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WILDLIFE RESPONSES TO RECREATION AND ASSOCIATED VISITOR PERCEPTIONS

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Abstract. Outdoor recreation has the potential to disturb wildlife, resulting in energetic costs, impacts to animals' behavior and fitness, and avoidance of otherwise suitable habitat. Mountain biking is emerging as a popular form of outdoor recreation, yet virtually nothing is known about whether wildlife responds differently to mountain biking vs. more traditional forms of recreation, such as hiking. In addition, there is a lack of information on the ''area of influence'' (within which wildlife may be displaced from otherwise suitable habitat due to human activities) of different forms of recreation. We examined the responses of bison (*Bison bison*), mule deer (*Odocoileus hemionus*), and pronghorn antelope (*Antilocapra americana*) to hikers and mountain bikers at Antelope Island State Park, Utah, by comparing alert distance, flight distance, and distance moved. Within a species, wildlife did not respond differently to mountain biking vs. hiking, but there was a negative relationship between wildlife body size and response. We determined the area of influence along trails and off-trail transects by examining each species' probability of flushing as perpendicular distance away from a trail increased. All three species exhibited a 70% probability of flushing from on-trail recreationists within 100 m from trails. Mule deer showed a 96% probability of flushing within 100 m of recreationists located off trails; their probability of flushing did not drop to 70% until perpendicular distance reached 390 m. We calculated the area around existing trails on Antelope Island that may be impacted by recreationists on those trails. Based on a 200-m ''area of influence,'' 8.0 km (7%) of the island was potentially unsuitable for wildlife due to disturbance from recreation.

Few studies have examined how recreationists perceive their effects on wildlife, although this has implications for their behavior on public lands. We surveyed 640 backcountry trail users on Antelope Island to investigate their perceptions of the effects of recreation on wildlife. Approximately 50% of recreationists felt that recreation was not having a negative effect on wildlife. In general, survey respondents perceived that it was acceptable to approach wildlife more closely than our empirical data indicated wildlife would allow. Recreationists also tended to blame other user groups for stress to wildlife rather than holding themselves responsible.

The results of both the biological and human-dimensions aspects of our research have implications for the management of public lands where the continued coexistence of wildlife and recreation is a primary goal. Understanding wildlife responses to recreation and the ''area of influence'' of human activities may help managers judge whether wildlife populations are experiencing stress due to interactions with humans, and may aid in tailoring recreation plans to minimize long-term effects to wildlife from disturbance. Knowledge of recreationists' perceptions and beliefs regarding their effects on wildlife may also assist public lands managers in encouraging positive visitor behaviors around wildlife.

Key words: American bison; disturbance; flight distance; flush response; hiking; mountain biking; mule deer; outdoor recreation; pronghorn antelope; visitor perceptions.

INTRODUCTION

Millions of visitors annually are attracted to public lands to engage in recreational activities. Because outdoor recreation is the second leading cause for the decline of federally threatened and endangered species on public lands (Losos et al. 1995), and the fourth leading cause on all lands (Czech et al. 2000), natural resource managers are becoming increasingly concerned about impacts of recreation on wildlife (Knight and Gutzwiller 1995). Recent assessments have suggested that recreation may have pronounced effects on wildlife individuals, populations, and communities by affecting behavior and fitness and by altering interspecific interactions (e.g., Boyle and Samson 1985, Knight and Cole 1995*a*). To manage for coexistence between wildlife and recreationists, managers should be aware of the potential consequences of recreation for wildlife.

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In addition, because natural resource managers must contend simultaneously with both ecological and social issues, integration of corresponding biological and social data on recreational impacts is necessary for informed decision making (Manfredo et al. 1995). Recreationists' perceptions regarding their effects on wildlife may influence their behavior on public lands. Knowledge of these perceptions can help managers encourage positive behaviors and increase visitor compliance with regulations (Purdy et al. 1987, Klein 1993).

Hiking and mountain biking are rapidly increasing in popularity as forms of outdoor recreation. Mountain biking in particular is one of the fastest-growing outdoor activities, with 43.3 million persons participating at least once in 2000 (USDA Forest Service and National Oceanic and Atmospheric Administration 2000). While researchers have examined the responses of wildlife to pedestrians, there is a lack of information on the responses of wildlife to mountain bikers. Despite this lack of knowledge, mountain biking is banned in all federal wilderness areas and on many other public lands, in part because it is assumed to be more disturbing for wildlife than hiking. Currently, it is not known whether wildlife respond differently to these activities.

Disturbance from recreation may have both immediate and long-term effects on wildlife. The immediate response of many animals to disturbance is a change in behavior, such as cessation of foraging, fleeing, or altering reproductive behavior (Knight and Cole 1991). Over time, energetic losses from flight, decreased foraging time, or increased stress levels come at the cost of energy resources needed for individuals' survival, growth, and reproduction (Geist 1978). In addition, the presence of humans in wildlife habitat may result in animals avoiding parts of their normal range (Hamr 1988, Gander and Ingold 1997). This loss of otherwise suitable habitat may be sufficient to reduce the carrying capacity of some public lands for wildlife (Light and Weaver 1973). The energetic cost for wildlife of responding to disturbance from recreation can also affect the carrying capacity of wildlife habitat (Stalmaster 1983). In some cases, wildlife may habituate to predictable disturbance from recreation, but in other cases they may not: mountain sheep (*Ovis canadensis*) and white-tailed deer (*Odocoileus hemionus*) did not habituate to pedestrians and snowmobiles, respectively (MacArthur et al. 1982, Moen et al. 1982).

The immediate behavioral responses of wildlife to recreation (e.g., flush response, alert and flight distances, distance moved) have conventionally been used to compare the degree of disturbance presented by different activities. The ''area of influence'' (Miller et al. 2001) may also be indicative of the relative impacts of recreational activities. Area of influence is defined as the area that parallels a trail or line of human movement within which wildlife will flush from a particular activity with a certain probability (Miller et al. 2001). Because most recreationists (except wildlife watchers and photographers) do not go out of their way to approach wildlife, the ''area of influence'' may provide a more meaningful estimate of disturbance than flight distances measured as a human directly approaches an animal. Wildlife avoidance of otherwise suitable habitat, therefore, can be assessed by the ''area of influence'' concept through examination of the probability of wildlife flushing within a certain distance of a trail.

The impetus for our research was the dearth of empirical studies that had examined wildlife responses to mountain biking, the lack of data regarding the area of influence of recreational activities, and the need for integration of ecological and social data on recreational impacts to wildlife. Our specific objectives were to (1) compare the behavioral responses of wildlife to hiking and mountain biking, (2) identify factors influencing wildlife response, (3) assess the area of influence around each activity, and (4) compare recreationists' perceptions of their effects on wildlife with corresponding empirical data. From our research, we suggest management and education implications for public lands where coexistence of wildlife and recreation is a primary goal.

Study Area

Antelope Island is a 104-km² (11 330-ha) island located in the southeast corner of the Great Salt Lake (40°59′ N, 112°12′ W) and accessed by a causeway from Syracuse, Utah. A north–south ridge of mountains forms the backbone of the island and provides 600 m of relief from lake level to high point. The only sources of fresh water on the island are springs that emerge from the Lake Bonneville terrace level. Exotic annual grasses, primarily cheatgrass (*Bromus tectorum*) and threeawn (*Aristida* spp.), dominate the lower elevations of the island, the result of an altered fire regime and historic overgrazing by livestock (Wolfe et al. 1999). Some higher slopes exhibit a grassland–sagebrush (*Artemisia tridentata*) community, with small stands of juniper (*Juniperus osteosperma*) and bigtooth maple (*Acer grandidentatum*) occurring only in protected canyons (Wolfe et al. 1999). Portions of the eastern side of the island have been reseeded with perennial grasses or a grass–legume mixture (Wolfe et al. 1999). Between 1952 and 1972, maximum summer and minimum winter temperatures averaged 32.7°C and −6.2°C, respectively (Wolfe et al. 1999).

Approximately 650 American bison (*Bison bison*), 50 pronghorn antelope (*Antilocapra americana*), 225 mule deer, and 90 bighorn sheep inhabit Antelope Island (J. Sullivan, *personal communication*). The bison herd is managed to remain at 550–700 individuals (winter herd size) by an annual roundup and sale. The mule deer population naturally fluctuates. The pronghorn and bighorn populations were reintroduced to the island in 1993 and 1997, respectively, and continue to increase in size. Hunting is not currently allowed on Antelope Island.

Currently, the park attracts about 400 000 visitors annually (J. Sullivan, *personal communication*). Recreation occurs year-round, but is concentrated in the spring and early summer and temporally overlaps with the peak fawning/calving season for the island's large ungulates. A 40-km network of backcountry trails, located on the northern half of the island, is used exclusively by hikers, mountain bikers, and horseback riders. The southern half of the island is not accessible to the public except on rare occasions and by the discretion of the park management. Currently, there is interest in expanding the trail system and allowing visitors into the southern portion of the island.

METHODS

Behavioral responses to recreation

We examined the behavioral responses of bison, pronghorn antelope, and mule deer to hiking and mountain biking on Antelope Island from May through August 2000 and April through June 2001. Bighorn sheep were not studied after initial observations indicated that recreationists rarely encountered sheep near trails. Horseback trials were unsuccessful given the limitations of the study area and design. Trials involving all three species of wildlife were performed along designated recreation trails. Trials with mule deer only were also conducted along a randomly chosen, off-trail line of movement to assess the response of mule deer to persons hiking or biking off designated trails. Experimental hiking and biking trials were performed by two people; an assistant acted as the recreationist while a researcher (A. R. Taylor) collected data as a hidden observer. The recreationist moved at a typical pace for each activity, did not stop to look at the animals, and avoided talking during the trial. Necessary communication between observer and recreationist was conducted via handheld radios. We recorded the following responses when an animal or group of animals were observed within 500 m of the trail: (1) alert distance (the distance between the recreationist and the animals when they first became visibly alert to the recreationist), (2) flush response (whether or not the animals took flight in response to the recreationist's presence), (3) flight distance (the distance between the recreationist and the animals when they took flight from the recreationist), (4) distance moved (the distance traveled by the animals from their initial position until they stopped fleeing), and (5) perpendicular distance (the shortest straight-line distance between the trail and the initial position of the animals; Fig. 1). All distances were measured to the nearest meter with a Bushnell Yardage Pro 800 Compact laser rangefinder (Bushnell, Overland Park, Kansas, USA). We tracked animals that continued fleeing out of sight to estimate distance moved. For groups of animals, distances were measured to the first animal that exhibited a particular response. Animals were not approached directly and the recreationist did not leave the trail during a trial, thus her activity was performed tangentially to animals. Visual landscape cues were used to mark initial animal locations. Beanbags were dropped on the trail to mark wildlife responses during a trial so that distances could be measured after the trial was completed. This ensured that the recreationist's activity during a trial appeared continuous to the animals being sampled.

Trials were conducted from 0600 to 1200 and 1700 to 2100 daily to avoid stressing animals during the hottest part of the day, and to coincide with periods of higher animal activity. Starting locations for hiking and biking were randomly chosen to avoid traveling the trails in the same pattern each day. Because wildlife on Antelope Island are not marked, we could not avoid sampling individuals multiple times nor could we quantify the frequency of repeat sampling. Experimental trials were not performed on a section of trail more than once per day to reduce the chances of resampling the same individuals within a short period of time.

Disturbance context

Wildlife responses to recreationists are likely influenced by a suite of variables that may change with each situation (Steidl and Anthony 1996). An animal may choose to flush from a recreationist based on the size of the group with which it is foraging, or depending on its age or sex (Knight and Cole 1995*b*). We follow Steidl and Anthony's example in terming these variables the ''disturbance context.'' We examined the influence of 13 different variables on the behavioral responses of bison, pronghorn, and mule deer (Table 1). The effects of these covariates on wildlife response were considered simultaneously in our analyses.

Visitor perceptions

To quantify recreationists' perceptions of their impacts on wildlife, we conducted an on-site survey during April through June 2001. Visitors were asked how close they felt was acceptable for recreationists to approach wildlife (corresponding to wildlife flight distance), how far they thought animals moved if they fled from recreationists (corresponding to distance moved), to what degree they believed wildlife were being affected by recreation, and which recreational user group they felt was most responsible for causing stress to wildlife. Visitors were also asked what management actions they would support on Antelope Island. We surveyed visitors from each of the island's three user groups (hikers, mountain bikers, and horseback riders), and did not survey individuals more than once.

Statistical analyses

The information-theoretic model selection approach synthesized by Burnham and Anderson (1998) was used to analyze the wildlife response data. To determine

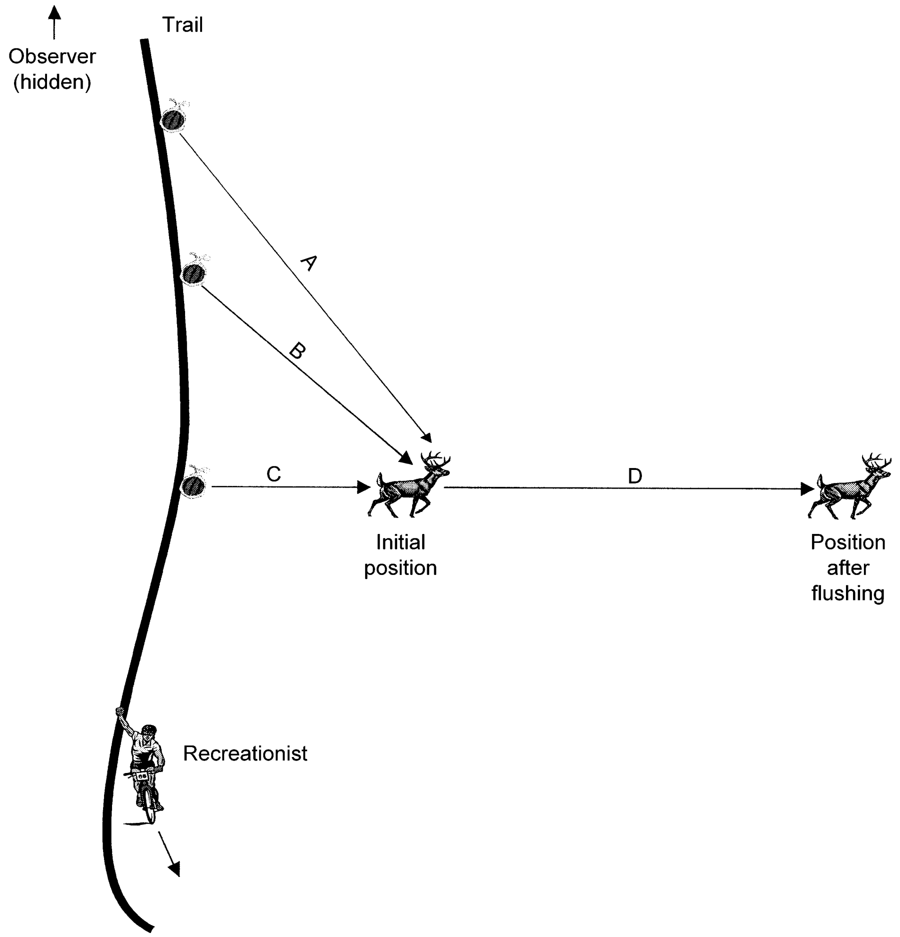

FIG. 1. Representation of response distances: A, alert distance; B, flight distance; C, perpendicular distance; D, distance moved. Markers on the trail represent beanbags dropped to mark response distance locations along trail. The observer remained hidden behind a rock, shrub, or topography during the trial. The mountain biker figure at the lower end of the trail represents the position of the recreationist after the trial has been completed.

the difference in wildlife response to hiking vs. mountain biking, a candidate set of 15 a priori multiple linear regression models was developed for each species/response distance combination (e.g., bison alert distance or mule deer flight distance; Appendix 1). These models included parameters for trial type (hiking or biking), trail position (on- or off-trail, mule deer only) and the variables comprising disturbance context (Table 1). Proc REG (SAS Institute 2001) was used to determine Akaike's Information Criterion (AIC) for each a priori model. The AIC values for each model were used to calculate AIC_c (a small-sample correction to AIC), ΔAIC_c (the difference between the model with the lowest AIC_c and each subsequent model), model likelihood, and the Akaike weight (an indicator of the relative support for that model exhibited by the data; Appendix 1). The parameter estimates from each candidate set of models were model-averaged to arrive at a prediction of the mean distance of interest for each species/distance combination. The same set of models was used to determine wildlife responses to both hiking and biking. Therefore, the predicted mean distances for each activity differ only in the value of the trial type variable, the values of all other variables being held constant across the model set. To estimate model-selection uncertainty, the variance estimates of each model in the candidate set were model-averaged using the delta method (Seber 1982:7–9). The model-averaged estimates of precision (standard errors) are therefore unconditional on any one model but are conditional on the a priori set of models and on the data collected during this study. The response distances were $\log_e$ transformed to correct for non-normality.

To examine the relative importance of the factors influencing wildlife response (the disturbance context), Proc IML (SAS Institute 2001) was used to sum the Akaike weights for each variable over the subset of models that included that variable (Burnham and Anderson 1998:140–141). This procedure allowed us to quantify the weight of evidence for the importance of each variable, and avoids the fallacy of regarding as unimportant variables that are not included in the best

TABLE 1. Variables measured to examine influence of disturbance context on wildlife behavioral responses on Antelope Island, Utah, 2000–2001.

Variable name	Definition	Type	Species
Trail type	hiking or biking	categorical	B, MD, PH
Trail position	on or off designated trail	categorical	MD
Encounter distance	distance at which recreationist became visible to animals	continuous	B, MD, PH
Perpendicular distance	shortest distance between animals' initial position and trail	continuous	B, MD, PH
Encounter × perpendicular	interaction between encounter and perpendicular distances	continuous	B, MD, PH
Time of day	morning or evening	categorical	B, MD, PH
Location	north or south end of island	categorical	B, MD, PH
Time of day × location	interaction between time of day and side of island	categorical	B, MD, PH
Total group size	size of wildlife group including all sexes and ages	continuous	B, MD, PH
Adult males	number of adult males in group	continuous	B, MD, PH
Adult females	number of adult females in group	continuous	MD, PH
Subadults	number of animals older than calves but younger than adults	continuous	B
Young of year	number of individuals <1 year old	continuous	B, MD, PH
Recreationist position	position of the recreationist relative to the animals during a trial: downhill, level, or uphill from the group	categorical	MD, PH
Cover	amount of cover around animals' initial position: none, some, or total cover (refers to how well vegetation blocked researchers' view of animals)	categorical	MD

Note: Species codes: B, bison; MD, mule deer; and PH, pronghorn.

model from the model selection procedure (Anderson et al. 2001).

Logistic regression was used to determine the area of influence around persons on trails. A candidate set of nine a priori models was developed using perpendicular distance and the disturbance context variables to predict flush response (Appendix 2). The same nine candidate models were used for each species (bison, mule deer, and pronghorn). Program MARK (White and Burnham 1999) was used to select the best model from the candidate set based on each model's AIC_c value. The parameter estimates from the best logistic regression model were used to calculate the mean probability of animals flushing as perpendicular distance increased.

Visitor responses to survey questions were analyzed using SPSS v.10.1 (SPSS 2000). Frequencies, crosstabs procedures, and ANOVA were used to compare visitor perceptions to research data and to examine perceptions across the three user groups on the island.

RESULTS

Wildlife responses to hiking and mountain biking

We performed 98 trials to bison, 88 trials to pronghorn, 110 on-trail trials to mule deer, and 60 off-trail trials to mule deer. Hiking and mountain biking trials were evenly distributed among total trial numbers. Trials in which one or more measurements were not obtained were deleted from our analyses. Linear regression models indicated that there was little difference in alert distance, flight distance, or distance moved between hiking and biking for all three species, with the exception of mule deer flight distance (Fig. 2). Although statistical significance is not assessed with the information-theoretic approach, the large degree of overlap between the 95% confidence intervals for hiking and biking is indicative of a lack of biological difference between wildlife responses to these activities (Table 2; see Schenker and Gentleman [2001] for a discussion of using confidence interval overlap to assess statistical significance). R^2 values ranged between 0.16 and 0.80 for the best models in each set. Models predicting animal distances moved generally explained less variation in the response variable than models predicting alert or flight distances (Appendix 1). Mule deer responses were greater to off-trail trials than to on-trail trials for alert distance and distance moved (Fig. 2). We observed interspecific differences across all response distances: pronghorn exhibited the greatest response to both hiking and biking, whereas bison showed the smallest response, once response distances were averaged across the two activities (Table 2).

Disturbance context

The importance of the disturbance context variables and their direction of effect differed among species and response distances (Table 3). We considered a variable to be consequential if the importance value from Table 3 was >0.5, meaning that half or more of the total Akaike weight for the model set was represented by models that contained that variable. There was a positive relationship between encounter distance (i.e., the distance a recreationist first became visible to wildlife) and alert distance. Similarly, increasing alert distance generally increased flight distance. For bison and pronghorn, flight distance was positively related to distance moved. Perpendicular distance was a meaningful element of the disturbance context for all distances and in most species/distance combinations. In most cases, the larger the perpendicular distance between the trail and an animal, the greater the distance of the wildlife

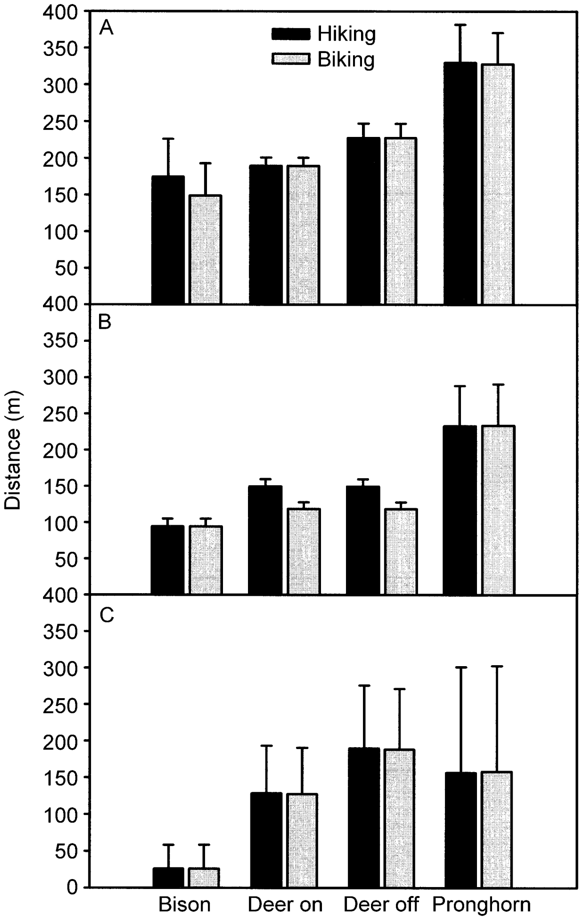

FIG. 2. Wildlife responses to hiking and mountain biking: (A) alert distance, (B) flight distance, (C) distance moved. ''Deer on'' indicates trials done on-trail to deer; ''deer off'' indicates trials done off-trail to deer. Bison and pronghorn trials were performed on-trail only. Error bars represent one standard error of the mean.

response. The position of the recreationist on the trail (whether below the animals, level with them, or above them) was important in determining deer alert distance, deer flight distance, and pronghorn distance moved (recreationist position was not measured for bison because they were almost always level with the recreationist). Animals responded most to recreationists above them and least to recreationists below them. Time of day (morning or evening) and wildlife group size were somewhat important in predicting response distances. Mule deer alert distance was greater in the evening, but bison flight distance and mule deer distance moved were greater in the morning. Larger group sizes tended to increase wildlife response distances. Group composition was relatively unimportant in predicting wildlife response except for deer flight distance and distance moved, which increased as the number of males in the group increased. Location on the island (north end, heavy trail use; south end, no public trails) did not influence wildlife response. Finally, for alert distance and distance moved, responses of deer to off-trail recreationists were greater than deer responses to on-trail recreationists.

Area of influence

Of 98 trials to bison, 75 groups (77%) of animals flushed to the treatment. Forty-nine of 88 pronghorn groups (56%) flushed to the treatment. Of 110 on-trail trials to mule deer, 66 groups flushed (60%); 58 of 60 mule deer groups (97%) flushed to off-trail trials. Because the previous analysis (for response distances) indicated that there was little difference between hiking and mountain biking, and because the best logistic regression model did not include the variable ''trial type,'' the data for hiking and mountain biking were combined for this analysis. The best logistic regression model included the variables species, perpendicular

TABLE 2. Means and 95% confidence intervals for alert distance, flight distance, and distance moved for bison, pronghorn, and mule deer on- and off-trail.

Response distance and species	*n*	Hiking		Biking		Combined	
		Mean	95% CI	Mean	95% CI	Mean	95% CI
Alert distance							
Bison	91	174.54	(99.10, 307.41)	148.91	(84.30, 263.04)	162.94	(92.37, 287.38)
Mule deer on trail	104	189.48	(168.56, 213.00)	189.51	(168.84, 212.71)	189.49	(168.66, 212.89)
Mule deer off trail	53	227.54	(192.27, 269.27)	227.57	(192.49, 269.04)	227.55	(192.35, 269.19)
Pronghorn	82	330.04	(243.14, 448.00)	327.74	(253.90, 423.07)	328.93	(247.98, 436.30)
Flight distance							
Bison	75	94.04	(75.14, 117.71)	94.06	(75.37, 117.39)	94.05	(75.24, 117.56)
Mule deer on trail	62	149.62	(131.45, 170.32)	118.45	(101.61, 138.08)	137.33	(119.20, 158.21)
Mule deer off trail	50	149.63	(131.54, 170.21)	118.45	(101.68, 138.00)	137.33	(119.30, 158.11)
Pronghorn	46	233.20	(147.46, 368.81)	233.93	(146.00, 374.80)	233.55	(147.12, 370.76)
Distance moved							
Bison	75	25.91	(3.90, 172.34)	26.00	(3.91, 172.95)	25.95	(3.90, 172.61)
Mule deer on trail	47	128.30	(50.41, 326.52)	127.31	(50.83, 318.84)	127.94	(50.52, 323.99)
Mule deer off trail	39	189.49	(81.03, 443.12)	188.02	(82.36, 429.26)	188.95	(81.48, 438.18)
Pronghorn	43	156.19	(33.41, 730.28)	157.82	(34.12, 730.02)	156.98	(33.75, 730.17)

Notes: Means are presented for hiking, mountain biking, and the mean of the two activities. Confidence intervals are based on the log-normal distribution so that no interval includes negative values for distances. All distances are in meters.

distance, trail position (on-trail or off-trail), and cover (none, some, and total; Appendix 2). On Antelope Island, cover typically referred to shrub (vegetation <3 m tall) density around the animals' initial position. In ''no cover'' trials, we had a full view of the wildlife at the onset of the trial. ''Some cover'' indicated that shrubs partially blocked our initial view of the animals. In ''total cover'' trials, our initial view was almost totally obscured. Wildlife flushing probabilities (Fig. 3) were graphed for a cover value of 0 (no cover), which was most often observed for wildlife in our study. As the value of the cover variable increased (to some cover and total cover), flushing probability decreased for a given perpendicular distance. Two other models had ΔAIC_c values <2, indicating that there was substantial support in the data for these models (Burnham and Anderson 1998; Appendix 2). The second best model was identical to the best model but lacked the cover variable, and is approximated by using a cover value of 0 in the best model. The third best model contained the variable ''young of the year'' instead of cover. The young of the year variable applied to bison only; larger numbers of calves tended to increase the probability of bison flushing at a given perpendicular distance.

As perpendicular distance increased, the probability of animals taking flight from a recreationist decreased (Fig. 3). There were no interspecific differences in flush response and therefore probability of flushing. This contrasts with the results of the previous analysis, in which response distances differed between the three species. At 100 m from a trail, bison, mule deer, and pronghorn showed approximately a 70% probability of taking flight from a person on that trail (Fig. 3). For mule deer, the area of influence around off-trail trials was much greater than that for on-trail trials. At 100 m from the line of movement of an off-trail trial, mule deer showed a 96% probability of flushing; that probability did not drop to 70% until the perpendicular distance increased to 390 m.

Visitor perceptions

We distributed 205 surveys to hikers, 230 to mountain bikers, and 205 to horseback riders on Antelope Island. Generally, recreationists failed to perceive that they were having as great an effect on wildlife as our biological data indicated. To compare measured flight distance with visitor perceptions of how close wildlife will allow humans to approach, we asked the question ''How close do you feel it is acceptable for recreationists to approach wildlife?'' The question was phrased in this way because it is difficult for people to estimate actual wildlife flight distances. User groups did not differ in their view of how close recreationists should approach wildlife (hikers, $F_{2,409} = 0.506$, $P = 0.945$; mountain bikers, $F_{2,396} = 0.027$, $P = 0.974$; horseback riders, $F_{2,401} = 1.877$, $P = 0.154$), but their combined perceptions differed greatly from actual wildlife flight distances (Fig. 4). Most recreationists felt that it was acceptable to approach wildlife at a much closer distance (mean acceptable distance to approach = 59.0 m) than wildlife in our experimental trials would typically allow a human to approach (mean flight distance of all species = 150.6 m).

Visitor perceptions of distance moved by wildlife were not substantially different from actual distances moved by wildlife during experimental trials. Recreationists thought bison were less likely to run long distances during flight than either mule deer or pronghorn; this perception was supported by our biological data. Forty percent of visitors surveyed believed that bison moved between 30.5 and 91.4 m in response to recreationists; this perception corresponds to the mean distance moved by bison (26.0 m) in our study. Seventy-eight percent of recreationists surveyed believed that deer and pronghorn move either more than 91.4 m or out of sight in response to recreationists; these perceptions correspond fairly well to the mean distance moved by deer and pronghorn in our study.

Of all visitors surveyed, 46%, 53%, and 54%, respectively, felt that bison, deer, and pronghorn were being negatively affected by recreation on Antelope Island. Fewer horseback riders than hikers or mountain bikers believed that recreation was having a negative effect on wildlife (Fig. 5). Generally, recreationists held members of other user groups responsible for stress or negative impacts to wildlife rather than holding members of their own recreational user group responsible (Fig. 6). These differences were significant overall ($\chi^2 = 47.349$, df = 4, $P < 0.001$). Survey respondents showed much support for penalizing recreationists who chased or intentionally stressed wildlife, and moderate support for closing trails to recreation in the spring (during fawning/calving season for wildlife) and for establishing minimum approach distances to wildlife. Visitors expressed little support for allowing only one type of recreational use on island trails, having fewer trails on the island, for requiring visitors to watch an educational video about the effects of recreation on wildlife, and for allowing recreation only on the north (developed) end of the island.

DISCUSSION

Wildlife responses to hiking and mountain biking

Our results indicate that there is little difference in wildlife response to hikers vs. mountain bikers. Certain qualities of each activity may have affected wildlife responses. While both activities involve humans traveling by non-motorized means on or off designated trails, hikers retain their human form while mountain bikers appear unlike humans because they are on a bicycle. Typically, pedestrians induce a more intense wildlife response than do motorized vehicles, perhaps because animals react most to the human form (Richens and Lavigne 1978, Eckstein et al. 1979, MacArthur et al. 1982, Freddy et al. 1986). However, mountain bikers

TABLE 3. Importance values (as calculated by summing Akaike weights across all possible models) and direction of effects (where substantial) of disturbance context variables.

				Disturbance context variables			
Response distance	Species	Trial type	Trial position	Encounter distance	Perpendicular distance	Time of day	Location
Alert distance	B	**0.63**, +	NA	**1.00**, +	**0.59**, +	0.34	0.31
	MD	0.30	**0.93**, −	**1.00**, +	**1.00**, +	**0.73**, +	0.30
	PH	0.24	NA	**1.00**, +	**1.00**, +	NA	0.32
Flight distance	B	0.26	NA	0.29	**0.88**, +	**0.55**, −	0.33
	MD	**0.94**, +	**0.53**, −	**0.53**, +	**1.00**, +	0.43	0.47
	PH	0.25	NA	0.22	**0.65**, +	0.44	NA
Distance moved	B	0.25	NA	0.25	0.25	0.32	0.32
	MD	0.25	**0.71**, −	0.24	0.27	**0.67**, −	0.35
	PH	0.30	NA	0.28	0.35	NA	**0.64**, +

Notes: Importance values >0.5 were considered consequential and are in bold type. A "+" indicates a positive relationship between the variable and the response distance measured; a "−" indicates a negative relationship between the same. NA denotes variables that were not considered for that species/distance combination. Species abbreviations: B = bison, MD = mule deer, and PH = pronghorn.

travel at a higher speed and are less apt to be talking than hikers, which may cause mountain biking to be less predictable for wildlife. The lack of difference in wildlife responses to hiking vs. biking may be attributable to a balance between the disturbing attributes of each activity.

Our finding that there was little difference between mountain biking and hiking contrasts with the results of a recent study on the responses of bighorn sheep to hikers, mountain bikers, and vehicles. In this case, the researchers found that sheep exhibited a greater probability of flushing, longer distances moved, and longer response durations when disturbed by hikers compared to mountain bikers or vehicles (Papouchis et al. 2001). The difference in findings between these studies, however, may be attributable to a difference in methodology. Papouchis et al. compared the responses of sheep approached directly and off-trail by hikers with those of sheep approached tangentially on a road or trail by mountain bikers and vehicles. Generally, wildlife exhibit a stronger response to humans that approach them directly and to humans located off designated trails (MacArthur et al. 1982, Moen et al. 1982, Knight and Cole 1995*a*, Miller et al. 2001). Therefore, the differences in sheep response to hiking and mountain biking seen in Papouchis et al.'s study may be as much attributed to the different approach methods and trial positions as to the different forms of recreation.

We also found that for alert distance, flight distance, and distance moved, a gradient of response existed among the three species studied on Antelope Island. Bison exhibited the shortest response distances and pronghorn the longest distances. The differences in response may be attributable to the specific characteristics of each species. The bison are rounded up annually and therefore may be more tolerant of human disturbance than the other species studied. Bison also have poorer eyesight than either mule deer or pronghorn, and tend to stand their ground when facing a predator rather than taking flight (Hirth 2000). Both white-tailed deer (*Odocoileus virginianus*) and mule deer typically use surrounding cover to avoid detection by a predator (Hirth 2000). Mule deer in our study were often observed to flee only to the nearest cover before stopping, and were more often observed in some cover when a trial was initiated. Because increasing cover generally decreased wildlife response, mule deer in cover could be expected to show a lesser response than animals in the open. Pronghorn as a species typically inhabit open, arid regions, in which their best defense against predators is early detection, rapid flight, and fleeing long distances. In addition, our study was conducted during the summer months on Antelope Island, when wildlife would be more likely to experience heat stress during exertion. Pronghorn exhibit several cooling mechanisms that would enable them to dissipate heat generated during flight better than either mule deer or bison (Vaughn 1986:462). The trend of decreasing response with increasing body size seen in our study merits further investigation. If supported by future studies, this pattern may provide a way to assess the relative response of different species to recreation, and allow managers to establish buffers that protect the most sensitive species from disturbance.

Our study did not attempt to address differences in wildlife response that might be caused by variations in recreationist behaviors, such as group size (of humans), silent vs. talking recreationists, people who stop their activity to look at wildlife, or visitors accompanied by dogs. It is expected that these factors would change wildlife response distances and the likelihood of animals flushing from recreationists, and should be taken into consideration when estimating levels of disturbance to wildlife from recreation at specific sites (Knight and Cole 1995*b*).

Disturbance context

Of the variables comprising disturbance context, encounter distance and perpendicular distance were ex-

TABLE 3. Extended.

Disturbance context variables						
Group size	Adult M	Adult F	Subadults	Young of year	Position	Cover
0.25	0.25	NA	0.25	0.24	NA	NA
0.65, +	0.36	0.39	NA	NA	**0.67**, +	0.32
0.26	0.42	0.27	NA	NA	0.29	NA
0.85, +	0.36	NA	0.24	0.28	NA	NA
0.44	**0.79**, +	0.41	NA	NA	**0.51**, +	0.42
0.57, +	0.21	0.48	NA	NA	0.25	NA
0.27	0.23	NA	0.31	0.50	NA	NA
NA	**0.94**, +	0.36	NA	NA	0.24	**0.62**, −
0.63, +	0.30	0.46	NA	NA	**0.85**, +	NA

tremely important in predicting wildlife response. Encounter distance (the distance at which a recreationist first became visible to animals) influenced alert distance for all three species because it established the upper limit at which wildlife could respond. Encounter distance was also an important variable in shaping the flush responses of bald eagles to river recreationists in Alaska (Steidl and Anthony 1996). In both studies, response distance (alert distance in our study, flight distance in Steidl and Anthony's) increased as encounter distance increased. Because our study took place in an open grassland environment with few visual obstructions, encounter distances were typically long because wildlife could see recreationists at great distances. Animals that encounter recreationists at great distances may be more affected by recreational activities than animals with limited encounter distances, as when vegetation shields recreationists from wildlife (Stalmaster and Newman 1978). The results of our study are most applicable for parks and natural areas with an open environment rather than a wooded community type.

Perpendicular distance (the shortest distance between wildlife and a recreationist on a trail) played a role in determining alert and flight distances in all three species. Interestingly, as perpendicular distance decreased, alert and flight distances decreased, indicating that animals close to the trail became alert and consequently fled at shorter distances than animals located far from the trail. Recarte et al. (1998) believed that fallow deer (*Dama dama*) perceived their linear transects (analogous to trails in this study) as predictable sources of disturbance and took flight in relation to the minimum distance to which an observer could approach. In our study, typical perpendicular distances

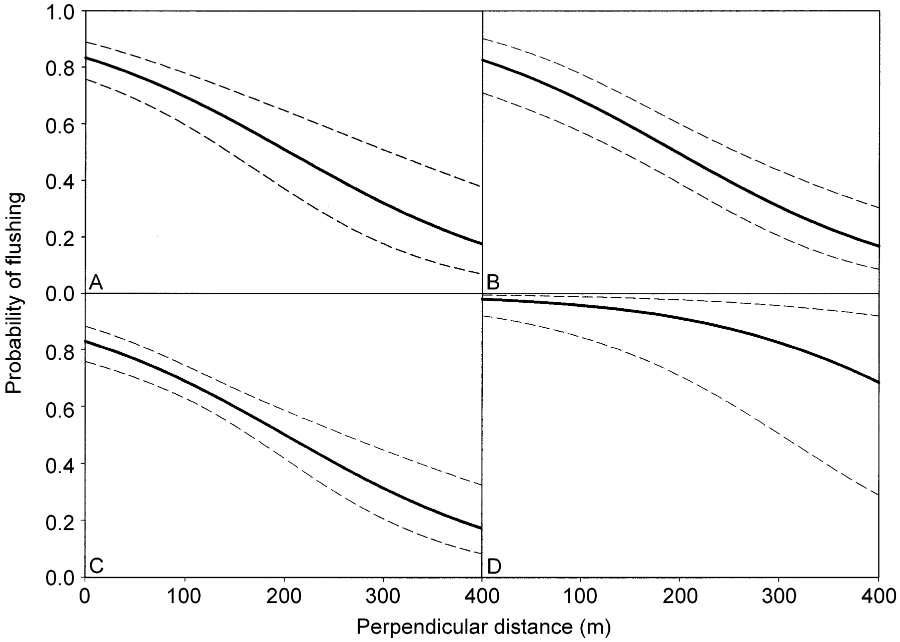

FIG. 3. Probability of wildlife flushing with increasing perpendicular distance: (A) bison, (B) pronghorn, (C) deer on-trail, (D) deer off-trail. Dashed lines indicate 95% confidence limits on probability.

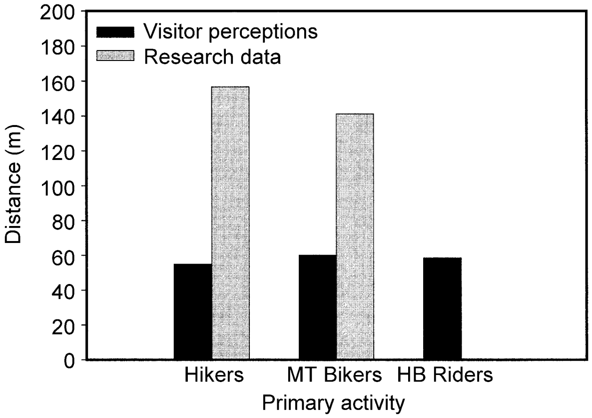

FIG. 4. Visitor perceptions of acceptable approach distance vs. wildlife flight distance. How close survey respondents believed it is acceptable for different user groups to approach wildlife contrasted with wildlife flight distances (from empirical data averaged across bison, deer on- and off-trail, and pronghorn). Research data on wildlife flight distances to equestrians (HB riders) were not collected in this study.

ranged between 50 m and 200 m, and few groups of animals were observed very close to trails. It is possible that these animals were those most habituated to trail-based recreation, and therefore showed little response when less habituated animals would already have fled (Whittaker and Knight 1999, Miller et al. 2001).

Time of day (morning or evening), animal group size and composition, and the position of the recreationist relative to the group also influenced wildlife response distances. Flight distances in bison, deer, and pronghorn were greater during morning trials than during evening trials, indicating a greater tolerance of recreationists during the evening (after 1700 hours [i.e., 5:00 P.M.]). This was previously found to be true in moose (*Alces alces*), elk (*Cervus elephus*), and mule deer (Altmann 1958), and may be related to the importance of evening as a feeding period during the heat of a continental summer.

Generally, the larger the group size of wildlife, the greater their response distances were. This finding contrasts with a previous study in which larger groups took flight less frequently than smaller groups (Recarte et al. 1998), but may be due to the tendency of gregarious animals to follow the lead of certain individuals in the group (Knight and Cole 1995*a*). For example, one animal beginning to flush often appeared to cue other group members to flush as well. In addition, one member of a group often continued to run after others had stopped, which occasionally spurred the stopped animals to begin running again. It is possible that larger groups have a greater chance of containing a particularly wary animal that will flush at large distances from a disturbance, thereby encouraging less wary animals to take flight at greater distances than they otherwise would.

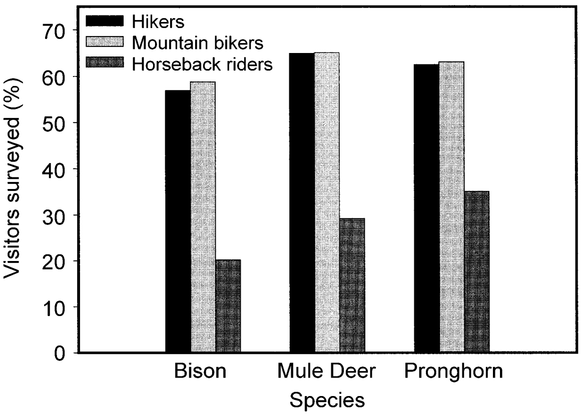

FIG. 5. Visitor perceptions of recreation effects. Values are the percentage of survey respondents in each user group who believed that bison, pronghorn, and mule deer may be negatively affected by recreation.

The presence of adult males reduced alert distance in pronghorn (similar to Hamr [1988] and Recarte et al. [1998]), but increased flight distance and distance moved in mule deer. Male deer often appeared more vigilant and wary than female deer on Antelope Island. Finally, a recreationist located above wildlife elicited a stronger response than a recreationist located level with or below wildlife. Due to the topography of Antelope Island, humans approaching animals from below are generally closer to the water, and therefore further from the interior of the island and typical escape terrain.

In many cases, it is difficult to make generalizations regarding the importance of external variables to wildlife response because studies are conducted with a variety of methods (A. Taylor and R. Knight, *unpublished manuscript*). For example, some researchers approach wildlife directly while others approach tangentially;

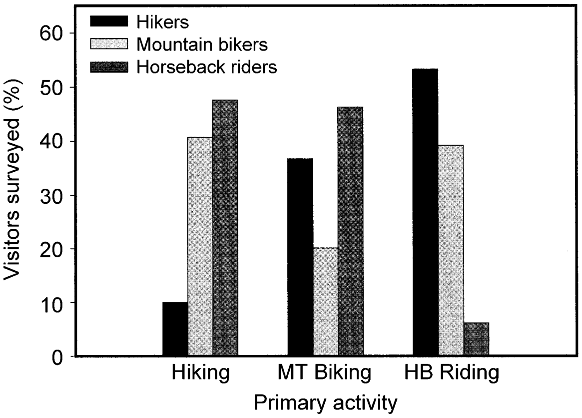

FIG. 6. Visitor perceptions of user group responsibility. Values are the percentages of survey respondents within each primary activity (user group) holding either hikers, mountain bikers, or horseback riders most responsible for stress to wildlife.

data collected using these different approach methods should not be compared.

Area of influence

The area of influence around a recreationist on a trail did not differ between mountain biking and hiking. This may mean that wildlife do not differentiate between hikers and bikers, but are instead reacting to the presence of a moving human on a trail, regardless of the person's activity. However, the area of influence differed considerably between on-trail and off-trail trials. This may reflect the spatial and temporal predictability of on-trail versus off-trail activities. Previous studies have indicated that animals react most to spatially unpredictable activities (Schultz and Bailey 1978, MacArthur et al. 1982, Hamr 1988, Miller et al. 2001). On-trail recreation may appear more predictable to wildlife because it occurs frequently and along a particular line of movement, and animals may habituate to this type of activity (Knight and Cole 1995*a*, Whittaker and Knight 1999).

Bison, mule deer, and pronghorn exhibited a 70% probability of flushing within 100 m of a trail. Increasing cover (from none to some to total cover) decreased the probability of wildlife flushing to recreationists. Therefore, although the area of influence of recreational activity is smaller on-trail than off-trail, it is still likely that animals will take flight from on-trail recreation, particularly if they are encountered in the open. Inherent in the flushing response is the potential for decreased energy acquisition and increased energy expenditure, and the possibility of animals avoiding suitable habitat due to recreational pressure. Thus, even on-trail recreation may have negative energetic consequences for wildlife and could result in displacement from otherwise suitable habitat (Miller et al. 2001). If wildlife on Antelope Island are able to habituate to human activity, the effects of recreation on animal populations may decrease over time. However, there is little evidence at this time to suggest that habituation may be occurring. The pronghorn on Antelope Island did not habituate to largely predictable recreational use over a three-year period following the opening of trails on the island, and in fact used areas that were significantly farther from trails than they had prior to the start of recreational use on the island (Fairbanks and Tullous 2002).

Visitor perceptions

Approximately 50% of visitors surveyed on Antelope Island did not believe that recreation was having a negative impact on wildlife. Our finding corresponds to the general public impression that recreation is benign and does not affect wildlife (Flather and Cordell 1995). In addition, visitor perceptions of wildlife flight distance differed remarkably from our research data. This was also the case in the only other study where wildlife responses to recreation and the perceptions of recreationists regarding those responses have been simultaneously measured (Stalmaster and Kaiser 1998). If visitors believe that they can approach wildlife more closely than animals will actually allow, then recreationists will disturb wildlife in a majority of encounters. Because flushing from recreational activity may come at the cost of energy needed for normal survival, growth, and reproduction (Geist 1978), and because it may cause animals to avoid otherwise suitable habitat (Hamr 1988, Gander and Ingold 1997, Miller et al. 2001), it is important that recreationists understand that their activities can flush wildlife and may make suitable habitat unavailable. By understanding and altering recreationists' perceptions with regard to their impacts on wildlife, public lands managers can influence visitor behavior and reduce the potential negative effects of recreation for wildlife.

There was little support among respondents for many of the management actions suggested on our survey. This may be because recreationists generally do not believe that they have an impact on wildlife, or because they believe that other user groups are more responsible for disturbing wildlife. In northwestern Washington, river recreationists also showed little support for restrictions on recreation, ostensibly because they did not understand that bald eagles were affected by recreation (Stalmaster and Kaiser 1998). Additional research integrating ecological and social data on recreational impacts is needed to fully examine the link between visitor perceptions, recreationist behavior, and public support for management actions that may reduce the impacts of recreation to wildlife.

RECOMMENDATIONS

Management

We found no biological justification for managing mountain biking any differently than hiking, if management decisions were to be based only on wildlife responses to each activity. However, because bikers travel faster than hikers, they may cover more ground in a given time period than hikers, thus having the opportunity to disturb more wildlife per unit time. Addressing the potential for mountain bikers to have a greater effect than hikers on wildlife will require knowledge of the typical distance traveled by bikers vs. hikers and their relative proportions among visitors to public lands. Importantly, because wildlife reacted most strongly to recreationists off trails, visitors should stay on designated trails to reduce disturbance to wildlife. Based on a 200-m area of influence around recreational trails (i.e., wildlife exhibit a 70% probability of flushing within 100 m on either side of the trail), 8.0 km^2 of 113.3 km^2 (7%) of Antelope Island may be potentially unsuitable for diurnal wildlife use due to disturbance from recreation. A decrease in suitable habitat may reduce the carrying capacity of public lands for wildlife (Light and Weaver 1973). This may be of particular concern where ''islands'' of public lands are surrounded by urban or suburban development, because wildlife in these areas may not be able to extend their home ranges to include less disturbed habitat (Miller et al. 2001). If management objectives include minimizing disturbance to wildlife habitat, new trails should follow existing edges and avoid water and forage resources, wildlife travel corridors, and escape terrain.

In addition, managers should investigate and consider visitor perceptions when planning management actions to separate wildlife and recreation, because visitors are more likely to comply with regulations when they understand how wildlife will benefit (Purdy et al. 1987). For example, survey respondents on Antelope Island tended to support the placement of minimum approach distances (buffer zones) around wildlife and tended to oppose the idea of fewer trails on the island.

The area of influence concept may provide a valuable measurement of potential habitat avoidance due to disturbance, and an estimate of the overall influence of recreational trails on wildlife habitat. Flight distance may be used as an assessment of the tolerance zone that an animal places between itself and a potential danger or disturbance (Altmann 1974). Flight distance has also been shown to be the best behavioral indicator of stress in wildlife (Stemp 1983). Therefore, we recommend that buffer zones or minimum approach distances (based on wildlife flight distances) be used to discourage recreationists from approaching wildlife too closely and causing them to flee. However, if such buffer zones are used for trail-based activities, data on wildlife flight distances should be collected by approaching animals tangentially rather than directly, so that the appropriate distance is used to determine the buffers.

Finally, the responses of wildlife to horseback riders need to be investigated. Horseback riding is another common use of non-motorized recreational trails, yet no study has addressed the comparative effects of equestrians on wildlife. Horseback riders in our survey tended to believe that they had the least impact on wildlife of any user group, and they were generally less supportive of management actions to protect wildlife. It is unclear whether these perceptions have a biological basis.

Education

We recommend that visitor education programs focus on informing recreationists about their potential effects on wildlife. Recreationists tend to believe that their activities are benign because they are dispersed over large areas (Flather and Cordell 1995). However, the majority of recent assessments suggest that recreation can affect wildlife individuals, populations, and communities. Recreationists need to be aware of wildlife responses such as flight distances and increased stress levels, the possibility for reduced carrying capacity of public lands, and the fact that each additional user may have a small yet cumulative impact on the environment.

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APPENDIX A

Tables showing values used in linear regression models to compare responses of wildlife to hiking and mountain biking are available in ESA's Electronic Data Archive: *Ecological Archives* A013-014-A1.

APPENDIX B

A table showing values used in logistic regression models to compare responses of wildlife to hiking and mountain biking is available in ESA's Electronic Data Archive: *Ecological Archives* A013-014-A2.