THERMAL ECOLOGY AND ECOLOGICAL ENERGETICS OF CALIFORNIA SPOTTED OWLS

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Abstract. In this study, we used open-circuit respirometry and the doubly labeled water technique (DLW) to examine the thermal ecology and ecological energetics of California Spotted Owls (*Strix occidentalis occidentalis*). Our physiological and behavioral observations indicated that Spotted Owls are less heat tolerant than typical birds. At temperatures above the thermoneutral zone (18.2–35.2°C), resting metabolic rate increased 1.48 times faster than predicted allometrically, and behavioral responses to heat stress (increased breathing rate, ptiloerection, gaping, and wing drooping) occurred at relatively modest temperatures, 30–34°C. Our data support the hypothesis that Spotted Owls prefer old-growth and late seral stage forests because they provide favorable microclimates. Our metabolic measurements reveal that Spotted Owls have exceptionally low energy requirements. Their basal metabolic rate, 10.13 ± 0.46 J g^{-1} hr^{-1}, is only 82% of that predicted allometrically for owls. Field metabolic rate (FMR) of five adults provisioning dependent young averaged 249 ± 60 kJ day^{-1}, only 34% of that predicted for comparably sized non-passerine birds. We calculated Spotted Owl prey requirements from our FMR data, laboratory determinations of assimilation efficiency (77%), and the body composition of representative prey types. On average, Spotted Owls feeding young can meet their own energy needs by consuming one northern flying squirrel (*Glaucomys sabrinus*) every 1.8 days or one woodrat (*Neotoma fuscipes*) every 3.7 days.

Key words: doubly labeled water, energetics, field metabolic rate, food consumption, Strix occidentalis occidentalis, *thermal ecology, thermoregulation.*

Ecología Térmica y la Energética Ecológica de *Strix occidentalis occidentalis*

Resumen. En este estudio usamos respirometría de circuito abierto y la técnica de agua doble-marcada (DLW) para examinar la ecología térmica y la energética ecológica de la lechuza moteada californiana (*Strix occidentalis occidentalis*). Nuestras observaciones fisiologicas y comportamentales indican que las lechuzas moteadas son menos tolerantes a temperaturas elevadas que las aves en general. A temperaturas sobre de la zona de neutralidad térmica (18.2–35.2°C), la tasa metabólica basal se incrementó 1.48 veces más rápido que la predicha alométricamente, y la respuesta en el comportamiento a la tensión térmica (incremento en la tasa respiratoria, erección de las plumas, jadeo y el reposo de las alas) ocurrió a temperaturas relativamente bajas (30–34°C). Nuestros datos son consistentes con la hipótesis que las lechuzas moteadas prefieren bosques maduros y en etapas avanzadas de suseción debido a su microclima favorable. Nuestras medidas metabólicas indican que las lechuzas moteadas tienen requerimientos energéticos excepcionalmente bajos. Su tasa metabólica basal, 10.13 ± 0.46 J g^{-1} hr^{-1}, representa solo el 82% del valor predicho para lechuzas. La tasa metabólica de campo (TMC) de cinco adultos que se encuentraban criando polluelos promedió 249 ± 60 kJ day^{-1}, solamente un 34% del valor predicho para aves no-paserinas de tamaño comparable. Calculamos los requisitos de alimentación para lechuzas moteadas usando nuestros datos de TMC, las determinaciones en el laboratorio de la eficiencia de la asimilación (77%), y la composición corporal de varios tipos de alimentos. En promedio, las lechuzas moteadas criando polluelos pueden mantenerse alimentandose de una ardilla (*Glaucomys sabrinus*) cada 1.8 días o una rata (*Neotoma fuscipes*) cada 3.7 días.

INTRODUCTION

Throughout most of its range the Spotted Owl (*Strix occidentalis*) exists at very low population densities that have declined from historical levels. As with the Northern Spotted Owl (*S. o. caurina*), demographic studies of the California Spotted Owl (*S. o. occidentalis*) strongly suggest population declines throughout its range (Steger et al. 1999, USDA 2000, Blakesley et al. 2001, Seamans et al. 2001). Spotted Owl life-history strategy, characterized by limited dispersal ability, deferred reproductive maturity, low reproductive rate, and specialized habitat requirements, makes them vulnerable to environmental perturbations, chief among which are habitat de-

struction and alteration. The close association of Spotted Owls with old-growth and late seral-stage forests is well documented (Gutiérrez et al. 1992, Moen and Gutiérrez 1997), but the basis for this distributional limitation remains poorly understood. Several potential factors have been proposed (Verner et al. 1992) including prey diversity, abundance, and accessibility; availability of suitable nesting and roosting sites; favorable microclimate; and protection from predators. Obviously, these factors are not mutually exclusive, and all may contribute to determining habitat selection in this species.

In this study we investigated the ecological energetics of California Spotted Owls, focusing primarily on the possible role of thermoregulatory constraints on habitat selection and on the energy and prey requirements of Spotted Owls provisioning offspring. It has been suggested that Spotted Owls are less heat tolerant than birds in general, and this is one of the explanations offered for their preference for old-growth and mature forests (Barrows and Barrows 1978, Barrows 1981, Ganey et al. 1993). Moreover, although Spotted Owl diet composition is well documented (Verner et al. 1992, Williams et al. 1992), we lack quantitative information concerning prey requirements. The importance of prey as a factor limiting avian reproductive success remains unclear, but understanding energy and prey requirements is fundamental to assessing habitat quality and suitability.

METHODS

We captured five juvenile owls in Lassen National Forest, California (40°20′N, 121°35′W), between mid-August and early September 1992, transported them to the University of California, Davis, and housed them individually in indoor animal chambers (3.3 m × 2.7 m × 2.2 m high) that were equipped with two perches. Owls were trained to the fist using standard falconry techniques, but were maintained free-flying within their respective chambers except during the assimilation efficiency study, when they were tethered to a perch. Free-flying owls were fed 1–2 live mice (*Mus musculus*) per day, whereas tethered owls were fed intact, dead mice. We weighed owls to the nearest gram with a K-tron electronic balance (Phoenix, Arizona) weekly and during metabolic measurements. We returned the owls to Lassen National Forest and released them in areas known to contain Spotted Owls upon the study's conclusion in July 1993.

RESTING METABOLIC RATE

We determined resting metabolic rates by measuring oxygen consumption (VO_2) of owls during both the active phase (20:00–03:00) and rest phase (08:00–14:30) of their daily cycle. Owls fasted for a minimum of 24 hr and had been resting in the dark at a stable temperature for at least 1 hr prior to measurement. To determine VO_2, we weighed each owl to the nearest 1 g with a calibrated electronic balance and placed it in a 19-L airtight opaque plastic metabolism chamber (35 cm high × 29 cm diameter) housed within a temperature-controlled cabinet. During measurements, owls perched on a 5-cm-diameter rope-wrapped perch that was mounted 5 cm above the metabolism chamber floor. Temperature within the metabolism chamber was monitored using three copper-constantan thermocouples that were calibrated against a mercury thermometer certified by the National Bureau of Standards. Dry, CO_2-free air passed through a 5-L Tylan mass-flow controller (Carson, California) calibrated with a bubble meter (Levy 1964) and into the metabolism chamber at between 2.1 to 3.2 L min^{-1}, which resulted in chamber air attaining 95% equilibrium in 19–29 min (Lasiewski et al. 1966). Because buildup of chamber humidity due to an animal's evaporative water loss can interfere with evaporative cooling at high temperatures (Lasiewski et al. 1966), we employed higher airflow rates (mean = 2.72 L min^{-1}) at air temperatures > 35°C. We can estimate the relative humidity (RH) that prevailed within the metabolism chamber during RMR measurements at 40°C if we assume the owls dissipated all of their metabolic heat evaporatively. At 40°C, mean VO_2 was 0.745 mL g^{-1} hr^{-1}. For a 691-g owl this is equivalent to a metabolic heat production of 172 J min^{-1}, which would require evaporation of 71.0 mg of water per min. Based on an airflow rate of 3.15 L min^{-1} at 40°C, we estimate mean RH within the metabolism chamber to have been 42% (Lasiewski et al. 1966). Using a higher airflow rate would have lowered RH within the metabolic chamber, but 42% RH is not excessive and we do not think humidity affected our RMR measurements at higher temperatures.

We determined the fractional concentration of O_2 in inlet and outlet chamber air (both dry and

CO$_2$-free) with an Applied Electrochemistry S3-A oxygen analyzer (Sunnyvale, California; calibrated using N$_2$-dilution, Fedak et al. 1981), and calculated VO$_2$ with equation 2 of Hill (1974). We calculated rates of metabolic heat production assuming 20.1 kJ of heat were produced per liter of O$_2$ consumed by fasted birds. We weighed owls before and after each VO$_2$ measurement and used their mean mass in our calculations. No more than two measurements were made per owl per day. Metabolic measurements were made between January and June on owls that were in full basic plumage (i.e., not molting).

BEHAVIORAL RESPONSES TO TEMPERATURE

We monitored behavioral responses to gradually increasing ambient temperature by placing individual owls on a perch within a Percival temperature-controlled cabinet (Boone, Iowa; 0.6 × 0.6 × 1.2 m). The cabinet was ventilated at 3.75 L min^{-1} and was equipped with a dim red light (4 W) and a one-way observation window. Each measurement period began with a 30-min equilibration period at a temperature of 26°C. We observed behavior as temperature increased from 26°C in 2°C increments, with the bird allowed to equilibrate to each stable temperature for 15 min. For each observation, we recorded dew point within the chamber (General Eastern 1100DP dew point hygrometer, Waterton, Massachusetts), breathing rate (the time required for 10 breaths), body width (a measure of ptiloerection), and behavior (e.g., exposure of foot pads, panting, gular fluttering, drooping of wings). We measured body width using a ruler attached to the back wall of the chamber. We concluded observations when the bird began to gular-flutter continuously. Beginning at 30°C, and following each observation, we recorded body temperature using a Physitemp model BAT-12 thermocouple thermometer (Clifton, New Jersey) with an Omega 27-gauge hypodermic-needle thermocouple probe (Stamford, Connecticut) that was inserted 2 cm into the pectoral muscle. We were unable to measure the body temperature of one uncooperative owl. We calibrated the thermocouple against a mercury thermometer certified by the National Bureau of Standards. During our behavioral observations at ambient temperatures (T_a) > 32°C, relative humidity (calculated from dew point) within the environmental chamber averaged 27.1% (19.9–36.0%).

FIELD METABOLIC RATE

We used the doubly labeled water (DLW) technique (Speakman 1997) to measure rates of CO$_2$ production (VCO$_2$) of free-living adult Spotted Owls that were provisioning young during the 1992–1995 breeding seasons. We captured 16 owls using either an extendible noose pole or a mist net, but successfully recaptured only 6 of them, 3 males and 3 females. All captured owls were previously banded as part of a long-term U.S. Forest Service demography study, and sex was known based on body mass, morphometric measures, and vocalizations. Upon initial capture, we weighed each owl to the nearest 5 g (Pesola balance, Baar, Switzerland) and injected it with 1.5 mL of water containing either >95 atoms % ^{18}O and 16.8 MBq ^{3}H (tritiated method; $n = 10$, 4 recaptures), or 67 atoms % ^{18}O and 33 atoms % ^{2}H (deuterated method; $n = 6$, 2 recaptures). We initially used the double-sample DLW method, which involved holding the bird for 1.5 hr following injection to allow the injectate to equilibrate with body water before taking an initial blood sample. We only recaptured one of five doubly sampled owls, however, so we switched to the single-sample DLW method (Nagy et al. 1984, Webster and Weathers 1989) during the 1994 season. With this technique, birds are released immediately after capture and injection, which minimizes stress and increases recapture success. Birds were recaptured approximately 24 ($n = 5$) or 48 ($n = 1$) hr after release. We collected blood samples from four uninjected adult owls to determine natural background isotope abundance, which averaged 0.2016 ± 0.0016 atoms % ^{18}O and 0.01544 ± 0.00044 atoms % ^{2}H.

Blood samples from tritiated birds were flame-sealed in heparinized glass capillary tubes and refrigerated until micro-distilled under vacuum to obtain pure water. We determined the ^{18}O content of triplicate 8-μL subsamples of the pure water from these samples by proton activation and subsequent counting of the ^{18}F thus produced (Packard model 5210 gamma counter, Meriden, Connecticut). We conducted these analyses at the Crocker Nuclear Laboratory, University of California, Davis. Coefficients of variation in ^{18}O standards were <1%. We measured ^{3}H activity of duplicate samples by liquid scintillation using toluene-PPO (2, 5-diphenyloxazole) cocktail and a Packard model 1600 CA

liquid scintillation analyzer (Meriden, Connecticut). Blood samples from deuterated birds were stored in flame-sealed hematocrit tubes until analyzed for $^{18}O/^{16}O$ and $^2H/H$ ratios at the University of Groningen, The Netherlands.

We computed CO_2 production of the doubly sampled bird using the equations of Lifson and McClintock (1966) as modified by Nagy (1975, 1983). For single-sample owls, we computed CO_2 production using equation 2 of Webster and Weathers (1989) using the mean body water fraction (0.617; range 0.602–0.628) determined by ^{18}O dilution and the logarithm of the initial isotope ratio obtained from the doubly sampled birds ($n = 5$). We converted CO_2 production to energy expenditure assuming an energy equivalent of 27.6 kJ per L CO_2, based on a diet of northern flying squirrels (*Glaucomys sabrinus*; dry matter = 10% fat, 90% protein) and energy equivalents for uricotelic carnivores (Gessaman and Nagy 1988).

ASSIMILATION EFFICIENCY AND PREY BODY COMPOSITION

We determined assimilation efficiency of four owls that were tethered to floor perches during five-day feeding trials. We provided owls with dead mice daily and determined the mass of food consumed by subtracting the mass of any uneaten portions that remained after feeding from the mass of prey provided. We weighed each owl at the start and end of the trial and collected all pellets and fecal material from a clear plastic sheet below each perch. We weighed and dried pellets and feces to constant mass at 50°C, and stored them in airtight bags. The gross energy content ($J\ g^{-1}$) of dried samples of mice ($n = 16$), pellets ($n = 20$), and feces (1 pooled sample per owl) was determined by bomb calorimetry by Dr. Barbara Oskroba at Colorado State University.

We determined proximate body composition of 17 northern flying squirrels and 16 mice, using the Kjeldahl procedure (Horwitz 1975) to determine protein content and a Soxtec system for fat analysis (Horwitz 1975). In addition, gross energy content ($kJ\ g^{-1}$) of mice ($n = 16$), northern flying squirrels ($n = 17$), and dusky-footed woodrats (*Neotoma fuscipes*; $n = 6$) was determined by bomb calorimetry by Dr. Barbara Oskroba. The woodrats, which were captured in Lassen National Forest, were partially dehydrated when we received them and we were unable

to determine their body water content. We assumed their water content was the same as that of flying squirrels (0.702) for our prey consumption calculations.

STATISTICAL ANALYSES

We used least-squares regression to determine the relationship between resting metabolic rate (RMR) and ambient temperatures above and below the thermoneutral zone. We compared RMR between rest and active phases using ANCOVA and paired two-tailed *t*-tests. To analyze behavioral responses to increasing ambient temperature we utilized least-squares regression. We compared prey energy values using ANOVA and prey fat and water content using independent two-tailed *t*-tests. We used independent two-tailed *t*-tests to compare male and female body mass, mass-specific field metabolic rate (FMR), and water efflux. To determine the relationships between FMR and mass loss and water flux we used least-squares regression. Except where indicated, values are presented as mean ± 1 SD.

AUTHORIZATIONS

Spotted Owls were captured and maintained in captivity under authority of (1) a Memorandum of Understanding dated 28 July 1992 (amended annually), between the University of California, Davis, the U.S. Forest Service, and the California Department of Fish and Game (CDFG), (2) CDFG scientific collecting permits Nos. 7125, 6137, 6914, and 22168-AM, and (3) University of California Animal Use and Care Protocol No. 5423. Field metabolic rate measurements using tritiated water were authorized by University of California Radiation Use Authorization No. 0942, the State of California Department of Health Services Radioactive Material License No.1334–57, and the Office of the Forest Supervisor, Lassen National Forest.

RESULTS

RESTING METABOLIC RATE

The mean body mass of owls during the laboratory metabolic measurements was 700 ± 43 g (range 640–743 g; $n = 5$). We characterized the relation of resting metabolic rate (RMR) to T_a using Newton's law of cooling (Scholander et al. 1950; Fig. 1). We fitted lines to the data below 20°C and above 36°C using least-squares regression. Measurements made during the rest and
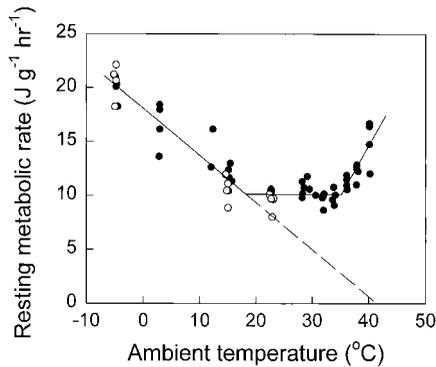
FIGURE 1.   Relation of California Spotted Owl resting metabolic rate to ambient temperature. Measurements during the rest phase of the daily cycle (shaded circles) do not differ significantly from those during the active phase (unshaded circles). Lines below the lower critical temperature (18.2°C) and above the upper critical temperature (35.2°C) are described by text equations 1 and 2.

FIGURE 2.   Relation of breathing rate (A) and owl body width (ptiloerection index) (B) to ambient temperature in California Spotted Owls. Symbols denote different individuals.

active phases of the daily cycle did not differ and, hence, we pooled the data (for data below 20°C, ANCOVA: $F_{1,20} = 0.1$, $P = 0.81$ for intercept and $F_{1,21} = 0.02$, $P = 0.88$ for slope; within the thermoneutral zone, paired t-test: $t_3 = 2.1$, $P = 0.13$). The thermoneutral zone extended from 18.2°C to 35.2°C.

We calculated basal metabolic rate (BMR) as the mean of the thermoneutral metabolic rate determined for each owl separately ($n = 3$–7 measurements per owl). BMR averaged 10.13 ± 0.46 J g^{-1} hr^{-1} or 170 ± 13 kJ day^{-1} ($n = 5$).

Below the lower critical temperature (T_{lc}) of 18.2°C, metabolic rate increased linearly with declining temperature as described by the equation

$$y = 18.1 - 0.436x$$
$$(r^2 = 0.87, \ s_{yx} = 1.59, \ s_b = 0.04, \ n = 23) \quad (1)$$

where y is RMR in J g^{-1} hr^{-1} and x is T_a in °C. This relation extrapolates to zero metabolism at $T_a = 41.5$°C, which is 0.6°C above the mean thermoneutral body temperature (T_b) of 40.9°C.

The RMR of three of the four owls measured at temperatures above the upper critical temperature (T_{uc}), 35.2°C, increased exponentially with increasing T_a by inspection. However, we fit a linear relation to the data to facilitate comparisons with other species. Above the T_{uc}, RMR is described by the equation
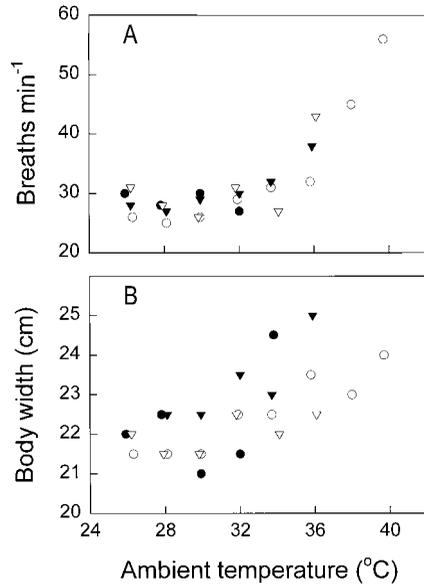
$$y = -23.0 + 0.941x$$
$$(r^2 = 0.60, \ s_{yx} = 1.4, \ s_b = 0.24, \ n = 12) \quad (2)$$

where y is RMR in J g^{-1} hr^{-1} and x is T_a in °C.

BEHAVIOR AT VARIOUS TEMPERATURES

There was no relationship between breathing rate and ambient temperature at or below ca. 32°C (Fig. 2A; $r^2 = 0.02$, $P = 0.64$). Above 32°C, however, breathing rate increased linearly with temperature as described by the equation

$$y = -112.1 + 4.18x$$
$$(r^2 = 0.87, \ s_{yx} = 23.7, \ s_b = 0.66, \ n = 8) \quad (3)$$

where y is breaths min^{-1} and x is ambient temperature in °C.

The ptiloerection (body width) index showed a similar functional response to temperature (Fig. 2B). At temperatures up to 30°C, the degree of ptiloerection was independent of temperature ($r^2 = 0.05$, $P = 0.47$). The degree of ptiloerection increased with temperature at or above 30°C as described by the equation

$$y = 15.7 + 0.21x$$
$$(r^2 = 0.35, \ s_{yx} = 2.6, \ s_b = 0.08, \ n = 16) \quad (4)$$

TABLE 1. Assimilation efficiency of captive California Spotted Owls consuming a diet of mice (*Mus musculus*).

Owl	Mean body mass, g	Mice eaten, g day^{-1}	Ingested energy (I) kJ day^{-1}	Excreta + pellets, g day^{-1}	Excreted energy (E) kJ day^{-1}	I–E, kJ day^{-1}	Assimilation efficiency	% mass change
1	651	32.9	277.6	4.5	47.3	230.3	0.83	–2.9
2	646	25.3	213.7	5.4	59.1	154.6	0.72	1.3
3	604	40.6	342.0	4.7	52.3	289.7	0.85	7.9
4	783	27.9	235.7	6.8	73.4	162.3	0.69	2.5
Mean	671	31.7	267.2	5.3	58.0	209.2	0.77	2.2
SD	78	5.8	48.9	0.9	9.8	55.0	0.07	3.9

where y is ptiloerection index in cm and x is ambient temperature in °C.

Body temperature of two of the three owls for which we obtained multiple measurements increased with temperature above 30°C as follows:

$$y = 35.4 + 0.185x$$
$$(r^2 = 0.83, \ s_{yx} = 1.4, \ s_b = 0.04, \ n = 6) \quad (5)$$

where y is body temperature in °C and x is ambient temperature in °C. However, there was no relationship between body temperature and ambient temperature for a third owl ($r^2 = 0.00$, $P = 0.99$).

Three of the four owls began to gape and droop their wings slightly at 34°C, while the remaining owl first panted and then gular-fluttered at this temperature. Two owls began continuous gular flutter at 36°C, whereas the fourth owl initiated gular flutter at 40°C.

ASSIMILATION EFFICIENCY AND PREY BODY COMPOSITION

California Spotted Owl assimilation efficiency, based on a diet of mice, averaged 77 ± 7% (Table 1).

Gross energy values (dry mass basis) differed among prey species with laboratory mice being highest (23.0 ± 1.2 kJ g^{-1}) followed by flying squirrels (19.3 ± 0.5 kJ g^{-1}) and wood rats (17.7 ± 1.3 kJ g^{-1}) (ANOVA: $F_{2,36} = 93.0$, $P < 0.001$).

Fat content as a percent of dry mass differed between flying squirrels (3.00 ± 0.50%) and laboratory mice (24.2 ± 4.9%, $t_{27} = 17.8$, $P < 0.001$). Water content of flying squirrels and mice also differed (70.2 ± 1.4% and 65.1 ± 1.4% of body mass, respectively; $t_{27} = 9.9$, $P < 0.001$). The fresh mass of flying squirrels was 105 ± 12 g ($n = 17$).

FIELD METABOLIC RATE AND WATER FLUX

Small errors in isotope measurements can result in large errors in CO_2 production if either absolute isotope turnover is low, or the rate of water flux is high, relative to the rate of CO_2 production (Nagy 1980). Both circumstances were true in our study. Accordingly, we evaluated the potential error in our CO_2 measurements by calculating isotope turnover rates. Turnover ratios were consistent with reliable CO_2 measurements for 5 of the 6 owls we recaptured. For Owl E, hydrogen turnover was 97.1% of oxygen turnover, which is very high and implies low reliability for this owl's CO_2 measurement. Owl E's VCO_2, 0.33 mL CO_2 g^{-1} hr^{-1}, was much lower than that of the other owls. Excluding Owl E, hydrogen turnover for the other five owls was 84 ± 6% of oxygen turnover, implying errors of <10% in CO_2 production. Final O_2 concentration averaged 77 ± 9% of initial O_2 concentration for the five owls, which could yield errors in CO_2 production as large as 30% for a 1% error in isotope measurements (Nagy 1980). Lack of a significant correlation between H:O turnover and CO_2 production ($r = -0.46$, $P = 0.43$) or between O_2 turnover and CO_2 production ($r = -0.53$, $P = 0.36$) for the five owls indicates an absence of systematic bias. Random errors would tend to cancel out, and an error as large as 30% in any one FMR measurement would produce only a 4–8% error in mean FMR. Excluding Owl E's low CO_2 production value increases mean FMR by 7.3% and broadens the 95% confidence interval from ± 65 kJ day^{-1} to ± 75 kJ day^{-1}, because of the decrease in sample size. Although mean FMR is not significantly different with or without Owl E ($t_9 = 0.44$, $P = 0.67$), we feel Owl E's CO_2 production is unreliable and should be excluded from the

TABLE 2. Body mass, field metabolic rate (FMR), and water influx of California Spotted Owls provisioning dependent young.

Owl	Sex	Mean mass, g	% mass change	FMR mL CO_2 g^{-1} hr^{-1}	FMR kJ day^{-1}	Water influx, mL H_2O kg^{-1} day^{-1}
A	M	553	–0.9	0.90	328	174
B	M	503	–2.9	0.64	212	71
C	M	528	–2.8	0.83	289	101
D	F	615	–3.2	0.44	179	162
E	F	664	0	0.33[a]	147[a]	112
F	F	616	–1.3	0.58	237	89
Mean		580	–1.9	0.68	249	118
SD		56	1.3	0.19	60	38

[a] FMR measurements for this owl were unreliable (see results section) and were not included in the mean.

mean. Its water efflux value is not subject to the same potential errors, however, and we have retained it.

Body mass of DLW owls did not differ significantly between males (528 ± 25 g) and females (632 ± 28 g; $t_4 = 3.49$, $P = 0.07$; Table 2). The lack of a significant difference in mass is likely attributable to small sample sizes ($n = 3$ of each sex), since it is well established that this species is sexually size-dimorphic (Blakesley et al. 1990). Mass-specific CO_2 production did not differ between the sexes ($t_3 = 2.5$, $P = 0.09$) averaging 0.79 ± 0.13 and 0.51 ± 0.10 mL CO_2 g^{-1} hr^{-1} for males and females, respectively, although values did not overlap. There was no relationship between FMR and mass loss during the measurement interval ($r^2 = 0.04$, $P = 0.71$), indicating that birds that lost more mass were not more likely to have higher FMR values.

Water efflux averaged 129 ± 38 mL H_2O kg^{-1} day^{-1} and did not differ between sexes ($t_4 = 0.43$, $P = 0.71$). Water influx averaged 118 ± 38 mL H_2O kg^{-1} day^{-1} (Table 2). There was no relationship between FMR and either water efflux ($r = 0.13$, $P = 0.82$) or influx ($r = 0.25$, $P = 0.68$). We derived a water budget for Spotted Owls based on our DLW measurements of total water intake, calculations of metabolic water production from FMR, and estimations of preformed water intake from prey. Of the total water influx of 68.4 mL day^{-1}, 40% was derived from drinking (Table 3).

DISCUSSION

THERMOREGULATION

Although our physiological and behavioral observations confirm previous suggestions that Spotted Owls are more sensitive to high ambient temperature (T_a) than typical birds (Barrows and Barrows 1978, Barrows 1981, Ganey et al. 1993), we found substantial differences between the temperature responses of our California

TABLE 3. Water budget of free-living California Spotted Owls feeding nestlings in Lassen National Forest, California.

Category	Water influx, mL day^{-1}	% total
Total water influx (TWI)	68.4	100
Metabolic water[a] (MW)	5.1	7.5
Preformed water (PW = TWI–MW)	63.3	92.5
Water in food[b] (WIF)	35.7	52.2
Drinking water (DW = PW–WIF)	27.6	40.4

[a] Metabolic water was estimated from CO_2 production using the relationship 0.567 mL L^{-1} CO_2.
[b] Water in food was estimated from consumption rates of flying squirrels (based on field metabolic rate) and a prey water content of 70.23%.

Spotted Owls and the Mexican Spotted Owls (*S. o. lucida*) studied by Ganey et al. (1993). These differences may reflect (1) the methods used to measure metabolic rate, (2) seasonal or plumage effects, (3) differences in body size (571 g for Mexican Spotted Owls vs. 700 g for California Spotted Owls), or (4) local (population-level) adaptations. Physiological differences between the two subspecies persist after accounting allometrically for size differences, however, and our discussion emphasizes other possible explanations for the observed differences between these subspecies.

The California Spotted Owl's upper critical temperature (T_{uc}), 35.2°C, is lower than the avian average of 38.2°C (Weathers 1981), but markedly higher than the 17.5°C or 25.2°C T_{uc} reported for Mexican Spotted Owls by Ganey et al. (1993; their T_{uc} varied depending upon the statistical model used to describe metabolism). Furthermore, whereas the thermoregulatory profile of California Spotted Owls conforms to the typical three-segment model (Fig. 1), that of Mexican Spotted Owls was best described by a two-segment model that lacked a thermoneutral zone (Ganey et al. 1993:653). Below the lower critical temperature, resting metabolic rate (RMR) increased with decreasing T_a at a rate of 0.039 mL O_2 (g hr °C)$^{-1}$ in Mexican Spotted Owls versus 0.022 mL O_2 (g hr °C)$^{-1}$ in California Spotted Owls. Thus, the Mexican Spotted Owls' thermal conductance was 80% higher than that of California Spotted Owls, as might be expected since Mexican Spotted Owls were "molting heavily during the testing period" (Ganey et al. 1993), whereas California Spotted Owls were not molting. Thermal conductance of California and Mexican Spotted Owls was 104% and 170%, respectively, of that predicted for rest-phase non-passerine birds (Aschoff 1981).

The basal metabolic rates (BMR) of California and Mexican Spotted Owls also differ markedly. Mexican Spotted Owl BMR (16.88 J g^{-1} hr^{-1}, Ganey et al. 1993) is 30% higher than predicted for a 571-g owl (Wijnandts 1984), whereas that of California Spotted Owls (10.13 J g^{-1} hr^{-1}) is only 82% of the prediction for a 700-g owl (Wijnandts 1984). Mexican Spotted Owls were molting heavily when their BMR was determined, a circumstance that probably increased their BMR by about 18% (Ganey et al. 1993). Accounting for the effects of molt, the mass-specific BMR of Mexican Spotted Owls is still about 37% higher than that of California Spotted Owls, suggesting population-level differences. The degree to which BMR varies between populations is poorly known. BMR differs by up to 20% in House Sparrow (*Passer domesticus*) populations (Hudson and Kimsey 1966) and by up to 18% in White-crowned Sparrow (*Zonotrichia leucophrys*) populations (Maxwell and King 1976); thus the 37% difference between Spotted Owl populations seems large. Ganey et al. (1993) noted that their Spotted Owls were sometimes active during metabolic trials, which may have contributed to their higher estimated BMRs.

The slope of the line relating RMR to T_a at temperatures exceeding T_{uc}, termed the coefficient of heat strain (h_s), provides an integrated measure of a species' response to heat (Weathers 1981). Above T_{uc}, RMR increased linearly with increasing T_a in Mexican Spotted Owls at a rate of 0.008 mL O_2 (g hr °C)$^{-1}$ (three-segment model; Ganey et al. 1993). In contrast, three of four California Spotted Owls exhibited an exponential increase in metabolic rate above T_{uc} similar to that found in Burrowing Owls (*Athene cunicularia*, Coulombe 1970). Because the relation between RMR and T_a above T_{uc} is linear in most avian species (Weathers 1981), we fit a linear relation to our data (Fig. 1) to facilitate comparisons. The value of h_s in California Spotted Owls, 0.047 mL O_2 (g hr °C)$^{-1}$, is 5.9 times that of Mexican Spotted Owls. The h_s of Mexican Spotted Owls is only 22% of that predicted for a 571-g bird (Weathers 1981). Although the Mexican Spotted Owl's incomplete plumage would facilitate heat loss when $T_a < T_b$, and thereby contribute to a reduction in h_s, its h_s is unreasonably low. For the 26 bird species included in Weathers' (1981) analysis, h_s averaged 105% of predicted values (range 54% to 210%). Adjusted for body mass, h_s of the Mexican Spotted Owls is less than half that of the next lowest species. Such a low h_s would imply unusual tolerance to heat stress. In contrast, h_s of California Spotted Owls is 148% of the predicted value, as would be expected of a heat-intolerant species. The exceptionally low h_s reported for Mexican Spotted Owls by Ganey et al. (1993) is thus questionable and may reflect a systematic measurement error.

The differences in metabolic profiles of Mexican and California Spotted Owls are larger than would be expected based on known plumage,

seasonal, or population effects (reviewed by Dawson and O'Connor 1996). Ganey et al. (1993) did not provide sufficient information to permit an evaluation of their data's accuracy, but the small size of their metabolism chamber (20-cm diameter; 45% smaller than ours) may have precluded full mixing of chamber air, led to higher effective chamber temperatures, and confounded their results. Ganey et al. (1993) did not state how they measured T_a within their metabolism chamber. If they assumed it equaled T_a within the temperature-controlled incubator that housed the metabolism chamber, the owl's proximity to the chamber walls could have elevated T_a within the chamber and affected their results. Owls in their study consistently initiated thermally induced behaviors at lower temperatures than did ours. For example, Mexican Spotted Owls began rapid gular fluttering at ambient temperatures no higher than 32.5°C, whereas no owls in our study initiated gular flutter at temperatures less than 34°C. Two of three owls we observed began to gular-flutter continuously at 36°C, the third at 40°C. (Our behavioral observations were of owls within a 432-L controlled-temperature cabinet.) Ganey et al. (1993) found elevated body temperatures at $T_a \geq 25°C$, whereas we found no increase in T_b until T_a exceeded 30°C.

Despite differences in the physiological and behavioral data, both our study and Ganey et al.'s (1993) support the hypothesis that Spotted Owls are relatively intolerant of high temperatures. On a landscape scale, Spotted Owls prefer relatively cool old-growth or late seral stage forests characterized by high structural diversity, large numbers of residual trees, and a high degree of canopy closure (LaHaye et al. 1997, Moen and Gutiérrez 1997). On a finer scale, owls may select roost sites that are exposed to wind to facilitate convective cooling (Hayes and Gessaman 1980) and that are located in shaded areas with minimal direct solar radiation. For example, California Spotted Owl roost sites occur more frequently on north-facing slopes (Bias and Gutiérrez 1992), which receive less direct solar radiation than other slope aspects. Ganey and Balda (1994) concluded that the consistent selection of dense, closed-canopy forests for roosting by Mexican Spotted Owls may indicate that the owls were seeking a favorable microclimate.

Air temperature within a closed-canopy forest should reasonably approximate a Spotted Owl's effective environmental temperature at warmer temperatures (Campbell and Norman 1998). Accordingly, we evaluated T_a during the warmest months of the year (June–September) at Lassen National Forest, based on ten years (1990–1999) of weather data (NOAA National Data Center) recorded near Mineral, CA (40°21′N, 121°36′W) at an elevation of 1486 m. This elevation is at the lower end of the owls' elevational range in the Lassen National Forest and, thus, much of the habitat utilized by Lassen owls should have lower temperatures than those recorded at Mineral. The data indicate that Spotted Owls in the Lassen region rarely encounter ambient temperatures that exceed their T_{uc}. For the 10-year period, 14% of days during the summer period had maximum temperatures that exceeded 30°C, but only 2% had temperatures between 34°C and 36°C. Less than 1% of days had temperatures equaling or exceeding the California Spotted Owl's T_{uc} of 35°C. The close agreement between maximum long-term T_a and the owl's T_{uc} provides strong support for temperature's importance in shaping Spotted Owl distribution.

FIELD METABOLIC RATE AND PARENTAL EFFORT

Owls (order Strigiformes) as a group have much lower metabolic rates than other birds. Their BMR averages 66% and their metabolizable energy (ME) intake averages 76% of that predicted for non-passerine birds (Wijnandts 1984). Even among a group known for low metabolic rates, the California Spotted Owl stands out as exceptional. Its BMR is 18% lower and its ME intake 44% lower than predicted by Wijnandts' (1984) strigiform equations, suggesting that its FMR should also be relatively low. Indeed, the FMR of California Spotted Owls ($n = 5$) is a remarkably low 249 kJ day^{-1} (Table 2), only 34% of that predicted for a 563-g non-passerine bird (Williams et al. 1993). Such an extreme departure from allometric expectation is unusual, but internal consistency between our various independent measures of Spotted Owl energetics adds confidence to our conclusion. Mass-specific FMR of California Spotted Owls averages 128% of the mass-specific ME intake determined during assimilation efficiency trials (0.41 vs. 0.32 kJ g^{-1} day^{-1}, respectively), as would be expected given the greater activity levels of owls in the field. Additionally, the BMR of California Spot-

ted Owls constitutes 58% of FMR, as expected from allometric predictions (Walsberg 1983) (calculated for the owls whose FMR we measured using a mean BMR of 10.13 J g^{-1} hr^{-1} and Table 2 body-mass values). All of our metabolic measurements thus indicate remarkably low rates of energy expenditure by California Spotted Owls.

Spotted Owls are sit-and-wait or ''perch and pounce'' predators (Forsman 1976, Verner et al. 1992), and their low FMR suggests a low level of parental effort. The physiological work rate of parent birds can be expressed as the FMR: BMR ratio (Drent and Daan 1980), with a high ratio implying a relatively high level of parental effort. The FMR of Spotted Owls provisioning young averaged 1.84 ± 0.51 × BMR, a value at the low end of the range of 1.3–6.7 × BMR reported for breeding birds (Masman et al. 1989, Weathers and Sullivan 1989, Peterson et al. 1990), and well below the proposed maximum sustainable effort values of 4.0 × BMR (Drent and Daan 1980) and 5–5.7 × BMR (Weathers and Sullivan 1989). Compared with many other bird species, Spotted Owls clearly do not work hard to provision their offspring.

Whether the Spotted Owl's low FMR and FMR:BMR values primarily reflect food limitation or some other factor(s) is unknown. Indeed, the extent to which food availability limits reproductive success of birds is controversial. Direct measurements of reproductive effort indicate that most bird species do not work to their physiological capacity when rearing young, contra earlier expectations (for review see Weathers and Sullivan 1989). This and other evidence suggests that parent birds may not be routinely food limited. Yet, in some species reproductive success is improved by providing breeding adults with supplemental food (Simons and Martin 1990). The importance of prey as a limit on reproductive success is thus unclear but undoubtedly varies among species and temporally within species.

FOOD AND WATER REQUIREMENTS

The remarkably low FMR of California Spotted Owls necessarily translates into correspondingly low prey requirements. We can estimate prey consumption rates from the FMR data using gross energy content values for flying squirrels and woodrats (adjusted to wet mass values), and the assimilation efficiency of the captive owls

(Table 1). Assimilation efficiency averaged 0.77, which is typical for owls in general as well as for other bird species eating similar diets (reviewed in Castro et al. 1989). Northern flying squirrels are the principal prey item of California Spotted Owls in the Lassen region (Verner et al. 1992, Williams et al. 1992), although two species of woodrat (*Neotoma fuscipes* and *N. cinerea*) are also taken (Verner et al. 1992). Body mass of northern flying squirrels in Lassen National Forest averages 103 g for both sexes and all ages (Williams et al. 1992). Although flying squirrels have a slightly higher gross energy content than woodrats (19.3 vs. 17.7 kJ g^{-1} dry mass, respectively, and 5.75 vs. 5.45 kJ g^{-1} wet mass, respectively), they are only about 50% as large (103 g vs. 221 g, respectively). Thus, woodrats provide considerably more gross energy per prey item than do flying squirrels (1205 kJ vs. 592 kJ on average, respectively). Based on our owl FMR data (Table 2) and assuming a diet composed exclusively of northern flying squirrels, Spotted Owls would need to consume 56 ± 12 g of squirrel per day while provisioning dependent offspring. Thus, on average, they would need to consume about one flying squirrel every 1.8 days to meet their own energy requirements. On a woodrat diet, they would need to consume 59 ± 13 g daily, which equates to one woodrat every 3.7 days.

In addition to prey energy content considerations, woodrat densities are generally higher than flying squirrel densities within their respective ranges (Rosenberg and Anthony 1992). These factors have implications for Spotted Owl home ranges as there is a strong correlation between diet and home-range size. Zabel et al. (1995) found a strong negative linear relationship between breeding season home-range size and the proportion of woodrats in the diet of Northern Spotted Owls. Optimal foraging models predict that home-range size is influenced by energy requirements and the abundance of available prey (Schoener 1968, 1983, Stephens and Krebs 1986). Thus, maintenance of larger home ranges by Spotted Owls and their dependence in Lassen National Forest on a smaller and less dense prey species (flying squirrels) suggest the need for increased foraging effort. Nevertheless, our FMR results from a Spotted Owl population that primarily exploits flying squirrels indicate that even with these considerations, their FMR

during the dependent juvenile stage is remarkably low.

The Spotted Owls' water influx rate as determined by doubly labeled water is 93% of that predicted for a non-passerine bird of their size (Williams et al. 1993), whereas their field metabolic rate is only 34% of predicted. Thus, compared with their rate of energy expenditure, Spotted Owls have relatively high rates of water flux. Indeed, their water economy index (WEI), 0.29 mL kJ^{-1}, is higher than that of most other birds (Nagy and Peterson 1988), suggesting that they are profligate water users. Many carnivorous and frugivorous birds obtain sufficient water from their food and do not need to drink (Goldstein and Skadhauge 2000). California Spotted Owls do not drink under laboratory conditions, but they do drink in the field (JAB and PJH, pers. obs.) and acquire about 40% of their total water requirement by drinking (Table 3). Why California Spotted Owls have such relatively high rates of water flux under field conditions is unknown, but their greater need for water in the field may contribute to their old growth habitat preference.

ACKNOWLEDGMENTS

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