This is contribution 2005-011 to the Pacific Biological Survey.

Literature Cited

Kraus, F., and A. Allison. 2004. New records of reptiles and amphibians from Milne Bay Province, Papua New Guinea. Herpetological Review 35: 413–418.

McDiarmid, R. W., J. A. Campbell, and T. A. Touré. 1999. Snake Species of the World: A Taxonomic and Geographic Reference. Vol. 1. The Herpetologists' League, Washington, DC.

McDowell, S. B. 1974. A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice P. Bishop Museum. Part I. Scolecophidia. Journal of Herpetology 8:1–57.

Wallach, V. 1993. The supralabial imbrication pattern of the Typhlopoidea (Reptilia: Serpentes). Journal of Herpetology 27:214–218.

———. 1995. A new genus for the *Ramphotyphlops subocularis* species group (Serpentes: Typhlopidae), with description of a new species. Asiatic Herpetological Research 6:132–150.

———. 1996a. Two new blind snakes of the *Typhlops ater* species group from Papua New Guinea (Serpentes: Typhlopidae). Russian Journal of Herpetology 3:107–18.

———. 1996b. The systematic status of the *Ramphotyphlops flaviventer* (Peters) complex (Serpentes: Typhlopidae). Amphibia-Reptilia 17:341–359.

Accepted: 11 August 2005.

Appendix 1

Specimens Examined

Typhlops depressiceps.—Papua New Guinea: New Ireland Province: Weitin River Valley, 13 km north, 10.5 km west of river mouth, 4.503°S, 152.937°E, 240 m (BPBM 11904).

Typhlops inornatus.—Papua New Guinea: Milne Bay Province: Bunisi Village, 10.0171°S, 149.6002°E, 1420 m (BPBM 17236); Siyomu Village, 10.0145°S, 149.5970°E, 1300 m (BPBM 17237); Ikara Village, 9.9801°S, 149.6311°E, 800 m (BPBM 17238); Morobe Province: Upper Watut River, near Bulolo (BPBM 2772); along Dunch River, 5.6 km northwest of summit Mt. Shungol, 6.8162°S, 146.6915°E, 750 m (BPBM 17844–45).

Journal of Herpetology, Vol. 39, No. 4, pp. 595–603, 2005

Effects of Body Mass, Feeding, and Circadian Cycles on Metabolism in the Lizard *Sceloporus occidentalis*

John H. Roe,[1,2] William A. Hopkins,[1,3] and Larry G. Talent[4]

[1]*University of Georgia, Savannah River Ecology Laboratory, Aiken, South Carolina 29802, USA*
[4]*Oklahoma State University, Stillwater, Oklahoma 74078 USA; E-mail: talentl@okstate.edu*

Abstract.—We examined aspects of pre- and postprandial metabolism in the diurnally active Western Fence Lizard, *Sceloporus occidentalis*, by measuring rates of oxygen consumption (Vo_2) and carbon dioxide production (Vco_2) at 30°C. *Sceloporus occidentalis* exhibited strong circadian variation in metabolism that continued throughout digestion, with diurnal peaks in metabolism up to four times as high as nocturnal minimum values (standard metabolic rate, SMR). Metabolism increased with increasing body size (mass range = 3.65–19.02 g), with mass exponents ranging from 0.61–0.82. Metabolism of lizards fed meals equivalent to 1.4, 2.9, and 3.9% of their body mass was elevated above fasting metabolism, although significant differences in metabolism were not detected among the three meal sizes. Maximum metabolism during digestion was from 1.2–1.3 times that of maximum fasting metabolism, a value similar to that of other small, frequently feeding lizards. Specific dynamic action (SDA) ranged from 2.38–22.02 mL O_2 and 1.54–14.54 mL CO_2, or 0.05 –0.44 kJ, which is equivalent to 9.4–17.0% of the ingested energy. Mean respiratory quotients (RQ) ranged from 0.65–0.68, indicating lipids were the primary energy substrate used during both fasting and digestion.

Knowledge of metabolic energy expenditure patterns has provided a framework for investigating physiological, behavioral, and ecological adaptations in reptiles (e.g., Congdon et al., 1982). Measuring metabolism permits identifica-

[2] Corresponding Author. Present address: Applied Ecology Research Group, University of Canberra, Canberra, Australian Capitol Territory 2601, Australia; E-mail: roe@aerg.canberra.edu.au
[3] E-mail: hopkins@srel.edu

tion of sources of individual variation and broad-scale patterns of energy use at multiple levels of biological organization. For example, among-species comparisons of metabolism suggest ecological and phylogenetic relationships greatly influence energy expenditure in reptiles (Andrews and Pough, 1985; Secor and Diamond, 2000). Studies of metabolism have also identified how temperature, body mass, time of day, sex, and season influence variation in ecological energetics among individuals or populations (Beaupre, 1993; Beaupre et al., 1993; Angiletta, 2001).

A rich empirical database on lizard metabolism has facilitated comparisons among lizards and between lizards and other taxa (e.g., Bennett and Dawson, 1976; Andrews and Pough, 1985; Waldshmidt et al., 1987, Christian et al., 1997). However, the influence of feeding on metabolism in lizards remains relatively underexplored compared to other aspects of their physiology. A growing literature base on standard metabolic rate (SMR, the metabolic rate of a postabsorptive animal at rest at a specified temperature during the inactive phase of its circadian cycle; Bennett and Dawson, 1976) and specific dynamic action (SDA, the increased energy expenditure associated with digestion, assimilation, and biosynthesis; Kleiber, 1975) has demonstrated how important the relationship between foraging ecology and metabolism is for understanding energy use in snakes (Secor and Diamond, 2000; Secor, 2001). More complete knowledge of SDA in lizards, which also vary widely in foraging ecology (Cooper, 1994), could yield valuable insight on energy use patterns among lizards, and between lizards and other groups of reptiles.

In this study, we examined aspects of pre- and postfeeding metabolism in a phrynosomatid lizard, the Western Fence Lizard (*Sceloporus occidentalis*). Our aims were to determine whether circadian cycles, body mass, and meal size influenced oxygen consumption and carbon dioxide production rates (Vo_2 and Vco_2, respectively).

Materials and Methods

Study Species.—*Sceloporus occidentalis* is a diurnally active phrynosomatid found in a variety of habitats and ranges from Mexico to Canada between the California coast and western Utah in the United States. Foraging behavior in *Sceloporus* spp. is generally classified as sit-and-wait, and most individuals feed frequently and usually have food in their stomach during the active season (Cooper, 1994; Niewiarowski and Waldshmidt, 1992). We established a research colony of *S. occidentalis* at the Savannah River Ecology Laboratory in Aiken, South Carolina, with the parental stock originating from the San Joaquin Valley, California. Within six weeks of hatching, lizards were maintained in a room with a 10:14 L:D cycle (photophase starting at 0630 and scotophase at 1630) and a temperature range of 29–32°C. Lizards were housed in plastic cages (52 × 36 × 18 cm) with screen lids. Each cage contained sand, a hide plate for refuge, a water dish, a dish filled with a calcium supplement (Rep-cal™), and a basking platform under a full spectrum lamp (40–60 W) at one end for thermoregulation. Lizards were fed crickets dusted with vitamin supplement (Rep-cal Herptivite™) daily. To eliminate variation due to sex, we only used males ($N = 11$, F_1–F_3 generations) between 3.65–19.02 g. Minimum size for sexual maturity in male *S. occidentalis* is approximately 12 g, which can be attained at the age of four months in captivity, or approximately two years in the wild (Talent et al., 2002).

Metabolic Measurements.—We measured metabolic rates of *S. occidentalis* indirectly as Vo_2 and Vco_2 using a computer controlled, closed system respirometer (Micro Oxymax, Columbus Instruments, Columbus, OH) described by Hopkins et al. (1999, 2004). Metabolic measurements occurred between 27 October 2003 and 26 February 2004. For each lizard, we measured fasting metabolism in two separate trials, and once after eating crickets equal to 1.44 ± 0.04 (± SE), 2.90 ± 0.07, and 3.92 ± 0.14% of lizard body mass. A meal size of approximately 4% represents the upper limit of what *S. occidentalis* would reliably eat in the laboratory. First and last metabolic trials for each lizard were under fasting conditions, and order of feeding trials was determined by the lizard's motivation to eat. Before each metabolic trial, lizards were fasted for 48 h to ensure that they were postabsorptive. For feeding trials, lizards were offered 1–13 crickets (depending on meal and body size) between 0745 and 0815 h. Mass of crickets was determined on an electronic balance (to the nearest milligram) before being offered to the lizards. Any uneaten crickets were removed and their mass determined once lizards no longer showed interest in feeding, and the mass eaten was calculated as the difference between crickets offered and crickets remaining. Lizards were then placed in individual glass respirometry chambers (600 mL for lizards < 9 g, and 1100 mL for lizards > 9 g) within an environmental cabinet in constant darkness at 30°C, which is within the range of active body temperatures experienced by this species in the wild (Bennett and Gleeson, 1976). Each chamber was covered with paper to reduce external stimuli. The respirometer was started between 0840 and 0900 h, and the first measurement occurred 2.7–3.3 h after feeding. Each chamber was sampled at one-hour intervals for 48 h, a time frame within which other frequently feeding, small lizards complete digestion (Beaupre et al.,

1993; Robert and Thompson, 2000; Iglesias et al., 2003). After every third sample, chambers were refreshed with dry ambient air (dried over a column of Drierite) equaling seven times the chamber headspace (volume of the chamber minus the volume of the lizard). Air was pumped from each respiratory chamber through a drying column containing magnesium perchlorate before passing through a gas sensor. Rates of gas exchange were calculated and adjusted for standard temperature and pressure by the respirometer software (Micro-Oxymax, vers. 6.09, Columbus Instruments, Columbus, OH). Lizards were undisturbed throughout metabolic measurements. After each trial, lizards were returned to their cages (outside of the environmental cabinet) and allowed access to water until subsequent metabolic measurements began.

Data Handling and Analysis.—Prior to all analyses, all metabolic variables and body mass were $\log_{10}$-transformed to better approximate normal distributions and equal variances. Because fasting metabolism was measured during two trials for each lizard, we present fasting metabolism as the mean of the two trials for each measurement period and use mean values in all analyses. Because lizards commonly exhibit daily fluctuations in metabolism resulting from activity and circadian rhythms, procedures to eliminate the influence of elevated gas exchange rates associated with such variation are required for accurate estimates of SMR. We estimated SMR for each individual by truncating the upper 75% of metabolic measurements and taking the mean of the remaining 25% of measurements. For this dataset, the 11 lowest of 45 Vo_2 and Vco_2 measures constitute the lower 25% of values. Similar techniques that use a standardized lower proportion of the measures have been successfully used to estimate SMR in reptiles that exhibit daily Vo_2 variation (Dorcas et al., 2004; Hopkins et al., 2004; Roe et al., 2004). We examined the functional relationship between SMR and body mass using regression analysis.

Similar to that of fasting metabolic measurements, measurements of digestive metabolism are complicated by variance of gas exchange rates associated with circadian rhythms and activity as well. Curve smoothing methods can be used to reduce the influence of undesired sources of metabolic variation from digestive metabolic estimates (Andrade et al., 1997; Powell et al., 1999; Hopkins et al., 2004; Roe et al., 2004). However, the variance associated with circadian rhythms was so great in *S. occidentalis* that such smoothing techniques could not be adopted. Instead, we estimated the total volume of oxygen consumed and carbon dioxide produced during fasting and digesting trials as the integral of total Vo_2 and Vco_2 (Fig. 1). These total gas exchange

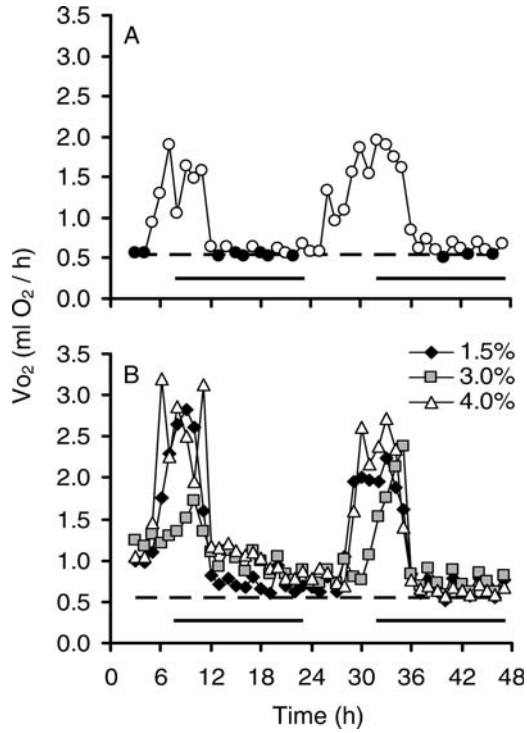

FIG. 1. Oxygen consumption of a representative *Sceloporus occidentalis* (7.17 g) while fasting (A) and after eating crickets equivalent to 1.4, 2.9, and 3.9% of their body mass (B) at 30°C in complete dark. Time "zero" corresponds to the approximate time of meal ingestion (0800) in feeding trials. The solid horizontal lines represent scotophase periods to which lizards were entrained in captivity. The horizontal dashed line represents standard metabolic rate (SMR), and the filled circles on graph A represent the Vo_2-values used to calculate SMR after the upper 75% were removed.

rates represent the sum of numerous components, including SMR, circadian rhythms, activity, and digestion. To examine effects of body mass and meal size on volumes of total O_2 consumed and CO_2 produced, we used repeated measures ANCOVA with lizard body mass (g) as the covariate and a specified compound symmetry covariance structure (PROC MIXED Model, SAS, vers. 8.1, SAS Institute, Cary, NC, 1999). Additionally, we used post hoc tests to examine which treatment groups differed from one another (Solutions for fixed effects, SAS, vers. 8.1, SAS Institute, Cary, NC, 1999). We then examined the functional relationship between body mass, meal size, and O_2 consumption and CO_2 production, using multiple regression analysis. These regression equations allowed us to estimate SDA for any combination of body and meal sizes by subtracting predicted gas volumes for a particular meal size from volumes for a meal

TABLE 1. Results of repeated measures ANCOVA for the effects of body mass (g) and meal size (% body mass) on metabolism of *Sceloporus occidentalis* (3.65–19.02 g) while fasting and while digesting meals equivalent to 1.4, 2.9, and 3.9% of their body mass at 30°C.

Effect	Num df	Den df	*F*	*P*
$1\log_{10}$ (maximum Vo_2/SMR)				
$\log_{10}$-mass	1	9	1.66	0.230
meal size	3	30	1.11	0.361
$\log_{10}$ (Vo_2-max digesting/Vo_2-max fasting)				
$\log_{10}$-mass	1	9	0.77	0.403
meal size	2	20	0.14	0.867
$\log_{10}$ total mL O_2				
$\log_{10}$-mass	1	9	65.50	< 0.001
meal size	3	30	4.01	0.016
$\log_{10}$ total ml CO_2				
$\log_{10}$-mass	1	9	44.71	< 0.001
meal size	3	30	3.08	0.042

size of zero (i.e., fasting gas exchange volume), while holding body mass constant. We then converted SDA to kJ expended (19.8 J per mL O_2 consumed; Secor and Diamond, 2000), and expressed SDA as the percentage of ingested energy used during digestion (SDA coefficient, Jobling, 1981). Energy content of crickets was determined by bomb calorimetry at the University of Georgia's Poultry Science Lab. Mean energy content of crickets was 5.8 kJ g^{-1} wet mass.

Increases in metabolism associated with circadian rhythms were estimated by calculating the ratio of maximum Vo_2 to SMR during fasting trials. Metabolic elevations resulting from a combination of circadian rhythms and digestion were estimated by calculating the maximum Vo_2:SMR ratio during digestion. We attempt to distinguish increases in metabolism attributed to circadian rhythms from those of digestion by comparing maximum Vo_2 during digestion to maximum Vo_2 during fasting (Vo_2 max digestion/Vo_2 max fasting). We examined the effects of body mass and meal size on both the maximum Vo_2/SMR and the Vo_2 max digestion/Vo_2 max fasting ratios using repeated measures ANCOVAs with lizard body mass (g) as the covariate in the model, and no specified covariance structure.

We calculated the respiratory quotient (RQ; the ratio of CO_2 produced to O_2 consumed) for each feeding treatment. RQ allows inference about the substrates used for aerobic catabolism (Withers, 1992). Significance was assessed at $P < 0.05$ for all statistical analyses, and values are reported as mean ± 1 SE.

RESULTS

Sceloporus occidentalis exhibited circadian cycles in metabolism both while fasting and during digestion of all meal sizes, with the lowest metabolic values occurring between 2100 and 0900 h each day (Fig. 1). The mean of the lower 25% of metabolic values results in an estimate of SMR that transects the majority of data points representing resting, baseline metabolism during the scotophase period to which lizards were entrained. The relationship between SMR and body mass (g) is described by the following equations: $\log_{10}$ SMR (O_2) = 0.731 × $\log_{10}$ body mass − 0.831 ($r^2 = 0.82$, $P < 0.001$), and $\log_{10}$ SMR (CO_2) = 0.824 × $\log_{10}$ body mass − 1.124 ($r^2 = 0.77$, $P = 0.001$). The mean RQ during fasting was 0.68 ± 0.01.

Maximum Vo_2/SMR ratios were generally higher during digestion (4.2 ± 0.5 [1.4%], 4.4 ± 0.4 [2.9%], and 4.2 ± 0.3 [3.9%]) compared to fasting (3.4 ± 0.2), but these differences were not statistically significant and did not vary among meal sizes (Table 1). Slopes of the relationship between maximum Vo_2/SMR ratios and body mass were similar among feeding treatments ($F_{3,27} = 0.41$, $P = 0.748$ for the interaction between $\log_{10}$ mass and meal size). The Vo_2 max digestion/Vo_2 max fasting ratio did not differ among meal size treatments (Table 1). Peak Vo_2 during digestion was only 25–30% higher than peak Vo_2 while fasting. Metabolic rate for 10 of 11 lizards in the highest feeding treatment returned to levels equal to or below prefeeding SMR within 48 h after feeding, and metabolic rate in all lizards returned to within 5% of the range (difference between peak digestive metabolism and SMR) within 45 h of feeding.

The total volume of O_2 consumed and CO_2 produced was influenced by body mass and feeding (Table 1). However, post hoc tests indicated that rates of gas exchange did not differ among meal sizes for fed individuals, and volumes of O_2 consumed and CO_2 produced during digestion of meals equivalent to 1.4% of body mass were not different from fasting lizards ($P = 0.06$ for O_2, $P = 0.20$ for CO_2; Fig. 2). Slopes of the relationship between body mass and gas exchange rates were similar among feeding treatments and ranged from 0.609–0.791 for O_2 ($F_{3,27} = 0.67$, $P = 0.579$ for interaction between $\log_{10}$ mass and meal size) and from 0.611–0.824 for CO_2 ($F_{3,27} = 0.74$, $P = 0.535$ for the interaction between $\log_{10}$ mass and meal size). The overall relationship between body mass (g), meal size (% of body mass), and ml O_2 consumed was significant ($r^2 = 0.78$, $P < 0.001$) and is described by the following equation: $\log_{10}$ mL O_2 = 1.08 + (0.683 × $\log_{10}$ body mass) + (0.024 × meal size). The relationship between body mass (g), meal size (% of body mass), and ml CO_2 produced was also significant ($r^2 = 0.73$, $P < 0.001$) and is described by the following equation: $\log_{10}$ ml CO_2 = 0.907 + (0.698 × $\log_{10}$ body mass) + (0.023 × meal

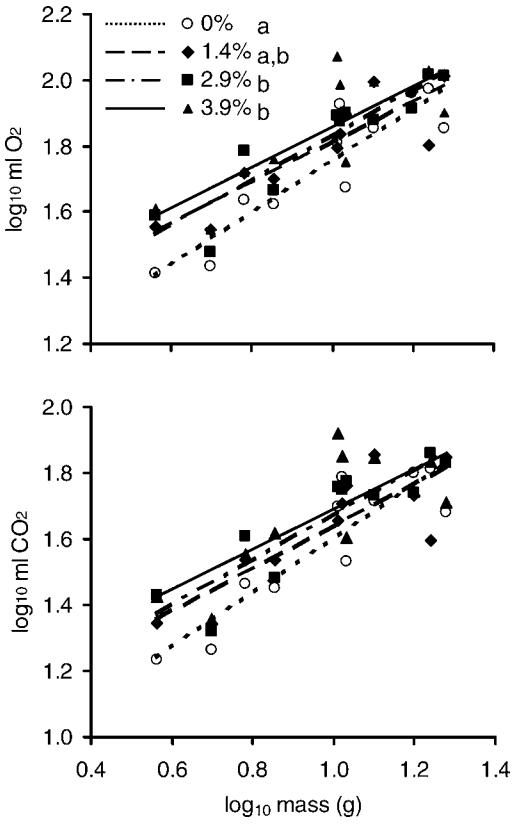

FIG. 2. Relationships between metabolism (cumulative volume of oxygen consumed and carbon dioxide produced) and body mass in *Sceloporus occidentalis* during fasting (0%) and after eating crickets equivalent to 1.4, 2.9, and 3.9% of their body mass at 30°C. Similar letters indicate no difference between meal size treatments.

size). The above equations represent total gas exchange rates (i.e., SMR + circadian cycles + SDA), not just that associated with digestion. Mean RQs during digestion were 0.65 ± 0.01, 0.68 ± 0.01, and 0.67 ± 0.01 for the 1.4, 2.9, and 3.9% meal sizes, respectively.

DISCUSSION

Circadian Cycles.—Sceloporus occidentalis exhibited cyclic oscillations in metabolism indicative of a circadian cycle (endogenous rhythm) because variation persisted in constant dark in both fasting and digesting states. The timing of elevated metabolism was consistent with the diurnal activity pattern of this species (Underwood, 1981; Sabo, 2003). Metabolism typically increased within a few hours of the start of photophase, peaked just prior to scotophase, and dropped to resting levels shortly thereafter (Fig. 1). The range of maximum Vo_2/SMR ratios for both fasting and feeding *S. occidentalis* (3.4–4.4) were consistent with differences between daily maximum and minimum Vo_2 for *S. occidentalis* reported previously (1.8–5.4, Jameson et al., 1977), and within the range typical of squamates in general (1.5–5.0, Waldshmidt et al., 1987). Circannual variation of circadian activity rhythms in laboratory colonies of *Sceloporus virgatus* maintained in constant photothermal regimes were observed by Stebbins (1963), but because our study spanned only four months, we could not fully examine whether our *S. occidentalis* colony exhibits such seasonal changes in activity or metabolism. However, we did not observe any obvious changes in the circadian metabolic pattern in *S. occidentalis* over the short duration of this study.

The degree of metabolic increase during digestion has been demonstrated to equal or surpass that of other metabolically demanding activities in some reptiles, particularly those that ingest large meals at infrequent intervals (Secor and Diamond, 1998; Secor et al., 2000). Such observations have led to the question of whether the energetic cost of digestion conflicts with simultaneously competing systems that also require considerable energy. In the lizard *Varanus exanthematicus* and the snake *Python morulus*, energy used during short bursts (several minutes) of postprandial exercise was greater than that used for exercise or digestion alone, suggesting an additive response where neither system is compromised when operating simultaneously (Secor et al., 2000; Bennett and Hicks, 2001). That *S. occidentalis* exhibited circadian cycles in metabolism during digestion suggests such cycles are an integral aspect of energy use, even in the presence of other physiologically demanding states. However, in contrast to short bursts of intense activity, elevated energy demands during circadian cycles are more prolonged (several hours). The persistence of the circadian rhythm during digestion has also been observed in the lizard *Eulamprus quoyii* (Iglesias et al., 2003), and in the snakes *Nerodia fasciata fasciata* (Hopkins et al., 2004) and *Lamprophis fuliginosus* (Roe et al., 2004). Many free-ranging squamates, including *Sceloporus*, have circadian metabolic cycles (Waldshmidt et al., 1987) and frequently have food in their guts, both of which require energy. Taken together, the above examples indicate that trade-offs in energy use between SDA and circadian cycles and at least some levels of activity do not occur in some squamates, perhaps because the ability to simultaneously digest food while performing other functions (e.g., foraging, mating, defending territories, avoiding predation) is critical to fitness. For example, many squamates consume meals and continue to actively forage, and the ability of oxygen delivery systems to meet the aerobic demands of multiple systems at once

would be advantageous to these animals (Bennett and Hicks, 2001).

Body Mass.—When comparing metabolism between studies and among taxa with variable body mass, describing relationships between body mass and whole body metabolism is preferred over reporting mass-specific rates because of the confounding effects of ratios (Packard and Boardman, 1988). As expected, whole body metabolism in *S. occidentalis* was strongly influenced by body mass, and metabolism scaled with body mass similarly during fasting and digestion. Mass exponents during digestion (0.609–0.824) were similar to those during fasting (0.731–0.824). Fasting mass exponents were also within the range of values reported for *S. occidentalis*, other lizards, and squamates in general during fasting (Bennett and Dawson, 1976; Andrews and Pough, 1985).

Digestive Metabolism.—The magnitude of the digestive metabolic response is a function of meal size in many lizards. Increases in SDA or digestive scopes with increasing meal size have been previously documented in *Sceloporus merriami* (1.7–7.1% of body mass; Beaupre et al., 1993), *Varanus albigularis* (6.0–9.3% of body mass; Secor and Phillips, 1997), and *Varanus exanthematicus* (5–15% of body mass; Hicks et al., 2000). Although metabolism during digestion was elevated above fasting in *S. occidentalis*, we detected no statistical difference in metabolism among fed individuals for the various meal sizes in our repeated measures design. A slight trend toward higher metabolism with increasing meal size in fed individuals is apparent, but the narrow range of meal sizes may have precluded detection of a significant effect (Fig. 2). However, because the high feeding treatment represented the upper limit of what *S. occidentalis* would voluntarily and reliably eat in the laboratory, testing a wider range of meal sizes was not possible and probably not relevant to *S. occidentalis*. Additionally, our metabolic estimates represent the sum of several components, including digestion, activity, and circadian cycles. To compare our estimates among meal sizes requires the assumption that activity and circadian cycles were similar among fasting lizards and those in all meal-size treatments. Because of the risk of disturbing animals (Zaidan, 2003), we did not monitor lizards during metabolic measurements, which is necessary to identify whether levels or frequency of spontaneous activity differed between trials. Without such surveillance, we were also reluctant to arbitrarily remove any values suspected to be activity-related from the dataset, for increases in metabolism may also be attributable to changes in alertness or other cryptic factors (Feder and Feder, 1981). Consequently, subtle changes in activity or circadian rhythms that we were unable to detect and account for could offset changes in digestive metabolism, potentially confounding our SDA estimates.

Metabolic rate in 10 of 11 lizards returned to levels below or equal to SMR within 48 h after ingesting the largest meal size, and all lizards returned to within 5% of the range (difference between peak digestive metabolism and SMR) within 45 h of feeding. This time frame for completion of digestion is consistent with the time required for metabolism to return to fasting levels in other frequently feeding, small lizards after feeding (Beaupre et al., 1993; Robert and Thompson, 2000; Iglesias et al., 2003, Pan et al., 2005). We consider a return from peak metabolism to within 5% of SMR to indicate a return to fasting levels in *S. occidentalis*, for squamates sometimes fail to completely return to prefeeding fasting levels many days after digestion is complete (Hopkins et al., 2004; Roe et al., 2004).

The incremental increase in metabolism of one physiological state relative to another provides a comparative measure of energy demand associated with that state. Most studies on digestive metabolism in lizards typically report the incremental increase in $\dot{V}O_2$ during digestion above fasting (digestive scope) as a measure of the postprandial metabolic response (Table 2). Maximum $\dot{V}O_2$ during digestion was 1.2–1.3 times higher than maximum fasting $\dot{V}O_2$ in *S. occidentalis*, which is consistent with that of most lizards (1.0–2.5) digesting meals equivalent to 1.4–20% of their body mass at 30–37°C (Table 2). However, digestive scopes in *Varanus* spp. (1.8–10.4) tend to be higher than most lizards studied to date. Many lizards in the genus *Varanus* feed infrequently on large meals (Losos and Greene, 1988; Secor and Phillips, 1997), and it is likely that the larger postprandial $\dot{V}O_2$ increase relative to other lizards is related to the substantial cost of up-regulating the gut from a quiescent fasting state following infrequent feeding events (Secor and Phillips, 1997). Similar correlations between feeding habits and digestive responses have been described in snakes (Secor and Diamond, 2000).

Although the factorial increase in peak metabolism during digestion relative to fasting is a useful comparative measure, this variable provides only a snapshot of energy demands during food processing. Additional variables, including the energy cost of SDA (expressed as cumulative milliliters O_2 consumed and milliliters CO_2 produced, or their energetic equivalents), or as a percentage of ingested energy (SDA coefficient), also provide valuable information on digestive costs, but are not always reported (Table 2). Based on our regression equation, male *S. occidentalis* between 3.65 and 19.02 g consume 2.38–22.02 mL O_2 and produce 1.54–14.54 mL CO_2 above fasting for SDA after

TABLE 2. Specific dynamic action in lizards.

Species	Mass (g)	T (C)	Digestive scope	SDA Coefficient[a]	Meal size (% body mass)	Meal type (kJ g^{-1} wet mass)	Citation
Angolosaurus skoogi	53–73	30	1.5	NR	7.0	Carrots	Clarke and Nicolson, 1994
Eulamprus tympanum	8–11	30	1.1–2.4	NR	4.2–5.7 [b]	Meal worms (NR)	Robert and Thompson, 2000
E. quoyii	19.2–34.7	30	1.5–1.9[c]	7.5–8.1	3.7–6.8 [b]	Meal worms (11.4)	Iglesias et al., 2003
Eumeces chinensis	21–38	30	1.5–2.0	8.5–16.9	3.9–12.4[b]	Meal worm, frog meat (11.8–14.1)	Pan et al., 2005
Sceloporus merriami	3.3–4.7	32–37	1.3–1.8	NR	10–15	Crickets (NR)	Niewiarowski and Waldshmidt, 1992
S. merriami	3.5–5.9	32–36	NR	2.4–4.0	1.7–7.1 [b]	Crickets (6.7) [d]	Beaupre et al., 1993
S. occidentalis	3.7–19.0	30	1.2–1.3	9.4–17.1	1.4–3.9	Crickets (5.8)	This study
Uta stansburiana	1–5	30	1.3	NR	1.9–9.5 [b]	Meal worms (NR)	Roberts, 1968
Varanus albigularis	6200–9200	30	6.7–10.4	17–24	6.0–9.3	Various foods (6.53–7.97)	Secor and Phillips, 1997
V. exanthematicus	260–660	35	1.8–6.3	NR	5–15	Mice, rats (NR)	Hicks et al., 2000
V. exanthematicus	145–900	35	1.95	NR	20	Lizard food (NR)	Bennett and Hicks, 2001

NR refers to values not reported. See text for description of metabolic variables.
[a] Expressed as a percentage of ingested energy.
[b] Estimated from range of wet mass fed and body mass, representing upper and lower extremes of relative meal sizes.
[c] Estimated from graphs.
[d] Converted to kJ g^{-1} wet mass assuming 74% water content.

eating meals weighing between 1.4–3.9% of their body mass. The energy cost of SDA for meals this size is 0.05–0.44 kJ, which is equivalent to 9.4–17% of the ingested energy. In the only other investigation where SDA (ml O_2) was reported for similar-sized lizards, 3.5–5.9 g *S. merriami* fed meals equivalent to 1.7–7.1% of their body mass consumed 0.74–3.24 mL O_2 (Beaupre et al., 1993), values slightly lower but within the range of similar-sized *S. occidentalis* in this study. Additional comparisons can be made for SDA coefficients, which range from 2.4–24% in lizards. SDA coefficients were very similar for *S. occidentalis* and *Eulamprus chinensis*, but there is little overlap among the other species for which this value is reported (Table 2). SDA coefficients rank in the following order: *Vatanus albigularis* > *S. occidentalis* and *E. chinensis* > *Eulampus quoyii* > *S. merriami* (Table 2); however, assessing whether such variance can be attributed to ecological, behavioral, or phylogenetic differences is not possible at this point. Differences in a meal's proximate composition (e.g., protein and energy content) can complicate comparisons of SDA coefficient (Pan et al., 2005). Energy densities of meals fed to lizards in studies of digestive metabolism vary considerably and are often not reported (Table 2). Clearly, more complete knowledge of the digestive metabolic response in lizards is necessary to examine patterns of digestive energy expenditure among lizards, and between lizards and other groups of reptiles.

Respiratory quotients (RQ) are used as an index of the energy substrate used to fuel aerobic metabolism. RQs are generally 1.0 for carbohydrate, 0.84 for protein, and 0.70 for lipid metabolism (Withers, 1992). RQs in *S. occidentalis* during both fasting and digestion ranged between 0.65 and 0.68, suggesting that oxidation of lipids is the primary source of energy during these states. Our RQ values for *S. occidentalis* were similar to those of other reptiles while fasting and at rest, which generally are around 0.7 (Bennett and Dawson, 1976; Litzgus and Hopkins, 2004). However, none of the studies of lizard digestive metabolism that we reviewed reported RQ during digestion. Lipids were likely readily available as an energy source for the lizards in this study, because they were from a captive colony and likely had high lipid reserves.

Both their wide biological diversity and tractability as experimental subjects has stimulated a great deal of comparative research in lizards (e.g., Andrews and Pough, 1985; Vitt and Pianka, 1994). In particular, comparative investigations of lizards have revealed a suite of ecological, behavioral, and physiological correlates of foraging modes (Anderson and Karasov, 1981; Huey and Pianka, 1981; Nagy et al., 1984; Cooper 1994). Traits such as foraging behavior and feeding frequency may also influence the digestive metabolic response in lizards, but such comparisons are currently constrained by both the limited number of species and the lack of consistency of variables examined in studies to date. At a minimum, future studies of the digestive metabolic response in lizards should include estimates of the total cost of digestion (e.g., SDA, SDA coefficient) in addition to digestive scope, as well as details on the energy content of meals.

Examining digestive metabolism in lizards representing a range of body mass and fed a range of meal sizes allows functional relationships between these variables to be described, facilitating comparisons across investigations and among the rich diversity of lizard species.

Acknowledgments.—We thank S. Durant for her assistance with this project and the Poultry Research Laboratory at the University of Georgia for determination of cricket caloric content. Comments from S. Beaupre and two anonymous reviewers improved an earlier version of this manuscript. Animal care and use protocols were approved by the University of Georgia's Institutional Animal Care and Use Committee (A1999-10024-c2). This research as supported by the Environmental Remediation Sciences Division of the Office of Biological and Environmental Research, U.S. Department of Energy through the Financial Assistant Award DE-FC09-96SR18546 to the University of Georgia Research Foundation. Partial support for manuscript completion was provided by the University of Canberra's Vice Chancellor's Postgraduate Research Scholarship and the W. J. Weeden award to JHR.

Literature Cited

Anderson, R. A., and W. H. Karasov. 1981. Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. Oecologia 49:67–72.

Andrade, D. V., A. P. Cruz-Neto, and A. S. Abe. 1997. Meal size and specific dynamic action in the rattlesnake *Crotalus durissus* (Serpentes: Viperidae). Herpetologica 53:485–493.

Andrews, R. M., and F. H. Pough. 1985. Metabolism of squamate reptiles: allometric and ecological relationships. Physiological Zoology 58:214–231.

Angiletta, M. J. 2001. Variation in metabolic rate between populations of a geographically widespread lizard. Physiological and Biochemical Zoology 74:11–21.

Beaupre, S. J. 1993. An ecological study of oxygen consumption in the Mottled Rock Rattlesnake, *Crotalus lepidus*, and the Black-Tailed Rattlesnake, *Crotalus molossus molossus*, from two populations. Physiological Zoology 66:437–454.

Beaupre, S. J., A. E. Dunham, and K. L. Overall. 1993. Metabolism of a desert lizard: the effects of mass, sex, population of origin, temperature, time of day, and feeding on oxygen consumption. Physiological Zoology 66:128–147.

Bennett, A. F., and W. R. Dawson. 1976. Metabolism. *In* C. Gans (ed.), Biology of the Reptilia. Vol. 5. Physiology A, pp. 127–223. Academic Press, New York.

Bennett, A. F., and T. T. Gleeson. 1976. Activity metabolism in the lizard *Sceloporus occidentalis*. Physiological Zoology 49:65–79.

Bennett, A. F., and J. W. Hicks. 2001. Postprandial exercise: prioritization or additivity of the metabolic responses? Journal of Experimental Biology 204: 2127–2132.

Christian, K. A., R. V. Baudinette, and Y. Pamula. 1997. Energetic costs of activity by lizards in the field. Functional Ecology 11:392–397.

Clarke, B. C., and S. W. Nicolson. 1994. Water, energy, and electrolyte balance in captive Namib Sand-Dune Lizards (*Angolosaurus skoogi*). Copeia 1994:962–974.

Congdon, J. D., A. E. Dunham, and D. W. Tinkle. 1982. Energy budgets and life histories of reptiles. *In* C. Gans and H. H. Pough (eds.), Biology of the Reptilia. Vol. 13, pp. 233–271. Academic Press, New York.

Cooper, W. E. 1994. Prey chemical discrimination, foraging mode, and phylogeny. *In* L. J. Vitt and E. R. Pianka (eds.), Lizard Ecology, Historical and Experimental Perspectives, pp. 95–116. Princeton Univ. Press, Princeton, NJ.

Dorcas, M. E., W. A. Hopkins, and J. H. Roe. 2004. Thermal dependency of standard metabolic rate in the Eastern Diamondback Rattlesnake (*Crotalus adamanteus*). Copeia 2004:145–151.

Feder, M. E., and J. H. Feder. 1981. Diel variation in oxygen consumption in three species of Philippine Gekkonid lizards. Copeia 1981:204–209.

Hicks, J. W., T. Wang, and A. F. Bennett. 2000. Patterns of cardiovascular and ventilatory response to elevated metabolic states in the lizard *Varanus exanthematicus*. Journal of Experimental Biology 203:2437–2445.

Hopkins, W. A., C. L. Rowe, and J. D. Congdon. 1999. Elevated trace element concentrations and standard metabolic rate in Banded Water Snakes (*Nerodia fasciata*) exposed to coal combustion wastes. Environmental Toxicology and Chemistry 18:1258–1263.

Hopkins, W. A., J. H. Roe, T. Phillipi, and J. D. Congdon. 2004. Standard and digestive metabolism in the Banded Water Snake, *Nerodia fasciata fasciata*. Comparative Biochemistry and Physiology A 137: 141–149.

Huey, R. B., and E. R. Pianka. 1981. Ecological consequences of foraging mode. Ecology 62:991–999.

Iglesias, S., M. B. Thompson, and F. Seebacher. 2003. Energetic cost of a meal in a frequent feeding lizard. Comparative Biochemistry and Physiology A 135:377–382.

Jameson, E. W., A. A. Heusner, and R. Arbogast. 1977. Oxygen consumption of *Sceloporus occidentalis* from three different elevations. Comparative Biochemistry and Physiology A 56:73–79.

Jobling, M. 1981. The influence of feeding on the metabolic rate of fishes: a short review. Journal of Fisheries Biology 18:385–400.

Kleiber, M. 1975. The Fire of Life: An Introduction to Animal Energetics. Krieger, Huntington, NY.

Litzgus, J. D., and W. A. Hopkins. 2004. Effect of temperature on the metabolic rate of the Mud Turtle (*Kinosternon subrubrum*). Journal of Thermal Biology 28:595–600.

Losos, J. B., and H. W. Greene. 1988. Ecological and evolutionary implications for diet in monitor lizards. Biological Journal of the Linnean Society 35:379–407.

Nagy, K. A., R. B. Huey, and A. F. Bennett. 1984. Field energetics and foraging mode of Kalahari lacertid lizards. Ecology 65:588–596.

Niewiarowski, P. H., and S. R. Waldshmidt. 1992. Variation in metabolic rates of a lizard: use of SMR in ecological contexts. Functional Ecology 6:15–22.

PACKARD, G. C., AND T. J. BOARDMAN. 1988. The misuse of ratios, indices, and percentages in ecophysiological research. Physiological Zoology 61:1–9.

PAN, Z.-C., X. JI, H.-L. LU, AND X.-M. MA. 2005. Influence of food type on specific dynamic action of the Chinese Skink *Eumeces chinensis*. Comparative Biochemistry and Physiology A 140:151–155.

POWELL, M. K., J. MANSFIELD-JONES, AND R. E. GATTEN JR. 1999. Specific dynamic effect in the Horned Frog, *Ceratophrys cranwelli*. Copeia 1999:710–717.

ROBERT, K. A., AND M. B. THOMPSON. 2000. Influence of feeding on the metabolic rate of the lizard, *Eulamprus tympanum*. Copeia 2000:851–855.

ROBERTS, L. A. 1968. Oxygen consumption in the lizard *Uta stansburiana*. Ecology 49:809–819.

ROE, J. H., W. A. HOPKINS, J. W. SNODGRASS, AND J. D. CONGDON. 2004. The influence of circadian rhythms on pre- and post-prandial metabolism in the snake *Lamprophis fuliginosus*. Comparative Biochemistry and Physiology A 139:159–168.

SABO, J. L. 2003. Hot rocks or no hot rocks: overnight retreat availability and selection by a diurnal lizard. Oecologia 136:329–335.

SECOR, S. M. 2001. Regulation of digestive performance: a proposed adaptive response. Comparative Biochemistry and Physiology A 128:565–577.

SECOR, S. M., AND J. A. DIAMOND. 1998. A vertebrate model of extreme physiological regulation. Nature 395:659–662.

———. 2000. Evolution of regulatory responses to feeding in snakes. Physiological and Biochemical Zoology 73:123–141.

SECOR, S. M., AND J. A. PHILLIPS. 1997. Specific dynamic action of a large carnivorous lizard, *Varanus albigularis*. Comparative Biochemistry and Physiology A 117:515–522.

SECOR, S. M., J. W. HICKS, AND A. F. BENNETT. 2000. Ventilatory and cardiovascular responses of pythons (*Python molurus*) to exercise and digestion. Journal of Experimental Biology 203:2447–2454.

STEBBINS, R. C. 1963. Activity changes in the Striped Plateau Lizard with evidence on influence of the parietal eye. Copeia 1963:681–691.

TALENT, L. G., J. N. DUMONT, J. A. BANTLE, D. M. JANZ, AND S. G. TALENT. 2002. Evaluation of Western Fence Lizards (*Sceloporus occidentalis*) and Eastern Fence Lizards (*Sceloporus undulatus*) as laboratory reptile models for toxicological investigations. Environmental Toxicology and Chemistry 21:899–905.

UNDERWOOD, H. 1981. Circadian organization in the lizard, *Sceloporus occidentalis*: the effects of blinding, pinealectomy and melatonin. Journal of Comparative Physiology 141:537–547.

VITT, L. J., AND E. R. PIANKA. 1994. Lizard Ecology, Historical and Experimental Perspectives. Princeton Univ. Press, Princeton, NJ.

WALDSHMIDT, S. R., S. M. JONES, AND W. P. PORTER. 1987. Reptilia. *In* T. J. Panadian and F. J. Vernberg (eds.), Animal Energetics. Vol. 2, pp. 553–619. Academic Press, New York.

WITHERS, P. C. 1992. Comparative Animal Physiology. Saunders College Publishing, New York.

ZAIDAN, F. 2003. Variation in cottonmouth (*Agkistrodon piscivorus*) resting metabolic rates. Comparative Biochemistry and Physiology A 134:511–523.

Accepted: 16 August 2005.

Journal of Herpetology, Vol. 39, No. 4, pp. 603–609, 2005

Diminutive New Species of *Uperoleia* Grey (Anura: Myobatrachidae) from the Vicinity of Darwin, Northern Territory, Australia

JEANNE E. YOUNG,[1,2] MICHAEL J. TYLER,[3] AND SALLY A. KENT[1]

[1]*School of Science and Primary Industries, Charles Darwin University, Darwin, Northern Territory, 0909, Australia*
[3]*School of Earth and Environmental Sciences, University of Adelaide, South Australia, 5005, Australia*

ABSTRACT.—A diminutive new species of *Uperoleia* (male snout–vent length, SVL, 17.3–21.3 mm female, SVL 21.8 mm) is described from 30 km south of Darwin, Northern Territory, Australia. The combination of small size, possession of maxillary and premaxillary teeth, and a completely exposed frontoparietal fontanelle distinguish the species from all other *Uperoleia*. The variation in number of pulses and duration of the advertisement call distinguish the species from the other sympatric *Uperoleia* species, *Uperoleia inundata* and *Uperoleia lithomoda*, as well as from the other Northern Territory species. The proximity of the type locality to Darwin highlights the current inadequate state of knowledge of the northern Australian frog fauna.

Since Moore's (1961) work listing 14 species of anurans in the Northern Territory of Australia, 30 additional species have been reported. All five anuran families found in Australia are repre-

[2] Corresponding Author. Present address: P. O. Box 237, Melrose Park Business Centre, South Australia, 5039, Australia; E-mail: jeanne.young@cdu.edu.au

sented: Bufonidae, Hylidae, Myobatrachidae, Microhylidae, and Ranidae (Tyler and Davies, 1986; Cogger, 2002). Among the myobatrachids, the genus *Uperoleia*, with seven species, is dominant. Currently, 24 species are recognized in *Uperoleia*, a genus with limited morphological diversity (Tyler et al., 1981a,b,c; Davies and Littlejohn, 1986; Davies et al., 1986). Despite the conservative morphology within the *Uperoleia*, the following characters are effective in species recognition: extent of exposure of the frontoparietal fontanelle, presence or absence of maxillary and premaxillary teeth, extent of dermal glands, degree of webbing and fringing on the toes, and advertisement call characteristics (Tyler et al., 1981a; Davies and Littlejohn, 1986; Davies et al., 1986). Other characters (e.g., size, dorsal color pattern, rugosity of the dorsum) are reliable at the extremes of expression (i.e., very large or very small size), and useful in situations where intermediate expressions occur provided there is an understanding of the intraspecifc variation across the range (Davies and Littlejohn, 1986; Davies et al., 1986). Recently, Brodie et al. (1998) investigated the significance of some distinguishing features of color and defense behavior in *Uperoleia*. Although it could be anticipated that additional undescribed species of *Uperoleia* could be found in remote areas, one of us (JEY) located a population only 30 km south of Darwin. The advertisement call of this species is distinct from those of the several species known in the northern periphery of the Northern Territory. Here we describe this new species of frog.

Materials and Methods

The specimens examined are deposited in the Northern Territory Museum (NTM), Darwin, Northern Territory and the South Australian Museum (SAMA), Adelaide, South Australia. Measurements were taken to the nearest 0.1 mm with dial callipers under a binocular dissection microscope following procedures of Tyler et al. (1981a). The following measurements were used: eye diameter (ED); eye to naris distance (EN); internarial span (IN); body length from snout–vent length (SVL); and tibia length (TL). Standard measures of head length and width were not taken because in most *Uperoleia* large parotoid glands cover the side of the head obscuring the tympana (Tyler et al., 1981a; Davies and Littlejohn, 1986; Davies et al., 1986). Radiography and alizarin staining were used to determine the extent of exposure of the frontoparietal fontanelle. Calls were recorded on a Sony tape recorder (Model TC-150) with the gain control bypassed and an Electro-Voice microphone (PL11). The analysis of call pulse and duration of three *Uperoleia inundata* and three individuals of the new species was completed using Adobe™ Audition 1.5 for Windows.

On the night of 20 March 2001 between 2245 and 0045 h the calling location and associated air and call site temperatures were measured for seven male individuals of the new species at the type locality (12°32′15″E, 131°07′17″S; Fig. 1) in the Howard River catchment. Relative humidity and air temperature were measured using a hand held HM34C Vaisala, and the cloud cover and wind conditions were qualitatively noted. Each male was located by triangulating on the call, and the air temperature at the call site was taken 2 cm and 1 m above the animal using a thermocouple.

Uperoleia daviesae sp. n.
Figures 2 and 3

Holotype.—NTM 26524. An adult male collected at the type locality in the Howard River catchment (12°32′15″E, 131°07′17″S) 30 km southeast of Darwin, Northern Territory, Australia (Fig. 1) on 10 March 2001 by J. E. Young, K. A. Christian, I. Morris and G. Sawyer.

Paratypes.—There are 17 paratypes of which 16 are males: NTM R26521–23, 26525–28 collected with the holotype, NTM R27496–97 collected by J. E. Young and S. A. Kent on 30 March 2001 and SAMA R260271–78 collected at the type locality by J. E. Young and M. J. Tyler, on 16 March 2001.

Diagnosis.—A minute species (SVL: male 17.3–21.3 mm; female, 21.8 mm; Fig. 2), characterized by (1) presence of teeth on the maxilla and premaxilla; (2) a completely exposed frontoparietal fontanelle; (3) indistinct dermal glands; (4) eye to naris distance greater than internarial span (EN/IN 1.12–2.00); (5) short hind limbs (TL/SVL 0.26–0.36); (6) toes unfringed with slight basal webbing; (7) orange-red to red inguinal pigmentation; and (8) a short raspy call with 22 pulses.

Comparison with Other Species.—*Uperoleia daviesae* is a dentate species; a feature that is shared with six congeners, *Uperoleia fusca*, *Uperoleia laevigata*, *Uperoleia marmorata*, *Uperoleia mjobergi*, *Uperoleia martini*, and *Uperoleia tyleri*. Of these species, *U. marmorata*, *Uperoleia martini*, and *U. tyleri*, are all larger than *U. daviesae*, have moderately, well-developed or hypertrophied parotoid glands, and have a partially exposed or unexposed frontoparietal fontanelle (Tyler et al., 1981a; Davies and Littlejohn, 1986; Davies et al., 1986). *Uperoleia fusca*, *U. laevigata*, and *U. mjobergi* overlap in size with *U. daviesae* but are distinguished by possessing an unexposed frontoparietal fontanelle and well-developed or hypertrophied parotoid glands. Only some individuals of *Uperoleia micromeles* have vestiges of teeth sporadically present on the premaxillaries

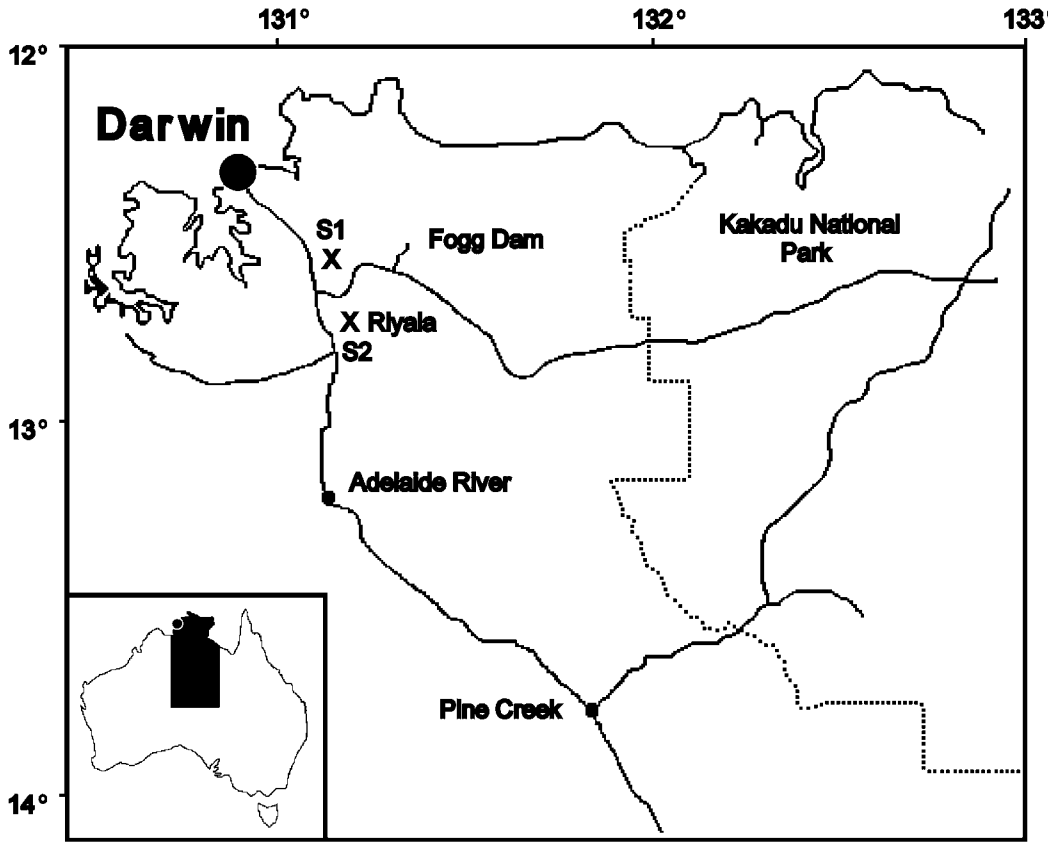

FIG. 1. Map of locations of *Uperoleia daviesae* sp. n. in the Darwin region of the Northern Territory of Australia. S1 designates the type locality of *U. daviesae* sp. n. in the Howard River catchment and S2 indicates an additional locality where *U. daviesae* was found in the Elizabeth River catchment.

and the maxillaries, and this species also differs from *U. daviesae* because it has a poor to moderately exposed frontoparietal fontanelle, an IN > EN (EN/IN 0.83–0.90), moderate to well-developed dermal glands and well fringed toes (Tyler et al., 1981a).

Uperoleia arenicola, *Uperoleia capitulata*, *Uperoleia mimula*, *Uperoleia minima*, *Uperoleia rugosa*, and *Uperoleia trachyderma* are all edentate species that overlap in size with *U. daviesae* (Tyler et al., 1981c; Davies and Littlejohn, 1986; Davies et al., 1986) but not in geographic distribution. Additionally, *U. capitulata*, *U. mimula*, *U. minima*, and *U. rugosa* differ from *U. daviesae* in having a poorly exposed or unexposed frontoparietal fontanelle and well-developed dermal glands, and all but *U. minima* have fringed toes. *Uperoleia arenicola* and *U. trachyderma* have well-developed parotoid glands and fringed toes, but the frontoparietal fontanelle is widely exposed similar to *U. daviesae*. *Uperoleia trachyderma* also has a dorsum densely covered with fine, conical tubercles, which is unique among the *Uperoleia* (Tyler et al., 1981c; Davies et al., 1986).

Only two congeners are sympatric with *U. daviesae*: *U inundata* and *U. lithomoda*, and both species are edentate. *Uperoleia inundata* is a larger species (male 23–28 mm, female 24–28 mm; *U. daviesae* male 17.3–21.3 mm, female 21.8 mm) with well-defined dermal glands, a smooth

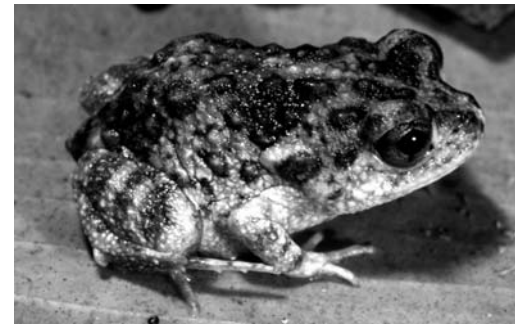

FIG. 2. Dorsolateral view of living *Uperoleia daviesae* sp. n. (male; SVL 18.6 mm). Specimen not collected.

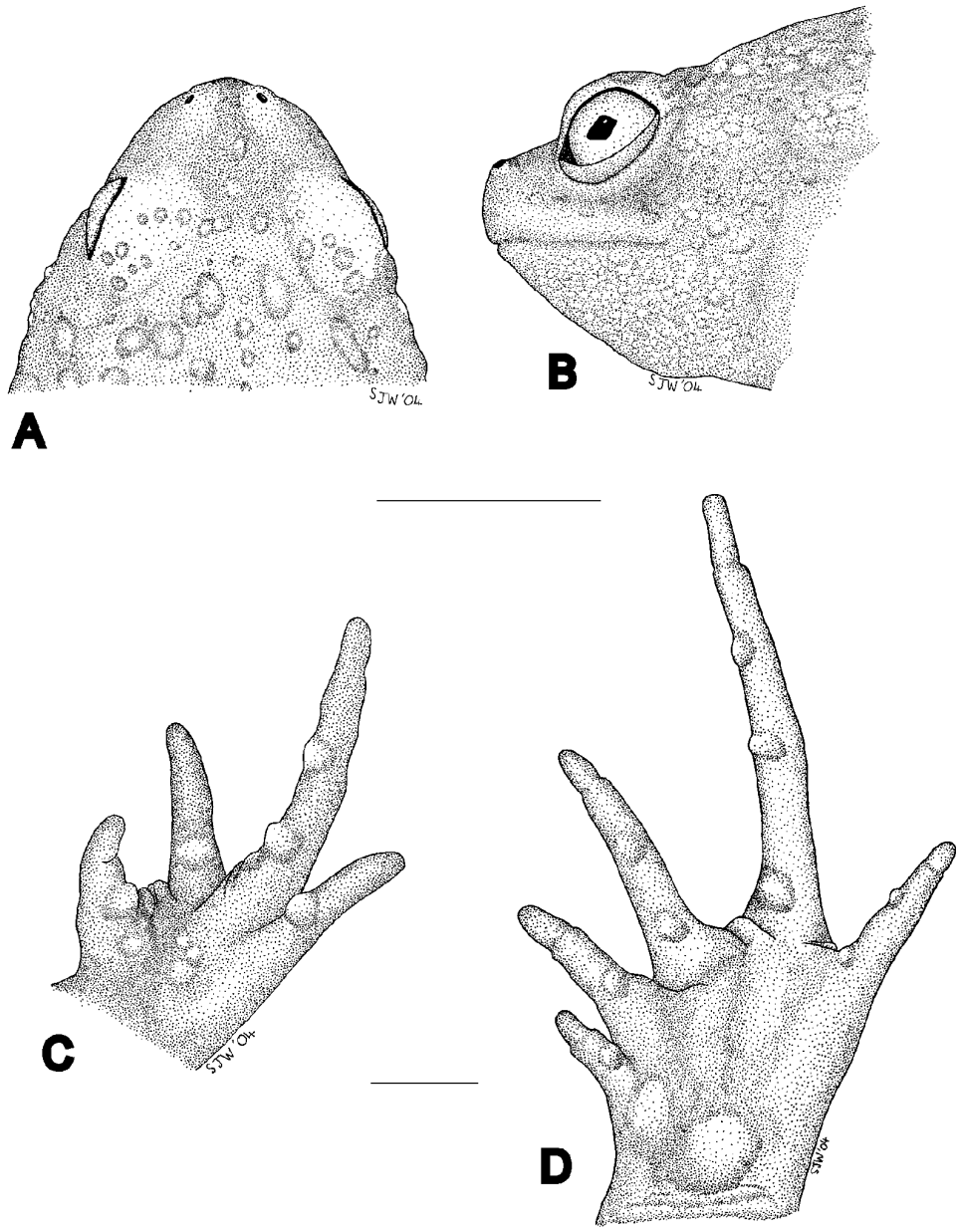

FIG. 3. *Uperoleia daviesae* sp. n., holotype (NTM 26524). (A) Dorsal and (B) lateral views of head (scale = 5 mm); ventral views (scale = 1 mm) of (C) hand and (D) foot.

dorsum, and light orange inguinal pigmentation (Tyler et al., 1981a). *Uperoleia lithomoda* overlaps in size (male 16.7–23.5, female 19.5–24.5) with *U. daviesae* but can be distinguished by the well-defined dermal glands and a strongly defined pattern on the dorsum (in particular dark, crescentic, slightly raised markings usually medial to the parotoid glands; Tyler et al., 1981a; Davies et al., 1986). The calls of three species are easily distinguished by ear; *U. inundata* has a long "raspy" call, *U. daviesae* a short raspy call and *U. lithomoda* a sharp "click." The number of pulses per call also differs but the pulse variation is not easily ascertained by ear (see "Vocalizations").

Description of Holotype.—Maxillary and premaxillary teeth present. Vomerine teeth absent. Frontoparietal fontanelle completely exposed. Snout short, truncated when viewed from above and slightly rounded in lateral profile (Fig. 3A,B). Eye–naris distance (EN) considerably greater

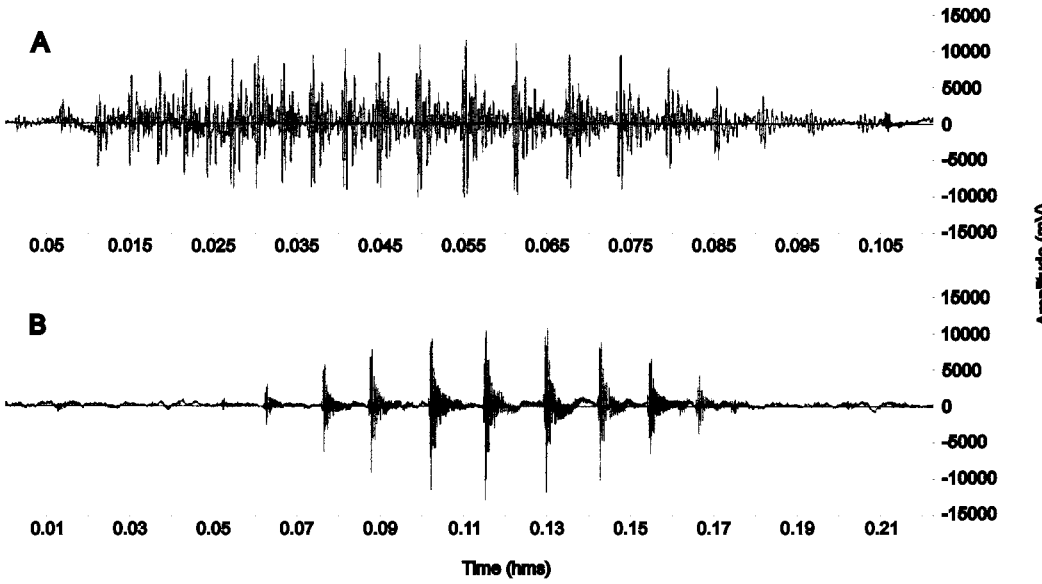

FIG. 4. Sonograms of advertisement calls of (A) *Uperoleia daviesae* sp. n. and (B) *Uperoleia inundata*, recorded at type locality, on 16 December 2001, 2100 h (Air temperature = 25°C, Relative humidity = 90%). Note that the call duration axes are scaled independently.

than IN (EN/IN 1.64). Canthus rostralis poorly defined and straight. Tympanum not visible (Fig. 2). Fingers long, slender, unfringed with small subarticular tubercles; order of length 3 > 4 > 2 > 1 (Fig. 3C). Palmar tubercles poorly developed. Hind limbs short (TL/SVL 0.33). Toes long, unfringed and with slight basal webbing; order of length 4 > 3 = 5 > 2 > 1 (Fig. 3D). Metatarsal tubercles small and oblique (Fig. 2). Subarticular tubercles moderate. Dorsal surface of frog with indistinct dermal glands. Dorsum with scattered and slightly raised tubercles. Cloacal flap absent. Ventral surface of body finely granular. Male with unilobular, submandibular vocal sac.

Measurements of Holotype.—Measurements in millimeters SVL 19.3; TL 6.4; ED 2.8; EN 1.8; IN 1.1.

Coloration.—Dorsal surface pale grey in preservative with pale brown tubercles surrounded by black. Parotoid glands pale cream. A faint yellow midvertebral stripe. Ventral surface cream with darker grey pigment on the submandibular area.

In life, dorsal surface light grey with a light purple tone (Fig. 2). Tubercles brown to red-brown surrounded by black. Parotoid glands pale red-brown; midvertebral stripe pale orange; groin orange-red.

Variations.—Females are larger than males and lack submandibular pigmentation, but otherwise all specimens are morphologically very similar to the holotype. All specimens have a pale grey ground color with darker patches that are associated with the dorsal tubercles, which vary from brown to red-brown. The groin color varies from orange-red to red, and the midvertebral stipe varies from pale yellow to pale red.

Vocalization.—The vocalizations of *Uperoleia* species can be described as a single short click or a longer squelch, with the major variation in call structure being in the duration and number of pulses per call (Tyler et al., 1981a; Davies and Littlejohn, 1986). The call of *U. daviesae* is easily distinguished from that of the sympatric *U. inundata* because *U. daviesae* has a shorter call duration (97 msec; range = 97–98 msec) with a greater number of pulses (22; $N = 3$; Fig. 4A) compared to the *U. inundata* call duration of 142 msec ($N = 3$) with 11 pulses ($N = 3$; Fig. 4B). The duration and pulses reported here for *U. inundata* agree with the previously published values of 145.5 msec duration ($N = 4$; range = 127–160) with 12.5 pulses (range = 11–14; Tyler et al., 1981a). The call of *U. lithomoda*, also sympatric with *U. daviesae*, has a call duration of 27.8 msec, with 1–4 pulses (Tyler et al., 1981a; Davies et al., 1986).

Physiology.—In a comparative study of rates of evaporative water loss (EWL) and cutaneous resistance (R_c) among northern Australian frogs, Young et al. (2005) found *U. daviesae* (referred to as *Uperoleia* sp. nov.) has no cutaneous resistance to EWL ($R_c = -0.1 \pm 0.9$ sec cm^{-1}; surface area specific EWL = 8.9 ± 1.4 mg cm^{-1} h^{-1}), which means water evaporates from the skin at a rate similar to a free water surface. Under desiccating conditions, *U. daviesae* assumes a low flat posture

FIG. 5. (Upper) Open Savannah/*Grevillea* woodland at the type locality and (Lower) a call chamber (indicated by white arrow) used by *Uperoleia daviesae* sp. n.

(without limbs folded to the body) to minimize water losses from the ventral surfaces.

Distribution and Ecology.—*Uperoleia daviesae* was originally found within the Koolpinyah sand sheet of the Howard River catchment (Fig. 1). Also, it has been found in sand sheet areas of the Elizabeth River catchment (12°33′07″E, 131°07′02″S). Recent surveys document populations of *U. daviesae* at 16 additional locations, all within the Howard River sand sheet (W. Freeland, pers. comm.).

The type locality habitat is open Savannah/*Grevillea* woodland, on ephemerally flooded sands with short to medium-height grasses; sedges and herbs are dominant in the understory (Fig. 5). The main breeding areas are characterized by shallow pools with small mounds (possibly termite) with clumps of grass growing over the tops (Fig. 5), sparse tea tree *Leptospermum* spp., and *Banksia*. Several species of carnivorous plants, such as sundews (*Drosera* spp.) and bladderworts (*Utricularia* spp.), are common within the habitat. Populations of this species have been found throughout the Howard River catchment in similar habitat to the type locality. A population found in the Elizabeth River catchment has been found in a similar habitat and soil structure.

Uperoleia daviesae was observed to call in high numbers in early January through February, in chorus with the *U. inundata* and *U. lithomoda*. *Uperoleia lithomoda* called from higher areas, where laterite formations and medium to tall grass clumps occur, whereas *U. inundata* call within the same shallow inundated herbland as *U. daviesae*. *Uperoleia inundata* and *U. daviesae* begin calling in mid to late December if the habitat is inundated. Some individuals of both of these species have been observed calling sporadically after rain prior to habitat inundation. In 2001–2002, *U. daviesae* called only in low numbers in March, and finished calling before *U. inundata*.

Most male *U. daviesae* were observed calling from small chambers at the base of sand mounds within flooded grassland (Fig. 5), either on wet sand or in very shallow water. However, on nights of intense calling, males called from either the tops of the sand mounds or in open sandy patches adjacent to or within flooded shallow pools. Males of *U. daviesae* call in small groups across an area, rather than as scattered individuals as in the case of *U. inundata*.

On the night of 20 March 2001, the calling location and associated air and call site temperatures were measured for seven males. The general weather conditions were clear skies, a light breeze and a relative humidity of 88% (air temperature = 25.5°C). Six males were calling from chambers in the base of sand mounds and one on the top of a sand mound partially obscured by a short grass clump. The calling site temperature for those males in chambers ranged from 29.5–29.7°C, and was 29.1°C for the individual on the top of the sand mound. The average air temperature at 1 m above ground was 26.1 ± 0.6°C.

Etymology.—The specific epithet *daviesae* honors Margaret Davies, whose published contributions have substantially expanded knowledge of the genus *Uperoleia*.

DISCUSSION

The information available thus far suggests *U. daviesae* is restricted to the sand sheets of the Howard River and the Elizabeth River catchments in the Northern Territory. The species has not been identified outside of these catchments in recent surveys (W. Freeland, pers. comm.). Additional surveys across a broader range of northern Australia designed to target *U. daviesae* would be valuable to confirm this restricted distribution. We are aware that another species of frog, *Cyclorana cryptotis*, was previously thought to be restricted to Western Australia and Northern Territory but recently was found to inhabit areas of Northern Queensland (Tyler et al., 1982; McDonald, 1998).

Although the current distribution of *U. daviesae* is tentative owing to limited surveys, the identification is certain based on the small size, the presence of the maxillary and premaxillary teeth, and the distinct advertisement call.

Acknowledgments.—We thank S. Walker (call analyses, sketches), J. Brazier (field assistance), M. Armstrong and K. Beggs (photography), I. Morris and G. Sawyer (call recordings), J. Kirby (graphics editing) and GNP Pty Ltd (additional locality information). Thanks also to K. Christian, S. Donnellan, and C. Saison for advice and comments on the manuscript. Research was conducted with approval from the Animal Ethics Committee of Charles Darwin University in Darwin, Northern Territory, Australia (Reference A99024). Specimens were collected under supervision of P. Horner from Northern Territory Museum and under a permit granted to M. Tyler from Northern Territory Parks and Wildlife Commission.

Literature Cited

Brodie Jr., E. D, C. R. Williams, and M. J. Tyler. 2000. Evolution of aposematic behavior and coloration in the Australian frog genus *Uperoleia*. Journal of Herpetology 32:136–139.

Cogger, H. G. 2002. Reptiles and Amphibians of Australia. Reed New Holland, Sydney, New South Wales, Australia.

Davies, M., and M. J. Littlejohn. 1986. Frogs of the Genus *Uperoleia* Grey (Anura: Leptodactylidae) in south-eastern Australia. Transactions of the Royal Society of South Australia 109:111–143.

Davies, M., K. R. McDonald, and C. Corben. 1986. The genus *Uperoleia* Grey (Anura: Leptodactylidae) in Queensland, Australia. Proceedings of the Royal Society of Victoria 98:147–188.

McDonald, K. R. 1998. First Queensland record of the burrowing frog *Cyclorana cryptotis* Tyler and Martin 1977 (Anura: Hylidae). Transactions of the Royal Society of South Australia 122:85–86.

Moore, J. A. 1961. The Frogs of Eastern New South Wales. Bulletin of the American Museum of Natural History 121:155–385.

Tyler, M. J., and M. Davies. 1986. Frogs of the Northern Territory. Conservation Commission of the Northern Territory, Darwin, Northern Territory, Australia.

Tyler, M. J., M. Davies, and A. A. Martin. 1981a. Australian frogs of the leptodactylid genus *Uperoleia* Grey. Australian Journal of Zoology Supplementary Series 79:1–64.

———. 1981b. New and rediscovered frogs from the Derby-Broome area of Western Australia. Records of the Western Australian Museum 9:147–172.

———. 1981c. Frog fauna of the Northern Territory: new distributional records and the description of a new species. Transactions of the Royal Society of South Australia 105:149–154.

———. 1982. Biology, morphology and distribution of the Australian fossorial frog *Cyclorana cryptotis* (Anura: Hylidae). Copeia 1982:260–264.

Young, J. E., K. A. Christian, S. Donnellan, C. R. Tracy, and D. Parry. 2005. Comparative analysis of cutaneous evaporative water loss in frogs demonstrates correlation with ecological habits. Physiological Biochemistry and Zoology 78: 847–856.

Accepted: 18 August 2005.