



Rates of Metabolism and Water Flux in Free-Ranging Racers, *Coluber constrictor*

Author(s): Michael V. Plummer and Justin D. Congdon

Source: *Copeia*, Vol. 1996, No. 1 (Feb. 2, 1996), pp. 8-14

Published by: [American Society of Ichthyologists and Herpetologists \(ASIH\)](#)

Stable URL: <http://www.jstor.org/stable/1446937>

Accessed: 21/03/2013 13:39

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



American Society of Ichthyologists and Herpetologists (ASIH) is collaborating with JSTOR to digitize, preserve and extend access to *Copeia*.

<http://www.jstor.org>

- in a labrid fish: how care might evolve. *Ethology* 84:319-333.
- , F. WERNERUS, AND R. R. WARNER. 1989. Female choice and the mating cost of peripheral males. *Anim. Behav.* 36:875-884.
- WARNER, R. R., AND P. LEJEUNE. 1985. Sex change limited by parental care: a test using four Mediterranean labrid fishes, genus *Symphodus*. *Mar. Biol.* 87:89-99.

DEPARTMENT OF MARINE SCIENCES, UNIVERSITY OF PUERTO RICO, BOX 5000, MAYAGUEZ,

PUERTO RICO 00709. PRESENT ADDRESS: DEPARTMENT OF ZOOLOGY, UNIVERSITY OF HAWAII AT MANOA, EDMONDSON HALL, 2538 THE MALL, HONOLULU, HAWAII 96822. Send reprint requests to KA. Submitted: 31 Oct. 1994. Accepted: 19 April 1995. Section editor: R. Winterbottom.

Copeia, 1996(1), pp. 8-14

Rates of Metabolism and Water Flux in Free-Ranging Racers, *Coluber constrictor*

MICHAEL V. PLUMMER AND JUSTIN D. CONGDON

A combination of temperature-sensitive radiotelemetry and doubly labeled water was used to determine daily activity periods, thermal profiles, water flux rates, and field metabolic rates (FMR) of free-ranging racers (*Coluber constrictor*) in a temperate mesic habitat during summer. Results were compared to published values on the closely related, ecologically similar coachwhip (*Masticophis flagellum*). Racers were active from about 0900-1800 h. Most snakes were in positive water balance. Rates of water influx (9.49 ml/d) and efflux (9.13 ml/d) were related to rates of body mass change (mean = 0.35%/d) and were about four times greater than those of *Masticophis* inhabiting a more xeric habitat. Mean activity temperature (32°C), FMR (0.157 ml CO₂/g/h), mass-specific daily metabolic energy expenditure (94.5 kJ/kg/d), calculated values of resting metabolism (20.3 kJ/kg/d), and activity metabolism (74.2 kJ/kg/d) in *Coluber* were all similar to those of *Masticophis*. We did not detect any relationship between FMR and either distance moved per day, frequency of activity, or body temperature. Water flux rates were greater in females than in males, but we observed no differences between sexes in body temperature or FMR. Compared to intermolt racers, molting racers had higher body temperatures and FMRs (2%, 15%) and lower water fluxes (17%, 25%), but none of these differences was significant. Compared to early in the activity season, racers in late season had lower body temperatures, were less active, and moved less. Water flux and FMR also decreased (13%, 21%), but the differences were not significant.

GEOGRAPHIC variation in the life history of a reptile species may result from different patterns of energy acquisition and allocation among populations (Congdon et al., 1982; Dunham et al., 1989; Waldschmidt et al., 1987). In snakes, such variation has been demonstrated for different populations of *Crotalus lepidus* using doubly labeled water techniques (DLW, S. Beaupre, unpubl.). However, estimates of field metabolic rates for snakes using DLW techniques are sparse. Such information is available for only two species of free-ranging viperids (*Crotalus cerastes*, Secor, 1992, 1994; *C. lepidus*,

S. Beaupre, unpubl.), one free-ranging colubrid (*Masticophis flagellum*, Secor, 1992, 1994), and one captive viperid in an outdoor enclosure (*Vipera berus*, Bradshaw et al., 1987). Recent reviewers of reptilian energetics have emphasized the need for more DLW studies on a variety of taxa, including snakes (Spotila and Standora, 1985; Lillywhite, 1987; Waldschmidt et al., 1987), and in a variety of habitats that will allow mesic-xeric comparisons (Benabib and Congdon, 1992). Most DLW studies on free-ranging lizards (Anderson and Karasov, 1981; Congdon and Tinkle, 1982; Nagy et al., 1984) and all

studies of free-ranging snakes (Secor, 1992, 1994; S. Beaupre, unpubl.) have been conducted only in warm xeric habitats.

The closely related, often synonymized (e.g., Schatti, 1987), New World snake genera *Coluber* and *Masticophis* contain morphologically and ecologically similar species characterized by having a slender body form, diurnal heliothermy, high preferred body temperature, high level of activity, wide foraging range, active defense, and rapid locomotion (Fitch, 1963, Brown and Parker, 1982; Secor, 1992). These morphological and behavioral attributes may be linked to certain physiological processes. For example, although *Coluber* and *Masticophis* have resting metabolic rates which are indistinguishable from other squamates (Bennett and Dawson, 1976; Andrews and Pough, 1985), total aerobic and anaerobic energy production during activity greatly exceeds that of more sedentary snakes (e.g., *Crotalus*, *Lichanura*; Ruben, 1976, Secor, 1992, 1994). Data from a pooled sample of *Coluber* and *Masticophis* (hereafter referred to as *Coluber/Masticophis*) revealed that their metabolic rates exceed those of some mammals during initial phases of activity (Ruben, 1976) and are among the highest reported for all reptiles (Lillywhite, 1987). Aerobic scopes for *Coluber/Masticophis* equal or exceed those known for any other reptile (Ruben, 1976; Walton et al., 1990). The high aerobic capacity in *Coluber/Masticophis* relative to that in *Crotalus* (Ruben, 1976) determined in the laboratory has recently been verified in free-ranging *Masticophis* and *Crotalus* with DLW data (Secor, 1992, 1994; Secor and Nagy, 1994).

In this paper, we use DLW techniques to determine water flux and field metabolic rates of racers, *C. constrictor*, in a population inhabiting a mesic habitat and in which patterns of activity and movement are known (Plummer and Congdon, 1994). We attempt to answer the following questions: (1) What are the water flux rates and metabolic rates of free-ranging *Coluber*? (2) Do these rates vary with body temperature, activity, movement, sex, or time? (3) How do water flux rates and field metabolic rates in *Coluber* compare with those of the ecologically and phylogenetically similar *Masticophis* from a much more xeric habitat?

MATERIALS AND METHODS

The study area centered on Field 3-412 and Ellenton Bay on the Department of Energy's Savannah River Site near Aiken, South Carolina. Field 3-412 is an old field (abandoned in 1952) on the lowland floodplain terrace of the

Savannah River. The primary vegetation consisted of grassland (67%) interspersed with *Lespedeza* spp., various forbs, woody shrubs, and bare soil (J. R. Jensen, M. E. Hodgson, J. Pinder, B. S. Collins, and H. E. Mackey Jr., Savannah River Operations Office Rep. DP-MS-87-111, 1987, unpubl.). Other vegetation included thickets (22%) of plum (*Prunus angustifolia*) and blackberry (*Rubus* spp.) and scattered clumps of trees (6%) consisting of oak (*Quercus laurifolia*) and pine (*Pinus taeda*). The old field was surrounded by mixed hardwood forest and planted pine forests of various ages. Ellenton Bay was an approximate 10-ha Carolina bay typical of the area. A more detailed description of the climate and aquatic habitats associated with the bay area can be found in Gibbons (1990).

We collected six female and five male racers in wire-mesh funnel traps set along a permanent aluminum drift fence surrounding Ellenton Bay (Gibbons, 1990). We sexed and measured (SVL, mass) racers and implanted temperature-sensitive radiotransmitters (Model CHP-2P, Telonics, Inc., Mesa, AZ) into them following the procedures of Reinert (1992). Transmitter mass was a maximum of 5% of snake mass. After implantation, we injected racers intraperitoneally with 3 ml/kg body mass of water containing 95 atoms ^{18}O per 100 atoms of total oxygen and 0.45 mCi of ^3H per ml. After approximately 12 h, we drew blood from the caudal vein and released the racers at their capture locations. Soon after release, two males were killed by predators (Plummer and Congdon, 1992), and one male died from an unknown cause. We monitored the remaining eight snakes and took blood samples between 20 July and 18 Oct. 1989. Body mass did not differ between males ($n = 2$, 122 ± 18.9 g) and females ($n = 6$, 135 ± 24 g; $t = 0.70$, $df = 6$, $P > 0.50$). Every 10 days, we captured snakes briefly to collect blood samples, which yielded repeated measures of FMR and water flux for each individual. We reinjected snakes every 20 days to replenish isotopes, allowed them to reach equilibrium, and took additional blood samples. We flame-sealed blood samples in heparinized capillary tubes in the field and stored them at 10 C. We analyzed blood samples by liquid scintillation spectrometry for ^3H and proton-activation analysis for ^{18}O (Wood et al., 1975; Nagy, 1980). We calculated water flux rates using equations (4) and (6) of Nagy and Costa (1980). We calculated field metabolic rates with equation (2) of Nagy (1980). We converted rates of CO_2 production from ml CO_2/gh to J/d according to the relationship $25.1 \text{ J}/\text{ml } \text{CO}_2$ (Nagy, 1980). We calculated mean CO_2 production and

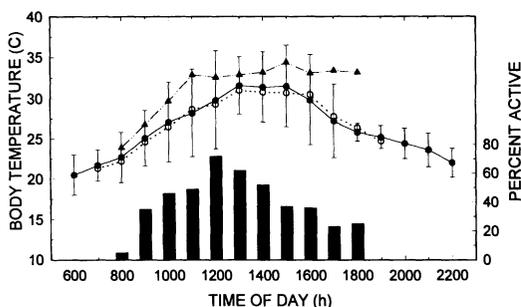


Fig. 1. Diel variation in activity and body temperature of *Coluber constrictor*. Solid circles and line indicate mean \pm 1 SD body temperatures of eight racers measured hourly on seven different days from July–Sept. For racers that were relocated once daily from July–Sept., the open circles and dotted line indicate mean body temperatures of all racers, the triangles and dashed line indicate mean body temperatures of active or basking racers, and the bars indicate the percent of snakes that were active or basking pooled across all days. Excluded from the analysis in the last case were those racers that were inactive because of ecdysis (Plummer and Congdon, 1994). Mean body temperature of snakes was assumed to be approximately 20 C from 2200–0600 h.

water flux rates of each snake from the repeated samples and used the mean CO_2 values to calculate daily energy allocation. We compared means for each snake from 20 July–15 Sept. to means from 16 Sept.–14 Oct. to investigate possible differences in FMR and water fluxes in early and late portions of the activity season.

We estimated postabsorptive standard metabolic rate (SMR) for a range of body temperatures from published data on *Coluber* (Stinner, 1987; Walton et al. 1990), *Masticophis* (Secor, 1992), and *Coluber/Masticophis* (Ruben, 1976). The resulting regression equation was metabolic rate ($\text{ml O}_2/\text{gh}$) = 1.16×10^{-5} temperature^{2.554} ($r = 0.92$, $P < 0.001$, $n = 11$). The predictions of metabolic rate from this model were similar to those from a more general model for reptiles (Bennett and Dawson, 1976) and slightly lower than those from a model for squamates (Andrews and Pough, 1985). To convert O_2 consumed to CO_2 produced, we assumed a respiratory quotient of 0.74 which is the expected value for the metabolism of proteins with an end product of uric acid (Schmidt-Nielsen, 1990).

We relocated each racer once daily at approximately the same time each day and plotted its location on an aerial photograph of the study area which we later digitized. At each relocation, we noted observations on activity, behavior, habitat, snake condition, and measure-

ments of body temperature. Snakes were “inactive” if their location was < 5 m straight-line distance from the previous day’s location and “active” if their location was ≥ 5 m from the previous day’s location. We determined individual thermal profiles of racers by telemetrically recording the body temperature of each racer every 1 h from just before dawn until after dusk on seven different days from July–Sept.

Statistical analyses were conducted with SYSTAT (1992). When our data did not meet the assumptions of parametric tests even when transformed, we used Spearman, Mann-Whitney, and Wilcoxon nonparametric tests. Unless otherwise stated, means are presented with their standard deviations.

RESULTS

Racers were active from approximately 0900–1800 h (Fig. 1). After an initial warm-up period each morning, active racers maintained body temperatures of about 32–33 C (Fig. 1). A diel thermal profile indicated that an average racer (including active and inactive snakes) spent approximately 6 h at a body temperature of 20.0 C, 6 h at 22.5 C, and 3 h each at 25.0, 27.5, 30.0, and 32.5 C (Fig. 1). We used the times spent at these body temperatures and the estimated standard metabolic rate to calculate a daily maintenance energy expenditure of 2.68 kJ/d for a racer of average mass (132 g).

Most snakes were in positive water balance; during the study, five snakes gained body mass (mean mass gain = 11.1%), two snakes lost body mass (mean mass loss = 8.7%), and one snake maintained body mass (Table 1). Body mass change per day was related to both water influx (Spearman correlation, $r_s = 0.76$, $P < 0.05$, $n = 8$) and efflux ($r_s = 0.76$, $P < 0.05$, $n = 8$). Water fluxes and FMR were unrelated to distance moved per day (influx, $r_s = 0.57$, $P > 0.05$, $n = 8$; efflux, $r_s = 0.57$, $P > 0.05$, $n = 8$; FMR, $r_s = 0.48$, $P > 0.10$, $n = 8$) or to level of activity (influx, $r_s = -0.13$, $P > 0.10$, $n = 7$; efflux, $r_s = -0.13$, $P > 0.10$, $n = 7$; FMR, $r_s = -0.07$, $P > 0.10$, $n = 7$). Water fluxes, but not FMR, were related to body temperature (influx, $r_s = 0.74$, $P < 0.05$, $n = 8$; efflux, $r_s = 0.74$, $P < 0.05$, $n = 8$; FMR, $r_s = 0.29$, $P > 0.10$, $n = 8$). Neither water fluxes nor FMR were related to body mass (influx, $r_s = 0.57$, $P > 0.05$, $n = 8$; efflux, $r_s = 0.57$, $P > 0.05$, $n = 8$; FMR, $r_s = 0.48$, $P > 0.10$, $n = 8$). A paired comparison analysis revealed that body temperatures decreased in late season (early = 28.5 ± 1.46 C, late = 25.5 ± 0.99 C; $t = -5.03$, $P < 0.01$, $df = 5$). Accompanying the temperature decrease

TABLE 1. BODY MASS (BM), BM CHANGE, TOTAL NUMBER OF DAYS MONITORED, FIELD METABOLIC RATE (FMR), WATER FLUXES AND BODY TEMPERATURES OF RACERS. Except for no. days monitored, values represent means for individual snakes. Mean movement rate (MR), home range size (HR), and percent of days active are from Plummer and Congdon (1994).

Snake no.	BM (g)	BM change %/d	Tot. no. days	FMR (mlCO ₂ /g/h)	Water		T _b (C)	MR (m/d)	HR (ha)	% days active
					influx (ml/d)	efflux (ml/d)				
01	164.9	-0.01	49	0.148	16.14	16.14	28.0	135	13.7	74
02	126.1	0.67	72	0.142	08.14	07.50	28.1	116	18.4	75
03	135.4	-0.18	73	0.145	05.82	06.00	27.2	73	12.7	69
07	133.1	0.48	54	0.187	07.10	06.63	25.9	104	7.9	82
08	164.0	1.46	23	0.194	18.83	17.10	31.3	74	6.7	63
09	110.0	0.99	31	0.152	09.35	08.57	27.0	134	20.5	75
10	114.0	-0.44	63	0.148	05.87	06.25	26.3	83	5.3	67
11	108.7	-0.16	34	0.136	04.71	04.82	24.2	—	—	—
Mean	132.0	0.35	50	0.157	09.49	09.13	27.2	104	12.2	72
SE	7.9	0.23	7	0.008	01.83	01.68	0.7	7.1	2.2	2

in individuals was a 21% decrease in FMR and 13% decreases for both water influx and efflux but none of these decreases were significant (FMR, early = 0.162 ± 0.028 ml CO₂ [gh]⁻¹, late = 0.128 ± 0.053 ml CO₂ [gh]⁻¹, $t = 0.84$, $P > 0.40$, $df = 5$; influx, early = 9.99 ± 4.89 ml/d, late = 8.65 ± 6.12 ml/d, $t = -0.55$, $P > 0.60$, $df = 5$; efflux, early = 9.63 ± 4.41 ml/d, late = 8.33 ± 6.16 ml/d, Wilcoxon, $W = -5.0$, $P > 0.60$, $n = 6$). The power of each of these paired comparisons tests was $< 10\%$.

A paired comparison analysis of intermolt and molting racers showed that molting racers increased FMR (15%) and body temperature (2%) and decreased water flux (efflux 17%, influx 25%) but none of these changes was significant (FMR, molt = 0.153 ± 0.025 ml CO₂ [gh]⁻¹, intermolt = 0.133 ± 0.029 ml CO₂ [gh]⁻¹, $t = 1.12$, $P > 0.30$, $df = 6$; temperature, molt = 26.8 ± 1.9 C, intermolt = 26.4 ± 1.6 C, $t = 0.42$, $P > 0.60$, $df = 6$; influx, molt = 6.69 ± 1.80 ml/d, intermolt = 8.90 ± 5.44 ml/d, $t = -1.34$, $P > 0.20$, $df = 6$; efflux, molt = 7.03 ± 0.63 ml/d, intermolt = 8.42 ± 2.02 ml/d, $W = 0.0$, $P > 0.90$, $n = 7$). The power of each of these paired comparisons tests was $< 15\%$. Water influx and efflux, but not FMR or body temperature, differed between male and female racers (FMR, Mann-Whitney, $U = 1.0$, $P > 0.05$, $n = 8$; temperature, $U = 3.0$, $P > 0.30$, $n = 8$; influx, $U = 0$, $P < 0.05$, $n = 8$; efflux, $U = 0$, $P < 0.05$, $n = 8$).

DISCUSSION

Racers in this study displayed the diurnal heliothermy, high preferred body temperature, high level of activity, wide foraging range, ac-

tive defense, and rapid locomotion that generally typifies *Coluber* (Fitch, 1963, Brown and Parker, 1982; Secor, 1992). In addition, the specific body temperatures and activity levels were similar to those reported for racers by other workers (summary in Hammerson, 1987). Decreased body temperatures in the late season (this study) were accompanied by late season decreases in activity and movement (Plummer and Congdon, 1994), and we anticipated concurrent decreases in water flux and FMR (Secor, 1994). Although water flux and FMR were reduced by 13% and 21%, respectively, in the late portion of the activity season, the lack of statistical significance probably resulted from our failure to extend the study late enough in the activity season and by the low statistical power of the tests because of low sample sizes.

Other proximate factors might also affect FMR and water fluxes. For example, water flux rates scale with body mass among a variety of vertebrate and invertebrate taxa (Nagy and Peterson, 1988), but we could not detect such differences in *Coluber* perhaps because of the small range in body mass of our snakes (109–165 g). Also, ecdysis is known to affect the behavior and physiology of snakes in ways which should affect FMR and water flux (e.g., level of activity, body temperature selection, resting metabolic rate; Gans et al., 1968; Taylor and Davies, 1981; Peterson et al., 1993). Compared to intermolt snakes, molting racers were much less active (Plummer and Congdon, 1994). We suspect that our chances of detecting significant differences in either FMR, temperature, or water flux would have been greater if most of our "molting" blood samples had not also included, to various degrees, periods of intermolt for the same indi-

TABLE 2. MEAN ACTIVITY, MOVEMENTS, BODY TEMPERATURES (T_b), BODY MASS (BM), BODY MASS CHANGE, WATER INFLUX, FIELD METABOLIC RATES (FMR), AND DAILY ENERGY EXPENDITURES ON FMR, SMR, AND FMR-SMR (ENERGY EXPENDED ABOVE SMR ON ALERTNESS, DIGESTION, ACTIVITY, LOCOMOTION, ETC.) OF *Coluber* (PLUMMER AND CONGDON, 1994; PRESENT STUDY) WITH A COMPARISON TO THOSE OF *Masticophis flagellum* (SECOR, 1992, 1994). Daily energetic expenditures for *Coluber* were calculated based on a daily thermal profile of 6 h each at body temperatures of 20 C and 22.5 C and 3 h each at 25 C, 27.5 C, 30 C, and 32.5 C.

	<i>Coluber</i>	<i>Masticophis</i>
No. snakes	8	11
Daily activity (%)	72	76
Movement rate (m/d)	104	186
Home range (ha)	12	53
Mean T_b when active (C)	32	33
Mean T_b in burrow (C)	25	29
BM (g)	132.0	123.7
BM change (%/d)	0.35	0.24
Water influx (ml/kg/d)	71.9	19.7
FMR (mlCO ₂ /g/h)	0.157	0.154
FMR (kJ/kg/d)	94.5	94.7
SMR (kJ/kg/d)	20.3	21.8
FMR-SMR (kJ/kg/d)	74.2	72.9

vidual. In addition, the lack of significance probably was influenced by the low statistical power of the tests because of low sample sizes.

Most variables relating to the behavior and physiology of *C. constrictor* from a mesic habitat are remarkably similar to those of the ecologically and phylogenetically similar *M. flagellum* from a xeric habitat (Table 2). One major difference was the approximately four times greater water flux rate in *Coluber* compared to *M. flagellum*. The comparison of water influx rates of *Coluber* to *M. flagellum* suggests that *Coluber* is not constrained by water and either obtains more water in its food or drinks water that is generally available in its habitat. For example, water was continually available for drinking throughout the study at Ellenton Bay. A similar magnitude of difference in water flux rates to that between *Coluber* and *Masticophis* was found in sceloporine lizards from mesic compared to xeric habitats (Benabib and Congdon, 1992). Some snakes from xeric habitats have lower rates of evaporative water loss compared to those from mesic habits (Gans et al., 1968), but the specific mechanisms for water conservation which appear to be present in *M. flagellum*, and lacking in *Coluber*, are unknown.

Another major difference between *Coluber* and *M. flagellum* was a lower rate of movement

in *Coluber*. Because our racers were adult, summer-active, and postreproductive, much of the movement we observed probably was related to foraging (Gibbons and Semlitsch, 1987; Plummer and Congdon, 1994). The generally lower availability of food energy in deserts for reptiles (Congdon, 1989) may require foraging movements of greater frequency and distance in *Masticophis*.

The energetic cost of movement in *Coluber* is not trivial and is more than was commonly thought for snakes in general (Walton et al., 1990). An average racer at 30 C traveling by lateral undulation at a median aerobically sustainable speed of 0.35 km/h would expend approximately 0.63 ml O₂ [gh]⁻¹ (Walton et al., 1990). Assuming that racers move for 5 h in the average 9-h activity period each day, the expenditure for movement would require about 6 kJ, or 60% of the daily energetic expenditure above SMR (which includes energy expended on alertness, digestion, activity, and locomotion (Secor and Nagy, 1994; Table 2). A cost of 60% of the energy expended each day suggests that the cost of locomotion in *Coluber* represents a substantial part of its total annual energy budget. A similar cost of activity is exhibited by another active, widely foraging squamate (*Cnemidophorus tigris*; Anderson and Karasov, 1981). The absence of a relationship between FMR and movement in *Coluber* perhaps was because average daily movement is a poor indicator of total activity in snakes (S. Beaupre, unpubl.). For example, the ratio of the actual path traveled compared to the straight-line distance between daily relocations ranged from 1.4 in *Masticophis* to 1.8–2.4 in *C. cerastes* (Secor, 1992, 1994; Brown and Lillywhite, 1992). Another source of error, based on the high ranking of *C. constrictor* among snake species in the proportion of captured individuals which contain identifiable food (84–90%; Shine, 1986), is a probable high frequency of feeding. A high frequency of feeding in snakes may result in a high proportion of the FMR being contributed by the cost of maintaining a continuously active digestive tract and frequent digestion (Secor and Nagy, 1994; Secor et al., 1994).

Mass-specific metabolic expenditures of both summer-active *Coluber* and *Masticophis* are approximately 90 kJ/kg per day (Table 2) which is approximately 4.5 times greater than that expended by these snakes in the resting state and almost 50 times greater than that expended by hibernating garter snakes (*Thamnophis sirtalis*, Costanzo, 1985). The results of this study further confirm the high metabolic capability previously determined in the laboratory for *Col-*

uber/*Masticophis* (Ruben, 1976) and for *Masticophis* in the field (Secor, 1992, 1994). The FMRs are greater than those reported for crotaline snakes (Secor, 1992, 1994; S. Beaupre, unpubl.) but lower than those reported for iguanid (Nagy, 1982; Benabib and Congdon, 1992), teiid (Anderson and Karasov, 1988), and lacertid lizards (Bradshaw et al., 1987). The extensive DLW data on free-ranging lizards permit comparisons within and among species which differ in time of activity, habitat, foraging mode, morphology, and phylogeny (e.g., Anderson and Karasov, 1981; Benabib and Congdon, 1992; Nagy et al., 1984). In free-ranging snakes, however, DLW data are still inadequate to make extensive generalizations relating metabolic levels with behavior, ecology, or phylogeny (Lillywhite, 1987), notwithstanding the elegant comparative studies of Secor (1992, 1994) and Secor and Nagy (1994) on the widely foraging *M. flagellum* and the sit-and-wait *C. cerastes* and that of S. Beaupre (unpubl.) on interpopulation variation in life histories of *C. lepidus*.

In summary, our study of the rates of metabolism and water flux in *Coluber* from a mesic area compared to those of *Masticophis* from a more xeric area indicates that metabolic rates are phylogenetically conservative whereas water flux rates are more variable ecologically. Moreover, for wide foragers, the energetic cost of activity may be high. Similar examples of FMR, water flux, and cost of activity have been reported in various lizard species suggesting that such patterns may be general in squamates.

ACKNOWLEDGMENTS

We thank J. Haskins for his assistance in the field, R. Seigel for providing his mark-recapture data on *Coluber* at Ellenton Bay, R. Anderson for assisting with the doubly labeled water, and S. Secor and S. Beaupre for providing their unpublished manuscripts. Statistical advice was provided by J. W. Gibbons and P. Niewiarowski. The manuscript was read by J. W. Gibbons, R. Kennett, P. Niewiarowski, and H. Whiteman. Technical assistance provided by R. Fischer, J. W. Gibbons, T. Mills, and R. Seigel is gratefully acknowledged. This study was approved by the University of Georgia Animal Care and Use Committee and by the Savannah River Ecology Laboratory Safety Committee. This research was supported by a sabbatical leave from Harding University (MVP), the Visiting Faculty Research Participation Program of the University of Georgia's Savannah River Ecology Laboratory (MVP), and by contract DE-AC09-

76SROO-819 between the US Department of Energy and SREL.

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.
- , AND ———. 1988. Energetics of the lizard *Cnemidophorus tigris* and life history consequences of food-acquisition mode. *Ecological Monographs* 58:79-110.
- ANDREWS, R. M., AND F. H. POUGH. 1985. Metabolism of squamate reptiles: allometric and ecological relationships. *Physiol. Zool.* 58:214-231.
- BENABIB, M., AND J. C. CONGDON. 1992. Metabolic and water-flux rates of free-ranging tropical lizards *Sceloporus variabilis*. *Physiol. Zool.* 65:788-802.
- BENNETT, A. F., AND W. R. DAWSON. 1976. Metabolism, p. 127-223. *In: Biology of the Reptilia*. Vol. 5. C. Gans and W. R. Dawson (eds.). Academic Press, New York.
- BRADSHAW, S. D., H. SAINT GIRONS, G. NAULEAU, AND K. A. NAGY. 1987. Material and energy balance of some captive and free-ranging reptiles in western France. *Amphib. Reptil.* 8:129-142.
- BROWN, T. W., AND H. B. LILLYWHITE. 1992. Autecology of the Mojave Desert sidewinder, *Crotalus cerastes cerastes*, at Kelso Dunes, Mojave Desert, California, USA, p. 279-308. *In: Biology of the pitvipers*. J. A. Campbell and E. D. Brodie (eds.). Selva Press, Tyler, TX.
- BROWN, W. S., AND W. S. PARKER. 1982. Niche dimensions and resource partitioning in a Great Basin desert snake community, p. 59-81. *In: Herpetological communities*. N. J. Scott (ed.). US Fish and Wild. Ser. Wild. Res. Rep. 13, Washington, DC.
- CONGDON, J. D. 1989. Proximate and evolutionary constraints on energy relations of reptiles. *Physiol. Ecol.* 62:356-373.
- , AND D. W. TINKLE. 1982. Energy expenditure in free-ranging sagebrush lizards (*Sceloporus graciosus*). *Can. J. Zool.* 60:1412-1416.
- , A. E. DUNHAM, AND D. W. TINKLE. 1982. Energy budgets and life histories of reptiles, p. 233-271. *In: Biology of the Reptilia*. Vol. 13. Physiology D. C. Gans and F. H. Pough (eds.). Academic Press, New York.
- COSTANZO, J. P. 1985. The bioenergetics of hibernation in the eastern garter snake *Thamnophis sirtalis sirtalis*. *Physiol. Zool.* 58:682-692.
- DUNHAM, A. E., B. W. GRANT, AND K. L. OVERALL. 1989. Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. *Ibid.* 62:335-355.
- FITCH, H. S. 1963. Natural history of the racer, *Coluber constrictor*. *Univ. Kansas Publ. Mus. Nat. Hist.* 15:351-488.
- GANS, C., T. KRAKAUER, AND C. V. PAGANELLI. 1968. Water loss in snakes: interspecific and intraspecific variability. *Comp. Biochem. Physiol.* 27:747-761.
- GIBBONS, J. W. 1990. Turtle studies at SREL: a re-

- search perspective, p. 19–44. *In*: Life history and ecology of the slider turtle. J. W. Gibbons (ed.). Smithsonian Institution Press, Washington, DC.
- , AND R. D. SEMLITSCH. 1987. Activity patterns, p. 396–421. *In*: Snakes: ecology and evolutionary biology. R. A. Seigel, J. T. Collins, and S. S. Novak (eds.). MacMillan, New York.
- HAMMERSON, G. A. 1987. Thermal behaviour of the snake *Coluber constrictor* in west-central California. *J. Therm. Biol.* 12:195–197.
- LILLYWHITE, H. B. 1987. Temperature, energetics, and physiological ecology, p. 422–477. *In*: Snakes: ecology and evolutionary biology. R. A. Seigel, J. T. Collins, and S. S. Novak (eds.). MacMillan, New York.
- NAGY, K. A. 1980. CO₂ production: analysis of potential errors in the doubly-labeled water method. *Am. J. Physiol.* 238:466–473.
- . 1982. Energy requirements of free-living iguanid lizards, p. 49–59. *In*: Iguanas of the world. G. M. Burghardt and A. S. Rand (eds.). Noyes Publ. Park Ridge, NJ.
- , AND D. P. COSTA. 1980. Water flux in animals: analysis of potential errors in the tritiated water method. *Am. J. Physiol.* 238:454–465.
- , AND C. C. PETERSON. 1988. Scaling of water flux rate in animals. *Univ. California Pub. Zool.* 120:1–172.
- , R. B. HUEY, AND A. F. BENNETT. 1984. Field energetics and foraging mode of Kalahari lacertid lizards. *Ecology* 65:588–596.
- PETERSON, C. R., A. R. GIBSON, AND M. E. DORCAS. 1993. Snake thermal ecology: the causes and consequences of body-temperature variation, p. 241–314. *In*: Snakes: ecology and behavior. R. A. Seigel and J. T. Collins (eds.). McGraw-Hill, Inc., New York.
- PLUMMER, M. V., AND J. D. CONGDON. 1992. Life history: *Coluber constrictor*. Predation. *Herpetol. Rev.* 23:80–81.
- , AND ———. 1994. Radiotelemetric study of activity and movements of racers (*Coluber constrictor*) associated with a Carolina Bay in South Carolina. *Copeia* 1994:20–26.
- REINERT, H. K. 1992. Radiotelemetric field studies of pitvipers: data acquisition and analysis, p. 185–197. *In*: The biology of pitvipers. J. A. Campbell and E. D. Brodie (eds.). Selva Publ. Co., Tyler, TX.
- RUBEN, J. A. 1976. Aerobic and anaerobic metabolism during activity in snakes. *J. Comp. Physiol.* 109:147–157.
- SCHATTI, B. 1987. The phylogenetic significance of morphological characters in the holarctic racers of the genus *Coluber* Linnaeus, 1758 (Reptilia, Serpentes). *Amphib. Reptil.* 8:401–418.
- SCHMIDT-NIELSEN, K. 1990. Animal physiology. Cambridge Univ. Press, New York.
- SECOR, S. M. 1992. Activities and energetics of a sit-and-wait foraging snake, *Crotalus cerastes*. Unpubl. Ph.D. diss., Univ. of California, Los Angeles.
- . 1994. Ecological significance of movements and activity range for the sidewinder, *Crotalus cerastes*. *Copeia* 1994:631–645.
- , AND K. A. NAGY. 1994. Bioenergetic correlates of foraging mode for the snakes *Crotalus cerastes* and *Masticophis flagellum*. *Ecology* 75:1600–1614.
- , E. D. STEIN, AND J. DIAMOND. 1994. Rapid upregulation of snake intestine in response to feeding: a new model of intestinal adaptation. *Am. J. Physiol.* 266 (Gastrointest. Liver Physiol. 29):G695–G705.
- SHINE, R. 1986. Ecology of a low-energy specialist: food habits and reproductive biology of the Arafura filesnake (Acrochordidae). *Copeia* 1986:424–437.
- SPOTILA, J. R., AND E. A. STANDORA. 1985. Energy budgets of ectothermic vertebrates. *Am. Zool.* 25: 973–986.
- STINNER, J. N. 1987. Cardiovascular and metabolic responses to temperature in *Coluber constrictor*. *Amer. J. Physiol.* 253:222–227.
- SYSTAT, INC. 1992. SYSTAT for windows: statistics. Ver. 5. Evanston, IL.
- TAYLOR, B. M., AND P. M. C. DAVIES. 1981. Changes in the weight dependence of metabolism during the sloughing cycle of the snake *Thamnophis sirtalis parietalis*. *Comp. Physiol.* 69:113–119.
- WALDSCHMIDT, S. R., S. M. JONES, AND W. P. PORTER. 1987. Reptilia, p. 553–619. *In*: Animal energetics. Vol. 2. P. J. Vernberg and T. J. Pandian (eds.). Academic Press, New York.
- WALTON, M., B. C. JAYNE, AND A. F. BENNETT. 1990. The energetic cost of limbless locomotion. *Science* 249:524–527.
- WOOD, R. A., K. A. NAGY, N. S. MACDONALD, S. T. WAKAKUWA, J. R. BECKMAN, AND H. KAAZ. 1975. Determination of oxygen-18 in water contained in biological samples by charged-particle activation. *Anal. Chem.* 47:646–650.
- SAVANNAH RIVER ECOLOGY LABORATORY, DRAWER E, AIKEN, SOUTH CAROLINA 29802. PRESENT ADDRESS: (MVP) DEPARTMENT OF BIOLOGY, BOX 2251, HARDING UNIVERSITY, SEARCY, ARKANSAS 72143. Send reprint requests to MVP. Submitted: 3 March 1995. Accepted: 23 May 1995. Section editor: J. R. Spotila.