- Conservation Letters Open Access
A journal of the Society for Conservation Biology

Quiet, Nonconsumptive Recreation Reduces Protected Area Effectiveness

Authors

- Sarah E. Reed, Adina M. Merenlender

1.

- **First published:** 28 June 2008Full publication history
- **DOI:** 10.1111/j.1755-263X.2008.00019.xView/save citation
- **Cited by:** 37 articles

Sarah E. Reed, Center for Landscape Analysis, The Wilderness Society, 655 Montgomery St., Suite 1000, San Francisco, CA 94111, USA. Tel: (415) 398-1111 x109; fax: (415) 398-1632. E-mail: sarah_reed@tws.org

Abstract

Protected areas around the world were created with the goals of preserving biodiversity and providing nature-based recreation opportunities for millions of people. This dual mandate guides the management of the majority of the world's protected areas, but there is growing evidence that quiet, nonconsumptive recreation may not be compatible with biodiversity protection. We combined noninvasive survey techniques and DNA verification of species identifications to survey for mammalian carnivores in 28 parks and preserves in northern California. Paired comparisons of neighboring protected areas with and without recreation revealed that the presence of dispersed, nonmotorized recreation led to a five-fold decline in the density of native carnivores and a substantial shift in community composition from native to nonnative species. Demand for recreation and nature-based tourism is forecasted to grow dramatically around the world, and our findings suggest a pressing need for new approaches to the designation and management of protected areas.

Introduction

Every day, millions of people use the world's protected areas for the recreation, education, and tourism opportunities that they provide. In the United States, for example, the number of people who participated in day hiking increased by nearly 800% between 1960 and 2000 (Figure 1). The majority of global protected areas permit public access (IUCN Categories Ib-VI; **IUCN 1994**), and key reserve networks, including national park systems in Europe, North America, and Australia, operate under a dual mandate to provide recreational opportunities while conserving natural resources. Although many researchers have noted the harmful impacts of motorized recreation and extractive land uses on the conservation effectiveness of protected areas (for example, **Liu *et al.* 2001**), “quiet,” nonconsumptive activities, such as hiking and wildlife viewing, are widely assumed to be benign uses. The demand for nature-based tourism is forecasted to grow dramatically in urban regions (**Cordell *et al.* 2005**), as well as in global biodiversity hotspots (**Christ *et al.* 2003**), and quantitative information is needed to understand the trade-offs between public use and species protection.

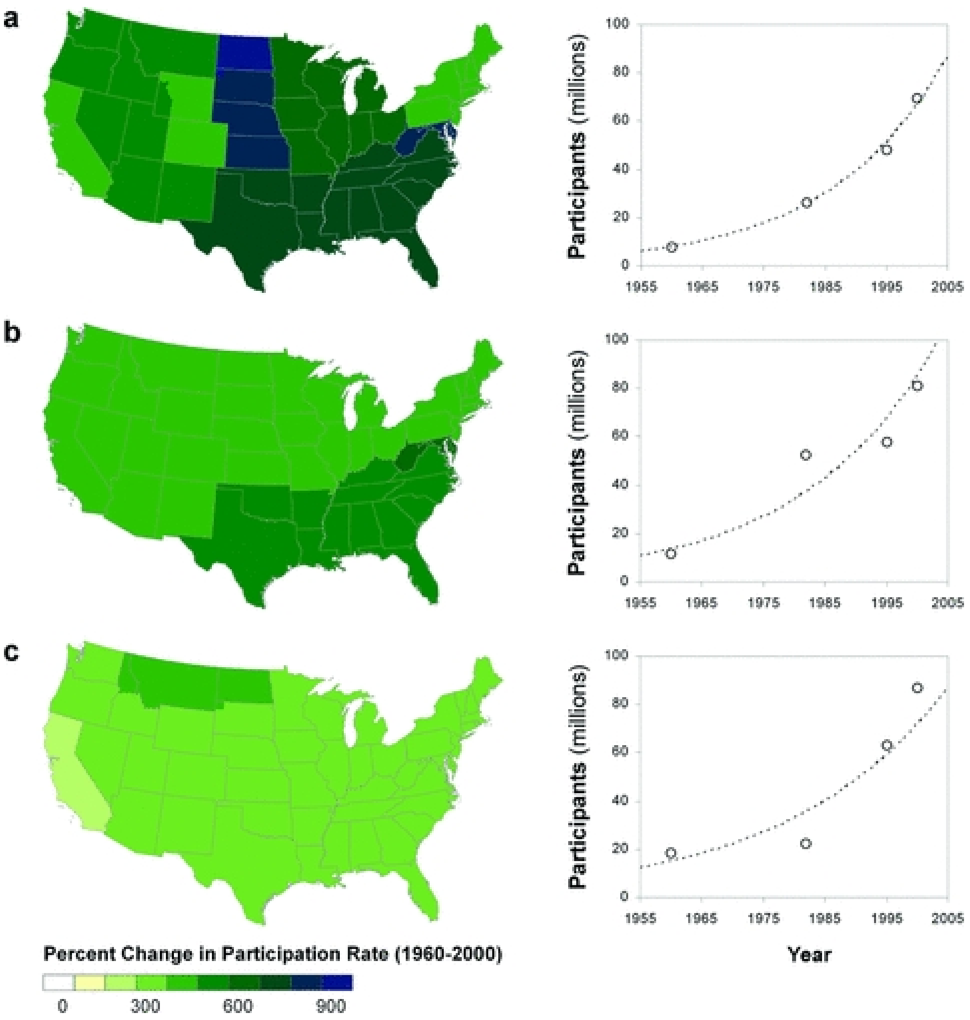

Figure 1.

Change in the rate and total number of U.S. citizens participating in three quiet, nonconsumptive recreational activities from 1960–2000. Geographic regions, participation rates, and numbers of participants in (a) day hiking, (b) bicycling, and (c) wildlife viewing are derived from the National Surveys on Recreation and the Environment (NSRE) conducted in 1960, 1982, 1995, and 2000 (http://www.srs.fs.usda.gov/trends/nrse/nrse2.html). NSRE surveys in 1960 and 1982 included individuals 12 years and older, whereas surveys in 1995 and 2000 included individuals 16 years and older. Dashed lines represent the best-fit exponential curves for changes in the number of participants over time.

Recreation is an important issue for ecologists and conservation planners to consider, because access for recreation is a key component of plans to generate public support and revenue for land conservation. Public parks and open space preserves are the primary places that most people access nature, and contact with nature has a range of human health benefits (**Frumkin 2001**). Ecologists have identified recreation as an ecosystem service supporting human populations (**Chan** ***et al.*** **2006**), and similarly, recreational opportunities are valued by economists as natural resource amenities driving economic growth and residential development patterns (**Hansen** ***et al.*** **2002**). Outdoor recreation enthusiasts are vocal advocates for land conservation (for example, **TNC 2005**), and public access is an important platform for generating tax and bond revenue for protected area acquisition.

However, recreation may not always be compatible with the conservation objectives of land protection. Recreation is the second leading cause of endangerment to species occurring on U.S. federal lands (**Losos** ***et al.*** **1995**), and there is growing evidence that nonmotorized activities have negative impacts on a wide range of wildlife species (**Knight & Gutzwiller 1995**). For example, recreational activity correlates with decreases in species abundances and activity levels (**Garber & Burger 1995**), causes wildlife to flee (**Papouchis** ***et al.*** **2001**) or avoid otherwise suitable habitat (**Taylor & Knight 2003**), and alters species composition and behavior (**Ikuta & Blumstein 2003**).

Few studies have examined recreation impacts in multiple parks or preserves (for example, **Forrest & St. Clair 2006**) or made comparisons between sites that do and do not permit recreation (for example, **Cole 1995**). In addition, the impacts of nonconsumptive recreation on mammalian carnivores are rarely investigated (for example, **Nevin & Gilbert 2005**). To understand how recreation impacts wildlife populations at the scale of resource management decisions, we need to examine recreation as a landscape-scale human disturbance process affecting whole species communities and ecosystems.

We surveyed the composition and density of mammalian carnivores to evaluate how biodiversity in protected areas was affected by the presence of quiet, nonconsumptive recreation. Here, we define quiet, nonconsumptive recreation to include dispersed, nonmotorized activities such as hiking, biking, and horseback riding. Wide-ranging and low-density carnivores are sensitive to human disturbance in fragmented landscapes (**Riley** ***et al.*** **2003**), and changes in carnivore composition and abundance can have cascading effects on prey species and vegetation communities (**Crooks & Soulé 1999**). In addition, research on habitat fragmentation has shown that variability in carnivore species' responses can be useful for identifying thresholds of human disturbance (**Crooks 2002**).

To minimize variation in habitat quality and landscape context among study sites, which could confound our ability to detect the impacts of recreation, we made paired comparisons of protected areas with recreation and nearby protected areas without recreation. We conducted transect searches for scats to maximize detections of a suite of carnivore species (**Reed & Leslie 2005**). Because visual identifications of sympatric carnivore scats can be highly unreliable (**Fernandez** ***et al.*** **1997**), we developed molecular genetic methods to confirm species identifications (**Bidlack** ***et al.*** **2007**).

Methods

We used a paired-site design to investigate how the presence of quiet, nonconsumptive recreation affects mammalian carnivore communities in 28 protected areas in Marin, Sonoma, and Napa Counties in northern California (122° 12′ to 122° 51′ W, 38° 0′ to 38° 37′ N; Figure 2). This region has a Mediterranean climate and is dominated by mixed oak woodlands. Over 1755 km^2 (23.3%) of land in the study area is under some form of protection. Nearly 60% of the protected land area is open to public access, 12.6% permits restricted access, and 27.4% is closed to the public (**BAOSC 2004**). The study area includes 25 incorporated cities and towns, and these protected areas are popular recreation destinations for the more than seven million residents of the greater San Francisco Bay Area. There is growing pressure on government agencies to purchase additional land for recreation and to expand public access in existing protected areas (**Wells 2000**).

Figure 2.

- Open in figure viewer
- Download Powerpoint slide

Locations of 14 pairs of protected areas with and without quiet, nonconsumptive recreation in northern California. To protect the privacy of landowners, only the center points of sites, their relative areas, and lines connecting paired sites are shown.

We first identified 14 parks and open space preserves that permitted public access for quiet, nonconsumptive recreational activities. We then used a spatial database of protected lands for the study region (**BAOSC 2004**) to identify 14 nearby (< 5 km) protected areas that did not permit recreation. Protected areas closed to recreation included public- and privately-owned biological preserves ($n = 1$ and 3, respectively) and private ranches with conservation easements ($n = 10$). Seven of these sites had private residences, three permitted limited access for research and educational activities, and two had narrow easements for regional trails along portions of their perimeters. The light and infrequent activities on these sites strongly contrasted with the regular and intense visitation to the public recreation areas.

We defined protected area perimeters according to the sites' administrative boundaries. Several sites were contiguous with other protected areas, but we did not include adjacent reserves in our calculations unless they were managed by the same individual or agency and permitted the same range of uses. Some protected areas were open to grazing by cattle and horses, including those that did ($n = 3$) and did not permit recreation ($n = 7$).

Pairs of protected areas were selected to be as similar in size, vegetation cover and adjacent land uses as possible (Table 1). We used ArcGIS 9.1 (ESRI, Redlands, CA, USA) to calculate site and landscape characteristics of the selected sites, and we used a paired-sample t-test (**Zar 1999**) to compare protected areas with and without recreation. Paired sites were located a mean of 1.8 km (range: 0–5.3 km) apart. The mean area of sites that permitted recreation was greater than the mean area of sites that did not permit recreation, but the there was no evidence for a difference between paired sites ($P = 0.49$). On average, sites without recreation were 79 m higher in elevation ($P = 0.0012$), but there was no evidence for a difference in slope ($P = 0.93$). All protected areas were located in oak woodland habitat, and sites with recreation had an average of 9.6% more hardwood forest cover ($P = 0.061$). Pairs of sites were located a similarly close to roads ($P = 0.89$), and the density of development was greater adjacent to protected areas that permitted recreation ($P = 0.10$). While these comparisons revealed some differences in protected area characteristics, the differences between paired sites were small relative to the total range of variability in the study system (Table 1), and the paired-site design represents our best effort to isolate the effects of recreation from other factors affecting carnivore distributions.

Table 1. Comparison of six site and landscape characteristics (mean ± s.d.) for protected areas with ($n = 14$) and without recreation ($n = 14$). The mean difference and probability of a Type I error (P) of paired comparisons are given for each variable, as well as the range of values throughout the study area.

Comparison	Study area range	Site type		Mean difference	
		Recreation	No recreation		
Area (ha)	0–2694.0	363.3 ± 491.7	254.5 ± 300.7	108.9	0.
Elevation (m)	0–832.0	183.0 ± 134.6	261.5 ± 164.6	–78.6	0.
Slope (°)	0–60.61	13.46 ± 6.39	13.54 ± 5.13	–0.09	0.
Hardwood cover (%)	0–100	51.01 ± 29.26	41.39 ± 26.00	9.61	0.
Distance to roads (m)	0–9486.8	408.5 ± 303.0	422.2 ± 257.7	–13.7	0.
Development density within 500	0.02–1940.62	7.54 ± 10.60	2.27 ± 1.90	5.28	0.

Comparison	Study area range	Site type		Mean difference
		Recreation	No recreation	
m (parcels/km^2)				

Our research focused on six common species: native coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and gray foxes (*Urocyon cinereoargenteus*), and nonnative red foxes (*Vulpes vulpes*), domestic dogs (*Canis familiaris*), and domestic cats (*Felis catus*). We conducted transect searches for scats to maximize detections of multiple carnivores (**Reed & Leslie 2005**) and to provide an index of species' densities (**Harrison *et al.* 2004**). We surveyed the study sites between June and September 2005. We visited each site once, and we visited paired protected areas within 24 hours of one another to minimize possible sources of temporal variation (**Sanchez *et al.* 2004**). We searched eight 500-m line transects in protected areas with recreation and four 500-m line transects in protected areas without recreation. To investigate how our observations were influenced by the locations of trails or land uses adjacent to protected areas, we stratified the transect locations on- and off-trail in the recreation areas and between the edges and interiors of all sites.

We collected and recorded the GPS point location of each probable mammalian carnivore scat detected during the transect searches. Because the ground cover in oak woodlands is relatively open, we estimate that we were able to detect scats within approximately 2 m of the transect search line. We stored each scat in a paper bag with a clay desiccant packet (Texas Technologies, Cedar Park, TX, USA). We also recorded the GPS point location for all domestic dog scats detected during the transect searches.

We developed molecular genetic methods to confirm species identifications for the collected scats (**Bidlack *et al.* 2007**) because visual identifications of scats from closely related species can be highly unreliable (**Fernandez *et al.* 1997**). We extracted and amplified DNA from collected scats between October 2005 and May 2006. We took two subsamples (approximately 500 mg) of each scat within 3 d of collection and stored them in a –80 °C freezer. We extracted DNA using Qiagen QIAamp DNA Stool extraction kits (Qiagen, Inc., Valencia, CA, USA) according to the manufacturer's instructions and stored extracted DNA in a –80 °C freezer.

We performed PCR amplification of DNA using Qiagen Taq PCR Master Mix kits (Qiagen, Inc.). We used HCarn200 (**Bidlack *et al.* 2007**) and CanidL1 (**Paxinos *et al.* 1997**) primers to amplify the first 196 bp of the mitochondrial cytochrome b gene. Each 20 µl PCR reaction contained 10 µl Qiagen Taq PCR Master Mix, 1 µl 10 µM HCarn200 primer, 1 µl 10 µM CanidL1 primer, 6 µl deionized H_20, and 2 µl diluted (1:50) DNA template. Thermal cycling was initiated at 94 °C for 2 minutes, followed by 40 cycles of 94 °C for 1 minute, 54 °C for 1 minute, and 72 °C for 2 minutes. All PCR reactions included at least one negative control to monitor for contamination, and we used electrophoresis to check each reaction for successful amplification. We repeated DNA amplification for all samples that failed to amplify in the first PCR reaction, and when necessary, we used additional subsamples to ensure a minimum sample size of 75% of the scats collected in each site.

We used restriction fragment length polymorphisms (RFLP) to identify amplified DNA fragments to species. We first digested PCR products with Hpa II (New England Biolabs, Ipswich, MA, USA) to separate canids from felids. Hpa II does not cut fragments from any of the three canid species (coyote, gray fox, and red fox) but cuts fragments from both felid species (bobcat and domestic cat) at 140 bp. We then digested samples identified as canid with HpyCH4 V (New England Biolabs). HpyCH4 V does not cut fragments from coyote, but cuts gray fox at 67 and 85 bp and red fox at 136 bp. We digested samples identified as felid with Bsl I (New England Biolabs). Bsl I does not cut fragments from bobcat, but cuts domestic cat at 150 bp.

Each 10 µl digest reaction contained 3.75 µl deionized H_20, 1 µl digest buffer, 0.25 µl restriction enzyme, and 5 µl PCR product. Reactions were incubated for 4–6 hours, according to manufacturer's instructions. We used electrophoresis to separate the products for 40 minutes on a 1.7% agarose gel and visualized the predicted cutting patterns using ethidium bromide and UV light. Failed or ambiguous digests were repeated, and digests that failed twice were excluded from further analysis.

All statistical analyses were performed using JMP 6.0 (SAS Institute, Cary, NC, USA). We used log-likelihood ratio tests (G-test; **Zar 1999**) to compare how frequently we detected each species in protected areas with and without recreation. We used paired-sample t-tests to compare native and nonnative species diversity and species densities between protected areas with and without recreation. Species densities were calculated as the number of scats detected divided by the length of transects searched (**Harrison *et al.* 2004**). We approximated the total scat densities along each transect by extrapolating the proportions of species detected in each site to the samples that we were unable to identify in the laboratory. For example, in a site where laboratory identifications were evenly divided between coyotes and bobcats, we assumed that half of the unknown scats were from coyotes and half from bobcats. We verified that extrapolating the species origin of unknown scats did not influence the results of our analysis by repeating all of the density comparisons including only those scat samples that were successfully identified in the laboratory. Paired-sample t-tests were also used to compare species densities between transects located on- and off-trail in the recreation sites, and species densities between the edges and interiors of all sites. Lastly, we used nonparametric Wilcoxon rank-sum tests to confirm the results of all paired comparisons, but statistical results are only reported for the parametric tests.

Results

The presence of quiet, nonconsumptive recreation correlated with a substantial shift in the composition of the carnivore community in California protected areas. A greater mean number of native species was detected in protected areas that did not permit recreation (Figure 3) ($P = 0.0011$) and bobcats in particular were detected more frequently in protected areas without recreation ($P = 0.013$). On the other hand, more nonnative species were detected in protected areas that permitted recreation (Figure 3) ($P < 0.001$), and domestic dogs were detected more frequently in the recreation areas ($P < 0.001$).

Figure 3.

- Open in figure viewer
- Download Powerpoint slide

Native and nonnative species diversity in protected areas with and without recreation. Mean numbers of species detected and standard errors are given for each type of site. Two asterisks (**) indicate a mean difference between paired sites with Type I error of $P < 0.01$, and three asterisks (***) indicate a difference with $P < 0.001$.

Densities of coyotes and bobcats were more than five times lower in protected areas that permitted recreation (Figure 4) ($P < 0.001$ and $P = 0.0029$, respectively), and we observed declines in density for both species between all 14 pairs of protected areas. Domestic dogs were not detected in protected areas without recreation, but we detected substantial densities (7.69 ± 2.57 scats km^{-1}) of dogs in the recreation areas (Figure 4) ($P = 0.0052$). We did not find evidence of any effects of trail location or protected area edge on the distributions of native carnivores. With the exception of domestic dogs, there was no evidence for differences in species' densities between transects located on- or off-trail or between transects located at the edges or interiors of the protected areas (Table 2).

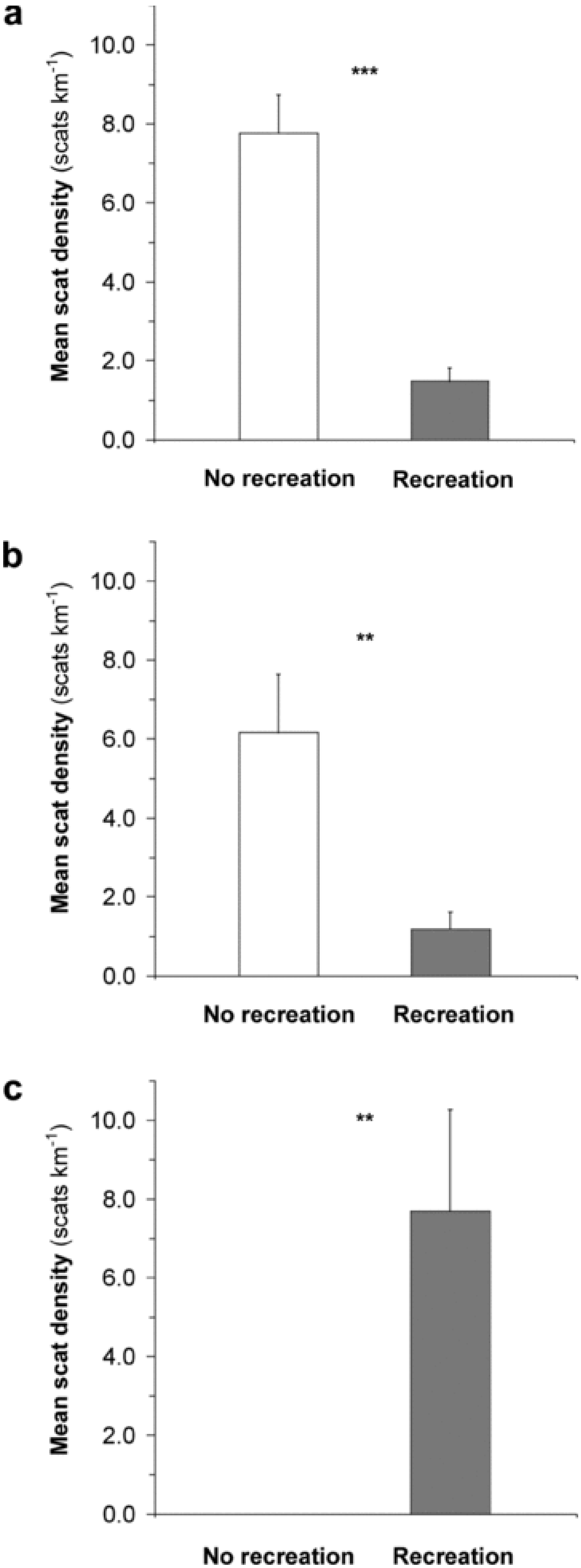
a
Mean scat density (scats km^{-1})
10.0
8.0
6.0
4.0
2.0
0.0
***
No recreation
Recreation
b
Mean scat density (scats km^{-1})
10.0
8.0
6.0
4.0
2.0
0.0
**
No recreation
Recreation
c
Mean scat density (scats km^{-1})
10.0
8.0
6.0
4.0
2.0
0.0
**
No recreation
Recreation

Figure 4.

- Open in figure viewer
- Download Powerpoint slide

Densities of (a) coyotes, (b) bobcats, and (c) domestic dogs in protected areas with and without recreation. Mean numbers of scats detected per kilometer of transect surveyed and standard errors are given for each type of site. Two asterisks (**) indicate a mean difference between paired sites with Type I error of $P < 0.01$, and three asterisks (***) indicate a difference with $P < 0.001$.

Table 2. Distribution of carnivore detections within protected areas. Densities (mean ± s.d.) of all species detected on transects at the edges versus the interiors of all sites, and on- versus off-trail in sites that permitted recreation. Paired comparisons with reasonable evidence of a mean differences (Type I error approaching 0) are indicated with bold type

Site type	Transect location	Mean scat density (scats km^{-1})					
		Coyote	Bobcat	Gray fox	Red fox	Dom. cat	Dom.
No recreation	Edge	8.72 ± 4.71	5.27 ± 4.16	0.73 ± 1.52	0.23 ± 0.58	0.30 ± 1.12	0
	Interior	7.75 ± 5.14	7.92 ± 12.22	0.21 ± 0.52	0.32 ± 0.90	0	0
Recreation	Edge	1.38 ± 1.40	1.09 ± 1.79	0.30 ± 0.64	0	0.15 ± 0.31	**12.49 ±**
	Interior	1.57 ± 1.72	1.23 ± 1.50	0.25 ± 0.92	0.03 ± 0.13	0.28 ± 0.77	**3.24 ± 5**
	On-trail	1.78 ± 1.90	1.23 ± 1.79	0.28 ± 0.74	0	0.17 ± 0.48	**11.53 ±**
	Off-trail	1.13 ± 1.70	1.10 ± 1.31	0.22 ± 0.67	0.03 ± 0.11	0.31 ± 0.68	**1.73 ± 2**

Discussion

The results of our carnivore surveys indicate that quiet, nonconsumptive recreation has a consistent and site-level impact on the distribution and densities of native carnivore species, and consequently, the effectiveness of protected areas for biodiversity conservation. Protected areas with recreation had more nonnative carnivores and dramatically lower densities of native species. We describe the effect of recreation as consistent, because we observed declines in native carnivore densities between all 14 pairs of protected areas, even those that were directly adjacent to one another. In addition, we suggest that the effect of recreation functions at the site level, because we did not observe effects of protected area edge or the locations of trails for any species except domestic dogs. The configuration of recreational trails may be important for determining recreation impacts in larger landscapes with more dispersed activities (for example, **Taylor & Knight 2003**). However, for moderately sized protected areas (50–2000 ha) near urban development, the key variable seems to be whether or not the site is open to public access.

Our paired-site study design helped us to isolate the effects of recreation from other sources of variation affecting carnivore distributions, including regional geographic variation, landscape context, and habitat characteristics. In addition, transect searches for scats, paired with DNA verification of species identifications, provided an efficient and accurate method for assessing the impacts of recreation in a large number of sites at a landscape scale. The detectability of scats likely varied between on- and off-trail transects, but it is not clear how much this variability affected the results. Although scats may have been obscured by vegetation along off-trail transects, scats also may have been crushed or otherwise removed from busy recreational trails. Regardless, there is no evidence to suggest that within recreation sites, native carnivores avoided recreational trails. This result is consistent with other studies that have found that carnivores often select low-traffic roads and trails as travel corridors (**Whittington** ***et al.*** **2005**).

Declines in native carnivores and introductions of nonnative species can alter the trophic structure of ecosystems and lead to unsustainable predation pressure on native birds and small mammals (**Crooks & Soulé 1999**). Two of the three nonnative carnivores that we detected in the recreation areas are strongly human-commensal species: domestic cats and domestic dogs. Cats and dogs are introduced to protected areas by people in a variety of ways; they accompany humans as companion pets, they are allowed to roam from nearby homes, or in the case of cats, they are managed in feral colonies (**Castillo & Clarke 2003**).

We detected domestic dogs more frequently and in much greater densities in the recreation areas. Domestic dogs are often a particular focus of protected area management policy, due to concerns about their impacts on resources as well as conflicts among user groups (**Miller** ***et al.*****2001**). Many public agencies exclude dogs from recreation areas or require dogs to be on leash (**Forrest & St. Clair 2006**), and an investigation of how mammalian carnivores respond to these different dog management policies is underway.

The design of our study did not address the mechanisms of human disturbance affecting carnivores in recreation areas; however, prior researchers have documented various behavioral responses of wildlife species to recreational disturbances, including flight (**Papouchis** ***et al.*** **2001**), avoidance (**Taylor & Knight 2003**), and reduction in habitat use (**Fairbanks & Tullous 2002**). Our analysis extends the results of these behavioral studies to characterize recreational disturbance to wildlife at a landscape scale, and the native carnivore declines that we observed provide us with an estimate of the cost, in terms of biodiversity and habitat suitability, of opening protected areas to public access.

Certainly, access for outdoor recreation will continue to be an important component of plans to generate public support and revenue for land conservation (for example, **Wells 2000**). When protected areas are designated for biodiversity conservation, development of nature-based tourism can yield economic benefits for local communities (**Eagles** ***et al.*** **2002**) and recreation areas provide health and ecosystem services for human populations (**Frumkin 2001**; **Chan** ***et al.*** **2006**). On the other hand, given the biodiversity crises we are facing around the world, public access needs to be balanced with the protection of native species and ecosystems.

Recent evidence indicates that participation in nature-based recreation may be declining (**Pergams & Zaradic 2008**). Our study focused on recreational activity in local parks, which has not necessarily declined in the same manner as visitation to national-level public lands, and may be increasing (for example, **OSMP 2005**). In fact, pressures on protected areas near urban centers could be even greater due to increasing oil costs and a declining economy, which may limit visitation to more distant parks.

A variety of management strategies have been proposed to minimize the impacts of recreation on wildlife, such as limiting the number of visitors via a permit system (**Garber & Burger 1995**), restricting public access to certain times of the year (**Klein** ***et al.*** **1995**), or closing a portion of a protected area to recreation and setting it aside as a biological preserve (**Ikuta & Blumstein 2003**). However, recreation impacts vary nonlinearly with use in a variety of ecosystems (for example, **Cole 1986**), such that a small number of visitors can have a disproportionate impact on sensitive species. In addition, many public agencies have limited resources for monitoring recreational use and enforcing compliance with management policies (**Forrest & St. Clair 2006**). These limitations suggest that it may be more effective to allocate recreational uses and conservation targets among different sites, and this approach will require a diverse suite of land conservation strategies.

Private lands play an important role in biodiversity protection, in part because private properties frequently occupy lower-elevation, higher-productivity lands than public protected areas (**Hansen** ***et al.*** **2002**; **Maestas** ***et al.*** **2003**). Our paired comparisons in hardwood rangelands indicate that a further advantage of private reserves is the absence of human recreational use, and these results provide strong support for conservation strategies that incorporate private lands. For example, conservation easements, which generally limit public access (**Rissman** ***et al.*** **2007**), may be particularly valuable for protecting biodiversity in areas with high demand for recreation. Ultimately, these considerations should be incorporated into the design of reserve networks. Conservation planning should take into account not only the spatial distribution of species, but also the demand for recreational use and other human activities, and the compatibility of those activities with long-term conservation objectives.

Editor : Richard Krannich

Acknowledgments

We are grateful to the Audubon Canyon Ranch, California Academy of Sciences, California Department of Fish and Game, California State Parks, Marin Agricultural Land Trust, Marin County Open Space District, Napa City Parks, Napa County Parks, Napa Land Trust, Sonoma County Agricultural Preservation and Open Space District, Sonoma County Regional Parks, Sonoma Land Trust, Sonoma State University, and numerous private landowners for permission to survey their properties. The Hopland Research and Extension Center provided equipment and logistical support for field surveys, and the laboratory of P. J. Palsbøll provided equipment and guidance for genetic analyses. We thank J. S. Brashares, D. A. Newburn, R. L. Pressey, D. M. Theobald, and two anonymous reviewers for helpful comments, which improved this manuscript. S.E.R. was supported by a National Science Foundation Graduate Research Fellowship, Sigma Xi Grant-In-Aid-of-Research, Phi Beta Kappa Doctoral Fellowship, Budweiser Conservation Scholarship, Switzer Environmental Fellowship and the Department of Environmental Science, Policy and Management.

Ancillary

References

- Bay Area Open Space Council (BAOSC) (2004) *Bay Area Protected Lands Database [Shapefile]*. Available from http://openspacecouncil.org/projects/bapldb. Accessed 2004.
- Bidlack, A.L., Reed S.E., Palsbøll P.J., Getz W.M. (2007) Characterization of a western North American carnivore community using PCR-RFLP of cytochrome b obtained from fecal samples. *Conserv Genet* **8**, 1511–1513.
  - CrossRef |
  - CAS |
  - Web of Science® Times Cited: 1
- Castillo, D., Clarke A.L. (2003) Trap/neuter/release methods ineffective in controlling domestic cat “colonies” on public lands. *Nat Area J* **23**, 247–253.
  - Web of Science® Times Cited: 10
- Chan, K.M.A., Shaw R., Cameron D.R., Underwood E.C., Daily G.C. (2006) Conservation planning for ecosystem services. *PLOS Biol* **4**, 2138–2152.
  - CrossRef |
  - CAS |
  - Web of Science® Times Cited: 55
- Christ, C., Hillel O., Matus S., Sweeting J. (2003) *Tourism and biodiversity: mapping tourism's global footprint*. Conservation International, Washington , D.C .
- City of Boulder Open Space and Mountain Parks (OSMP) (2005) *Visitor master plan*. Available from http://www.ci.boulder.co.us/files/openspace/pdf_VMP/Final-VMP.pdf. Accessed 4 April 2008.
- Cole, D.N. (1986) Recreational impacts on backcountry campsites in Grand Canyon National Park, Arizona, USA. *Environ Manag* **10**, 651–659.
  - CrossRef |
  - Web of Science® Times Cited: 16 |
  - ADS

- Cole, D.N. (1995) Experimental trampling of vegetation I: relationship between trampling intensity and vegetation response. *J Appl Ecol* **32**, 203–214.
    - CrossRef |
    - Web of Science® Times Cited: 39
- Cordell, H.K., Green G.T., Leeworthy V.R., Stephens R., Fly M.J., Betz C.J. (2005) United States of America: outdoor recreation. Pages 245–264 in G.Cushman, A.J.Veal, J.Zuzanek, editors. *Free time and leisure participation: international perspectives*. CABI Publishing, Wallingford , U.K.
    - CrossRef |
    - Web of Science® Times Cited: 4
- Crooks, K.R. (2002) Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conserv Biol* **16**, 488–502.
    - Wiley Online Library |
    - Web of Science® Times Cited: 95
- Crooks, K.R., Soulé M.E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature***400**, 563–566.
    - CrossRef |
    - CAS |
    - Web of Science® Times Cited: 314 |
    - ADS
- Eagles, P.F.J., McCool S.F., Haynes C.D. (2002) *Sustainable tourism in protected areas: guidelines for planning and mana- gement*. IUCN, Gland and Cambridge , United Kingdom .
    - CrossRef
- Fairbanks, W.S., Tullous R. (2002) Distribution of pronghorn (*Antilocarpa americana ord*) on Antelope Island State Park, Utah, USA, before and after establishment of recreational trails. *Nat Area J* **22**, 277–282.
    - Web of Science® Times Cited: 8
- Fernandez, G.J., Corley J.C., Capurro A.F. (1997) Identification of cougar and jaguar feces through bile acid chromatography. *J Wildlife Manage* **61**, 506–510.
    - CrossRef |
    - Web of Science® Times Cited: 9
- Forrest, A., St. Clair C.C. (2006) Effects of dog leash laws and habitat type on avian and small mammal communities in urban parks. *Urban Ecos* **9**, 51–66.
    - CrossRef
- Frumkin, H. (2001) Beyond toxicity: human health and the natural environment. *Am J Prev Med* **20**, 234–240.
    - CrossRef |
    - PubMed |
    - CAS |
    - Web of Science® Times Cited: 21
- Garber, S.D., Burger J. (1995) A 20-yr study documenting the relationship between turtle decline and human recreation. *Ecol Appl* **5**, 1151–1162.
    - CrossRef |
    - Web of Science® Times Cited: 45
- Hansen, A.J., Rasker R., Maxwell B. *et al* . (2002) Ecological causes and consequences of demographic change in the New West. *BioScience* **52**, 151–162.
    - CrossRef |
    - Web of Science® Times Cited: 67
- Harrison R.L., Clarke P.S., Clarke C.M. (2004) Indexing swift fox populations in New Mexico using scats. *Am Midl Nat* **151**, 42–49.
    - CrossRef |
    - Web of Science® Times Cited: 6
- Ikuta, L.A., Blumstein D.T. (2003) Do fences protect birds from human disturbance? *Biol Conserv* **112**, 447–452.
    - CrossRef |
    - Web of Science® Times Cited: 28
- Klein, M.L., Humphrey S.R., Percival H.F. (1995) Effects of ecotourism on distribution of waterbirds in a wildlife refuge. *Conserv Biol* **9**, 1454–1465.
    - Wiley Online Library |
    - Web of Science® Times Cited: 42

- Knight, R.L., Gutzwiller K.J. (1995) *Wildlife and recreationists: coexistence through management and research*. Island Press, Washington , D.C .
- Liu, J., Linderman M., Ouyang Z., An L., Yang J., Zhang H. (2001) Ecological degradation in protected areas: the case of Wolong Nature Reserve for giant pandas. *Science* **292**, 98–101.
  - CrossRef |
  - PubMed |
  - CAS |
  - Web of Science® Times Cited: 127 |
  - ADS
- Losos, E., Hayes J., Phillips A., Wilcove D., Alkire C. (1995) Taxpayer-subsidized resource extraction harms species. *BioScience* **45**, 446–455.
  - CrossRef |
  - Web of Science® Times Cited: 10
- Maestas, J.D., Knight R.L., Gilgert W.C. (2003) Biodiversity across a rural land-use gradient. *Conserv Biol* **17**, 1425–1434.
  - Wiley Online Library |
  - Web of Science® Times Cited: 45
- Miller, S.G., Knight R.L., Miller C.K. (2001) Wildlife responses to pedestrians and dogs. *Wildlife Soc Bull* **29**, 124–132.
  - Web of Science® Times Cited: 36
- Nevin, O.T., Gilbert B.K. (2005) Perceived risk, displacement and refuging in brown bears: positive impacts of ecotourism? *Biol Conserv* **121**, 611–622.
  - CrossRef |
  - Web of Science® Times Cited: 15
- Papouchis, C.M., Singer F.J., Sloan W.B. (2001) Responses of desert bighorn sheep to increased human recreation. *J Wildlife Manage* **65**, 573–582.
  - CrossRef |
  - Web of Science® Times Cited: 42
- Paxinos, E., McIntosh C., Ralls K., Fleischer R. (1997) A noninvasive method for distinguishing among canid species: amplification and enzyme restriction of DNA from dung. *Mol Ecol* **6**, 483–486.
  - Wiley Online Library |
  - PubMed |
  - CAS |
  - Web of Science® Times Cited: 59
- Pergams, O.R.W., Zaradic P.A. (2008) Evidence for a fundamental and pervasive shift away from nature-based recreation. *Proc Roy Acad Sci* **105**, 2295–2300.
  - CrossRef |
  - PubMed |
  - Web of Science® Times Cited: 11 |
  - ADS
- Reed, S.E., Leslie E.F. (2005) Patterns of carnivore co-occurrence on the North Rim, Grand Canyon National Park. Pages 309–316 in C.Van Riper, D.J.Mattson, editors. *The Colorado Plateau II: biophysical, socioeconomic and cultural research*. University of Arizona Press, Tucson .
  - Web of Science®
- Riley, S.P.D., Sauvajot R.M., Fuller T.K. *et al* . (2003) Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conserv Biol* **17**, 566–576.
  - Wiley Online Library |
  - Web of Science® Times Cited: 40
- Rissman, A.R., Comendant T., Lozier L. *et al* . (2007) Conservation easements: private use and biodiversity protection. *Conserv Biol* **21**, 709–718.
  - Wiley Online Library |
  - PubMed |
  - Web of Science® Times Cited: 10
- Sanchez, D.M., Krausman P.R., Livingston T.R., Gipson P.S. (2004) Persistence of carnivore scat in the Sonoran Desert. *Wildlife Soc B* **32**, 366–372.
  - Wiley Online Library |

  - Web of Science® Times Cited: 7
- Taylor, A.R., Knight R.L. (2003) Wildlife responses to recreation and associated visitor perceptions. *Ecol Appl* **13**, 951–963.
  - CrossRef |
  - Web of Science® Times Cited: 41
- The Nature Conservancy (TNC) (2005) Outdoor recreation and conservation groups urge congress to preserve vital conservation tax incentive tool [press release]. Available from http://www.nature.org/pressroom/press/press1851.html. Accessed 18 January 2008.
- Wells, J. (2000) *Greenbelt gaining ground in Sonoma County[news story]*. Available from http://www.sfgate.com/cgi-bin/article.cgi?file=/chronicle/archive/2000/09/28/MN9975.DTL. Accessed 18 January 2008.
- Whittington, J., St. Clair C.C., Mercer G. (2005) Spatial responses of wolves to roads and trails in mountain valleys. *Ecol Appl* **15**, 543–553.
  - CrossRef |
  - Web of Science® Times Cited: 23
- The World Conservation Union (IUCN). (1994) *Guideline for protected area management categories*. IUCN, Gland, Switzerland and Cambridge , United Kingdom .
- Zar, J.H. (1999) *Biostatistical analysis*. 4th edn. Prentice Hall, Upper Saddle River, New Jersey .