

ACTIVITY PATTERNS OF NESTING MEXICAN SPOTTED OWLS¹

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Abstract. We collected 2,665 hr of behavioral information using video surveillance on 19 Mexican Spotted Owl (*Strix occidentalis lucida*) pairs between 25 April and 26 July 1996. Prey deliveries per day increased as the nesting season progressed, with an average of 2.68 prey deliveries during incubation, 4.10 items during brooding, and 4.51 items during the nestling phase. The highest delivery rates were concentrated between 1–3 hours before sunrise (02:00–05:00) and 1–3 hours after sunset (18:00–21:00). Trip duration during diurnal hours increased 14 fold from incubation through the nestling phase, compared with a 7.2 fold increase during nocturnal hours. Nest bout duration decreased during both diurnal (36%) and nocturnal hours (76%) across the nesting season. Nest attentiveness decreased as the nesting season progressed, from 97% during the incubation phase to 47% during the nestling phase. Owls attended nests at higher rates during diurnal hours than nocturnal hours across all nesting phases. Activity patterns of Mexican Spotted Owls showed marked cyclical changes in response to ecological factors. Fluctuations in nesting behavior were related to changes in nesting phase and time of day.

Key words: activity patterns, Mexican Spotted Owl, nest attentiveness, nesting behavior, prey delivery rates, *Strix occidentalis lucida*, video surveillance.

INTRODUCTION

Quantification of life history characteristics is important in identifying the relationship between behavioral patterns and fitness, detecting and mitigating for anthropogenic impacts, and understanding an animal's energetic needs under certain ecological conditions. Many investigators have quantified changes in raptor behavior during diurnal nesting phases, but few studies have examined comparable behaviors for nocturnal raptors (Marti 1974, Bosakowski 1989), with no relevant data for Mexican Spotted Owls (*Strix occidentalis lucida*). Our objectives for this study were to examine diel and cyclical patterns in nesting behavior of Mexican Spotted Owls, and to relate changes during nesting phases to energetic costs of reproduction.

METHODS

STUDY AREA

We studied the activity patterns of Mexican Spotted Owls during the 1996 nesting season in the Sacramento Mountains of the Lincoln Na-

tional Forest, Otero County, in south-central New Mexico (Delaney et al. 1997). The Sacramento Mountains are part of the Basin and Range East Unit as designated by the Mexican Spotted Owl recovery team (Rinkevich et al. 1995a). White fir (*Abies concolor*) and Douglas fir (*Pseudotsuga menziesii*) dominate the area, with southwestern white pine (*Pinus strobiformis*) and ponderosa pine (*P. ponderosa*) making up a minor component (Alexander et al. 1984). Elevation ranges between 2,300–2,700 m.

VIDEO SURVEILLANCE

We used black and white, charge-coupled device (CCD), video cameras with night vision to monitor Mexican Spotted Owl nesting behavior (Delaney et al. 1998). We chose video surveillance because it: (1) did not require owls to be captured, (2) provided both nocturnal and diurnal recording capabilities, (3) facilitated real-time, behavioral analyses *a posteriori*, (4) could be operated remotely with minimal impact, and (5) provided observations at the nest, which are considered the least biased and most accurate way of assessing the diet of raptors (Bielefeldt et al. 1992, Mersmann et al. 1992). Cameras mounted in waterproof, heavy-gauge plastic, switch boxes (12.9 × 6.7 × 4.1 cm) were placed an average of 6.9 m (range 3.0–10.1 m) from

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nests in adjacent trees. Professional grade video recorders provided 24-hr continuous coverage per VHS tape. Cameras and video recorders were powered by 12-volt, rechargeable batteries that were replaced every 24–36 hr. All cameras and related equipment were removed after the 1996 nesting season.

SPOTTED OWL BEHAVIOR

We estimated the starting date for nest sites where we did not have adequate reproductive data by backdating from juvenile departure dates. We divided the nesting cycle into three stages: incubation (eggs present: day 0–32), brooding (small chicks attended by adult: day 33–47), and nestling (larger chicks typically unattended in nest: day 48–until fledgling). To determine temporal variation in spotted owl behavior across the nesting season, we measured the following parameters: (1) prey delivery rate—number of prey items delivered to a nest over the incubation, brooding, and nestling phases, (2) nest attentiveness—percentage of total time spent on the nest per diurnal, nocturnal (based on sunrise and sunset), or 24-hr period, (3) nest departures—number of trips from the nest by an attending adult (presumably the female), (4) trip duration—length of time spent away from the nest per departure, and (5) nest bout duration—length of time that an adult owl (presumably female) attended the nest between departures. Trip and nest bout duration are considered to be inversely related, that is, if an owl is away from the nest it is considered on a trip. Parameters were not separated by sex because owls were not distinguishable later in the season by the time spent at the nest, therefore these data represent combined behavioral information from owl pairs instead of from individual owls. These data were part of a larger study investigating the effects of aerial and ground-based disturbances on spotted owl reproductive success and productivity and were collected during non-manipulated days.

PELLET COLLECTION

Pellets were collected opportunistically at Mexican Spotted Owl nest sites during the 1996 nesting season to corroborate prey use data from video surveillance and direct behavioral observation. Protocols developed by S. DeRosier and J. P. Ward Jr. (unpubl. data) were used to identify and quantify prey remains from pellets. Prey

items were counted and identified from reconstructed skeletons or skulls, whichever provided the highest count (Forsman et al. 1984). We quantified all prey items by relative frequency, and determined the percent biomass for the five most common prey groups: woodrats (*Neotoma* sp.), white-footed mice (*Peromyscus* sp.), voles (*Microtus* sp.), pocket gophers (*Thomomys* sp.), and rabbits (*Sylvilagus* sp.). Relative frequency of prey is expressed as the number of items of a given species or group divided by the total number of items found. Prey biomass was calculated as a product of the total number of items by the average mass (g) for that species or group. Biomass estimates for prey groups were estimated based on body mass of mammals consumed by Mexican Spotted Owls occurring in the Sacramento Mountains (J. P. Ward Jr., unpubl. data). We assumed that the items found in each pellet was representative of the true proportion of each prey species within the owl's diet. Values were calculated from totals across all territories.

DATA ANALYSIS

We used SPSS 7.5 for Windows (SPSS Inc. 1997) to perform statistical analyses. Whenever appropriate, multiple observations at a single nest were averaged before inferential tests, so that the sample size was the number of nests examined. We used a two-factor analysis of variance to assess the significance of variability between nocturnal and diurnal owl responses (factor 1), and among temporal phases during the nesting season (factor 2). We used Dunnett's T3 multiple comparison procedure (Dunnett 1980) to interpret differences among temporal phases and to account for heterogeneous variance among phases when interactions between factors were absent. When interactions were present between factors, a separate *t*-test between nocturnal and diurnal responses was computed for each phase. To examine whether there was a treatment effect on spotted owl behavior during non-manipulated days due to noise testing, we used linear regression to correlate between stimulus distance and nesting behavior before and after disturbance events. Type I errors were maintained for the set of *t*-tests by applying a Bonferroni adjustment to the *t*-test significance levels (Zar 1984). An alpha level = 0.05 was adopted for all tests or set of multiple comparisons. Means \pm SE are presented in the text.

RESULTS

We collected 2,665 hr of behavioral information through video surveillance on 19 Mexican Spotted Owl pairs during the 1996 nesting season ($\bar{x} = 140.3 \pm 22.7$ hr nest⁻¹). A total of 1,021 hr of spotted owl behavior was recorded during diurnal periods, 60 hr during nocturnal periods, and 1,584 hr during 24-hr periods. Nest sites were typically videotaped twice per week from 25 April through 26 July. Nineteen territories provided diurnal information on spotted owl behavior, whereas only eight territories supplied nocturnal and 24-hr activity. Initiation dates for incubation of spotted owl nests began on approximately 28 March through 25 April, eggs hatched from approximately 20 April through 7 May, and young fledged from 24 May through 10 July. Seventeen of 19 spotted owl nests were reproductively successful, producing an average of 1.5 ± 0.2 young per occupied nest ($\bar{x} = 1.7 \pm 0.2$ young per successful nest). We did not observe any nest abandonment or failure due to camera placement; however, two sites failed for unrelated reasons. Noise disturbance testing did not appear to influence spotted owl behavior during subsequent non-manipulated days. We found no statistical relationship between stimulus distance and any of the behavioral parameters recorded during this study.

PREY DELIVERIES

Prey deliveries increased as the nesting season progressed, with an average of 2.68 prey deliveries 24-hr⁻¹ during incubation, 4.10 items during brooding, and 4.51 items during the nestling phase. More prey was delivered to nests during nocturnal than diurnal periods across the incubation, brooding, and nestling phases (Table 1). Owls delivered 0.37 prey items hr⁻¹ during nocturnal hours, and only 0.03 deliveries hr⁻¹ during diurnal hours across the nesting season. The highest prey delivery rates were during crepuscular hours, between 1–3 hr before sunrise (02:00–05:00) and 1–3 hr after sunset (18:00–21:00). Peaks in prey deliveries shifted from 03:00 and 19:00 during the incubation phase to 04:00 and 21:00 during the nestling phase. The number of prey deliveries appeared to increase with owl age and the number of owlets per nest, although the sample size was too small to determine statistical significance. Owl territories with one juvenile ($n = 3$) made an average of 4.09

± 0.61 prey deliveries 24-hr⁻¹ through nesting weeks 5–8, compared with 4.87 ± 0.38 for territories with two juveniles ($n = 3$), and 7.75 ± 1.39 for one territory with three juveniles. On 15 occasions during the 1996 nesting and post-nesting season, spotted owls were observed foraging during diurnal hours. All foraging attempts were made from trees where owls were initially found roosting and appeared to be opportunistic in nature, with only short foraging flights observed in each case. No foraging attempts were made from nests.

PELLET ANALYSIS

Between April and July 1996, we collected 308 prey items from 17 pairs of owls in the Sacramento Mountains. Mammals dominated the diet accounting for 89.3% of the total number of prey items compared with only 5.8% for insects and 4.9% for birds. The five most common mammalian prey items were deer mice (*Peromyscus boylii* and *P. maniculatus*; 34.7%), voles (*Microtus mexicanus* and *M. longicaudus*; 19.5%), woodrats (*Neotoma mexicana*; 17.5%), pocket gophers (*Thomomys bottae*; 8.8%), and rabbits (*Sylvilagus* sp.; 5.8%). Woodrats represented the highest percentage of prey biomass in the owl's diet (37.4%), followed by rabbits (20.3%), pocket gophers (16.8%), peromyscid mice (13.5%), and voles (12.0%). Video surveillance corroborated data from our pellet analysis suggesting that deer mice, voles, and woodrats were the most common prey species delivered to spotted owl nests in the Sacramento Mountains. We were unable to determine the relative body size or identity of all prey items delivered to the nest. In many cases we were only able to determine that the owl had prey. This limited our ability to estimate the relative frequency and biomass of prey being delivered to the nest.

NEST ATTENDANCE

Spotted owls attended nests for longer periods during both incubation and brooding than during the nestling phase, whereas there was no difference in attendance rates between incubation and brooding phases. The largest decrease in nest attendance occurred at the onset of the nestling phase. Owls attended nests at higher rates during diurnal hours than nocturnal hours across all nesting phases (Table 1).

TABLE 1. Variation in prey deliveries, attendance, nest departures, mean trip and nest bout durations by nesting phase and time of day for Mexican Spotted Owl territories in Sacramento Mountains, New Mexico, 1996. Data presented are means \pm SE (*n*).

Behavior	Incubation	Brooding	Nestling	Time of day effects ^a	Time of day/phase interactions ^b
Prey deliveries					
day	0.39 \pm 0.25 (9)	0.24 \pm 0.06 (15)	0.85 \pm 0.17 (16)	< 0.01	0.64
night	2.27 \pm 0.05 (8)	3.76 \pm 0.17 (8)	4.03 \pm 1.08 (8)		
combined	1.33 \pm 0.59 (8)	2.00 \pm 0.37 (8)	2.43 \pm 0.36 (8)		
Nest attendance (%)					
day	99.53 \pm 0.10 (15)	91.54 \pm 2.18 (8)	61.48 \pm 3.63 (8)	< 0.03	0.52
night	95.25 \pm 0.30 (15)	68.12 \pm 5.81 (8)	32.26 \pm 5.04 (8)		
combined	97.39 \pm 18.87 (15)	79.83 \pm 10.45 (8)	46.87 \pm 10.45 (8)		
Nest departures					
day	0.30 \pm 0.07 (15)	0.89 \pm 0.14 (15)	2.55 \pm 0.20 (15)	< 0.01	0.35
night	2.83 \pm 0.14 (8)	4.10 \pm 0.28 (8)	4.50 \pm 0.28 (8)		
combined	1.56 \pm 1.00 (8)	2.50 \pm 0.65 (8)	3.52 \pm 0.56 (8)		
Mean trip duration (hr) ^c					
day	0.12 \pm 0.02 (6)	0.79 \pm 0.30 (9)	1.68 \pm 0.19 (15)	> 0.05	0.65
night	0.20 \pm 0.02 (2)	0.57 \pm 0.18 (8)	1.44 \pm 0.21 (8)		
Nest bout duration (hr)					
day	5.95 \pm 0.46 (8)	5.95 \pm 0.75 (8)	3.82 \pm 0.50 (16)	< 0.02	0.01 ^d
night	3.01 \pm 0.38 (2)	1.54 \pm 0.68 (10)	0.71 \pm 0.47 (8)		

^a Significance level for comparison between day and night periods across all nesting phases.

^b Significance level of interaction in ANOVA by phase and time of day.

^c Mean trip durations were significantly different between incubation and nestling phases for both day and night periods.

^d Mean values differed between day and night for each nesting phase.

TRIP ACTIVITY

The onset and cessation of owl activity from the nest varied greatly across the nesting season. During the incubation phase, spotted owls left their nests an average of 7.8 ± 5.0 min after sunset ($n = 10$), and returned 31.4 ± 9.7 min before sunrise ($n = 8$). During the brooding phase, owls left their nests 26.8 ± 11.5 min before sunset ($n = 10$) and returned 26.6 ± 17.3 min after sunrise ($n = 10$). Similar onset and cessation rates were not available during the nestling phase because owls did not return to nests long enough for us to calculate these rates. Owls left nests less frequently during incubation than during the nestling phase. We observed more trips during nocturnal than diurnal hours across all nesting phases (Table 1).

Diurnal nesting bouts were longer than nocturnal bouts during each phase. Trip durations did not differ between night and day in any phase (Table 1). From incubation to the nestling phase, nest bout durations decreased 36% during diurnal periods (largest decrease occurring between brooding and nestling) and 76% during

nocturnal periods (largest decrease between incubation and brooding). Conversely, from incubation to the nestling phase, trip durations increased significantly during both diurnal (1,400%) and nocturnal hours (720%; Table 1).

During the incubation phase, trip durations were brief with little variation. All diurnal trips were < 15 min (range 0.0–22.8 min), with 83% of nocturnal trips < 15 min (0.6–75.0 min). In comparison, nesting bouts during incubation were longer and more variable (Table 1). Nesting bouts also were about 40 times longer than trip durations during diurnal hours ($F_{1,13} = 115.43$, $P < 0.001$) and about 15 times longer during nocturnal hours ($F_{1,13} = 54.59$, $P < 0.02$). Diurnal nesting bouts also were longer than trip durations during the brooding ($F_{1,16} = 38.73$, $P < 0.01$) and nestling phases ($F_{1,30} = 11.77$, $P < 0.01$), but not for nocturnal hours during the brooding ($F_{1,13} = 1.46$, $P > 0.05$) or the nestling phase ($F_{1,15} = 2.19$, $P > 0.05$). The increase in nest departures and trip durations corresponded with a decrease in nest attentiveness as the nesting season progressed (Table 1).

DISCUSSION

A bird's behavior during the nesting season is an important determinate of its ultimate reproductive success or failure (Hohman 1986). Food availability and abundance, nest attendance, trip duration, and other factors, are thought to strongly affect fledging rates. Mexican Spotted Owls showed marked cyclical changes in their activity rates that we attribute to increased pressure in providing for young.

PREY DELIVERIES

The increase in prey deliveries across the nesting season was due largely to an increase in nocturnal deliveries. Such a change may be explained by increased energy demands by the young for growth and thermoregulation, and also from greater female involvement in procuring prey. This has been documented in other raptor species. Nesting Prairie Falcons (*Falco mexicanus*) increased prey delivery rates with nesting phase (Holthuijzen 1990), and nesting Barred Owls (*S. varia*) increased foraging activity to obtain food for young (Fuller 1979, Tester 1987).

Diurnal foraging activity has been documented for Mexican Spotted Owls (this study), California Spotted Owls (*S. o. occidentalis*; Laymon 1991), Northern Spotted Owls (*S. o. caurina*; Forsman et al. 1984, Sovern et al. 1994), Barred Owls (Fuller 1979, Tester 1987), and Barn Owls (*Tyto alba*; Bunn 1972). We agree with Sovern et al. (1994) that most diurnal foraging by spotted owls is an opportunistic response to available prey in proximity to an owl's roost location (Forsman et al. 1984). Our observed diurnal prey delivery rate of 0.36 prey 12-hr⁻¹ (average diurnal period across nesting season) is similar to the 0.32 prey 12-hr⁻¹ for Northern Spotted Owls in Oregon (Sovern et al. 1994). Laymon (1991) suggested that nesting California Spotted Owls regularly foraged during the day because of increased pressure upon adults to provide for juveniles. The fact that 11 of the 15 diurnal foraging attempts we observed during the nestling phase and after juveniles had fledged is consistent with that hypothesis. Our results suggest that prey delivery activity increases with brood size, as has been reported by Holthuijzen (1990) for Prairie Falcons; this may explain the levels of diurnal foraging activity we observed. Brood size, foraging territory quality, and prey avail-

ability may explain most of the observed variability between and within individual spotted owls.

The 2-hr shift in dawn and dusk prey delivery peaks may reflect prey availability during those periods. Peromyscid mouse activity above ground is primarily nocturnal (Falls 1968), with adult activity peaking during early morning and evening hours (Seabloom et al. 1994). Similar activity patterns also have been found for woodrats (Justice 1960). Wiley (1971) found that woodrats were active approximately 30 min before complete darkness to 30 min before sunrise. Fifty-four percent of a woodrat's nocturnal movements were made between 20:30–22:30, with 75% of such movements occurring before midnight (Wiley 1971). Spotted owls may synchronize foraging activity according to prey activity patterns, as documented for Eurasian Kestrels (*F. tinnunculus*; Rijnsdorp et al. 1981) and Prairie Falcons (Holthuijzen 1990). The 1-hr delay in peak prey deliveries that we observed during evening hours also could have been due to changes in photoperiod over the course of the nesting period. Unfortunately, prey activity patterns are not known in sufficient detail to determine whether they can account for the cyclical shift in owl foraging activity. The observed variation may allow owls to adjust to local, seasonal, or annual fluctuations in prey abundance (Ward and Block 1995).

The high level of reproductive success and production we observed during this study may be due to prey abundance (Snyder and Snyder 1973, Newton 1979), as well as the type of prey utilized (Ganey 1992). Mexican Spotted Owls consume animals from five mammalian orders (*Insectivora*, *Chiroptera*, *Carnivora*, *Lagomorpha*, and *Rodentia*), five avian orders (*Galliformes*, *Strigiformes*, *Apodiformes*, *Piciformes*, and *Passeriformes*), one reptilian suborder (*Lacertilia*), and from a variety of insect genera (Ward and Block 1995). Mammals are taken more frequently than any other group, and gain even greater importance when biomass is considered. Ward and Block (1995) documented an increase in owl production when moderate to high levels of peromyscid mice, voles, and woodrats were consumed. The frequencies of these prey genera were nearly significant in predicting Mexican Spotted Owl reproductive success (Ward and Block 1995). We observed relatively high levels of these common prey groups within our pellet

collection (71.7%; Delaney et al., unpubl. data), which is consistent with values presented by Ward et al. for the Sacramento Mountains (68.5%; cited in Ward and Block 1995) and by Ganey (1992; 61–83%) over a range of Mexican Spotted Owl sites in Arizona.

NEST ATTENDANCE

The high level of nest attendance we observed for Mexican Spotted Owls during the incubation phase is similar to the 97% attendance rates of incubating Prairie Falcons (Holthuijzen 1990), and Broad-winged Hawks (*Buteo platypterus*; Matray 1974). Comparable attendance levels during brood rearing suggest that adult presence throughout the brooding phase is important to the survival of chicks. Similar observations were made for brooding Peregrine Falcons (*Falco peregrinus*; Enderson et al. 1973) and Prairie Falcons (Holthuijzen 1990). The decline in nest attendance in the nestling phase coincided with an increase in nest departures, trip durations, and prey deliveries (Delaney et al. 1997).

Female spotted owls left the nest infrequently and for short periods of time during the incubation phase, especially during the hottest portion of the day from 10:00–14:00. Such behavior may have evolved as a way of protecting eggs from solar radiation damage in areas of high elevation, as well as reducing the risk from predation, and may explain the high level of nest attentiveness we observed. Extreme heat may be more detrimental to embryo survival and development than cooling (Fyfe and Olendorff 1976). Trips off the nest may have been timed to avoid exposing eggs to periods of extreme daily temperatures, may have coincided with daily food availability, may have been based on limiting nest detection by predators, and/or may just be a function of prime resting time for spotted owls. The increase in trip frequency and duration as the nesting season progressed suggests that ambient temperatures have a diminishing effect, and that temperature becomes less important as juveniles gain the ability to thermoregulate.

Spotted owls tended to leave the nest earlier and arrive back later, relative to sunset and sunrise, respectively, as the nesting season progressed. Such changes could be due to increasing day length, which reduces the available time period for nocturnal activities, or due to changes in the level of parental care. Clark (1975) found similar patterns in nest departure activity for

Short-eared Owls (*Asio flammeus*). We agree with Fuller (1979) and Wijnandts (1984) that owl departure activity is closely related with time of sunset and sunrise, but only as it relates to the incubation and brooding phase. During the nestling phase, parental responsibilities increased, especially during diurnal periods, and activity patterns of spotted owls became more variable. This was illustrated in our inability to determine the onset and cessation of spotted owl activity at the nest during the nestling phase.

Great-horned Owls, Northern Goshawks (*Accipiter gentilis*), Red-tailed Hawks (*Buteo jamaicensis*), and Golden Eagles (*Aquila chrysaetos*) are considered potential predators of spotted owls (Rinkevich et al. 1995b). During this study we videotaped one attempted nest predation on an owlet by a juvenile Red-tailed Hawk. There are only two reports of apparent predation on Mexican Spotted Owls, one by a Great-horned Owl (Ganey 1988) and the other by a Golden Eagle (Rinkevich et al. 1995b). Due to the apparent infrequent nature of predation at spotted owl nests, we believe that owl nesting behavior is more strongly regulated by thermal effects.

These results provide baseline life history characteristics that are currently lacking for spotted owls. Such information needs to be determined before resource managers can adequately detect changes in spotted owl reproductive success, productivity, and nesting behavior due to anthropogenic disturbances. Nest attentiveness, trip frequency, nest departures, trip duration, and nest bout duration did not statistically differ between comparable manipulated and non-manipulated days, suggesting that experimental testing did not influence these variables. Prey delivery rate was the only variable correlated with disturbance distance. Delaney et al. (1999) suggest that human activities in close proximity to spotted owl territories may affect prey delivery rates and should be limited during peak periods of spotted owl foraging activity.

These data were collected during a good reproductive year; behavioral patterns may change under other circumstances. Replication in other locations and years are needed to determine the general applicability of these patterns. Finally, variation in prey availability and abundance among owl territories may influence prey delivery rates, nest attendance, trip duration, and nest bout duration. An understanding of food availability and abundance in each territory would

help clarify causes underlying the patterns observed during this study.

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