 95% confidence intervals for the means. Sample sizes are shown in the base of the bars.

Until now the supposition that marmots can adjust their behavior to avoid negative demographic consequences when confronted with regular human presence has been based on potentially ambiguous behavioral data (Neuhaus & Mainini 1998; Louis & Le Berre 2000). Our demographic results support this hypothesis in the case of Olympic marmots and demonstrate the importance of using demographic data when evaluating the impacts of recreational activities on animal populations.

Comparison of Behavioral and Demographic Results

If one relied on a single behavioral metric to evaluate the probable impacts of disturbance on marmots—and perhaps other species—the conclusions would depend on the behavioral trait examined. The flushing experiments revealed that Olympic marmots in areas of high tourist traffic responded to the approach of a human in much the same way as alpine marmots in highly visited tourist areas (Mainini et al. 1993; Neuhaus & Mainini 1998; Louis & Le Berre 2000), flushing only when humans approached quite close (Fig. 2). Nevertheless, these data provided inconclusive information about the potential for associated demographic effects. The reduced flushing responses in marmots regularly exposed to humans could have indicated that these marmots had learned that the danger presented by a car or human is low; that regularly visited marmots were energetically stressed and therefore the cost of lost foraging opportunity was higher than for unvisited marmots; or that regularly visited marmots were less wary because they had been "desensitized" to movement, potentially leaving them vulnerable to predation.

The increased frequency with which marmots at high-use sites looked up to scan for predators when foraging further complicates the story (Fig. 2). This behavioral change was consistent with an increased wariness (perhaps because the marmots were anticipating disturbance), and may have signified a reduced susceptibility to predation. Nevertheless, the resulting increase in total looking-up time potentially limited food consumption. Finally, if one compared only the amount, or temporal distribution, of time spent foraging between the two groups of marmots, one might have concluded that there was no cost associated with disturbance.

The demographic data, on the other hand, were unambiguous. Olympic marmots successfully accommodated current levels of tourism without changes in reproduction or survival. The behavioral changes neither caused nor were symptomatic of a negative energy balance. Body mass, which influences marmot reproductive success (Hacklaender & Arnold 1999) and infant survival (Lenihan & Van Vuren 1996), was essentially unaffected by visitation level. The 100% overwinter survival of radio-tagged marmots, normal fall-to-spring apparent survival of tagged infants, and similar reproductive output at both types of sites all suggest that energy balance is similar across sites. The similarity of reproductive and infant survival rates at high-use sites to historic Olympic marmot rates from a period of population stability and to those of related species (Fig. 4) also indicate that marmots at high-use sites are not energetically stressed. Likewise, the reduced flight response of marmots at high-use sites does not appear to indicate a functional reduction in antipredator behavior, because we detected no effect of visitation level on active-season survival of radio-tagged marmots.

The similarity of marmot behavior at the low-use demographic sites and the low-use behavioral sites support our low-use designations for the demographic sites. For our low-use sites, our research activities represented all or most of the animals' exposure to humans. We visited our low-use sites $\leq$25 days each summer, often briefly for telemetry checks. Marmots at high-use sites were disturbed many times each day by cars, hikers, or both (Table 1; Fig. 1), in addition to research-related activities.

Olympic Marmots and Tourists: Recommendations for Management

We do not recommend changes in current visitor management for the purpose of protecting marmots from direct disturbance by humans. Marmots at our seven high-use demographic study sites experienced the highest tourist pressure of any marmots currently found in Olympic National Park, without exhibiting reductions in key demographic rates. It is also unlikely that recently documented extinctions were directly caused by tourism because most extinct colonies would have experienced disturbance levels similar to those we studied.

Nevertheless, as wildlife viewing opportunities become rarer and park visitation increases, it may be necessary to increase efforts to keep hikers on designated trails and drivers in their cars. Predictability of human behavior is important to marmots (Mainini et al. 1993) and other wildlife (Papouchis et al. 2001). Although only once during our activity budget observations did a marmot flee from a tourist, during the course of our trapping and telemetry operations we regularly saw drivers leave their cars and pursue marmots in an effort to photograph them, following them or sitting a few meters from their burrows for as long as 40 minutes. This clearly does not constitute predictable behavior. Education and enforcement efforts could be targeted to reduce this kind of direct harassment. If tourism levels grow substantially and concerns persist about marmot populations, it would be wise to reexamine marmot responses as a threshold response to disturbance is possible (Creel et al. 2002).

We also caution that our results may not apply to marmots that recolonize or are reintroduced to popular tourist areas. Alpine marmots apparently habituate to

humans during the first summer of life (Neuhaus & Mainini 1998). If true for Olympic marmots, 2-year-olds emigrating or transplanted from low-use sites might be sensitive to disturbance. No marmots immigrated to a high-use site during our study, so we could not evaluate the effects of disturbance on naïve adult marmots.

Finally, we emphasize that our finding that tourism does not negatively affect demographic rates of Olympic marmots speaks only to the impact of direct disturbance. Our results in no way preclude the possibility that tourism may indirectly influence marmots if humans are subsidizing predators or otherwise altering the ecosystem.

Conclusions

Although our results are specific to Olympic marmots, we have demonstrated the potential for confusion that can arise if one relies on behavioral studies alone to assess impacts of recreational disturbance on populations. Demographic studies designed a priori to evaluate population performance are preferable but often impractical—the costs are too high and the delays too long. Nevertheless, we expect there are other taxa for which existing demographic data could be used in a post hoc analysis similar to ours. This approach allowed us to test for biologically important demographic costs to Olympic marmots without incurring additional field expenses or delays. By eliminating from further consideration one potential cause of observed marmot declines, we may have prevented unpopular and unnecessary restrictions on tourism.

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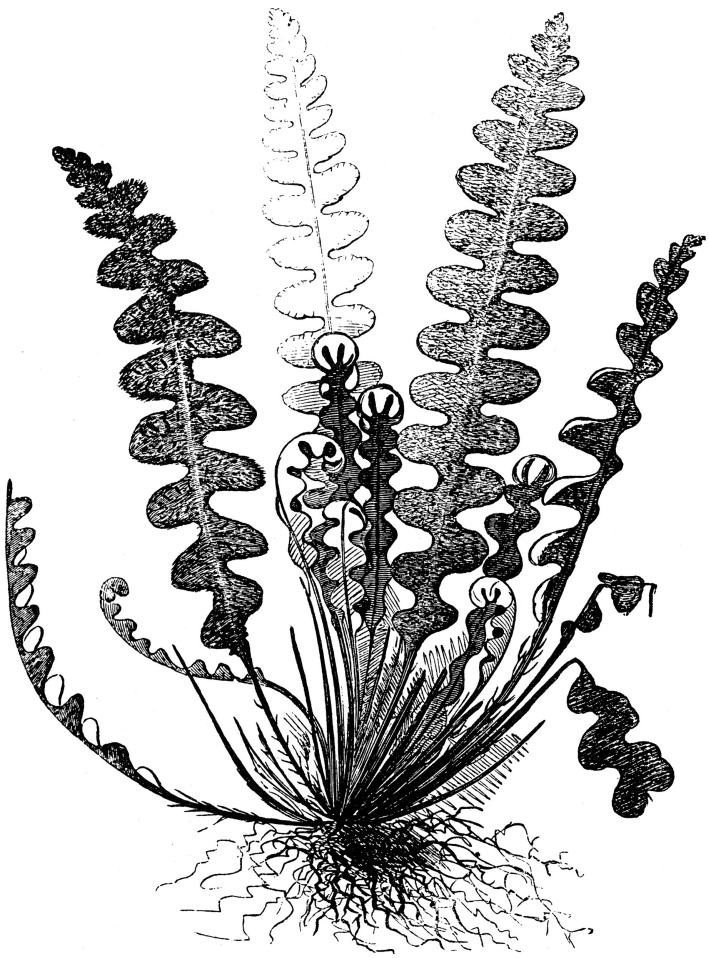
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