EFFECTS OF HELICOPTER NOISE ON MEXICAN SPOTTED OWLS

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Abstract: Military helicopter training over the Lincoln National Forest (LNF) in southcentral New Mexico has been severely limited to protect nesting Mexican spotted owls (Strix occidentalis lucida). To evaluate nesting and nonnesting spotted owl responses to helicopter noise, we measured flush frequency, flush distance, alert behavior, response duration, prey delivery rates, female trips from the nest, and nest attentiveness during manipulated and nonmanipulated periods, 1995–96. Chain saws were included in our manipulations to increase experimental options and to facilitate comparative results. We analyzed stimulus events by measuring noise levels as unweighted one-third-octave band levels, applying frequency weighting to the resultant spectra, and calculating the sound exposure level for total sound energy (SEL) and the 0.5-sec equivalent maximum energy level (LEQmax 0.5-sec) for helicopters, and the 10-sec equivalent average energy level (LEQavg 10-sec) for chain saws. An owl-weighting (dBO) curve was estimated to emphasize the middle frequency range where strigiform owls have the highest hearing sensitivity. Manipulated and nonmanipulated nest sites did not differ in reproductive success (P = 0.59) or the number of young fledged (P = 0.12). As stimulus distance decreased, spotted owl flush frequency increased, regardless of stimulus type or season. We recorded no spotted owl flushes when noise stimuli were >105 m away. Spotted owls returned to predisturbance behavior within 10–15 min after a stimulus event. All adult flushes during the nesting season occurred after juveniles had left the nest. Spotted owl flush rates in response to helicopters did not differ between nonnesting (13.3%) and nesting seasons (13.6%; P = 0.34). Spotted owls did not flush when the SEL noise level for helicopters was ≤102 dB (92 dBA) and the LEQ level for chain saws was ≤59 dB (46 dBA). Chain saws were more disturbing to spotted owls than helicopter flights at comparable distances. Our data indicate a 105-m buffer zone for helicopter overflights on the LNF would minimize spotted owl flush response and any potential effects on nesting activity.

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Key words: chain saws, disturbance, flush response, helicopters, Mexican spotted owls, noise, response thresholds, sound measurements, Strix occidentalis lucida.

To maintain tactical proficiency for low-level search-and-rescue missions, military air crews require frequent training. Recently, low-level training flights have come under scrutiny for their potential effects on wildlife, which has led to reductions in military access to potential training areas (Holland 1991). Holloman Air Force Base (HAFB), located in southcentral New Mexico, lacks sufficient area and habitat diversity to conduct effective helicopter training operations, but the Sacramento Ranger District of the LNF in the Sacramento Mountains contains the habitat diversity necessary to conduct such training operations. However, to avoid potential effects on nesting Mexican spotted owls (hereafter, spotted owl), military helicopters have been precluded from flying over the LNF during the February–August nesting season. To gain year-long access to the forest for training of the 48th Rescue Squadron (48 RQS), HAFB had to determine if and to what extent their activities might affect nesting spotted owls.

Much of the information about noise effects on raptors is anecdotal and fails to quantitatively measure either the stimulus or a behavioral response related to the animal's fitness. Predictive models for the relation between disturbance dosage and quantifiable effects are even more scarce (Awbrey and Bowles 1990, Grubb and Bowerman 1997). Although many types of human disturbance can affect birds of prey (Fyte and Olendorff 1976), very little research has addressed the effects of human activity on owls (Wesemann and Rowe 1987; J. C. Bednarz and

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The objectives of this study were (1) record, characterize, and quantify helicopter overflights at spotted owl roost sites during a post- or nonnesting season (1995) and at active nest sites during the nesting season (1996); (2) develop a dose-response threshold relation for quantifying spotted owl behavioral responses to variation in noise levels and stimulus distances; (3) determine if helicopter overflights affect spotted owl reproductive success (successful nests) or productivity (young fledged); and (4) develop disturbance-specific management guidelines to minimize potential effects from helicopter overflights on the LNF.

STUDY AREA

This study was located within the Sacramen- to Ranger District of the LNF in southcentral New Mexico, Otero County. This area was chosen for its large population of spotted owls and its importance as a potential training site for the 48 RQS. Vegetation is primarily Rocky Mountain conifer forest (Brown and Lowe 1980) dominated by Douglas-fir (Pseudotsuga menziesii) with some southwestern white pine (Pinus strobiiformes) and ponderosa pine (P. ponderosa; Alexander et al. 1984). Elevation in the mountainous terrain ranges between 1,372 and 2,957 m.

METHODS

Surveys and Territory Selection

Territories were surveyed between 15 June and 6 July 1995 and between 15 March and 15 April 1996. We selected territories for our study based on (1) presence of mated pairs of spotted owls, and (2) no captures or manipulations prior to our research. During the 1996 nesting season, a third criterion required pairs to be reproductively active. Seven female and 6 male spotted owls were tested in the nonnesting season. During the nesting season, we concentrated on testing females because of their nest fidelity. Sample sizes in both the nonnesting and nesting seasons were limited by the number of pairs that fit the foregoing criterion.

Vocal imitations of spotted owl calls (Forsman 1983) were used during nocturnal and diurnal point surveys to locate both nonnesting and nesting spotted owls. During nocturnal surveys, we determined initial spotted owl locations between dusk and 2200 (all times reported as Mountain Standard Time). Spotted owl positions were triangulated by plotting compass bearings on topographic maps so that each area could be visited for diurnal surveys (predawn to 0800), when we followed spotted owls to a daytime roost. During the 1995 nonnesting season, we then radioed the location to the 48 RQS for an overflight later that day or conducted a chainsaw manipulation. Upon finding a spotted owl during the 1996 nesting season, we attempted to determine its reproductive status by feeding it live mice. Nesting spotted owls take prey back to the nest, while nonreproductive spotted owls either cache or eat the prey (Forsman 1983). Once a territory was determined to be reproductively active, the nest location was recorded for future testing. To minimize interactions with spotted owls, we used the least number of mice necessary to determine reproductive activity.

Spotted Owl Behavior and Response Measures

We documented spotted owl behavior during manipulated and nonmanipulated periods by direct observation (camouflaged blinds 25–30 m from nest or roost) and through video surveillance. To evaluate spotted owl response behavior to helicopter and chainsaw manipulations and contrast it with pre- and postmanipulated behavior, we measured the following: (1) flush frequency = proportion of manipulations that elicited a flight response; (2) flush distance = distance (m) flown by a spotted owl in response to a sound stimulus; (3) alert behavior = number of head movements averaged per 5-min block, before, during and after manipulations; (4) time to alert = minutes between start of a manipulation and when a spotted owl initially responded with a head movement in the direction of the manipulation; (5) response duration = minutes following a noise stimulus until a disturbed spotted owl returned to prestimulus behavior; (6) prey deliveries = number of prey deliveries recorded at each nest site (calculated per hour for diurnal, nocturnal, and 24-hr periods); (7) trips = number of times the attending female left the nest (calculated per hour for diurnal, nocturnal, and 24-hr periods); and (8)
nest attentiveness = proportion of time the adult female spotted owl spent on the nest through the nesting season (calculated for diurnal, nocturnal, and 24-hr periods, as well as for nesting phases; see Delaney et al. 1999).

**Video Surveillance**

Because our use of video was a new and unique application of the various hardware components, we had to design, construct, test, and modify our video surveillance system before applying it in the field (Delaney et al. 1998). We used Marshall black-and-white, miniature video cameras (Marshall Electronics, Culver City, California, USA) with night vision to monitor spotted owl behavior. (Use of trade names does not imply endorsement by the U.S. Forest Service Rocky Mountain Research Station, U.S. Air Force, U.S. Army Construction Engineering Research Laboratories, or Northern Arizona University to the exclusion of other potentially suitable products.) In addition to the 6 infrared light-emitting diodes (LEDs) on the camera board, 9-LED supplemental light sources were constructed to approximately double night-vision capabilities. Panasonic industrial-grade video recorders provided up to 24-hr coverage/VHS tape (Panasonic Corporation of America, Secaucus, New Jersey, USA). Between 9 April and 27 May 1996, cameras were placed at 20 nest sites in adjacent trees, averaging 6.9 m from nests (range = 3.0–10.3 m). A 15-m, power-line-and-coaxial-cable down line and a 60-m trunk line were used to minimize potential disturbance to spotted owls by offsetting the recorder and batteries to an out-of-sight tarpaulin blind. Between 25 April and 3 July 1996, video surveillance systems at 19 successful nests yielded >2,655 hr of spotted owl behavior coverage. All cameras and related equipment were removed after the 1996 nesting season.

**Sound Measurements**

**Instrumentation and Recording.**—Sony TCD-D7, digital audio tape (DAT) recorders continuously recorded all noise events, along with exact time and date (Sony Corporation of America, New York, New York, USA). We attached a Bruel & Kjaer (B&K) Type 4149, 1.3-cm condenser microphone (Bruel & Kjaer, Naerum, Denmark) with a 7.5-cm wind screen to a B&K Model 2639 preamplifier, mounted the microphone on a 1-m stick, and placed the unit directly under a spotted owl location (roost or nest) about 1 m from the tree trunk. Using 3 10-m connecting cables attached to the preamplifier, we located the B&K Model 2804 power supply and DAT recorder at our observation point in a camouflaged blind 25–30 m from the spotted owls. A 1.0-kHz, 94-dB calibration signal from a B&K Type 4250 sound level calibrating system was recorded before and after each recorded manipulation. This signal provided an absolute, standardized reference point for sound levels and spectra when data were later reduced via a B&K Type 2144 frequency analyzer. All noise data were analyzed at the U.S. Army Construction Engineering Research Laboratories, Champaign, Illinois, USA.

**Sound Metrics.**—We used 3 sound metrics in this study: (1) SEL = the sound exposure level, which represents total sound energy for helicopters; (2) $LEQ_{avg, 0.5-sec} = \text{the 0.5-sec equivalent average peak energy level for helicopters}$; and (3) $LEQ_{avg, 10-sec} = \text{the 10-sec equivalent average energy level for chain saws}$. Noise is defined as sound that is undesired or that constitutes an unwarranted disturbance; it can alter animal behavior or normal functioning. We analyzed noise events as unweighted one-third-octave band levels, applied frequency weighting to the resultant spectra, and calculated the above metrics. Chain saw noise was relatively steady and most appropriately described by the average sound level, LEQ, over a specified time interval (10-sec). Helicopter noise was more varied and could not be described as well by the average noise level. Aircraft noise events are typically described in terms of SEL, which correlates well with human annoyance to aircraft noise. However, SEL levels cannot be meaningfully compared to LEQ levels; therefore, we also represented helicopters with LEQ for comparison with chain saws.

Frequency weighting is an algorithm of frequency-dependent attenuation that simulates the hearing sensitivity of the study subjects. Frequency weighting discriminates against sound which, while easily measured, is not heard by the subjects. Flat-weighting (or absence of any weighting function) does not emphasize any portion of the frequency spectrum and therefore represents the true sound level and frequency for a noise stimulus event (Fig. 1). The commonly used A-frequency weighting attenuates noise energy according to human hearing range and sensitivity and generally will not be appropriate for animal species. However,
**A. Helicopter**

![Graph showing Band LEQ (dB) for different noise levels.

- **Owl-weighted**
- **A-Weighted**
- **Unweighted**

**B. Chain Saw**

![Graph showing Band LEQ (dB) for different noise levels.

- **Owl-weighted**
- **A-Weighted**
- **Unweighted**

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1/3 OCTAVE SPECTRUM CENTER FREQUENCIES (Hz)

Fig. 1. (A) A comparison of owl-, A-, and unweighted equivalent maximum (helicopter) and average (chain saw) noise energy levels (LEQs) for a 60-m helicopter manipulation on 5 June 1996, and (B) a 60-m chain saw manipulation on 11 June 1996 at the same Mexican spotted owl territory in the Sacramento Mountains, New Mexico.
it is useful to present A-weighted noise levels (dBA), as well as more appropriately weighted levels, because this weighting algorithm occurs on sound-level meters and is ubiquitously used.

Because both flat- and A-weighting do not accurately reflect the way a spotted owl hears noise, we developed an estimated owl-weighting (dBO) curve. An audiogram describes hearing range and sensitivity and provides information on which a frequency weighting algorithm can be based for a specific species. Available information indicates hearing is quite similar among members of a taxonomic order. Within the order Strigiformes, we found audiograms for 2 species (great horned owl [Bubo virginianus], barn owl [Tyto alba]) within the same Suborder (Strigi) as spotted owls. These audiograms were used to approximate frequency-weighted noise levels for spotted owls. This owl-weighting emphasized the middle frequency range where test spotted owls had the highest hearing sensitivity (Trainer 1946, Konishi 1973).

**Field Manipulations**

We conducted a pilot test in January 1995 on HAFB and at an inactive nest site on the LNF to determine experimental flight profiles and microphone placement. Helicopter manipulations occurred between 1 and 22 August 1995 and between 30 April and 25 July 1996. Chain saw manipulations were conducted between 9 July and 23 September 1995 and between 11 June and 26 July 1996. We manipulated 28 spotted owl territories (13 in 1995 and 22 in 1996, with 7 sites manipulated in both years). Twenty-five of these sites received both helicopter and chain saw manipulations, while the remaining 3 sites received only 1 chain saw or helicopter manipulation (Table 1). We tried to minimize the overall number of manipulations and to maximize the time between manipulations, while still striving to conduct as complete an array of manipulations as possible during the incubation, nestling, and fledgling phases of the nesting season. However, because of administrative and logistical delays, as well as to remain conservative in our approach, only 3 chain saw tests and 8 helicopter flights were conducted during incubation. The average interval between consecutive manipulations, regardless of type or season, was 12.8 days (range = 4–79).

During the 1995 field season, spotted owls were manipulated after the normal nesting cycle so that any behavioral responses could not have an adverse effect on nesting success or productivity. Only after spotted owls showed minimal responses during nonnesting did we focus manipulations on nesting spotted owls. Helicopter manipulations were comparable between seasons but, as explained below, a threshold validation approach was taken with chain saws during the 1996 nesting season to limit potential experimental effects. Therefore, we could only compare helicopter and chain saw results for the nonnesting season. This research was conducted under a U.S. Forest Service subpermit to the U.S. Fish and Wildlife Service Region 2 Endangered Species and Special Purpose-Master-Migratory Bird Permits.

**Helicopters.—** Helicopter tests were conducted with the actual aircraft used by the 48 RQS (Sikorsky, HH-60G, Pave Hawk, twin-jet helicopters). The blade design of the HH-60G greatly reduces blade-slap (‘whopping’ sound) of an approaching helicopter. Spotted owl territories were randomly presented with 1 of 3 controlled helicopter flight profiles on any 1 day: (1) 15-m vertical, (2) 30-m vertical–30-m lateral, and (3) 60-m vertical. All flights were above tree canopy. The 15-m flight represented a minimum altitude that 48 RQS pilots would rarely fly during training missions. The 60-m profile represented the maximum diurnal altitude and a minimum nocturnal flight altitude. The 30-m vertical–30-m lateral profile approximated a more typical daytime overflight. At each site, we tried to conduct all 3 diurnal profiles during both the nonnesting and nesting.

<table>
<thead>
<tr>
<th>Season</th>
<th>Helicopter</th>
<th>Chain saws</th>
<th>Season totals</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Manipulations</td>
<td>Sites</td>
<td>Manipulations</td>
</tr>
<tr>
<td>Nesting (1996)</td>
<td>57</td>
<td>22</td>
<td>55</td>
</tr>
<tr>
<td>Totals</td>
<td>81</td>
<td>26</td>
<td>80</td>
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</table>
seasons, plus at least 1 nocturnal profile during the nesting season.

Terrain, tree heights, and variation among pilots caused deviations from the intended profiles. To account for these variations and to facilitate a comparison with chain saw results, we calculated straight-line distances from spotted owl to helicopter for all aircraft manipulations. We used field observations of aircraft from 2 to 3 positions of varying elevation and lateral offset, measured tree and spotted owl heights, topographic features, pilot information (Global Positioning System [GPS] flight path data, aircraft altitude, crew observations), and triangulation for these calculations, which we estimated to be ± 10% accurate. In addition to calculating closest distance, we also calculated spotted owl-to-aircraft distance during the approach, using flight speed data to determine the distance at which spotted owls first responded to approaching helicopters. We conducted only 1 pass/flight over any roost or nest site per day, with the entire manipulation lasting <10 min in total audible duration and <30 sec in the immediate vicinity of the spotted owls. Helicopter speed was 150–170 km/hr (80–90 knots).

To define the specific flight line, we positioned 2 1-m-diameter red, helium-filled weather balloons above the canopy approximately 50 m on either side of a spotted owl’s position. To position nocturnal flights, we used flashlights (4 D-cell Mag Lites; Mag Instruments, Ontario, California, USA) pointed skyward in conjunction with the pilots’ night-vision capabilities. Diurnal flights usually occurred between 1200 and 1300 and nocturnal flights between 2000 and 2200. The 48 RQS developed a pilot’s in-flight guide which detailed all spotted owl territories and access routes so pilots could circumvent nontarget and control sites en route to manipulated sites.

**Chain Saws.**—Stihl Model 025, 44-cc chain saws were used for noise testing (Stihl, Virginia Beach, Virginia, USA). To satisfy LNF fire and safety restrictions, bars and chains were removed and there was no actual cutting during manipulation testing. However, the noise levels and frequency spectra were similar for chain saws tested with and without bars and chains. We used forest vegetation to hide the operator and eliminate visibility as an influencing factor as we ran chain saws continuously for 5 min, alternately revving for 10 sec and idling for 10 sec. In 1995, nonnesting spotted owls were exposed to chain saw noise from 1 of 5 randomly selected initial distances (30, 45, 60, 75, and 90 m). If spotted owls flushed during the initial presentation, the test was ended for that day and the next scheduled manipulation was initiated 15–30 m farther away to establish a distance-response threshold. If the initial manipulation did not cause a flush, the next manipulation about 5–7 days later was presented 15 m closer. Because 60 m was the greatest distance at which chain saws elicited a flush response in 1995, only distances ≥60 m were examined in 1996 (60, 105, 250, and 400 m). This approach minimized potential effects on nesting spotted owls.

**Habituation**

We used experimental testing and treating sites as their own controls to evaluate possible habituation to repeated noise stimuli. At the end of the 1996 nesting season, we exposed 4 previously unmanipulated sites and 4 manipulated sites to 1 helicopter and 1 chain saw manipulation each, and we compared spotted owl flush response. Helicopter flights followed the most aggressive 15-m profile, while chain saw tests were run at 60 m to remain consistent with our conservative approach to nesting season manipulations. In addition, manipulated sites were used as their own self-controls throughout the study. We measured temporal changes in spotted owl response toward disturbance based on seasonal (response duration and time-to-alert) as well as proximate scales (alert responses pre-, during, and postmanipulation).

**Data Analyses**

Numbers of manipulated sites and sample sizes for individual analyses varied due to different inclusion criteria, missing data, 7 sites being manipulated in both years, and not all sites receiving both helicopter and chain saw manipulations. We used SPSS 7.5 for Windows (SPSS 1997) to perform descriptive statistics, independent-samples t-test for comparing mean values of young fledged and variation in sound levels, Tukey’s HSD test in the 1-way analysis of variance for comparing distances for alert, react, and flush responses, and linear regression for exploring the relation between noise levels and distance by type and between net differences in prey deliveries before and after manipulations. We used net differences in prey deliveries because of repeated-measures limitations. We cal-
culated a potential threshold distance for zero-difference with a 95% calibration interval (Graybill 1976). We used a 1-tailed Fisher's exact test to assess $2 \times 2$ contingency tables for flush response variability with manipulation type, stimulus distance, nesting season and phase, and for reproductive success between experimental and control sites (Zar 1984). To evaluate mean alert response (i.e., head movements) for 5-min intervals pre-, during, and postmanipulation, we used a nonparametric, Multi-Response Permutation Test for matched pairs (PTMP; Mielke and Berry 1982; Slauson et al. 1991. User manual for BLOSSOM statistical software, unpublished. National Ecological Research Center, U.S. Fish and Wildlife Service, Fort Collins, Colorado, USA). We used power analyses (Steidl et al. 1997) on reproductive success and productivity for comparisons between experimental and control sites. All means are reported ± SD. We considered alpha levels of $P < 0.05$ significant.

RESULTS

Manipulation Summary

We presented 161 helicopter and chain saw manipulations during the 1995 nonnesting and the 1996 nesting seasons (Table 1). The fledgling phase received 30 helicopter and 43 chain saw manipulations. The nestling phase received 19 helicopter and 9 chain saw manipulations, and the incubation phase received 8 helicopter and 3 chain saw manipulations. We were not able to compare spotted owl response levels between diurnal and nocturnal periods because, due to scheduling and logistical difficulties, there were only 5 nocturnal helicopter flights over spotted owl nests during the nesting season. Because we analyzed only first exposures (when $>1$ occurred) for each categorical manipulation distance at each site for flush response, our effective sample size by distance was reduced to 126: 58 helicopters ($4 \leq 30$ m, 13 at 30–45 m, 15 at 46–60 m, 20 at 61–105 m, 6 at $>105$ m) and 68 chain saws (6 at 30 m, 3 at 45 m, 23 at 60 m, 3 at 75 m, 2 at 90 m, 16 at 105 m, 13 at 250 m, 2 at 400 m). The 8 helicopter and 8 chain saw postexperiment habituation manipulations were in addition to this sample of 126.

Reproductive Success

 Manipulated and nonmanipulated nest sites did not differ in reproductive success (Fisher's exact test: $P = 0.59$) or the number of young fledged ($t_{20} = 0.95$, $P = 0.12$). We conducted power analyses based on data from 17 experimental and 5 control sites. Power levels were 0.22 for detecting a 10% difference in reproductive success between nests and 0.11 for productivity. Power increased to 0.29 and 0.16 for detecting a 15% difference, and 0.36 and 0.21 for a 20% difference. Fifteen of 17 manipulated spotted owl nest sites produced 1.4 young/occupied nest (1.6 young/successful nest), while all 5 nonmanipulated sites were successful in producing 1.8 young/occupied nest and 1.8 young/successful nest. Neither of the failed pairs flushed nor exhibited any unusual response to manipulations during the nesting season. One pair lost their chick to predation 9 days after the last manipulation, while apparently infertile eggs at the other site never hatched, despite normal incubation.

Flush Response and Associated Thresholds

Distance Thresholds.—As stimulus distance decreased, spotted owl flush frequency increased (Fig. 2), regardless of stimulus type (Tables 2, 3) or season (nesting, nonnesting). We recorded no spotted owl flushes when the noise stimulus was $>105$ m distant. Only 2 flushes occurred at $>60$ m stimulus distance (1 helicopter at 89 m, 1 chain saw at 105 m). Chain saws consistently elicited higher response rates than helicopters at similar distances (Fig. 2). At $\leq 60$ m stimulus distance during the nonnesting season, response to chain saws (72%) was greater than response to helicopters (20%; Fisher's
exact test: P < 0.01). In 11 instances at 6 territories (46% of the 24 helicopter flights during nonnesting), spotted owls did not flush in response to helicopter noise that averaged 21 dBA louder than chain saw manipulations that did cause a flush at the same territory (Fig. 3). All flushes recorded during the nesting season occurred after fledging; no flushes were elicited by manipulations during the incubation and nesting phases. Overall, helicopters elicited 0% spotted owl response when beyond 105 m, 14% within 105 m, 19% within 60 m, and 50% within 30 m.

Spotted owl flush rates did not differ between nesting (13.6%) and nonnesting (13.3%) seasons for helicopter manipulations at ≤105 m (Fisher’s exact test: P = 0.34; Table 2). Flush rates were lower during the incubation and nesting phases (0%) than during the fledging phase (28%; Fisher’s exact test: P = 0.04). Adults also roosted farther from juveniles as the number of days postfledging increased (1–20 days: \( \bar{x} = 9.7 \) m, \( n = 10 \); 21–40 days: \( \bar{x} = 18.2 \) m, \( n = 15 \); 41–60 days: \( \bar{x} = 29.3 \) m, \( n = 11 \)). After 20 days, adult flush distance was typically less than adult-to-juvenile distance (21–40 days: \( \bar{x} = 10.8 \) m, \( n = 2 \); 41–60 days: \( \bar{x} = 13.7 \) m, \( n = 3 \)). An adult spotted owl flew closer to a juvenile during only 1 of these latter 5 manipulations, however, regardless of adult flush distances, new diurnal roosts averaged only 6.5 m farther from juveniles.

Table 3. Chain saw manipulations eliciting a Mexican spotted owl flush response during the 1995 nonnesting and 1996 nesting seasons in the Sacramento Mountains, New Mexico.

<table>
<thead>
<tr>
<th>Season</th>
<th>Stimulus distance (m)</th>
<th>Number of presentations</th>
<th>Number of flushes</th>
<th>Flush frequency (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nonnesting (1995)</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>30</td>
<td>6</td>
<td>5</td>
<td>83.3</td>
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<tr>
<td>45</td>
<td>3</td>
<td>2</td>
<td>66.7</td>
<td></td>
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<td>60</td>
<td>9</td>
<td>6</td>
<td>66.7</td>
<td></td>
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<td>75</td>
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<td>90</td>
<td>2</td>
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<td>105</td>
<td>23</td>
<td>13</td>
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<td>≤105</td>
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<td>1995 season totals</td>
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<tr>
<td>Nesting (1996)</td>
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<tr>
<td>60</td>
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<td>16</td>
<td>1</td>
<td>6.3</td>
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<tr>
<td>400</td>
<td>2</td>
<td>0</td>
<td>0.0</td>
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</tr>
<tr>
<td>1996 season totals</td>
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<tr>
<td>Chain saw totals</td>
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<tr>
<td>45</td>
<td>45</td>
<td>15</td>
<td>22.1</td>
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</table>

*To minimize additional potential disturbance at nest sites, only chain saw distances ≥60 m were tested in 1996; therefore, season totals are not comparable.*
Noise Thresholds.—During the nonnesting season, spotted owls did not flush when the SEL noise level for helicopters was $\leq 104$ dBO (92 dBA) and the LEQ level for chain saws was $\leq 65$ dBO (51 dBA). During the nesting season, spotted owls did not flush when the SEL sound level for helicopters was $\leq 102$ dBO (92 dBA) and the LEQ level for chain saws was $\leq 59$ dBO (46 dBA). These dBO levels represent the noise level thresholds below which there were no spotted owl flush responses for the stimulus type and season indicated. Noise levels recorded near nest sites before and after disturbance trials were usually 25–35 dB (reaching upwards of 40 dB on windy days). Helicopters typically became audible at approximately 2,000 m.

Owl-, A-, and flat-weighting curves differed for 2 equidistant helicopter and chain saw trials at the same site (Figs. 1A,B). Within the mid-frequency range, helicopters were louder than chain saws; yet, more of the total chain saw noise energy was in the midfrequency range where estimated spotted owl sensitivity was greatest. Helicopter energy level peaked at the lower end of the spectrum below the estimated spotted owl hearing sensitivity range. This difference partially explains the higher response rates for chain saws at lower noise levels than for helicopters (Fig. 4).

Alert Response

Spotted owls exhibited alert responses (i.e., head movements) when helicopters were an average of 403 ± 148 m away ($n = 34$; Fig. 5) but showed no response when helicopters were >660 m distant. Distances between helicopter and spotted owl for react responses (i.e., wing and body movements; $\bar{x} = 124 \pm 59$ m, $n = 2$) and flush responses (i.e., flight; $\bar{x} = 45 \pm 28$ m, $n = 7$) were shorter than for alert responses (Tukey's HSD: $P < 0.01$). The stimulus distances for react and flush responses did not differ (Tukey's HSD: $P = 0.75$), but sample sizes were very limited. However, the indicated trend was for severity of response type to increase as stimulus distance decreased.

We compared average head-movements/5 min for the 30–60 min prior to a manipulation (i.e., the mean of all 5-min, premanipulation means), the 5-min interval of the manipulation, and the 30–60 min following the manipulation. Spotted owls responded to noise stimuli with more alert movements ($\bar{x} = 7.4 \pm 5.6$, $n = 91$)
than during premanipulation intervals (\( \bar{x} = 1.6 \pm 1.5, n = 84; \) PTMP: \( P < 0.01 \); Fig. 6). Spotted owls typically returned to premanipulation behavior in the third 5-min interval (between 10–15 min) after a stimulus event. Only the first (3.1 ± 3.7, \( n = 57; \) PTMP: \( P = 0.01 \)) and second 5-min intervals (2.6 ± 3.0, \( n = 51; \) PTMP: \( P = 0.08 \)) following a manipulation had greater frequencies of head movements than premanipulation levels.

**Habituation**

**Experimental Testing.**—Three of 4 previously unmanipulated spotted owls flushed in response to helicopter flights, while none of the 4 previously manipulated spotted owls flew (Table 4; Fisher’s exact test: \( P = 0.07 \)). During chain saw testing, 2 of the 4 unmanipulated spotted owls flushed, while no manipulated spotted owls flew (\( P = 0.21 \)). Spotted owls may have habituated to the manipulations during successive exposures, and more so to helicopters than to chain saws. However, sample sizes were too small to establish significance for indicated trends.

**Seasonal Change in Response Duration.**—Response duration was consistently longer for chain saws than helicopters, was inversely related to stimulus distance, and generally decreased as the nesting season progressed. Mean response duration following helicopter flights dropped from 10.3 ± 9.4 min (\( n = 14 \)) in July to 8.2 ± 5.5 min (\( n = 12 \)) in August. Mean response durations following chain saw manipulations were 22.2 ± 22.3 min (\( n = 19 \)) in July and 10.7 ± 8.6 min (\( n = 5 \)) in August. Response durations following chain saw manipulations were 1.3–2.2 times longer than following helicopter flights.

Response duration averaged 16.6 ± 16.8 min (\( n = 47 \)) when stimuli were ≤60 m away, and 7.0 ± 7.9 min (\( n = 25 \)) when stimuli were >60 m away. Spotted owls required 11.6 ± 10.5 min (\( n = 24 \)) to return to prior resting condition after helicopter flights of ≤60 m, compared to only 6.0 ± 8.8 min (\( n = 11 \)) when flights were >60 m away. Response durations for chain saws were 21.1 ± 20.9 min (\( n = 23 \)) at ≤60 m and 7.4 ± 7.6 min (\( n = 14 \)) at >60 m, which was 1.2–1.8 times longer than helicopter durations.

**Table 4.** Habituation testing of helicopter and chain saw noise stimuli at 4 manipulated Mexican spotted owl nest sites and 4 previously unmanipulated sites in the Sacramento Mountains, New Mexico, 1996.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Unmanipulated</th>
<th>Manipulated</th>
<th>Unmanipulated</th>
<th>Manipulated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dates</td>
<td>8–25 Jul</td>
<td>8–22 Jul</td>
<td>19–23 Jul</td>
<td>16–26 Jul</td>
</tr>
<tr>
<td>Flushes</td>
<td>3 (75%)</td>
<td>0</td>
<td>2 (50%)</td>
<td>0</td>
</tr>
<tr>
<td>Distance (m, SLD)*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>36.5</td>
<td>42.8</td>
<td>60.0</td>
<td>60.0</td>
</tr>
<tr>
<td>Range</td>
<td>33–40</td>
<td>40–47</td>
<td>60.0</td>
<td>60.0</td>
</tr>
<tr>
<td>Owl-weighting (dB)*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>101.7</td>
<td>100.9</td>
<td>69.9</td>
<td>68.5</td>
</tr>
<tr>
<td>Range</td>
<td>99.8–102.3</td>
<td>64.9–72.9</td>
<td>65.2–74.5</td>
<td></td>
</tr>
<tr>
<td>A-weighting (dB)*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>95.5</td>
<td>90.4</td>
<td>56.4</td>
<td>56.0</td>
</tr>
<tr>
<td>Range</td>
<td>89.9–91.4</td>
<td>51.3–59.7</td>
<td>53.8–60.5</td>
<td></td>
</tr>
</tbody>
</table>

* SLD = straight-line distance between stimulus and spotted owl.
* dB = decibels.
* Only 1 noise level recording was available for analysis.
Seasonal Change in Time to Alert.—Time to alert increased as the nesting season progressed and as stimulus distance increased. Spotted owls exhibited alert responses after only 0.6 ± 0.7 min (n = 13) during helicopter flights in July, compared with 1.4 ± 1.4 min (n = 9) in August and 1.6 ± 0.6 min (n = 6) in September. Spotted owl response was quicker during chain saw manipulations: <0.2 ± 0.4 min (n = 22) in June, >0.2 ± 0.4 min (n = 13) in July, 0.3 ± 0.5 min (n = 6) in August, and 0.5 min (n = 1) in September. When helicopter flights were ≤60 m away, spotted owls responded in 1.0 ± 1.0 min (n = 21) compared to 1.2 ± 1.0 min (n = 10) for flights >60 m. Spotted owls responded to chain saws in 0.1 ± 0.2 min (n = 26) at distances ≤60 m, and in 0.3 ± 0.5 min (n = 16) when saws were >60 m away. Time to alert was consistently 3.0–10.0 times longer for helicopters than for chain saws.

Prey Delivery Rates and Related Behaviors

Over 81% of all prey deliveries within the nesting season (n = 387) occurred during nocturnal hours (n = 16 spotted owl territories). Mean prey deliveries per hour were highest (1.00) at 0400, when >18% of all prey were delivered (Fig. 7). Prey deliveries per hour averaged 0.03 during diurnal hours compared with 0.37 during nocturnal hours, which translates to 0.36 prey deliveries/12-hr diurnal period and 4.20 deliveries/12-hr nocturnal period.

There were only 7 instances of full 24-hr video records 1–2 days before and immediately after a manipulation. Net differences in prey deliveries for the 24-hr periods after and before noise manipulations (postmanipulation deliveries minus premanipulation deliveries) for the 24-hr periods after and before helicopter and chain saw manipulations at 4 Mexican spotted owl nest sites in the Sacramento Mountains, New Mexico, 1996. Shading along the distance axis indicates the 95% calibration interval (± 68 m) around the estimated potential threshold distance (96 m) for zero-difference in prey deliveries (Graybill 1976).

Fig. 7. Mean prey deliveries per hour (Mountain Standard Time [MST]) averaged across the entire nesting season for Mexican spotted owls in the Sacramento Mountains, New Mexico, 1996.

Fig. 8. The linear regression and 95% prediction interval between stimulus distance and net difference in prey deliveries (postmanipulation deliveries minus premanipulation deliveries) for the 24-hr periods after and before helicopter and chain saw manipulations at 4 Mexican spotted owl nest sites in the Sacramento Mountains, New Mexico, 1996. Shading along the distance axis indicates the 95% calibration interval (± 68 m) around the estimated potential threshold distance (96 m) for zero-difference in prey deliveries (Graybill 1976).

DISCUSSION

Research Effects

Spotted owls tend to be less affected by nearby, nonthreatening human activity than most other raptor species. Sovern et al. (1994) found both nesting and nonnesting spotted owls became accustomed to observers sitting quietly 25–50 m away in only 10–15 min. Our use of blinds and their placement, along with the microphones, 1–4 hr in advance of manipulations provided additional visual and temporal buffering. Monitoring spotted owl behavior during those premanipulation hours and through unattended video camera coverage at other times confirmed undisturbed, normal activity. While
monitored spotted owls were aware of the cameras, we recorded no unusual behaviors or changes in activity patterns in response to their presence. In fact, spotted owls that used the camera trees, and sometimes the same branch, for perching continued to do so after camera placement. Neither locator balloons, which were above the canopy and obscured by intervening vegetation, nor flashlights with direction-al beams pointed skyward were normally visible to manipulated spotted owls. Our data collection activities did not seem to affect spotted owl responses to experimental manipulations.

Reproductive Success

Other noise disturbance research suggests aircraft overflights alone have a negligible effect on raptor reproductive success and young fledged per nest (Platt 1977, Anderson et al. 1989, Ellis et al. 1991). We believe the small, nonsignificant decrease in reproductive success between manipulated (n = 17) and nonmanipulated (n = 5) sites in our study was attributable to natural attrition inherent in the larger manipulation sample.

Our ability to detect a biologically meaningful difference in reproductive success and productivity between manipulated and nonmanipulated nests was limited by population size. Sample sizes of 116 nests for measuring success and 362 nests for measuring productivity would have been required to reach an adequate power level of 0.80. With only 30–50 spotted owl territories reproductively active on the Sacramento Ranger District each year, and only about 80% of those sites successfully producing young in a good year, adequate power levels can never be reached.

Although we were not able to relate the number of flushes or the number of manipulations to the number of young fledged, both parameters should be addressed in noise disturbance research (Awbrey and Bowles 1990). Helicopter-induced flushes have been found to affect the number of young gyrfalcons (Falco rusticolus) that fledged in Alaska (Platt 1977), while Awbrey and Bowles (1990) hypothesized flushes may be the best predictor of eventual reproductive loss.

Flush Response

The proportion of spotted owls flushing in response to a manipulation was negatively related to stimulus distance and positively related to noise level. Grubb and King (1991), McGarigal et al. (1991), Stalmaster and Kaiser (1997), and others reported similar findings for bald eagles (Haliaeetus leucocephalus), with response to human activity increasing as stimulus distance decreased. Platt (1977) describes a comparable pattern for gyrfalcon response to helicopter flights.

The dose-response relations of flush frequency with distance (Fig. 2) and noise level (Fig. 4) indicated that chain saws, although not as loud as helicopters, caused spotted owls to respond from farther away and at higher frequencies. Results for both stimuli are consistent with a model derived from 9 studies of aircraft disturbance effects on several species of nesting raptors (Bowles et al. 1990), which predicts increasing flush probability with increasing noise levels.

Temporal Variation in Spotted Owl Flush Response.—Most studies have not examined the effects of human activities during the incubation and fledgling phases of the nesting season, primarily because of concerns over causing early nesting failure and premature fledging by juveniles (Awbrey and Bowles 1990). However, we observed a strong dichotomy in response behavior between prefledging and postfledging periods, with female spotted owls only flushing after their chicks had left the nest. Spotted owls, like other raptors, appear reluctant to leave the nest during the incubation and nestling phases (Craig and Craig 1984, Fraser et al. 1985, Anderson et al. 1989, Ellis et al. 1991). For bald eagles, flush frequency increased as the nesting season progressed and nest attendance declined, with the highest response rate occurring postfledging (Grubb and Bowerman 1997).

The fact that adult spotted owls were more likely to flush in response to manipulations later in the reproductive cycle also suggests a decrease in adult defensive or protective behavior as juveniles mature. Because adult spotted owls roosted at increasing distances from maturing juveniles, flush distance may become less critical as the fledgling phase progresses, especially because adults did not flush farther than their original distance from juveniles. Although season and nesting phase influence avian response to disturbance (Thiessens 1957, Knight and Temple 1956), prior experience, habituation, and animal temperament may be more important factors (Hart 1985, Manci et al. 1988).
fact, prior experience may be the best indicator of animal response to overflights (Bowles 1995).

**Distance and Sound Thresholds.**—Our distance-response threshold for spotted owls was similar to that of most other raptor species exposed to aircraft overflights (N. F. R. Snyder et al. 1978. An evaluation of some potential impacts of the proposed Dade County training jetport on the endangered Everglade Kite, unpublished report. U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, Maryland, USA; Craig and Craig 1984, Anderson et al. 1989). For example, Grubb and Bowserman (1997) recommended helicopter survey flights remain >150 m from bald eagle nests and be <1 min in duration. Despite the aggressive nature of our testing regime (i.e., close proximity, repeated exposure, little or no prior experience), spotted owl behavioral responses were minimal when noise disturbance stimuli were >105 m away, and reproduction was not detrimentally affected. Because the 48 RQS varies every flight path during normal training operations over the forest, spotted owls on the LNF would not likely receive as much military helicopter disturbance within any year as the manipulated pairs received during this study.

Distance was a better predictor of spotted owl response to helicopter flights than noise levels. Even when we controlled for distance, noise levels varied among helicopter flights more than among chain saw manipulations. Helicopter noise varied not only with distance but also with rotor pitch, rotor torque, power levels, pilot technique, aircraft loading, speed, topography, and weather. Awbrey and Bowles (1990) described distance as the most commonly used surrogate for noise exposure in the animal effects literature, and suggested distance may be the best representative for the relation between stimulus and response measures. Grubb and King (1991) determined distance was the single most important predictor of bald eagle response in a classification tree model. Their model ranked noise sixth, behind distance, duration of disturbance, visibility, number of disturbances per event, and stimulus position relative to the affected eagle.

**Helicopters Versus Chain Saws.**—Few researchers have directly compared differences in raptor responsiveness between aerial and ground-based disturbances. In our study, ground-based disturbances elicited a greater flush response than aerial disturbances. Nesting bald eagles in Arizona showed the highest response frequency and severity of response to ground disturbances, followed by aquatic and aerial disturbances (Grubb and King 1991). Awbrey and Bowles (1990), in their meta-analysis of noise disturbance research on raptors, noted aircraft overflights were less detrimental than common ground-based activities such as hiking.

Spotted owls may have perceived helicopters as less threatening than chain saws because of their shorter duration, gradual crescendo in noise levels, minimal visibility, and lack of association with human activity. Helicopters would have elicited greater spotted owl response if exposure times were increased through slower maneuvers such as hovering. Chain saws started abruptly with an associated startle effect, whereas approaching helicopters were always preceded by a gradual increase in noise levels. Disturbing activities in close proximity to a spotted owl's location may also be more visible and therefore elicit a greater response than an activity farther away, regardless of noise level. However, we believe visibility had very limited effect on our results; helicopters were usually not visible, or only briefly so, to spotted owls roosting within or beneath the forest canopy. Grubb and Bowerman (1997) found aircraft visibility had little effect on bald eagle responsiveness. Although chain saws were also operated out of sight of reference spotted owls in all but a few instances, field crews had to set up recording equipment beneath the spotted owls for both types of manipulations. Subsequent chain saw operation may have been associated more with this ground-based human activity. In addition, raptors may be less disturbed by aerial manipulations because of their use of that medium (Gilmer and Stewart 1983).

**Alert Response**

Spotted owls initially responded to noise disturbances by turning toward the source. This orienting, alert response is an example of an animal's awareness of the disturbance through increased readiness to respond (Archer 1979, Brown 1990). Orienting response becomes progressively less frequent with repeated exposure to the same stimuli (Archer 1979). The relatively quick return to predisturbance behavior we documented is consistent with Ellis (1981), who showed heart rates of prairie falcons (Falco mexicanus) exposed to aircraft overflights returned to predisturbance levels within 5 min.
Our mean alert response threshold (403 m) corroborates a regional U.S. Fish and Wildlife Service policy that recommends a 400-m buffer zone around spotted owl nest sites (C. Torez, U.S. Fish and Wildlife Service, personal communication).

Habituation

Habituation is defined as an animal’s progressive loss in responsiveness toward a stimulus and is an important determinant in overall response behavior (Peeke and Herz 1973). Although statistically insignificant due to small sample size, experimental spotted owls were less likely to flush (0 of 8) in response to helicopter and chain saw manipulations later in the season than control spotted owls (5 of 8 or 62%), suggesting that spotted owls may have been habituating to manipulation testing. Platt (1977) and Anderson et al. (1989) observed a similar decrease in flush response to aircraft overflights between experienced and relatively naive raptors. In northcentral Michigan, a pair of nesting bald eagles near a military air base was 14% less responsive and the median distance to aircraft eliciting a response was half that (400 m vs. 800 m) of 5 other pairs more remotely located (Grubb et al. 1992). In addition, response duration decreased and time to alert increased during the 1996 field season. However, we consider these trends weaker evidence for habituation because the influence of seasonal factors, such as nesting phase, cannot be differentiated.

Prey Delivery Rates and Related Behaviors

The effects of human activity on a raptor’s ability to procure prey during the nesting season has not been well documented (Awbrey and Bowles 1990). Holthuijzen et al. (1990) found that prey delivery rates did not differ between experimental and control sites for prairie falcons exposed to construction and mining activity. Comparable examples for nocturnal raptors are lacking. We found prey delivery rates were highly and positively correlated with stimulus distance. Thus, manipulations in close proximity to spotted owl territories may affect prey delivery rates. The estimated threshold for detrimentally affecting prey deliveries (96 m) indicates a subblushing response consistent with the 105-m flush threshold and emphasizes the potential importance of this threshold distance.

However, these threshold findings are based on a specific range of manipulations per territory; changes in stimulus frequency, duration, timing, and distance could strongly influence overall spotted owl response behavior.

Weather conditions should be considered when determining the effects of human activity on raptors (Schueck and Marzluff 1995). To control for possible weather effects, we did not conduct any manipulations during periods of inclement weather. This approach was consistent with the training protocol for the 48 RQS, which limited activity during such periods. However, factors such as precipitation, wind, and clouds can limit foraging ability of raptors (Brown et al. 1988, Bosakowski 1989, Fleming and Smith 1990) and thereby place greater importance on the next available foraging times, when disturbance could become more critical.

MANAGEMENT IMPLICATIONS

This research differs from previous noise disturbance studies by a unique combination of factors: (1) interpretation of noise levels via owl-weighting, which is more specific to the subject animal’s hearing sensitivity than the generalized and less applicable A- or flat-weighting; (2) field experimentation with a threatened species in its natural habitat during a normal nesting season; and (3) controlled experimentation with the same resource and military aircraft, personnel, and flight profiles that initially raised the question of potential disturbance. A progressive, incremental, and conservative approach made this experimentation possible with no resultant negative effect on spotted owl activity or productivity.

Potentially detrimental noise levels were our initial and primary concern, but stimulus distance evolved as a more easily defined, quantified, and managed characteristic. Spotted owl response data were readily analyzed by distance because manipulation stimuli were presented by distance. In addition, distance results also directly translate into practical management implications. However, any application of our spotted owl response distances to develop management protocols for spotted owls elsewhere is inherently limited because it is predicated on having the same stimulus in a context similar to our experimentation. Alternatively, considering spotted owl response in terms of noise levels enables our results to be more generally ap-
plied, with due caution, to other types of helicopters under more varying conditions. This distinction is explained by the fact that noise level at the target species is the final measure of stimulus noise, whereas distance is only 1 of numerous intermediate factors (such as terrain, vegetation, atmospheric conditions, stimulus type, size, operation, etc.) that can affect noise level at the target.

Nonetheless, our data indicate the following recommendations for management of helicopter noise near Mexican spotted owls:

(1) At comparable distances, helicopter overflights were less disturbing to spotted owls than chain saws. This result validates, for this species and aircraft, the already established pattern that ground-based activities are typically more disturbing to raptors than aerial activities.

(2) Spotted owls did not flush when helicopter SEL noise levels were ≤102 dBA (92 dBA). Hence, helicopter noise levels below this threshold should not detrimentally affect nesting spotted owls.

(3) A 105-m radius, hemispherical protection zone should eliminate spotted owl flush response to helicopter overflights on the LNF. Zero flush response beyond 105 m for both helicopters and the more disturbing chain saws support this conclusion. Detrimental effects on prey delivery rates should also be minimized because the estimated threshold for this subflushing response (96 m) was <105 m.

(4) Short duration, single pass, single aircraft overflights had little effect on spotted owls. Other flight maneuvers involving circling, hovering, landing, etc., with potential increases in duration, proximity, or noise levels were not included in our experimentation.

(5) Our behavioral data indicate diurnal flights will likely have less potential for disrupting critical spotted owl activity than nocturnal flights. However, during nighttime hours, the 3 hr following sunset and preceding dawn were most important. Helicopter overflights between these nocturnal hours should minimize effects on spotted owl behavior.

(6) Considering the frequency of our manipulation testing, we recommend separating potential owl overflights along the same route by at least 7 days. Because flights over the same sites were separated as much as possible to minimize effects during our testing, data on the potential effects of more frequent overflights are lacking. However, actual rescue training flights avoid using the same route and therefore should not affect the same nest site twice in a breeding season.

(7) Although multiple flights over any 1 site are not recommended, our trend data indicate the likelihood of habituation with repeated exposures and as the nesting season progressed. Thus, naive, unexposed spotted owls may be more affected than spotted owls that have previously experienced overflights.

(8) Spotted owl flush response to helicopter overflights did not differ between the nesting and nonnesting seasons. Within the context of our experimentation, we found no substantive evidence that helicopter overflights during the nesting season detrimentally affected spotted owl success or productivity.

In conclusion, these research findings are specific to Mexican spotted owls and Pave Hawk helicopters, as well as to the seasons and habitat associated with our testing. Therefore, extrapolation to different avian genera or species, or other aircraft and locations, must be done with caution. For example, changes in forest type or elevation alone may influence prey availability and delivery rates, which may in turn influence spotted owl response behavior. We also caution against use of these findings to infer how spotted owls would respond under different circumstances that were not directly tested, such as spotted owl responses during early courtship and incubation, responses to >1 helicopter or overflight, or responses in different nesting habitat or under different foraging conditions. While our research was effective in answering the original, specific disturbance question, these results must be qualified by the limiting context of their derivation when applied to broader managerial questions.

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