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THERMAL REGIMES OF MEXICAN SPOTTED OWL NEST STANDS

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ABSTRACT—To evaluate the hypothesis that spotted owls (*Strix occidentalis*) select habitats with cool microclimates to avoid high daytime temperatures, I sampled thermal regimes in nest areas used by Mexican spotted owls (*S. o. lucida*) in northern Arizona. I sampled air temperature at 30-min intervals in 30 pairs of nest and random sites from May through August and used the resulting thermal profiles to estimate a suite of diurnal temperature parameters. I estimated diurnal energy use and evaporative water loss, and compared these estimates and temperature parameters between nest and random areas. Owl nest areas were significantly cooler than random areas, and estimated evaporative water loss was significantly lower in nest areas than in random areas. In contrast, there was little difference in estimated diurnal energy use between nest and random areas. These results support the hypothesis that Mexican spotted owls select cool habitats. Use of these cooler habitats apparently reduces diurnal evaporative water loss relative to random areas, suggesting that water balance might be more important in habitat selection by spotted owls than previously realized. However, selection of cool nest areas apparently does not result in large energy savings, at least in this high-elevation study area (mean elevation at nest areas in this study was 2,230 m).

RESUMEN—Para evaluar la hipótesis de que búhos moteados (*Strix occidentalis*) seleccionan hábitats con micro-climas frescos para huir de las altas temperaturas durante el día, muestree temperaturas en áreas de nidificación usadas por búhos moteados mexicanos (*S. o. lucida*) en el norte de Arizona. La temperatura ambiental fue medida en intervalos de 30 minutos en 30 pares de nidos y sitios seleccionados al azar durante los meses de mayo a agosto y los perfiles termales resultantes fueron usados para estimar diversos parámetros de temperaturas diurnas. Estimé el uso diurno de energía y la pérdida de agua por evaporación y comparé estas estimaciones y parámetros de temperaturas entre nidos y sitios seleccionados al azar. Las áreas de nidificación de búhos son significativamente más frías que áreas elegidas al azar, y estimaciones de pérdida de agua por evaporación fueron considerablemente más bajas en nidos que en áreas elegidas al azar. En contraste, hubo poca diferencia en la estimación de uso diurno de energía entre áreas de nidificación comparada a áreas seleccionadas al azar. Estos resultados corroboran la hipótesis de que los búhos moteados mexicanos seleccionan hábitats frescos. El uso de estos hábitats frescos aparentemente reduce la pérdida diurna de agua por evaporación, lo que sugiere que el balance de agua puede ser más importante que lo antes pensado en la selección de hábitats por los búhos moteados. Sin embargo, la selección de nidos en áreas frescas aparentemente no se traduce en grandes ahorros de energía al menos en grandes alturas (la altura promedio de las áreas de nidificación en este estudio fue 2,230 m).

Spotted owls (*Strix occidentalis*) frequently inhabit late-seral forests throughout their range (Gutiérrez et al., 1995), but reasons underlying use of such forests are not well understood. Among explanatory hypotheses proposed (reviewed by Carey, 1985; Gutiérrez, 1985), one suggests that the owls are poorly adapted to high temperatures and, therefore, seek cool habitats during warm weather (Barrows and Barrows, 1978; Barrows, 1981).

Several lines of evidence support the temperature and heat stress hypothesis. First, spotted owls are heavily feathered compared to many other owls inhabiting temperate zones and have feathers extending to the toes, apparently reducing or negating the ability to use the toes as an avenue for heat dissipation (Barrows, 1981). Second, spotted owls typically roost and nest in cool microsites during warm weather (e.g., Barrows, 1981; Forsman et al.,

1984; Ganey and Dick, 1995; Gutiérrez et al., 1995). Third, laboratory and field studies generally have supported the hypothesis (Ganey et al., 1993; Teng, 1998; Weathers et al., 2001).

Despite the evidence that owls select cool habitats for nesting and roosting, reasons underlying such selection remain uncertain. Teng (1998) compared thermal environments of owl roost and random sites in interior forests in northwestern California and estimated that roosting in randomly sampled areas would increase energy costs for thermoregulation by 5 to 34% per day and evaporative water loss by up to 5% per day relative to the sampled roost sites. Weathers et al. (2001) studied metabolic rate and water flux in the field using doubly-labeled water, determined that rates of water flux were high relative to metabolic rates, and suggested that minimizing water loss also might contribute to the preference of the owl for cooler environments.

Thus, heat stress, energy use, and water balance all have been proposed as factors underlying selection of late-successional habitats by spotted owls. Understanding the relative importance of these factors is important in assessing habitat quality and suitability for this owl (Weathers et al., 2001). However, directly assessing the relative importance of these factors experimentally in the field is essentially impossible, because free-ranging owls cannot be forced to use particular environments for comparative purposes.

In this study, I sampled thermal regimes in nest areas used by Mexican spotted owls (*S. o. lucida*), which occur in mountains and canyons throughout much of the American Southwest and into Mexico (Gutiérrez et al., 1995). My proximate objectives were to: 1) quantify thermal regimes in owl nest areas and random areas; 2) estimate owl energy and water use in these areas; and 3) compare these parameters between nest areas and random areas. Ultimately, I hoped to provide insights into habitat selection by this owl.

METHODS—This study was conducted in the Coconino National Forest, Coconino County, north-central Arizona. This forest encompasses 8,169 km^2, ranging from approximately 800 to 3,850 m in elevation. Temperature and precipitation vary widely across this elevational gradient, with mean minimum and maximum temperatures for July ranging from 6 to 14°C and 21 to 45°C, respectively. Mean annual precipitation ranges from 28 to >90 cm and falls mainly in 2 seasons. The wettest season occurs from July through October, with most precipitation occurring during thunderstorms. Winter snows typically occur from December through March (United States Department of Agriculture, 1995).

Selection of Nest and Random Areas—Sampling included all known spotted owl nest locations (n = 106) within the Coconino National Forest as of 1993, when available data on owl locations were compiled (United States Department of the Interior, 1995). To ensure that the sample adequately represented variability in owl nesting habitat, I stratified owl nest locations by 3 ''landscape types'' typically occupied by owls in this forest. Montane mixed-conifer landscapes occurred at relatively high elevations (≥2,400 m) in mountainous terrain featuring mosaics of mixed-conifer forests, dominated by Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), or both, and ponderosa pine (*Pinus ponderosa*). Canyon mixed-conifer landscapes occurred at lower elevations in deep canyons. These landscapes featured diverse topography and mosaics of forest types interspersed with large cliffs, rock outcroppings, or both. Pine-oak (*Quercus*) landscapes typically occurred at intermediate elevations (2,000 to 2,350 m) in rolling terrain featuring elevated plains, cinder cones, and small canyons. Mixtures of ponderosa pine and ponderosa pine-Gambel oak (*Q. gambelii*) forest dominated these areas.

Owl nest locations were assigned to landscape types using data from the Terrestrial Ecosystem Survey (TES; United States Department of Agriculture, 1995). This data set incorporated information on soils, vegetation, and climatic conditions in defining a set of ecological ''map units'' showing potential vegetation. Ganey and Benoit (2002) documented strong associations between owl occupancy and particular TES map units representing the above landscape types.

Owl nest-site locations were overlaid on a polygon coverage showing TES map units in a geographical information system (GIS; Arcview; ESRI, Redlands, California) environment to identify the TES map unit associated with each nest site. Map units 611, 613, 653, and 654 were used to identify montane mixed-conifer, map unit 555 identified canyon mixed-conifer, and map units 582, 584, and 565 identified the primary pine-oak associations used by nesting owls within the study area (see United States Department of Agriculture, 1995, and Ganey and Benoit, 2002, for further details).

I randomly selected 10 nest locations from each landscape type, with the constraint that an individual owl territory could be included in the sample only once. Using the GIS, I randomly selected a point within a 1-km radius of each nest location to serve

as a paired random location. Given patterns of owl movements and home range sizes, it can reasonably be assumed that areas within 1,000 m are available to resident owls (Ganey and Dick, 1995; Gutiérrez et al., 1995) and, therefore, could be selected as nest areas. Random locations were constrained to forested habitats, and any random points not falling in forested habitat were reselected until a point in forested habitat resulted. Thus, the sample consisted of 30 pairs of nest locations and random locations, with 10 pairs from each landscape type, and with all random points representing forested habitats.

Field Sampling—Coordinates for nest locations and random locations were located in the field using a global positioning system receiver (Garman GPS 12; Garmin International, Inc., Olathe, Kansas). Once the location was reached, the nearest tree ≥20 m in height was used as the sample point. Thus, I did not attempt to locate actual nest sites or structures, and samples represented nest stands and random stands rather than nests. For simplicity, I will refer to nest and random sample locations as areas hereafter.

At each sample point, a data logger attached to a nylon line was hung in the tree at a height of 8 m, the mean perch height for 36 radio-marked owls in 6 study areas in Arizona and New Mexico (n = 1,852 roosts sampled, SE = 0.09 m, 95% confidence interval = 7.96 to 8.31 m; unpubl. data). Loggers were hung in the interior of the tree crown, to ensure that they remained in shade for most of the day. Data loggers used (Optic Stowaway model WTA08-05+37; Onset Computer Corporation, Bourne, Massachusetts) sampled ambient temperature (°C) with an accuracy of 0.2°C and a resolution of 0.16°C, and were set to record at 30-min intervals. I placed loggers in trees beginning on 1 May 2001 and left them in place through August 2001. Spotted owls in this area typically roost in the nest area throughout this time period, even in years when they do not nest (pers. observ.).

Because of the time required to access sampling areas and place loggers in trees, I did not complete placing loggers until 10 June 2001. Thus, pairs of loggers came online on different dates throughout this period, meaning that sampling periods were not equal in length for all pairs of areas. I staggered placement order among the 3 landscape types to ensure that all were represented equally throughout the period required to place loggers, always placed loggers at paired nest areas and random areas on the same day, and standardized time periods covered by paired loggers for analysis.

I also sampled habitat characteristics that might influence thermal regime, including elevation, slope, aspect, canopy cover, and basal area. Elevation (m) was obtained from the GPS location. Percent slope was estimated with a clinometer. Two estimates were obtained, 1 up-slope and 1 down-slope, then averaged to estimate overall slope. Aspect (degrees) was measured along the main slope axis using a compass. Canopy cover was sampled using a sighting tube along 2 perpendicular 10-m transects randomly oriented and centered beneath the data logger. Presence or absence of overhead cover was recorded at 1-m intervals along these transects, with overall percent canopy cover computed as: number of hits/20 × 100. Basal area was estimated from the sample point using a 10-factor basal-area-factor prism. At each visit to a sampling area, I recorded wind speed and relative humidity in the shade at a height of 2 m using a Kestrel 3000 pocket weather station (Nielsen–Kellerman, Chester, Pennsylvania). These measures were used to compute mean wind speed and relative humidity for each site.

Data Analysis—I used the sampled thermal profiles to calculate a suite of diurnal temperature parameters for each nest area and random area (Table 1). I focused on the diurnal period because these owls actively forage at night, and, with the exception of nesting females, are not restricted at night to the areas where thermal regimes were sampled. Diurnal periods were estimated using a table of sunrise and sunset times for Flagstaff, Arizona (United States Naval Observatory; www.mach.usno.navy.mil/cgi-bin/aa_rstablew.pl).

I estimated resting energy use and evaporative water loss by owls using equations from the literature. Both Ganey et al. (1993) and Weathers et al. (2001) provided equations relating ambient temperature to resting metabolic rate. I used the more recent equations in Weathers et al. (2001) to relate owl energy use to thermal regimes at nest areas and random areas. I used an equation from Ganey et al. (1993) to estimate evaporative water loss, however, because Weathers et al. (2001) did not provide an equation for this purpose. I again focused on the diurnal period, both for reasons discussed above and because these owls actively forage at night. Neither activity budgets at night nor energetic costs for flight and foraging bouts were known for this owl.

I estimated resting metabolism rate (RMR; J/g/h) for each 0.5-h sampling interval using the following equations (Weathers et al., 2001):

below T_{lc} ($T_a < 18.2$°C): $RMR = 18.1 - 0.436(T_a)$;
within the thermoneutral zone (T_a 18.2 to 35.2°C): $RMR = 10.13$;
above T_{uc} ($T_a > 35.2$°C): $RMR = -23.0 + 0.941(T_a)$,

where T_a = ambient temperature for the sample interval, and T_{lc} and T_{uc} refer to the lower and upper critical temperatures, respectively (18.2 and 35.2°C; Weathers et al., 2001). I converted RMR to energy used (kJ) for each sampling interval, arbitrarily basing this calculation on a male Mexican spotted owl (mean mass = 509 g; Gutiérrez et al., 1995), and

TABLE 1.—Temperature parameters estimated at 30 Mexican spotted owl (*Strix occidentalis lucida*) nest areas and paired random areas in northern Arizona, May through August 2001. All parameter estimates cover the diurnal period, when owls were largely restricted to nest areas. Also shown are metabolic parameters estimated and direction of a priori predictions concerning differences between nest and random areas, where relevant.

Parameter estimated	A priori prediction
Mean daily temperature (°C)	Random area > nest area
Mean daily maximum temperature (°C)	Random area > nest area
Mean overall maximum temperature (°C)[1]	Random area > nest area
Mean % of time with temperature >35.2°C[2]	Random area > nest area
Mean % of days with temperature >35.2°C[2]	Random area > nest area
Mean daily minimum temperature (°C)	None
Mean % of time with temperature <18.2°C[3]	None
Resting energy use (kJ)	Random area > nest area
Evaporative water loss (mL/kg/day)	Random area > nest area

[1] Mean of overall maximum temperatures encountered per area during sampling period (as opposed to mean daily maximum temperature).

[2] Upper critical temperature (T_{uc}; Weathers et al., 2001).

[3] Lower critical temperature (T_{lc}; Weathers et al., 2001).

estimated diurnal resting energy use by summing across all diurnal sampling intervals within a day.

Energy use likely was underestimated, because owls perform maintenance activities (preening, stretching) during the day, sometimes socialize or forage during the day, often will be digesting prey captured during the night, and undergo molt during the breeding season (Forsman, 1981). All of these activities require energy, but estimates of energy costs for these activities were not available for spotted owls. This bias should not affect comparisons between nest areas and random areas.

I estimated evaporative water loss (EWL; mg H_2O/g/h) as:

$$EWL = 1.08 \exp(0.043T_a)$$

after Ganey et al. (1993), then converted EWL to mL/kg/day to facilitate comparisons with Weathers et al. (2001). EWL might have been overestimated because the equations used were derived under dry conditions (Ganey et al., 1993) and EWL should be greater under such conditions than under field conditions. I did not expect the magnitude of this bias to be great in this relatively dry (Table 2) study area, however.

Consistent with the idea that owls select roosting areas to provide favorable microclimates and reduce energy and water use, I evaluated a suite of a priori predictions regarding differences in diurnal temperature and metabolic parameters between nest areas and random areas (Table 1). I tested predictions us-

TABLE 2—Characteristics of paired Mexican spotted owl (*Strix occidentalis lucida*) nest areas and random areas (n = 30) in northern Arizona, May through August 2001. P-values from Wilcoxon signed-ranks test, except for aspect (Watson-Williams F-test for 2 circular means).

	Nest areas		Random areas		Difference[1]		
Variable	Mean	*SE*	Mean	*SE*	Mean	95% CI[2]	*P*
Slope (%)	38.5	5.5	20.6	3.6	−17.2	−26.2, −8.1	<0.001
Basal area (m^2/ha)	37.9	2.6	25.4	2.0	−13.1	−19.4, −6.9	0.001
Elevation (m)	2228.5	35.9	2251.9	30.8	16.3	−17.2, 49.7	0.714
Canopy cover (%)	75.2	1.4	53.8	2.2	−21.6	−26.5, −16.6	<0.001
Aspect (deg)	359.3	57.5[3]	79.3	124.8[3]			0.090
Mean wind speed (km/h)	2.2	0.2	3.5	0.7	1.3	−0.2, 2.7	0.004
Mean relative humidity (%)	28.8	2.3	26.8	2.4	−2.0	−4.3, 0.3	0.039

[1] Difference = random area value − nest area value.

[2] 95% confidence interval (lower bound, upper bound).

[3] Circular standard deviation.

TABLE 3—Diurnal weather parameters in paired Mexican spotted owl (*Strix occidentalis lucida*) nest areas and random areas ($n = 30$) in northern Arizona, May through August 2001. Variables were first summarized within, then averaged across areas (mean ± *SE* = 101.5 ± 2.3 days sampled per area). *P*-values from Wilcoxon signed-ranks test comparing paired nest areas and random areas. Diurnal periods were estimated using a table of sunrise and sunset times for Flagstaff, Arizona.

	Nest areas		Random areas		Difference[1]		
Variable	Mean	*SE*	Mean	*SE*	Mean	95% CI[2]	*P*
Mean diurnal temperature (°C)	20.7	0.2	22.4	0.3	1.8	1.3, 2.3	<0.001
Mean % of time with temperature > 35.2°C	0.4	0.1	2.0	0.4	1.6	0.8, 2.5	<0.001
Mean % of days with temperature >35.2°C	6.9	2.0	22.5	2.9	15.5	8.4, 22.7	<0.001
Mean % of time with temperature <18.2°C	32.8	1.2	27.0	1.1	−5.8	−8.0, −3.6	<0.001
Mean daily minimum temperature (°C)	11.7	0.4	11.8	0.3	0.1	−0.6, 0.8	0.599
Mean daily maximum temperature (°C)	28.0	0.5	31.5	0.4	3.2	2.0, 4.4	<0.001
Mean overall maximum temperature (°C)[3]	35.3	0.6	38.0	0.2	2.7	1.4, 3.9	<0.001

[1] Difference = random area value − nest area value.

[2] 95% confidence interval (lower bound, upper bound).

[3] Mean of absolute maximum temperatures encountered per area during the sampling period (as opposed to mean daily maximum).

ing Wilcoxon signed-ranks tests (Conover, 1980) to compare the appropriate parameter between paired nest areas and random areas. I also used Wilcoxon tests to compare habitat characteristics between nest areas and random areas, except for aspect. I compared aspect between nest areas and random areas using the Watson-Williams *F*-test for 2 circular means (Zar, 1974:321). I evaluated relationships between temperature parameters and habitat characteristics of nest areas and random areas using Pearson's product-moment correlation coefficient (Zar, 1974: 236–237). I pooled areas within the 3 landscape types recognized, because I was interested in differences between owl nest areas and random areas in all landscape types, rather than in potential differences between landscape types.

Because the Wilcoxon tests evaluated the difference between paired sites, I report mean differences and 95% confidence intervals around those differences. I also report means and standard errors for nest areas and random areas, however, because these parameter estimates also are of interest.

RESULTS—Paired nest areas and random areas were separated by 635.6 ± 39.8 (*SE*) m, on average. Nest areas occurred on steeper slopes than random areas and had greater basal area and canopy cover. Elevation and aspect did not differ between nest areas and random areas. Relative humidity was greater and wind speeds were lower in nest areas than in random areas (Table 2).

Patterns with respect to temperature parameters generally agreed with a priori predictions (Tables 1, 3). Mean diurnal temperature, mean daily maximum temperature, mean overall maximum temperature, and mean proportions of time and days with temperature $> T_{uc}$ all were greater in random areas than in nest areas. Mean minimum temperatures did not differ between nest areas and random areas, but temperatures $< T_{lc}$ occurred more often in nest areas than in random areas. Temperatures $> T_{uc}$ never were recorded in 50% of nest areas and occurred infrequently in nest areas overall. Temperatures $> T_{uc}$ occurred in 100% of random areas and occurred on more days in random areas, but still accounted for a relatively small portion of the diurnal period. Mean overall maximum temperature at nest areas approximated T_{uc} as estimated by Weathers et al. (2001). Thus, all parameters indicated that owl nest areas were cooler than random areas.

Temperature parameters were correlated with some habitat characteristics, but most relationships were relatively weak (Table 4). Among habitat characteristics that differed between nest areas and random areas, percent slope was not significantly correlated with any temperature parameters, whereas both basal area and canopy cover were inversely correlated with both mean and maximum daily temperatures. This relationship was stronger for

TABLE 4—Pearson's product-moment correlation coefficients (r) and associated P-values between habitat characteristics and selected diurnal temperature parameters estimated at Mexican spotted owl (*Strix occidentalis lucida*) nest areas and paired random areas ($n = 60$) in northern Arizona, May through August 2001.

	Mean temperature		Minimum temperature		Maximum temperature	
Habitat variable	r	P	r	P	r	P
Slope (%)	−0.080	0.549	−0.080	0.546	−0.204	0.122
Elevation (m)	−0.434	0.001	0.455	0.001	−0.364	0.004
Basal area (m^2/ha)	−0.276	0.035	0.314	0.015	−0.325	0.012
Canopy cover (%)	−0.588	0.001	−0.076	0.567	−0.578	0.001

canopy cover than for basal area in both cases. Elevation also was significantly correlated with temperature parameters, but did not differ between paired nest areas and random areas (Table 2).

In contrast to my prediction, thermal regimes in nest areas did not result in lower estimated diurnal energy use relative to random areas. Energy use was slightly but consistently greater in nest areas (Table 5), apparently due to the greater amount of time within the diurnal period when temperatures fell below T_{lc} (Table 3). In contrast, estimates of evaporative water loss were significantly lower in nest areas, supporting the a priori prediction.

DISCUSSION—This study clearly supported the hypothesis that areas used by Mexican spotted owls for nesting are cooler during the day, on average, than the surrounding environs. Differences between pairs of nest areas and random areas were relatively small but consistent in direction for most parameters (Table 3). This finding was consistent with observed habitat characteristics of sampled nest areas and random areas. The greater canopy cover and basal area in nest areas (Table 2) should contribute to reduced solar radiation, higher relative humidity, and cooler ambient temperature (Table 4).

Weathers et al. (2001) noted that ambient temperatures in their study area rarely exceeded T_{uc} for spotted owls and suggested that this agreement between ambient temperatures encountered and the T_{uc} of the owls strongly supported the importance of temperature in shaping owl distribution. Temperatures $>T_{uc}$ occurred in all random areas sampled in this study, and on an average of >22% of days sampled in these areas (Table 3). In contrast, such temperatures occurred in only 50% of nest areas sampled, and on approximately 7% of days sampled in these areas, on average. Because it was impossible to ensure that data loggers remained in shade all day, these parameters overestimate ambient temperatures in the shade and more accurately represent conditions that an owl perched in occasional sunlight would

TABLE 5—Estimated resting energy use and evaporative water loss for a hypothetical Mexican spotted owl (*Strix occidentalis lucida*) during the diurnal period, May through August 2001. Parameters were estimated from thermal profiles sampled in 30 nest areas and paired random areas in northern Arizona. Energy use and evaporative water loss were estimated for a male owl (mass = 509 g; Gutiérrez et al., 1995) using equations from Weathers et al. (2001) and Ganey et al. (1993), respectively. P-values from Wilcoxon signed-ranks test comparing paired nest areas and random areas. Diurnal periods were estimated using a table of sunrise and sunset times for Flagstaff, Arizona.

	Nest areas		Random areas		Difference[1]		
Variable	Mean	*SE*	Mean	*SE*	Mean	95% CI[2]	P
Energy use (kJ)	76.5	0.3	75.7	0.2	−0.9	−1.3, −0.4	0.002
Evaporative water loss (mL/kg/day)	65.8	0.7	71.5	0.9	5.7	4.0, 7.4	<0.001

[1] Difference = random area value − nest area value.
[2] 95% confidence interval (lower bound, upper bound).

encounter. Nevertheless, the mean maximum temperature encountered in nest sites (35.3°C) closely approximates T_{uc}, providing additional support for the importance of temperature regimes in influencing habitat selection.

My results suggested, however, that owls do not gain an energetic advantage from use of these cool environments. Estimated resting energy use during the diurnal period was slightly greater in nest areas than in random areas (Table 5), because ambient temperature fell below the T_{lc} for greater proportions of the day in nest areas (Table 3), forcing owls to expend energy for thermoregulation. As noted earlier, energy use likely is underestimated here, but this bias should be equal for nest areas and random areas and likely is small. Sovern et al. (1994) estimated that nesting and non-nesting northern spotted owls (*S. o. caurina*) respectively spent approximately 83 and 90% of diurnal hours resting during the breeding season, and diurnal activity also seems to be limited in Mexican spotted owls (Delaney et al., 1999).

In contrast to the observed pattern with respect to energy use, estimated evaporative water loss was approximately 8.7% lower in nest areas than in random areas (Table 5). California spotted owls (*S. o. occidentalis*) acquire roughly 40% of their total water requirements by drinking (Weathers et al., 2001), but many Mexican spotted owls occupy drainages lacking permanent streams (pers. observ.). During the driest months of the year (May and June), stock tanks provide the main source of free water in these areas. These tanks are relatively common but might not contain water during extremely dry periods and often are located either in open areas or some distance from owl nest areas and roost areas or both. Owls might be reluctant to use tanks where they occur in forest openings, especially during the day, and flying to and from these water sources would increase energy requirements. Minimizing water loss in such areas thus could be highly advantageous, suggesting that water balance might be an important factor in habitat selection (see also Weathers et al., 2001).

Several complicating factors deserve mention here. First, I did not sample ambient temperature at actual roost or nest microsites, but only in general nest areas. Owls might select microsites within these areas that provide thermal advantages and reduce energy use. More important, this study presents a simplistic view of thermal environments of sampled areas, because factors other than ambient temperature also affect these environments. Relative humidity, wind speed, and solar and long-wave radiation (Hayes and Gessaman, 1980) might be important, particularly as they interact with topography and vegetation. Sampling these factors was beyond the scope of this study, however.

Because of these limitations, relative comparisons of energy and water use between nest areas and random areas remain speculative. For example, greater wind speeds in random areas could increase convective cooling there, which could increase energy use relative to estimates presented here. Better information on the effects of wind (and other environmental factors) on energy and water use thus will be required to fully understand the ramifications of these data.

The data presented here clearly document differences in thermal regimes between nest areas and random areas available to spotted owls and provide further support for the hypothesis that spotted owls select cool nest areas. The implications of those differences on energy and water use are less clear. Nevertheless, the hypothesis that use of cool habitats reduces water use by spotted owls seems to be supported. In contrast, selection of cool sites does not seem to have large consequences in terms of energy use.

Given that owls select cool nest areas, my results provide further support for the importance of canopy cover as an important correlate of spotted owl habitat (e.g., Grubb et al., 1997; Ganey et al., 2003). Of those habitat variables that differed between nest areas and random areas, canopy cover was most highly correlated with both mean and maximum diurnal temperature (Table 4). Thus, this variable might be important in identifying the types of cool forest stands used by spotted owls and should be included in forest-sampling schemes where identifying such stands is an objective.

The finding that owl nest areas are cooler than random areas does not rule out other factors as influences on habitat selection by owls. The same types of structural features that result in cooler microclimates might be correlated with factors such as prey abundance or pro-

tection from predators. For example, relatively dense forests with closed canopies and high basal area might provide improved hiding cover for owls in general, and especially for inexperienced juvenile owls. Such forests also might provide more and better den structures for small mammals. In fact, it seems unlikely that habitat selection is based solely on thermal constraints, and more likely that such constraints interact with other factors, such as prey abundance and protective cover.

Finally, thermal environments vary among areas, and the relative importance of thermal environments on owl habitat selection might vary among areas. For example, mean temperatures in random areas in this study were lower than mean temperatures in owl roost areas sampled by Teng (1998) in northwestern California. This might indicate that thermal constraints on habitat selection were less important in my study area, where owls occur at relatively high elevations, than in areas where spotted owls occur at lower elevations and routinely are exposed to warmer temperatures.

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