THESIS

IMPLICATIONS OF OUTDOOR RECREATION FOR WILDLIFE CONSERVATION IN PROTECTED AREAS

Submitted by

Courtney Louise Larson

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Spring 2015

Master's Committee:

Advisor: Kevin R. Crooks
Co-Advisor: Sarah E. Reed

Richard L. Knight

ABSTRACT

IMPLICATIONS OF OUTDOOR RECREATION FOR WILDLIFE CONSERVATION IN PROTECTED AREAS

Outdoor recreation is an ecosystem service provided by most protected areas worldwide, and it is usually assumed to be compatible with conservation goals. Since participation in outdoor recreation is growing globally, this presents a dilemma for conservation planners and protected area managers who must manage this demand for recreation while working to protect species. In this thesis, I present the results of a systematic review that summarizes and analyzes the scientific literature on the effects of recreation on animals (Chapter 1). I then describe the findings of a field study in which my co-authors and I measured and modeled recreation in a network of reserves in order to understand variability in human use of reserves (Chapter 2).

An increasing number of studies are discovering negative effects of recreation on animals. My co-authors and I used a systematic review process to analyze 218 articles on recreation impacts on wildlife, without restrictions on geographic area, taxonomic group, or recreation activity. We quantified trends in publication rates and outlets, identified major knowledge gaps, and assessed evidence for negative and positive effects of recreation. Although publication rates are low and knowledge gaps remain, the evidence was clear with over 93% of reviewed articles documenting at least one effect of recreation on wildlife. Birds (39% of articles) and mammals (37%) were the focus of the majority of recreation studies, whereas research on 1) amphibians, reptiles, and fish, 2) locations in South America, Asia, and Africa, and 3) responses at the population and community levels was lacking. Although responses are

likely to be species-specific in many cases, some taxonomic groups (e.g., passerine birds, shorebirds, ungulates, and coral) had more evidence of an effect of recreation. Counter to public perception, non-motorized activities had more evidence of a recreation effect than motorized activities, and snow-based activities had more evidence of an effect than other activities.

In the second chapter, we sought to understand the variation in recreation activity at a network of reserves in San Diego County, California. We empirically measured spatial and temporal variability in recreation to identify biophysical and socioeconomic factors that influenced activity patterns. We measured recreation with remotely-triggered cameras and an expert opinion survey, and we used random forest models to identify important factors and make predictions to unsampled reserves. Accessibility variables (e.g., numbers of housing units, parking lots, and entrances), trail density, and the number of nearby reserves were important variables with strong positive relationships with visitation levels. This predictive model has applications for reserve planning as human populations continue to grow, and can be used to compare species exposure to recreation to prioritize future study and potential conservation interventions. Understanding the variability in visitation patterns can help inform protected area management policies that will more effectively balance human recreation with biodiversity conservation.

ACKNOWLEDGEMENTS

I would first like to thank my co-advisors, Sarah Reed and Kevin Crooks, for their guidance and support throughout each of the stages of this project, including future work. I am lucky to have advisors who are excellent mentors as well as inspiring scientists. Thank you to my co-author Adina Merenlender for help in planning this project and for her improvements to manuscripts, and to Rick Knight for serving on my committee and providing helpful suggestions along the way. I would like to thank Ron Rempel, Yvonne Moore, Kristine Preston, and Emily Perkins of the San Diego Management and Monitoring Program and Jeff Tracey and Robert Fisher of the U.S. Geological Survey Western Ecological Research Center for sharing spatial data and for assistance and advice in planning and implementing my fieldwork. Thank you to Andra Bontrager of the Wildife Conservation Society for digitizing trails, and to Grete Wilson-Henjum, Rachel Larson, Toryn Shafer, and Nicole Kirwan for their hard work reviewing and sorting camera trap images. Many rangers, reserve managers, and other reserve staff helped with the logistics for my fieldwork and responded to my survey, for which I am grateful. This research was supported by a grant from the California Department of Fish and Wildlife and also by the Wildlife Conservation Society, the Colorado State University Graduate School, GIS Colorado, and the Warner College of Natural Resources. I am grateful to my parents Elaine and Steve Larson and siblings Hannah and Owen Larson for inspiring my enthusiasm for science and the outdoors. Finally, I would like to thank my husband, Jeff Carroll, for helping me to believe I could be a scientist.

TABLE OF CONTENTS

ABSTRACT ii
ACKNOWLEDGEMENTS iv
CHAPTER ONE 1
Introduction 1
Methods 4
Results 9
Discussion 14
Tables 20
Figures 22
LITERATURE CITED 28
CHAPTER TWO 37
Introduction 37
Methods 40
Results 46
Discussion 49
Tables 53
Figures 55
LITERATURE CITED 61
APPENDIX I 67
APPENDIX II 80

CHAPTER ONE[1]

EFFECTS OF RECREATION ON ANIMALS REVEALED AS WIDESPREAD THROUGH A GLOBAL SYSTEMATIC REVIEW

Introduction

Participation in outdoor recreation, ranging in scope from international ecotourism to local park visits, is growing globally. In the United States, the number of participants in outdoor recreation increased by 7.5% and total visitor days increased by 32.5% between 2000 and 2009 (Cordell 2012). Driven in part by rapid growth in international tourism (UNWTO 2014), recreation and ecotourism are also expanding in the developing world (O'Connor et al. 2009); visits to protected areas in Africa, Asia, and Latin America increased approximately 2.5 to 5% between 1992 and 2006 (Balmford et al. 2009).

Recreation is commonly assumed to be compatible with biodiversity conservation, in contrast to more well-known threats such as population growth and residential development at protected area edges (Wittemyer et al. 2008; Wade & Theobald 2010) or subsistence use within reserves to help sustain local livelihoods (Naughton-Treves et al. 2005). Most protected areas have a dual mandate to conserve biodiversity and improve human welfare through resource use or outdoor recreation (Naughton-Treves et al. 2005; Reed & Merenlender 2008). Accordingly, recreation is permitted in over 94% of the land in International Union for Conservation of Nature (IUCN) protected areas globally (categories Ib-VI; Eagles et al. 2002; IUCN & UNEP 2014). In the United States and other developed nations, providing opportunities for outdoor recreation has historically been an important reason for the designation of protected areas (Becken & Job

---

[1] Manuscript co-authored with Sarah E. Reed, Adina M. Merenlender, and Kevin R. Crooks

2014), while in the developing world, ecotourism has been embraced as a potential win-win solution for poverty alleviation and conservation (Naughton-Treves et al. 2005). Furthermore, there are numerous benefits of outdoor recreation for human health and communities. People with access to natural areas have lower mortality rates (McCurdy et al. 2010), and outdoor play promotes mental and physical health in children (Louv 2005). Recreation and ecotourism can also be a source of economic revenue for protected areas and the communities around them, and can help garner support for conservation (Bushell & Eagles 2007; Zaradic et al. 2009).

Despite these benefits, there is growing recognition that non-consumptive outdoor recreation can have negative impacts on biological communities. Recreation is a leading factor in endangerment of plant and animal species on United States federal lands (Losos et al. 1995), and is a threat to birds in 65% of biodiversity hotspots (Steven & Castley 2013). Effects of recreation on animals include behavioral responses such as increased flight and vigilance (Mainini et al. 1993; Naylor et al. 2009); changes in spatial or temporal habitat use (George & Crooks 2006; Rogala et al. 2011); declines in abundance, occupancy, or density (Banks & Bryant 2007; Reed & Merenlender 2008); physiological stress (Müllner et al. 2004; Arlettaz et al. 2007); reduced reproductive success (Beale & Monaghan 2005; Finney et al. 2005); and altered species richness and community composition (Riffell et al. 1996; Kangas et al. 2010). Many species respond similarly to human disturbance and perceived predation risk, forcing a trade-off between risk avoidance and fitness-enhancing activity such as foraging or caring for young (Frid & Dill 2002).

Although there is a growing body of empirical studies of the effects of recreation on animals, a recent global and systematic review does not exist. Early reviews (Boyle & Samson 1985; Pomerantz et al. 1988; Duffus & Dearden 1990; Knight & Gutzwiller 1995) provide valuable definitions and conceptual frameworks, but were not systematic and need updating to reflect literature published in recent decades. In addition, contemporary reviews have restricted their scope by location or habitat type (Marzano & Dandy 2012; Sato et al. 2013; Barros et al. 2014), taxonomic group (Wolfe et al. 2000; Stankowich 2008; Showler et al. 2010; Martínez-Abraín et al. 2010; Steven et al. 2011), or recreation activity (Orams 2002; Newsome et al. 2004; Parsons 2012).

We conducted a systematic review of the published scientific literature to synthesize global effects of recreation across all animal taxa. Such a review facilitates the evidence-based conservation necessary to help bridge the gap between conservation science and practice (Pullin & Knight 2009). To aid decision-makers faced with dilemmas about managing the demand for recreation while trying to fulfill mandates to protect species, it is critical to understand the degree to which biodiversity conservation and recreation are compatible, and under what circumstances. First, we examined trends in recreation research, including publication rates over time, geographic distribution, and study design. Second, we investigated which taxonomic groups were most commonly studied, and which had more or less evidence for effects of recreation. Similarly, we examined which recreation activities and types of responses (e.g., behavioral, abundance, or survival) were most frequently measured, and what effects were observed. Finally, we summarized the management strategies proposed by the authors to avoid or mitigate these effects.

Methods

Selection of articles

We systematically searched for articles using the Institute for Scientific Information Web of Science database (Thompson Reuters, New York, NY, USA). Our search included all years available in the database at the time of the search (1900-2012) in a broad list of journals (n=166) from four categories within Web of Science: biodiversity conservation, ecology, zoology, and behavioral sciences. From this list, we removed journals that were not published in English, or could not be reasonably expected to publish articles on recreation and wildlife. To reduce the effect of dissemination bias in our analysis, we included articles published in regional and lesser-known journals as well as the most widely-read publications (Barto & Rillig 2012). Our search did not locate book chapters, articles published in journals not indexed in Web of Science, and articles in the gray literature. Within the list of journals, we used keywords "touris*" and "recreat*" to search for tourism and recreation articles in Web of Science. We did not include taxonomic keywords since titles and abstracts often refer only to their focal species.

Using titles, abstracts, and the full text as needed, we determined whether each article would be included and recorded the reason for rejection if necessary (Pullin & Stewart 2006). We excluded consumptive activities (e.g. hunting); however, studies examining consumptive activities as a source of disturbance for non-target species were retained. We rejected articles if they a) did not study one or more animal species; b) did not directly test effects of non-consumptive recreation; c) did not collect empirical data (e.g., were review or simulation articles); d) studied the effects of recreation infrastructure (e.g., trails or ski lifts) rather than recreation activity; or e) examined recreation as a vector for invasive species dispersal or disease transmission. Experimental treatments designed to mimic recreational activities were included.

Data collection

Data collected from each article included publication information, geographic location, study design, taxonomic group(s), recreation activities, response types, effects found, and management recommendations (Table 1). For articles that studied multiple species, recreation activities, or response types, we treated each combination of variables as a separate "test," rather than attempting to determine an overall effect for each article. For example, Banks and Bryant (2007) examined the effects of hiking and dog-walking on bird abundance and richness, so we recorded four tests in our database. While tests from the same study often rely on the same animal populations, locations, and data collection efforts, we examined the results of each test separately since effects often differed.

Publication trends and geographic distribution

We summarized the number of articles by publication year, journal category, country, continent, and habitat type. We calculated Spearman correlations to assess trends in the number of articles per year, both for the articles included in the review and for the overall publication volume in the selected journals. Journals were classified into eight broad categories, and articles were assigned to one or more habitat classes on the basis of authors' descriptions (Table 1).

Study design

To examine how recreation studies have been designed and conducted, we recorded the proportion of articles that used an experimental design and included controls and replication. For our purposes, any kind of an experimental treatment (e.g., experimental boat passes near a raptor nest; Steidl & Anthony 2000) counted as an experimental design, and any treatment or site without recreation counted as a control. We also examined the method used to measure recreation: direct observation with human observers, experimental treatment (e.g., researchers simulating recreation activities), expert opinion, remote monitoring (e.g., automatic counters), permitted use (e.g., whether a site was open to a specific recreational activity), or proxy variables (e.g., car counts).

Recreation effect

The "effect" variable, which was the response variable for several of our research questions, was a binary variable indicating whether the recreation effect documented by the authors was statistically significant (as defined by the authors). We used the percent of tests documenting a statistically significant effect of recreation as a measure of the amount of evidence for a recreation impact in our comparisons among taxonomic groups, recreation activities, and response types. We caution that a statistically significant effect of recreation does not necessarily provide insight into the effect's magnitude or biological significance. Further, authors may include significant results while omitting non-significant findings due to publication bias (Lortie et al. 2007). However, we believe this approach is meaningful as a representation of the weight of evidence that currently exists, and comparisons across taxonomic groups, recreation activities, and response types can be informative for better-studied groups.

We categorized all significant effects as negative, positive, or unclear. Negative responses were consistent with the following effects of recreational disturbance at the community, population, or individual (behavioral or physiological) levels: 1) community: decreased diversity; 2) population: decreased survival, reproduction, occurrence, or abundance; 3) behavioral: behavior typically assumed to reflect negative responses to anthropogenic disturbance, e.g. decreased foraging or increased vigilance; and 4) physiological: physiological condition typically assumed to reflect disturbance effects, e.g. decreased weight or increased stress. Conversely, positive responses were in the opposite direction. We were unable to classify some responses and labeled them “unclear.” Examples of unclear effects were behavioral responses that did not have obvious fitness consequences (e.g., decreased vocalizing) and tests with non-linear responses (e.g., highest reproductive success at an intermediate level of recreation). We note that positive responses do not necessarily imply positive outcomes for biodiversity conservation; for example, an increase in species diversity could be attributable to an increase in non-native species.

Taxonomic groups, recreation activities, and response types

We examined differences in research focus and evidence for recreation effects among six broad taxonomic groups: amphibians, birds, fish, invertebrates, mammals, and reptiles. We then divided groups with sufficient sample size (≥15 tests on ≥5 different species) into narrower taxonomic classifications (Classes for invertebrates and fish; Orders for birds, mammals, and reptiles; amphibians were omitted due to small sample size), and subdivided Classes or Orders with sufficient sample sizes (≥15 tests on ≥5 different species) again into Orders or Families. We also grouped species by their IUCN status (IUCN 2014).

We grouped recreation activities into 18 types (Table 1) and created broader categories for more general comparisons: winter terrestrial (snow and ice-based activities such as skiing and snowmobiling), summer terrestrial (land activities not requiring snow or ice), and aquatic activities. We also compared non-motorized and motorized activities. Finally, we categorized response types into diversity, survival, reproduction, abundance, occurrence, behavior, and physiological measures, as well as "other" responses (e.g., sex ratio).

Management recommendations

To qualify the management recommendations noted in the articles and provide a useful synthesis for land managers, we categorized recommended management actions as follows: spatial restrictions, capping visitation, increasing visitor education, temporal restrictions, improving infrastructure, adding or changing rules, enforcement of existing rules, staff training, or "other" (Table 2). Calls for additional research, although common in the literature, were not considered management recommendations.

Statistical analysis

To assess gaps in the literature, we used chi-square goodness of fit tests to determine if the distribution of articles differed significantly from an even distribution. We performed this test for journal type; habitat type; continent; IUCN status; taxonomic groups, starting with the broadest groups and progressing down to Family when possible; recreation activities; and response types. We used logistic regression models to compare the amount of evidence for overall, negative, and positive recreation effects where sample sizes were sufficient, which we defined as 15 tests. Since multiple tests were often extracted from a single article, we included the article identifier as a random effect in each of the regression models.

Results

Our initial keyword search resulted in a list of 1770 articles. After careful review, the final list included 218 articles (Appendix SI) with results for 1611 tests. Articles were rejected when authors: did not study one or more wildlife species (37.3%), did not directly test an effect of recreation on wildlife (35.7%), tested the effects of consumptive recreation only (9.1%), tested effects of recreation infrastructure only (2.4%), conducted review studies (1.2%), examined recreation as a mechanism for the spread of invasive species or disease (1.1%), conducted modeling or simulation studies (0.6%), or did not include statistical tests of the effects of recreation (0.3%).

Publication trends and geographic distribution

The earliest articles discovered by our search were published in 1981, and the peak year was 2008 with 23 articles. Although total publication volume rose from 1981 to 2012, so did the proportion of articles that met our criteria (Spearman's rank correlation r_s=0.842, p<0.001; Fig. 1). Recreation studies were not evenly distributed among journal types (χ^2=208.67, p<0.0001). Most of the included articles were published in conservation (40.4%) and wildlife (19.3%) journals, followed by ecology (15.1%), taxa-specific (10.6%), ecosystem or region-specific (9.6%), and behavior journals (3.2%); very few articles were published in general biology (0.9%) or other (0.9%) journal categories.

Geographically, studies of recreation on wildlife were not evenly distributed among continents (χ^2=147.74, p<0.0001) or habitat types (χ^2=220.16, p<0.0001). Most studies were conducted in North America (37.6%), Europe (24.3%), and Oceania (15.1%), and relatively few in South America (9.2%), Asia (5.1%), Africa (4.6%), and Antarctica (3.7%; Fig. 2a). The

United States accounted for 27.5% of the articles, followed by Australia (8.7%), New Zealand (6.4%), Spain (5.5%), the United Kingdom (4.6%), Canada (4.1%), and Antarctica (3.7%). Most studies were conducted in forest (22.1%), marine (16.1%), grassland (11.5%), and shoreline (9.4%) habitats (Fig. 2b). The least well-studied habitat types were tundra (2.7%), polar (2.1%), and desert (1.2%), as well as human-modified habitat (agricultural and urban, representing 5.7% of articles combined).

Study design

Approximately one-third (35%) of the articles contained an experimental component, and 60% contained controls. Most articles (83%) had replication of study sites, treatments, or groups. Of the methods used to measure recreation, direct observation was the most common (35.6% of articles), followed by experimental treatment (19.2%), expert opinion (15.6%), and proxy variables (15.4%). Permitted use as a measure of recreation was less common (9.7%), as was remote monitoring (4.5%).

Taxonomic groups

Research effort in our sample of articles was imbalanced among taxonomic groups, at the broadest level (χ^2=193.74, p<0.0001) and among bird (χ^2=21.30, p=0.0016) and mammal (χ^2=16.73, p=0.0050) Orders and invertebrate Classes (χ^2=9.88, p=0.0072; Fig. 3). Birds (39% of articles) and mammals (37%) were the focus of the majority of recreation studies, followed by invertebrates (12%), reptiles (5%), fish (5%), and amphibians (1%). Studies of a single species were more common (67.1%) than those that examined at least two species. Among birds, the most commonly researched Orders were Passeriformes (passerine birds; 36.0% of studies), Charadriiformes (wading birds and gulls; 19.2%), Sphenisciformes (penguins; 7.6%), and Accipitriformes (hawks, eagles, vultures; 5.8%). Research on mammals focused mainly on ungulates (27.2%), carnivores (27.2%), cetaceans (11.0%), and rodents (9.7%). The greatest proportion of invertebrate studies (28.2%) focused on the effects of snorkeling or SCUBA diving on corals, followed by studies on arachnids (10.3%), bivalves (10.3%), and cephalopods (7.7%). The most commonly studied fish Order was Actinopterygii (ray-finned fish; 58.3%), followed by "other" Orders (33.3%), including Chondrichthyes (sharks, stingrays). Research on reptiles focused on Orders Squamata (lizards, snakes; 75.0%) and Testudines (turtles; 25.0%).

We identified the IUCN status of the focal species for 72.4% of tests; the remaining tests examined multiple species or species not evaluated by the IUCN. The distribution of these 258 species into IUCN status groups was uneven (χ^2=800.39, p<0.0001); most (82.7%) had a least concern status, followed by near threatened (6.7%), vulnerable (4.3%), endangered (3.9%), data deficient (2.0%), and critically endangered (0.4%). Endangered species included three mammals (black howler monkey *Alouatta pigra*, Hector's dolphin *Cephalorhynchus hectori*, and the Barbary macaque *Macaca sylvanus*), three fish (dusky grouper *Epinephelus marginatus*, Nassau grouper *Epinephelus striatus*, and the brownstriped gaunt *Anisotremus moricandi*), two birds (Egyptian vulture *Neophron percnopterus* and the yellow-eyed penguin *Megatypes antipodes*), the boulder star coral *Montastraea annularis*, and the wood turtle *Glyptemys insculpta*. The only critically endangered species was the Western lowland gorilla *Gorilla gorilla gorilla*.

Of the 218 articles analyzed, 93% documented at least one impact of recreation on individuals, populations, or communities. Negative effects of recreation were most frequent (59.2%), followed by unclear (26.0%) and positive (14.8%) effects. Most (83.0%) of the unclear effects were behavioral responses. At the broadest taxonomic level, logistic regression showed that evidence of negative (*F*=15.43, p<0.0001) and positive (*F*=4.19, *p*=0.002) effects differed significantly among taxa, but overall effects did not (*F*=1.37, *p*=0.243; Fig. 3). Invertebrates (mean±SE: 48.1±3.4% of tests) and reptiles and amphibians together (39.0±6.5%) had the most negative effects, and fish (12.0±2.7%) and birds (8.5±1.1%) had the most positive effects.

For birds, the number of positive effects differed among Orders (*F*=3.30, *p*=0.003) and were most frequent in Passeriformes (passerine birds; 25.2±6.1%). Evidence of negative (*F*=1.85, *p*=0.088) or overall (*F*=2.01, *p*=0.062) effects did not differ among Orders. Evidence of negative effects varied among Charadriiformes Families (*F*=6.15, *p*=0.003) and was greatest in Charadriidae (e.g., plovers, lapwings; 46.5±11.5%). Among Passeriformes Families, Corvidae (e.g., crows, choughs) had the most positive effects (41.1±8.8%; *F*=7.60, *p*=0.0007). Mammal Orders did not differ in overall evidence of recreation impacts (*F*=1.75, *p*=0.121), but did for negative (*F*=6.47, p<0.0001) and positive (*F*=6.87, p<0.0001) effects. Rodentia had the most positive effects (27.5±7.1%) and Artiodactyla (even-toed ungulates) had the most negative effects (44.3±5.1%). Invertebrates differed among Classes in evidence of overall (*F*=8.86, *p*=0.0002) and negative (*F*=4.71, *p*=0.0099) effects; the “other” class (e.g. corals, crabs) had the most evidence for overall and negative effects (84.1±5.1% overall and 56.1±4.7% negative) and Arachnida (spiders) had the least (45.6±1.2% overall and 25.2±8.5% negative). Finally, fish Classes differed in evidence of overall (*F*=12.96, *p*=0.0004) and negative (*F*=15.76, *p*=0.0001) effects; the “other” grouping (e.g., sharks, stingrays) had more evidence for overall and negative effects (63.8±6.3% overall and 37.2±8.4% negative) than Actinopterygii (ray-finned fish; 32.5±5.1% overall and 9.3±3.6% negative). Low sample sizes precluded comparison of amphibian or reptile taxa.

Recreation activities

The articles in our sample examined a wide variety of recreation activities, but did not study them evenly (Fig. 4a; χ^2=2368.4, p<0.0001). Summer terrestrial activities were the most common, comprising 70.2% of activities, followed by aquatic (20.8%) and winter terrestrial (5.4%). Motorized forms of recreation, including off-highway vehicles, snowmobiles, and motorized boats, were examined in only 11.6% of articles. The most commonly-studied specific activity was hiking (27.7% of articles).

Winter terrestrial, summer terrestrial, and aquatic activities varied in evidence of overall (F=5.09, p=0.0062) and negative (F=14.05, p<0.0001) effects. Winter terrestrial had the most evidence of overall (73.2±5.5% of tests) and negative (35.9±6.0%) effects. Non-motorized activities had more negative effects than motorized activities (33.8±1.4% versus 22.3±3.0%; F=11.47, p=0.0007). Evidence of overall (F=2.75, p=0.0001), positive (F=2.64, p=0.0003), and negative (F=6.10, p<0.0001) recreation effects varied across individual recreation activities (Fig. 4b). Activities with the most evidence of overall effects included cross-country skiing and snowshoeing (79.3±7.5% of tests), alpine skiing (77.6±8.1%), fishing from shore (73.1±8.7%), and beach use (71.2±5.3%).

Response types

Response types were not examined evenly (χ^2=1051.6, p<0.0001); behavioral (35.0%) and abundance (20.7%) responses to recreation were the most common (Fig. 5a). Only 7.1% of tests measured species richness or diversity and 2.5% measured survival. The evidence of overall (F=5.69, p<0.0001) negative (F=17.7, p<0.0001), and positive (F=2.58, p=0.025) effects varied significantly among response types (Fig. 5b). Physiological responses had the most overall effects (61.6±4.1% of tests), followed by diversity/richness (57.2±6.6%) and behavioral (54.5±2.3%) responses; reproductive responses (34.0±5.2%) had the fewest overall effects. Physiological (49.6±4.1%) and diversity (48.2±6.6%) responses had the most negative effects, while behavioral responses had the most positive effects (10.0±1.2%).

Management recommendations

More than one-third (35%) of the included articles did not provide management recommendations (Table 2). Of those that did include recommendations, the most common types were spatial restrictions (29.2%), capping visitation (14.6%), and visitor education (13.0%). Enforcement of existing rules (6.1%) and staff training (1.2%) were the least frequently suggested management strategies.

Discussion

Although published research on recreation effects on animals increased by an order of magnitude from 1981 to 2012, the proportion of the literature devoted to the subject remains small (0.11% of our target journals in the highest year) and many gaps in knowledge remain. This research may not be reaching a broad audience even among conservation scientists; over 20% of articles were published in journals specific to a taxonomic group, geographic region, or ecosystem, whereas few were published in the broadest journals. The articles had a strong geographic bias toward North America, Europe, and Australia. This is troubling, since South America, Africa, and Asia contain most of the world's biodiversity hotspots (Myers et al. 2000) as well as popular ecotourism destinations including Brazil, South Africa, Thailand, and Indonesia (Christ et. al. 2003); we see an immediate need for recreation impact studies in these areas. A surprising number of studies were conducted in Antarctica, as a result of a growing ecotourism industry that often includes visits to penguin colonies (Pfeiffer & Peter 2004).

Further, the distribution of articles among broad taxonomic groups was skewed in favor of birds and mammals, a trend consistent with conservation science as a whole (Clark & May 2002). However, these are large, diverse groups that still warrant more research; for example, passerine birds were the most frequently studied bird Order in our set of articles, but the 69 species examined therein comprised only ~1% of the 5,000+ species in the Order. There is also an urgent need to understand more about the potential effects of recreation on invertebrates, fish, reptiles, and amphibians. We found only two articles on amphibians, but their rapid worldwide decline and known sensitivity to human disturbance (Welsh & Ollivier 1998; Houlahan et al. 2000) highlight the need to understand whether recreation could be a contributing factor. In general, current research on recreation effects on animals does not include many species of urgent conservation concern; less than 10% of species studied are globally threatened (IUCN status of critically endangered, endangered, or vulnerable). This mismatch between conservation priorities and current research effort must be addressed, since impacts of recreation often occur inside protected areas meant to conserve imperiled species. Finally, few articles (32.9%) examined more than one species, and studies of species from multiple trophic levels were especially rare (4.6%). More research is needed on community-level effects of recreation including potential cascading effects (e.g., Leighton et al. 2010).

Over 80% of articles measured recreation as a categorical variable, typically with ≤3 levels. Though this approach is simple to implement and analyze, it limits the ability of researchers to evaluate how responses may change with different recreation intensities. The typically-assumed response relationship of wildlife to human disturbance is curvilinear, where impacts increase quickly with more disturbance, then remain relatively constant (Monz et al. 2013); however, little empirical evidence exists to support this assumption. Future research should measure recreation across intensity gradients to help verify the existence of thresholds and examine the shape of these relationships.

Evidence of recreation impacts on wildlife was clear, with over 93% of reviewed articles documenting at least one effect of recreation. As expected, the majority of these effects were negative. Among birds, Family Charadriidae (e.g., plovers, lapwings) had considerable evidence of negative effects of recreation, consistent with a recent study that found that species from this Order (Charadriiformes) were more frequently threatened by tourism than other bird Orders (Steven & Castley 2013). Among mammals, Order Artiodactyla had the most evidence of negative effects, mostly consisting of behavioral responses to recreation activity (Wolfe et al. 2000; Stankowich 2008), which were more likely to show a response to recreation than most other response types. For invertebrates, stony corals (Class Anthozoa) frequently showed negative effects – such as physical damage or reduced abundance – in areas frequented by recreational divers (Hawkins et al. 1999; Zakai & Chadwick-Furman 2002). For fish, negative physiological effects of wildlife viewing were documented for Class Chondrichthyes (e.g., sharks, stingrays; Semeniuk & Rothley 2008; Semeniuk et al. 2009), and negative effects of diving on fish communities have also been recorded (Hawkins et al. 1999).

Evidence of positive effects of recreational activity was much less common. Birds, particularly passerines and corvids, had more evidence of positive effects compared to the other broad taxonomic groups. Many corvids are urban adaptors (Marzluff & Neatherlin 2006), and several studies found that they quickly become habituated to human disturbance, allowing them to tolerate or even thrive in the presence of recreationists (Storch & Leidenberger 2003; Jiménez et al. 2011), sometimes at the expense of other species (Gutzwiller et al. 2002). Of the mammals, rodents had the most evidence of positive effects. All but one of these effects were behavioral, and most resulted from habituation, for example reduced flight responses in areas with higher recreation (Griffin et al. 2007; Cooper et al. 2008).

We also found that non-motorized activities had more evidence of negative effects than motorized activities. Motorized activities are often expected to be more harmful because of their speed, noise, and spatial extent (Stankowich 2008), but our results suggest the opposite across a wide range of study locations and taxa. A few articles (3.2%) directly compared motorized and non-motorized activities; four mammals (guanaco *Lama guanicoe*, wolverine *Gulo gulo*, coyote *Canis latrans*, and bobcat *Lynx rufus*) showed behavioral or occurrence responses to non-motorized but not motorized recreation (George & Crooks 2006; Krebs et al. 2007; Malo et al. 2011), whereas the reverse was found for Hector's dolphin (*Cephalorhynchus hectori*) behavior (Bejder et al. 1999) and ghost crab (*Ocypode quadrata*) abundance (Steiner & Leatherman 1981). Our results also suggest that winter terrestrial activities may affect animals more than other activities, though the number of articles was small. A recent review of winter recreation effects on animals (Sato et al. 2013) supports this conclusion, finding that over half of the reviewed articles reported overall detrimental effects, particularly on birds and on species richness and diversity.

Overall, authors observed individual-level (behavioral and physiological) effects more frequently than most population-level (occurrence, abundance, and reproduction) effects. Though they appeared in few articles, survival and diversity impacts were relatively frequently observed, and are important to understand for conservation purposes. Authors of behavioral studies tended to measure more responses in a single study than authors of population-level studies, potentially increasing the likelihood of finding significant effects. Behavioral metrics may also be popular because they can be simpler to measure and have been proposed as a proxy for demographic parameters (Wildermuth et al. 2013). Nonetheless, behavioral metrics might not always reflect the true population consequences of anthropogenic disturbance (Gill et al. 2001). Study duration can also influence conclusions; one long-term study found that low-level recreation had an effect on dolphin habitat use that was not observed in a short-term behavioral study (Bejder et al. 2006a, 2006b), while another found that short-term behavioral responses did not result in changes in the distribution or relative abundance of waterbirds (Guillemain et al. 2007). Habituation to recreation is a behavioral response that was discussed in many (39.4%) of the included articles, but whether habituation is a beneficial outcome is unclear and warrants further study (Bejder et al. 2006a; Baudains & Lloyd 2007).

Though most articles documented recreation effects, few presented specific, achievable steps to minimize impacts. Over one-third of the articles did not describe any management or mitigation actions, and many more contained only vague suggestions. We see a strong need for empirical tests of the effectiveness of management actions, which were rare. Encouraging examples of successful mitigation actions do exist, such as educating divers about avoiding damage to coral reefs (Medio et al. 1997), using volunteers to deter harassment of fur seals (Acevedo-Gutiérrez et al. 2011), and installing fences to establish disturbance-free areas (Ikuta & Blumstein 2003; Cassini et al. 2004). This type of practical evaluation of management strategies is critical in assessing the ability of protected areas to meet demands for both recreational opportunities and the conservation of biodiversity. Interviewing practitioners would be a useful direction for future research in order to assess the type and extent of management strategies currently being employed. We also emphasize that even where management recommendations are provided in the scientific literature, it is unclear to what extent they are received by practitioners (Cook et al. 2013); a search of unpublished reports and other communications on the subject would help inform how well conservation scientists are reaching decision-makers.

The effects of recreation on animals is still a relatively unknown and low-profile topic in the conservation science literature, despite growing evidence that detrimental impacts can occur from a wide variety of recreational activities. Further, anthropogenic disturbance associated with recreation and tourism – such as habitat conversion for roads and resorts, pollution from vehicles, and the spread of invasive species – are likely to have additional effects (Steven & Castley 2013), increasing the overall impact of recreation. Recreation effects may also act synergistically with other threats to biodiversity, such as urbanization and climate change. This is a troubling problem for managers and conservation practitioners, since recreation is an integral part of protected areas worldwide (Becken & Job 2014). Finding an appropriate balance between biodiversity conservation and outdoor recreation is complicated, especially since impacts vary among species and recreation activities. We must start by simply acknowledging that these uses are not necessarily compatible for all species, in all locations. This will make it easier to justify additional research on this topic, establish restrictions on recreation, and encourage changes in the behavior of recreationists, leading to improved conservation outcomes.

Tables

Table 1. List of variables collected from articles included in the systematic review of the effects of recreation on animals, with descriptions or a list of categories and the type of data collected.

Category	Variable	Description or list of categories	Data type
Publication	Author(s)		text
	Title		text
	Journal		text
	Journal type	Behavior, conservation, ecology, ecosystem/region-specific, general biology, taxa-specific, zoology/wildlife, other	categorical
	Publication year		numeric
Geographic	Continent		categorical
	Country		text
	Habitat type	Agricultural, beach, desert, forest, freshwater, grassland, marine, polar, shoreline, urban, scrub/shrub, tundra, wetland, other	categorical
Study design	Measure of recreation*	Direct observation, experimental treatment, expert opinion, remote monitoring, permitted use, proxy	categorical
	Experiment	Was it an experimental study?	yes/no
	Control	Did the study include a control treatment? (e.g. a "no-recreation" site)	yes/no
	Replication	Did the study replicate treatments, study sites, observation periods, etc?	yes/no
Effect	Effect*	Did the authors find a significant recreation impact?	yes/no
	Effect direction*	Positive, negative, unclear	categorical
Taxonomic	Multiple species	Were multiple species studied?	yes/no
	Taxa group	Amphibian, bird, fish, invertebrate, mammal, reptile	categorical
	Scientific name*		text
	Common name*		text
Recreation	Activity*	Alpine ski/snowboard, beach use, biking, boat (non-motorized), camping, cross-country ski/snowshoe, dog-walking, equestrian, fishing (shore), hiking, running, motorized (boat), motorized (land), swimming/diving, wildlife feeding, wildlife viewing (boat), wildlife viewing (land), other	categorical
Response	Type*	Abundance, behavioral, diversity/richness, occurrence, physiological, reproductive, survival, other	categorical
Management	Recommendations	Cap visitation, improve infrastructure, rule change, staff training, spatial restrictions, temporal restrictions, visitor education, none, other	categorical

* For articles that studied multiple species, recreation activities, or response variables, we treated each combination of variables as a separate "test," and recorded the information marked with an asterisk (*) for each test individually.

Table 2. General management recommendations suggested by authors of articles included in the systematic review of the effects on recreation on animals.

Recommendation	Examples	Frequency (%)
Spatial restrictions	Designate a trail-free area within protected area; establish minimum approach distances to animals	29.2
Cap visitation	Limit the number of visitors that can enter the area per day	14.6
Visitor education	Educate SCUBA divers about the impacts of human contact on coral; instruct visitors about effects of noise on sensitive species	13.0
Temporal restrictions	Limit recreational access during the breeding season	11.3
Physical improvements	Restore habitat; install fencing around sensitive areas	8.5
Rule change	Restrict boat speed in sensitive areas; prohibit wildlife feeding	8.1
Other	Species translocations; increased use of private land for conservation	8.1
Enforcement	Enforce leash laws; keep people on trails	6.1
Staff training	Train staff in visitor education	1.2
No recommendations		35.2

Figures

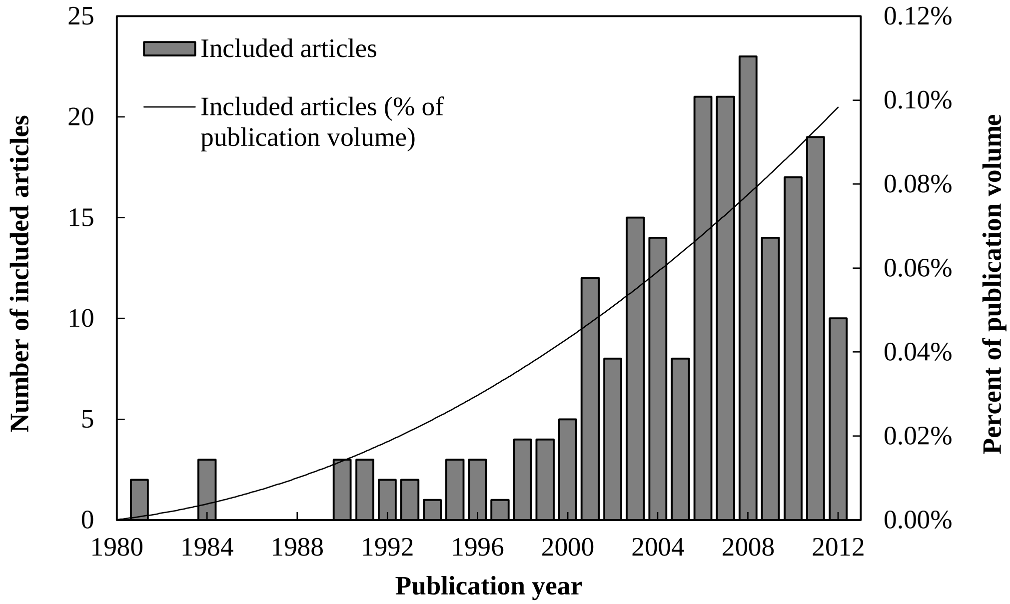
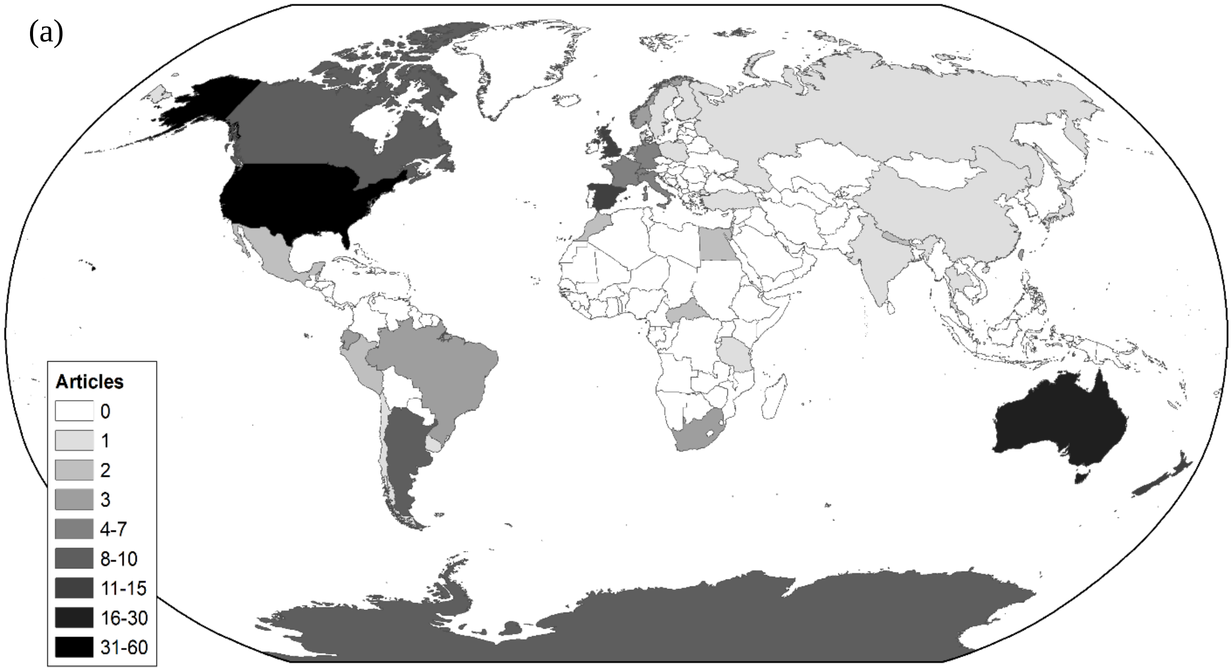


Figure 1. Published articles on the effects of recreation on animals by publication year, shown as raw numbers (shaded bars) and as a percent of the overall publication volume of the journal set used in the systematic review (trendline; a second order polynomial function).

(a)



(b)

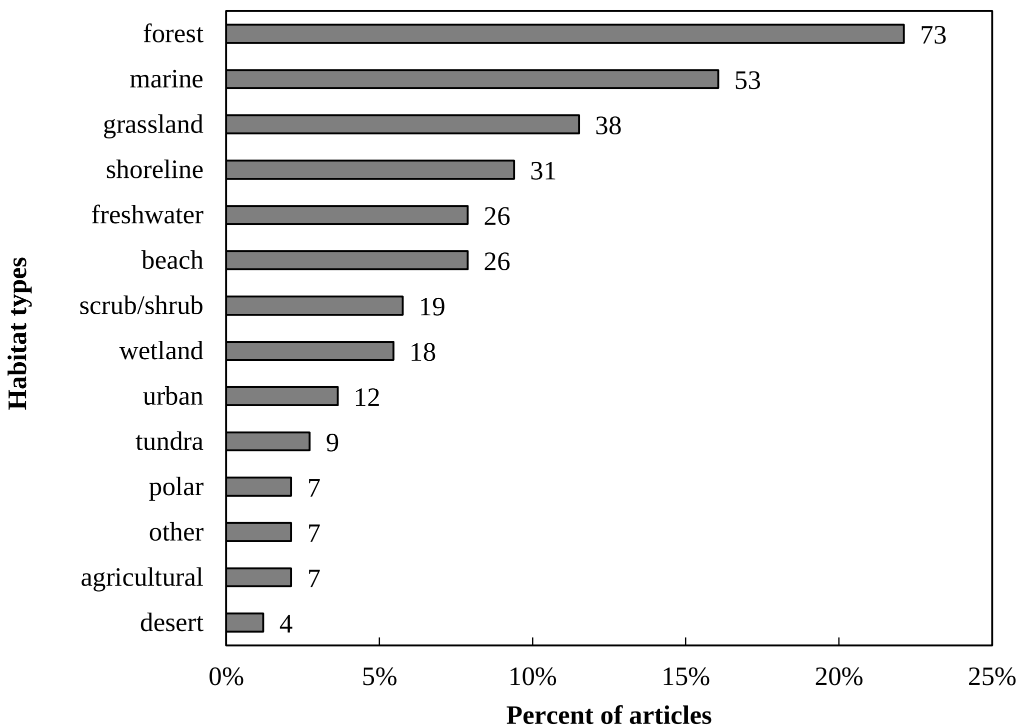
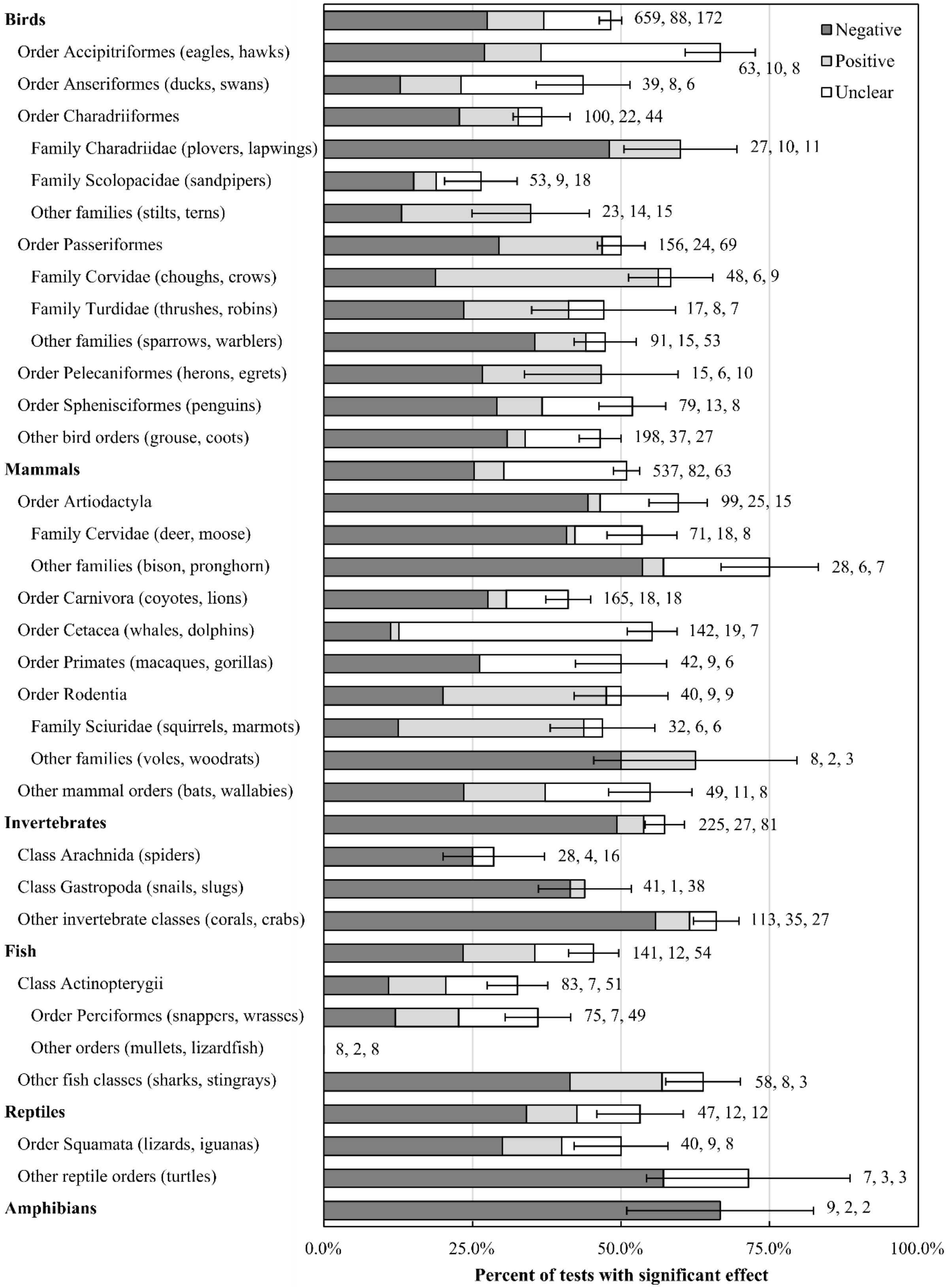


Figure 2. Distribution of published articles on the effects of recreation on animal species by a) the country where the study was conducted, and b) the major habitat type(s). Since some studies involved multiple habitat types, the sum (330) is greater than the total number of articles (218). Numbers following bars represent the number of articles in each category.



Birds
Order Accipitriformes (eagles, hawks)
Order Anseriformes (ducks, swans)
Order Charadriiformes
Family Charadriidae (plovers, lapwings)
Family Scolopacidae (sandpipers)
Other families (stilts, terns)
Order Passeriformes
Family Corvidae (choughs, crows)
Family Turdidae (thrushes, robins)
Other families (sparrows, warblers)
Order Pelecaniformes (herons, egrets)
Order Sphenisciformes (penguins)
Other bird orders (grouse, coots)
Mammals
Order Artiodactyla
Family Cervidae (deer, moose)
Other families (bison, pronghorn)
Order Carnivora (coyotes, lions)
Order Cetacea (whales, dolphins)
Order Primates (macaques, gorillas)
Order Rodentia
Family Sciuridae (squirrels, marmots)
Other families (voles, woodrats)
Other mammal orders (bats, wallabies)
Invertebrates
Class Arachnida (spiders)
Class Gastropoda (snails, slugs)
Other invertebrate classes (corals, crabs)
Fish
Class Actinopterygii
Order Perciformes (snappers, wrasses)
Other orders (mullets, lizardfish)
Other fish classes (sharks, stingrays)
Reptiles
Order Squamata (lizards, iguanas)
Other reptile orders (turtles)
Amphibians
659, 88, 172
63, 10, 8
39, 8, 6
100, 22, 44
27, 10, 11
53, 9, 18
23, 14, 15
156, 24, 69
48, 6, 9
17, 8, 7
91, 15, 53
15, 6, 10
79, 13, 8
198, 37, 27
537, 82, 63
99, 25, 15
71, 18, 8
28, 6, 7
165, 18, 18
142, 19, 7
42, 9, 6
40, 9, 9
32, 6, 6
8, 2, 3
49, 11, 8
225, 27, 81
28, 4, 16
41, 1, 38
113, 35, 27
141, 12, 54
83, 7, 51
75, 7, 49
8, 2, 8
58, 8, 3
47, 12, 12
40, 9, 8
7, 3, 3
9, 2, 2
Negative
Positive
Unclear
0.0%
25.0%
50.0%
75.0%
100.0%
Percent of tests with significant effect

Figure 3. Evidence of an effect of recreation by taxonomic group, as measured by the proportion of tests that were statistically significant. For articles that studied multiple recreation activities, species, or response variables, each combination of variables was treated as a separate test. Common names are example species that were present in the reviewed articles. We present taxonomic groups that have at least 15 tests and 5 species represented; the remaining taxa are included in "other" categories for comparative purposes. Numbers following bars show the number of tests, number of articles, and count of unique species. Articles that studied functional groups or communities rather than individual species (e.g., insectivorous birds) were added to the most relevant "other" category and were not counted as species. Error bars show standard error.

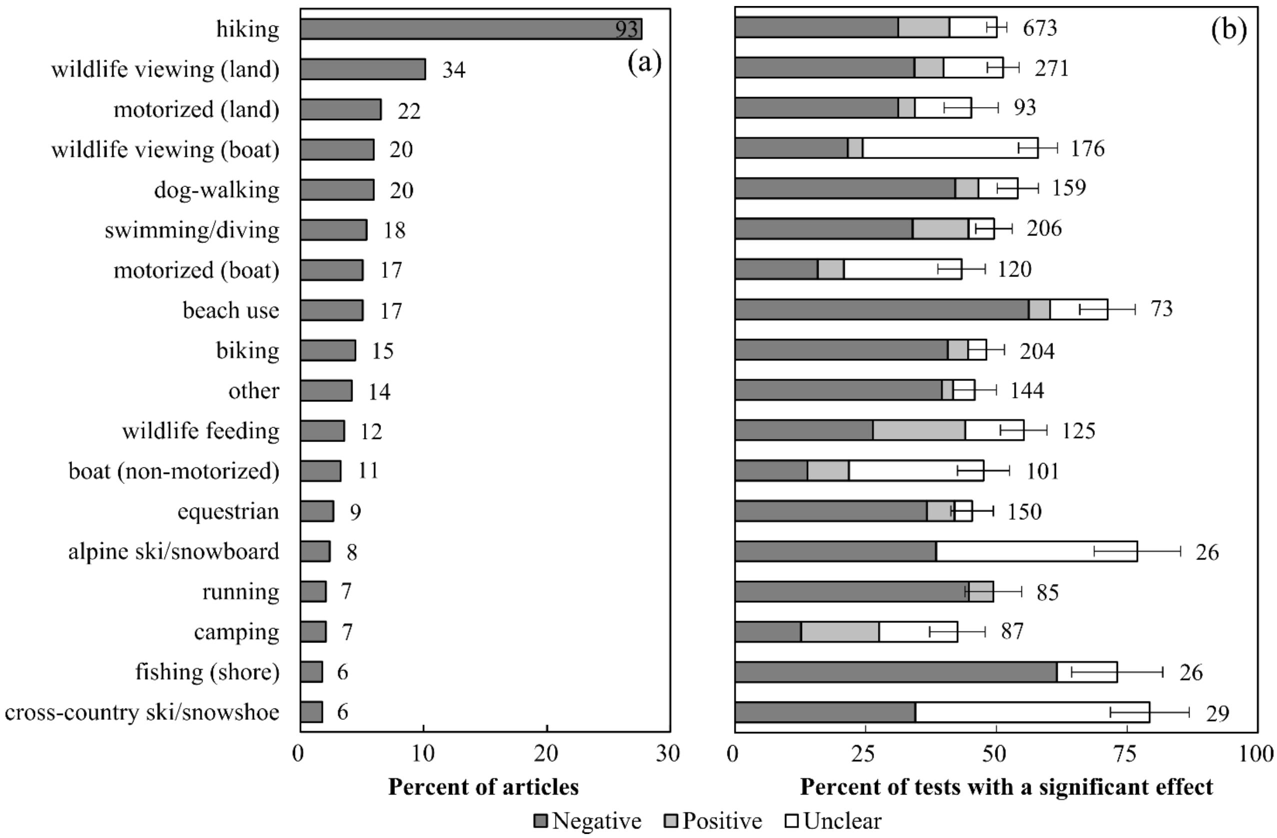


Figure 4. Recreation activities included in the systematic review of the effects of recreation on wildlife. Panel (a) shows the percent of articles that included each recreation activity (numbers of articles follow the bars), and panel (b) shows the percent of tests in which a statistically significant effect of recreation on an animal species was observed (number of tests follow the bars). Total percentages are categorized into negative, positive, and unclear effects of recreation. Error bars show standard error.

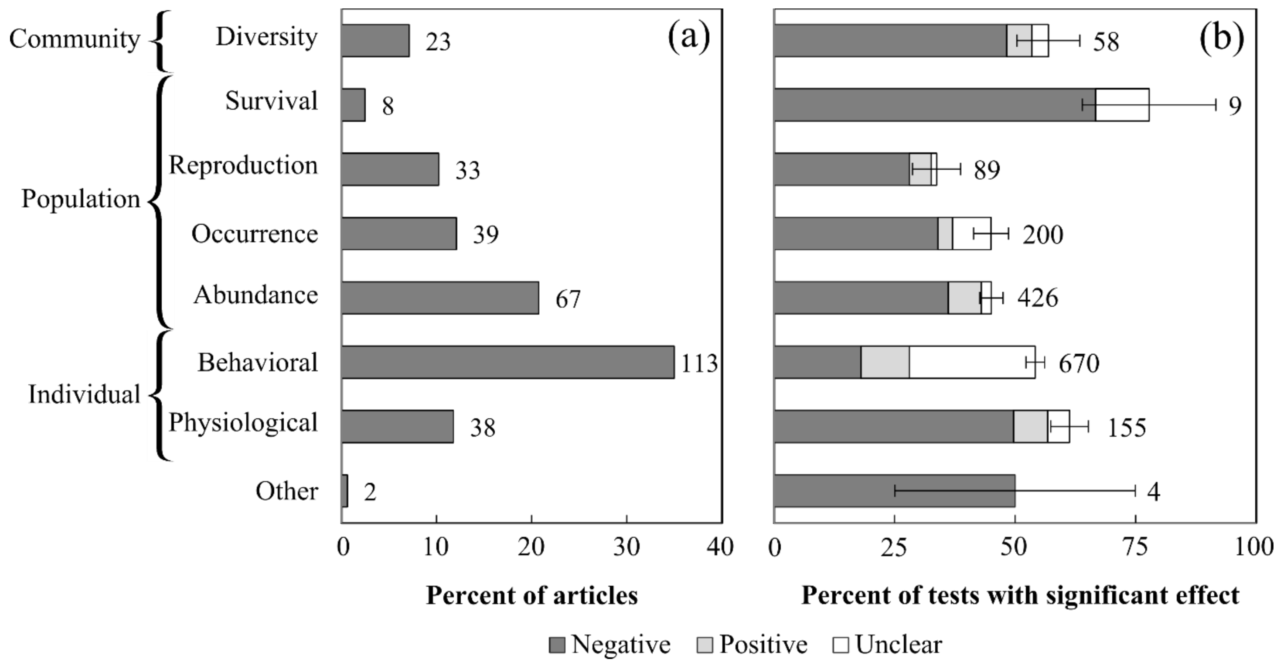


Figure 5. Types of animal responses to recreation in the articles included in the systematic review of the effects of recreation on wildlife, categorized by community-, population-, and individual-level response types. Panel a) shows the percent of articles in which each response type is tested (numbers of articles follow the bars). Panel b) shows the percent of tests in which a statistically significant effect of recreation on an animal species was observed (number of tests follow the bars). Total percentages are divided into negative, positive, and unclear effects of recreation. Error bars represent standard error.

LITERATURE CITED

Acevedo-Gutiérrez, A., L. Acevedo, and L. Boren. 2011. Effects of the presence of official-looking volunteers on harassment of New Zealand fur seals. Conservation Biology **25**:623–627.

Arlettaz, R., P. Patthey, M. Baltic, T. Leu, M. Schaub, R. Palme, and S. Jenni-Eiermann. 2007. Spreading free-riding snow sports represent a novel serious threat for wildlife. Proceedings of the Royal Society B: **274**:1219–1224.

Balmford, A., J. Beresford, J. Green, R. Naidoo, M. Walpole, and A. Manica. 2009. A global perspective on trends in nature-based tourism. PLoS Biol **7**:e1000144.

Banks, P. B., and J. V. Bryant. 2007. Four-legged friend or foe? Dog walking displaces native birds from natural areas. Biology Letters **3**:611–613.

Barros, A., C. Monz, and C. Pickering. 2014. Is tourism damaging ecosystems in the Andes? Current knowledge and an agenda for future research. AMBIO:1–17.

Barto, E. K., and M. C. Rillig. 2012. Dissemination biases in ecology: effect sizes matter more than quality. Oikos **121**:228–235.

Baudains, T. P., and P. Lloyd. 2007. Habituation and habitat changes can moderate the impacts of human disturbance on shorebird breeding performance. Animal Conservation **10**:400–407.

Beale, C. M., and P. Monaghan. 2005. Modeling the effects of limiting the number of visitors on failure rates of seabird nests. Conservation Biology **19**:2015–2019.

Becken, S., and H. Job. 2014. Protected areas in an era of global-local change. Journal of Sustainable Tourism **22**:507–527.

Bejder, L., S. M. Dawson, and J. A. Harraway. 1999. Responses by Hector's dolphins to boats and swimmers in Porpoise Bay, New Zealand. Marine Mammal Science **15**:738–750.

Bejder, L., A. Samuels, H. Whitehead, and N. Gales. 2006a. Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. Animal Behaviour **72**:1149–1158.

Bejder, L., A. Samuels, H. Whitehead, N. Gales, J. Mann, R. Connor, M. Heithaus, J. Watson-Capps, C. Flaherty, and M. Krützen. 2006b. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. Conservation Biology **20**:1791–1798.

Boyle, S. A., and F. B. Samson. 1985. Effects of nonconsumptive recreation on wildlife: a review. Wildlife Society Bulletin **13**:110–116.

Bushell, R., and P. F. J. Eagles. 2007. Tourism and protected areas: benefits beyond boundaries. CABI: Cambridge, MA.

Cassini, M. H., D. Szteren, and E. Fernández-Juricic. 2004. Fence effects on the behavioural responses of South American fur seals to tourist approaches. Journal of Ethology **22**:127–133.

Christ, C., O. Hillel, S. Matus, and J. Sweeting. 2003. Tourism and biodiversity: mapping tourism's global footprint. Conservation International, Washington, D.C.

Clark, J. A., and R. M. May. 2002. Taxonomic bias in conservation research. Science **297**:191–192.

Cook, C. N., M. B. Mascia, M. W. Schwartz, H. P. Possingham, and R. A. Fuller. 2013. Achieving conservation science that bridges the knowledge–action boundary. Conservation Biology **27**:669–678.

Cooper, C. A., A. J. Neff, D. P. Poon, and G. R. Smith. 2008. Behavioral responses of Eastern gray squirrels in suburban habitats differing in human activity levels. Northeastern Naturalist **15**:619–625.

Cordell, H. K. 2012. Outdoor recreation trends and futures: a technical document supporting the Forest Service. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC.

Duffus, D. A., and P. Dearden. 1990. Non-consumptive wildlife-oriented recreation: a conceptual framework. Biological Conservation **53**:213–231.

Eagles, P. F. J., S. F. McCool, and C. D. Haynes. 2002. Sustainable tourism in protected areas: guidelines for planning and management. World Commission on Protected Areas Best Practice Protected Area Guidelines Series No. 8. IUCN, Gland, Switzerland.

Finney, S. K., J. W. Pearce-Higgins, and D. W. Yalden. 2005. The effect of recreational disturbance on an upland breeding bird, the golden plover *Pluvialis apricaria*. Biological Conservation **121**:53–63.

Frid, A., and L. M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology **6**:11.

George, S. L., and K. R. Crooks. 2006. Recreation and large mammal activity in an urban nature reserve. Biological Conservation **133**:107–117.

Gill, J. A., K. Norris, and W. J. Sutherland. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biological Conservation **97**:265–268.

Griffin, S. C., T. Valois, M. L. Taper, and L. Scott Mills. 2007. Effects of tourists on behavior and demography of Olympic marmots. Conservation Biology **21**:1070–1081.

Guillemain, M., R. Blanc, C. Lucas, and M. Lepley. 2007. Ecotourism disturbance to wildfowl in protected areas: historical, empirical and experimental approaches in the Camargue, Southern France. Biodiversity and Conservation **16**:3633–3651.

Gutzwiller, K. J., S. K. Riffell, and S. H. Anderson. 2002. Repeated human intrusion and the potential for nest predation by gray jays. Journal of Wildlife Management **66**:372–380.

Hawkins, J. P., C. M. Roberts, T. V. Hof, K. D. Meyer, J. Tratalos, and C. Aldam. 1999. Effects of recreational scuba diving on Caribbean coral and fish communities. Conservation Biology **13**:888–897.

Houlahan, J. E., C. S. Findlay, B. R. Schmidt, A. H. Meyer, and S. L. Kuzmin. 2000. Quantitative evidence for global amphibian population declines. Nature **404**:752–755.

Ikuta, L. A., and D. T. Blumstein. 2003. Do fences protect birds from human disturbance? Biological Conservation **112**:447–452.

IUCN. 2014. The IUCN Redlist of Threatened Species. Version 2014.2. Available from http://www.iucnredlist.org (accessed September 10, 2014).

IUCN and UNEP. 2014. The World Database on Protected Areas (WDPA). UNEP-WCMC, Cambridge, UK.

Jiménez, G., J. A. Lemus, L. Meléndez, G. Blanco, and P. Laiolo. 2011. Dampened behavioral and physiological responses mediate birds' association with humans. Biological Conservation **144**:1702–1711.

Kangas, K., M. Luoto, A. Ihantola, E. Tomppo, and P. Siikamäki. 2010. Recreation-induced changes in boreal bird communities in protected areas. Ecological Applications **20**:1775–1786.

Knight, R. L., and K. Gutzwiller. 1995. Wildlife and recreationists: coexistence through management and research. Island Press, Washington, D.C.

Krebs, J., E. C. Lofroth, and I. Parfitt. 2007. Multiscale habitat use by wolverines in British Columbia, Canada. Journal of Wildlife Management **71**:2180–2192.

Leighton, P. A., J. A. Horrocks, and D. L. Kramer. 2010. Conservation and the scarecrow effect: can human activity benefit threatened species by displacing predators? Biological Conservation **143**:2156–2163.

Lortie, C. J., L. W. Aarssen, A. E. Budden, J. K. Koricheva, R. Leimu, and T. Tregenza. 2007. Publication bias and merit in ecology. Oikos **116**:1247–1253.

Losos, E., J. Hayes, A. Phillips, D. Wilcove, and C. Alkire. 1995. Taxpayer-subsidized resource extraction harms species. BioScience **45**:446–455.

Louv, R. 2005. Last child in the woods: saving our children from nature-deficit disorder. Algonquin Books, Chapel Hill, NC.

Mainini, B., P. Neuhaus, and P. Ingold. 1993. Behaviour of marmots *Marmota marmota* under the influence of different hiking activities. Biological Conservation **64**:161–164.

Malo, J., P. Acebes, and J. Traba. 2011. Measuring ungulate tolerance to human with flight distance: a reliable visitor management tool? Biodiversity and Conservation **20**:3477–3488.

Martínez-Abraín, A., D. Oro, J. Jiménez, G. Stewart, and A. Pullin. 2010. A systematic review of the effects of recreational activities on nesting birds of prey. Basic and Applied Ecology **11**:312–319.

Marzano, M., and N. Dandy. 2012. Recreationist behaviour in forests and the disturbance of wildlife. Biodiversity and Conservation **21**:2967–2986.

Marzluff, J. M., and E. Neatherlin. 2006. Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. Biological Conservation **130**:301–314.

McCurdy, L. E., K. E. Winterbottom, S. S. Mehta, and J. R. Roberts. 2010. Using nature and outdoor activity to improve children's health. Current Problems in Pediatric and Adolescent Health Care **40**:102–117.

Medio, D., R. F. G. Ormond, and M. Pearson. 1997. Effect of briefings on rates of damage to corals by scuba divers. Biological Conservation **79**:91–95.

Monz, C. A., C. M. Pickering, and W. L. Hadwen. 2013. Recent advances in recreation ecology and the implications of different relationships between recreation use and ecological impacts. Frontiers in Ecology and the Environment **11**:441–446.

Müllner, A., K. Eduard Linsenmair, and M. Wikelski. 2004. Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). Biological Conservation **118**:549–558.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature **403**:853–858.

Naughton-Treves, L., M. B. Holland, and K. Brandon. 2005. The role of protected areas in conserving biodiversity and sustaining local livelihoods. Annual Review of Environment and Resources **30**:219–252.

Naylor, L. M., M. J. Wisdom, and R. G. Anthony. 2009. Behavioral responses of North American elk to recreational activity. Journal of Wildlife Management **73**:328–338.

Newsome, D., D. N. Cole, and J. L. Marion. 2004. Environmental impacts associated with recreational horse-riding. Pages 61-82 in R. Buckley, editor. Environmental Impacts of Ecotourism. CABI Publishing, Wallingford, UK.

O'Connor, S., R. Campbell, H. Cortez, and T. Knowles. 2009. Whale watching worldwide: tourism numbers, expenditures and economic benefits, a special report from the International Fund for Animal Welfare prepared by Economists at Large. International Fund for Animal Welfare, Yarmouth, MA.

Orams, M. B. 2002. Feeding wildlife as a tourism attraction: a review of issues and impacts. Tourism Management **23**:281–293.

Parsons, E. C. M. 2012. The negative impacts of whale-watching. Journal of Marine Biology **2012**:1–9.

Pfeiffer, S., and H.-U. Peter. 2004. Ecological studies toward the management of an Antarctic tourist landing site (Penguin Island, South Shetland Islands). Polar Record **40**:345–353.

Pomerantz, G. A., D. J. Decker, G. R. Goff, and K. G. Purdy. 1988. Assessing impact of recreation on wildlife: a classification scheme. Wildlife Society Bulletin **16**:58–62.

Pullin, A. S., and T. M. Knight. 2009. Doing more good than harm – building an evidence-base for conservation and environmental management. Biological Conservation **142**:931–934.

Pullin, A. S., and G. B. Stewart. 2006. Guidelines for systematic review in conservation and environmental management. Conservation Biology **20**:1647–1656.

Reed, S. E., and A. M. Merenlender. 2008. Quiet, nonconsumptive recreation reduces protected area effectiveness. Conservation Letters **1**:146–154.

Riffell, S. K., K. J. Gutzwiller, and S. H. Anderson. 1996. Does repeated human intrusion cause cumulative declines in avian richness and abundance? Ecological Applications **6**:492–505.

Rogala, J. K., M. Hebblewhite, J. Whittington, C. A. White, J. Coleshill, and M. Musiani. 2011. Human activity differentially redistributes large mammals in the Canadian Rockies national parks. Ecology and Society **16**: http://www.ecologyandsociety.org/vol16/iss3/art16.

Sato, C. F., J. T. Wood, and D. B. Lindenmayer. 2013. The effects of winter recreation on alpine and subalpine fauna: a systematic review and meta-analysis. PLoS ONE **8**:e64282.

Semeniuk, C. A. D., S. Bourgeon, S. L. Smith, and K. D. Rothley. 2009. Hematological differences between stingrays at tourist and non-visited sites suggest physiological costs of wildlife tourism. Biological Conservation **142**:1818–1829.

Semeniuk, C. A. D., and K. D. Rothley. 2008. Costs of group-living for a normally solitary forager: effects of provisioning tourism on southern stingrays *Dasyatis americana*. Marine Ecology Progress Series **357**:271–282.

Showler, D. A., G. B. Stewart, W. J. Sutherland, and A. S. Pullin. 2010. What is the impact of public access on the breeding success of ground-nesting and cliff-nesting birds. CEE Review **05-010**: http://www.environmentalevidence.org/wp-content/uploads/2014/07/SR16.pdf.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biological Conservation **141**:2159–2173.

Steidl, R. J., and R. G. Anthony. 2000. Experimental effects of human activity on breeding bald eagles. Ecological Applications **10**:258–268.

Steiner, A. J., and S. P. Leatherman. 1981. Recreational impacts on the distribution of ghost crabs *Ocypode quadrata* fab. Biological Conservation **20**:111–122.

Steven, R., and J. G. Castley. 2013. Tourism as a threat to critically endangered and endangered birds: global patterns and trends in conservation hotspots. Biodiversity & Conservation **22**:1063–1082.

Steven, R., C. Pickering, and J. G. Castley. 2011. A review of the impacts of nature based recreation on birds. Journal of Environmental Management **92**:2287–2294.

Storch, I., and C. Leidenberger. 2003. Tourism, mountain huts and distribution of corvids in the Bavarian Alps, Germany. Wildlife Biology **9**:301–308.

UNWTO. 2014. UNWTO Tourism Highlights, 2014 edition. World Tourism Organization, Madrid, Spain.

Wade, A. A., and D. M. Theobald. 2010. Residential development encroachment on U.S. protected areas. Conservation Biology **24**:151–161.

Welsh, H. H., and L. M. Ollivier. 1998. Stream amphibians as indicators of ecosystem stress: a case study from California's redwoods. Ecological Applications **8**:1118–1132.

Wildermuth, R. P., J. D. Anadón, and L. R. Gerber. 2013. Monitoring behavior: assessing population status with rapid behavioral assessment. Conservation Letters **6**:86–97.

Wittemyer, G., P. Elsen, W. T. Bean, A. C. O. Burton, and J. S. Brashares. 2008. Accelerated human population growth at protected area edges. Science **321**:123–126.

Wolfe, S. A., B. Griffith, and C. A. G. Wolfe. 2000. Response of reindeer and caribou to human activities. Polar Research **19**:63–73.

Zakai, D., and N. E. Chadwick-Furman. 2002. Impacts of intensive recreational diving on reef corals at Eilat, northern Red Sea. Biological Conservation **105**:179–187.

Zaradic, P. A., O. R. W. Pergams, and P. Kareiva. 2009. The impact of nature experience on willingness to support conservation. PLoS ONE **4**:e7367.

CHAPTER TWO[2]

WIDE VARIATION IN HUMAN ACTIVITY IN A SOUTHERN CALIFORNIA RESERVE SYSTEM AND POTENTIAL IMPLICATIONS FOR ANIMAL CONSERVATION

Introduction

In the United States and other developed nations, providing opportunities for outdoor recreation has been an important motivation for the establishment of protected areas (Becken & Job 2014). Recreation is beneficial for human health and community livelihoods (Louv 2005; McCurdy et al. 2010) and can help raise support and funds for land conservation (Bushell & Eagles 2007; Zaradic et al. 2009). Participation in outdoor recreation is growing. In the United States, the number of participants grew 7.5% between 2000 and 2009 and total visitor days increased by 32.5%, and these trends are expected to continue until at least 2060 (Cordell 2012).

Outdoor recreation is usually assumed to be compatible with conservation goals and is permitted in most protected areas worldwide, including 94% of the land area in IUCN protected areas (Eagles et al. 2002; IUCN & UNEP 2014). However, emerging research demonstrates that recreation can have damaging effects on plants and animals (Sato et al. 2013; Monz et al. 2013; Barros et al. 2014). This threat is widespread, as recreation activity is listed as a threat to birds in 65% of the world's biodiversity hotspots (Steven & Castley 2013), and our systematic review found that recreation had at least one demonstrated effect on animals in 93% of published studies (Chapter 1). This creates a dilemma for conservation practitioners and protected area managers who must manage the demand for outdoor recreation while fulfilling mandates to protect species and ecological communities.

[2] Manuscript co-authored with Sarah E. Reed, Adina M. Merenlender, and Kevin R. Crooks

To inform decisions about recreation in protected areas, managers need reliable data on basic recreation measures rather than “best guesses” (McClaran & Cole 1993; Griffin et al. 2010). Visitation measures such as the number of visitors, their spatial and temporal distribution, and their chosen recreational activity can help managers understand and mitigate potential impacts on ecological communities by identifying areas of particularly high use, allocating staff, and monitoring compliance with regulations (Cessford & Muhar 2003; Hadwen et al. 2007). There are a variety of approaches for collecting visitation data, ranging from expert opinion data ((Martin et al. 2012), remote monitoring using trail counters, remotely-triggered cameras, or GPS devices (Pettebone et al. 2010; Beeco et al. 2014), visual observations (Arnberger et al. 2005), or visitor surveys (Termansen et al. 2004), with no clear consensus on the best methods (Watson et al. 2000; Cessford & Muhar 2003; Wolf et al. 2012). Regardless of the monitoring method, managing the diverse threats to wildlife posed by recreation requires a better understanding of how, where, and when impacts are occurring (Becken & Job 2014), particularly at the landscape scale where monitoring efforts are rare (Monz et al. 2010; Braunisch et al. 2011; Rösner et al. 2013).

San Diego County, California is an excellent location to study human disturbance on wildlife because of its large human population and high levels of biodiversity and endangerment. It is the fifth most populous county in the United States with over three million residents (U.S. Census Bureau 2013). The county is located in a hotspot of global biodiversity that is home to over 500 vertebrate species (Myers et al. 2000), and it is among the counties with the greatest number of endangered plants and animals in the continental United States (Dobson et al. 1997). The San Diego area’s Multiple Species Conservation Program (MSCP) was one of the first multiple species Habitat Conservation Plans developed under the Endangered Species Act and was designed to protect 85 plant and animal species (CA Department of Fish and Game 2012). San Diego County's MSCP reserves are managed by a variety of city, county, and state agencies as well as private organizations, and they vary in size and distance from urbanized areas as well as the likely intensity of recreational use. This gradient presents a natural experiment over which recreational activity can be measured and compared across multiple spatial scales.

Our goal was to empirically measure spatial and temporal variability in recreation across a network of MSCP reserves in San Diego County, California, and to identify biophysical and socioeconomic factors that influenced observed differences in activity patterns. Specifically, we modeled reserve visitation to understand how accessibility variables (e.g., nearby housing density, number of entrances), landscape variables (e.g., proximity of similar reserves, distance from coast), and reserve attributes (e.g., slope, vegetation type, trail length and density) contributed to the levels of hiking, mountain biking, and horseback riding in our study reserves, and how visitation varied between weekdays and weekend days. We also used our models to extrapolate predicted levels of human visitation to a larger network of similar reserves in San Diego County and used data from a survey of expert opinion to validate these predictions. Understanding the drivers of reserve visitation can help to estimate human activity at unmeasured reserves, make predictions about the effects of future changes in the reserve network, and inform reserve design and land management. Further, overlaying recreation models with species distributions can help set priorities for further study on species that are currently facing high levels of recreation.

Methods

Reserve selection

To select the reserves for field study and for prediction, we identified sites that were publicly owned, included in the MSCP, and were at least 100 ha in area. We sought the opinion of local biologists, reserve managers, and rangers to inform our final selection of 18 field study reserves along an expected gradient of recreation activity (Fig. 6). An additional 28 reserves were selected for the prediction set. Prediction reserves were dispersed over a larger spatial extent than the field study reserves, so for consistency we eliminated reserves that were 2 or more standard deviations away from the mean value from the field reserves for 4 or more of the 24 predictor variables. Both the field study and prediction sets included reserves open and closed to the public.

Field data collection

At each reserve, we used maps and field visits to identify all official entrances and stratified them into three categories: staging areas were primary access points with parking lots; trailheads were established entrances that appeared on reserve maps and were accessible by car (often with street parking); and connectors were entrances that were typically difficult to access by car, sometimes unmarked, and were generally used by people entering from an adjacent neighborhood or another reserve. At closed reserves, we identified the service roads that intersected the reserve boundary as the most likely entry points for unauthorized use. Unofficial (typically user-created) entrances were common but difficult to locate systematically and were not included in our sampling design.

We used remotely-triggered cameras (Bushnell Trophy Cam) to document human activity at reserve entrances from July to October 2013. We installed cameras at all staging areas and trailheads and a random sample of at least 50% of connectors, with the exception of one reserve (Mission Trails) with an unusually large number of entrances, where we placed cameras at all 4 staging areas, 6 of 11 trailheads, and 1 of 4 connectors. In total, we established 83 camera locations across the 18 reserves, with each camera installed for one 14-day period. Cameras were placed near the entrance to the reserve, attached to a tree or metal post buried at least 30 cm into the soil, and concealed with vegetation where possible. Cameras were set to capture a single photo at each motion trigger, and to take no more than one photo every ten seconds. Although unofficial entrances were not monitored, unauthorized uses of official entrances (e.g., after-hours use or prohibited forms of recreation) were captured by the cameras and included in our counts.

Visitation estimates from field data

For cameras that operated for more than 14 days, we randomly truncated either the beginning or the end of the sampling period, resulting in even 14-day sampling periods for analysis. For cameras that recorded more than 2,000 photos during the sampling period (n = 22), we subsampled the data to reduce time spent sorting photos. The goal of our subsampling procedure was to randomly select photos but to avoid selecting large numbers of blank photos triggered by wind, which affected many cameras from late morning to mid-afternoon. To do this, we first identified cameras strongly affected by wind (n = 14 out of 22), which had continuous blocks of photos with moving vegetation or blank photos. We then used the distribution of photos across the hours of the day from the eight cameras that were not heavily affected by wind to establish proportions of photos to subsample randomly from each hour from each of the 22 cameras.

We viewed each photo and counted the number of individual hikers, mountain bikers (referred to as bikers), and people riding or leading horses (referred to as equestrians). We recorded the direction of travel in order to quantify the imbalance of people entering versus exiting the reserve. We expected that this imbalance was attributable to sampling error (e.g., the camera was unable to capture bicycles going downhill due to their speed, but did capture them going uphill in the other direction), or to visitors entering and exiting through different entrances, including unofficial entrances. These imbalances were sometimes trivial and sometimes substantial, so we felt it was important to incorporate them into our reserve-level estimates of visitation.

We created visitation estimates from the camera data, using the following equation to produce a reserve-level visitation estimate, defined as the number of single-person visits to a site per day (Watson et al. 2000):

$$V_i = \sum \frac{N_j + k\tilde{S} + l\tilde{T} + m\tilde{C}}{2} + \left|\sum B_j\right|$$

Here, V_i is visitation at reserve i and N_j is the mean individuals per day (going either direction) detected by the camera at entrance j. S, T, and C represent individuals per day at k staging areas, l trailheads, and m connectors not sampled with cameras, respectively; these are modeled as the median of the individuals per day from other entrances of the same type. The sum of individuals from all entrances is divided by 2 because we assume each visitor passed by a camera twice – once entering and once exiting, and then these are summed to aggregate to the reserve level. B_j is the mean imbalance in individuals per day at entrance j. This represents the total number of individuals entering the reserve minus the number of individuals exiting the reserve at entrance j, and can have positive or negative values. These imbalances at each entrance are summed to produce the net imbalance at the reserve level, and are added to the reserve level camera detections to produce visitation estimate V_i. We calculated separate estimates for mean visitation by hikers, bikers, equestrians, and total visitors per weekday, weekend day, and all days for each site. We divided our visitation estimates by the area of each site to produce estimates of recreation intensity (people/hectare/day).

Expert opinion survey

As an additional source of information about recreation levels in the reserve network, we designed and implemented a survey to systematically collect expert-opinion data regarding the reserves and their visitation patterns (Appendix II). The survey was administered via the online survey platform Survey Gizmo, and was distributed to rangers and other on-the-ground staff by their supervisors. The survey was open from May 28 to November 5, 2013. All responses were anonymous, although respondents identified their employer (e.g., City of San Diego). The survey asked staff to choose the reserves with which they are the most familiar from a list of publicly-owned parks, ecological reserves, and open space preserves, and to estimate the number of visitors on an average weekday and weekend day, as well as other questions including seasonality of recreational activity and unauthorized use. Respondents selected from five categorical ranges in visitation: 0-9, 10-49, 50-199, 200-499, and 500 or more people per day. We used the midpoint of these categories in comparisons with estimates from the field data and modeling approaches (750 was the midpoint selected for the 500 or more category). We used the survey data as an independent source of information to help validate both the empirical estimates and the model predictions of visitation to the reserves.

Recreation predictors and modeling

We hypothesized that visitation could be modeled by several groups of predictor variables (Termansen et al. 2004; Neuvonen et al. 2010; Siderelis et al. 2011): accessibility (number of entrances and parking lots, and the housing density within different travel times); reserve attributes (slope, elevation, vegetation, trail length and density); and landscape context (distance from coast, number of similar reserves within different travel times). We derived these variables from spatial datasets using ArcGIS and from field visits to the reserves (Table 3). For the housing density and substitution predictors, we included a series of variables calculated at varying travel-time buffer distances from the reserve (Wade & Theobald 2010) since we suspected that their effects were scale-dependent but did not know the appropriate scale (Wilmers et al. 2013). We created the travel time buffers using county roads data (SanGIS/SANDAG Data Warehouse) that included the average driving speed for each class of roads, from which we calculated the time to cross each 1 m pixel. For pixels without roads, we assigned a walking speed of 5 km/hour (Theobald et al. 2010). We then created cost distance surfaces for each reserve using ArcGIS 10.1, and uses these to calculate the number of housing units and substitute reserves within several travel times.

We used random forests (RF) to model the level of recreation and the level of recreation intensity (visitors per hectare per day), by all visitors, hikers, and bikers. We did not model equestrian recreation due to low counts and limited variability of equestrian visitation to the study sites. Since prior knowledge of recreation in this system was minimal, exploratory analyses were better suited to our goals than confirmatory hypothesis-testing techniques. RF modeling is well-suited to exploratory analysis since it can handle a large number of predictor variables – including cases in which the number of predictor variables greatly exceeds the number of observations – and it does not require the analyst to make many assumptions about the distributions of or correlations among predictor and response variables (Prasad et al. 2006; Hochachka et al. 2007; Cutler et al. 2007). They have been shown to perform favorably in comparison with other commonly used modeling methods in ecology (Knudby et al. 2010; Oppel et al. 2012).

We used the randomForests package in R to build the RF models (Breiman 2001). Based on preliminary exploration and the tuneRF function in the randomForests package, we used twice the default number of variables for splitting at each node (mtry=16) for all visitors and hikers, and the default number of variables (mtry=8) for bikers. The number of trees for all models was 1,000. We log-transformed the response variables to limit the influence of extreme outliers (Knudby et al. 2010). We used the RF models to identify important variables, using the importance function in the randomForest package. The importance value for a given variable is calculated as the percent increase in the mean squared error (MSE) of the model when the values of that variable are randomly permutated. We also constructed partial dependence plots for variables identified as important to examine the shape of the relationship between predictor and response variables. We assessed the RF model fit and performance using the percent of variance explained and Pearson correlations between the predicted and observed values.

Recreation prediction

We made predictions about the level of recreation by all visitors, hikers, and bikers within field and prediction reserves using the predict function of the randomForest package. However, because maps of trail networks were not consistently available in a digital format, we were unable to collect trail length and density variables for the prediction reserves. Therefore, we made predictions from new RF models that did not include these variables.

Results

Field data

The cameras recorded 142,456 photos over 1,379 camera-days, of which 78,551 were categorized. These included 41,336 photos of humans and 1,944 wildlife photos, as well as 28,079 blank pictures. Mean (±SD) human visitation for field study reserves was 211.3±447.8 (range: 0-1,943) people per day (Fig. 7). The busiest reserve (Mission Trails) was an outlier with visitation estimated to be 5.4 times higher than the next highest (Tecolote Canyon, 361 people/day). Mean recreation intensity was 0.28±0.36 (range: 0-1.22) people per hectare per day. Across nearly all reserves, most recreationists were hikers (86.2%) with fewer bikers (12.5%) and equestrians (1.4%); however, the number of bikers was similar to or exceeded the number of hikers at some reserves (i.e., Del Mar Mesa and Tecolote Canyon). Across all reserves, estimated visitation was on average 1.95 times higher (paired $t=2.38$, $p=0.029$) on weekend days (319.8±642.8) than on weekdays (163.9±368.1).

Fourteen of the field study reserves also received responses in the expert opinion survey. Survey responses and empirical estimates of recreation were strongly and positively correlated ($r = 0.650$, $p = 0.012$; Fig. 8a). Further, the ranked order of reserves did not differ significantly between the two estimation methods (Wilcoxon signed rank test; $V = 57$, $p = 0.808$).

Recreation modeling

The RF models performed well, especially for the all visitors model (Table 4); the correlation between predicted and observed values ($r = 0.954$, $p < 0.0001$; Fig. 8b) and the percentage of variation explained (55.7%) were both high. The hiker and biker models also performed reasonably well with correlations between predicted and observed values of 0.964 ($p < 0.0001$) and 0.843 ($p < 0.0001$), and 47.1 and 44.6% of variation explained.

As a group, accessibility variables were the most important across all models, but the individual variables with the highest importance varied (Fig. 9). For both the all visitors and hiking model, housing units within 10 minutes was the most important variable (% increase in MSE: 11.49% for the all visitors model, 10.08% for hikers), with other housing variables having slightly lesser importance (2.69 - 8.07% for all visitors, 4.29 - 7.34% for hikers). Whether a reserve was open to the public and the number of parking lots were also important in both the all visitor (7.85% and 4.36%) and the hiking (7.44% and 4.77%) models. For the biking model, housing units within 10, 20, 30, and 40 minutes all had high importance values (7.33-8.70%). The number of entrances was also important in the biking model (6.86%). Accessibility variables had a positive relationship with visitation estimates across all three models, and the shape of the relationship between housing units and visitation was typically characterized by a rapid increase in visitation at some threshold of housing units (Fig. 10).

Landscape context variables, specifically the number of substitute reserves within 20 and 30 minutes, were also important in the three models to varying extents. The number of substitute reserves was positively related to visitation for travel times of 20 minutes or greater. Substitute reserves within 20 and 30 minutes were the most important for the all visitors (4.77 and 2.63%) and hiker (5.26 and 5.08%) models, and within 30 and 40 minutes were the most important for the biker model (2.46 and 2.00%). Distance from the coast was important only in the biking model (3.04%), and had a negative relationship with visitation.

Finally, most reserve attributes had only moderate importance in the RF models. Trail variables had some importance in each model, including trail density for all visitors (2.88%), trail density (3.25%) and unofficial trail density (3.29%) for hikers, and trail length (6.35%) and trail density (2.20%) for bikers. Trail length and density had a positive relationship with visitation in all cases. Slope range was somewhat important for the all visitors model (2.44%), with thresholds at slope ranges of approximately 50 and 60 degrees (Figure 5), at which point visitation increased dramatically. Elevation range (1.18%) had a negative relationship and herbaceous cover (2.38%) had a positive relationship with visitation in the biking model.

Recreation predictions

Running the RF models without the trail variables had little effect on their performance; correlations between modeled and empirically-estimated levels of recreation and percent variance explained were similar to the models containing the trail variables (Table 4). Modeled visitation levels at the prediction reserves for all visitors (43.1±8.1 per day), hikers (18.3±2.7 per day), and bikers (4.2±0.7 per day) were lower than modeled visitation at the field reserves (all $t > 2.1$, all $p < 0.049$). The expert opinion survey responses and the modeled visitation values at all reserves were positively and relatively strongly correlated ($r = 0.544$, $p = 0.0009$; Fig. 8c). However, the ranked order of the reserves differed between the survey responses and model predictions (Wilcoxon signed rank test; $V = 441$, $p = 0.013$).

Discussion

Understanding drivers of recreation activity

We found that recreational activity varied widely among the reserves in this diverse and spatially-expansive network. We successfully modeled this variation using easily-measured predictors relating to the accessibility and spatial arrangement of reserves. In our study system, the most important drivers of recreation activity were related to reserve accessibility. Housing density surrounding the reserves was a strong, positive predictor of recreational activity. Specifically, the number of housing units within 10 minutes of reserves was the most important variable in our all visitor and hiker models, and was important in the biker models along with housing units within 20, 30, and 40 minutes. Bikers generally travel at higher speeds than hikers, and our results indicate that they seek out reserves with longer trail networks, consistent with findings of Becco et al. (2014). They are thus likely willing to travel further to reach such sites, which could explain the importance of housing units within greater travel times for bikers. The number of entrances and parking lots were also associated with higher visitation. Accessibility (sometimes measured as travel cost) has been identified as an important factor in analyses of visitation in other protected area networks (Termansen et al. 2013).

The effects of nearby reserves that could act as substitutes were moderately important for all models, but more important for hikers than bikers. We expected that the number of substitutes would be negatively related to visitation since they would compete with each other for visitors (Termansen et al. 2008), yet our RF models show a positive correlation, particularly in the moderate travel time buffers (20 and 30 minute). We suspect clusters of reserves may have acted as an attractant because of trail networks spanning multiple reserves, or due to visitors' greater awareness of the vicinity as a destination for recreation.

Predicted visitation levels from the RF models were low compared to the empirical estimates and expert opinion data. Despite removing from the prediction set reserves that differed excessively from the field reserves, several predictor variables differed considerably between field and prediction sites. A few of these were important variables, such as housing units within 50 and 60 minutes, the number of entrances, and substitute reserves within 20 and 30 minutes, and for each of these the field reserves had greater means than the prediction reserves. These discrepancies could help explain the consistently low modeled visitation levels at prediction reserves. Nonetheless, despite the underestimation of absolute levels of recreation, our predictive models performed well, with strong correlations between predicted and observed values across sampled reserves and relatively high percentage of variation explained.

We note that both the visitation and recreation intensity measures used in this analysis are averages across the sampling period, which reduces any temporal peaks in recreation. Further, our measure of recreation intensity assumes that recreationists are spread evenly across the reserve area. This is unlikely because it is known that recreationists concentrate near entrances, facilities, and attractions (van der Zee 1990; Monz et al. 2010). Spatially or temporally concentrated activity can have diverse effects on animals (Stalmaster & Kaiser 1998; Kerbiriou et al. 2009; Malo et al. 2011), and future research should explicitly examine how peak visitation events may influence animals differently than steady rates. Identifying threshold levels of recreation at which animal responses increase or asymptote (Monz et al. 2013) would be useful information for wildlife and land managers.

Applications of the recreation model

The population of the San Diego region is expected to grow by 40% between 2008 and 2050, and housing is expected to increase by 34% during this time period (San Diego Association of Governments 2010), leading to continued urban sprawl. Reserves that are currently at the urban fringe may experience rapid housing growth at their borders. Our models can help land managers project growth in recreation as nearby housing units increase. For example, if housing units within 30 minutes of a reserve grew from approximately 100,000 to 160,000, a 16% increase, we would expect visitation to be 1.4 times higher than the previous level. Further, variables that may have some flexibility at the time of reserve establishment, such as the number of parking lots and the total trail length, can be used by planners and managers to concentrate visitor use into certain areas or to project the influence of changes on the overall level of visitation. These examples show how knowledge of the driving factors behind recreation activity can help with current reserve management and future conservation planning.

Further, our results imply that, at least in this system, obtaining rough estimates of the level of recreation in these reserves using our model is not difficult. Nearly all of the important variables we identified were easy to measure using freely-available GIS data (e.g,, parcels, elevation). Additionally, the estimates from the expert opinion survey were strongly correlated with those derived from empirical field measurements. Considering that there were relatively few survey responses per reserve, this is an intriguing result, especially since expert opinion data is rarely considered as an option for visitor monitoring (Cessford & Muhar 2003; Arnberger et al. 2005) or used to create visitation estimates (but see Rösner et al. 2013). Our survey may have been successful because the respondents had extensive experience working on the ground in the reserves; respondents averaged 113 (±117) days per year and over 7.7 (±5.9) years working in the reserves. In protected area networks with experienced staff, a systematic survey may be a quick and simple approach to develop coarse estimates of visitation. Further, rangers and other on-the-ground staff are aware of unauthorized human activity, such as going off trail or into closed areas, which other visitor count methods may have difficulty detecting (Rösner et al. 2013). However, local and regional reserves are less likely to have dedicated staff than state or federally managed reserves. It can also be difficult to validate survey data, especially if reserves have many entrances or large seasonal variation in recreational use.

Our recreation modeling approach could be used to examine the exposure of threatened animal species to recreation, for example by correlating presence, occupancy, or abundance of animal species with predicted levels of recreation. Species with strong positive correlations would be expected to have higher exposure to recreation than those with negative or non-significant correlations. An analysis of species exposure to recreation could help prioritize species for future research and guide land management policy. These methods could also be applied in other contexts to examine different suites of important drivers of recreation for a variety of animal species. Few of the existing studies of the effects of recreation on animals suggest specific management actions that could reduce impacts, and fewer still test the effectiveness of management actions (Chapter 1). Our approach brings us closer to addressing this gap by improving our understanding of the drivers and spatial patterns of recreation. From this, we can predict visitation levels at unsampled reserves, forecast changes in visitation in response to population growth or altered reserve management, and prioritize both species and locations within the reserve network where conflict may be occurring between recreation and animal occurrence. We depend on protected areas to provide opportunities for recreation while conserving biodiversity, but we must take steps to ensure that these uses are compatible.

Tables

Table 3. Predictor variables used to model visitation in study reserves.

Category	Predictor(s)	Abbreviation(s)	Data source(s)
Accessibility	Housing units (within 10, 20, 30, 40, 50, and 60 minutes of travel time)	HOUS_10, HOUS_20, HOUS_30, HOUS_40, HOUS_50, HOUS_60	Parcel data, roads data
	Number of parking lots	PKG	Field visits, reserve maps and websites, aerial imagery
	Number of entrances	ENT	Field visits, reserve maps and websites, aerial imagery
	Open to the public	OPEN	Reserve websites, reserve managers
Reserve attributes	Area	AREA	Calculated in ArcGIS 10.1
	Official trail length	TR_LNG	Digitized trails from aerial imagery
	Official trail density	TR_DNS	Digitized trails from aerial imagery, reserve area
	Unofficial trail length	UTR_LNG	Digitized trails from aerial imagery
	Unofficial trail density	UTR_DNS	Digitized trails from aerial imagery, reserve area
	Lakes	LAKE	Aerial imagery
	Elevation range	ELEV	Elevation
	Slope range	SLP	Derived from elevation
	Vegetation (percent cover herbaceous, shrub, hardwood)	HEB, SHB, HDW	Vegetation
Landscape context	Distance from coast	CDIST	Calculated in ArcGIS 10.1
	Number of nearby reserves (within 10, 20, 30, and 40 minutes of travel time)	SUB_10, SUB_20, SUB_30, SUB_40	Roads data

Table 4. Random forest model performance, as measured by the percentage of variation explained (pseudo R^2) and the Pearson correlation coefficient (r) between the modeled and empirically-estimated levels of visitation at field study reserves, with and without trail length and density variables. All correlations are statistically significant at the $p = 0.05$ level or smaller.

	With trail variables		Without trail variables	
	r	% variation explained	r	Mean % variation explained
All visitors	0.954	55.69	0.921	56.32
Hikers	0.964	47.13	0.956	46.83
Bikers	0.843	44.62	0.845	44.51

Figures

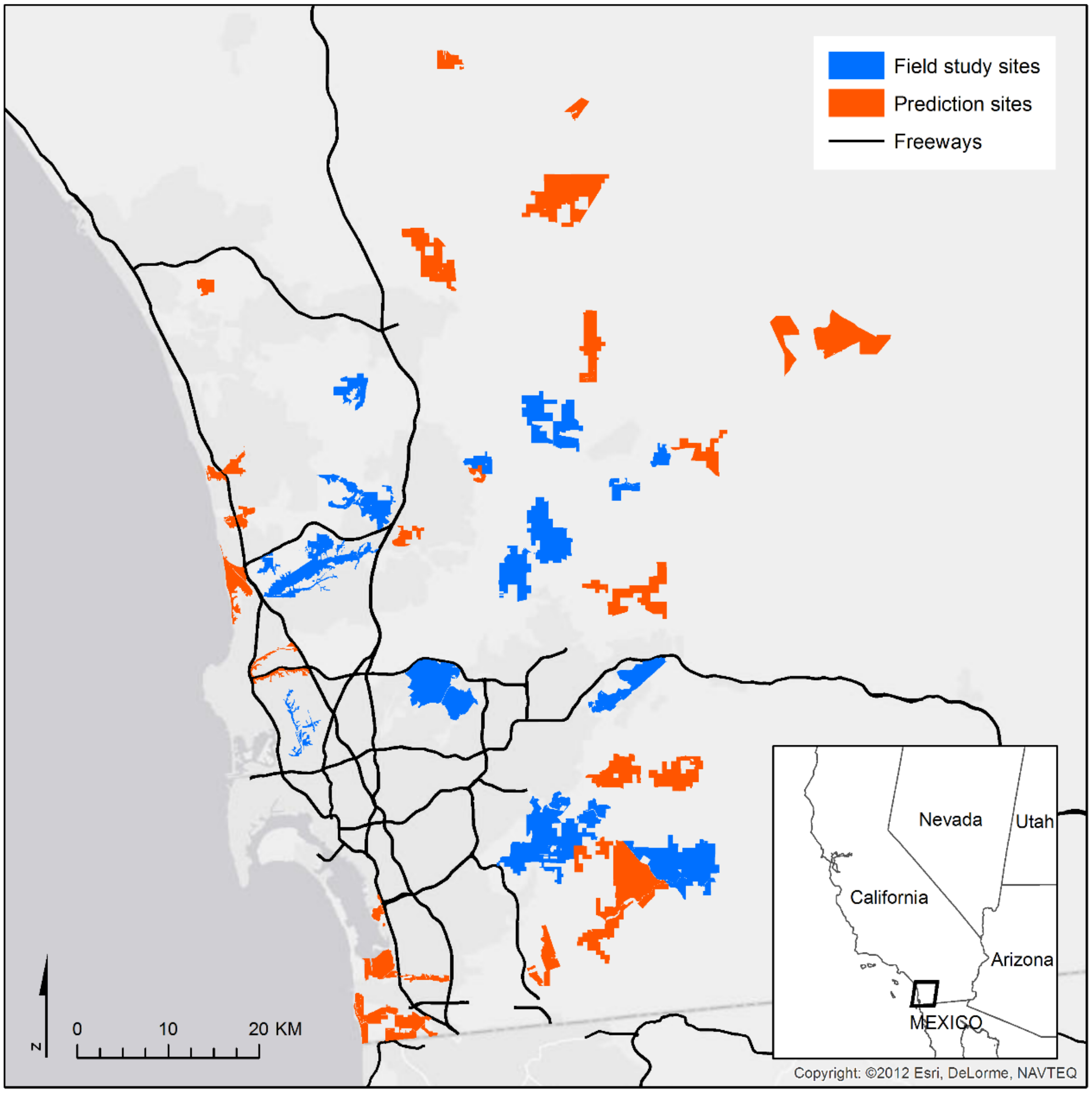


Figure 6. Field study reserves (n =18) and prediction reserves (n = 28) in San Diego County, California.

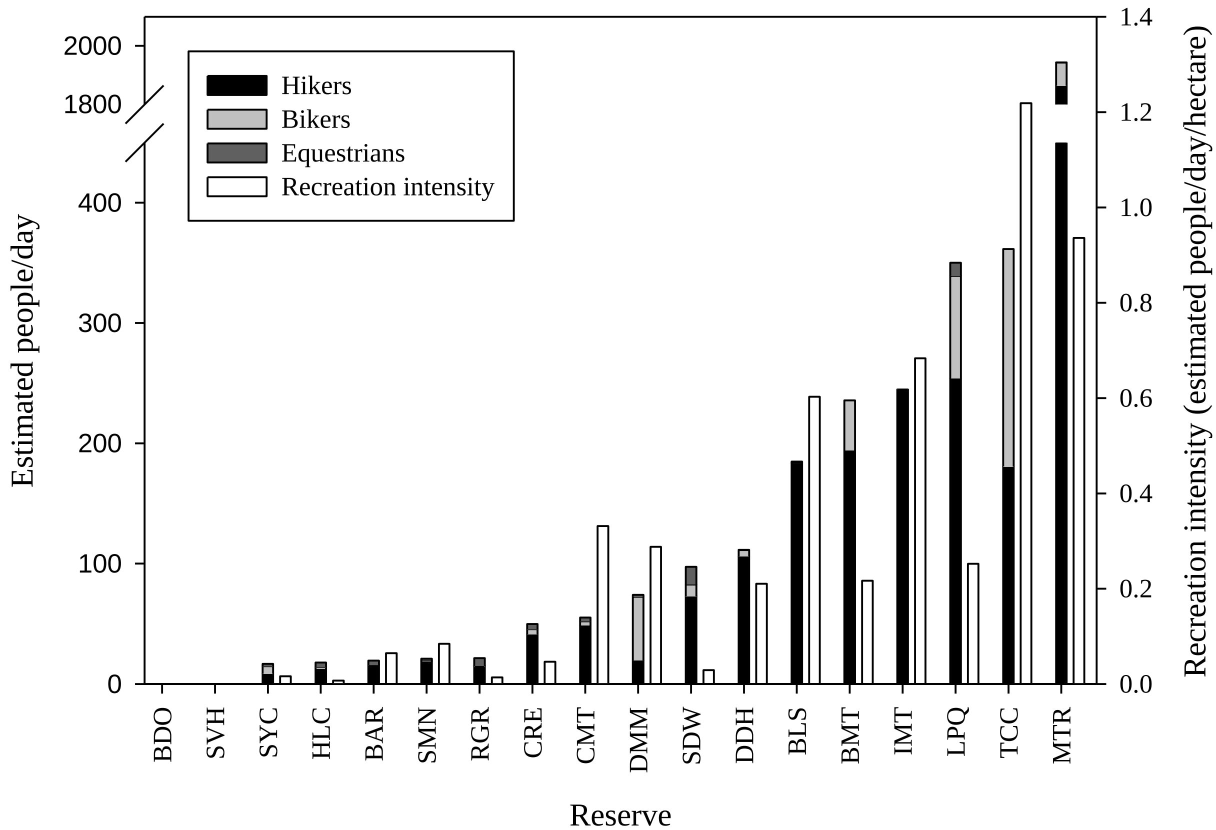


Figure 7. Visitation estimates for hikers, bikers, and equestrians at the 18 field study reserves. The left axis shows recreation estimates divided into activity type, and the right axis shows total visitation intensity (visitors per area).

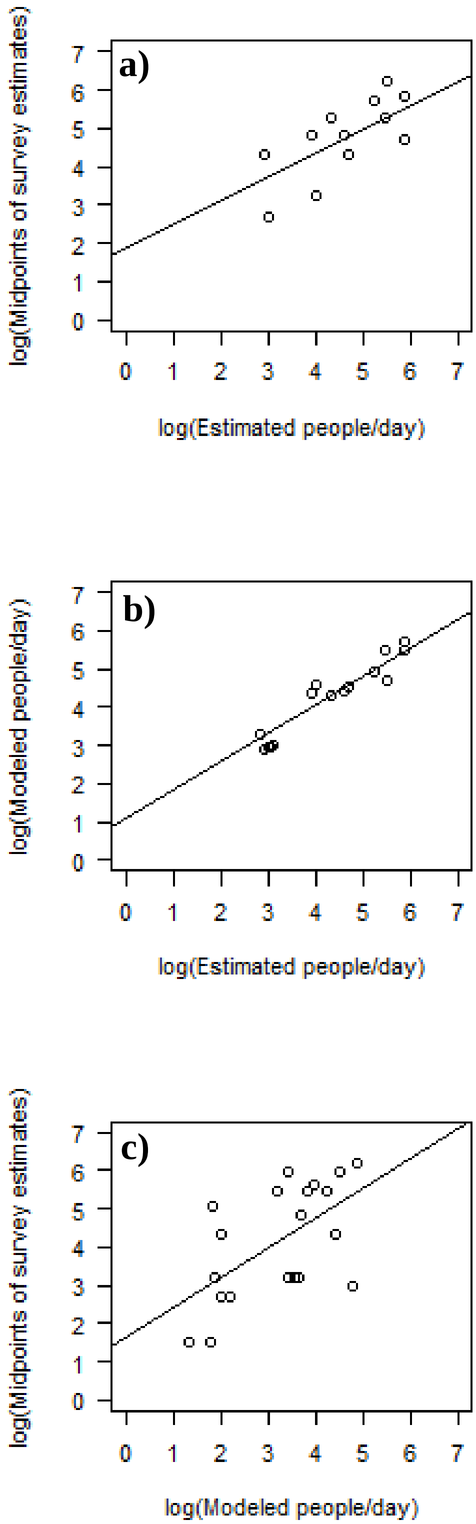


Figure 8. Scatterplots comparing a) empirical recreation estimates and estimates derived from an expert opinion survey for field reserves (n=14); b) empirical recreation estimates and modeled recreation for field reserves (n=18); and c) modeled recreation and estimates derived from an expert opinion survey for field and prediction reserves (n=34).

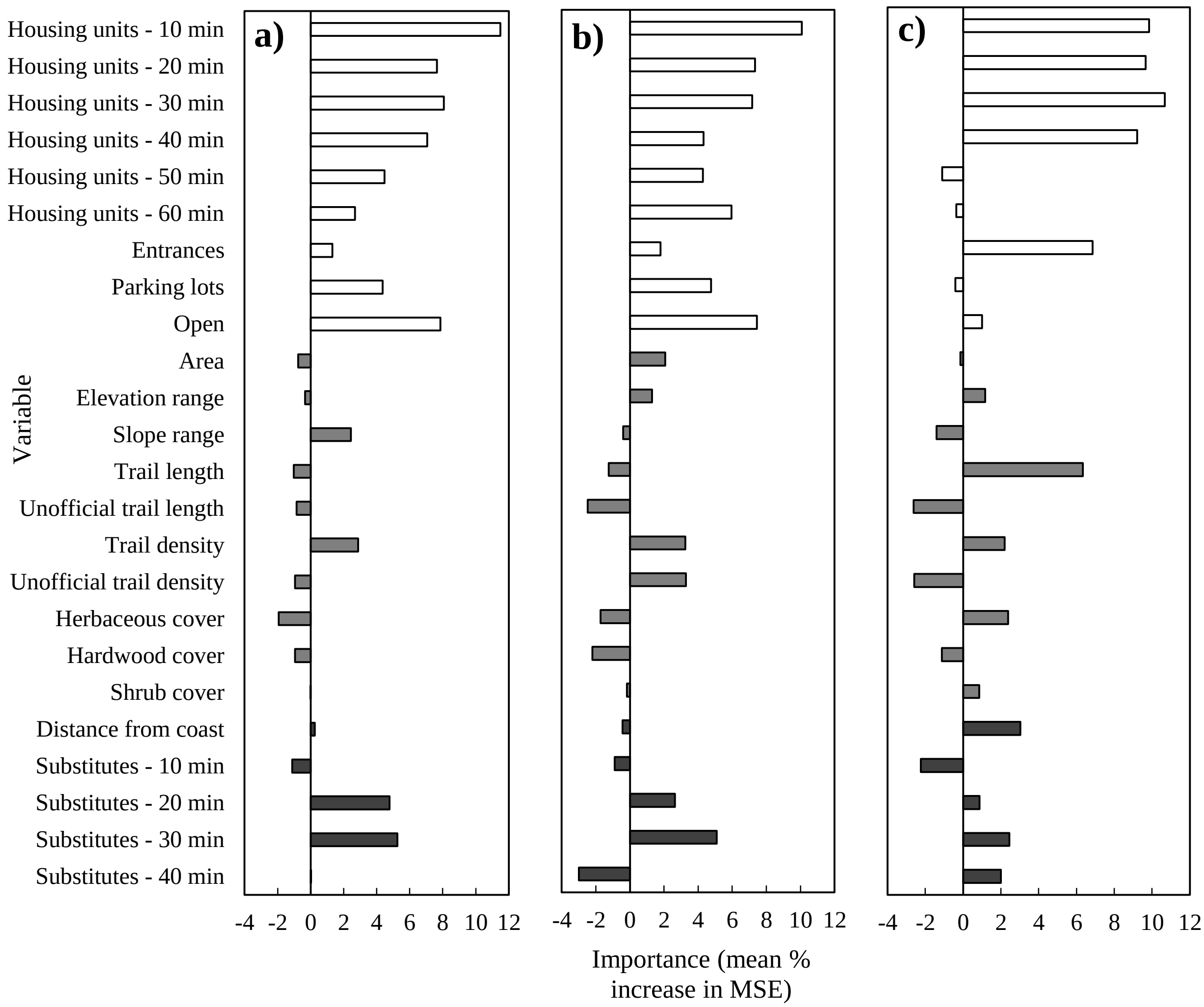
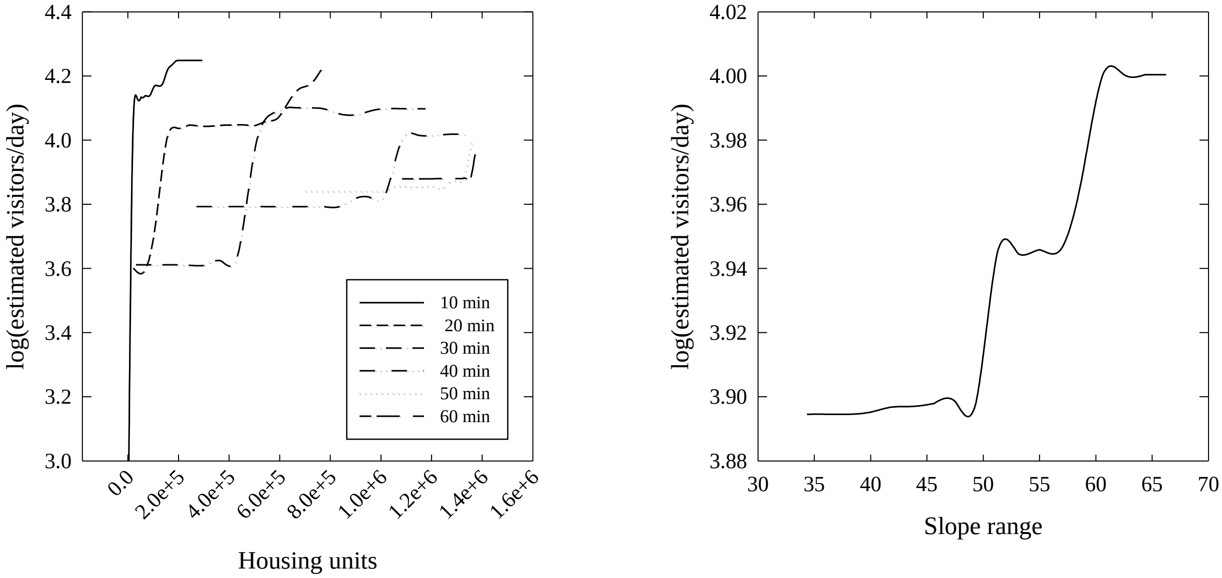
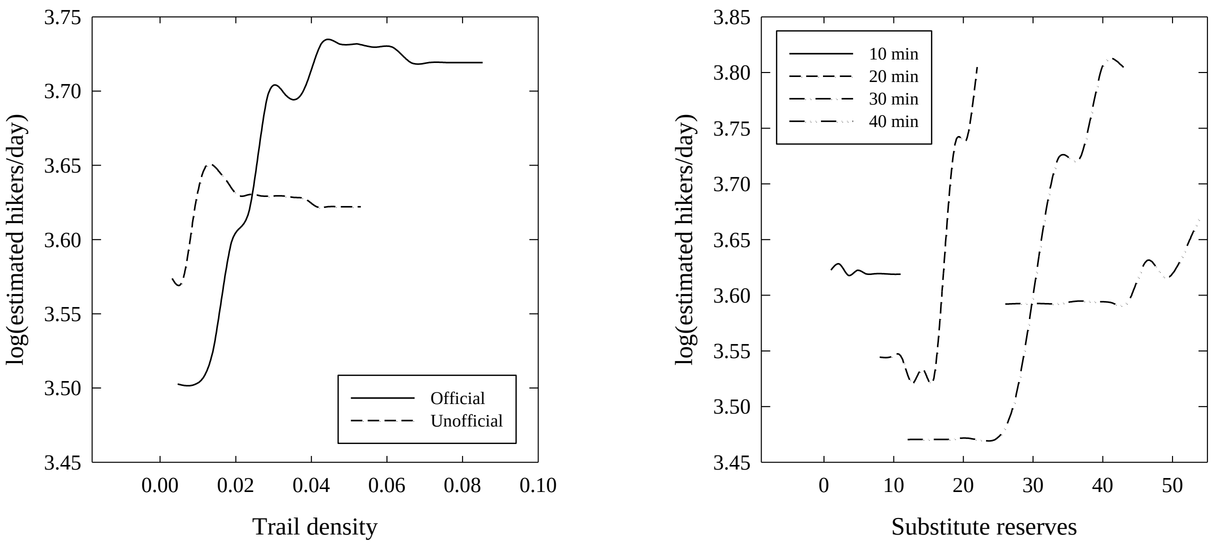


Figure 9. Variable importance plots for a) all visitors; b) hikers; and c) bikers. A high value indicates that a variable is important to the regression model because when this variable is randomly permuted, there is a relatively large change in the error (MSE) across all trees. A negative value means that the error decreased when the variable was randomly permuted and indicates very low importance. Accessibility variables have white bars, reserve attribute variables have medium gray bars, and landscape context variables have dark gray bars.

a)


log(estimated visitors/day)
Housing units
10 min
20 min
30 min
40 min
50 min
60 min
0.0
2.0e+5
4.0e+5
6.0e+5
8.0e+5
1.0e+6
1.2e+6
1.4e+6
1.6e+6
log(estimated visitors/day)
Slope range

b)


log(estimated hikers/day)
Trail density
Official
Unofficial
log(estimated hikers/day)
Substitute reserves
10 min
20 min
30 min
40 min

c)

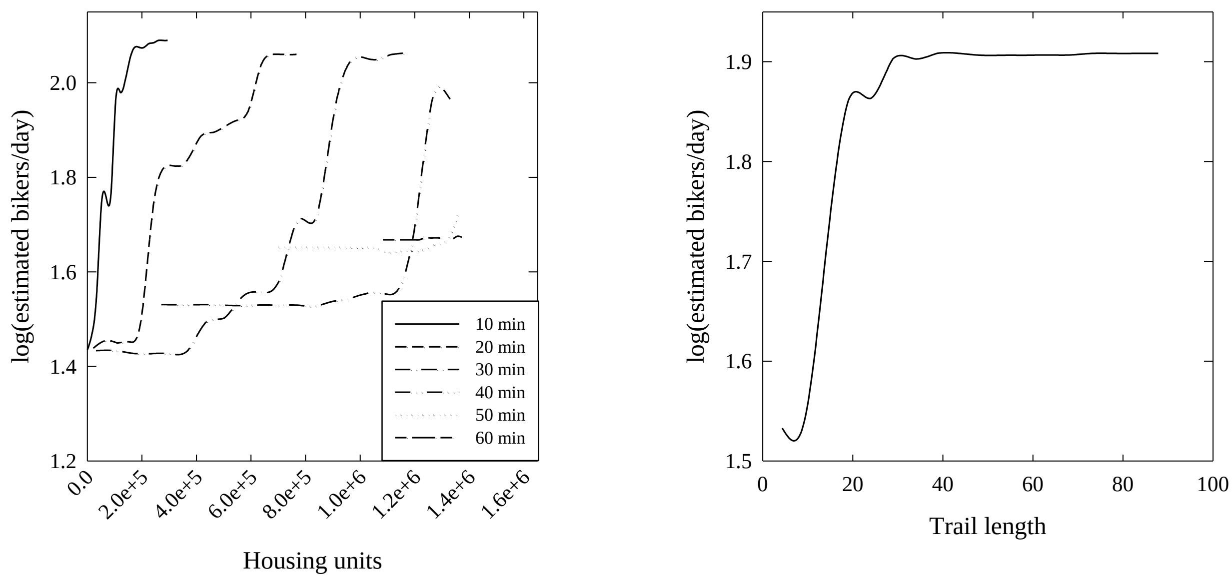


Figure 10. Partial dependence plots for selected predictor variables for random forest models for a) all visitors, b) hikers, and c) bikers at a network of reserves in San Diego County, CA, USA. Partial dependence plots show the relationship between a predictor and a response variable after averaging out the effects of other predictor variables in the model.

LITERATURE CITED

Arnberger, A., W. Haider, and C. Brandenburg. 2005. Evaluating visitor-monitoring techniques: a comparison of counting and video observation data. Environmental Management **36**:317–327.

Barros, A., C. Monz, and C. Pickering. 2014. Is tourism damaging ecosystems in the Andes? Current knowledge and an agenda for future research. AMBIO:1–17.

Becken, S., and H. Job. 2014. Protected areas in an era of global-local change. Journal of Sustainable Tourism **22**:507–527.

Beeco, J. A., J. C. Hallo, and M. T. J. Brownlee. 2014. GPS visitor tracking and recreation suitability mapping: tools for understanding and managing visitor use. Landscape and Urban Planning **127**:136–145.

Braunisch, V., P. Patthey, and R. Arlettaz. 2011. Spatially explicit modeling of conflict zones between wildlife and snow sports: prioritizing areas for winter refuges. Ecological Applications **21**:955–967.

Breiman, L. 2001. Random forests. Machine Learning **45**:5–32.

Bushell, R., and P. F. J. Eagles. 2007. Tourism and protected areas: benefits beyond boundaries: the Vth IUCN World Parks Congress. CABI.

CA Department of Fish and Game. 2012. Summary of Natural Community Conservation Plans (NCCPs). Available from http://www.dfg.ca.gov/habcon/nccp/.

Cessford, G., and A. Muhar. 2003. Monitoring options for visitor numbers in national parks and natural areas. Journal for Nature Conservation **11**:240–250.

Cordell, H. K. 2012. Outdoor recreation trends and futures. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC, USA.

Cutler, D. R., T. C. Edwards, K. H. Beard, A. Cutler, K. T. Hess, J. Gibson, and J. J. Lawler. 2007. Random forests for classification in ecology. Ecology **88**:2783–2792.

Dobson, A. P., J. P. Rodriguez, W. M. Roberts, and D. S. Wilcove. 1997. Geographic distribution of endangered species in the United States. Science **275**:550–553.

Eagles, P. F. J., McCool, C. D. Haynes, United Nations Environment Programme, World Tourism Organization, and International Union for Conservation of Nature and Natural Resources. 2002. Sustainable tourism in protected areas: guidelines for planning and management. IUCN--the World Conservation Union, Gland, Switzerland.

Griffin, T., S. Moore, G. Crilley, S. Darcy, and S. Schweinsberg. 2010. Protected area management: collection and use of visitor data. Vol. 1: Summary and recommendations. Cooperative Research Centre for Sustainable Tourism, Griffith University, Gold Coast, Queensland.

Hadwen, W. L., W. Hill, and C. M. Pickering. 2007. Icons under threat: Why monitoring visitors and their ecological impacts in protected areas matters. Ecological Management & Restoration **8**:177–181.

Hochachka, W. M., R. Caruana, D. Fink, A. Munson, M. Riedewald, D. Sorokina, and S. Kelling. 2007. Data-mining discovery of pattern and process in ecological systems. The Journal of Wildlife Management **71**:2427–2437.

IUCN, and UNEP. 2014. The World Database on Protected Areas (WDPA). UNEP-WCMC, Cambridge, UK.

Kerbiriou, C., I. Le Viol, A. Robert, E. Porcher, F. Gourmelon, and R. Julliard. 2009. Tourism in protected areas can threaten wild populations: from individual response to population viability of the chough Pyrrhocorax pyrrhocorax. Journal of Applied Ecology **46**:657–665.

Knudby, A., A. Brenning, and E. LeDrew. 2010. New approaches to modelling fish–habitat relationships. Ecological Modelling **221**:503–511.

Louv, R. 2005. Last child in the woods: Saving our children from nature-deficit disorder. Algonquin Books.

Malo, J., P. Acebes, and J. Traba. 2011. Measuring ungulate tolerance to human with flight distance: a reliable visitor management tool? Biodiversity and Conservation **20**:3477–3488.

Martin, T. G., M. A. Burgman, F. Fidler, P. M. Kuhnert, S. Low-Choy, M. Mcbride, and K. Mengersen. 2012. Eliciting expert knowledge in conservation science. Conservation Biology **26**:29–38.

McClaran, M. P., and D. N. Cole. 1993. Packstock in wilderness: use, impacts, monitoring, and management. US Department of Agriculture, Forest Service, Intermountain Research Station.

McCurdy, L. E., K. E. Winterbottom, S. S. Mehta, and J. R. Roberts. 2010. Using nature and outdoor activity to improve children’s health. Current Problems in Pediatric and Adolescent Health Care **40**:102–117.

Monz, C. A., D. N. Cole, Y.-F. Leung, and J. L. Marion. 2010. Sustaining visitor use in protected areas: future opportunities in recreation ecology research based on the USA experience. Environmental Management **45**:551–562.

Monz, C. A., C. M. Pickering, and W. L. Hadwen. 2013. Recent advances in recreation ecology and the implications of different relationships between recreation use and ecological impacts. Frontiers in Ecology and the Environment **11**:441–446.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature **403**:853–858.

Neuvonen, M., E. Pouta, J. Puustinen, and T. Sievänen. 2010. Visits to national parks: Effects of park characteristics and spatial demand. Journal for Nature Conservation **18**:224–229.

Oppel, S., A. Meirinho, I. Ramírez, B. Gardner, A. F. O'Connell, P. I. Miller, and M. Louzao. 2012. Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. Biological Conservation **156**:94–104.

Pettebone, D., P. Newman, and S. R. Lawson. 2010. Estimating visitor use at attraction sites and trailheads in Yosemite National Park using automated visitor counters. Landscape and Urban Planning **97**:229–238.

Prasad, A. M., L. R. Iverson, and A. Liaw. 2006. Newer classification and regression tree techniques: Bagging and random forests for ecological prediction. Ecosystems **9**:181–199.

Rösner, S., E. Mussard-Forster, T. Lorenc, and J. Müller. 2013. Recreation shapes a "landscape of fear" for a threatened forest bird species in Central Europe. Landscape Ecology **29**:55–66.

San Diego Association of Governments. 2010. 2050 regional growth forecast. San Diego, California.

SanGIS/SANDAG Data Warehouse. San Diego Geographic Information Sources - JPA/San Diego Association of Governments (SANDAG). Available from http://www.sangis.org/Download_GIS_data.htm.

Sato, C. F., J. T. Wood, and D. B. Lindenmayer. 2013. The effects of winter recreation on alpine and subalpine fauna: A systematic review and meta-analysis. PLoS ONE **8**:e64282.

Siderelis, C., R. L. Moore, and J.-H. Lee. 2011. A mixed logit model of visitors' national park choices. Society & Natural Resources **24**:799–813.

Stalmaster, M. V., and J. L. Kaiser. 1998. Effects of recreational activity on wintering bald eagles. Wildlife Monographs:3–46.

Steven, R., and J. G. Castley. 2013. Tourism as a threat to critically endangered and endangered birds: global patterns and trends in conservation hotspots. Biodiversity and Conservation **22**:1063–1082.

Termansen, M., C. J. McClean, and F. S. Jensen. 2013. Modelling and mapping spatial heterogeneity in forest recreation services. Ecological Economics **92**:48–57.

Termansen, M., C. J. McClean, and H. Skov-Petersen. 2004. Recreational site choice modelling using high-resolution spatial data. Environment and Planning A **36**:1085–1099.

Termansen, M., M. Zandersen, and C. J. McClean. 2008. Spatial substitution patterns in forest recreation. Regional Science and Urban Economics **38**:81–97.

Theobald, D. M., J. B. Norman, and P. Newman. 2010. Estimating visitor use of protected areas by modeling accessibility: a case study in Rocky Mountain National Park, Colorado. Journal of Conservation Planning **6**:1–20.

U.S. Census Bureau. 2013. State and County QuickFacts. 2010 Census Briefs. American Community Survey. Available from http://census.gov/prod/cen2010/briefs/c2010br-01.pfd.

Van der Zee, D. 1990. The complex relationship between landscape and recreation. Landscape Ecology **4**:225–236.

Wade, A. A., and D. M. Theobald. 2010. Residential development encroachment on U.S. protected areas. Conservation Biology **24**:151–161.

Watson, A. E., D. N. Cole, D. L. Turner, and P. S. Reynolds. 2000. Wilderness recreation use estimation: a handbook of methods and systems. U.S. Department of Agriculture, Ogden, UT.

Wilmers, C. C., Y. Wang, B. Nickel, P. Houghtaling, Y. Shakeri, M. L. Allen, J. Kermish-Wells, V. Yovovich, and T. Williams. 2013. Scale dependent behavioral responses to human development by a large predator, the puma. PLoS ONE **8**:e60590.

Wolf, I. D., G. Hagenloh, and D. B. Croft. 2012. Visitor monitoring along roads and hiking trails: How to determine usage levels in tourist sites. Tourism Management **33**:16–28.

Zaradic, P. A., O. R. W. Pergams, and P. Kareiva. 2009. The impact of nature experience on willingness to support conservation. PLoS ONE **4**:e7367.

APPENDIX I

Articles about the effects of recreation on animals that were included in the systematic review process (Chapter 1).

Addessi, L. 1994. Human disturbance and long-term changes on a rocky intertidal community. Ecological Applications **4**:786–797.

Amo, L., P. López, and J. Martin. 2006. Nature-based tourism as a form of predation risk affects body condition and health state of *Podarcis muralis* lizards. Biological Conservation **131**:402–409.

Arlettaz, R., P. Patthey, M. Baltic, T. Leu, M. Schaub, R. Palme, and S. Jenni-Eiermann. 2007. Spreading free-riding snow sports represent a novel serious threat for wildlife. Proceedings of the Royal Society B **274**:1219–1224.

Ayres, E., J. N. Nkem, D. H. Wall, B. J. Adams, J. E. Barrett, E. J. Broos, A. N. Parsons, L. E. Powers, B. L. Simmons, and R. A. Virginia. 2008. Effects of human trampling on populations of soil fauna in the McMurdo dry valleys, Antarctica. Conservation Biology **22**:1544–1551.

Banks, P. B., and J. V. Bryant. 2007. Four-legged friend or foe? Dog walking displaces native birds from natural areas. Biology Letters **3**:611–613.

Barros, F. 2001. Ghost crabs as a tool for rapid assessment of human impacts on exposed sandy beaches. Biological Conservation **97**:399–404.

Baudains, T. P., and P. Lloyd. 2007. Habituation and habitat changes can moderate the impacts of human disturbance on shorebird breeding performance. Animal Conservation **10**:400–407.

Beale, C. M., and P. Monaghan. 2005. Modeling the effects of limiting the number of visitors on failure rates of seabird nests. Conservation Biology **19**:2015–2019.

Behie, A. M., M. S. M. Pavelka, and C. A. Chapman. 2010. Sources of variation in fecal cortisol levels in howler monkeys in Belize. American Journal of Primatology **72**:600–606.

Bejder, L., S. M. Dawson, and J. A. Harraway. 1999. Responses by Hector's dolphins to boats and swimmers in Porpoise Bay, New Zealand. Marine Mammal Science **15**:738–750.

Bejder, L., A. Samuels, H. Whitehead, and N. Gales. 2006a. Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. Animal Behaviour **72**:1149–1158.

Bejder, L., A. Samuels, H. Whitehead, N. Gales, J. Mann, R. Connor, M. Heithaus, J. Watson-Capps, C. Flaherty, and M. Krützen. 2006b. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. Conservation Biology **20**:1791–1798.

Berman, C. M., J. Li, H. Ogawa, C. Ionica, and H. Yin. 2007. Primate tourism, range restriction, and infant risk among *Macaca thibetana* at Mt. Huangshan, China. International Journal of Primatology **28**:1123–1141.

Bhattacharya, T., T. Bashir, K. Poudyal, S. Sathyakumar, and G. K. Saha. 2012. Distribution, occupancy and activity patterns of goral (*Nemorhaedus goral*) and serow (*Capricornis thar*) in Khangchendzonga Biosphere Reserve, Sikkim, India. Mammal Study **37**:173–181.

Bishop, M. J. 2008. Displacement of epifauna from seagrass blades by boat wake. Journal of Experimental Marine Biology and Ecology **354**:111–118.

Blom, A., C. Cipolletta, A. M. H. Brunsting, and H. H. T. Prins. 2004. Behavioral responses of gorillas to habituation in the Dzanga-Ndoki National Park, Central African Republic. International Journal of Primatology **25**:179–196.

Bolduc, F., and M. Guillemette. 2003. Human disturbance and nesting success of common eiders: interaction between visitors and gulls. Biological Conservation **110**:77–83.

Borkowski, J. 2001. Flight behaviour and observability in human-disturbed sika deer. Acta Theriologica **46**:195–206.

Borkowski, J. J., P. J. White, R. A. Garrott, T. Davis, A. R. Hardy, and D. J. Reinhart. 2006. Behavioral responses of bison and elk in Yellowstone to snowmobiles and snow coaches. Ecological Applications **16**:1911–1925.

Bowen, K. D., and F. J. Janzen. 2008. Human recreation and the nesting ecology of a freshwater turtle (*Chrysemys picta*). Chelonian Conservation and Biology **7**:95–100.

Braunisch, V., P. Patthey, and R. Arlettaz. 2011. Spatially explicit modeling of conflict zones between wildlife and snow sports: prioritizing areas for winter refuges. Ecological Applications **21**:955–967.

Bright, A., G. R. Reynolds, J. Innes, and J. R. Waas. 2003. Effects of motorised boat passes on the time budgets of New Zealand dabchick, *Poliocephalus rufopectus*. Wildlife Research **30**:237–244.

Bright, A., J. R. Waas, and J. Innes. 2004. Correlations between human-made structures, boat-pass frequency and the number of New Zealand dabchicks (*Poliocephalus rufopectus*) on the Rotorua Lakes, New Zealand. New Zealand Journal of Ecology **28**:137–142.

Burger, J., and M. Gochfeld. 2007. Responses of emperor penguins (*Aptenodytes forsteri*) to encounters with ecotourists while commuting to and from their breeding colony. Polar Biology **30**:1303–1313.

Burger, J., M. Gochfeld, C. D. Jenkins, and F. Lesser. 2010. Effect of approaching boats on nesting black skimmers: using response distances to establish protective buffer zones. Journal of Wildlife Management **74**:102–108.

Cardoni, D. A., M. Favero, and J. P. Isacch. 2008. Recreational activities affecting the habitat use by birds in Pampa's wetlands, Argentina: implications for waterbird conservation. Biological Conservation **141**:797–806.

Cassini, M. H., D. Szteren, and E. Fernández-Juricic. 2004. Fence effects on the behavioural responses of South American fur seals to tourist approaches. Journal of Ethology **22**:127–133.

Claudet, J., P. Lenfant, and M. Schrimm. 2010. Snorkelers impact on fish communities and algae in a temperate marine protected area. Biodiversity and Conservation **19**:1649–1658.

Cobley, N. D., and J. R. Shears. 1999. Breeding performance of gentoo penguins (*Pygoscelis papua*) at a colony exposed to high levels of human disturbance. Polar Biology **21**:355–360.

Colman, J. E., B. W. Jacobsen, and E. Reimers. 2001. Summer response distances of Svalbard reindeer *Rangifer tarandus platyrhynchus* to provocation by humans on foot. Wildlife Biology **7**:275–284.

Coma, R., E. Pola, M. Ribes, and M. Zabala. 2004. Long-term assessment of temperate octocoral mortality patterns, protected vs. unprotected areas. Ecological Applications **14**:1466–1478.

Comor, V., J. Orgeas, P. Ponel, C. Rolando, and Y. R. Delettre. 2008. Impact of anthropogenic disturbances on beetle communities of French Mediterranean coastal dunes. Biodiversity and Conservation **17**:1837–1852.

Constantine, R. 2001. Increased avoidance of swimmers by wild bottlenose dolphins (*Tursiops truncatus*) due to long-term exposure to swim-with-dolphin tourism. Marine Mammal Science **17**:689–702.

Constantine, R., D. H. Brunton, and T. Dennis. 2004. Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. Biological Conservation **117**:299–307.

Cooper, C. A., A. J. Neff, D. P. Poon, and G. R. Smith. 2008. Behavioral responses of Eastern gray squirrels in suburban habitats differing in human activity levels. Northeastern Naturalist **15**:619–625.

Cornelius, C., S. A. Navarrete, and P. A. Marquet. 2001. Effects of human activity on the structure of coastal marine bird assemblages in central Chile. Conservation Biology **15**:1396–1404.

Cunha, A. A. 2010. Negative effects of tourism in a Brazilian Atlantic forest National Park. Journal for Nature Conservation **18**:291–295.

Dans, S. L., M. Degrati, S. N. Pedraza, and E. A. Crespo. 2012. Effects of tour boats on dolphin activity examined with sensitivity analysis of Markov chains. Conservation Biology **26**:708–716.

De la Torre, S., C. T. Snowdon, and M. Bejarano. 2000. Effects of human activities on wild pygmy marmosets in Ecuadorian Amazonia. Biological Conservation **94**:153–163.

Devney, C. A., and B. C. Congdon. 2009. Testing the efficacy of a boundary fence at an important seabird breeding colony and key tourist destination. Wildlife Research **36**:353–360.

Diego-Rasilla, F. J. 2003. Human influence on the tameness of wall lizard, *Podarcis muralis*. Italian Journal of Zoology **70**:225–228.

Duchesne, M., S. D. Côté, and C. Barrette. 2000. Responses of woodland caribou to winter ecotourism in the Charlevoix Biosphere Reserve, Canada. Biological Conservation **96**:311–317.

Dyck, M. G., and R. K. Baydack. 2004. Vigilance behaviour of polar bears (*Ursus maritimus*) in the context of wildlife-viewing activities at Churchill, Manitoba, Canada. Biological Conservation **116**:343–350.

El Alami, A., E. Van Lavieren, A. Rachida, and A. Chait. 2012. Differences in activity budgets and diet Between semiprovisioned and wild-feeding groups of the endangered Barbary macaque (*Macaca sylvanus*) in the Central High Atlas Mountains, Morocco. American Journal of Primatology **74**:210–216.

Ellenberg, U., T. Mattern, and P. J. Seddon. 2009. Habituation potential of yellow-eyed penguins depends on sex, character and previous experience with humans. Animal Behaviour **77**:289–296.

Fairbanks, W. S., and R. Tullous. 2002. Distribution of pronghorn (*Antilocapra americana* Ord) on Antelope Island State Park, Utah, USA, before and after establishment of recreational trails. Natural Areas Journal **22**:277–282.

Fernández-Juricic, E., M. D. Jimenez, and E. Lucas. 2002. Factors affecting intra- and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. Canadian Journal of Zoology/Revue Canadienne de Zoologie **80**:1212–1220.

Fernández-Juricic, E., R. Vaca, and N. Schroeder. 2004. Spatial and temporal responses of forest birds to human approaches in a protected area and implications for two management strategies. Biological Conservation **117**:407–416.

Fernández-Juricic, E., M. P. Venier, D. Renison, and D. T. Blumstein. 2005. Sensitivity of wildlife to spatial patterns of recreationist behavior: a critical assessment of minimum approaching distances and buffer areas for grassland birds. Biological Conservation **125**:225–235.

Fernández-Juricic, E., E. F. Zahn, T. Parker, T. Stankowich, and others. 2009. California's endangered Belding's savannah sparrow (*Passerculus sandwichensis beldingi*): tolerance of pedestrian disturbance. Avian Conservation and Ecology-Écologie et conservation des oiseaux **4**:1.

Ficetola, G. F., R. Sacchi, S. Scali, A. Gentilli, F. De Bernardi, and P. Galeotti. 2007. Vertebrates respond differently to human disturbance: implications for the use of a focal species approach. Acta Oecologica **31**:109–118.

Finney, S. K., J. W. Pearce-Higgins, and D. W. Yalden. 2005. The effect of recreational disturbance on an upland breeding bird, the golden plover *Pluvialis apricaria*. Biological Conservation **121**:53–63.

Fowler, G. S. 1999. Behavioral and hormonal responses of Magellanic penguins (*Spheniscus magellanicus*) to tourism and nest site visitation. Biological Conservation **90**:143–149.

Galicia, E., and G. A. Baldassarre. 1997. Effects of motorized tourboats on the behavior of nonbreeding American flamingos in Yucatan, Mexico. Conservation Biology **11**:1159–1165.

Garber, S. D., and J. Burger. 1995. A 20-year study documenting the relationship between turtle decline and human recreation. Ecological Applications **5**:1151–1162.

George, S. L., and K. R. Crooks. 2006. Recreation and large mammal activity in an urban nature reserve. Biological Conservation **133**:107–117.

Giese, M. 1996. Effects of human activity on Adelie penguin *Pygoscelis adeliae* breeding success. Biological Conservation **75**:157–164.

Gill, J. A., K. Norris, and W. J. Sutherland. 2001. The effects of disturbance on habitat use by black-tailed godwits *Limosa limosa*. Journal of Applied Ecology **38**:846–856.

Glover, H. K., M. A. Weston, G. S. Maguire, K. K. Miller, and B. A. Christie. 2011. Towards ecologically meaningful and socially acceptable buffers: response distances of shorebirds in Victoria, Australia, to human disturbance. Landscape and Urban Planning **103**:326–334.

Goldstein, M. I., A. J. Poe, L. H. Suring, R. M. Nielson, and T. L. McDonald. 2009. Brown bear den habitat and winter recreation in south-central Alaska. Journal of Wildlife Management **74**:35–42.

Griffin, S. C., T. Valois, M. L. Taper, and L. Scott Mills. 2007. Effects of tourists on behavior and demography of Olympic marmots. Conservation Biology **21**:1070–1081.

Grubb, T. G., D. K. Delaney, W. W. Bowerman, and M. R. Wierda. 2010. Golden eagle indifference to heli-Skiing and military helicopters in northern Utah. Journal of Wildlife Management **74**:1275–1285.

Guillemain, M., R. Blanc, C. Lucas, and M. Lepley. 2007. Ecotourism disturbance to wildfowl in protected areas: historical, empirical and experimental approaches in the Camargue, Southern France. Biodiversity and Conservation **16**:3633–3651.

Gutzwiller, K. J., and S. K. Riffell. 2008. Does repeated human intrusion alter use of wildland sites by red squirrels? Multiyear experimental evidence. Journal of Mammalogy **89**:374–380.

Gutzwiller, K. J., S. K. Riffell, and S. H. Anderson. 2002. Repeated human intrusion and the potential for nest predation by gray jays. The Journal of Wildlife Management **66**:372–380.

Hawkins, J. P., and C. M. Roberts. 1992. Effects of recreational SCUBA diving on fore-reef slope communities of coral reefs. Biological Conservation **62**:171–178.

Hawkins, J. P., and C. M. Roberts. 1993. Effects of recreational scuba diving on coral reefs: trampling on reef-flat communities. Journal of Applied Ecology **30**:25–30.

Hawkins, J. P., C. M. Roberts, T. V. Hof, K. D. Meyer, J. Tratalos, and C. Aldam. 1999. Effects of recreational scuba diving on Caribbean coral and fish Communities. Conservation Biology **13**:888–897.

Hayward, M., and G. Hayward. 2009. The impact of tourists on lion *Panthera leo* behaviour, stress and energetics. Acta Theriologica **54**:219–224.

Heil, L., E. Fernandez-Juricic, D. Renison, A. M. Cingolani, and D. T. Blumstein. 2007. Avian responses to tourism in the biogeographically isolated high Cordoba Mountains, Argentina. Biodiversity and Conservation **16**:1009–1026.

Heyman, W., L. Carr, and P. Lobel. 2010. Diver ecotourism and disturbance to reef fish spawning aggregations: It is better to be disturbed than to be dead. Marine Ecology Progress Series **419**:201–210.

Hines, K. N. 2011. Effects of ecotourism on endangered northern Bahamian rock iguanas (*Cyclura cychlura*). Herpetological Conservation and Biology **6**:250–259.

Hodgson, A. J., H. Marsh, and P. J. Corkeron. 2004. Provisioning by tourists affects the behaviour but not the body condition of Mareeba rock-wallabies (*Petrogale mareeba*). Wildlife Research **31**:451–456.

Holcomb, K., J. K. Young, and L. R. Gerber. 2009. The influence of human disturbance on California sea lions during the breeding season. Animal Conservation **12**:592–598.

Holmes, N. D. 2007. Comparing king, gentoo, and royal penguin responses to pedestrian visitation. Journal of Wildlife Management **71**:2575–2582.

Holmes, N., M. Giese, and L. K. Kriwoken. 2005. Testing the minimum approach distance guidelines for incubating toyal penguins *Eudyptes schlegeli*. Biological Conservation **126**:339–350.

Hsieh, Y.-L., Y.-S. Lin, and I.-M. Tso. 2003. Ground spider diversity in the Kenting uplifted coral reef forest, Taiwan: a comparison between habitats receiving various disturbances. Biodiversity and Conservation **12**:2173–2194.

Hsu, C., C. Chen, and H. Hsieh. 2009a. Effects of sediment compaction on macroinfauna in a protected coastal wetland in Taiwan. Marine Ecology Progress Series **375**:73–83.

Hsu, M. J., C.-C. Kao, and G. Agoramoorthy. 2009b. Interactions between visitors and Formosan macaques (*Macaca cyclopis*) at Shou-Shan Nature Park, Taiwan. American Journal of Primatology **71**:214–222.

Hulbert, I. A. R. 1990. The response of ruddy shelduck *Tadorna ferruginea* to tourist activity in the Royal Chitwan National Park of Nepal. Biological Conservation **52**:113–123.

Ikuta, L. A., and D. T. Blumstein. 2003. Do fences protect birds from human disturbance? Biological Conservation **112**:447–452.

Ilarri, M. D. I., A. T. de Souza, P. R. de Medeiros, R. G. Grempel, and I. M. de L. Rosa. 2008. Effects of tourist visitation and supplementary feeding on fish assemblage composition on a tropical reef in the Southwestern Atlantic. Neotropical Ichthyology **6**:651–656.

Iverson, J. B., S. J. Converse, G. R. Smith, and J. M. Valiulis. 2006. Long-term trends in the demography of the Allen Cays Rock Iguana (*Cyclura cychlura inornata*): human disturbance and density-dependent effects. Biological Conservation **132**:300–310.

Jayakody, S., A. M. Sibbald, I. J. Gordon, and X. Lambin. 2008. Red deer *Cervus elephus* vigilance behaviour differs with habitat and type of human disturbance. Wildlife Biology **14**:81–91.

Jayakody, S., A. M. Sibbald, R. W. Mayes, R. J. Hooper, I. J. Gordon, and X. Lambin. 2011. Effects of human disturbance on the diet composition of wild red deer (*Cervus elaphus*). European Journal of Wildlife Research **57**:939–948.

Jiménez, G., J. A. Lemus, L. Meléndez, G. Blanco, and P. Laiolo. 2011. Dampened behavioral and physiological responses mediate birds' association with humans. Biological Conservation **144**:1702–1711.

Kaiser, M. S., and E. K. Fritzell. 1984. Effects of river recreationists on green-backed heron behavior. The Journal of Wildlife Management **48**:561–567.

Kangas, K., M. Luoto, A. Ihantola, E. Tomppo, and P. Siikamäki. 2010. Recreation-induced changes in boreal bird communities in protected areas. Ecological Applications **20**:1775–1786.

Karp, D. S., and R. Guevara. 2011. Conversational noise reduction as a win–win for ecotourists and rain forest birds in Peru. Biotropica **43**:122–130.

Karp, D. S., and T. L. Root. 2009. Sound the stressor: how hoatzins (*Opisthocomus hoazin*) react to ecotourist conversation. Biodiversity and Conservation **18**:3733–3742.

Keeley, W. H., and M. J. Bechard. 2011. Flushing distances of ferruginous hawks nesting in rural and exurban New Mexico. Journal of Wildlife Management **75**:1034–1039.

Keller, V. E. 1991. Effects of human disturbance on eider ducklings *Somateria mollissima* in an estuarine habitat in Scotland. Biological Conservation **58**:213–228.

Kerbiriou, C., I. Le Viol, A. Robert, E. Porcher, F. Gourmelon, and R. Julliard. 2009. Tourism in protected areas can threaten wild populations: from individual response to population viability of the chough *Pyrrhocorax pyrrhocorax*. Journal of Applied Ecology **46**:657–665.

King, J. M., and J. T. Heinen. 2004. An assessment of the behaviors of overwintering manatees as influenced by interactions with tourists at two sites in central Florida. Biological Conservation **117**:227–234.

Klailova, M., C. Hodgkinson, and P. C. Lee. 2010. Behavioral responses of one western lowland gorilla (*Gorilla gorilla gorilla*) group at Bai Hokou, Central African Republic, to tourists, researchers and trackers. American Journal of Primatology **72**:897–906.

Klein, M. L., S. R. Humphrey, and H. F. Percival. 1995. Effects of ecotourism on distribution of waterbirds in a wildlife refuge. Conservation Biology **9**:1454–1465.

Krebs, J., E. C. Lofroth, and I. Parfitt. 2007. Multiscale habitat use by wolverines in British Columbia, Canada. Journal of Wildlife Management **71**:2180–2192.

Lafferty, K. D. 2001a. Disturbance to wintering western snowy plovers. Biological Conservation **101**:315–325.

Lafferty, K. D. 2001. Birds at a southern California beach: seasonality, habitat use and disturbance by human activity. Biodiversity and Conservation **10**:1949–1962.

Lafferty, K. D., D. Goodman, and C. P. Sandoval. 2006. Restoration of breeding by snowy plovers following protection from disturbance. Biodiversity and Conservation **15**:2217–2230.

Lamb, J. B., and B. L. Willis. 2011. Using coral disease prevalence to assess the effects of concentrating tourism activities on offshore reefs in a tropical marine park. Conservation Biology **25**:1044–1052.

Laroche, R. K., A. A. Kock, L. M. Dill, and W. H. Oosthuizen. 2007. Effects of provisioning ecotourism activity on the behaviour of white sharks Carcharodon carcharias. Marine Ecology Progress Series **338**:199–209.

Leighton, P. A., J. A. Horrocks, and D. L. Kramer. 2010. Conservation and the scarecrow effect: Can human activity benefit threatened species by displacing predators? Biological Conservation **143**:2156–2163.

Lemon, M., T. P. Lynch, D. H. Cato, and R. G. Harcourt. 2006. Response of travelling bottlenose dolphins (*Tursiops aduncus*) to experimental approaches by a powerboat in Jervis Bay, New South Wales, Australia. Biological Conservation **127**:363–372.

Lenth, B. E., R. L. Knight, and M. E. Brennan. 2008. The effects of dogs on wildlife communities. Natural Areas Journal **28**:218–227.

Lott, D. F., and M. McCoy. 1995. Asian rhinos *Rhinoceros unicornis* on the run? Impact of tourist visits on one population. Biological Conservation **73**:23–26.

Lusseau, D. 2003a. Male and female bottlenose dolphins *Tursiops spp*. have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. Marine Ecology Progress Series **257**:267–274.

Lusseau, D. 2003b. Effects of tour boats on the behavior of bottlenose dolphins: using Markov chains to model anthropogenic impacts. Conservation Biology **17**:1785–1793.

Lusseau, D. 2004. The hidden cost of tourism: detecting long-term effects of tourism using behavioral information. Ecology and Society **9**:2.

Lusseau, D. 2005. Residency pattern of bottlenose dolphins *Tursiops spp*. in Milford Sound, New Zealand, is related to boat traffic. Marine Ecology Progress Series **295**:265–272.

Lusseau, D. 2006. The short-term behavioral reactions of bottlenose dolphins to interactions with boats in Doubtful Sound, New Zealand. Marine Mammal Science **22**:802–818.

Lynch, H. J., W. F. Fagan, and R. Naveen. 2010. Population trends and reproductive success at a frequently visited penguin colony on the western Antarctic peninsula. Polar Biology **33**:493–503.

Madsen, J. 1998. Experimental refuges for migratory waterfowl in Danish wetlands. I. Baseline assessment of the disturbance effects of recreational activities. Journal of Applied Ecology **35**:386–397.

Mainini, B., P. Neuhaus, and P. Ingold. 1993. Behaviour of marmots *Marmota marmota* under the influence of different hiking activities. Biological Conservation **64**:161–164.

Maljković, A., and I. M. Côté. 2011. Effects of tourism-related provisioning on the trophic signatures and movement patterns of an apex predator, the Caribbean reef shark. Biological Conservation **144**:859–865.

Mallord, J. W., P. M. Dolman, A. F. Brown, and W. J. Sutherland. 2007. Linking recreational disturbance to population size in a ground-nesting passerine. Journal of Applied Ecology **44**:185–195.

Malo, J., P. Acebes, and J. Traba. 2011. Measuring ungulate tolerance to human with flight distance: a reliable visitor management tool? Biodiversity and Conservation **20**:3477–3488.

Mann, S. L., R. J. Steidl, and V. M. Dalton. 2002. Effects of cave tours on breeding *Myotis velifer*. The Journal of Wildlife Management **66**:618–624.

Maréchal, L., S. Semple, B. Majolo, M. Qarro, M. Heistermann, and A. MacLarnon. 2011. Impacts of tourism on anxiety and physiological stress levels in wild male Barbary macaques. Biological Conservation **144**:2188–2193.

Markovchick-Nicholls, L., H. M. Regan, D. H. Deutschman, A. Widyanata, B. Martin, L. Noreke, and T. Ann Hunt. 2008. Relationships between human disturbance and wildlife land use in urban habitat fragments. Conservation Biology **22**:99–109.

Martin, J., L. de Neve, J. Antonio, V. Polo, and M. Soler. 2004. Factors affecting the escape behaviour of juvenile chinstrap penguins, *Pygoscelis antarctica*, in response to human disturbance. Polar Biology **27**:775–781.

Martin, J., P. L. Fackler, J. D. Nichols, M. C. Runge, C. L. McIntyre, B. L. Lubow, M. C. McCluskie, and J. A. Schmutz. 2011. An adaptive-management framework for optimal control of hiking near golden eagle nests in Denali National Park. Conservation Biology **25**:316–323.

Martinez, E., M. B. Orams, M. D. M. Pawley, and K. A. Stockin. 2012. The use of auditory stimulants during swim encounters with Hector's dolphins (*Cephalorhynchus hectori hectori*) in Akaroa Harbour, New Zealand. Marine Mammal Science **28**:E295–E315.

McClung, M. R., P. J. Seddon, M. Massaro, and A. N. Setiawan. 2004. Nature-based tourism impacts on yellow-eyed penguins *Megadyptes antipodes*: does unregulated visitor access affect fledging weight and juvenile survival? Biological Conservation **119**:279–285.

McGrann, M. C., G. R. Wright, R. J. Dial, and A. M. McGrann. 2006. Off-highway vehicle impact on the flat-tailed horned lizard, *Phrynosoma mcallii*, in the Colorado Desert of Southern California. California Fish and Game **92**:67–80.

McMillan, M. A., J. C. Nekola, and D. W. Larson. 2003. Effects of rock climbing on the land snail community of the Niagara escarpment in southern Ontario, Canada. Conservation Biology **17**:616–621.

Milazzo, M. 2011. Evaluation of a behavioural response of Mediterranean coastal fishes to novel recreational feeding situation. Environmental Biology of Fishes **91**:127–132.

Milazzo, M., I. Anastasi, and T. J. Willis. 2006. Recreational fish feeding affects coastal fish behavior and increases frequency of predation on damselfish *Chromis chromis* nests. Marine Ecology Progress Series **310**:165–172.

Miller, J. R., and N. T. Hobbs. 2000. Recreational trails, human activity, and nest predation in lowland riparian areas. Landscape and Urban Planning **50**:227–236.

Miller, S. G., R. L. Knight, and C. K. Miller. 1998. Influence of recreational trails on breeding bird communities. Ecological Applications **8**:162–169.

Moore, M. J. C., and R. A. Seigel. 2006. No place to nest or bask: effects of human disturbance on the nesting and basking habits of yellow-blotched map turtles (*Graptemys flavimaculata*). Biological Conservation **130**:386–393.

Morrison, M. L., R. J. Young, J. S. Romsos, and R. Golightly. 2011. Restoring forest raptors: influence of human disturbance and forest condition on Northern Goshawks. Restoration Ecology **19**:273–279.

Müllner, A., K. Eduard Linsenmair, and M. Wikelski. 2004. Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). Biological Conservation **118**:549–558.

Naylor, L. M., M. J. Wisdom, and R. G. Anthony. 2009. Behavioral responses of North American elk to recreational activity. Journal of Wildlife Management **73**:328–338.

Neuhaus, P., and B. Mainini. 1998. Reactions and adjustment of adult and young alpine marmots *Marmota marmota* to intense hiking activities. Wildlife Biology **4**:119–123.

Neumann, W., G. Ericsson, and H. Dettki. 2010. Does off-trail backcountry skiing disturb moose? European Journal of Wildlife Research **56**:513–518.

Osinga, N., S. B. Nussbaum, P. M. Brakefield, and H. A. Udo de Haes. 2012. Response of common seals (*Phoca vitulina*) to human disturbances in the Dollard estuary of the Wadden Sea. Mammalian Biology - Zeitschrift für Säugetierkunde **77**:281–287.

Paksuz, S., and B. Özkan. 2012. The protection of the bat community in the Dupnisa Cave System, Turkey, following opening for tourism. Oryx **46**:130–136.
Papouchis, C. M., F. J. Singer, and W. B. Sloan. 2001. Responses of desert bighorn sheep to increased human recreation. Journal of Wildlife Management **65**:573–582.
Parent, C., and P. J. Weatherhead. 2000. Behavioral and life history responses of eastern Massasauga rattlesnakes (*Sistrurus catenatus catenatus*) to human disturbance. Oecologia **125**:170–178.
Patterson, M. E., J. D. Fraser, and J. W. Roggenbuck. 1991. Factors affecting piping plover productivity on Assateague Island. Journal of Wildlife Management **55**:525–531.
Patthey, P., S. Wirthner, N. Signorell, and R. Arlettaz. 2008. Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems. Journal of Applied Ecology **45**:1704–1711.
Peters, K. A., and D. L. Otis. 2007. Shorebird roost-site selection at two temporal scales: is human disturbance a factor? Journal of Applied Ecology **44**:196–209.
Pfeiffer, S., and H.-U. Peter. 2004. Ecological studies toward the management of an Antarctic tourist landing site (Penguin Island, South Shetland Islands). Polar Record **40**:345–353.
Phillips, G. E., and A. W. Alldredge. 2000. Reproductive success of elk following disturbance by humans during calving season. Journal of Wildlife Management **64**:521–530.
Picciulin, M., L. Sebastianutto, A. Codarin, A. Farina, and E. A. Ferrero. 2010. In situ behavioural responses to boat noise exposure of *Gobius cruentatus* (Gmelin, 1789; fam. Gobiidae) and *Chromis chromis* (Linnaeus, 1758; fam. Pomacentridae) living in a marine protected area. Journal of Experimental Marine Biology and Ecology **386**:125–132.
Pineiro, A., I. Barja, G. Silvan, and J. Carlos Illera. 2012. Effects of tourist pressure and reproduction on physiological stress response in wildcats: management implications for species conservation. Wildlife Research **39**:532–539.
Preisler, H. K., A. A. Ager, and M. J. Wisdom. 2006. Statistical methods for analysing responses of wildlife to human disturbance. Journal of Applied Ecology **43**:164–172.
Randler, C. 2006. Disturbances by dog barking increase vigilance in coots *Fulica atra*. European Journal of Wildlife Research **52**:265–270.
Reed, S. E., and A. M. Merenlender. 2008. Quiet, nonconsumptive recreation reduces protected area effectiveness. Conservation Letters **1**:146–154.
Reed, S. E., and A. M. Merenlender. 2011. Effects of management of domestic dogs and recreation on carnivores in protected areas in Northern California. Conservation Biology **25**:504–513.
Reimers, E., S. Eftestøl, and J. E. Colman. 2003. Behavior responses of wild reindeer to direct provocation by a snowmobile or skier. Journal of Wildlife Management **67**:747–754.
Reimers, E., F. L. Miller, S. Eftestøl, J. E. Colman, and B. Dahle. 2006. Flight by feral reindeer Rangifer *tarandus tarandus* in response to a directly approaching human on foot or on skis. Wildlife Biology **12**:403–413.
Riffell, S. K., K. J. Gutzwiller, and S. H. Anderson. 1996. Does repeated human intrusion cause cumulative declines in avian richness and abundance? Ecological Applications **6**:492–505.
Rode, K. D., S. D. Farley, J. Fortin, and C. T. Robbins. 2007. Nutritional consequences of experimentally introduced tourism in brown bears. Journal of Wildlife Management **71**:929–939.

Rode, K. D., S. D. Farley, and C. T. Robbins. 2006. Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. Biological Conservation **133**:70–80.

Rode, K. D., S. D. Farley, and C. T. Robbins. 2006. Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. Ecology **87**:2636–2646.

Rodgers, J. A., and S. T. Schwikert. 2002. Buffer-zone distances to protect foraging and loafing waterbirds from disturbance by personal watercraft and outboard-powered boats. Conservation Biology **16**:216–224.

Rodríguez-Prieto, I., and E. Fernández-Juricic. 2005. Effects of direct human disturbance on the endemic Iberian frog *Rana iberica* at individual and population levels. Biological Conservation **123**:1–9.

Rodriguez-Prieto, I., E. Fernández-Juricic, J. Martín, and Y. Regis. 2009. Antipredator behavior in blackbirds: habituation complements risk allocation. Behavioral Ecology **20**:371–377.

Romero, L. M., and M. Wikelski. 2002. Exposure to tourism reduces stress-induced corticosterone levels in Galápagos marine iguanas. Biological Conservation **108**:371–374.

Rouphael, A. B., and G. J. Inglis. 2001. "Take only photographs and leave only footprints"?: An experimental study of the impacts of underwater photographers on coral reef dive sites. Biological Conservation **100**:281–287.

Rouphael, A. B., and G. J. Inglis. 2002. Increased spatial and temporal variability in coral damage caused by recreational scuba diving. Ecological Applications **12**:427–440.

Sanecki, G. M., K. Green, H. Wood, and D. Lindenmayer. 2006. The implications of snow-based recreation for small mammals in the subnivean space in south-east Australia. Biological Conservation **129**:511–518.

Schierding, M., S. Vahder, L. Dau, and U. Irmler. 2011. Impacts on biodiversity at Baltic Sea beaches. Biodiversity and Conservation **20**:1973–1985.

Schlacher, T. A., and L. Thompson. 2012. Beach recreation impacts benthic invertebrates on ocean-exposed sandy shores. Biological Conservation **147**:123–132.

Schummer, M. L., and W. R. Eddleman. 2003. Effects of disturbance on activity and energy budgets of migrating waterbirds in south-central Oklahoma. Journal of Wildlife Management **67**:789–795.

Schurr, M., A. Fuentes, E. Luecke, J. Cortes, and E. Shaw. 2012. Intergroup variation in stable isotope ratios reflects anthropogenic impact on the Barbary macaques (*Macaca sylvanus*) of Gibraltar. Primates **53**:31–40.

Sebastianutto, L., M. Picciulin, M. Costantini, and E. A. Ferrero. 2011. How boat noise affects an ecologically crucial behaviour: the case of territoriality in *Gobius cruentatus* (Gobiidae). Environmental Biology of Fishes **92**:207–215.

Seip, D. R., C. J. Johnson, and G. S. Watts. 2007. Displacement of mountain caribou from winter habitat by snowmobiles. Journal of Wildlife Management **71**:1539–1544.

Semeniuk, C. A. D., S. Bourgeon, S. L. Smith, and K. D. Rothley. 2009. Hematological differences between stingrays at tourist and non-visited sites suggest physiological costs of wildlife tourism. Biological Conservation **142**:1818–1829.

Semeniuk, C. A. D., and K. D. Rothley. 2008. Costs of group-living for a normally solitary forager: effects of provisioning tourism on southern stingrays *Dasyatis americana*. Marine Ecology Progress Series **357**:271–282.

Semenova, O. V. 2008. Ecology of ground beetles in an industrial city. Russian Journal of Ecology **39**:444–450.

Sheppard, N., K. A. Pitt, and T. A. Schlacher. 2009. Sub-lethal effects of off-road vehicles (ORVs) on surf clams on sandy beaches. Journal of Experimental Marine Biology and Ecology **380**:113–118.

Shively, K. J., A. W. Alldredge, and G. E. Phillips. 2005. Elk reproductive response to removal of calving season disturbance by humans. Journal of Wildlife Management **69**:1073–1080.

Sibbald, A. M., R. J. Hooper, J. E. McLeod, and I. J. Gordon. August. Responses of red deer (*Cervus elaphus*) to regular disturbance by hill walkers. European Journal of Wildlife Research **57**:817–825.

Skagen, S. K., R. L. Knight, and G. H. Orians. 1991. Human disturbance of an avian scavenging guild. Ecological Applications **1**:215–225.

Skagen, S. K., C. P. Melcher, and E. Muths. 2001. The interplay of habitat change, human disturbance and species interactions in a waterbird colony. American Midland Naturalist **145**:18–28.

Smith-Castro, J. R., and A. D. Rodewald. 2010. Effects of Recreational Trails on Northern Cardinals (Cardinalis cardinalis) in Forested Urban Parks. Natural Areas Journal **30**:328–337.

St Clair, J. J. H., G. E. García-Peña, R. W. Woods, and T. Székely. 2010. Presence of mammalian predators decreases tolerance to human disturbance in a breeding shorebird. Behavioral Ecology **21**:1285–1292.

Stalmaster, M. V., and J. L. Kaiser. 1998. Effects of recreational activity on wintering bald eagles. Wildlife Monographs:3–46.

Stamation, K. A., D. B. Croft, P. D. Shaughnessy, K. A. Waples, and S. V. Briggs. 2010. Behavioral responses of humpback whales (*Megaptera novaeangliae*) to whale-watching vessels on the southeastern coast of Australia. Marine Mammal Science **26**:98–122.

Steckenreuter, A., R. Harcourt, and L. Moeller. 2011. Distance does matter: close approaches by boats impede feeding and resting behaviour of Indo-Pacific bottlenose dolphins. Wildlife Research **38**:455–463.

Steidl, R. J., and R. G. Anthony. 1996. Responses of bald eagles to human activity during the summer in interior Alaska. Ecological Applications **6**:482–491.

Steidl, R. J., and R. G. Anthony. 2000. Experimental effects of human activity on breeding bald eagles. Ecological Applications **10**:258–268.

Steiner, A. J., and S. P. Leatherman. 1981. Recreational impacts on the distribution of ghost crabs *Ocypode quadrata* fab. Biological Conservation **20**:111–122.

Stensland, E., and P. Berggren. 2007. Behavioural changes in female Indo-Pacific bottlenose dolphins in response to boat-based tourism. Marine Ecology Progress Series **332**:225–234.

Stockin, K. A., D. Lusseau, V. Binedell, N. Wiseman, and M. B. Orams. 2008. Tourism affects the behavioural budget of the common dolphin *Delphinus sp*. in the Hauraki Gulf, New Zealand. Marine Ecology Progress Series **355**:287–295.

Storch, I., and C. Leidenberger. 2003. Tourism, mountain huts and distribution of corvids in the Bavarian Alps, Germany. Wildlife Biology **9**:301–308.

Swarthout, E. C. H., and R. J. Steidl. 2003. Experimental effects of hiking on breeding Mexican spotted owls. Conservation Biology **17**:307–315.

Tadesse, S. A., and B. P. Kotler. 2012. Impact of tourism on Nubian Ibex (*Capra nubiana*) revealed through assessment of behavioral indicators. Behavioral Ecology **23**:1257-1262.

Taylor, A. R., and R. L. Knight. 2003. Wildlife responses to recreation and associated visitor perceptions. Ecological Applications **13**:951–963.

Thiel, D., S. Jenni-Eiermann, V. Braunisch, R. Palme, and L. Jenni. 2008. Ski tourism affects habitat use and evokes a physiological stress response in capercaillie *Tetrao urogallus*: a new methodological approach. Journal of Applied Ecology **45**:845–853.

Thiel, D., E. Menoni, J.-F. Brenot, and L. Jenni. 2007. Effects of recreation and hunting on flushing distance of capercaillie. Journal of Wildlife Management **71**:1784–1792.

Thomas, K., R. G. Kvitek, and C. Bretz. 2003. Effects of human activity on the foraging behavior of sanderlings *Calidris alba*. Biological Conservation **109**:67–71.

Titus, J. R., and L. W. VanDruff. 1981. Response of the common loon to recreational pressure in the Boundary Waters Canoe Area, northeastern Minnesota. Wildlife Monographs:3–59.

Tratalos, J. A., and T. J. Austin. 2001. Impacts of recreational SCUBA diving on coral communities of the Caribbean island of Grand Cayman. Biological Conservation **102**:67–75.

Trathan, P. N., J. Forcada, R. Atkinson, R. H. Downie, and J. R. Shears. 2008. Population assessments of gentoo penguins (*Pygoscelis papua*) breeding at an important Antarctic tourist site, Goudier Island, Port Lockroy, Palmer Archipelago, Antarctica. Biological Conservation **141**:3019–3028.

Trulio, L. A., and J. Sokale. 2008. Foraging shorebird response to trail use around San Francisco Bay. Journal of Wildlife Management **72**:1775–1780.

Tsounis, G., L. Martinez, L. Bramanti, N. Viladrich, J. Gili, A. Martinez, and S. Rossi. 2012. Anthropogenic effects on reproductive effort and allocation of energy reserves in the Mediterranean octocoral *Paramuricea clavata*. Marine Ecology Progress Series **449**:161–172.

Tull, J. C., and P. F. Brussard. 2007. Fluctuating asymmetry as an indicator of environmental stress from off-highway vehicles. Journal of Wildlife Management **71**:1944–1948.

Ulrich, W., M. Zalewski, I. Hajdamowicz, M. Stańska, W. Ciurzycki, and P. Tykarski. 2010. Tourism disassembles patterns of co-occurrence and weakens responses to environmental conditions of spider communities on small lake islands. Community Ecology **11**:5–12.

Uyarra, M. C., and I. M. Côté. 2007. The quest for cryptic creatures: impacts of species-focused recreational diving on corals. Biological Conservation **136**:77–84.

Van der Zande, A. N., J. C. Berkhuizen, H. C. van Latesteijn, W. J. ter Keurs, and A. J. Poppelaars. 1984. Impact of outdoor recreation on the density of a number of breeding bird species in woods adjacent to urban residential areas. Biological Conservation **30**:1–39.

Van der Zande, A. N., and P. Vos. 1984. Impact of a semi-experimental increase in recreation intensity on the densities of birds in groves and hedges on a lake shore in The Netherlands. Biological Conservation **30**:237–259.

Velando, A., and I. Munilla. 2011. Disturbance to a foraging seabird by sea-based tourism: Implications for reserve management in marine protected areas. Biological Conservation **144**:1167–1174.

Veloso, V. G., E. S. Silva, C. H. S. Caetano, and R. S. Cardoso. 2006. Comparison between the macroinfauna of urbanized and protected beaches in Rio de Janeiro State, Brazil. Biological Conservation **127**:510–515.

Walker, B. G., P. D. Boersma, and J. C. Wingfield. 2005. Physiological and behavioral differences in Magellanic penguin chicks in undisturbed and tourist-visited locations of a colony. Conservation Biology **19**:1571–1577.

Walker, B. G., P. Dee Boersma, and J. C. Wingfield. 2006. Habituation of adult magellanic penguins to human visitation as expressed through behavior and corticosterone secretion. Conservation Biology **20**:146–154.

Weinrich, M., and C. Corbelli. 2009. Does whale watching in Southern New England impact humpback whale (*Megaptera novaeangliae*) calf production or calf survival? Biological Conservation **142**:2931–2940.
Williams, R., and E. Ashe. 2007. Killer whale evasive tactics vary with boat number. Journal of Zoology **272**:390–397.
Yalden, D. W. 1992. The influence of recreational disturbance on common sandpipers *Actitis hypoleucos* breeding by an upland reservoir, in England. Biological Conservation **61**:41–49.
Yalden, D. W. 1990. Recreational disturbance of large mammals in the Peak District. Journal of Zoology **221**:293–298.
Yalden, P. E., and D. W. Yalden. 1990. Recreational disturbances of breeding golden plovers *Pluvialis apricarius*. Biological Conservation **51**:243–262.
Yasué, M., and P. Dearden. 2006. The potential impact of tourism development on habitat availability and productivity of Malaysian plovers *Charadrius peronii*. Journal of Applied Ecology **43**:978–989.
Zakai, D., and N. E. Chadwick-Furman. 2002. Impacts of intensive recreational diving on reef corals at Eilat, northern Red Sea. Biological Conservation **105**:179–187.
Zielinski, W. J., K. M. Slauson, and A. E. Bowles. 2008. Effects of off-highway vehicle use on the American marten. Journal of Wildlife Management **72**:1558–1571.
Zuberogoitia, I., J. Zabala, J. A. Martínez, J. E. Martínez, and A. Azkona. 2008. Effect of human activities on Egyptian vulture breeding success. Animal Conservation **11**:313–320.

APPENDIX II

Expert opinion survey that was distributed using an online survey platform (Survey Gizmo) to reserve managers, rangers, and other reserve staff (Chapter 2).

San Diego NCCP Reserves Recreation Survey

Reserve selection

This survey is part of a collaborative project between the California Department of Fish and Wildlife, the Wildlife Conservation Society, Colorado State University, University of California - Berkeley, and the San Diego Management and Monitoring Program to assess the impacts of recreation on wildlife in San Diego County NCCP reserves. The goal of this survey is to gain information from local experts about recreational use in San Diego reserves. If you have any questions about the survey, please contact Courtney Larson at courtney.larson@colostate.edu. We are interested in learning about the type and amount of recreation that occurs on reserves. Please choose the 3-5 reserves for which you are most familiar with this information. The reserves you choose now will be the ones you are asked about in the remainder of the survey. See the reserves on a Google map.*

[Note: in the online survey these were arranged in a table by managing agency]

[ ] Batiquitos Lagoon Ecological Reserve
[ ] Border Field State Park
[ ] Black Mountain Open Space Park
[ ] Barnett Ranch Open Space
[ ] City of Chula Vista Central City Preserve
[ ] Crestridge Ecological Reserve
[ ] Canada De San Vicente
[ ] Carlsbad Highlands Ecological Reserve
[ ] Hollenbeck Canyon Wildlife Area
[ ] McGinty Mountain Ecological Reserve
[ ] Otay Mountain Ecological Reserve
[ ] Plaisted Creek Ecological Reserve
[ ] Rancho Jamul Ecological Reserve
[ ] San Elijo Lagoon Ecological Reserve
[ ] San Felipe Valley Wildlife Area
[ ] Sycuan Peak Ecological Reserve
[ ] Cuyamaca Rancho State Park
[ ] Palomar Mountain State Park
[ ] Torrey Pines State Natural Reserve
[ ] Otay Ranch Preserve
[ ] Otay Valley Regional Park
[ ] Daley Ranch Open Space Preserve

[ ] City of Poway Open Space
[ ] Iron Mountain
[ ] Lake Poway Recreation Area
[ ] Carmel Mountain Open Space Preserve
[ ] Del Mar Mesa Open Space
[ ] El Capitan Reservoir Open Space
[ ] Los Penasquitos Canyon Preserve
[ ] Marian Bear Natural Park
[ ] Mission Trails Regional Park
[ ] Rose Canyon Open Space
[ ] Sabre Springs
[ ] San Dieguito River Park
[ ] Scripps Miramar Open Space
[ ] Sutherland Reservoir Open Space
[ ] Tecolote Canyon Natural Park
[ ] Boulder Oaks Open Space Preserve
[ ] Del Dios Highlands Open Space Preserve
[ ] Goodan Ranch and Sycamore Canyon Preserve
[ ] Hellhole Canyon Preserve
[ ] Oakoasis Preserve
[ ] Ramona Grasslands Preserve
[ ] San Vicente Highlands Open Space Preserve
[ ] Santa Ysabel Open Space Preserve
[ ] Simon Preserve
[ ] Tijuana River Valley Regional Park
[ ] Volcan Mountain Wilderness Preserve
[ ] Wilderness Gardens Open Space Preserve
[ ] San Diego Bay National Wildlife Refuge: Sweetwater Marsh Unit
[ ] San Diego Bay National Wildlife Refuge: South San Diego Bay Unit
[ ] San Diego National Wildlife Refuge
[ ] Tijuana Slough National Wildlife Refuge
[ ] Blue Sky Ecological Reserve

Visitor estimates

What is your estimate of the number of people entering the reserve(s) on an average weekday?
1 = very low, 10 or fewer people per day
2 = low, 10-49 people per day
3 = moderate, 50-199 people per day
4 = high, 200-499 people per day
5 = very high, 500 or more people per day

	1	2	3	4	5
Reserve 1					
Reserve 2					
Reserve 3					

What is your estimate of the number of people entering the reserve(s) on an average weekend day? Please type in your estimate of the level of use using the following scale:
1 = very low; 10 or fewer people per day
2 = low; 10-49 people per day
3 = moderate; 50-199 people per day
4 = high; 200 - 499 people per day
5 = very high; 500 or more people per day

	1	2	3	4	5
Reserve 1					
Reserve 2					
Reserve 3					

What types of recreation occur at the reserve(s) on an average weekday? Please type in your estimate of the level of use using the following scale:
1 = very low; 10 or fewer people per day
2 = low; 10-49 people per day
3 = moderate; 50-199 people per day
4 = high; 200 - 499 people per day
5 = very high; 500 or more people per day

	Hiking	Biking	Horseback riding	Dog-walking	Off-highway vehicles	Other (please specify in Comments)
Reserve 1						
Reserve 2						
Reserve 3						

Comments:
____
____

What types of recreation occur at the reserve(s) on an average weekend day? Please type in your estimate of the level of use using the following scale:
1 = very low; 10 or fewer people per day
2 = low; 10-49 people per day
3 = moderate; 50-199 people per day
4 = high; 200 - 499 people per day
5 = very high; 500 or more people per day

	Hiking	Biking	Horseback riding	Dog-walking	Off-highway vehicles	Other (please specify in Comments)
Reserve 1						
Reserve 2						
Reserve 3						

Comments:
____
____

What is your estimate of the number of people entering the reserves on an average weekday during each season? Please type in your estimate using the following scale:
1 = very low; 10 or fewer people per day
2 = low; 10-49 people per day
3 = moderate; 50-199 people per day
4 = high; 200 - 499 people per day
5 = very high; 500 or more people per day

	Dec, Jan, Feb (wet season)	Mar, Apr, May (spring)	June, July (mild part of summer)	Aug, Sept (hot part of summer)	Oct, Nov ("California spring")
Reserve 1					
Reserve 2					
Reserve 3					

What is your estimate of the number of people entering the reserves on an average weekend day during each season? Please type in your estimate using the following scale:
1 = very low; 10 or fewer people per day
2 = low; 10-49 people per day
3 = moderate; 50-199 people per day
4 = high; 200 - 499 people per day
5 = very high; 500 or more people per day

	Dec, Jan, Feb (wet season)	Mar, Apr, May (spring)	June, July (mild part of summer)	Aug, Sept (hot part of summer)	Oct, Nov ("California spring")
Reserve 1					
Reserve 2					
Reserve 3					

Other reserve information

Do these reserves hold special events that draw large amounts of recreational users?
( ) Yes
( ) No

If possible, name the event(s), approximate dates, and your estimate of the number of attendees.

	Event name	Event dates	Number of attendees
Reserve 1			
Reserve 2			
Reserve 3			

Why do you think people choose to visit this reserve rather than others? Choose all that apply.

	Location	Trail length or difficulty	Amenities	Destinations (peaks, etc)	Wildlife viewing	Activities (biking, etc)	Other
Reserve 1							
Reserve 2							
Reserve 3							

Comments: ____

Are there any wildlife species that you think are affected by the presence of visitors in the reserves? Please name the species, and the effect(s) you think people might be having.

	Species	Effect
Reserve 1		
Reserve 2		
Reserve 3		

Are you aware of any kind of unauthorized use of the reserves?
( ) Yes
( ) No

Please list the unauthorized uses you are aware of.

	Unauthorized uses
Reserve 1	
Reserve 2	
Reserve 3	

Experience in reserves

Approximately how many days in the past year have you spent in each reserve?

	Days
Reserve 1	
Reserve 2	
Reserve 3	

How many years have you worked in each of the reserves?

	Years
Reserve 1	
Reserve 2	
Reserve 3	

Do you have any final comments or questions?

Thank you for taking our survey!