

**FINAL REPORT**

EXPLORING RELATIONSHIPS AMONG  
RECREATION, CANYONLAND HABITAT TYPES,  
AND MEXICAN SPOTTED OWLS IN NATIONAL PARKS  
AND BUREAU OF LAND MANAGEMENT STUDY  
AREAS IN SOUTHERN UTAH

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## EXECUTIVE SUMMARY

The primary goal of this research was to investigate potential effects of human recreation in canyon environments on territorial occupancy rates and reproduction of Mexican spotted owls (*Strix occidentalis lucida*), a threatened species. The research used observations of owl roost behavior and an analysis of territorial occupancy patterns to assess potential hiking and climbing impacts on the owls. In addition to work in Zion, research was conducted in Grand Staircase-Escalante National Monument, Capitol Reef National Park, and on Bureau of Land Management study areas in the vicinity of Cedar Mesa, and the Grand Gulch Primitive Area (Fig. 1; pg. 7). The research included direct field observation at 47 spotted owl territories distributed among the study areas in rocky canyon habitats. Following data collection, we analyzed roost behavior patterns, territorial occupancy rates, and reproductive success, and evaluated potential impacts of human-use, where we defined use-levels (high, medium, and low) based on direct observation of the numbers of visitors using canyons where spotted owls were detected (see Methods section for definitions of the use levels).

The roost behavior analysis was unable to distinguish differences between recreation use-level or the existence of fledglings in the adult territories because these factors were confounded. For example, all territories with fledglings were ranked as high-recreation sites, whereas territories without fledglings were identified as low-recreation sites. Therefore, we were unable to distinguish potential effects of high-recreation versus presence of fledglings. However, results from an analysis of fledgling roost behavior suggested that recreation may have affected components of fledgling behavior at roost sites, thus these relationships warrant further study. During observations of adult roost behavior, independent of recreation use-level, we observed that adult owls spent the majority of time resting quietly, and were rarely active during the day. Although we did observe owls primarily roosting, when we compared results to other studies (e.g., Sovern et al. 1994), we observed that roosting owls in canyon habitats were more active than owls in forest habitats. Willey (1998) observed similar results in his study in canyons of Utah. Our results also indicated that adult owls with fledglings at high-recreation territories were more vigilant than adults without fledglings at low-recreation territories, which matched predictions, but we were unable to distinguish if recreation or fledglings presence were responsible for observed differences in vigilance. We also observed that adult owls with fledglings at high-recreation sites showed a greater proportion of time conducting maintenance behaviors compared to adults without fledglings at low-recreation sites. These observations may be due to displacement behaviors, perhaps in response to recreational activity by humans within an owl's territory. Our results concerning human impacts on roosting owls were the opposite to conclusions of Swarthout and Steidl (2003), who noted when a "hiker" (treatment trial) walked past an owl nest, observers detected a decrease in time spent by female owls in maintenance behaviors. For juveniles, about half of the recorded fledgling behaviors were roosting, whereas the other half was spent in more active behaviors. This observation indicated that although spotted owls are nocturnal, fledglings spotted owls are active

during daytime hours.

We suspect, and it seems rather obvious, that active fledglings present in a territory cause adults to increase activity levels compared to adults without fledglings (Sovern et al. 1994). We also observed that it was much easier to find and observe adult owls when fledglings were present, thus adult owls with young were detected more frequently than adults without young. These differences in behavior among sites, i.e., with or without young imply that parental owls will exhibit unique sets of parental behaviors, and may also use habitats in different ways than non-parental owls, ultimately affecting things like detection probability, and population surveys.

During the study, fledglings in high- and low-recreation territories were observed spending approximately equal time roosting quietly but different amounts of time in maintenance and vigilance behaviors. Fledglings associated with high-recreation territories spent more time in maintenance behaviors and less time in vigilant behaviors. Again, we think this could be a form of displacement behavior by fledglings in response to high recreational activity by humans. However, it is unclear how being less vigilant at high-recreation territories could impact fledglings, thus we suspect that a decrease in vigilance has the potential to increase vulnerability to predators (i.e., via not being alert to predators). However, an increase in vigilance could also increase vulnerability to predators (i.e., via revealing location to predators). Before concluding that recreation is negatively related to fledgling behavior, more research towards understanding impacts of recreation on fledgling behavior needs to occur. Research investigating potential relationships between recreation and survival of fledglings before and after leaving their natal territories would be of interest to managers.

We recommend further research be initiated to examine differences between owl behaviors (i.e., both adults and fledglings) along a range of variables such as: human recreation, habitat type, time of day, sex, and mating status (i.e., whether adults are paired or single). It is not unreasonable to suggest that these variables could have been related to the behaviors we observed in this study, but unfortunately, with the limited data set, we did not test variables other than human recreation. We strongly urge future efforts to consider using radio or GPS-based telemetry to aid relocation and thus direct observation of the owls. Both Sovern et al. (1994) and Willey (1998) used VHF transmitters in behavior studies, which facilitated owl relocations. However, during our study, we visited 47 owl territories multiple times and were able to find roosting owls at only seven sites. We think various forms of telemetry could allow us to find a much larger sample of roosting birds, thus reduce uncertainty concerning owl behavior.

We also studied possible relationships between recreation, habitat, and owl site occupancy, colonization, extinction, and detection, and analyzed recreation, year, habitat, and fledgling production relationships. Results indicated that owls were not avoiding high-recreation sites during the 3-year study. The analysis also concluded that recreation did not appear to be negatively related to site occupancy, site colonization, or fledgling

production; nor was recreation positively related to site extinction. High recreation sites were occupied by spotted owls each year of our study, and fledglings were observed in these sites multiple years. Although we did not see a negative relationship between recreation and occupancy, we did see a possible relationship between habitat-type and occupancy. Mesic sites were estimated to have higher occupancy and recolonization rates and lower extinction rates when compared to xeric sites. Mesic sites appeared to be more stable (i.e., constant occupancy) than xeric sites. Mesic habitats may provide more favorable microclimates and habitat structure, roost and nest sites, and diverse habitats for the owl's prey (Barrows 1981, Ganey et al. 1993, Rinkevich and Gutiérrez 1996, Swarthout and Steidl 2001, Willey 1998, Willey and van Riper 2007, Willey and Willey 2010).

Spotted owls have a low ability to dissipate heat via evaporative cooling, thus they appear to use microclimates within both canyon and forest habitats to avoid high temperatures (Barrows 1981, Ganey et al. 1993, Weathers et al. 2001, Ganey et al. 2004). All though both mesic and xeric habitats have rocky canyon relief that provides shade, mesic habitats may possess more shaded relief via vegetation structure and narrower canyon walls (Rinkevich and Gutiérrez 1996). Both Rinkevich and Gutiérrez (1996) and Willey and Willey (2010) indicated the importance of water in the arid canyonlands of Southern Utah. Rinkevich and Gutiérrez (1996) surveyed 75% of Zion National Park for Mexican spotted owls and concluded that all of the accessible territories had perennial or ephemeral water sources; they compared these territories to randomly selected canyons, and 71% of unoccupied random canyon study sites had no water present. Willey and Willey (2010) trapped small mammals and surveyed for Mexican spotted owls in canyons within Grand Staircase Escalante National Monument. They showed within drought years, small mammal species richness and abundance was much lower than wet years. In addition, they observed lower owl occupancy, number of pairs among sites, and production of young within drought years. Thus wetter (i.e., mesic) habitats may experience less fluctuation in small mammal populations between wetter and dryer years, e.g., due to consistent presence of springs and canyon seeps, and as a result, these habitats may experience less fluctuation in prey availability and owl occupancy (Willey and Willey 2010).

Our research did not document a negative relationship between recreation and spotted owls, but future occupancy monitoring of spotted owl territories in Utah is recommended. The occupancy approach is a cost effective method to monitor territorial occupancy rates of spotted owls over multiple years. We recommend that future studies implement methods to estimate detection rates among different owl site states, including single owls, pairs, and pairs with fledglings, to provide corrected, unbiased estimates of true occupancy rate (see MacKenzie et al. 2006).



## INTRODUCTION

The Mexican spotted owl (*Strix occidentalis lucida*) is one of three subspecies in North America, with *lucida* considered distinct from the Northern (*S. o. caurina*) and California (*S. o. occidentalis*) forms based primarily on plumage and overall size (Gutiérrez et al. 1995). For example, *lucida* is somewhat lighter in appearance, smaller, and has larger “spots” than both *caurina* and *occidentalis*. There is also evidence for significant genetic differentiation among the subspecies (Barrowclough et al. 1999, 2005). Mexican spotted owls were listed as “threatened” in 1993 by the US Fish and Wildlife Service, in part, due to perceived threats from timber harvest and wildfire (Cully and Austin 1993).

The Mexican spotted owl has a relatively large geographic range, from Northern Utah, south through the four corners region of the U.S., then extending south to Michoacan, Mexico (Gutiérrez et al. 1995). Within this diverse region, the owl is widely distributed among forested mountain ranges and rocky canyonlands (USDI 1995). The Mexican spotted owl is strongly associated with mature coniferous forests, riparian woodlands, and narrow rocky canyons (Ganey and Balda 1989, Rinkevich and Gutiérrez 1996, Willey 1998, Mullet and Ward 2010).

In Utah, the Mexican spotted owl (henceforth, owl) is distributed within a fragmented rocky canyon environment (Rinkevich and Gutiérrez 1996, Willey and van Riper 2007) where steep cliffs generate microclimates and structures that allow the owl to establish nest sites and locate protected roosts (Barrows 1981, Ganey et al. 1993, Weathers et al. 2001, Ganey et al. 2004, Rinkevich and Gutiérrez 1996, Willey 1998, Willey and van Riper 2007). Studies of habitat use indicate that narrow rocky canyons

have structural elements that create many potential roost and nest locations (Rinkevich and Gutiérrez 1996, Willey 1998, Swarthout and Steidl 2001 2003). The variation in vegetation and geomorphology create a diversity of habitats for the owl's small mammalian prey (Rinkevich and Gutiérrez 1996, Willey 1998, Willey and Willey 2010). Within these rocky habitats the owl nests exclusively in caves or on ledges of steep cliffs, and no nests have been located in trees, although scattered stands are often present near nest sites (Willey 1998, Rinkevich and Gutiérrez 1996, Swarthout and Steidl 2003). Diet analyses indicate the owls primarily consumed small mammals, with a majority of identified prey in pellet samples consisting of woodrats (*Neotoma*) and mice (*Peromyscus*) (Wagner et al. 1982, Rinkevich 1991, USDI 1995).

In a study observing diurnal behaviors, Sovern et al. (1994) showed that Northern spotted owls primarily roosted in a single location with eyes closed during diurnal observation periods, and showed little vigilance or flight behaviors during the day; however, they noted that nesting pairs foraged more (1.9 times), and were more active, as compared to non-nesting owls. Willey (1998) recorded diurnal roost behavior in southern Utah and reported similar results to Sovern et al. (1994). For example, in canyon habitats, owls spent the majority of time at roosts resting, occasionally foraged or changed roost sites, and even though it was a relatively hot environment, the owls rarely were observed thermoregulating. Investigating nocturnal social behavior in Arizona, Ganey (1990) observed that owls called most frequently within two hours after sunset, with less frequent calling later in the evening and just before sunrise. Ganey (1990) observed that the owl used a wide variety of calls, including 4 note hoots, bark calls, and low whistles.

Because of its status as a threatened species (USDI 1995), and apparent dependence on economically important forests, spotted owls are of great interest to land managers, wildlife biologists, and the public. Southern Utah has experienced a steady increase in human visitation to canyon environments, and thus a large increase in human activity within canyons used by nesting spotted owls (USDI, 1995, Rinkevich and Gutiérrez 1996, Swarthout and Steidl 2001, 2003). For example, human recreational use was measured in select canyons by the National Park Service, Zion National Park, using official travel permits required by prospective users. Canyoneering permits for popular canyons, many occupied by spotted owls, increased by as much as 1,714% between 1998 and 2002 (Zion National Park, unpublished backcountry use records). Overall, the number of permits issued for narrow slot-type canyon day use increased 42% since 2003, and overnight camping permits increased 26%.

Humans recreating within spotted owl breeding habitat within the canyonlands has the potential for negative effects on the owl and its habitat (Swarthout and Steidl 2001, 2003). Although the owl is primarily a nocturnal predator, its diurnal activities could be affected by daytime visitation by humans (Delaney et al. 1999, Swarthout and Steidl 2001, 2003). LeFranc and Millsup (1984) summarized recreation impacts to raptors and suggested recreation was among the primary threats to many raptor species. Recreation has been shown to have both direct and indirect effects on raptors (Richardson and Miller 1997). For example, studies of diurnal raptors indicated that human activity was associated with decreased nest attendance and decreased hatching and fledging success (White and Thurow 1985), as well as lower prey delivery rates (Suter and Jones

1981, Fernandez and Azkona 1993, Delaney et al. 1999, Steidl and Anthony 2000).

Recreation by humans in the vicinity of raptors has been shown to alter foraging behavior (Knight et al. 1991, McGarigal et al. 1991, Swarthout and Steidl 2003) and was associated with nest abandonment (White and Thurow 1985).

With respect to impacts on spotted owls, previous studies addressed effects among different types of human disturbance, for example, Delaney (1999) provided evidence that chainsaw operation (a ground-based disturbance) elicited a greater flush response in nesting and post-nesting Mexican spotted owls than did over-flights by helicopters (an aerial disturbance). Working in canyon environments in Utah, Swarthout and Steidl (2001) directly approached roosting spotted owls to potentially induce and then record a variety of behavioral responses. They estimated, given a specific rate of hiker approach, the distance that provoked an owl to flush, and then observed post-flush flight distances. Swarthout and Steidl (2003) observed spotted owl nest behavior during trials where a “hiker” walked past an owl nest ( $n = 10$ ) in 15-minute blocks while an observer watched for changes in behavior, for example, female owl prey-handling time, vocalization rates, and various daytime maintenance behaviors. Results for hiker trials were compared to control (no hiker) periods. They observed decreases in female prey-handling time and in time performing maintenance behaviors.

To advance the knowledge of the owl’s population ecology in the canyonlands and explore potential human impacts, the broad goal of this research project was to investigate whether existing recreational hiking restrictions used by Federal agencies within the study areas prevented negative impacts on owls during the breeding season,

defined as March-August (USDI 1995). The first research question we addressed concerned whether spotted owl behavior was related to recreation by humans, thus we conducted an investigation of diurnal owl roost behavior to assess the impacts of human recreation on spotted owls. The second research question, and primary focus of our work, concerned the potential impacts of hiking-specific recreational activity on occupancy rates of spotted owl territories. To address this question, we conducted occupancy-surveys across a range of owl sites (i.e., territories) with differing levels of hiker use to examine territorial status of spotted owls under different conditions. Our third research question was about whether owl reproduction was related to recreation by humans. To address the third question, we estimated annual productivity for each owl territory by estimating fledglings produced per detected pair of owls during the study.

The field component of the research was conducted in study areas located across southern Utah's canyonlands: Zion and Capitol Reef National Parks, Grand Staircase-Escalante National Monument, and the Cedar Mesa-Elk Ridge highland (Figure 1.0). Zion National Park typically has the highest concentration of spotted owls in Utah, including at least 23 known territories within 59,500 hectares. The park has a long history (since the 1970s) of spotted owl research and monitoring (e.g., Kertell 1977), including an active monitoring program for occupancy and reproduction (Rinkevich and Gutiérrez 1996, Unpublished Records of Zion National Park, Springdale, UT). Capitol Reef National Park and Grand Staircase-Escalante National Monument include 19 known owl territories; Capitol Reef with ten historic territories across 98,000 hectares and Grand Staircase with nine territories in 769,000 hectares. Grand Staircase, Capitol Reef, and the

Cedar Mesa-Elk Ridge highland all have a history of spotted owl research and monitoring since the 1980s (Wagner et al. 1982, Willey 1998, Willey and van Riper 2007). Because Capitol Reef and Grand Staircase are adjacent management units, they may represent a contiguous area of habitat for the owl. The Cedar Mesa-Elk Ridge highland has historically included seven territories (USDI 1995).

Levels of recreational use differ among the research study areas (Fig. 1). Approximately half of the owl territories in Zion National Park occurred within popular human recreational use corridors (e.g., canyoneering routes or established trails). In Capitol Reef, only two of ten historic territories received regular visitation (typically less than ten visitors per week), and other territories were rarely visited (Gary Lenhart, park biologist, pers. com.). Grand Staircase-Escalante National Monument has nine territories that received low visitation, due in part to difficult access (William Booker, BLM Recreation Specialist, pers. com.). Owl territories on the Cedar Mesa-Elk Ridge highland received varying use, with most human activities in Fish and Owl Canyons due to the presence of ancient Native American ruins constructed by the Anasazi (Rick Boretti, BLM Wildlife Tech., pers. com.).

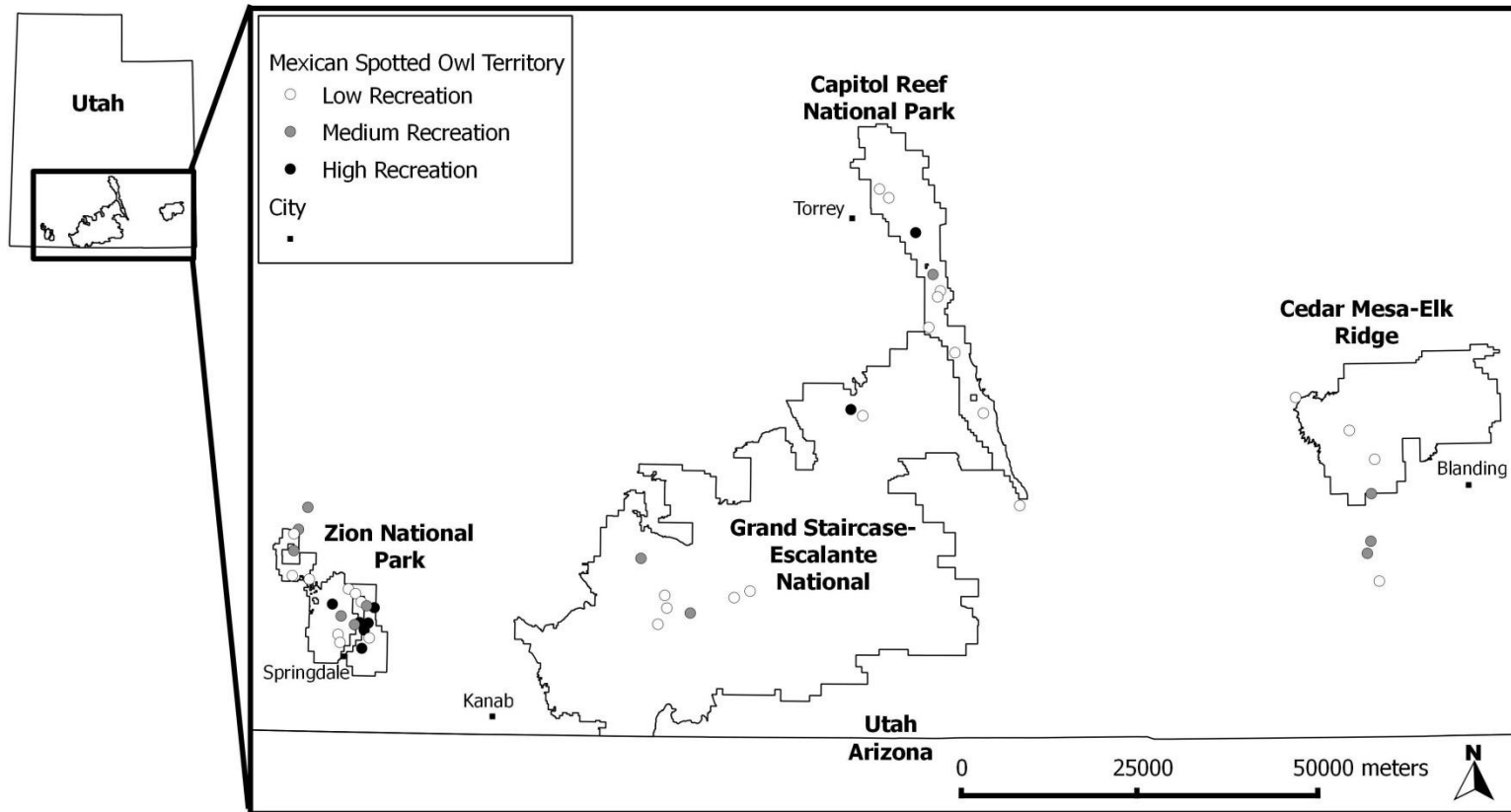


Figure 1. Zion and Capitol Reef National Parks, Grand Staircase-Escalante National Monument, and the Cedar Mesa-Elk Ridge highland study areas, southern Utah. Approximate locations of Mexican spotted owl territories are shown. The Cedar Mesa-Elk Ridge highland study area is composed of the Manti La-Sal National Forest (shown as a border) and Bureau of Land Management (BLM) lands (not illustrated).

### Research Study Areas

During 2008 through 2010, from July to early August (i.e., the post fledging period) each season, we investigated occupancy dynamics, roost behavior, and reproduction of spotted owls at 47 historic territories within four study areas (Fig. 1): Capitol Reef and Zion National Parks, Grand Staircase-Escalante National Monument (administered by the Bureau of Land Management), and on the Cedar Mesa-Elk Ridge highland, administered partly by the Bureau of Land Management (BLM) and the USDA Forest Service, Manti La-Sal National Forest. Ten historically active territories in Capitol Reef (CARE), nine territories in Grand Staircase-Escalante National Monument (GSENM), and seven territories in Cedar Mesa-Elk Ridge (CEDAR) were included in the sample (Willey 1998; Willey and Willey 2010); however, in Zion National Park (ZION), a sub-sample of historic sites was selected based on several limiting factors, including: relative human use, accessibility, and safety for researchers, resulting in 21 territories.

Zion National Park is located 1 km north of Springdale, Utah, and is characterized by a deep sandstone gorge dissected by side canyons and large vertical cliffs, and ranges in elevation from 1,345 to 2,141 m. Vegetation along canyon bottoms and north facing slopes in ZION was primarily mixed-conifer forest dominated by Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and ponderosa pine (*Pinus ponderosa*). Riparian vegetation included box elder, and bigtooth maple (*Acer grandidentatum*). South-facing aspects possessed scattered stands of ponderosa pine,



pinyon pine (*P. edulis*), and Utah juniper (*Juniperus utahensis*). GSENM (1,590 to 1,989 m elevation), located 30 km east of Kanab, is a maze-like region of steep canyons eroded deeply into the Grand Staircase uplift north of the Grand Canyon geologic formations. Vegetation was dominated by pinyon-juniper woodlands (PJ), with small pockets of mixed-conifer forest in cool canyon alcoves. Mesas and rolling uplands contained a mixture of PJ interspersed by blackbrush (*Coleogyne ramosissima*), alder leaf mountain mahogany (*Cercocarpus montanus*), and Indian ricegrass (*Achnatherum hymenoides*).

## **RELATIONSHIP BETWEEN RECREATION AND MEXICAN SPOTTED OWL ROOST BEHAVIOR IN SOUTHERN UTAH**

### Introduction

Because of its status as a threatened species (USDI 1995), and apparent dependence on economically important mature forest habitats, spotted owls are of great interest to land managers, wildlife biologists, and the public. During the past two decades the canyonlands region in southern Utah experienced a steady increase in human visitation, and as a result, a significant increase in human use in canyons used by nesting spotted owls (USDI 1995, Rinkevich and Gutiérrez 1996, Swarthout and Steidl 2001, 2003). For example, human recreational use was measured in select canyons by the National Park Service, Zion National Park, using official travel permits required by prospective users. Canyoneering permits for popular canyons, many occupied by spotted owls, increased by as much as 1,714% between 1998 and 2002 (Zion National Park, unpublished backcountry use records). Overall, the number of permits issued for narrow slot-type canyon day use has increased 42% since 2003, and overnight camping permits increased 26%.

Use by humans recreating within spotted owl breeding habitat within the canyonlands has the potential for negative impacts on the owl and its habitat (Swarthout and Steidl 2001, 2003). LeFranc and Millsup (1984) summarized recreation impacts to raptors and suggested recreation was among primary threats to many species. Recreation

has been shown to have both direct and indirect effects on raptors (Richardson and Miller 1997). For example, studies of diurnal raptors indicated human activity was associated with decreased nest attendance and decreased overall reproductive success (e.g., decreased hatching and fledging success) (White and Thurow 1985), and lowered prey delivery rates (Suter and Jones 1981, Fernandez and Azkona 1993, Delaney et al. 1999, Steidl and Anthony 2000). Recreation by humans in the vicinity of raptors has been shown to alter foraging behavior (Knight et al. 1991, McGarigal et al. 1991, Swarthout and Steidl 2003), and was associated with nest abandonment (White and Thurow 1985).

With respect to impacts to spotted owls, previous studies have addressed effects among different types of human disturbance, for example, Delaney (1999) showed chainsaw operation (a “ground-based” disturbance) elicited greater flush response in by nesting Mexican spotted owls than over-flights by helicopters (an aerial disturbance) during the same time periods. Working in canyon environments in Utah, Swarthout and Steidl (2001) directly approached roosting owls to induce and record a variety of behavioral responses. They estimated, given a specific rate of hiker approach, the distance that provoked an owl to flush and also observed post-flush flight distance. Swarthout and Steidl (2003) observed spotted owl nest behavior during trials where a “hiker” walked past an owl nest ( $n = 10$ ) in 15-minute blocks while an observer watched for changes in behavior, for example, female owl prey handling time, vocalization rates, and various daytime maintenance behaviors. Hiker trials were compared to a control (no hiker) period. They observed a decrease in time females spent handling prey and decreased time among maintenance behaviors.

In a study observing diurnal behaviors, Sovern et al. (1994) showed that Northern spotted owls primarily roosted quietly during diurnal observation periods, and showed little or no vigilant or flight activities; however, they noted that nesting pairs foraged more (1.9 times) and were more active during the day than non-nesting owls. Willey (1998) conducted diurnal roost observations in southern Utah's canyonlands and saw similar results to Sovern et al. (1994). For example, the owls in canyon habitats spent the majority of time at roosts resting quietly, rarely foraged or changed roost sites, and even though it was a relatively hot environment, the owls were rarely observed thermoregulating (Willey 1998). Investigating nocturnal social behavior in Arizona, Ganey (1990) observed that owls called most frequently within two hours after sunset, with less frequent calling later in the evening and just before sunrise. Ganey (1990) observed that the owl used a wide variety of calls, including 4 note hoots, bark calls, and low whistles.

To investigate diurnal behavior in canyon habitat and compare behaviors of owls associated with relatively high versus low levels of recreation, we conducted diurnal roost observations for owls associated with both high- and low-recreational use-level. We were interested in understanding the relationship between human visitation and owl diurnal roost behavior. Our questions related to roosts with relatively low human-use were: 1) do spotted owls spend most of the day roosting? 2) how much movements were conducted among roosts during the day? and 3) how much time was spent being vigilant to their surroundings? We predicted for roosts that experienced high recreation the spotted owls would exhibit more vigilance and move more to alternate roosts (e.g., flush

from one roost to another to avoid humans) than owls associated with low levels of recreation (Swarthout and Steidl 2001, 2003). To understand the relationships between fledglings and adult-owl behaviors we asked if owls with fledglings would be more vigilant than non-nesting residents? We predicted that owls with fledglings would be more vigilant than those without fledglings (Sovern et al. 1994).

In addition to our observations on roost behavior, we also designed an investigation of diurnal owl roost behavior involving field experiments to assess the impacts of human canyon hikers on spotted owls. From July-August 2010, we conducted field experiments that exposed roosting owls to a 3-hiker group who walked slowly, while talking in low voices through a treatment area with a roosting spotted owl. Our statistical design was a before/during/after (BDA, i.e., pre-treatment, hiker treatment, and post-treatment) contrast to estimate effects of hiker presence on roost behavior. During 2008-2010, 47 owl territories were available for study, but we were only able to locate roosting owls and conduct diurnal roost observations at seven territories because owls were not radio-tagged and difficult to find, thus 6 territories were located in ZION, and 1 in GSENM.

## Methods

### Diurnal Roost Observations

Diurnal roost behaviors of focal spotted owls were observed and recorded on data forms at seven occupied territories during the second half of the breeding season (July and August). A single observer visited a territory and attempted to locate a roosting owl, then established an observation point within 50 m of the focal owl. The observer allowed a 10-minute habituation period to pass, and then started recording behavior on a

standardized data form, where all behaviors and changes in behavior were recorded by time. Behaviors were assigned to seven categories: 1) roosting, which included: sitting with eyes open or closed; 2) thermoregulation: gular fluttering, feather erection, wing and tail movements, exposing the legs or foot pads for air flow, and movement from sunlight to shade; 3) foraging: foraging attempts; 4) moving: change of roost and shifting position at a roost; 5) socializing: calling, courtship, and allopreening; 6) vigilance: visually searching; and 7) maintenance: preening, stretching, regurgitating pellets, and defecation. Observers also recorded temperature (pocket thermometer), cloud cover (ocular estimation of percent sky covered), and wind speed (Kestrel anemometer) at the beginning and the end of the observation; sex (if possible) and age (i.e., fledgling or adult) of the roosting owl; and any presence of humans, other than the observer.

### Diurnal Roost Analysis

No foraging attempts were observed during this study, thus foraging was removed as a category before the final analysis. A two-by-six contingency table and chi-square analysis was used to test if total minutes of diurnal roost behavior recorded for the owls were independent of our two identified human-use levels. We used a rank of high or low, because no “medium” impact site could be identified among the territories studied, i.e., sites either had very common visitation, or it was rare.  $P \leq 0.05$  was the preselected significance value in all tests, where adults and fledglings were analyzed separately.

### Roost Behavior Experiments

In addition to our observations on roost behavior, we also designed an investigation of diurnal owl roost behavior involving field experiments to assess the impacts of human

visitation (i.e., hikers) on spotted owls. From July-August 2010, we conducted field experiments that exposed roosting owls to a 3-hiker group. Our statistical design was a before/during/after (BDA, i.e., pre-treatment, hiker treatment, and post-treatment) contrast to estimate effects of hiker presence on roost behavior. Each conditional period of the BDA experiment was 1-hr in length, thus totaling 3-hrs per experimental trial. Each experimental trial was conducted during the afternoon (1200 to 1600 hrs) on owls that had not been exposed to human presence during that day. The afternoon trial was selected to match experimental conditions with time when large number of hikers are in canyon areas and also to conduct experiments during high temperature periods when owls could be stressed by human presence.

To conduct the field experiments, one observer located a roosting owl and then positioned themselves 20-70m from the owl. Ten min passed to allow normal behavior of the owl to continue. The observer then initiated the BDA experiment first by observing pre-treatment behavior (1-hr); then hiker treatment behavior. Hikers passed tangentially by the owl twice during the 1-hr treatment period. Finally, the observer continued observations during post-treatment period for 1-hr.

## Results

During the 2008, 2009, and 2010 field seasons, we located roosting owls in six territories in ZION and one territory in GSENM, and collected a total of 4,036 minutes of roost behavior (Table 1). Recorded observations included 1,774 minutes for adult owls with fledglings at high-recreation territories and 472 minutes of adult owls without

fledglings located at low-recreation territories. We also recorded behavior data that included 1,535 minutes for fledglings at high-recreation territories and 255 minutes for fledglings at low-recreation territories. We did not observe diurnal roost behavior of adults at high-recreation sites without fledglings nor did we observe owls with fledglings at low-recreation territories. Clearly this sampling outcome was not optimal, thus important relationships could be confounded, for example the ability to examine differences between low and high recreation with respect to diurnal adult behavior. Nevertheless, the Chi-square analysis indicated that the distribution of behaviors for adult owls was unequal and potentially dependent on recreation level or presence of fledglings ( $P < 0.05$ ) (Table 1). Adult owls with fledglings at high-recreation territories spent more time in maintenance and vigilance behaviors and less time roosting than did adults without fledglings seen at low-recreation territories.

Chi-square results for fledgling owls indicated that the distribution of behaviors for fledglings was dependent on whether they occupied a high- or low-recreation site ( $P < 0.05$ ) (Table 2). Although fledglings in both types of sites (i.e., high or low recreation) spent approximately 50% of their time roosting, fledglings observed at high-recreation study sites spent more time performing maintenance behaviors (high-recreation = 13%; low-recreation = 4%) and showed less time in vigilant behaviors (high-recreation = 29%; low-recreation = 35%).

With regard to our attempt to conduct experiments, during the 2010 field season when scheduled work began, only one adult owl was observed roosting during day time hours in a low-recreation territory (unexposed to human presence that day), resulting in



only one successfully completed field experiment that exposed a male adult to a 3-hiker group. Our experimental design did not allow us to use observations of owls in high-recreation territories, because hikers were present during all three treatment periods. Because of this limited sampling, we did not complete a statistical analysis on the 3-hours of behavior data.

### Discussion

The roost observational analysis identified a significant difference in the frequency of various adult behaviors between types of roosts, but the difference may or may not have been related to recreation use level, i.e., it could have simply been due to presence or absence of fledglings. In other studies, Sovern et al. (1994) noticed that frequency rates in the different roost behaviors in pairs of adult owls with fledglings differed from that of pairs without fledglings. We were unable to test for such differences in this study. All the adults observed with fledglings were associated with high recreation sites, and all the adults observed without fledglings were associated with low recreation sites.

Similar to Sovern et al. (1994) and Willey (1998), we observed that adult owls spent the majority of time at roosts, apparently resting, and spending little time in active movements or social behaviors. Although the owls we observed in canyon environments primarily roosted quietly in stationary locations, we did observe that the owls were a bit more active during daytime hours than Northern spotted owls (Sovern et al. 1994), similar to the observations of Willey (1998). These results also indicate that adult owls

with fledglings at high-recreation territories were more vigilant than adults without fledglings at low-recreation territories. Although this result matches our predictions, we were unable to distinguish if recreation, fledglings, or both were responsible for differences in vigilance.

Our study differed from that of Sovern et al. (1994) and Willey (1998) in that we recorded and analyzed maintenance behaviors separately from roost behaviors, and then noticed that adult owls with fledglings at high-recreation territories spent a greater proportion of time in maintenance behaviors than adults without fledglings at low-recreation territories (Table 1). Conducting relatively more maintenance activities could be a form of displacement behavior in response to high-recreational activity by humans in an owl's nest area, but unfortunately we were unable to distinguish between recreation and fledgling presence.

The behavior results in this study showed an opposite relationship compared to a study by Swarthout and Steidl (2003) in canyon study areas. They observed decreased female maintenance behaviors in the presence of elevated human activity. In our study, nearly half of the recorded fledgling behaviors were roosting, whereas the other half of their diurnal behavior consisted of relatively more active behaviors. This observation indicates that although spotted owls are nocturnal, fledgling spotted owls are active during daytime hours. The presence of active fledglings may cause adults to conduct greater amounts of support behavior, thus higher overall activity than adults without fledglings (Sovern et al. 1994). We also observed that it was much easier to find and observe adult owls with fledglings, and thus adult owls with young were detected more

frequently than adults without young. This may suggest that parental owls are more active, and might select roosts in different microhabitats than owls with no young, thus observations of different owl behaviors.

Fledglings in high and low recreation territories were observed spending approximately equal time roosting quietly but different amounts of time in maintenance and vigilance behaviors. Fledglings associated with high-recreation territories spent more time in maintenance behaviors and less time in vigilant behaviors. Again, this suggests displacement behavior in response to high-recreational activity by humans, but it is unclear how being less vigilant in high-recreation territories could impact fledglings. Perhaps a decrease in vigilance has the potential to increase vulnerability to predators (i.e., via not being alert to predators). However, an increase in vigilance could also increase vulnerability to predators (i.e., via revealing location to predators). Before concluding that recreation is negatively related to fledgling behavior, more research needs to be conducted to better understand potential impacts of recreation on fledgling behavior, and furthermore, future efforts need to explore if recreation could be related to fledgling survival before and after leaving their natal territories.

In conclusion, the roost analyses identified a significant difference in fledgling behaviors and in adult behavior frequencies, but adult behavior difference may or may not be related to recreation. Further research should be initiated to examine differences between owl behaviors (i.e., both adults and fledglings) along a range of variables such as: human recreation, habitat type, time of day, owl sex, and mating status (i.e., whether adults are paired or single). It is not unreasonable to suggest that these variables could

have been related to the behaviors we observed, but unfortunately, with the limited data set, we did not test additional relationships outside of human recreation. Clearly radio transmitters will help observers locate and observe owls, and both Sovern et al. (1994) and Willey (1998) used radio transmitters. During our study, we visited 47 historically occupied owl territories multiple times for three years, but located roosting owls during the day at only seven sites.

Table 1. Summary of Chi-square analysis comparing diurnal roost behavior between adult Mexican spotted owls associated with high- and low- levels of recreation in southern Utah. Adult owls associated with high-recreation were also parents (i.e., they were also associated with fledglings), and adults associated with low-recreation were not parents (i.e., they were never observed with fledglings). Total minutes for each individual behavior associated with Low- and High- recreation use of territories. The proportion of total behavior is shown in parentheses. Maintenance = Maint, Movement = Move, and Thermoregulation = Thermo.

	Roost	Maint	Move	Social	Vigilant	Thermo	Total
Low	372 (0.79)	26 (0.06)	13 (0.03)	0 (0.00)	57 (0.12)	4 (0.01)	472
High	1066 (0.60)	205 (0.12)	66 (0.04)	33 (0.02)	387 (0.22)	17 (0.01)	1774
$X^2$	61.37						
df	5						
$P$	$6.3 \times 10^{-12}$						

Table 2. Summary of Chi-square analysis comparing diurnal roost behavior between fledgling Mexican spotted owls associated with high- and low- levels of recreation in southern Utah. Total minutes for each individual behavior associated with Low- and High- recreation territories. The proportion of total behavior is shown in parentheses. Maintenance = Maint, Movement = Move, and Thermoregulation = Thermo.

	Roost	Maint	Move	Social	Vigilant	Thermo	Total
Low	128 (0.50)	11 (0.04)	5 (0.02)	12 (0.05)	90 (0.35)	9 (0.04)	255
High	751 (0.49)	200 (0.13)	78 (0.05)	50 (0.03)	445 (0.29)	11 (0.01)	1535
$X^2$	38.47						
df	5						
$P$	$3.0 \times 10^{-7}$						

**ASSOCIATIONS BETWEEN RECREATION, SITE OCCUPANCY DYNAMICS,  
AND NUMBER OF FLEDGLINGS FOR MEXICAN SPOTTED OWLS IN  
SOUTHERN UTAH**

Introduction

During the past two decades, the canyonlands region of southern Utah experienced a steady increase in human visitation and, as a result, a significant increase in human activity in canyons used by nesting spotted owls (USDI 1995, Rinkevich and Gutiérrez 1996, Swarthout and Steidl 2001, 2003). For example, human recreational use was measured in select canyons by the National Park Service, Zion National Park, using official travel permits required by prospective users. Canyoneering permits for popular canyons, many occupied by spotted owls, increased by as much as 1,714% between 1998 and 2002 (Zion National Park, unpublished backcountry use records). Overall, the number of permits issued for narrow slot-type canyon day use has increased 42% since 2003, and overnight camping permits increased 26%.

Use by humans recreating within spotted owl breeding habitat within the canyonlands has the potential for negative impacts on the owl, and its habitat (Swarthout and Steidl 2001, 2003). LeFranc and Millsup (1984) summarized recreation impacts to

raptors and suggested it was among primary threats to many raptor species. Recreation has been shown to have both direct and indirect effects on raptors (Richardson and Miller 1997). For example, studies of diurnal raptors indicated human activity was associated with decreased nest attendance and hatching and fledging success) (White and Thurow 1985), and lower prey delivery rates (Suter and Jones 1981, Fernandez and Azkona 1993, Delaney et al. 1999, Steidl and Anthony 2000). Recreation by humans in the vicinity of raptors has been shown to alter foraging behavior (Knight et al. 1991, McGarigal et al. 1991, Swarthout and Steidl 2003), and was associated with nest abandonment (White and Thurow 1985).

With respect to impacts to spotted owls, previous studies have addressed effects among different types of human disturbance, for example, Delaney (1999) showed chainsaw operation (a “ground-based” disturbance) elicited greater flush response by nesting Mexican spotted owls than over-flights by helicopters (an aerial disturbance) during the same time periods. Working in canyon environments in Utah, Swarthout and Steidl (2001) directly approached roosting owls to induce and record a variety of behavioral responses. They estimated, given a specific rate of hiker approach, the distance that provoked an owl to flush and also observed post-flush flight distance. Swarthout and Steidl (2003) observed spotted owl nest behavior during trials where a “hiker” walked past an owl nest ( $n = 10$ ) in 15-minute blocks while an observer watched for changes in behavior, for example, female owl prey handling time, vocalization rates, and various daytime maintenance behaviors. Hiker trials were compared to a control (no hiker) period. They observed a decrease in time females spent handling prey and

decreased time among maintenance behaviors.

Given the evidence that human-use in canyons may affect nesting or roosting spotted owls (Swarthout and Steidl 2001, 2003), the goal of this study was to further examine potential impacts. The research questions concerning human use and owl site occupancy dynamics included: 1) was owl occupancy rate negatively associated with human use? 2) was colonization of owl sites negatively associated with human use?, and 3) was site extinction positively related to recreational use? In addition, we also identified a research question concerning human use and owl fledgling production: 1) was fledgling production per owl pair negatively associated with human use? The analysis of site occupancy dynamics and reproduction occurred across a range of potentially impacted territories (i.e., with differing levels of hiker use). Occupancy-based population analyses involve the investigation of a site's (in this case, an owl territory) occupancy-state dynamics and provided the opportunity to rigorously investigate the questions about human-use level (MacKenzie et al. 2006). We also examined a question about the impacts of habitat on occupancy dynamics, including: 1) was habitat (i.e., mesic or xeric) related to site occupancy, colonization, or extinction? To identify potential correlations among the response and predictor variables, and thus test hypotheses concerning slope coefficients, we used an Information-Theoretic approach (Burnham and Anderson 1998) to examine the relationship between recreational-use levels by humans and rates of spotted owl occupancy, detection, site-extinction, and site-colonization using occupancy models (MacKenzie et al. 2006). We explored site-specific habitat covariates to investigate possible relationships of habitat and rates of occupancy,

extinction, colonization, and detection, and used a Poisson-regression analysis to estimate fledgling production per pair of adult owls.

Raptors are considered sensitive to anthropogenic disturbances, but few studies have looked at human intrusion effects on spotted owl behavior (Delaney et al. 1999, Swarthout and Steidl 2001, 2003). Thus, little work has been completed on how intrusions might be related to spotted owl occupancy rate. We predicted that if hiker-based recreation in the canyonlands is adversely affecting owls, then we would observe decreased occupancy and colonization rates and increased rates of site extinctions in canyons that are used highly by recreationists. We also expected to see fewer fledged young in territories (henceforth: “sites”) associated with increased recreation. It was unclear what the relationship between recreation and detection probability could be; however, Swarthout and Steidl (2003) observed an increase in nesting owl vocalizations when hikers were present during evening periods. Alternatively, if owls habituate to human voices and other hiker noises, one might observe decreased vocal behaviors, and thus a reduction in detection rate during standardized surveys. We predicted that owls would habituate to humans such that sites with high levels of human use would show lowered response rates and less owl calling.

### Methods

Occupancy-based population analyses provide for the investigation of site state dynamics and relationships of site-specific covariates, for example habitat or human use (MacKenzie et al. 2006). We used an information-theoretic approach (Burnham and



Anderson 1998) to explore our research questions and examine the relationship between two site-specific covariates (recreational use and habitat type) and owl site occupancy parameters. Candidate models were developed using multiple-season occupancy modeling and a logit link, and Akaike's Information Criterion was used to rank models in each candidate set.

#### Hiker Use-Level Covariate

Recreation level varies as a site-specific model covariate among study areas and owl territories in Utah (MacKenzie et al. 2002). Thus, the site-level recreation covariates were assigned to three levels: high, medium, and low level of hiker presence for each spotted owl site. The use-levels were identified for each study site using a variety of approaches: trail cameras, permit records, and expert opinion from local area biologists; and then were represented in regression models as a continuous variable. Recreational use of many canyons in the study unit was well known by the biologists that work in these areas. Thus, expert opinions on the levels of use were influential in assigning use-levels for recreation at each site. ZION and CARE required backcountry permits to manage human use in numerous canyons, and documented permit records each year. However, to validate levels of use, we placed trail cameras that counted the number of individuals using a subsample of canyons in our study. Next, each owl site was given a final recreational-use rank for the analysis, then we modeled recreational-use as a continuous covariate with equal spacing between low-, medium-, and high-recreation, and finally we predicted both negative and positive trends associated with recreation (modeled as a continuous variable to streamline model predictions).

### Habitat Covariate

We created a site-specific habitat covariate that represented potential variation among owl sites and was represented in regression models as a categorical variable. As described in the study area section, the canyon landscapes vary in vegetation composition, climate, elevation, and topography. We observed that relatively cool and mesic habitats were present at higher-elevation study sites in our sample. These canyons contained a relatively high proportion of mixed conifer and riparian forest vegetation types (Rinkevich and Gutiérrez 1996, Willey and Van Riper 2007). In contrast, relatively drier, and more open, habitats were present at lower elevations with higher ambient temperatures and vegetation dominated by desert scrub vegetation (Brown 1982, Willey 1998, Willey and Willey 2010).

### Occupancy Visits

All spotted owl territories in the sample ( $n = 47$  sites) were surveyed using a standardized procedure (modified from USFWS 2003) that included two visits per owl site per year to estimate site occupancy using methods described by MacKenzie et al. (2003). During the 2008 field season, all 47 sites were visited. In 2009, 44 sites were visited, and in 2010, 43 sites were visited (Appendices A and B). Field surveys were conducted from 1 April through 31 August each year of the study (we defined this period as the “breeding season”). Within each owl territory, observers used a previously known relatively precise Universal Trans Mercator (UTM) spatial coordinate to locate the position of the owl nest site (typically a previously known nesting area or roost location).

Each standardized occupancy survey started with a systematic 1-hr search for signs of spotted owls (roosting owls, feathers, pellets) within a 2-km line transect centered at the UTM coordinate of the historic nest or roost site at each territory. The search period typically was conducted during 1-hr prior to sunset, but occasionally occurred during other daylight hours (especially when at remote sites). If no owls were located during the 1-hr search period, surveyors initiated standardized calling surveys for spotted owls along the 2-km transect imitating a variety of spotted owl calls. The calling protocol followed the standard protocol established for spotted owls (Forsman 1983, USFWS 2003). Observers established five calling stations spaced 500 m apart along the linear transect with station three (the midpoint) centered at the UTM coordinate of nest or commonly used roost site. Observers altered calling and listening for spotted owls from each survey point for 30 minutes. This procedure was repeated for each survey station until an owl was detected, or all five stations were called for spotted owls. If an owl was detected, additional calling sometimes occurred to verify location and the number of owls present, but calling by observers was kept to a minimum to reduce possible impacts on owls. If owls were heard or seen, the type of detection (vocal, visual, or both), estimated distance to the owl, time of detection, and sex of the owl (owls can be sexed by size or vocal behavior) were recorded. Observers attempted to keep survey effort ( e.g., length of search period), calling effort, and speed of each survey visit, equal among site visits and study areas.

In addition to occupancy visits, we also searched for fledglings and estimated the maximum number of fledglings produced per successful site (i.e., sites where pairs of

owls were detected and evidence of reproduction was identified). We did not account for imperfect detection of fledgling spotted owls, such that estimates of annual productivity could be biased low depending on the extent to which failed detections occurred.

### Occupancy Analyses

For the analysis of occupancy rate ( $\psi$ ),  $\psi$  was defined as the proportion of all owl sites that were occupied by owls. If occupancy status could be observed without error,  $\psi$  could be obtained by simply dividing the number of occupied sites ( $x$ ) by the total number of sites visited ( $s = 47$ ), thus the proportion of sites occupied was  $\psi = x / s$ . Because it is likely that owls were not always detected at every site,  $x$  could not be directly measured; instead,  $x$  was derived by estimating the probability of detecting an owl at a site if the site was occupied. The detection probability can be estimated by visiting sites multiple times during a primary survey period ( $T$ ) (MacKenzie et al. 2002, 2003, 2006, MacKenzie and Royle 2005), and a minimum of two visits is required to estimate detection probability within a primary survey period. In addition, this approach is robust to missing observations, and thus suitable for field studies (MacKenzie et al. 2002). It is important to note that although increased number of visits can generate a more accurate parameter estimates, after a point, additional visits do not appreciably increase the accuracy of the estimate of detection probability, especially for species with high detection rates and relatively high occupancy like spotted owls (MacKenzie et al. 2002, 2003, Block et al. in press).

Single-species, multiple-season occupancy modeling was used to estimate occupancy, detection, and site changes on the study area (MacKenzie et al. 2006). This

type of model allowed changes in occupancy to occur between years and also the use of covariates to evaluate possible mechanisms for observed changes. This approach has been used successfully for spotted owls, for example, to estimate changes in occupancy of Northern spotted owls due to barred owl presence (Olson et al. 2005). We used this model approach to estimate changes in  $\psi$ , recolonization ( $\gamma$ ), and extinction ( $\varepsilon$ ) rates for spotted owls in response to recreation and habitat.

Program Presence 3.0 Beta (Hines 2006) and R (R Development Core Team 2010) with its extension package unmarked (Fiske and Chandler 2010) were used to evaluate a 2-step process to estimate occupancy parameters (i.e., initial occupancy, extinction, recolonization, and detection probabilities). We evaluated detection models, then evaluated an *a priori* candidate model list using the best modeling approach estimated for detection. We ran all models using the default setting where initial occupancy in year one ( $\psi_t$ ) is directly estimated and  $\psi_{t+1}$  is derived using:  $\psi_{t+1} = \psi_t (1 - \varepsilon_t) + (1 - \psi_t)\gamma_t$ . To rank the candidate regression models and estimate relationships of recreation use-level, habitat, and  $\psi_t$ ,  $\varepsilon$ ,  $\gamma$ , and  $p$ , we used the small-sample-size corrected version of Akaike's Information Criterion ( $AIC_c$ ), and also used  $\Delta AIC_c$  to calculate the difference between the best model (smallest  $AIC_c$ ) and each model. In addition, Akaike weights ( $w_i$ ) were calculated and were used to evaluate the top model/models and used in model averaging. Within models, possible relationships between covariates and  $\psi_t$ ,  $\varepsilon$ ,  $\gamma$ , and/or  $p$  were evaluated using a logit link.

### Fledgling Analyses

After the occupancy analysis was completed, work was conducted on

reproduction data and the number of fledglings observed. We used data where territories were occupied during the study by a pair (i.e., sites where a pair was detected during occupancy visits), even if for only one season. We used the data set on fledglings to summarize reproduction and also to conduct an exploratory analysis using Poisson regression and certain covariates (i.e., habitat, recreation, and year) to evaluate possible factors related to the number of fledglings observed per pair. We predicted that if hiker-based recreation in the canyonlands is adversely affecting owls, then you would expect to see fewer fledged young in territories associated with increased recreation. After reviewing the results from the occupancy analysis, we predicted xeric territories would fledge fewer young when compared to mesic territories. Year covariates were explored in this analysis after observing seasonal differences in numbers of fledged young detected from 2008 to 2010 and noting that the majority of spotted owls do not breed every year (Gutiérrez et al. 1995).

R (R Development Core Team 2010) with its extension package AICcmodavg (Mazerolle 2010) was used to evaluate eight candidate models (Table 3.5). Because data were limited for xeric sites at high- and medium- recreation levels, we did not evaluate interaction models (Appendices A and B). To rank the candidate regression models and estimate relationships of recreation level, habitat, year and fledglings per pair were used  $AIC_c$ . Similar to the occupancy analysis,  $\Delta AIC_c$  and  $w_i$  were used to further evaluate Poisson regression models.

## Results

### Occupancy Results

All six analytical contrasts investigating the relationships among recreation, habitat, and the occupancy parameters were represented in the field sample of owl territories, although the combinations were not equally distributed among categories (Table 3). Fifty-seven percent of owl sites (total  $n = 47$ ) were associated with low recreation. Among the 16 sites classified as xeric, only one site was associated with high recreation, whereas seven of 31 (23%) mesic sites were associated with high recreation. Three of the 16 (19%) xeric sites were associated with medium recreation, and nine of 31 (29%) mesic sites were associated with medium recreation. Twelve of the xeric sites (75%) and 15 of the 31 (48%) mesic sites had low recreation levels.

During the 2008 field season surveys, we detected owls at 31 out of 47 sites (66%) (Appendices A and B), and detected 16 owl pairs and 15 single males among the study sites. We did not detect owls at the single high-recreation xeric site, but did detect owls at two of three medium-recreation xeric sites (67%) (1 male and 1 pair), six of 12 low-recreation xeric sites (50%) (2 males and 4 pairs), six of seven high-recreation mesic sites (86%) (2 males, 4 pairs, and 2 fledglings), seven of nine medium-recreation mesic sites (78%) (5 males, 2 pairs, and 1 fledgling), and 10 of 15 low-recreation mesic sites (67%) (5 males, 5 pairs, and 1 fledgling). Therefore, naïve occupancy rates were 0.50 for xeric sites and 0.74 for mesic sites in 2008.

In 2009, two occupancy visits, and in some cases, follow-up visits to search for

fledglings were conducted at 44 of 47 sites (Appendices A and B). We detected owls at 27 of 44 sites (61%), and detected 16 pairs and 11 single owls. As in 2008, we did not detect owls at the single high-recreation xeric site, but did detect owls at one of three medium-recreation xeric sites (33%) (1 pair), three of nine low-recreation xeric sites (33%) (1 male and 2 pairs), seven of seven high-recreation mesic sites (100%) (4 males, 3 pairs, and 4 fledglings), seven of nine medium-recreation mesic sites (78%) (4 males, 2 pairs, 1 female, and 4 fledglings), and nine of 15 low-recreation mesic sites (60%) (1 male, 8 pairs, and 7 fledglings). Therefore, naïve occupancy rates were 0.31 for xeric sites and 0.74 for mesic sites in 2009.

During the 2010 field season, we detected owls at 23 of 43 visited sites (53%) (Appendices A and B), and detected 14 pairs and nine single owls. We did not detect owls at the single high-recreation xeric site, but did detect owls at one of three medium-recreation xeric sites (33%) (1 male), three of 11 low-recreation xeric sites (27%) (1 male, 2 pairs, and 1 fledgling), six of seven high-recreation mesic sites (86%) (3 males, 3 pairs, and 2 fledglings), three of seven medium-recreation mesic sites (43%) (3 pairs), and 10 of 14 low-recreation mesic sites (71%) (3 males, 6 pairs, 1 female, and 4 fledglings). Therefore, naïve occupancy rates were 0.27 for xeric sites and 0.68 for mesic sites in 2010.

Following analyses of the candidate models exploring detection probability, the best model estimated constant detection across all sites and survey visits (Table 5). Therefore, we modeled detection as constant for additional models predicting relationships of site-level covariates (i.e., habitat and recreation) and occupancy,



extinction, and recolonization rates.

In the analysis of detection-corrected occupancy rates for the multi-season data, two models out-ranked other competing models (Table 6): both included the site-specific mesic/xeric habitat covariate when modeling  $\psi_t$  and  $\gamma$ , but they differed in how they modeled  $\varepsilon$ . These models outranked others that included effects of recreation on occupancy, extinction, and recolonization rates ( $\Delta AIC_c \geq 3.60$ ). The two top-ranked models represented 69.5% of the overall  $w_i$  (Table 6). From the top-ranked model,  $\psi_t$  was estimated as 0.75 (95% CI = 0.57 - 0.87) and 0.50 (95% CI = 0.27 - 0.73) for mesic and xeric sites, respectively. In addition, recolonization rate was estimated at 0.10 (95% CI = 0.02 - 0.37) for xeric sites and 0.53 (95% CI = 0.28 - 0.76) for mesic sites. In the top-ranked model,  $p$  was estimated as 0.89 (95% CI = 0.82 - 0.94) across all three years of study. Extinction rate in the top model was constant across years (0.25; 95% CI = 0.15 - 0.39). In the second highest ranked model ( $\Delta AIC_c = 0.70$ ),  $\psi_t$ ,  $\gamma$ , and  $p$  were modeled the same as in the top-ranked model, but  $\varepsilon$  was modeled with a site-specific habitat covariate. As in the top model, estimates of  $\psi_t$  and  $\gamma$  were higher on mesic sites in the second-best model. Additionally, in the second-best model,  $\varepsilon$  was also a function of habitat conditions and estimated to be lower on mesic sites (Table 7).

Although a recreation covariate was not present among the top two models, the third-ranked model contained both habitat and recreation covariates in the model for  $\psi_t$ . In this model, the coefficients for both covariates were positive, but 95% CIs overlapped zero (recreation: 0.297; 95% CI = -0.63 to 1.22; habitat: (0.99; 95% CI = -0.35 to 2.32) (Table 7). This model also estimated that extinction rate was negatively related to

recreation, but again the 95% CI overlapped zero (-0.54; 95% CI = -1.40 to 0.32).

To further investigate the relationships of recreation and  $\psi_t$ ,  $\varepsilon$ , and  $\gamma$ , we conducted model averaging but first removed all models with interaction terms. Model averaged results indicated that although habitat may have been associated with  $\psi_t$ ,  $\varepsilon$ , and  $\gamma$ , the relationship with parameters was quite small, or virtually absent (Figure 3). Model averaging indicated that if recreation is related, it was positively related to  $\psi_t$ , and  $\gamma$  and was negatively related to  $\varepsilon$ , but again, this relationship also appears to be quite small, or virtually absent.

### Fledgling Results

During the three year study, we detected 16 pairs in 2008, 16 pairs in 2009, and 14 pairs in 2010. Three sites were observed with fledglings during 2008, with a total of four fledglings detected (0.25 fledglings per owl pair) (Table 4). During 2009, 15 fledglings were detected (0.94 fledglings per pair) (Table 4). Seven fledglings (0.5 fledglings per pair) were detected in 2010 (Table 4).

After exploring the fledgling data using a Poisson regression, along with inclusion of covariates (i.e., habitat, recreation, and year), model ranking indicated habitat, year, and recreation were possibly related to fledgling production when compared to the NULL model (Table 3.5). Three models were within two  $\Delta AIC_c$  and represented 76% of the overall  $w_i$ . In the top-ranked model ( $AIC_c = 95.5$ ), habitat and year were both modeled as covariates to estimate fledglings per pair. That model estimated fledglings per pair as 0.34 (SE = 0.17) for mesic sites and 0.05 (SE = 0.06) for xeric sites in 2008; 1.11 (SE = 0.29) for mesic sites and 0.18 (SE = 0.18) for xeric sites in 2009; and 0.57 (SE = 0.22) for

mesic sites and 0.09 (SE = 0.10) for xeric sites in 2010. In the second highest ranked model ( $\Delta AIC_c = 1.1$ ), habitat was the only covariate, and fledglings per pair were estimated as 0.69 (SE = 0.14) for mesic sites and 0.10 (SE = 0.10) for xeric sites from 2008 to 2010. In the third ranked model ( $\Delta AIC_c = 1.9$ ), habitat, year, and recreation were all modeled as covariates to estimate fledglings per pair. That model was unable to estimate fledglings per pair in high-recreation xeric sites across all years, and it was also unable to estimate fledglings per pair in medium-recreation xeric sites in 2010. The model estimated fledglings per pair in medium-recreation xeric sites as 0.06 (SE = 0.07) in 2008 and 0.21 (SE = 0.22) in 2009; in low-recreation xeric sites as 0.05 (SE = 0.06) in 2008, 0.18 (SE = 0.18) in 2009, and 0.09 (SE = 0.09) in 2010; in high-recreation mesic sites as 0.41 (SE = 0.22) in 2008, 1.41 (SE = 0.54) in 2009, and 0.70 (SE = 0.32) in 2010; in medium-recreation mesic sites as 0.34 (SE = 0.17) in 2008, 1.18 (SE = 0.31) in 2009, and 0.59 (SE = 0.22) in 2010; and in low-recreation mesic sites as 0.28 (SE = 0.16) in 2008, 0.98 (SE = 0.30) in 2009, and 0.49 (SE = 0.21) in 2010.

Finally, we investigated coefficient estimates from the top three models (Table 8). The models estimated fledglings per pair were positively related to year 2009, year 2010, mesic habitat, and increased recreation, but all estimates have relatively large SE indicating a high level of uncertainty.

### Discussion

We predicted if hiker-based recreation in the Canyonlands was adversely affecting owls, then results would have shown decreased fledgling production, occupancy

rates, and colonization rates, and increased site extinction in canyons that were highly used by recreationists. However, the results did not support any of these predictions concerning human recreation, in fact, the results supported opposite relationships. However, there may be other variables that were responsible for territory occupancy patterns that we did not identify. We did observe a possible habitat and occupancy relationship, where mesic sites exhibited higher occupancy and recolonization rates and lower extinction rates when compared to xeric sites. Occupancy rates on mesic sites appeared to be more stable than on xeric sites during the study. Furthermore, mesic habitats were possibly related to higher fledgling production, but the estimates had relatively large associated uncertainty. It is possible that mesic habitats provided more favorable microclimates and habitat structure for roost and nest sites, and diverse habitats for the owl's prey than xeric sites, which is in agreement with previous research (Barrows 1981, Ganey et al. 1993, Rinkevich and Gutiérrez 1996, Swarthout and Steidl 2001, Willey 1998, Willey and van Riper 2007, Willey and Willey 2010).

Spotted owls have a low ability to dissipate heat via evaporative cooling, thus they appear to use microclimates within both canyon and forest habitats that allow them to avoid high summer temperatures (Barrows 1981, Ganey et al. 1993, Weathers et al. 2001, Ganey et al. 2004). Although both mesic and xeric habitats have rocky canyon relief that provides shade, mesic habitats may possess greater overall cover due to riparian vegetation structure and relatively narrow shaded canyon walls (Rinkevich and Gutiérrez 1996). Both Rinkevich and Gutiérrez (1996) and Willey and Willey (2010) indicated the importance of water in the arid canyonlands of southern Utah. Rinkevich

and Gutiérrez (1996) surveyed 75% of Zion National Park for Mexican spotted owls and concluded that all of the accessible territories had perennial water sources; they compared these territories to random canyons, and 71% of the unoccupied random canyons had no water present. Willey and Willey (2010) trapped small mammals and surveyed for Mexican spotted owls in canyons within Grand Staircase-Escalante National Monument and showed during drought years, small mammal species richness and abundance was much lower than wet years. In addition, they observed lower owl occupancy, fewer owl pairs, and lowered production of young within drought years. Perhaps wetter (i.e., mesic) habitats may experience less fluctuation in small mammal populations between wet and dry climate cycles, and as a result, show less fluctuation in owl occupancy (Willey and Willey 2010).

#### Management Implications

The results showed that human recreation was not negatively correlated with site occupancy or reproduction, thus we think that current management practices and imposed limits to recreational activity in the study areas have been adequate for protecting spotted owls. In Zion National Park, canyoneering permits for popular canyons, many occupied by spotted owls, increased by as much as 1,714% at some sites between 1998 and 2002 (Zion National Park, unpublished backcountry use records). During our surveys, we did not see a noticeable difference in human visitation to owl territories from 2008 thru 2010, but we did visit the territories that received the highest levels of human visitation, and owls were consistently detected at these sites. A large increase in recreation, such as

occurred between 1998 and 2002, could have had an initial negative impact on owl occupancy, but we were unable to identify such a relationship. Therefore, we recommend no changes to human use permit levels for the canyons we studied, but do strongly recommend long term monitoring of owl occupancy and human recreation to alert managers quickly to potential future impacts. We do not know what potential negative impacts an increase in recreational activity could have on owl occupancy and reproduction, but think that a safe strategy would include an early warning system of monitoring and maintaining future management options, for example, managers may need to alter permit limits and/or other methods of controlling human recreation in canyons.

Furthermore, it is possible that increased use of xeric sites by humans could ultimately have negative impacts on owls in xeric habitats. Our results did not indicate a negative interaction between recreation and xeric habitat, but we only had one high-recreation and three medium-recreation sites in our sample. Thus, we highlight the uncertainty for managers, and recommend continued monitoring of recreation, habitat quality, and owl occupancy and reproduction using a multistate occupancy model approach (Nichols et al. 2007, MacKenzie et al. 2009, MacKenzie et al. 2011). This type of modeling has been used to investigate the relationships of recreation and Golden Eagle (*Aquila chrysaetos*) occupancy and reproduction in Denali National Park, Alaska (Martin et al. 2009) and was further used in an adaptive management plan (Martin et al. 2011).

Table 3. Combinations of recreation and habitat variables identified for 47 Mexican spotted owl territories surveyed in 2008, 2009, and 2010, southern Utah.

	Xeric	Mesic	Total
High	1	7	8
Medium	3	9	12
Low	12	15	27
<b>Total</b>	<b>16</b>	<b>31</b>	<b>47</b>

Table 4. Mexican spotted owl occupancy and reproduction data 2008-2010.

Area	2008			2009			2010		
	Single	Pair	Young	Single	Pair	Young	Single	Pair	Young
Zion	9	10	4	7	11	13	6	12	6
Cedar Mesa	4	0	0	3	1	0	0	0	0
GSENM	1	3	0	1	2	2	2	1	0
Capitol Reef	1	3	0	0	2	0	1	1	1
<b>Totals:</b>	<b>15</b>	<b>16</b>	<b>4</b>	<b>11</b>	<b>16</b>	<b>15</b>	<b>9</b>	<b>14</b>	<b>7</b>
<b>Fledglings/pair:</b>	<b>0.25</b>			<b>0.94</b>			<b>0.50</b>		

Table 5. Summary of detection models for a Mexican spotted owl multi-year occupancy analysis (2008, 2009, and 2010) including potential effects of recreation (R) and habitat type (H).  $\psi$  = initial occupancy rate, 2008;  $\gamma$  = recolonization rate;  $\varepsilon$  = extinction rate; and  $p$  = detection probability. R = a recreation covariate indicating high, medium, or low recreation level and H = a habitat covariate indicating mesic or xeric canyon environments. Model coding: habitat: xeric = 1, mesic = 2; recreation: low = 1, medium = 2, high = 3. Models are ranked in terms of small-sample-size corrected version of Akaike's Information Criterion ( $AIC_c$ ). The relative difference in  $AIC_c$  values ( $\Delta AIC_c$ ),  $AIC_c$  model weight ( $w_i$ ), the number of parameters (k), and twice the negative log-likelihood value ( $-2\ln L$ ) are also given.

<b>Model</b>	<b><math>AIC_c</math></b>	<b><math>\Delta AIC_c</math></b>	<b><math>w_i</math></b>	<b>k</b>	<b><math>-2\ln L</math></b>
$\psi(H+R)$ , $\gamma(H+R)$ , $\varepsilon(H+R)$ , $p(\cdot)$	274.6	0	0.654	10	248.4
$\psi(H+R)$ , $\gamma(H+R)$ , $\varepsilon(H+R)$ , $p(R)$	277	2.4	0.193	11	247.5
$\psi(H+R)$ , $\gamma(H+R)$ , $\varepsilon(H+R)$ , $p(H)$	278	3.4	0.118	11	248.4
$\psi(H+R)$ , $\gamma(H+R)$ , $\varepsilon(H+R)$ , $p(H+R)$	280.4	5.9	0.034	12	247.3



Table 6. Result of model ranking of an *a priori* model list describing investigating spotted owl multi-year occupancy (2008 to 2010) including an analysis of recreation (R) and habitat (H), where:  $\psi$  = initial occupancy rate, 2008;  $\gamma$  = recolonization rate;  $\varepsilon$  = extinction rate; and  $p$  = detection probability. R = a recreation covariate indicating high, medium, or low recreation level and H = a habitat covariate indicating mesic or xeric canyon environments. Models were ranked using the small-sample-size corrected  $AIC_c$ . Values shown include:  $AIC_c$ ,  $\Delta AIC_c$ , model weight ( $w_i$ ), the number of parameters ( $k$ ), and twice the negative log-likelihood value ( $-2\ln L$ ).

Model	$AIC_c$	$\Delta AIC_c$	$w_i$	$k$	$-2\ln L$
$\psi(H), \gamma(H), \varepsilon(\cdot), p(\cdot)$	266	0	0.406	6	251.9
$\psi(H), \gamma(H), \varepsilon(H), p(\cdot)$	266.7	0.7	0.289	7	249.8
$\psi(H+R), \gamma(H), \varepsilon(R), p(\cdot)$	269.7	3.6	0.066	8	249.9
$\psi(H), \gamma(\cdot), \varepsilon(H), p(\cdot)$	270.1	4.0	0.054	6	256
$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	270.5	4.5	0.044	4	261.5
$\psi(H+R), \gamma(H+R), \varepsilon(\cdot), p(\cdot)$	271.1	5.1	0.031	8	251.4
$\psi(H+R), \gamma(H), \varepsilon(H+R), p(\cdot)$	271.4	5.4	0.027	9	248.6
$\psi(H+R), \gamma(H+R), \varepsilon(H), p(\cdot)$	272.2	6.1	0.019	9	249.3
$\psi(H+R), \gamma(H+R), \varepsilon(R), p(\cdot)$	272.6	6.6	0.015	9	249.7
$\psi(R), \gamma(\cdot), \varepsilon(R), p(\cdot)$	272.7	6.7	0.014	6	258.6
$\psi(H+R+H^*R), \gamma(H+R+H^*R), \varepsilon(\cdot), p(\cdot)$	274.1	8.1	0.007	10	248
$\psi(R), \gamma(R), \varepsilon(\cdot), p(\cdot)$	274.4	8.4	0.006	6	260.3
$\psi(H+R), \gamma(\cdot), \varepsilon(H+R), p(\cdot)$	274.5	8.5	0.006	8	254.7
$\psi(H+R), \gamma(H+R), \varepsilon(H+R), p(\cdot)$	274.6	8.5	0.006	10	248.4
$\psi(H+R), \gamma(R), \varepsilon(H), p(\cdot)$	275.3	9.3	0.004	8	255.5
$\psi(R), \gamma(R), \varepsilon(R), p(\cdot)$	275.5	9.5	0.004	7	258.6
$\psi(H+R), \gamma(R), \varepsilon(H+R), p(\cdot)$	277.6	11.6	0.001	9	254.7
$\psi(H+R+H^*R), \gamma(\cdot), \varepsilon(H+R+H^*R), p(\cdot)$	279.8	13.8	0.000	10	253.7
$\psi(H+R+H^*R), \gamma(H+R+H^*R), \varepsilon(H+R+H^*R), p(\cdot)$	281.9	15.9	0.000	13	244.9

Table 7. Estimated regression coefficients (and SE) from the three top-ranked models from Table 3.3., where:  $\psi$  = initial occupancy rate, 2008;  $\gamma$  = recolonization rate;  $\varepsilon$  = extinction rate; and  $p$  = detection probability. In addition, (recreation) = a recreation covariate indicating high, medium, or low recreation level and (habitat) = a habitat covariate indicating mesic or xeric canyon environments. Model coding: habitat: xeric = 1, mesic = 2; recreation: low = 1, medium = 2, high = 3.

Model	Intercept $\beta_0$ (SE)	Coefficient (SE)
$\psi(\text{habitat})$ , $\gamma(\text{habitat})$ , $\varepsilon(\cdot)$ , $p(\cdot)$		
$\psi(\text{habitat})$	-1.09 (1.091)	habitat ( $\beta_1$ ) = 1.10 (0.659)
$\gamma(\text{habitat})$	-4.45 (1.749)	habitat ( $\beta_1$ ) = 2.28 (0.992)
$\varepsilon(\cdot)$	-1.10 (0.335)	
$p(\cdot)$	2.11 (0.288)	
$\psi(\text{habitat})$ , $\gamma(\text{habitat})$ , $\varepsilon(\text{habitat})$ , $p(\cdot)$		
$\psi(\text{habitat})$	-1.08 (1.09)	habitat ( $\beta_1$ ) = 1.09 (0.663)
$\gamma(\text{habitat})$	-4.23 (1.633)	habitat ( $\beta_1$ ) = 2.17 (0.955)
$\varepsilon(\text{habitat})$	0.877 (1.336)	habitat ( $\beta_1$ ) = -1.118 (0.751)
$p(\cdot)$	2.12 (0.287)	
$\psi(\text{habitat} + \text{rec})$ , $\gamma(\text{habitat})$ , $\varepsilon(\text{rec})$ , $p(\cdot)$		
$\psi(\text{habitat} + \text{rec})$	-1.366 (1.189)	habitat ( $\beta_1$ ) = 0.986 (0.680) rec ( $\beta_2$ ) = 0.297 (0.471)
$\gamma(\text{habitat})$	-4.35 (1.70)	habitat ( $\beta_1$ ) = 2.24 (0.97)
$\varepsilon(\text{rec})$	-0.184 (0.775)	rec ( $\beta_1$ ) = -0.540 (0.438)
$p(\cdot)$	2.12 (0.286)	

Table 8. Exploratory models for the relationship between number of owl fledglings per pair and recreation, habitat, or year (2008-2010). Model ranks used a small-sample-size corrected Akaike's Information Criterion ( $AIC_c$ ). Model information includes:  $AIC_c$ ,  $\Delta AIC_c$ , model weight ( $w_i$ ), the number of parameters ( $k$ ), and twice the negative log-likelihood value ( $-2\ln L$ ).

<b>Model</b>	<b><math>AIC_c</math></b>	<b><math>\Delta AIC_c</math></b>	<b><math>w_i</math></b>	<b><math>k</math></b>	<b><math>-2\ln L</math></b>
~habitat+year	95.5	0.0	0.389	4	86.5
~habitat	96.6	1.1	0.223	2	92.3
~habitat+year+recreation	97.4	1.9	0.150	5	85.9
~habitat+recreation	98.6	3.2	0.079	3	92.1
~year	98.8	3.3	0.075	3	92.2
~year+recreation	99.6	4.1	0.050	4	90.6
NULL	101.2	5.8	0.022	1	99.1
~recreation	102.2	6.8	0.013	2	97.9

Table 9. Estimated regression coefficients and standard errors (SE) for the three top ranked regression models (see Table 3.5). Habitat and year were both modeled as categorical covariates. Recreation was modeled as a continuous covariate: low recreation = 0, medium recreation = 1, and high recreation = 2. Intercepts represent xeric, year 2008, and/or low recreation.

<b>Model</b>	<b>Coefficients</b>	<b>Estimate</b>	<b>SE</b>
~habitat+year	Intercept	-2.90	1.08
	Year 2009	1.19	0.56
	Year 2010	0.52	0.63
	Mesic Habitat	1.82	1.02
~habitat	Intercept	-2.30	1.00
	Mesic Habitat	1.94	1.02
~habitat+year+rec	Intercept	-2.98	1.08
	Year 2009	1.24	0.57
	Year 2010	0.55	0.63
	Mesic Habitat	1.72	1.03
	Recreation (0, 1, or 2)	0.18	0.23

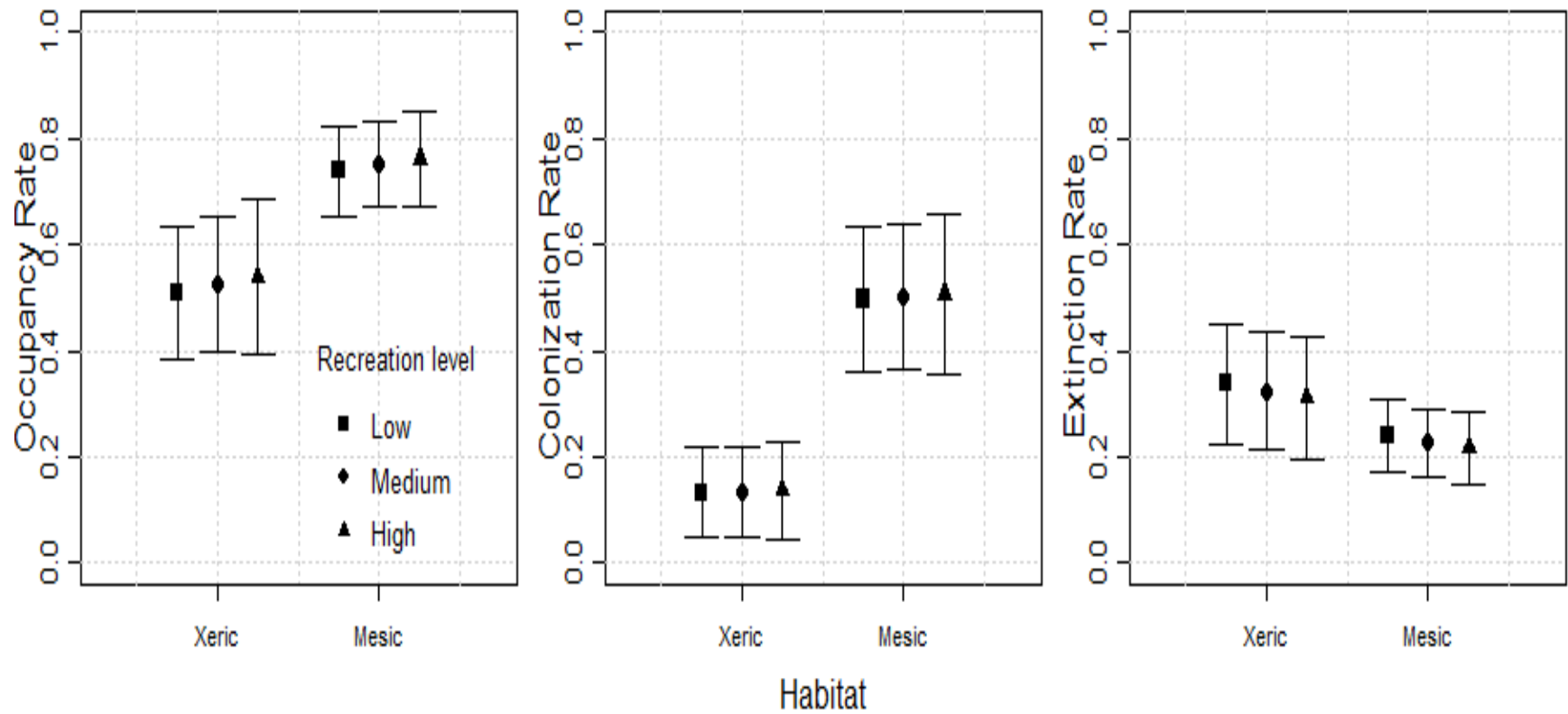


Figure 2. Model-averaged estimates of occupancy, colonization, and extinction rates for spotted owl territories in southern Utah, during the 2008, 2009, and 2010 field seasons. Occupancy Rate = initial occupancy rate, 2008. Error bars represent standard errors. Model average estimate of detection probability = 0.8915 (SE=0.0278).

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**APPENDIX B. CAPITOL REEF AND ZION NATIONAL PARKS OCCUPANCY AND REPRODUCTIVE DATA.**

Results of occupancy and reproductive visits to spotted owl territories within CARE and ZION in southern Utah, during the 2008, 2009, and 2010 field seasons. (R) represents recreation level. (H) represents habitat level. (-) indicates the site was not visited in the season, and (\*) indicates the sites was visited a total of one time in the season.

Study Areas	Site	R	H	2008		2009		2010	
				Detected		Detected		Detected	
				Adults	Fledglings	Adults	Fledglings	Adults	Fledglings
CARE	17	Low	Mesic	none	none	none	none	none	none
	18	Low	Xeric	none	none	none	none	none	none
	19	High	Xeric	none	none	none	none	none	none
	20	Medium	Xeric	male	none	none	none	none	none
	21	Low	Xeric	none	none	none	none	pair	1
	22	Low	Xeric	pair	none	none	none	none	none
	23	Low	Mesic	none	none	none	none	none	none
	24	Low	Xeric	pair	none	pair	none	male	none
	25	Low	Xeric	none	none	none	none	none	none
	26	Low	Xeric	pair	none	pair	none	none*	none*
ZION	27	Medium	Mesic	pair	none	pair	2	pair	none
	28	Low	Mesic	pair	none	none	none	female	none
	29	Medium	Mesic	pair	1	pair	2	none	none
	30	Medium	Mesic	male	none	none	none	none	none
	31	Low	Mesic	male	none	pair	none	pair	none
	32	Low	Mesic	none	none	pair	3	pair	none
	33	High	Mesic	male	none	male	none	male	none
	34	Medium	Mesic	male	none	female	none	-	-
	35	Low	Mesic	male	none	male	none	pair	none
	36	Low	Mesic	pair	1	pair	2	pair	2
	37	Low	Mesic	male	none	pair	none	pair	2
	38	Low	Mesic	male	none	none	none	male	none
	39	High	Mesic	pair	none	male	none	male	none
	40	Medium	Mesic	male	none	male	none	pair	none
	41	High	Mesic	pair	none	pair	2	pair	2
	42	Medium	Mesic	none	none	male	none	pair	none
	43	High	Mesic	male	none	male	none	male	none
44	High	Mesic	pair	none	pair	2	pair	none	
45	Low	Mesic	pair	none	pair	none	pair	none	
46	High	Mesic	pair	2	pair	none	pair	none	
47	Low	Mesic	pair	none	pair	none	male	none	