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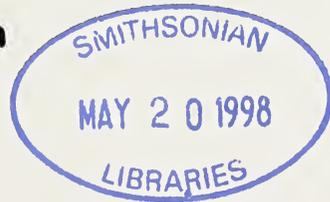
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DEPARTMENT OF HERPETOLOGY

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The Maryland Herpetological Society  
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### Meetings

The third Wednesday of each month, 7:30 PM at The Baltimore Zoo's Reptile House (except August and September due to The Mid-Atlantic Reptile Show). The Department of Herpetology meets informally on all other Wednesday evenings at the NHSM at 8:00 p.m.



# THERMAL TOLERANCE OF FIVE SPECIES OF LIZARD FROM MEXICO AND THE SOUTHWESTERN USA

Royce E. Ballinger, Julio A. Lemos-Espinal, and Geoffrey R. Smith

In ectotherms, the ability of an organism to maintain the appropriate internal environment is often dependent on the ability of the organism to use its external environment to maintain the proper body temperature (Huey and Stevenson 1979). Extremes in environmental temperatures are therefore challenges to an ectotherm's physiological well being. The response of lizards to thermal extremes has revealed apparently adaptive responses to cold, even sub-freezing temperatures (Lemos-Espinal and Ballinger 1992; Costanzo et al. 1993, 1995); however, at extremely high temperatures almost all reptiles lose the ability to coordinate their actions (i.e., they reach their critical thermal maximum; Pough and Gans 1982). Therefore, an important aspect of a reptile's thermal biology is its tolerance of high temperatures.

In this paper, we report on the thermal tolerances of five species of lizard from México and the southwestern USA. The thermal biology of the Mexican species (*Phrynosoma asio* and *Sceloporus mucronatus*) has not been well studied. Indeed, only rudimentary knowledge of field body temperatures is available for *P. asio* (Lemos-Espinal, Smith, and Ballinger unpubl.), and only a slightly more detailed analysis for *S. mucronatus* is available (Lemos-Espinal et al. in press). In addition, we investigate the influence of time of year, as well as sex on the thermal tolerance of *Sceloporus virgatus*, *S. scalaris*, and *S. jarrovi* from the Chiricahua Mountains of southeastern Arizona, USA. More is known about the thermal biology of these species, and the specific populations of these species than for the Mexican species (see Smith et al. 1993; Smith and Ballinger 1994a, b). We also compare the thermal tolerance of two populations of *S. jarrovi*, one at high elevation and one at low elevation.

## Materials and Methods

*Sceloporus virgatus* and *S. jarrovi* were collected in the vicinity of the Southwestern Research Station (1646 m) near Portal, Cochise County, Arizona. The habitat in this area is primarily pine-oak

woodland and has been previously described by Vinegar (1975). *Sceloporus virgatus* and *S. jarrovi* were collected in the vicinity of Rustler's Park (2500-2600 m). The habitat in this area is primarily wooded with talus slopes interspersed and has been described previously by Ballinger (1979), Smith et al. (1993). Lizards were collected and tested throughout 1974 and 1975. *Phrynosoma asio* were collected in the Cañón del Zopilote, north of Chilpancingo, Guerrero, México (600 m elevation), 14 km south of Mexcala, a small town on the Río Balsas. The area is situated in arid tropical scrub (the most xeric portion of the Bosque Tropical Caducifolio of Rzedowski 1988). *Sceloporus mucronatus* were collected near Sierra del Ajusco, México (3400 m elevation) at km 19 on the Ajusco-Tinaguistenco highway (México Highway 892) in an open area with basaltic rocks and lava interspersed with grassy patches (*Festuca amolissima*) and surrounded by a *Pinus hartwegii* forest.

Lizards were not allowed to acclimate to laboratory temperature before testing, and were tested within a few hours of capture. Thirty-one *P. asio*, 16 *S. mucronatus*, 81 *S. virgatus*, 99 *S. scalaris*, and 190 *S. jarrovi* were tested. Lizards were tethered on aluminum foil (to prevent substrate heating) under a heat lamp which caused lizards to heat up relatively rapidly. Tests were concentrated in the morning hours. Body temperatures were taken at the onset of muscle spasms, indicating they would no longer be able to escape from temperature conditions that would result in death, also known as the critical thermal maximum (CTM). Lizards were removed from the heat source and allowed to recover (individuals not immediately recovering were excluded from the analysis). Means are given  $\pm$  one standard error.

### Results

*Phrynosoma asio*. - Mean SVL of the lizards used in this study was  $90.1 \pm 2.2$  mm (N = 31, range = 72 - 120 mm), and Mean BM was  $39.0 \pm 2.7$  g (N = 31, range = 18 - 68 g). Mean indices of thermal tolerance are given in Table 1. Critical Thermal maximum and Gaping Temperature were not related to either measure of body size (SVL or BM) ( $P > 0.15$  in all cases). The temperature at which continuous escape occurred was negatively correlated with body mass, but not SVL (SVL: N = 31,  $R^2 = 0.10$ ,  $P = 0.08$ ; BM: N = 31,  $R^2 = 0.21$ ,  $P = 0.0009$ ;  $y = 39.6 + 0.055x$ ). Initial Escape Temperature also decreased with body size (SVL: N = 31,  $R^2 = 0.12$ ,  $P = 0.053$ ;  $y = 40.1 - 0.054x$ ; BM: N = 31,  $R^2 = 0.17$ ,  $P = 0.02$ ;  $y = 37.3 - 0.053x$ ).

Initial escape temperature did not differ between males and females (Table 2;  $df = 29$ ,  $t = -0.5$ ,  $P = 0.62$ ). Critical thermal maximum also did not differ between males and females (Table 2;  $df = 29$ ,  $t = 0.17$ ,  $P = 0.87$ ). Males did not differ from females in their continuous escape temperatures (Table 2;  $df = 29$ ,  $t = -0.19$ ,  $P = 0.85$ ), nor in their gaping temperatures (Table 2;  $df = 29$ ,  $t = 0.64$ ,  $P = 0.52$ ).

*Sceloporus mucronatus*. - Mean SVL of the lizards used in this study was  $81.7 \pm 2.6$  mm ( $N = 16$ , range = 65 - 95 mm), and Mean BM was  $24.7 \pm 2.4$  g ( $N = 16$ , range = 11 - 39 g). Mean indices of thermal tolerance are given in Table 1. Initial Escape Temperature and Gaping Temperature were not related to either measure of body size (SVL or BM ( $P > 0.70$  in all cases). The temperature at which continuous escape occurred was positively correlated with body size (SVL:  $N = 16$ ,  $R^2 = 0.38$ ,  $P = 0.011$ ;  $y = 33.1 + 0.085x$ ; BM:  $N = 16$ ,  $R^2 = 0.33$ ,  $P = 0.019$ ;  $y = 37.0 + 0.087x$ ). Critical Thermal Maximum also increased with body size (SVL:  $N = 16$ ,  $R^2 = 0.43$ ,  $P = 0.006$ ;  $y = 39.5 + 0.035x$ ; BM:  $N = 16$ ,  $R^2 = 0.35$ ,  $P = 0.015$ ;  $y = 41.5 + 0.035x$ ).

Initial escape temperature did not differ between males and females (Table 2;  $df = 14$ ,  $t = -0.96$ ,  $P = 0.36$ ). Critical thermal maximum also did not differ between males and females (Table 2;  $df = 14$ ,  $t = 0.82$ ,  $P = 0.43$ ). Males had slightly, but statistically significantly higher continuous escape temperatures (Table 2;  $df = 14$ ,  $t = 2.23$ ,  $P = 0.04$ ). Females had higher gaping temperatures on average than males (Table 2;  $df = 14$ ,  $t = -2.50$ ,  $P = 0.026$ ).

*Sceloporus virgatus*. - *Sceloporus virgatus* used in this study had a mean SVL of  $47.7 \pm 1.2$  mm ( $N = 82$ , range = 26 - 66 mm), and mean BM was  $3.8 \pm 0.3$  g ( $N = 63$ , range = 0.6 - 8.8 g). Mean indices of thermal tolerance are given in Table 3. The temperature at which initial escape occurred was not significantly related to either SVL or BM ( $P = 0.10$  and  $0.09$ , respectively). Continuous escape temperature increased with SVL ( $N = 79$ ,  $R^2 = 0.28$ ,  $P < 0.0001$ ;  $y = 30.0 + 0.14x$ ) and BM ( $N = 61$ ,  $R^2 = 0.23$ ,  $P = 0.0001$ ;  $y = 33.7 + 0.69x$ ). The temperature at which *S. virgatus* began to open their mouths was significantly and positively related to their SVL ( $N = 59$ ,  $R^2 = 0.36$ ,  $P < 0.0001$ ;  $y = 32.3 + 0.14x$ ) and BM ( $N = 51$ ,  $R^2 = 0.24$ ,  $P = 0.0003$ ;  $y = 36.4 + 0.53x$ ). Critical thermal maximum also positively correlated with SVL ( $N = 82$ ,  $R^2 = 0.52$ ,  $P < 0.0001$ ;  $y = 33.4 + 0.17x$ ) and BM ( $N = 63$ ,  $R^2 = 0.51$ ,  $P < 0.0001$ ;  $y = 37.6 + 0.89x$ ).

*Sceloporus virgatus* males and females did not have different mean initial escape temperatures ( $df = 80$ ;  $t = -0.07$ ,  $P = 0.94$ ), continuous

escape temperatures ( $df = 78$ ;  $t = -0.75$ ,  $P = 0.46$ ), gaping temperatures ( $df = 57$ ;  $t = -0.77$ ,  $P = 0.44$ ), and CTMs ( $df = 81$ ;  $t = 0.20$ ,  $P = 0.84$ ) (see Table 4). Monthly variation in CTM in *S. virgatus* was significant (Fig. 1; Kruskal-Wallis:  $df = 7$ ;  $H = 32.3$ ,  $P < 0.0001$ ).

*Sceloporus scalaris* - The lizards used in this study had a mean SVL of  $45.5 \pm 1.0$  mm ( $N = 99$ , range = 27 - 60 mm), and Mean BM was  $3.0 \pm 0.2$  g ( $N = 87$ , range = 0.5 - 7.9 g). Mean indices of thermal tolerance are given in Table 3. The temperature at which initial escape occurred was positively correlated with SVL ( $N = 98$ ,  $R^2 = 0.35$ ,  $P < 0.0001$ ;  $y = 29.5 + 0.12x$ ) and BM ( $N = 86$ ,  $R^2 = 0.19$ ,  $P < 0.0001$ ;  $y = 33.5 + 0.47x$ ). Continuous escape temperature increased as SVL ( $N = 99$ ,  $R^2 = 0.41$ ,  $p < 0.0001$ ;  $y = 34.2 + 0.09x$ ) and BM ( $N = 87$ ,  $R^2 = 0.29$ ,  $P < 0.0001$ ;  $y = 37.0 + 0.41x$ ) increased. The temperature at which *S. scalaris* began to open their mouths was positively related to their SVL ( $N = 64$ ,  $R^2 = 0.10$ ,  $P = 0.009$ ;  $y = 35.5 + 0.08x$ ) and BM ( $N = 87$ ,  $R^2 = 0.48$ ,  $P < 0.0001$ ;  $y = 40.3 + 0.062x$ ).

Male and female *S. scalaris* did not differ in initial escape temperature ( $df = 83$ ,  $t = 1.3$ ,  $P = 0.19$ ), continuous escape temperatures ( $df = 84$ ,  $t = -1.0$ ,  $P = 0.30$ ), gaping ( $df = 57$ ,  $t = -0.56$ ,  $P = 0.57$ ), and CTM ( $df = 84$ ,  $t = .37$ ,  $P = 0.71$ ) (see Table 4). There was significant monthly variation in CTM for these *S. scalaris* (Fig. 1; Kruskal-Wallis;  $df = 7$ ,  $H = 66.2$ ,  $P < 0.0001$ ).

*Sceloporus jarrovi* - Mean SVL in this study was  $67.2 \pm 1.0$  mm ( $N = 188$ , range = 42 -96 mm), and mean BM as  $11.5 \pm 0.6$  g ( $N = 130$ , range = 2.0 - 28.1 g). Mean indices of thermal tolerance are given in Table 3. No measures of thermal tolerance were significantly related to SVL ( $P > 0.08$  in all cases). The temperature at which initial escape occurred was positively correlated with BM ( $N = 128$ ,  $R^2 = 0.04$ ,  $P = 0.02$ ;  $y = 29.9 + 0.08x$ ). Critical Thermal Maximum also increased with BM ( $N = 130$ ,  $R^2 = 0.04$ ,  $P = 0.02$ ;  $y = 40.6 + 0.052x$ ). Very little variation in these indices in *S. jarrovi* was explained however. There was no significant relationship between the other two thermal tolerance indices and BM ( $P > 0.10$  in both cases).

Male and female *S. jarrovi* did not differ in initial escape ( $df = 183$ ,  $t = -0.9$ ,  $P = 0.36$ ), gaping temperature ( $df = 131$ ,  $t = -0.0004$ ,  $P = 1.00$ ), and CTM ( $df = 189$ ,  $t = 0.015$ ,  $P = 0.99$ ) (see Table 4). Females had slightly higher mean continuous escape temperatures ( $df = 184$ ,  $t = -2.58$ ,  $P = 0.0110$  (see Table 4). Mean CTM varied from month-to-month (Fig. 1; Kruskal-Wallis:  $df = 7$ ,  $H = 40.2$ ,  $P < 0.0001$ ). Individuals in the

high-elevation population did not have a significantly different mean CTM than individuals from the low-elevation population ( $41.5 \pm 0.17$  C ( $N = 104$ ) vs  $41.4 \pm 0.16$  C ( $N = 83$ );  $df = 185$ ,  $t = -0.45$ ,  $p = 0.66$ ).

### Discussion and Conclusions

The mean CTMs of the five species used in this study ranged from 41.4 C in *S. virgatus* and *S. jarrovi* to 44.1 C in *P. asio*. If only the *Sceloporus* species are considered, the range is even smaller, with the highest mean being *S. scalaris* at 42.3 C. Thus there appears to be little difference in field-acclimated CTMs within the four species of *Sceloporus*. However, the same could be said about the range of field active body temperatures of these four species: *S. virgatus* 33.4 C (Smith and Ballinger 1994a), *S. scalaris* 32.6 - 32.9 C (Smith et al. 1993), *S. jarrovi* 31.1 - 32.5 C (Smith and Ballinger 1994b), and *S. mucronatus* 31.5 C (Lemos-Espinal et al in press). *Phrynosoma asio*, on the other hand, appears to have a higher CTM than any of the *Sceloporus* considered here. The higher CTM may be a result of phylogenetic trends: *Phrynosoma* in general may have higher thermal tolerances than *Sceloporus*. Indeed, a study on *P. cornutum* found a relatively high CTM after acclimation (Ballinger and Schrank, 1970). *Phrynosoma asio* also has a higher mean active body temperature than any of the *Sceloporus* (except *S. virgatus*) studied here (33.0 C; Lemos-Espinal, Smith, and Ballinger, unpubl.).

In *S. mucronatus*, *S. virgatus* and *S. scalaris*, there were significant positive regressions of CTM on body size. At least some of the other indices of thermal tolerance in all five species were correlated with body size (negatively in the case of *P. asio*, but positively in the other species). These results suggest the possibility of ontogenetic changes in thermal tolerance in these species. They also suggest a continuous shift in tolerance rather than an abrupt switch at some threshold size. We found a very weak relationship between CTM and body size in *S. jarrovi*. Biologically the relationships observed probably do not reflect a shift in thermal tolerance during the life of *S. jarrovi*, since the amount of variation in thermal tolerance explained by measures of body size is very small. Other studies have failed to find significant differences in thermal tolerance due to size (Spellerberg 1972; Art and Claussen 1982) or age (i.e., adult vs. juvenile, Paulissen 1988).

Thermal tolerances may vary from month to month or season to season, just as preferred or activity body temperatures can (e.g., Patterson and Davies 1978; Smith et al. 1993; Smith and Ballinger

1994a; Lemos-Espinal et al., 1997). For example, Larson (1961) found that the critical thermal maximum (CTM) for *Sceloporus occidentalis* differed between winter and summer. Spellerberg (1972) found the same to be true in many Australian lizards. Similarly, Heatwole and Firth (1982) found that the voluntary maximum temperature of *Amphibolurus muricatus* differed between fall and spring/summer. For all three species for which data were available, CTM varied throughout the year. Several other studies have demonstrated similar trends in other species of lizards (Larson 1961; Spellerberg 1972; Heatwole and Firth 1982). Differences in thermal tolerances observed here may result from differences in acclimation because of seasonal change in temperatures experienced (individuals were not test at a single acclimation temperature, but at field acclimated temperatures). Acclimation has been shown to influence CTM in several species of lizards (Lowe and Vance 1955; Larson 1961; Ballinger and Schrank 1970; Corn 1971; Art and Clauseen 1982), but Kour and Hutchison (1970) found no acclimation effect in *Sceloporus occidentalis*. In addition to changes in temperature, changes in photoperiod may also influence the thermal tolerance of lizards (Lashbrook and Livezey 1970; but see Ballinger et al. 1969), suggesting seasonal changes in photoperiod may be influencing the thermal tolerance of these three species, and resulting in the variation observed in our study. Interestingly, *S. virgatus* maintain the same body temperature in winter and summer (Smith and Ballinger 1994b), whereas *S. scalaris* and *S. jarrovi* maintain higher body temperatures in summer than in winter (Smith et al. 1993; Smith and Ballinger 1994a).

Over its elevational range in the Chiricahua Mountains, *S. jarrovi* exhibits differences in life history characters, physiology, and thermal ecology (Vinegar and Hillyard 1972; Ballinger and Newlin 1975; Ballinger 1979; Middendorf and Simon 1988; Smith and Ballinger 1994a, c; Smith et al. 1994; Ballinger et al 1996), however in this study we did not observe any differences between the CTMs of high and low elevation populations of *S. jarrovi*. This is in contrast to the studies of Hertz and his colleagues studying *Anolis* along an elevational gradient in Puerto Rico (Hertz et al. 1979; Hertz 1981), and the study of Lemos-Espinal and Ballinger (1995) on *Sceloporus grammicus* from 3700 m and 4600 m in México. These studied found that CTM tended to decrease with increasing elevation.

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Table 1. Indices of thermal tolerance for *Phrynosoma asio* and *Sceloporus mucronatus* from México. See text for abbreviations. N is given in parentheses.

	<i>Phrynosoma asio</i>	<i>Sceloporus mucronatus</i>
INIT	35.3 ± 0.3 C (31)	37.3 ± 0.3 C (16)
CONT	37.3 ± 0.3 C (31)	40.0 ± 0.4 C (16)
GAPE	40.5 ± 0.3 C (31)	38.6 ± 0.2 C (16)
CTM	44.1 ± 0.2 C (31)	42.3 ± 0.6 C (16)

Table 2. Indices of thermal tolerance for male and female *Phrynosoma asio* and *Sceloporus mucronatus* from México. See text for abbreviations. N is given in parentheses.

	Males	Females
<i>Phrynosoma asio</i>		
INIT	35.1 ± 0.4 C (15)	35.4 ± 0.5 C (16)
CONT	37.2 ± 0.5 C (15)	37.4 ± 0.4 C (16)
GAPE	40.8 ± 0.5 C (15)	40.3 ± 0.4 C (16)
CTM	44.2 ± 0.5 C (15)	44.1 ± 0.2 C (16)
<i>Sceloporus mucronatus</i>		
INIT	37.1 ± 0.5 C (9)	37.7 ± 0.5 C (7)
CONT	40.6 ± 0.1 C (9)	39.2 ± 0.7 C (7)
GAPE	38.2 ± 0.2 C (9)	39.1 ± 0.3 C (7)
CTM	42.4 ± 0.1 C (9)	42.2 ± 0.3 C (7)

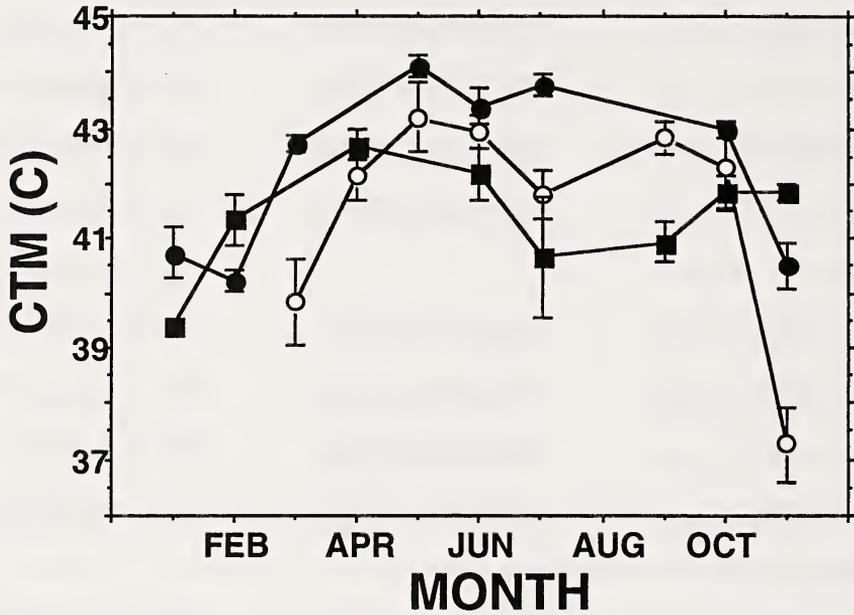
Table 3. Indices of thermal tolerance for *Sceloporus virgatus*, *S. scalaris*, and *S. jarrovi* from the Chiricahua Mountains of southeastern Arizona, USA. See text for abbreviations. N is given in parentheses.

	<i>S. virgatus</i>	<i>S. scalaris</i>	<i>S. jarrovi</i>
INIT	31.3 ± 0.2 C (82)	34.9 ± 0.2 C (98)	30.8 ± 0.2 C (185)
CONT	36.6 ± 0.3 C (80)	38.3 ± 0.2 C (99)	38.4 ± 0.2 C (186)
GAPE	38.6 ± 0.3 C (59)	39.1 ± 0.3 C (64)	36.1 ± 0.2 C (133)
CTM	41.4 ± 0.3 C (83)	42.3 ± 0.2 C (99)	41.4 ± 0.1 C (191)

Table 4. Indices of thermal tolerance for male and female *Sceloporus virgatus*, *S. scalaris*, and *S. jarrovi* from the Chiricahua Mountains of southeastern Arizona, USA. See text for abbreviations. N is given in parentheses.

	Males	Females
<i>Sceloporus virgatus</i>		
INIT	31.3 ± 0.2 C (54)	31.3 ± 0.3 C (28)
CONT	36.4 ± 0.4 C (52)	36.9 ± 0.5 C (28)
GAPE	38.4 ± 0.4 C (37)	38.9 ± 0.4 C (22)
CTM	41.5 ± 0.4 C (55)	41.4 ± 0.3 C (55)
<i>Sceloporus scalaris</i>		
INIT	35.0 ± 0.4 C (23)	35.5 ± 0.2 C (62)
CONT	38.4 ± 0.2 C (23)	38.4 ± 0.2 C (63)
GAPE	38.9 ± 0.4 C (17)	39.3 ± 0.4 C (42)
CTM	42.8 ± 0.2 C (23)	42.7 ± 0.2 C (63)
<i>Sceloporus jarrovi</i>		
INIT	30.7 ± 0.2 C (101)	31.0 ± 0.2 C (84)
CONT	38.0 ± 0.2 C (103)	38.8 ± 0.2 C (83)
GAPE	36.1 ± 0.3 C (69)	36.1 ± 0.3 C (64)
CTM	41.4 ± 0.2 C (105)	41.4 ± 0.1 C (86)

Figure 1. Variations in CTM as a function of month in *Sceloporusvirgatus* (open circles), *S. scalaris* (closed circles), and *S. jarrovi* (closed rectangles) from the Chiricahua Mountains of southeastern Arizona. Bars are  $\pm 1$  SE.



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## HYPOCALCEMIA IN IGUANAS

Thirty-nine iguanas under one year of age were evaluated over a three-month period in order to determine their calcium levels as part of their routine physical examinations or for other medical purposes. The iguanas were brought to the clinic for one or more of the following reasons: new pet, anorexia, lack of movement, swollen jaws or legs, kyphoscoliosis and weakness. For a variety of reasons, not all iguanas seen in this time period were tested. Blood calcium levels ranged from 3.0 to 14.5 with an average of 7.6 (normal 8.0 - 15.0). Low calcium was detected in 55% of the animals (21 out of 38) with the largest distribution of calcium levels in the 5.0 - 6.9 range. In iguanas with low blood calcium, the most common findings included improper diet, improper environmental temperature and lack of full spectrum lighting in the animals' habitats. Many of the iguanas experienced concurrent problems such as bacterial infections, endo- and exoparasites, starvation and trauma.

Iguanas are becoming increasingly popular as pets. They are offered for sale at prices as low as \$15.99. Most, however, are never seen by a veterinarian. A three-month study was undertaken at our facility in order to determine the incidence of hypocalcemia in iguanas under one year of age. In this time period, approximately seventy-five iguanas were examined for a variety of reasons. The study was limited to subjects under one year of age, since these are the animals most commonly sold through pet stores. Many people had purchased the iguanas on impulse and had no idea what to feed them or how to care for them. Most iguanas (approximately 90%) were kept at suboptimal temperatures. Ninety-five percent of the animals had endoparasites (pinworms). Full spectrum lighting was absent or used improperly in 85% of the cases. Blood calcium levels were determined in 38 individuals. Blood was drawn from the ventral tail vein into red top tubes and was spun and separated. Blood calcium levels were determined by commercial laboratories. The levels ranged from 3.0 to 14.5 with an average of 7.6 (normal 8.0 - 15.0). Low calcium was detected in 55% of the subjects (21 of 38) with the largest distribution of levels in the 5.0 - 6.9 range (Fig. 1). Eighty-four percent of the animals (32 of 38) showed evidence of metabolic bone disease (MBD). MBD usually results from a low calcium diet, but it may also be caused by lack of vitamin D<sub>3</sub>, excessive dietary phosphorus and, in rare cases, kidney, parathyroid, thyroid or liver disease (Boyer, 1991). Signs of MBD include flexible mandible (rubber

jaw - usually the first sign), round skull, failure to grow, long bone fractures, inability to move rapidly or raise the body off the ground, anorexia, twitching of the toes and limbs, scoliosis and kyphosis. Diagnosis of MBD is based upon clinical signs, blood calcium levels and radiographs.

Low blood calcium appears to be a frequently-encountered problem. Eighty-four percent of the iguanas under study displayed evidence of MBD. Hypocalcemia was detected in 55% of the iguanas through blood (serum) determination. The difference (29%) between the individuals who showed evidence of MBD and those detected via blood determination results from the fact that in individuals with early cases of MBD, the blood calcium levels have not yet dropped, and the body is maintaining normal serum calcium levels by drawing upon bone reserves. Causes of low blood calcium include low amounts of calcium in the diet (most common cause), vitamin D<sub>3</sub> deficiency, hypomagnesium, metabolic acidosis, hypoparathyroidism, excess urinary loss, steatorrhea, glucose and other rapidly-metabolized foods and excessive phosphorus (Lindman, 1967; Shils, 1970; Levy et al, 1974; Lewis, Morris, Hand, 1989; Boyer, 1991). The diets that were fed to the iguanas were lacking not only in calcium but in most other nutrients as well. Most of the iguanas were offered lettuce, strawberries, melon, crickets and meal worms. The body of knowledge regarding the dietary requirements of iguanas is still in its infancy. It is currently recommended for growing animals up to two years of age that the diet be 80% plant-based and 20% protein-based (Boyer, 1991). Plant-based foods offered should be predominantly high-fibrous, calcium-rich foods (collard greens, turnip greens, mustard greens, alfalfa, dandelions). If fed excessively, broccoli, kale, bok-choy, cabbage and related vegetables may be goitergenic. Fibrous greens should comprise 50% of the diet; thirty percent of the diet can consist of string beans, carrots, peppers, spinach, squash, bean sprouts, hibiscus flowers, nasturtiums and mulberry leaves. Fruits should be regarded as treats, fed to the iguana as one would feed a biscuit or a piece of rawhide to a dog. When compared with vegetables, fruits prove to be poor in nutritional value, and the sugar/starch content may induce abnormal hindgut fermentation. In the wild, green iguanas are folivores and at all ages of their life do not consume insects, arachnids, eggs or meat (Barbour, 1997; Iverson, 1980, 1982; Round et al, 1990). Animal protein based diets and high protein fat diets should not be fed (Barbour, 1997; Iverson, 1980, 1982; Rand et al., 1990).

Full spectrum lighting is required in order to maintain health. Ultraviolet light can be divided into UVA (blacklight, longwave, nearwave), UVB (middlewave, erythermal) and UVC (farwave, shortwave, germicidal) (Alberts, 1992) (Fig. 2). UVA and UVB are essential for good health (Gehrman, 1994). UVA results in brighter, more vibrant color and increase in appetite and reproductive behavior. UVB induces a chemical reaction in the skin for the production of vitamin D<sub>3</sub> (Alberts, 1994; Bernard, 1991; Barbour, 1997). Research has shown that iguanas fed a diet that was rich in calcium and vitamin D<sub>3</sub> and iguanas injected with supplemental vitamin D<sub>3</sub> fared poorly compared to individuals that were exposed daily to ultraviolet light (Bernard, 1991). When using the more frequently-sold lights, the distance from the light to the reptile should be no more than 18 inches; any questions should be directed to the manufacturer. Artificial lights, however, are not a substitute for sunlight and direct sunlight should be used whenever possible.

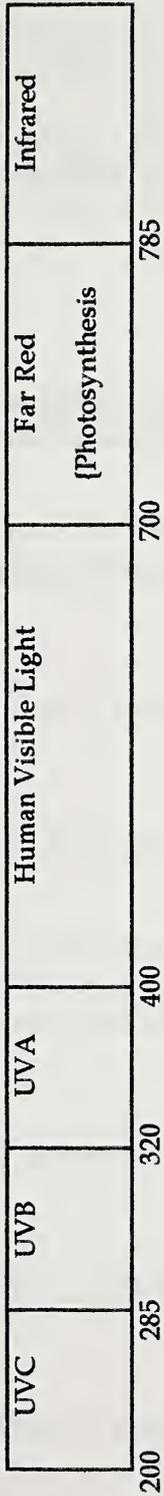
The correct environment temperature for iguanas should range from approximately 95° to 105° during the day with a slight decrease at night. At this temperature, appetite and activity are improved. In addition, this temperature allows for proper hindgut fermentation. Lower temperatures result in incomplete or partial digestion/fermentation and may alter bacterial flora.

To summarize, iguanas are becoming more popular as pets because of their low initial cost. Most iguanas, however, are never presented to veterinarians for physical examinations. Many people object to spending money on health care for a reptile for which they only paid \$15.00 or \$20.00. As a result, most iguanas die within a relatively short period of time. The majority of iguanas present to veterinarians show signs of illness. Unless proper nutritional needs, environmental temperature and lighting requirements are met, most can be expected to perish.

Figure 1. Calcium levels of green iguanas seen during a three month period in private veterinary practice.

Calcium level (mg/dl)	Number of iguanas
3.0 - 3.9	3
4.0 - 4.9	3
5.0 - 5.9	6
6.0 - 6.9	7
7.0 - 7.9	3
8.0 - 8.9	2
9.0 - 9.9	5
10.0 - 10.9	5
11.0 - 11.9	3
12.0 and up	2
	<hr/> 39

Figure 2. Light Bands; Wavelength in nanometers



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## STATUS OF CHORUS FROGS (GENUS *PSEUDACRIS*) IN SOUTHEASTERN COLORADO

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A gap exists in the distribution of chorus frogs in southeastern Colorado. New locality records extend the known range of chorus frogs in this area. The factors responsible for this distributional hiatus remain unknown, as does the specific identity of chorus frogs from this part of the range of the genus *Pseudacris*.

Chorus frogs (*Pseudacris triseriata*) are abundant and widespread in many areas of North America. However, existing information suggests that only a few widely scattered populations exist in the western Great Plains region south of the Platte River drainage (Conant and Collins 1991). A large distributional hiatus extends across southeastern Colorado (Hammerson 1982) and southwestern Kansas (Collins 1993). Herein we report several new records from southeastern Colorado, extending the known range of *Pseudacris* eastward approximately 20 to 60 km in the Colorado portion of the distributional gap.

The area bounded by latitudes 37° and 39° North and longitudes 105° and 102° West encompasses the southeastern portion of Colorado as well as a very narrow strip of extreme western Kansas. Within this area, almost all of which is in the Arkansas River drainage, only five *Pseudacris* localities were mapped by Hammerson (1982) and none by Collins (1993). Since the publication of Hammerson (1982), several new county records have been documented in southeastern Colorado, including Crowley (Bergman et al. 1996), Huerfano and Las Animas (Livo et al. 1995), and Kiowa (Mackessy et al. 1996) counties. Platz (1989) provided an additional published record for Lincoln County. Figure 1 shows these published localities as well as several previously unpublished localities. Localities are listed alphabetically by county in the appendix.

These records more than triple the number of known *Pseudacris* localities from the lower Arkansas drainage in southeastern Colorado. The new localities also help to fill in a major distributional gap between a

single record of *Pseudacris* collected in 1963 along the Cimarron River in extreme southeastern Colorado (UCM 32682) and the nearest localities to the north and northwest (Hammerson 1982:35). Similar gaps exist between the Cimarron River locality and localities to the east and south in Kansas, Oklahoma, and to a lesser extent, New Mexico (see range maps in Black and Sievert 1989, Collins 1993, Stebbins 1985, and Degenhardt et al. 1996).

Suitable habitat for *Pseudacris* exists within the distributional hiatus, and there are no abrupt changes in vegetation, soils, or land forms between occupied and apparently unoccupied areas (Küchler 1966, Hammond 1980, Hunt 1979). Additional field work is warranted, especially during the calling season, to determine whether the remaining distributional gap for *Pseudacris* is real or simply an artifact of the cryptic behavior of these small frogs outside of their calling season.

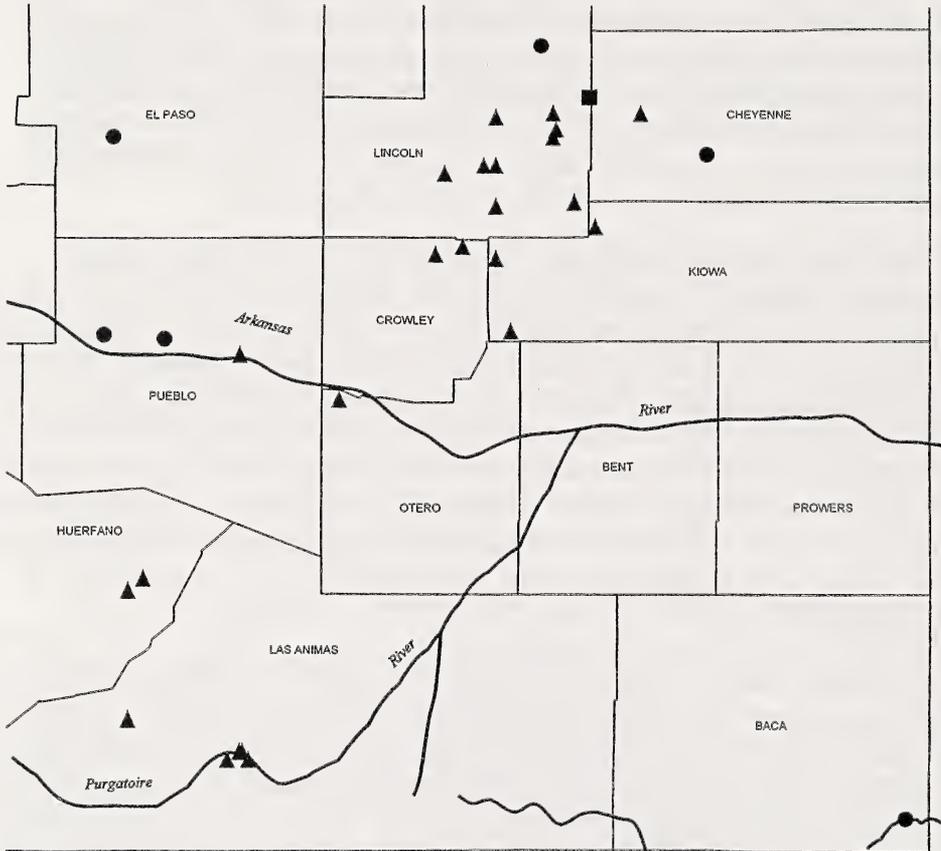
In addition, the specific identity of the chorus frogs in southeastern Colorado remains a matter to be determined. The chorus frog present in Colorado and throughout western North America generally has been regarded to be *Pseudacris triseriata*. Recently, Platz (1989) examined call and morphological attributes of three *Pseudacris* populations in Colorado and suggested that two species (*P. triseriata* and *P. maculata*) are present, with both occurring in the region from which our new records derive. Detailed analysis is required to differentiate between these two taxa. Hence, precise boundaries and possible areas of sympatry for these taxa remain to be elucidated in eastern Colorado.

Further, chorus frogs in Colorado exhibit a wide range in morphological and ecological variation (Pettus and Spencer 1964; Pettus and Angleton 1967; Miller 1977), including in large areas not sampled by Platz (1989). This leads to the possibility of additional, undescribed taxa. Until more detailed studies of genetic, morphological, and call variations are made, we feel that the species-level taxonomic status of *Pseudacris* in Colorado should be regarded as unresolved.

### Acknowledgments

Several students participated in observations of chorus frogs in southeastern Colorado, including Enoch Bergman, Ron Donoho, Justin Hobert, Chad Montgomery, and Kevin Waldron. We also appreciate the constructive comments of an anonymous reviewer.

Figure 1. Distribution of *Pseudacris* in southeastern Colorado (Closed circles-Localities mapped in Hammerson (1982); Closed rectangles - Locality reported by Platz (1989); Closed triangles - Localities reported in this paper, also including Bergman et al. (1996), Livo et al. (1995), and Mackessy et al. (1996). Some adjacent localities are represented by a single symbol.



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Appendix

**Cheyenne:** Ca. 50 frogs observed by S. P. Mackessy and students at pond on Co. Rd. 9 0.8 mi S jct Co. Rd. T (30 July 1996).

**Crowley:** Specimen collected (UNC-MNH #278) by S. P. Mackessy and students at pond on Co. Rd. 27 4.2 mi S jct Lincoln Co. Rd. D (4 June 1996) (Bergman et al. 1996); 4 adult frogs observed by S. P. Mackessy and students at pond on Co. Rd. BB 0.5 mi E jct Hwy 71 (4 June 1996).

**Huerfano:** Two specimens collected (UCM 57333-4) by L. J. Livo, D. Chiszar, and H. M. Smith on 19 May 1995 at 1.1 km east, 0.1 km south junction of Cucharas River with Walsen Arroyo (T27S, R65W, SE 1/4 Section 30) (Livo et al., 1995) and a chorus heard on 19 May 1995 by L. J. Livo, D. Chiszar, and H. M. Smith from wetlands at south end of Maria Reservoir (T27S, R65W, W 1/2 Section 28).

**Kiowa:** W side County Hwy 109, 0.1 mi S jct county road T (Mackessy et al., 1996); 2 frogs and numerous tadpoles observed at roadside pond on Co. Rd. 2 4.1 mi S Lincoln Co. line (5 June 1996); chorus heard at pond on Hwy 96 2.7 mi E jct Co. Rd. 3 (20 June 1996).

**Las Animas:** Chorus heard by L. J. Livo on 24 May 1995 at junction of Apishapa River and Trujillo Creek (T31S, R65W, Section 18) southwest of Aguilar (Livo et al., 1995). Choruses heard by G. A. Hammerson on 17 June 1993 from four localities ranging from 2.4 to 9.6 km east of Beshoar in T32S, R62W. Probable sections were 25, 22 or 27, 23 or 26, and 30.

**Lincoln Co:** Platz (1989) reported chorus frogs from Lincoln Co., 3 km west Aroya. S. P. Mackessy and students have observed chorus frogs from the following additional localities: 200 m W of county road 43, 1.0 mi N jct county road U; on S side of county road N ca. 0.3 mi E jct county road 31; 4 frogs observed Co. Rd. M 1.0 mi E jct Co. Rd 22 (20 August 1996); ca. 50 tadpoles (3 July 1996) and 50 froglets (13 August 1996) observed pond NE corner jct Co. Rd. M and Co. Rd. 22; 25 frogs, including 5 amplexing pairs, observed ca. 0.5 mi W of Co. Rd. 43, 1.3 mi S jct Hwy. 94 (1 June 1996); 2 frogs observed at pond on S side of Hwy 94 0.1 mi E jct Co. Rd. 32 (10 June 1996); 4 frogs observed and ca. 15 heard calling at pond on Co. Rd. 32 0.5 mi N jct Co. Rd. F (10 June 1996); 3 adult frogs and numerous tadpoles observed at pond on Co. Rd. 43 4.7 mi S jct Hwy 94 (5 June 1996); 1 adult and 3 tadpoles (regurgitated by *Thamnophis radix*) observed at pond on Co. Rd. 43 0.4 mi S jct Co. Rd. U (5 June 1996); 1 frog observed in ditch pond on Co. Rd. 32 0.4 mi S jct Co. Rd. F (5 June 1996); chorus heard at pond on Co. Rd. 32 at jct Co. Rd. N (14 June 1996); chorus heard at pond on Co. Rd. 32 0.8 mi N jct Co. Rd. W (21 June 1996); chorus heard at pond on Co. Rd. 32 1.3 mi S. jct Hwy 94 (21 June 1996); chorus heard at pond on Hwy 94 0.6 mi W

ect Co. Rd. 32 (21 June 1996); pond on Co. Rd. G 1.9 miles west of Cheyenne/Kiowa County lines (5 August 1996).

**Otero:** Chorus heard on 10 June 1988 by G. A. Hammerson east of Fowler (T22S, R59W, Section 15 or 22).

**Pueblo:** Chorus heard on 29 May 1995 by L. J. Livo from a marshy area 5 km west and 2 km south Boone along U. S. Highway 50 (T21S, R62W, S 1/2 Section 10).

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# A COMPARISON OF THE FEEDING BEHAVIOR OF TWO PIPIDS, *XENOPUS LAEVIS*, AND *HYMENOCHIRUS BOETTGERI* WITH EMPHASIS ON THE USE OF THE FORELIMBS

Typical pipid feeding behavior consists of shoveling food into the mouth by use of the forelimbs. *Xenopus laevis* displays this behavior. *Hymenochirus boettgeri* does not use its hands in the typical pipid mode as the webbing between the toes of the forelimbs may make this behavior maladaptive due to potential reduced respiratory capacity, increased susceptibility to predation, and reduced foraging efficiency. Both species utilize the claws on the hind feet to assist in feeding.

## Introduction

Anurans of the family Pipidae are well adapted to a thoroughly aquatic existence. Their broad flattened bodies, retention of larval lateral line systems, and loss of a tongue and eyelids have resulted in behaviors unique to this primitive Aglossid family. One of these behaviors involves the use of the forelimbs while feeding and foraging (Halliday and Adler, 1987; Wagner, 1955). Most anurans utilize their pectoral limbs to some extent while feeding. *Xenopus laevis* (African clawed frog), like most Pipids, use their "hands" extensively to shovel food into their mouth (Wagner, 1955). *Hymenochirus boettgeri* (dwarf African clawed frog), though, has webbing between the digits of its forelimbs. (Terent'ev, 1965). This fact makes feeding with its forelimbs in typical pipid fashion more difficult.

There is a definite paucity of data concerning the behavior of *H. boettgeri* except in its breeding (Rabb & Rabb, 1963) while *X. laevis* has been more thoroughly studied due to its use in medical research (Stewart, 1967). My study compares the use of the forelimbs while feeding in these two species. I also describe some associated feeding and locomotory behaviors in these two species.

## Materials and Methods

Five 2 to 5 cm *Xenopus laevis* were housed individually in 4 L squat fish bowls. The fish bowls were 3/4 filled with water without any

gravel or other amendments. These subjects were fed a varied diet of live earthworms (large and small), live adult guppies, live and dead arthropods, dry flaked and pelleted fish food, and raw meat.

Three 2 to 3 cm *Hymenochirus boettgeri* were housed communally in a 40 L aquarium. The aquarium was filled with water and contained floating *Ceratophyllum* sp. for the frogs to rest in, *Vallisneria spiralis* rooted in a gravel substrate, and several small stones and pieces of driftwood for hiding places.

The aquarium was filtered with an air-lift undergravel filter. Two more *H. boettgeri* were housed in a 4 L "pickle jar" with a few sprigs of *Cobomba* sp. rooted in a gravel substrate, and a few small stones. *H. boettgeri* were fed small live earthworms, pieces of large live earthworms, live baby guppies, live brine shrimp, live freshwater amphipods, and dry flaked and granular fish food.

### Results and Discussion

These two species share some feeding behaviors in common, but their foraging strategies and methods of handling food items differ substantially.

#### Description of *Xenopus laevis* Feeding Behavior

*Xenopus laevis* utilizes both a sit-and-wait and an active hunting approach to foraging. The sit-and-wait approach I observed was similar to that briefly described by Halliday and Adler (1987). When using a sit-and-wait strategy *X. laevis* spends considerable time in shallow water resting on the claws of the hind feet with only the eyes and nostrils penetrating the surface film. Their forelimbs are positioned anteriorly, with the palmar regions held supinate and the elbows flexed slightly in anticipation of prey capture. These frogs will remain in this position for a considerable duration if a prey item is suspended in view above the water surface, but out of reach. If the item drops into the water, *X. laevis* immediately lunges at and grabs the prey with its forelimbs. The frog then forces the victim into its mouth using its forelimbs to "shovel" the item into its mouth in typical Pipid fashion.

*X. laevis* also utilizes an active, hunting approach to foraging. This tactic is used while submerged. The frog swims in a random pattern along the substrate with both forelimbs positioned as previously

described. It will swim two or three strokes with its hind legs, then tilt its head towards the ground. The frog will reach into crevices between the gravel with its "hands", and in a circumductive movement of the forearm sweep detritus into its mouth. Then with a chewing motion, the frog will spit out inedible portions of this material. If a large item, such as a 4 or 5 cm earthworm is found, *X. laevis* will hold it between the fingers. Then with alternating movements of the left and right arm, it will move the prey into and out of the mouth. The frog continues manipulating the worm until it is positioned satisfactorily, then swallows it.

If the worm is too large to swallow, *X. laevis* will reach cranially with one or both of its hind feet (while holding the worm with both its jaws and fingers). With the plantar region facing anteriorly, the frog digs its claws into the top of the prey to tear off the protruding portion. The portion in its grasp is then swallowed. The use of these claws in feeding was briefly described by Wagner (1955) and as a facilitator to ecdysis by Mc Callum (1997).

#### Description of the Feeding Behavior of *Hymenochirus boettgeri*

The feeding behavior and use of the forelimbs by *Hymenochirus boettgeri* differs substantially from *X. laevis*. The former does not hunt or feed with its forelimbs in typical Pipid fashion. The forelimbs are not adducted while swimming as in most frogs, or held forward in typical Pipid fashion for feeding. Instead, the forelimbs are held pronate and used actively for swimming. When swimming to the surface for air, *H. boettgeri* uses the front limbs in either a breast stroke or dog paddle motion.

The front limbs are also used during foraging to turn over small pebbles or pieces of plant material, and to dig in the gravel for small worms and invertebrates. This species is not a sit-and-wait forager. It spends its time actively climbing about in vegetation, and scouring the substrate for prey. When it finds a small prey item, *H. boettgeri* moves stealthily towards it. Once close enough it lunges at the victim, using both the front and hind legs for propulsion (only the hind limbs are used for propulsion by *X. laevis*). The prey will be grabbed with the mouth only, and swallowed.

If this prey is large, *H. boettgeri* first attempts to tear it apart using its forelimbs by reaching cranially with the palmar region held pronate and digging the terminal phalanges into the prey. Using an

abductive movement of the forelimb, the frog attempts to tear off the protruding portion.

If this tactic is unsuccessful, the frog will use its hind legs as described in *X. laevis*. *Hymenochirus boettgeri*, however, does not hold the prey with its hands. This species is able to catch small fish fry, crustaceans, and other animals in this fashion. Undoubtedly the more binocular position of its eyes, not dorsal as in *X. laevis*, aid the effectiveness of this strategy.

The active foraging displayed by *X. laevis* would be less effective with webbed hands. This behavior would not sweep items into the mouth, but away from it like waving a paper fan at your face on a hot day. Furthermore, frogs with webbed feet that handle prey in typical Pipid fashion may damage this webbing, especially if the prey is small crayfish or other arthropod. Such injuries could subject these individuals to infection, and the frogs could temporarily lose the ability to swim with their front limbs. This could impede both prey capture and escape from predators.

Such damage could also impair the frog's respiratory capacity, as the well vascularized webbing of some Pipids has been suggested as an accessory respiratory organ (Wagner, 1955). If the webbing were damaged, this active hunter could experience reduced endurance while foraging due to lower oxygen uptake and carbon dioxide dissipation. The lowered respiratory capacity experienced due to webbing damage could also result in more frequent trips to the surface to breath. These frogs could be more frequently susceptible to predation from above while breathing, and would likely be more frequently susceptible to aquatic predators during trips from the substrate to the surface. These factors likely selected against primitive *H. boettgeri* that used their forelimbs for feeding.

No other Pipid genera endemic to either South America or Africa are known to display either webbed front feet, or *H. boettgeri*'s atypical Pipid feeding behavior. This seems to indicate that these characteristics have evolved recently in *H. boettgeri* from a typical Pipid ancestor. Consequently, these are probably advanced, not primitive, characteristics evolved for an aquatic active forager's lifestyle.

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## FIELD OBSERVATIONS ON THE BEHAVIOR OF CHIHUAHUA SPOTTED WHIPTAIL LIZARDS (*CNEMIDOPHORUS EXSANGUIS*)

Hobart M. Smith, David Chiszar, Clint Henke, Julio A. Lemos-Espinal  
and Frank van Breukelen

Burrowing and foraging behavior of two *Cnemidophorus exsanguis* in southwestern New Mexico is described. The hind legs were not used in burrowing, except for locomotion - only the forelegs, in both excavation and clearance. The elevated scanning posture, frequently intervening between excavation and clearance episodes, was assumed with brief initial vertical vibration of the head, and occasionally accompanied by spastic, digging-like movements of the free foreleg. The lizards were wary of large moving objects but unconcerned with stationary ones.

On June 11, 1997, one of us (HMS) was stationed for a few hours on the continental divide at 1890 m in the San Luis Mts. of Hidalgo Co., southwestern New Mexico, between Barnett and Whitewater canyons, on the north slope of Lang Peak (2060 m), while others in the party climbed the peak. The locality is about 2 km north of the new Mexico/Chihuahua border.

Between 10:00 and 11:30 a.m., two large adult, apparently gravid *Cnemidophorus exsanguis* were observed as they moved about within a few square meters of the road. The literature on this species is remarkably extensive (Stuart, 1991) in view of its relatively recent recognition (Lowe, 1956), but we are aware of no previous description of several behaviors here recorded.

Of special interest is the burrowing behavior of one of the lizards. It worked some 45 min on a burrow constructed de novo under a small stone (about 3x20x6 cm) on top of a mound of earth on one side of the road, created by a road scraper. The burrow, with two exits as well as the one entrance, ultimately collapsed after being dug some 20 cm under the rock.

The burrow was started by swipes of the forelegs, used alternately two or three times each. As displaced soil accumulated in

front of the burrow, the lizard would turn around and, holding the soil between the outstretched forelegs and the fore part of body, would push the soil away like a miniature, animated bulldozer. After two or three passes that cleared the displaced soil away, the lizard would turn around and resume digging, again with the forelegs. The burrow eventually was deepened enough that the body of the lizard was completely concealed, only part of the tail visible. At no time were the hind legs used directly for either excavation or clearance.

Initially the observer stood 2-3 m from the burrowing lizard, during which time it moved steadily between episodes of excavation and clearance. When the burrow was deep enough to prevent the lizard from seeing external movements while excavating, the observer changed to a sitting position 1.2 m from the burrow. Thereafter, the lizard regularly stopped still for 10-20 seconds, half-emerged from the burrow, apparently scanning the vicinity for any threat, before resuming clearing efforts. So posed, the fore part of body was held up by one or both forelegs extended vertically, but the body was held still and the head turned slightly no more than once or twice.

While scanning, the lizard exhibited two remarkable behaviors. Immediately upon adoption of the scanning stance, the lizard vibrated the head vertically over a distance of no more than 2-3 mm, for just a fraction of a second, then held still. The function of the vibration was not evident, but may well be bathyoptic and stereoscopic (facilitating distance and depth perception, and three-dimensional vision), as is apparently one function of the conspicuous push-ups of many phrynosomatid (and other) lizards (Walls, 1967: 342) - a function that has been very little explored whereas the social function of "signature displays" (Ferguson, 1977: 409-411) has dominated the literature on the subject. Maximum depth-perception could well be achieved by a much smaller movement arc in active, foraging lizards such as *Cnemidophorus* than would be the case in less active, ambushing lizards such as phrynosomatids (Anderson, 1993: 83).

A second remarkable behavior was the seemingly spasmodic, uncoordinated, erratic digging movement of whichever foreleg was free as the lizard held its scanning stance. Usually only one extended foreleg supported the fore part of the body, and the other foreleg was free. In that position, the free foreleg exhibited futile digging movements in mid-air. We interpret this behavior as representing conflict between two functional patterns: burrow excavation and antipredation vigilance. The result was the nonfunctional addition of digging movement to the

scanning pattern, conforming to the process called "superposition" by Eibl-Eibesfeldt (1975: 206).

Although these digging movements were malfunctioning with respect to excavation, they may have been ritualized signals indicating status or territory ownership, as Carpenter et al. (1970) described very similar motor patterns ("circumduction" was their name for the behavior) within the social repertoire of three species of "*Amphibolurus*" (now in three genera, *Amphibolurus*, *Ctenophorus* and *Pogona*).

Otherwise the behavior of the two *C. exsanguis* conformed with previous reports (e.g., Scudday and Dixon, 1973: 284; Schall and Pianka, 1980: 561) on foraging and approachability. Although both were almost constantly on the move, and skittishly aware of any extraneous movement, they showed little or no fear of stationary objects - an attribute Schall and Pianka (1980: 562) regarded as "temerarious." They periodically sought shade wherever available, and rested there for a few seconds. Their antagonism was weak, the larger occasionally chasing the smaller if it approached too closely, the latter then fleeing rapidly. Nevertheless, both twice rested together for 10-15 seconds in the shade of the observer.

After 11:30 a.m. the two lizards disappeared, presumably because of the heat (lower 30's C), and were not seen again during our stay there until 1:30 p.m.

#### Acknowledgments

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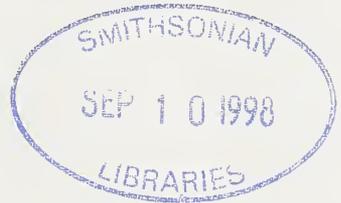
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COMPARATIVE METABOLIC RATE-TEMPERATURE CURVES  
OF FIVE SPECIES OF SNAKES OF THE FAMILIES  
VIPERIDAE, COLUBRIDAE AND LEPTOTYPHLOPIDAE

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# COMPARATIVE METABOLIC RATE-TEMPERATURE CURVES OF FIVE SPECIES OF SNAKES OF THE FAMILIES VIPERIDAE, COLUBRIDAE, AND LEPTOTYPHLOPIDAE

Mohamed K. Al-Sadoon and Nasr M. Abdo

## Abstract

Five snake species (*Vipera russelii*, *Malpolon monspessulanus insignitus*, *Coluber florulentus*, *Spalerosophis diadema*, and subadult and adult *Leptotyphlops microrhynchus*) belonging to the families Viperidae, Colubridae, and Leptotyphlopidae were collected from Pakistan, Egypt, and Saudi Arabia for the comparative study of their metabolic rate-temperature (M-T) curves. The resting oxygen consumption ( $\dot{v}O_2$ ) rates of each species were measured at ambient temperatures of 10 to 35°C in a double-chamber, volumetric closed system. The M-T curves and the linear regression lines were significantly ( $P < 0.05$ ) directly proportional in all species. A significant inverse proportionality of the metabolic rate weight-specific relationship was noticed in all species, but was more pronounced in the subadult and adult *L. microrhynchus*. The  $Q_{10}$  values though pointing to the thermal dependent shifts and preferred body temperature ranges, but the variations and similarities observed in these parameters could be attributed to geographical and environmental factors.

## Introduction

Extremes of temperature (Sturbaum, 1982) and water relations of reptiles are always critical and demanding for life, especially in arid regions (Cloudsley - Thompson, 1971, 1972, 1991), and the selection and regulation of a preferred body temperature (PBT) range by such ectotherms has been reported to be species-specific and as an important factor in ecological isolation (Bogert, 1949). Such thermoregulation is of paramount importance to counter changes in environmental temperature (Sturbaum, 1982). Several studies have been undertaken on the behavioral and physiological responses of reptiles to temperature (Cowles & Bogert, 1944; Bogert, 1959; Dawson and Templeton, 1963; Licht *et al.*, 1966; Cloudsley- Thompson, 1972; Hutchison, 1979 and Al-Sadoon, 1986, 1991).

Moreover, oxygen consumption at various temperature levels could be an indirect measure of oxidative metabolism in ectothermic animals such as reptiles (Al-Sadoon and Spellerberg, 1985a). The rate of oxygen consumption is expected to show a steady increase with the rise in the ambient temperature in a manner according to Van't Hoff's generalization (Gordon *et al.*, 1982). However, more recent studies (Al-Sadoon and Spellerberg, 1985b) have shown that such a relationship is not always linear.

Hence, we carried out allometric investigations on the metabolism of five snake species from various geographical locations and belonging to three different families, looking for any significant correlations in the patterns of their metabolic rate-temperature (M-T) curves and their  $Q_{10}$  values.

### Materials and Methods

#### *Experimental animals*

All experimental specimens were snakes *Vipera russi* ( $\bar{x}$  w = 54.6 g; SEM = 3.8) is a representative of the family Viperidae that had been collected from the cultivated lowlands of eastern Pakistan. It is solenoglyphous (i.e., has long hinged erectile front fangs), has very potent venom, and leads a nocturnal (scarcely diurnal) life. The family Colubridae is represented by the weakly-venomous, opisthoglyphous (back-fanged) diurnal snake *Malpolon monspessulanus insignitus* ( $\bar{x}$  w = 91.2 g; SEM = 4.5), which was collected from Alexandria, Egypt on the Mediterranean coast. The other two species of the family Colubridae were *Coluber florulentus* and *Spalerosophis diadema*, were collected from the Central desert regions of Saudi Arabia. Both are diurnal, non-venomous, aglyphous (without fangs) colubrids. The family Leptotyphlopidae was represented by sub-adults ( $\bar{x}$  w = 0.3 g; SEM 0.036) and adults ( $\bar{x}$  w = 2.3 g; SEM = 0.286) of *Leptotyphlops microrhynchus*. These thread-snakes or worm-snakes are burrowers that lead a subterranean nocturnal life. They were collected from the cultivated areas of Wadi Haniefa near to the city of Riyadh, in the Central Region of Saudi Arabia.

All experimental animals were kept in the serpentarium of the animal facility of the Zoology Department, College of Science, King Saud

University in Riyadh. They were kept in large transparent perspex tanks (100 x 50 x 45 cm) with netwire sliding tops. Each tank was provided with substratum of sand, to simulate the snakes' natural habitat. An automatic 100-watt lamp was placed overhead inside each tank to give a light period of 9 h per day that provided a thermal gradient of 20 to 40° C. The animals were fed laboratory-bred mice once every fortnight. The worm-snakes, were fed mealworms and other small insects. Water was provided *ad libitum*. In order to achieve a post-absorptive state, the animals were not fed for 5 days prior to experimentation.

### *Resting metabolic rate (RMR)*

The resting metabolic rate of the snakes was measured in terms of resting  $\dot{v} O_2$  rate (ml/ g/ h) using the double chamber, volumetric closed system of Al-Sadoon (1983) and Al-Sadoon and Spellerberg (1985a; 1987) at temperatures ranging from 10 - 35° C, with 5° C intervals. Scay something about time at each temperature.

Statistical analyses and figure drawings were carried out according to the model of Biosoft (1991). Two-tail t-test was employed for comparisons of the  $\bar{x} \pm 0.2$  of the different groups. All tests were considered significant at  $\alpha \leq 0.05$ .

## Results

### *Metabolic rate-temperature (M-T) curves*

Resting  $\dot{v} O_2$  (RMR) of the five snakes and the  $\bar{X} \dot{v} O_2$  of each one at the various experimental temperature levels are presented in Figs. 1 - 4. The linear regression analysis of the M-T curves clearly demonstrate that the  $\dot{v} O_2$  rate of each species increased directly with the temperature (Table 3.). On the other hand the values for *L. microrhynchus* subadults which have a smaller body mass ( $\bar{x} \pm 0.3g$ ), were significantly ( $P < 0.01$ ) higher than the adults ( $\bar{x} \pm 2.3g$ ). The observed/predicted (O/P)  $\dot{v} O_2$  of all species is around unity, but was very much reduced in the case of adult *L. microrhynchus* (Table 1). The M-T curve shapes are variable. Those of *S. diadema*, and of both the subadult and adult of *L. microrhynchus* are triphasic (Figs. 3 and 4). Those of *V. russelii* and *M. m. insignitus* depict a steady increase without any middle phase or plateau (Figs. 1 and 2). On the other

Table 1. The observed and predicted\* mean resting oxygen consumption values (ml/g/h) of the five snake species.

Species	20° C				30° C				35° C			
	observed	predicted	ratio (O/P)		observed	predicted	ratio (O/P)		observed	predicted	ratio (O/P)	
<i>V. russelii</i>	0.051	0.048	1.10		0.147	0.110	1.37		0.189	0.170	1.11	
<i>M. m. insignitus</i>	0.056	0.043	1.32		0.103	0.095	1.10		0.134	0.151	0.89	
<i>C. florulentus</i>	0.031	0.046	0.70		0.118	0.103	1.20		0.148	0.164	0.90	
<i>S. diadema</i>	0.075	0.049	1.53		0.098	0.109	0.90		0.140	0.173	0.81	
<i>L. microrhynchus</i> (Subadults)	0.519	0.159	3.30		0.596	0.374	1.60		0.663	0.594	1.12	
<i>L. microrhynchus</i> (Adults)	0.061	0.099	0.62		0.078	0.229	0.34		0.094	0.364	0.26	

\* Calculated for the three temperatures using the regression equations of Bennett and Dawson (1976) and Bennett (1982).

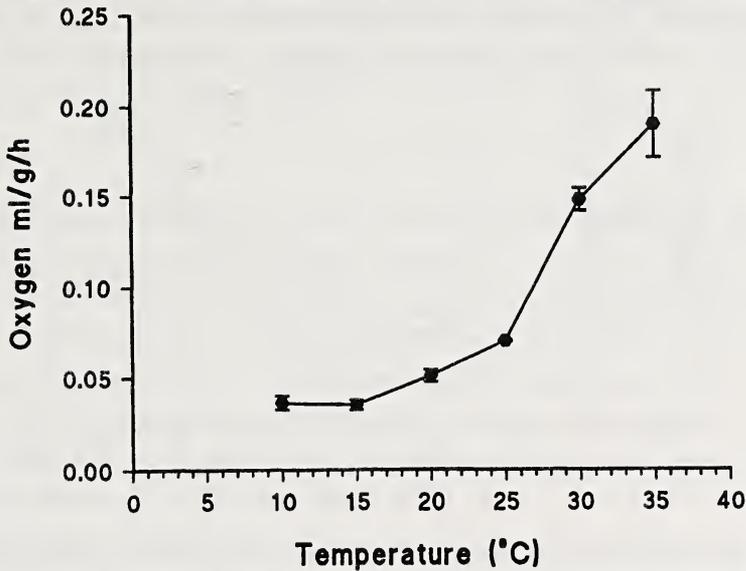


Fig. 1. Relationship between the oxygen consumption rates and the experimental temperatures of *vipers russelii*. Each point represents the mean of different individual snakes. Vertical lines represent standard errors (S.E.)

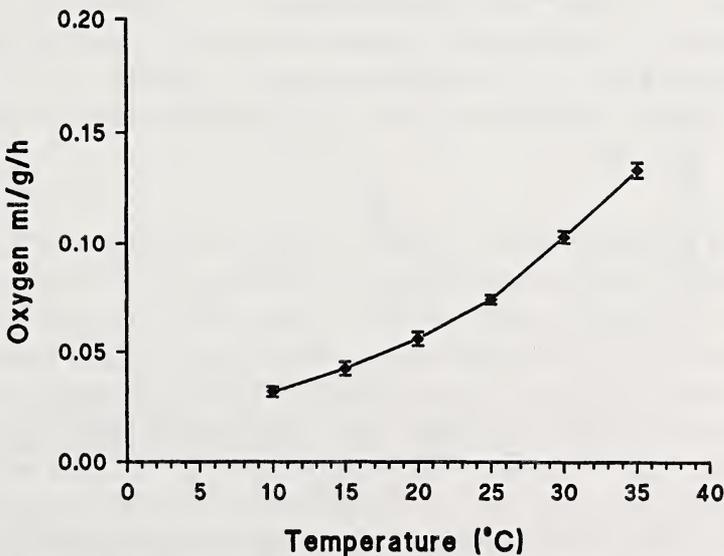


Fig. 2. Relationship between the oxygen consumption rates and the experimental temperatures of *Malpolon monspessulanus insignitus*. Each point represents the mean of different individual snakes. Vertical lines represent standard errors (S. E.)

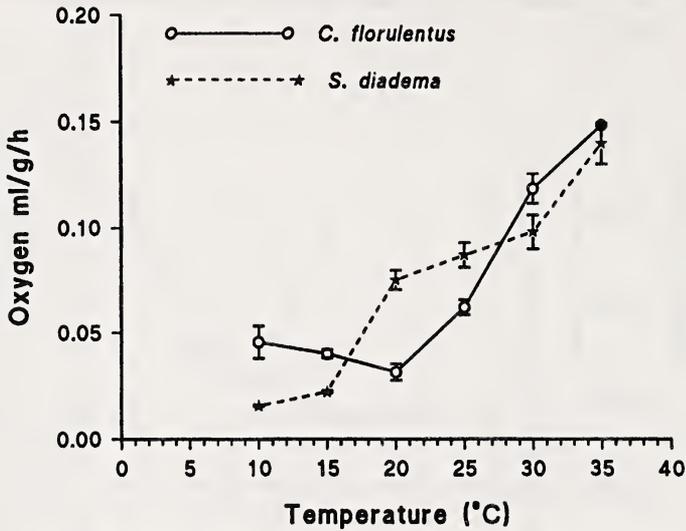


Fig. 3. Relationship between the oxygen consumption rates and the experimental temperatures of *Coluber florulentus* (O—O) and of *Spalerosophis diadema* (\*—\*). Each point represents the mean of different individual snakes. Vertical lines represent standard errors (S.E.)

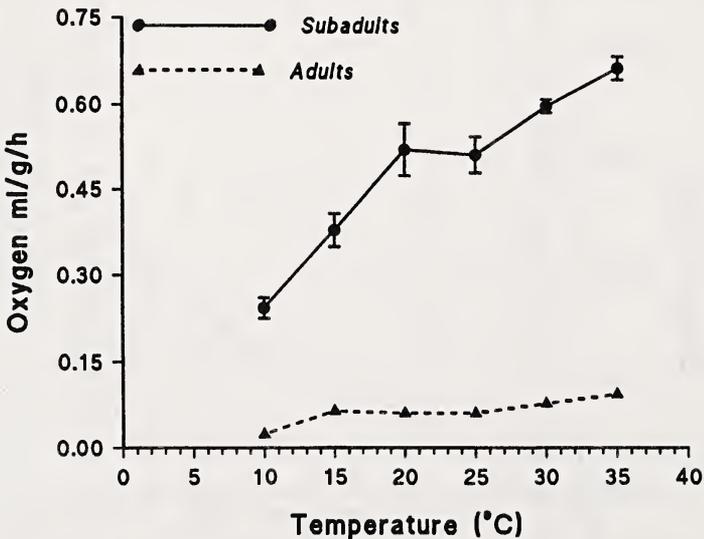


Fig. 4. Relationship between the oxygen consumption rates and the experimental temperatures *Leptotyphlops microrhynchus* (O—O, subadults) and (A—A adults). Each point represents the mean of different individual snakes. Vertical lines represent standard errors (S.E.)

hand, the M-T curve of *C. florulentus* shows a decreasing phase between 10°C and 20° C, followed by a steady increase similar to that of *V. russelii* and of *M. m. insignitus* (Figs. 1-3).

### *Q*<sub>10</sub> Values

Table 2 shows the *Q*<sub>10</sub> values of *L. microrhynchus* adults and subadults with an increasing phase for the subadults (2.4, 1.9 at 10-15 and 15-20°C) followed by a level plateau (1.0 at 20-25°C) then by an increase of 1.4 at 25-30° C. The adult *Q*<sub>10</sub> values show an increase of 7.4 at 10-15° C followed by a decrease of 0.9 at 15-20 and of 1.0 at 20-25°C, then an increase of 1.6 at 25-30° C. The *Q*<sub>10</sub> values of *S. diadema* have shown a rising phase of 11.6 at 15-20° C followed by a declining one of 1.3, 1.3 at 20-25°C and 25-30°C, respectively then followed by an increasing one of 2.0 at 30-35°C (Table 2).

The *Q*<sub>10</sub> values of *V. russelii* and *M. m. insignitus* have shown a very narrow plateau of a slight variation in thermal dependence. Those of *M. m. insignitus* depict a rising value of 1.8 at 15-20° C which becomes stationary at 1.8 at 20-25° C, then a slight increase of 1.9 at 25-30°C. Those of *V. russeiii* reach 2.1 at 15-20° C, then drop lightly to 1.9 at 20-25°C, before rising sharply to 4.4 at 25-30° C. On the other hand the *Q*<sub>10</sub> values of *C. florulentus* decrease to 0.8 and 0.6, respectively at 10-15 and 15-20° C, before rising sharply to 4.0 at 20-25° C. However, the overall *Q*<sub>10</sub> value for all species was around 2.0, but was only 1.2 for *L. microrhynchus* subadult (Table 2).

### Discussion

The RMR of the five snake species to varied according to species. However, the M-T curves and the *Q*<sub>10</sub> parameters were similarities among the species. Both of the *Q*<sub>10</sub> values and the shape of the M-T curves of subadult and adult *L. microrhynchus* were biphasic in. This burrowing, nocturnal species has cooler microhabitats in cultivated areas where it was been collected. Nevertheless, this cooler microhabitat can reach high temperature levels in summer, together with the whole desert area of the Central Region of Saudi Arabia. Hence this species is capable of surviving wide ranges of temperature within that habitat. This is also somewhat true for the diurnal snake *S. diadema*, which also inhabits the same desert habitat of the Central Region of Saudi Arabia. What could, however, refer to the range of its voluntary body temperature (VBT), which has been

Table 2. The thermal dependence ( $Q_{10}$  values) of resting oxygen consumption of the five snake species.

Species	$Q_{10}$ values of resting oxygen consumption.				
	10-15 C	15-20 C	20-25 C	25-30 C	30-35 C
<i>V. russelii</i>	1.0	2.1	1.0	4.4	1.7
<i>M.m. insignitus</i>	1.7	1.8	1.8	1.9	1.7
<i>C. florulentus</i>	0.8	0.6	4.0	3.6	1.6
<i>S. diadema</i>	2.0	11.6	1.3	1.3	2.0
<i>L. microrhynchus</i> (Subadults)	2.4	1.9	1.0	1.4	1.2
<i>L. microrhynchus</i> (Adults)	7.3	0.9	1.0	1.6	1.5
					1.7

Table 3. Linear regression analysis of the  $\dot{V}O_2$  of the five snake species.

Species	$\bar{X} \pm SEM^*$ (g)	XY correlation (r)	r <sup>2</sup>	P (t)
<i>V. russelii</i>	54.6 ± 3.8	0.93	0.86	P < 0.002
<i>M. m. insignitus</i>	91.1 ± 4.5	0.98	0.96	P < 0.002
<i>C. florulentus</i>	64 ± 10.8	0.87	0.76	P < 0.002
<i>S. diadema</i>	51. ± 1.73	0.97	0.95	P < 0.002
<i>L. microrhynchus</i> (Subadults)	0.3 ± 0.04	0.96	0.93	P < 0.002
<i>L. microrhynchus</i> (Adults)	2.3 ± 0.29	0.89	0.80	P < 0.002

\*SEM = Standard Error of Mean.

considered by Bennet and Dawson (1976) as a mechanism of metabolic homeostasis. On the other hand the M-T curves of the nocturnal viper, *V. russelii* and the diurnal colubrid *M. m. insignitus* have shown some degree of similarity in the steady increase as well as in the narrow range of low thermal dependence. This might indicate the damp habitats of both species. The former is collected from the damp cultivated areas of eastern Pakistan and the latter from the damp Mediterranean coast of Alexandria in northern Egypt. Similar observations of the effect of climate on the metabolic rate of various reptiles have been made by several research workers (Dawson and Templeton, 1963; Davies and Bennet, 1981; Al-Sadoon, 1983; Wheeler, 1984; Hailey and Davies, 1986; Zari, 1987 and Patterson and Davies, 1989).

An interesting feature was observed in the M-T curve of *C. florulentus*, where the  $Q_{10}$  values were low (decreasing) at the temperature range of 10-20°C. This has only been observed in cool, temperate snakes such as *Thamnophis sirtalis*, and has been interpreted by Aleksjuk (1971) as a mechanism of instantaneous temperature dependence shift. However, such a feature has never been observed before in any tropical or subtropical snake species. This low phase is, however, immediately followed by a sharp rising phase at 20-25° C. At higher temperatures (30-35° C), however, a low  $Q_{10}$  phase was observed that could be attributed to a physiological thermoregulation at high temperature by this diurnal desert snake.

Several researchers are of the opinion that the  $Q_{10}$  values are indicative of the three phase-shaped M-T curves of the majority of the tested snakes (Avery, 1976; Bennet and Dawson, 1976; Patterson and Davies, 1978, 1984, 1989; Andrews and Pough, 1985; Gatten Jr., 1985; and Zari, 1991). With the exception of *L. microrhynchus* the present results demonstrate that the O/P  $V_{O_2}$  values of all the snakes are around the value of a unit, which is a clear indication of their close similarity to the predictions of Bennet and Dawson (1976) and of Bennet (1982). The variable ratios attained by the subadult and adult *L. microrhynchus* could be attributed to the fact that the regression equations derived by Bennet and Dawson (1976) depict the interspecific relationships of large reptiles, while *L. microrhynchus* is of a very small body mass. Similar results were obtained by Al-Sadoon (1986), Al-Sadoon and Spellerberg (1987) and by Al-Sadoon and Abdo (1988, 1989, 1991).

The highest RMR was that of *L. microrhynchus* (subadults) which is of the lightest body mass of the snakes tested in the present study. This could be attributed to the mass-specific metabolism which is inversely proportional to the body mass. This feature is, however, also apparent, but with some minor anomalies in the position of the M-T curves worked out in the present study for all of the snakes tested. The most anomalous of those was that of the adult *L. microrhynchus* and it could well explain that anomaly. On the other hand, the  $Q_{10}$  values of the relatively heavier snakes were higher than those of the lighter ones. This is in good agreement with previous studies (Rao and Bullock, 1954; and Bennet and Dawson, 1976) and could be attributed to many factors, salient among which are climatic and environmental ones. More inter and intra-specific studies, especially those related to geographical barriers, are however needed for the better understanding of the ecophysiology of these reptiles.

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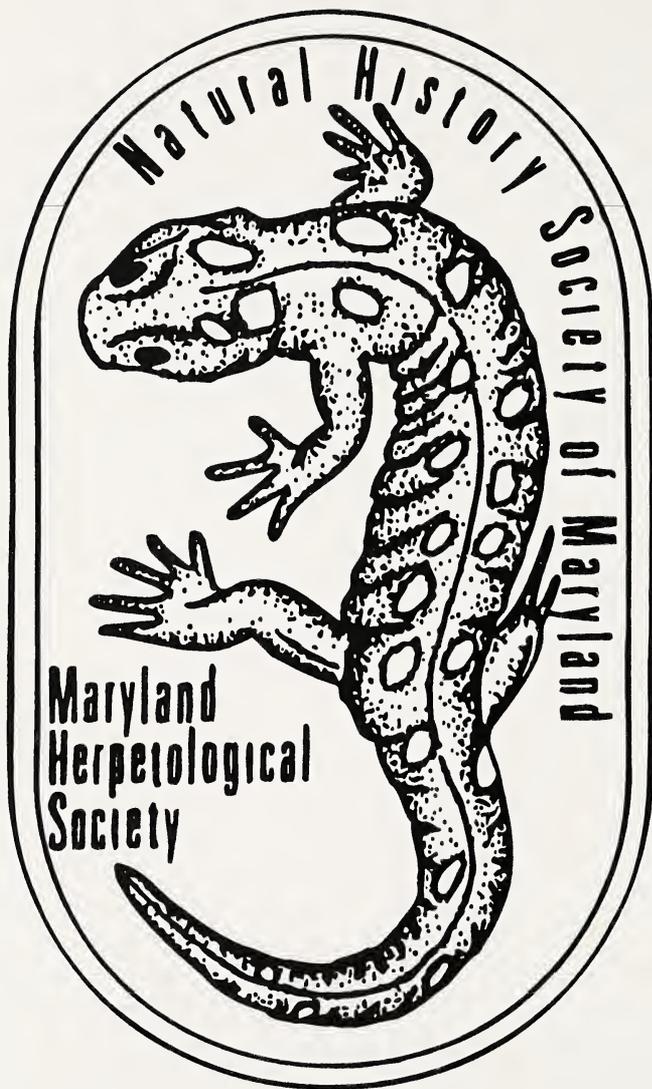
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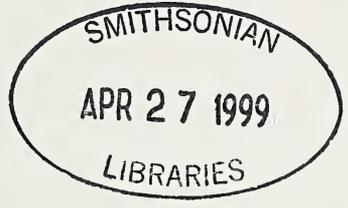
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# OSTEOLOGY OF *LEPTODACTYLUS LATINASUS* (ANURA: LEPTODACTYLIDAE) AND THE VALIDITY OF ITS SUBSPECIES

Maria L. Ponssa and E. O. Lavilla

## Abstract

The controversy on the validity of the subspecies of *Leptodactylus latinasus* is analyzed from an osteological point of view. The coincidence of diverse characters states of the skull, hyoid and pectoral girdle indicates that it is a monotypic species, in spite of some morphological differences (especially in the snout), observed among diverse populations.

## Introduction

After its description by Jiménez de la Espada (1875), the name *Leptodactylus latinasus*, was apparently overlooked, and was inadvertently replaced by *Leptodactylus prognathus* Boulenger (1888).

In 1964, Gallardo considered that this taxon was actually composed of two species, *L. prognathus*, inhabiting the eastern regions of Uruguay, Paraguay, Brazil and Argentina, and a new one, *L. anceps*, restricted to the dry, chacoan areas.

Since then, two antagonistic opinions arose: one supporting the existence of only one species with polymorphic populations, and the other that gave subspecific status to these differences. Among the contributions the following are the most relevant:

Barrio (1965) studied the nuptial call of *L. prognathus* and *L. anceps*, and due to their overall similarities, considered that they could be co-specific, and that the latter would be a chacoan subspecies of *L. prognathus*.

Heyer (1969) revalidated *Leptodactylus latinasus*, and later (Heyer 1978) considered *L. anceps* as a junior synonym of Jiménez de la Espada primarily based on Barrio's (op. cit.) results and some morphological overlap, but pointing out that chacoan populations could be differentiated from the coastal ones.

In the meantime, Limeses, Vignes and Tio (1972) showed some structural similarity in tongue structure and in the number of teeth of the premaxilla and maxilla in both entities.

Later authors (i.a. Cei, 1980, 1987; Gallardo, 1987; Gallardo and Varela, 1992; Lavilla, 1992), agreed with Barrio (1965) and considered *Leptodactylus latinasus* as a polytypic species, formed by the nominal subspecies and *L. latinasus anceps*.

In short, while nuptial call, some anatomical characters and some morphometric data showed similarities, diverse morphological and distributional characters showed differences, and due to the diversity of opinions available, we focused on the osteological analysis to contribute additional evidence to help solve the controversy.

### Material and Methods

Two groups of *Leptodactylus latinasus* (sensu lato) were analyzed, including:

- (a) Chacoan populations: Six individuals (three males and three females) from El Cadillal (Tucumán, Argentina), housed at Fundación Miguel Lillo collection (FML) as FML 02410/1-3, FML 02410/5, FML 02410/7 and FML 02410/9-10. The sample was assigned to "Tucumán", type locality of Gallardo's *L. anceps*.
- (b) Eastern populations: Six individuals (three males and three females) from Caseros (Prov. Buenos Aires, Argentina), housed at Museo Argentino de Ciencias Naturales Bernardino Rivadavia as MACN 6280-6285; this sample was considered by Gallardo (1964) as *Leptodactylus prognathus*, and was employed as a part of the comparative material in the original description of *L. anceps*.

Skeletons were prepared following Wassersug (1976) technique for stained and cleared vertebrates, and the analysis followed classical considerations employing the nomenclature proposed by Trueb (1993).

### Results and Discussion

The osteological analysis was focused on skull, hyobranchial skeleton, and pectoral girdle, and the following are common characters to the oriental (*Leptodactylus latinasus latinasus*) and chacoan (*Leptodactylus latinasus anceps*) populations:

Skull:

The frontoparietals, deeply forked, are usually fused to each other in the rear portion of the parietal region. They run from the posterior end of the foramen magnum to the posterior portion of the sphenethmoid, overlapping with it. The margins of the occipital region are fused to prootics and exoccipitals, and the frontoparietal fontanella is irregular and thin.

The nasals are subtriangular, in medial contact each other and with the sphenethmoid. The dorsal surface of each bone is sculptured, and are not in contact with the pars facialis of the maxilla, nor with the frontoparietals.

The quadrato-jugals, completely ossified and stick-like, are in contact with the squamosal and overlaps the maxilla.

The squamosals show the zygomatic ramus of each bone subtriangular, directed slightly outwards and not in contact with maxilla. The otic ramus do not contact the frontoparietals. The otic plate is subquadrangular, not reaching the crista parotica. The descendent ramus is grooved and in contact with the quadrato-jugals.

The cultriform process of the parasphenoid is lanceolate and with irregular tip, reaching the area between neopalatines. The bone covers the sphenethmoid up to the neopalatine level, but is not in contact with them. The alae are partially fused to prootics and exoccipitals.

The neopalatines are included in a cartilaginous matrix, and contact the sphenethmoid, vomers and the pars palatina of the maxilla.

In the pterygoids, the anterior ramus of each bone doesn't reach the neopalatines and are separated from the maxilla by a cartilaginous sheet. The medial ramus has not contact with parasphenoid alae. The posterior ramus is laminar, curved and joints the complex quadrato-jugal - squamosal.

The vomers of each side are in medial contact and superposed to the sphenethmoid. The alae are irregular and indented, forming the anterior and inner sides of choanae; the dentigerous process bears 11-14 teeth.

The prootics are dorsally sculptured, and fused to exoccipitals and with the posterior region of frontoparietals and parasphenoid.

The exoccipitals show widely separated occipital condyles, and a

---

cartilaginous and mineralized crista parotica.

The premaxillae are juxtaposed to the maxilla, and the dentigerous processes have 9-11 teeth. The allary process of each bone is quadrangular, perpendicular to the axial axis and directed dorsally or posterodorsally. The pars palatina is laminar, while the palatine process is variable, notched or entire.

The maxillae have 39-45 teeth that go beyond the pterygoid level, and the pars palatina and facialis are laminar. Of the three typical processes, the preorbital is blunt, the postorbital vestigial, and the pterygoid is absent. The maxillary arch is complete.

The sphenethmoid is tubular, ossified, and dorsally approaching the premaxilla.

#### Pectoral Girdle:

Sternal architecture shows a cartilaginous and mineralized omosternum, with the proximal end slightly expanded; the mesosternum is ossified, showing the proximal region with convergent, and distal region with subparallel sides; the xiphisternum is cartilaginous, mineralized and expanded, and the epicoracoids are cartilaginous and mineralized; in ventral view the right overlaps the left.

The clavicles are arched and fused to scapulae. The scapulae bear the pars glenoidalis smaller than pars acromialis, and the union with suprascapulae and with coracoids are cartilaginous. The glenoid cavity is surrounded by cartilage. Finally, the cleithrum show cartilaginous, mineralized tip.

#### Hyoid:

The hyoid plate is cartilaginous, mineralized and with parallel margins. Of its processes, the anterolaterals are perpendicular to the axial axis, the hials are thin, long and expanded shortly after the curvature, and the tirohyals are ossified and with cartilaginous tip.

The cricoid is a complete, cartilaginous and not mineralized ring, where the esophagic process is differentiated, as a triangular structure, with regular sides. The bronchial process is thin.

The arithenoids are not mineralized, and show triangular shape in lateral view.

Among the analyzed structures, only three characters showed differences between the so called *Leptodactylus latinasus latinasus* and *Leptodactylus latinasus anceps*, and includes:

The cartilaginous episternum is rounded, rhomboidal or chordiform in *L. l. latinasus*, and rounded in *L. l. anceps*.

The anterolateral processes of the hyoid are not distally expanded in *L. l. latinasus*, but show a distal expansion in *L. l. anceps*.

Finally, the posterolateral processes of the hyoid are thin, not distally expanded in *L. l. latinasus*, but some individuals of *L. l. anceps* may show an expanded tip.

The osteological analysis presented herein show an immense number of similarities between populations considered as different subspecies, and among the few differences, all of them show variable conditions in one or other set of examined skeletons.

In conclusion, the skeletal evidence indicates that *Leptodactylus latinasus* is a monotypic species with the following synonymy:

*Leptodactylus latinasus* Jiménez de la Espada, 1875

1875. *L. latinasus* Jiménez de la Espada. Vert. Viaje Pacif.:40.

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## DIFFERENTIAL SURVIVORSHIP OF LARVAL LEOPARD FROGS (*RANA PIPIENS*) EXPOSED TO TEMPORARY AND PERMANENT REDUCED pH CONDITIONS

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### Abstract:

The effect of pH in breeding environments on amphibian's reproductive success may be directly linked to the current environmental problems of acid rain and amphibian population decline. In this study, eggs obtained following hormonally induced ovulation were fertilized artificially at pH 6.2 and raised to the free swimming stage at seven pH levels between 3.5 and 8.1. In addition the effects of short-term exposure to acidic conditions were investigated by placing developing eggs at different stages into pH 4.5 for 24 hours and noting visible deformities and survivorship. Prolonged exposure to pH <4 was lethal. Exposure to pH < 5.6 for more than 24 hours resulted in high embryo mortality (75-100%). Short-term exposure to pH 4.5 yielded no significant decrease in embryonic survival. Prolonged exposure to reduced pH yielded developmental abnormalities with a higher frequency than 24 hour exposure. Abnormalities observed include caudal curling, failure to retract yolk plug, and thoracic swelling; these tadpoles exhibited 100% mortality.

### Introduction

Acid precipitation is a very common problem in the United States. The pH of ponds and lakes can be altered on either a short-term basis or sometimes even permanently. Because these are breeding sites for many amphibians, the effect of pH on amphibian development has received some study (Dunson et al., 1992). Whereas Pough and Wilson (1977) report that pH does not affect the rate of amphibian development, other investigators note that amphibian development does not occur below pH 4.5 and that various developmental abnormalities occur at higher pH levels (Beebe, 1986; Beebe et al., 1990; Beebe and Griffin, 1977; Pough and Wilson, 1977; Freda and Dunson, 1985b). The majority of recent work focuses on

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Key words: *Anura; Rana pipiens; Acid Rain; Larval Survivorship*

correlating population studies with environmental chemistry (see Dunson et al., 1992). This type of study is clearly important and applicable to conservation biologists. However, in spite of published records of lethal pH ( $LC_{50}$ ) for several species (Freda and Taylor, 1992; Corn and Vertucci, 1992) the need still exists for controlled laboratory studies of embryonic development and survivorship over a range of pH levels.

We hypothesized that reduced pH would reduce embryo survivorship in *Rana pipiens* significantly even greater than that of the  $LC_{50}$  level. We addressed two specific questions in this study. First, what pH would be fatal to developing *R. pipiens*? Second, what is the critical stage of development at which a fluctuation in pH would be harmful? *R. pipiens*, was used for two reasons both of which relate to its ecology. First, the species tends to breed in permanent ponds rather than ephemeral ponds such as those utilized by *Rana sylvatica* and many Bufonids and Ambystomatids (Dickerson, 1913; Clark and Hall, 1983; Cook, 1983; Pierce et al., 1984; Freda and Dunson, 1985b). Species that breed in ephemeral ponds are often more tolerant of low pH than are other species (Freda and Taylor, 1992). Therefore understanding the effect of reduced pH on a species that does not typically breed in ephemeral ponds should reveal more about the impact acid precipitation has on amphibian populations. Second, this species is one of many amphibian species whose populations are thought to be declining due to acid precipitation (Martin, 1990; Milstein, 1990).

## Materials and Methods

### Acquisition of Eggs

Adult male and female *R. pipiens* were purchased from a commercial supplier (Kons Inc.). Consequently, collection locality and subspecies are unknown. All frogs were refrigerated at 11° C to stimulate brumation until they were needed with an average time in brumation of 10 days.

Ovulation of gravid female frogs was induced by the injection of female anterior pituitary glands (Hamburger 1960) and progesterone into the abdominal cavity. Eggs were artificially fertilized using conventional methods (Hamburger, 1960; Pierce and Sikand, 1984). Specifically, testes

from two males were macerated in reconstituted soft water. Females were stripped of eggs and the sperm solution was delivered by pipette.

#### Water pH and Buffer System

To investigate pH effects, an artificial buffer system was used. The buffer system contained 1L of distilled water, 30mg  $MgSO_4$ , 30mg  $CaSO_4 \times 2H_2O$ , 2mg KCl (Pierce et al., 1987), 81mg  $Na_2HPO_4$ , and 128mg  $NaH_2PO_4 \times H_2O$ . This yields a pH=6.3. The pH was lowered by addition of dilute sulfuric acid. The control group was maintained in pH 8.1 pond water. Solutions were changed daily to ensure minimal temporal variation in pH.

#### Short-term Exposure to Reduced pH

To establish if there was a critical point in development at which a pH shift would be fatal, eggs were fertilized as above and then raised in pond water at pH 8.1 until they were temporarily exposed to acidic conditions. Approximately 150 eggs were placed into a pH 4.5 buffered solution at each of four developmental stages: (1) fertilization; (2) 24 h or gastrula; (3) 48 h or neurula; and (4) 72 h or tail bud. After 24 h exposure the eggs were returned to pond water at pH 8.1. These egg batches were kept separated until feeding began.

Three replicates of this experiment were run, each using eggs from a new female and two new males. The final stage of development reached was recorded and any deformities were noted. Data on the percentage of tadpoles that hatched after short-term exposure to reduced pH were analyzed using a one way Anova.

#### Extended Exposure to Reduced pH

To determine a critical lower limit of pH on development approximately 200 eggs obtained in the above manner were placed in each of seven separate dishes pH 3.5, 4.0, 5.0, 5.6, 6.3, and a control of pond water of pH 8.1 one hour after fertilization. The experiment was replicated once with eggs from two different females. The pH levels were maintained until feeding was initiated in free swimming tadpoles, approximately 1 week after hatching. Each day, solutions were changed and any eggs which stopped developing were removed to ensure that bacteria did not begin

to grow. The final stage of development reached was recorded and any visible deformities were noted. Data on the percentage of tadpoles that hatched in conditions of extended exposure to reduced pH were also analyzed using a one way Anova followed by a Duncan multi-range test.

The number surviving in both the short-term and extended exposure experiments were compared and analyzed using a two-way t-test.

## Results

### Short-term Exposure to Reduced pH

There was no significant difference ( $F=4.024$ ,  $p=0.08$ ) in the percent of tadpoles surviving to free swimming following short-term exposure to reduced pH at the different developmental stages; 80% to 98% survived in all cases.

Some developmental anomalies were noted. These anomalies include swelling of the thoracic region in which the embryo appears bloated around the pectoral girdle. Caudal curling, or a dramatic bend in the tail, was also noted and appeared not only in embryos in the egg, but also in free-swimming larva. All abnormal embryos died either before hatching or within the first week of hatching.

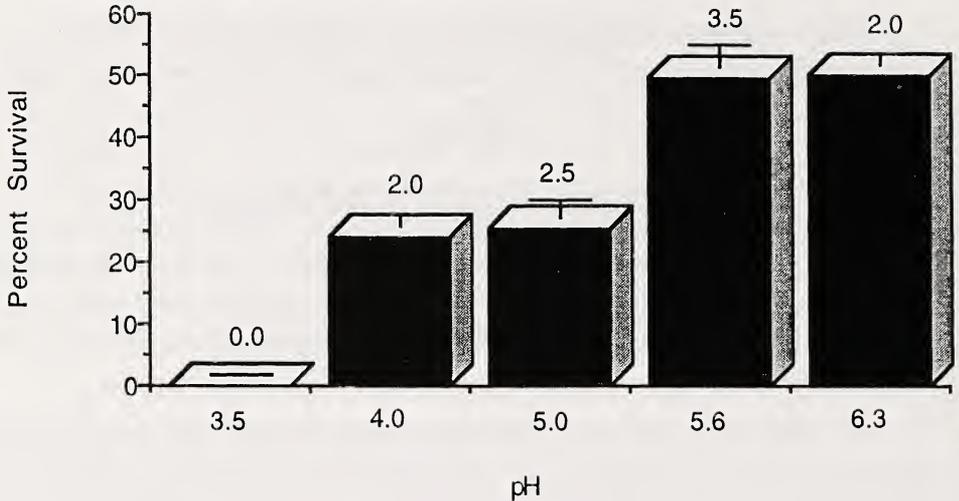
### Extended Exposure to Reduced pH

Percentage survival differed significantly with pH in the extended exposure experiment ( $F=81.901$ ,  $p<0.01$ ). The data indicate that a pH less than 4.0 is lethal (Fig. 1). Bacterial infection (*Pseudomonas fluorescens*), inhibition of yolk plug retraction, thoracic swelling and caudal curling occur at a pH less than 6.3.

Some eggs died of causes not visibly related to the study. These deaths occurred throughout the test period and showed no specific trend nor were they limited to any specific developmental stage. No deformities were visible in these individuals.

Mortality occurred most often at yolk plug retraction. Prior to this stage, development seemed normal. However, yolk plug retraction did not occur prior to neurulation as it should. This deformity was always fatal in the early stages of neurulation.

Fig. 1 Percent survival under extended pH stress. Numbers represent standard error.



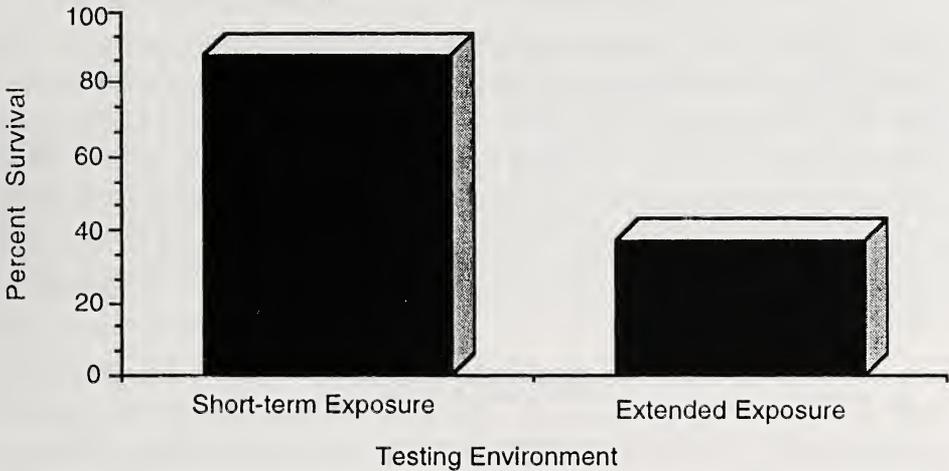
Two other visible deformities of tadpoles were thoracic swelling and caudal curling. Hatching success was significantly different ( $p < 0.05$ ) between pH 5.6 and pH 5.0 as was the percent surviving to free swimming stage.

Survival under conditions of extended exposure was significantly lower than short-term exposure conditions ( $T = -10.265$ ,  $p < 0.01$ ), as illustrated in Fig. 2.

### Discussion

The lethal effects of low pH have been noted by several authors. Dunson and Connell (1982) reported that *Xenopus laevis* failed to hatch at pH 4.3. Gosner and Black (1957) listed critical pH ranges for eleven species, including *Rana pipiens* (pH 3.9-4.1) and *Rana sylvatica* (pH 3.5-3.9). Grant and Licht (1993) found the critical pH of *R. sylvatica* (pH 4.0-4.5), *R. catesbeiana* (pH 4.0-4.5), and *H. versicolor* (pH 3.5-3.8). Freda and Taylor (1992) reported the  $LC_{50}$  for *R. pipiens* (pH 4.06), *R. clamitans* (pH 3.36) and *R. sylvatica* (pH 3.71). Similarly, Corn and Vertucci (1992) reported the  $LC_{50}$  of *Ambystoma tigrinum* (pH 5.3), *Bufo boreas* (pH 4.5), *Pseudacris triseriata* (pH 4.8), *R. pipiens* (pH 4.5) and *R. sylvatica* (pH 4.3). Pierce and Mont-

Fig 2. Percent survival to free swimming as a function of testing environment.



gomery (1989) found that *B. valliceps*, *B. woodhousei* and *Xenopus laevis* embryos exposed to pH 4.0 for three days showed no permanent effects. In the present study we found that fewer than 50% of *R. pipiens* larva survive prolonged exposure to pH < 5.6 Prolonged exposure to pH 3.5 was 100% lethal. However, we found no significant increase in mortality when exposed to pH 4.5 for 24 h. The difference in survival rate between prolonged exposure and short-term exposure to reduced pH was significant. This indicates that brief exposures to reduced pH, even to the LC<sub>50</sub> for a species, is significantly less lethal than prolonged exposure to the same pH.

The reason that a pH of 3.5 was lethal in this study may be correlated with the increase in development of bacteria (*Pseudomonas fluorescens*) which is known to inhabit low pH areas (Bergan, 1981; Jeter and Ingraham, 1981). High mortality in low pH could also be due to physiological factors. Dunson and Connell (1982) attributed the poor hatching success of *Xenopus laevis* eggs incubated in reduced pH to the blockage of some physiological process necessary for hatching. Salthe (1965) found that the amount of perivitelline fluid in *R. pipiens* eggs did not increase normally when the eggs were incubated in low pH. High mortality for *R. sylvatica* incubated at a pH of 3.5 has been attributed to sodium (Na) imbalance (Freda and Dunson, 1985b).

Reports of developmental anomalies and deformities are rather common in the literature. The deformities found in the current study, inability to retract the yolk plug, caudal curling of free swimming tadpoles, and the swelling of the thoracic region have been previously noted for other amphibian species (Pough and Wilson 1977; Pough, 1976; Pough and Wilson, 1977; Beattie and Tyler-Jones, 1992). Freda and Dunson (1985a) noted that embryos of other amphibian species exhibit curling within the egg when maintained at pH < 4.5. Bradford et al. (1992) reported a reduction in body size for embryonic *R. muscosa* acidic conditions. In addition, Gosner and Black (1957) noted deformities for frogs reared in low pH, but no description of these deformities was given.

Amphibian species are affected differently by pH. Pough and Wilson (1977) found significant pH tolerance differences in two species of salamanders, *Ambystoma jeffersonianum* and *A. maculatum*. Freda and Dunson (1985b) noted that *R. sylvatica* can breed in virtually all available ponds due to a high tolerance to low pH. Conversely, *B. calamita* will not reproduce successfully in acidic ponds, and *Bufo woodhousei* is absent from acidic ponds in Pennsylvania (Freda and Dunson 1986). Freda and Taylor (1992) reported that the *R. pipiens* and *B. americanus* tadpoles were more sensitive to acidic conditions than *R. clamitans*, *R. sylvatica* and *P. crucifer* and their tadpoles will actively avoid acidic conditions. *R. pipiens* are not as tolerant to reduced pH as other anuran species.

In the current study, prolonged exposure to low pH reduced survival whereas short-term exposure did not. This contradicts what Leftwich and Lilly (1992) found for *Bufo americanus*. They report that short-term exposure to reduced pH significantly hindered survival of embryos. However, they did not use a buffer system, nor did they monitor the pH throughout the study. Also, they only used eggs from one clutch from a single pair. Consequently, the results they achieved could be an artifact of the genotype of the parents as there is evidence to suggest a genetic or at least a maternal-factor basis for acid tolerance (Pierce and Sikand, 1985; Pierce and Wooten, 1992). At face value, however, their results suggest that *Bufo* may be more sensitive to brief exposure to low pH than *R. pipiens*.

Pierce and Montgomery (1989) assert that temporary reductions in pH occur more commonly in nature than does prolonged exposure to reduced pH. This would explain why certain areas of the North Eastern

United States, which have been permanently damaged by acid rain, have diminished amphibian populations or changing populations while those with only occasional acidic events may show less of a decline.

The natural mortality in normal conditions for developing *R. pipiens* is high. Merrell (1977) estimated the highest mortality for a population of *R. pipiens* in Minnesota to occur in the larval stage with nearly 95% of the larva failing to metamorphose. If our data are any indication of natural survival in fluctuating pH, it seems unlikely that temporary exposure to low pH could significantly affect a population. However, prolonged exposure to reduced pH could be detrimental to the population, even causing local extinctions.

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## ***SCELOPORUS POINSETTI: ITS TAXONOMIC AFFINITY WITH *MUCRONATUS****

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Populations of *Sceloporus poinsetti* and of *Sceloporus mucronatus* have not been reported to approach each other geographically, so that observations of a population near Huichapan, Hidalgo, Mexico exhibiting characters of both taxa is of interest. Specimens from nearby areas have consistently been referred to *S. mucronatus*. Yet 2 of 4 individuals from the Huichapan locality are identical with individuals of *S. poinsetti poinsetti* in most characters, whereas in certain characters of pattern 2 others are indefinite of identity, resembling, in certain features, some specimens of *S. mucronatus* from Veracruz. Review of examples from the region has helped to clarify the issue, a study from which this paper results.

*Sceloporus poinsetti* was described by Baird and Girard in 1854, *S. mucronatus* by Cope in 1885. The taxa have retained species status during more than a century following, with the exception that Boulenger referred to both as subspecies of *S. torquatus* (1885, 1897), he accepting the number of dorsal scales, length of the fourth toe and the tibia as diagnostic.

### Diagnostic Characters

Striking differences between these taxa have been given as those of pattern, particularly the caudal banding — distinct, broad, alternating dark and light bands, most distinct toward tip of tail in *S. poinsetti*, absent or not of equal width, incomplete near tip in — and the broad white margins of the nuchal collar and a broad light band behind occiput in *poinsetti* with narrow white collar borders in *S. mucronatus*, but no postoccipital light band.

Regarding Boulenger's consideration of these taxa as subspecies of *S. torquatus*, it is to be noted that throughout almost the entire range of *S. torquatus* the dorsal pattern alone is far different from and without tendency toward that of the *S. poinsetti-mucronatus* complex where the ranges approach each other. Furthermore, habitat of *S. torquatus* is at much higher elevation than that observed for most populations of *S. poinsetti* (Olson, 1990).

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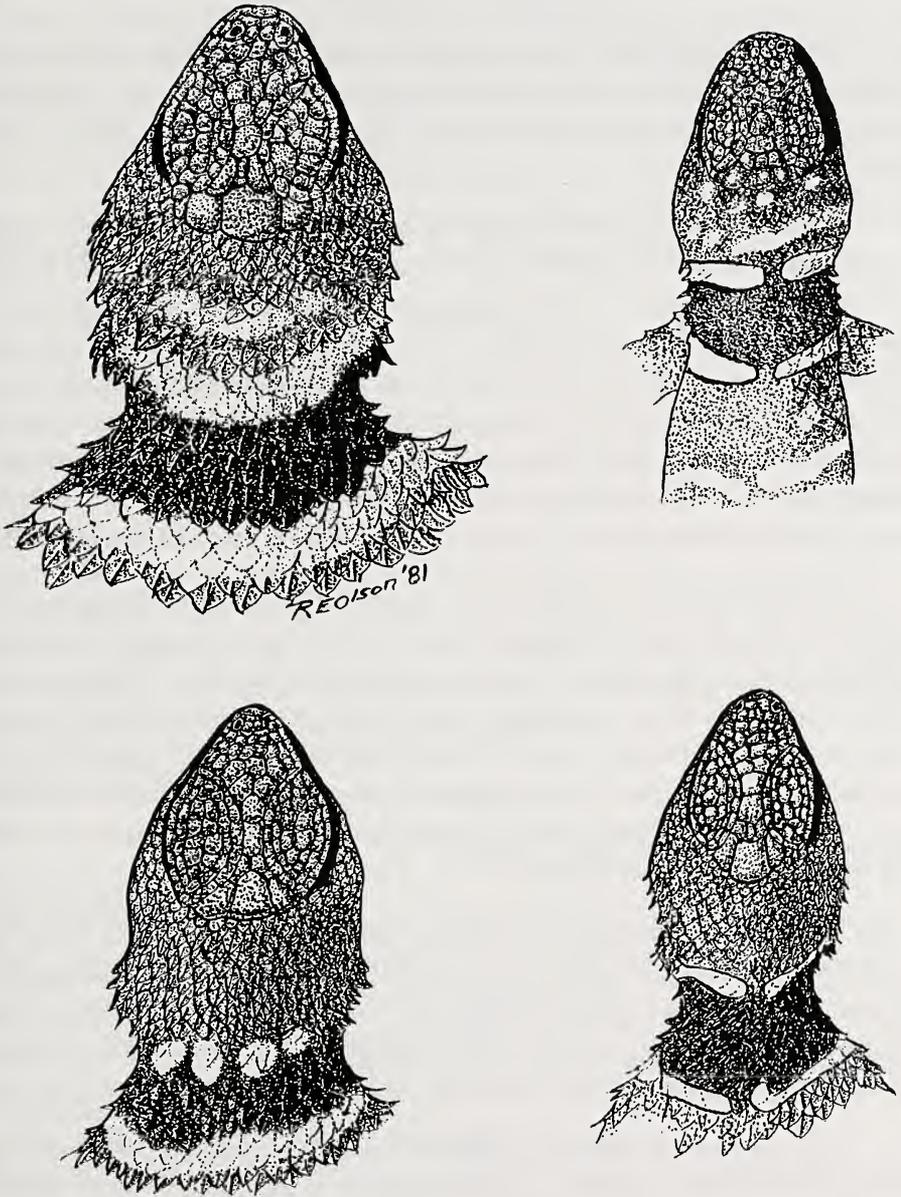


Figure 1. Anterior dorsal patterns of examples of *Sceloporus*. Upper left: #5863, 6.7 mi. SW Huichapan, Hidalgo, Mexico. Upper right: #5864, same locality as above. Lower left: #1223, W. Acultzingo, Veracruz, Mexico. Lower right: #5966, Ramirez, Veracruz.

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### Population Comparisons

Samples of *Sceloporus poinsetti* from various portions of its range in Mexico give indication of individuality of expression of each population. Some of these were compared with specimens from northern Mexico, Texas and New Mexico.

In all samples except Durango specimens (central and Western Texas, central New Mexico, southern Zacatecas, and Hidalgo) the nuchal collar is narrow (3 scales broad), the collar borders broad (2 or more scales), and there is a post-occipital light bar, almost as if an additional light collar border. Specimens from west of cd. Durango have broad, deep set nuchal collars (5 scales broad) broad borders (not distinctly so broad, however, because of the breadth of the collar itself), and a post-occipital light bar which often becomes indistinct in mature individuals. Thus *S. p. macrolepis* is quite distinct from other populations by virtue of pattern alone.

The pattern in most populations involves, to some degree, a series of 3 or 4 dark dorsal cross-bars. These tend to be indistinct in Zacatecas animals, and somewhat so in specimens from Hidalgo. Zacatecas specimens, especially larger examples, tend to be tan or dusky dorsally, in contrast to the gray to blue-gray of most populations, with barred dorsum mentioned above. (Zacatecas populations were often found to inhabit open, dry soil situations with elaborate burrow systems in the soil, unlike the usual saxicolous habitats.)

Males in northerly populations have medium to dark blue belly patches with heavy, black borders medially, these either contacting medially or not. I do not find these features in more southerly populations. Rather, the belly patches are medium to light blue, lack much of a border and are separated along the midline by a light area 6 or more scales across.

A specimen (REO 5864) from 6.7 mi. SW Huichapan, Hgo. is taken to be anomalous in pattern. This specimen is 54 mm svl. with well-defined throat bars. The dorsum is olive with paravertebrally arranged, cream-colored chevrons. The nuchal collar is olive-brown, the borders of which are cream-colored, broken medially. Caudal bars are moderately distinct. In this it closely resembles a juvenile of *S. mucronatus* (#1227) from near Puerto del Aire, Veracruz. Many specimens of *S. mucronatus* have alternating olive and black caudal bars; those from hilly areas above

Acultzingo, Veracruz often have sharply black-and-white barred tails. Adults from the Hidalgo locality bear weakly-barréd tails, and two (5862 & 5863) have continuous dark dorsal blotches rather than crossbars, whereas a third (5874) is nearly plain. The nuchal collars and borders resemble, in other respects, those of *S. poinsetti* elsewhere. It is to be noted that the collar borders are usually broader (ca. 1 1/2 scales) in specimens of *S. mucronatus* from Las Vigas and La Joya, Veracruz, and especially from Oaxaca, where the distinct caudal barring is again observed.

### Nearby

Examples from two other localities show influences of *S. poinsetti*. Two from Amealco, 15 km. SE Huichapan exhibit strong tendencies, MZFC 3461(a) having faint but equal-width tail bands, narrow collar (3-3 1/2 scales), with broad borders (1 1/2 scales), another, MZFC 3461(b), having broad black (3) and narrow white (1) tail bands, postoccipital bar, and medium (1-1 1/2) collar borders. Of 14 others from Ajacubo, 35 mi. SE Huichapan, 8 have distinct, equal or nearly equal width tail bands (3 of 14 have incomplete tails), 5 have a complete 1-2 scale broad postoccipital band, and 8 have broad collar borders. But two from 6 mi W Huichapan (UTEF), are not so similar as above (Table 1).

Table 1. Scalation.

	N	Dorsals	Ventrals	Femoral Pores	Preoculars
<b><u>HIDALGO</u></b>					
6.7 mi. SW Huichapan (REO)	4	32-39	44-50	10.9 (9-12)	1 (all)
8.5 mi. NE Pachuca (REO)	1	31	42	13-14	1
Ajacuba (MZFC)	14	28-39	39-51	13.0 (10-15)	1-2 (1.6)
Amealco (MZFC)	2	31.5	46	12-13	1
<b><u>TLAXCALA</u></b>					
4.5 mi. N Taxco (REO)	3	28-31	41-48		
20 mi. N Apizaco (REO)	5	28-31	41-48	12.6 (11-15)	1-2 (1.2)
<b><u>VERACRUZ</u></b>					
2 mi. ESE Las Vigas (REO)	5	26-30	39-43	12.2 (10-14)	1-2 (1.4)
0.6 mi. S Perote (REO)	2	29	----	11 (8-14)	1-2 (1.5)
1.2 mi. WNW La Joya (REO)	6	27-31	42-43	11.7 (10-14)	1-2 (1.1)
2-3.5 mi. WSW Acultzingo (REO)	4	33-38	44-50	15.0 (11-18)	1.0 (all)
ENE Puerto del Aire (REO)	2	36-37	47-49	15.0 (14-16)	1.0 (all)

Further by comparison, features of the taxa are similar or identical. Belly patches in adult males do not differ significantly. And the parallel medial lines on the throat in females are shared, as is the blue spot on the shoulders in the nuchal collar field. Supraoculars are in a double row in both, and scale counts are in agreement. Dentition features are so similar between the taxa (Figure 2.) as to be indistinguishable (Olson et al. 1986, 1987). Alvarez and Huerta (1973) show similar data.

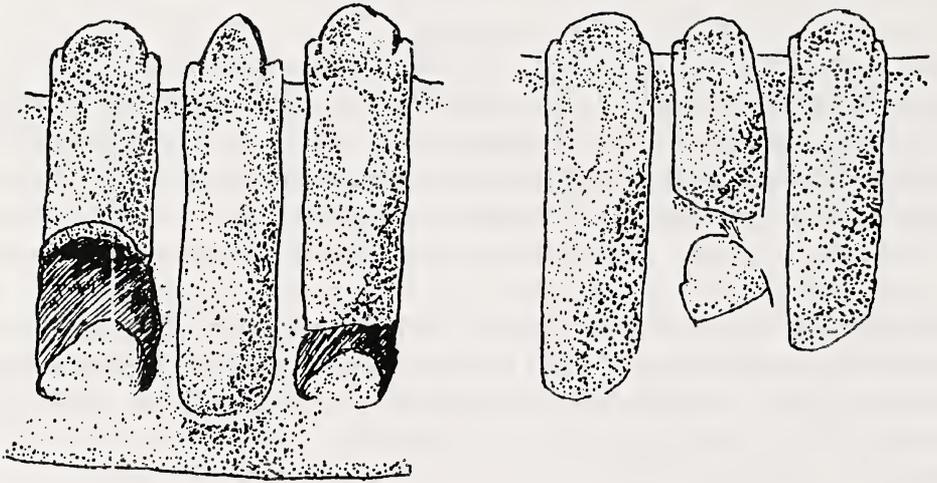


Figure 2 Dentition examples.

Left: lingual view of teeth 15-17 on left dentary. #11469, 3.8 mi. SE Arenal, Zacatecas, Mex.

Right: lingual view of teeth 13-15, left dentary. #11466, above Puerto del Aire, Veracruz, Mex.

### Discussion

The considerable overlap and intergrading of characters throughout the population complex, and features observed in the Hidalgo localities rendering many examples non-definitive as to classification lead to the conclusion that a single species is involved, and that the Huichapan area examples are intergrades. Since the name *S. poinsetti* appears some

30 years prior to *mucronatus*, the assemblage is to appear under the name *Sceloporus poinsetti*.

### Acknowledgments

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## CANNIBALISM IN *BOTHROPS ASPER*.

There are numerous records concerning cannibalism in snakes (Mitchell, 1986), this phenomenon occurs more commonly in captivity (Kiauber, 1972). Although there are reports of cannibalism in some species of "nauyacac" like *Bothrops jararaca*, *Botriechis nigroviridis*, *B. schlegeli*, *Porthidium nasutum* (Mitchell, 1986), and *Bothrops atrox* (Martins and Gordo, 1993), there is a general lack of information on one of the most common species of the group *B. asper*.

The "Laboratorio de Herpetologia Vivario de la UNAM Campus Iztacala," located in Mexico City has successfully maintained this species since 1986. On July 14<sup>th</sup>, 1993; a 7 year old female born in captivity and weighing 3,468 g. gave birth to 52 youngsters (mean SVL = 263 mm; TL = 305 mm; weight = 12 g), 35 of them were alive, 17 dead and in addition there were 5 infertile eggs found. At the beginning youngsters were raised in enclosures of wood and plastic construction (32 X 18 X 39 cm); in groups of 6 organisms. The bottom of the enclosure was covered with newspaper (with twice per week changes), and water was offered *ad libitum* in a plastic dish.

The literature refers that adults of this species feed mostly on small mammals as wild rats, mice and birds, while the youngsters prefer frogs and lizards (Mehrtens, 1987; Alvarez del Toro, 1982). In captivity this species, young of adult, easily accept rats or mice as food, so we fed the youngsters small mice (*Mus musculus*) once by week.

After three months the animals began to show eye problems due to bites that they were receiving from their "room mates." For this reason we separated them in groups of 2 organisms in each enclosure. The morning of October 18<sup>th</sup>, 1993, we found one of the youngsters (SVL = 350 mm; TL = 418 mm) swallowing up to the half of the body of its companion (SVL = 315 mm; TL = 365 mm); we carefully moved the snakes causing regurgitation. When the "prey" was completely released we could see that it was alive and in perfect condition, without a single sign of wounds. After this, both youngsters were separated and placed in individual cages, and no further problems arose.

Later, on November 12<sup>th</sup>, 1993; mid-morning, we detected the absence of an organism from one of the enclosures. The only youngster still in the cage (SVL = 298mm; TL = 348 mm) showed it swollen belly (Fig. 1). palpating the body of the snake, we could confirm that it was full with another snake.

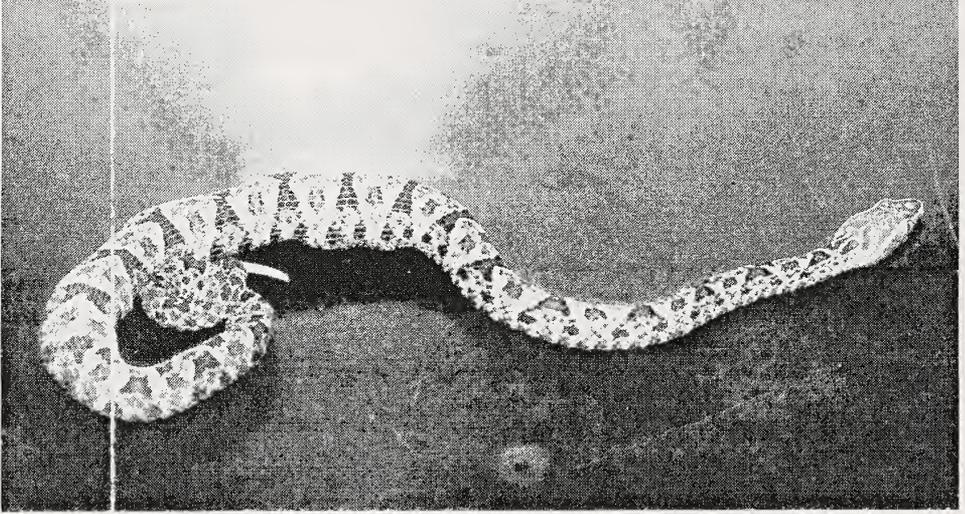


Figure 1. Youngster *Bothrops asper* showed swollen belly.

On January 27<sup>th</sup>, 1994 in the afternoon, another youngster swallowed its companion. We were waiting for the next day to obtain an x-ray series, but when we came for the organism, we found that the "prey" was regurgitated, probably due to its size (quite the same than its own). The regurgitated organism showed signs of advanced digestion especially on the head.

One of the most interesting observations resulting from this report, is the fact, that one snake swallowed another live snake. In most of cannibalism reports, there is a lack of knowledge regarding whether the "prey" was or was not dead or injured before it was swallowed; generally it is suggest that the "prey" was intentionally killed before swallowing, as it has been reported for the boid *Candoia carinata* swallowing an individual of *Charina b. bottae* (Michaels, 1985), or that it is already dead before swallowing (Mitchell, 1986).

In the other two cases we have referred regarding *B. asper* it is possible that the case was similar to the first related here, but we can not be assure because we did not observed the real ingestion process. It is also possible that they were attacked and injured or even killed previously to the ingestion, as it is known to occur in other species of "nauyacas" where the slightest movement provokes an attack.

The real causes of cannibalism are not well known in snakes; although many theories have been proposed (Mitchell, 1986), more information is needed to substantiate them. This prolific and relatively easy-to-maintain species can greatly contribute to the understanding of the phenomena.

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**BOOK REVIEW:**

***T. REX AND THE CRATER OF DOOM.* BY WALTER ALVAREZ. 1997. PRINCETON UNIVERSITY PRESS, PRINCETON, NEW JERSEY, 185 PP. HARDCOVER. US \$24.95. ISBN 0-691-01630-5. *THE GREAT DINOSAUR EXTINCTION CONTROVERSY.* BY CHARLES OFFICER AND JAKE PAGE. 1996. ADDISON-WESLEY, NEW YORK, 209 PP. HARDCOVER US \$25.00. ISBN 0-201-48384-X.**

*Jeffrey V. Yule*

Contemporary vertebrate diversity in general and reptilian diversity in particular are tied to a 65-million-year-old event known as the Cretaceous-Tertiary (K/T) extinction, which eradicated six entire reptilian orders: two of dinosaurs, three of aquatic reptiles, and one of pterosaurs. The subsequent diversification of both reptiles and mammals can only be fully understood in the context of this incident. Understandably, then, the K/T extinction has long been a matter of broad scientific interest. In 1980, an article whose authors included Nobel-laureate physicist Luis Alvarez and his geologist son Walter initiated an energetic scientific debate by arguing that a meteorite impact caused the extinction. The evidence presented for that claim was the presence of unusually high levels of the element iridium in the sediments marking the event. Although rare in the Earth's crust, iridium occurs in higher concentrations in meteorites, and the authors suggested an impact best explained the anomaly. Seventeen years later, there is still no consensus as to whether the Alvarez team's hypothesis is correct. Although it has gained many supporters, critics remain. Among the detractors are those who favor traditional, noncataclysmic explanations for the K/T extinction, such as shifts in climate and sea level. Others believe that the extinction — and the iridium anomaly — resulted from massive volcanism.

Two recent books address the impact vs. volcanism debate. Walter Alvarez's *T. rex and the Crater of Doom* sets forth the pro-impact argument, while Charles Officer's and Jake Page's *The Great Dinosaur Extinction Con-*

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*troversy* presents the evidence for volcanism. As is typical of works that treat unresolved scientific debates, the two books contradict one another's conclusions at every turn — but not with equal success. *T. rex and the Crater of Doom* presents an overview of the pro-impactors' evidence and discusses how it has been tested. *The Great Dinosaur Extinction Controversy*, on the other hand, focuses undue attention on peripheral issues while giving short shrift to matters of central interest. In particular, Officer and Page opt for flawed rhetorical strategies and ignore the difficulties they face in squaring their interpretations of key evidence with the conclusions of the broader geological community. Alvarez's discussion of the impact position suffers from none of these problems.

Although the title *T. rex and the Crater of Doom* suggests a particular concern with dinosaurs at the K/T extinction, Alvarez focuses on attempts to substantiate the impact hypothesis by addressing iridium anomalies and other geological evidence, including the smoking-gun evidence of the hypothesized reptile-killing impact: the crater itself. Alvarez presents a nontechnical account of the search for that key piece of evidence, now thought to be the Yucatán's Chicxulub (Cheek-shoe-lube) crater. He contextualizes the search within the broader framework of modern geology, discussing matters from radioactive dating and geological mapping to the shift of opinion that led geologists to recognize the importance of catastrophic as well as uniformitarian processes.

Alvarez is particularly successful at explaining just how devastating the impact of a 10-kilometer meteorite would have been. He effectively presents the unfamiliar in light of the familiar, comparing the object's diameter to that of modern-day San Francisco and describing its probable final velocity of 30 km/sec as 1,000 times faster than a car on the highway. His ability to provide useful perspective extends to other matters as well, as when he explains that the impact would have released enough energy to vaporize the meteorite within a second while producing a hole with a momentary depth of 40 km. This hole would have almost instantly collapsed to form a broader, shallower crater 150-200 km across. Under these circumstances, Alvarez writes, the "Earth would suffer cataclysmic damage in less time than it takes to read this sentence." To the author's credit, he makes that point clearly, briefly but ably covering matters from the vaporization of bedrock and subsequent atmospheric heating and forest fires to the effects of a giant tsunami, greenhouse gases, and acid rain.

Despite its strengths, however, Alvarez's account suffers from being too reader friendly, general, and nontechnical. Although end notes direct interested readers to a variety of sources for further details, he is at times more interested in offering marginally significant personal reminiscences than in addressing pertinent scientific matters. For instance, Alvarez ignores provisional answers that have been offered to some of the questions he raises — as when he writes that it is not clear whether the impacting object was a comet or a meteor and that no one has been able to satisfactorily explain why dinosaurs and other organisms went extinct while turtles, crocodiles, and a host of others did not. Both of these matters have been addressed in some detail by, among others, David Brez Carlisle, who has gone to especially great lengths to establish the impactor's cometary origin. Alvarez's failure to mention Carlisle's or other researchers' work on these and a variety of other matters represents a mild puzzle regardless of whether or not he accepts their conclusions. His account of the development of the impact hypothesis could only have benefited by addressing some of the matters he raises in greater detail. In general, though, while *T. rex and the Crater of Doom* does not treat the impact-volcanism debate comprehensively, it offers a clear and reasonably fair overview. The same cannot be said of *The Great Dinosaur Extinction Controversy*.

Officer — who, along with Charles Drake, formulated the explosive-volcanism hypothesis — has long argued for a volcanic cause for the K/T extinction. The well-publicized polarity of the impact-volcanism debates notwithstanding, however, the reader has a right to expect that some attention will be paid to counterarguments. Yet Officer and Page repeatedly downplay or ignore the existence of other reasonable points of view. Officer's assertion that shocked quartz associated with the K/T boundary layer was formed during volcanic explosions contradicts accepted beliefs about its diagnostic value in identifying impact sites, a consideration raised both in *T. rex and the Crater of Doom* and elsewhere (Carlisle 96; Glen 68). Although Officer and Neville Carter produced evidence of shocked quartz crystals associated with volcanic activity, Alvarez explains, their samples never quite matched the damaged crystals associated with known impact craters and the K/T boundary layer (97). In writing that volcanoes are "unquestionably responsible" (112) for iridium anomalies, Officer and Page similarly ignore opinions at variance with their own. At times that strategy is so obviously flawed that one wonders how the book

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ever saw print, especially in light of its other problems of consistency and rhetoric.

For example, Officer and Page twice devote attention to a 1984 opinion poll showing that a minority of German and British paleontologists, Soviet geoscientists, and American geophysicists accepted the Alvarez hypothesis (102-104; 186). This poll, they suggest, was wrongly ignored in a 1989 *Washington Post* article written by Richard Kerr. The reader is left to wonder just how important this supposed oversight might be — after all, the poll was five years old when Kerr “ignored” it and it is 12 years old now. Officer and Page invoke the 1984 poll again in attempting to argue that, as often happens with pathological science, opinion in favor of erroneous research initially rises towards 50 percent before falling off to oblivion (186). Here, they suggest that acceptance of the impact hypothesis is and should be falling off, yet their only evidence for such a shift in opinion is one outdated poll — a fact that they seek to excuse by noting that they are unaware of any recent surveys on the matter. Since graduate students working on theses or dissertations would be expected to undertake their own polling in such a situation, it is difficult to understand why these authors do not behave similarly in writing a book.

Among the many factors adversely affecting Officer’s and Page’s attempt to present their position, perhaps the most damaging is another rhetorical consideration. They give the appearance of trying to make their case in the style of a shrewd but cynical prosecutor — by executing a smear campaign against the defendant. While Alvarez is always civil and sometimes even gracious to his critics, Officer and Page generally are not. Alvarez comments that the frustrating ten-year search for the crater was actually a blessing, noting that “an early discovery of the impact site might have short-circuited the intense challenge to each bit of evidence that Chuck Officer compelled us to face.” At least occasionally, Alvarez also notes when other researchers’ opinions on key issues differ from his own. He writes, for example, that members of Officer’s so-called Dartmouth group are among a minority of researchers who don’t accept the presence of small glass particles called microtektites as evidence of an impact — this despite the fact that pro-impact researchers consider microtektites to be among their most important evidence. In a refreshing move away from the either-or thinking often characteristic of the impact volcanism debates,

Alvarez even concludes by suggesting that volcanism might play a role in the final explanation of events despite the fact that an impact appears to have been a more important factor (142-144). By contrast, Officer and Page attempt to make their case by impugning the integrity of pro-impact researchers and their work. They write, for instance, that "most of the 'science' performed by the Alvarez camp has been so inexplicably weak, and the response to it so eagerly accepted by important segments of the scientific press... that some skeptics have wondered if the entire affair was not, on the impact side, some kind of scam" (xiii). In what reads as a transparent attempt to make that very charge without being required to substantiate it, they immediately back away from their statement, noting that they lack the investigative skills necessary to substantiate such an allegation. Instead, they write, they will limit themselves to the "scientific merits of the case" (xiii). It is thus with some surprise that the reader later finds Officer and Page bringing personalities into their analysis.

Their sixth chapter opens by focusing on the late Luis Alvarez's alleged personal shortcomings, in particular arrogance and intolerance of disagreement. Once again, Officer and Page sound a modest note, writing that they lack the necessary skills to determine why a researcher would behave so poorly; instead, they reiterate, they will focus on the scientific merits of the case. Inexplicably, they then attempt the very sort of assessment of Luis Alvarez that they so recently admitted they were incapable of formulating. Eventually, they offer a brief and not especially convincing explanation for doing so. Based on the elder Alvarez's shortcomings, they finally reveal, it could have been predicted that "he would have had some trouble getting along with geologists and paleontologists" (82). Why this line of evidence would be crucial to making the volcanism argument is not clear. Moreover, the argumentative strategy employed in the rest of the book suggests that Officer's and Page's motivation for including their anti-Luis Alvarez section was to attack the most well-known researcher associated with the hypothesis in an effort to damage it by association. Such a strategy would certainly be in keeping with their generally scattershot approach. One of their main lines of argument is to portray those who take the opposite view as a wrong-headed group of potential flimflam artists. If there is any flimflam to be found in *The Great Dinosaur Extinction Controversy*, however, Officer and Page are the ones seeking to perpetrate it.

Inconsistencies as well as attempts at misdirection abound in their argument. For instance, they note that the publicity gained by the Alvarez hypothesis might have done harm to the environment by diverting attention from the current global extinction crisis (6) — a consideration which is neither here nor there insofar as their argument goes but which might gain them something if a reader were willing to dislike an environmentally unfriendly hypothesis. Still, they offer no evidence to support their claim. On the previous page, in fact, they contradict it. There, we find that the impact hypothesis is potentially ecofriendly since it might have drawn attention to the spate of extinctions currently being caused by human activities. At times, then, Officer's and Page's prose can best be characterized as muddled. The authors are at their best when they examine the scientific evidence, as when they outline the problems with the Chicxulub site as the "smoking-gun" crater (151-157). Unfortunately, these sections are not as common as they ought to be and even when they do turn up they tend to be exceedingly one-sided. In discussing the Chicxulub crater, for instance, they briefly report pro-impact researchers' conclusions only to summarily dismiss them. By contrast, in discussing the same matter Alvarez presents the pro-impactors' conclusions, a brief overview of pro-volcanists' critiques of those conclusions, and then an outline of the research pro-impactors undertook to address those critiques. While the pro-impact position deserves a careful cross-examination, Officer and Page have not offered one here. If, as they maintain, the public has been hoodwinked into accepting a hodgepodge of bad science as the genuine article, they have set themselves up for the job of debunking it, but they never fully engage that task.

Even among those who accept that an impact took place near the time of the K/T extinction, there is no agreement that the impact was the sole or even the most important factor in the extinction. It might turn out, as the University of Pennsylvania's Peter Dodson has recently suggested, that the dinosaurs were eliminated not by any one cause but, instead, by a "symphony of causes" (280), from changing sea level and climactic shifts to volcanism and mountain building. But more and more lately it appears that the relevant scientific communities see a connection between iridium and the extinction event that wiped out a fantastic array of Mesozoic reptiles. In setting forth its case, *T. rex and the Crater of Doom* may not thoroughly cover all the reasonable counterarguments, but it does recognize

that they exist. Regrettably, the various shortcomings of *The Great Dinosaur Extinction Controversy* provide little reason to question the impact hypothesis. While scientists need not necessarily be civil to one another to maintain their credibility, they must at least rely on argumentative strategies that play fair. By allowing himself to be associated with a work that fails to do so, Officer calls into question his entire argument. Thus, Officer's and Page's characterization of pro-impactors as pathologically self-deluded should be taken with a grain of salt. Although the pro-volcanism school might have a case to make, we will have to wait at least a while longer to see it in print.

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**BOOK REVIEW:**

***AMPHIBIANS AND REPTILES OF THE GREAT LAKES REGION*, BY JAMES H. HARDING, 1997, UNIVERSITY OF MICHIGAN PRESS, ANN ARBOR, MICHIGAN, VII-XVI + 1 78 PP. 83 PIS. II FIGS., 78 MAPS, ISBN 0-472-09628-1, CLOTH, \$49.50 AND ISBN 0-472-06628-5, PBK. \$19.95.**

In this modestly priced volume, Harding certainly achieved his stated aims to provide a specific reference guide for identification, distribution, and life history of those herptiles occurring within the Great Lakes Region, which includes the following states: Illinois, Indiana, Michigan, Minnesota, New York, Ohio, Pennsylvania, Wisconsin, as well as the Canadian Province of Ontario.

The introduction provides guidance on the importance of Amphibians and Reptiles in our Ecosystem, along with a brief introduction on the Conservation of the Herpetofauna, and a list of addresses for Governmental Agencies, which provide current legal information and permit requirements is given just prior to the Index. The introduction is followed by a section on definitions, origins, classification and checklist of species found within the Great Lakes Region.

Three to six pages are devoted to individual species accounts, along with color range maps for the 75 species and subspecies of Amphibians and Reptiles recorded from the region. Each species accounts includes traditional description, remarks on distribution, habitat, ecology, reproduction, growth, status, and Conservation. The author also provides descriptions for ten additional marginal and questionable species that possibly could turn-up in the Great Lakes Region.

The book is attractively laid out, and photo quality is consistently high throughout. The only drawback appears in the distributional maps, which can be deceiving, as they reflect the overall distribution, as seen in the major Field Guides, and not the true present distribution of each species. A much more accurate format would have been to show spot localities for museum specimens, literature accounts, or other reliable

observations, with different symbols for each. The author also fails to provide a key for the identification of the 75 taxa represented, although this can possibly be explained by the author having mentioned In the Preface, that the book was designed for non-specialist, although professional will find this volume of considerable importance as a reference for ecological data. The illustrations and maps are placed along with each species account, and not centrally located as in so many recent herpetological works. This certainly is a plus for anyone not familiar with the herpetofauna of their area.

I found no topographical errors in the text, and the book is printed on acid-free paper, with the font easy-on-the-eyes. Overall the book is attractively laid out, and the quality and accuracy of the text are exceptional, and should serve as an excellent guide for anyone interested in the Herpetofauna of northeastern and north-central United States.

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# HERPETOLOGICAL BIBLIOGRAPHY of INDONESIA



Indraneil Das

The archipelago of Indo-Malaya, stretching from the Andaman and Nicobar Islands, eastward to Timor, is the largest in the world (approximately 14,000 islands), and includes several political entities. Much of the land area and associated coastal water fall within the political boundaries of a single nation, that of the Republic of Indonesia. However, significant portions are controlled by India, Myanmar or Burma, Malaysia, and the Philippines. This work is a comprehensive bibliography of the scientific papers, magazine and newspaper articles, books, book reviews, museum catalogues, bibliographies, chapters from books, and theses that contain references to any species of amphibians and reptiles in this region. Both terrestrial and aquatic taxa are included. Languages in the cited literature include Bahasa Indonesia, Chinese, Dutch, English, French, German, Hungarian, Italian, Japanese, Latin, Polish, Portuguese, Russian, and Spanish.

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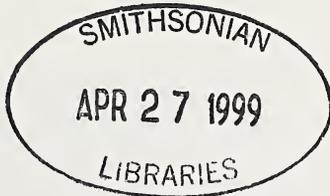
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The Maryland Herpetological Society  
Department of Herpetology, Natural History Society of Maryland, Inc.

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**MORPHOLOGICAL VARIATION AND RELATIONSHIP  
OF Rhadinaea bogertorum (SQUAMATA:  
COLUBRIDAE), AN ENDEMIC SNAKE OF THE  
SIERRA DE JUAREZ, OAXACA, MEXICO**

AURELIO RAMIREZ-BAUTISTA, MARIO MANCILLA-MORENO,  
HOBART M. SMITH, DAVID CHISZAR AND  
FRANK VAN BREUKELEN

Twenty-five previously unreported specimens of Rhadinaea bogertorum, five of R. macedougalli, and three of R. myersi, are described and compared. They appear to represent a single complex which also includes R. marcellae, for which the complex is named. Partial sympatry occurs between the former two of southern Atlantic slopes; R. myersi is dichopatric on southern Pacific slopes, and R. marcellae on northern Atlantic slopes. Rhadinaea macedougalli exhibits convergence with R. marcellae in some characters where their ranges are most closely approximated.

Rhadinaea bogertorum Myers has been known since its original description (Myers, 1974) only from two specimens (AMNH 100906-7). We here record variation in 25 previously unreported specimens of that species, and compare them with other recently collected material of the similar species, R. macedougalli and R. myersi.

All specimens of R. bogertorum are from the Sierra de Juárez, northern Oaxaca, México. New material we have examined is (museum acronyms as in Leviton et al., 1985): IBH (Instituto de Biología, UNAM) 06249 (2), 11.4 km NE Cerro Pelón; IBH 11280, Santiago Comaltepec; KU 187299-187303, 10.6 km N Cerro Pelón; LACM 130104, 7.2 rd mi SSE Vista Hermosa; MZFC (Museo de Zoología, Facultad de Ciencias) 04518, Santiago Comaltepec, km 80.5 on Tuxtepec-Oaxaca Hwy; MZFC 04520, Santiago Comaltepec, rd to San Isidro, km 190 on Tuxtepec-Oaxaca Hwy; UCM 49355-7, 49359, 49361-6, 49367, 49369-70, 52384, Vista Hermosa.

Rhadinaea macedougalli Smith and Langebartel has been known only from three specimens (Myers, 1974). We here report three additional ones

(UCM 41189, 52493, 52669) from Vista Hermosa, Oaxaca, and two (MZFC 9946, 9947) from San Martín Caballero, Oaxaca.

Rhadinaea myersi Rossman has also been known only from three specimens (Myers, 1974). We here report three additional animals, two (UCM 44516, 44518) from Río Sal, Lachao, Juquila, Oaxaca, and one (UCM 49353) from Santa Rosa, Lachao, Juquila, Oaxaca.

**Variation in R. bogertorum.** - All specimens have 8-8 supralabials, except for three hatchlings with 7-8, and one with 7-7. The 4th and 5th supralabials enter the orbit in all except those with 7 supralabials, in which either the 3rd and 4th, or the 4th only (one side of UCM 49363, with 7-8) enter the orbit. The infralabials vary from 9 to 11, the latter number was found (KU 187303, UCM 49357) on one side only in two specimens; the modal number is 10, occurring about twice as frequently as 9 (AMNH 100906, UCM 49355). The preoculars vary from 1 to 4, a single scale occurring on one side only in two specimens (UCM 49362-3), and on both sides in two others (UCM 49356-7), and four scales occurring on one side in one snake (UCM 49365); the modal number is two, occurring about twice as frequently as three. The postoculars are 2-2 in all specimens except two females (IBH 11280, MZFC 04518) with 1-2, and two males (UCM 49363, KU 187299) with 1-1. The temporals are 1-2-3 in all except one male (UCM 49366) with 1-2-2 on one side, and two males (KU 187302, UCM 49362) with 1-2-2 on both sides.

The dorsal scale rows are 17-17-17 in all except one male (KU 187303) with 17-17-16, one female (UCM 52384) with 16-17-17, a male (UCM 49365) with 15-17-17, and a male (UCM 49367) with 15-17-15. The ventrals are 160 to 170 in females ( $X = 165.2$ ,  $n = 13$ ), 144 to 158 ( $X = 153.7$ ,  $n = 14$ ) in males. The range of variation in males (15) exceeds that in females (11).

The umbilicus is evident in eight hatchlings. It involves one or two ventrals, usually just one. The anterior or single ventral interrupted varies from the 118th to the 137th, depending on the number of ventrals: it varies from 81 to 85 per cent of the total ventral count from the first ventral ( $X = 82.9$ ,  $n = 8$ ), or 15-19% of the total ventral count from the anal plate ( $X = 17.1$ ,  $n = 8$ ). The caudals (including the types) are 62-70 in females ( $X = 65.9$ ,  $n = 12$ ), 65-80 ( $X = 72.7$ ,  $n = 11$ ) in males.

The largest specimen is a female 581 mm TTL (total length), the largest male 510+ mm (snout-vent length (SVL) = 402 mm and tail length (TL) = 108 broken  $\pm$  8 mm). The smallest snake measured 116 mm TTL, 35 mm TL. However, most of the UCM specimens are hatchlings and so brittle that they could not be measured. The tail/total length ratio varied from 0.21 to 0.27 ( $X = 0.24$ ,  $n = 11$ ) in females, and from 0.25 to 0.30 ( $X = 0.28$ ,  $n = 8$ ) in males.

The color pattern of all specimens corresponds well with the description and figures of the species in Myers (1974: figs. 10-11). In the largest specimen (UCM 49355) no evidence exists of dark lines between the dark lateral sides; the vertebral dark line typical of the other specimens is completely lacking throughout the length of the body. Loss of distinctness of lines appears to be ontogenetic. In hatchlings both vertebral and dorsolateral dark lines (the latter on the adjacent edges of the 6th and 7th scale rows) are evident either anteriorly, posteriorly, or both. In larger individuals no evidence of the dorsolateral dark line remains.

The pale supraocular line deviates laterally far enough to engage the rear edge of the posterior supralabial in all specimens except MZFC 4520, although it borders that scale in this specimen and, in several others (UCM 49355, 49359, 49361) barely encroaches upon it. There is a narrow break in the same pale line, the length of only one scale, on both sides of one (UCM 49363) and one side of another specimen (UCM 49367). The labials, mental and rostral are frequently immaculate white, but the anterior two or three labials (both upper and lower) bear a few black flecks in about half the specimens, and in a few specimens similar flecks are also present on the mental and/or rostral.

Variation in R. macdougalli.- It was somewhat of a surprise to find that Thomas MacDougall, who collected all of the UCM specimens of the three species here dealt with, found R. macdougalli sympatric with R. bogertorum. All of the latter, however, were taken in 1972, whereas his R. macdougalli were collected in 1967 and 1970. It is therefore likely that the two species were not found in microsympatry, even though all are labelled "Vista Hermosa". How their habitats differ there remains to be determined. These specimens extend the known range of the species some 50 km northwestward from Yelagato, Oaxaca (Myers, 1974).

The five specimens we examined appear to conform reasonably well with those previously recorded (Myers, 1974). The supralabials are 8-8 in all, 4th and 5th entering the orbit; infralabials 10-10 except in one specimen with 9-10; preoculars 2-2 in two individuals, 2-3 in one, 3-3 in one snake, and indeterminate in one; postoculars 2-2 except in one specimen with 1-2; temporals 1-2-3 in all specimen; ventrals 134, 138 and 141 in three females, 127 and 130 in two males; umbilicus at ventral 110; caudals 63, 73 and 82 in three females, 71 and 76 in two males; scale rows 17-17-17 in all; TTL in one small female is 187 mm and in two adult females 321 and 350 mm, TL 53, 98 and 110 mm; TTL in one male 331 mm, TL 105 mm (the other male, a hatchling, is too brittle to measure); TL/TTL ratio in the measurable male is 0.32, in the females 0.28, 0.28 and 0.34. The hemipenial spines in the single adult male are about 20 in number.

The pale supraocular line is strongly displaced laterally, passing through the upper posterior part of the last supralabial, but is interrupted on both sides in three specimens (UCM 52493, MZFC 9946 - 9947), is complete on both sides in one specimen (UCM 52669), and is interrupted on only one side in one (UCM 41189). In the latter, the pale line itself is interrupted, but its black borders are united and continuous through that interruption of less than half of a scale length.

There is no dorsolateral dark line. In UCM specimens, the vertebral scales are dark edged and with slightly lighter centers in some parts of the dorsum, somewhat as in *R. marcellae* (Myers, 1974: fig. 11E), whereas in the MZFC specimens, these scales bear a reticulate pattern and are darker at the edges and center. In one specimen (UCM 52493) there is a black edged postparietal pale spot on four successive scales of the vertebral row, widest (1.5 scales) anteriorly; in two others (UCM 52669, MZFC 9947) there is a faint pale postparietal streak on four vertebral scales. In the UCM specimens, the scales in the fifth row are distinctly pale-centered, producing the effect of a pale lateral line, although anteriorly the line is very distinct and continuous, aligned with the postocular series. Much as in *R. marcellae*, in one specimen (UCM 41189) a postparietal spur extends mediad from the pale lateral line for a distance of two scales on one side, one scale on the other. The labials are mostly white, but a dark dot on their lower edge occurs on the anterior six to seven supralabials, and the anterior four infralabials. One similar black dot is present on each side of the rostral and mental.

This species differs from *R. bogertorum* most importantly in its lower number of ventrals (119 to 130 males, 124-141 in females vs 144 to 158 in males, 160 to 170 in females of *R. bogertorum*). The position of the umbilicus, at the 110th ventral in the single available hatchling, is lower than those of hatchlings *R. bogertorum* (118 - 137), but the difference is merely a reflection of the lower number of ventrals, because the relative position is the same, as indicated by its position as expressed in per cent of the total ventral count from the first ventral (82%) and from the anal plate (18%). A number of differences in pattern as tentatively suggested by Myers (1974) are substantiated, including more extensive spotting of the upper and lower lips in *R. macdougalli*; the absence of a vertebral dark line, whose place is taken by dark edging of the vertebral scales, the centers of which are slightly more pale than the adjacent ground color; the absence of a dark dorsolateral line, even in hatchlings; the presence of distinct pale centers of the scales in the 5th row; and the frequent hiatus in the postocular light line.

Of great interest is the resemblance of the three UCM specimens of *R. macdougalli* to *R. marcellae* in the supposedly partially diagnostic characteristics of a black-edged pale vertebral line and of postparietal transverse and median pale lines as figured and described in Nieto-Montes de Oca and Mendelson (1997). These peculiar similarities suggest that *R. macdougalli* might actually be a subspecies of *R. marcellae*, inasmuch as their ventral and caudal counts are very similar. However, *R. macdougalli* differs sharply from *R. marcellae* in the involvement of the 8th supralabial in the pale postocular stripe and in the smaller number of hemipenial spines (in the low 20's vs about 50), and accordingly we retain them as separate species. Material from the area between their present known range limits will be critical in verifying their species status.

**Variation in *R. myersi*.**- In the three previously unreported specimens, the supralabials are 8-8, with the 4th and 5th entering the orbit in all specimens; infralabials 10-10 in two specimens (UCM 49353, 44516), 9-9 in one (UCM 44518); preoculars 2-2 in two (UCM 44518, 44516), 3-3 in one (UCM 49353); postoculars 2-2 in all specimens; temporals 1-2-2 on one side of one (UCM 44518), 1-2-3 in others (UCM 44518, 49353); scale rows 17-17-17 in all snakes; ventrals 145 in one female (UCM 44516), 136 and 141 in two males (UCM 44518 and 49353 respectively); caudals 68 in

one female (UCM 44516), 84 in one male (UCM 44518); female the longest, 391 mm TTL, 110 mm TL; adult male 309 mm TTL, tail incomplete; hatchling male 137 mm TTL, 43 mm TL; ratio TL/TTL 0.28 in female, 0.31 in male.

This species is most closely similar to R. bogertorum and R. macdougalli, although both of the latter are restricted to Atlantic slopes, R. myersi to Pacific slopes, so far as known. The most salient distinction of the latter species from the former two is its intermediate number of ventrals, with only a slight overlap with R. macdougalli. In R. myersi the ventrals number 139-145 in two females, 132 to 141 in four males (vs 160 to 170 and 144 to 158, respectively, in R. bogertorum; 124 to 141 and 119 to 130, respectively, in R. macdougalli).

The pattern differences pointed out by Myers (1974) remain consistent in the present series. Most reliable is the more nearly parallel position of the pale postocular lines, which do not touch the posterior supralabial, contrary to the condition in both R. bogertorum and R. macdougalli. The black dorsal border of the lateral brownish zone lies prominently on the lateral edge of the 5th scale row, less upon the upper edge of the 4th; the scales of the 5th row are distinctly pale-centered. There is no dorsolateral dark line even in the hatchling. The vertebral dark line is virtually indistinguishable; only a little dark edging on the scales of that row distinguish them from adjacent scales. There is a narrow dark brown bar across the rostral. Spotting on the labials varies; in one specimen spots are present on most scales, whereas in the hatchling they are not evident at all, and on the other specimen there are scattered tiny flecks on most scales.

**Remarks.**- Among the eleven members of the decorata group as recognized by Myers (1974: 57), four (bogertorum, macdougalli, marcellae, myersi) comprise a distinct species complex we here designate the marcellae complex, inasmuch as R. marcellae Taylor (1949) was the earliest described. All are relatively high elevation species, occurring in cloud forest or in the pine-oak zone. Each of the last two is isolated in distribution, but the first two are partially sympatric at least grossly; it remains to be determined whether their habitats are similar or not.

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## The Report of the Snake Genus *Conophis* in South America is Erroneous

David L. Auth, Jean Mariaux, Joël Clary, David Chiszar,  
Frank van Breukelen and Hobart M. Smith

*Abstract.* The report of *Conophis lineatus* from Colombia, South America, is erroneous and based on *Liophis lineatus*. The similarities of the two genera suggest that they belong to the same tribe or subfamily.

The southern limit of distribution of *Conophis* has long been regarded as Costa Rica (Wellman, 1963; Peters and Orejas-Miranda, 1970; Villa et al., 1988). However, at least two records of *C. lineatus* are for more southern localities: Barranquilla, Colombia (Pérez-Santos and Moreno, 1988), and Coclé, Panama (Auth, 1994a). The latter record was promptly refuted, however (Auth, 1994b), with identification of the snake in question as *Liophis lineatus*, a species well known from Panama and northern South America (Michaud and Dixon, 1987).

The basis for the Colombia record was a specimen cited by Pérez-Santos and Moreno (1988: 129), MHNG 1368.98 (museum acronyms as in Leviton et al., 1985), which they did not examine, and whose identity has never been verified. We reexamined the specimen, and found that in reality it also represents *Liophis lineatus*, conforming in most details with the definition of the species in Michaud and Dixon (1987: 5). It is a well-preserved, adult female in good condition 681 mm TTL, 176 mm TL, taken between 1966 and 1968 by J. Garzoni for E. Kramer. Its pattern (Fig. 1) conforms with that of populations west of the Andes (Michaud and Dixon, 1987: 5), and differs from that of populations east of the Andes (Fig. 2). The body has three dark brown stripes, all extending to tail tip and originating on snout, where the median stripe is narrowly separated from the lateral stripes, which are continuous on rostral; median stripe nearly uniformly dark, with narrow, slightly darker brown edges, occupying three and two half scale rows on body, narrowing to two half rows on tail; lateral dark stripe passing posteriorly through eye and upper edges of supralabials, on neck involving the 5th scale row, adjacent half of the 4th and lower edge of the 6th; more posteriorly the lateral stripe descends to the 4th and 5th rows, and descends still farther at the point of scale row drop to the 3rd and 4th rows; on the tail it occupies the 2nd scale row and

ultimately the 1st. There are no markings whatever between the dark stripes, or ventral to the lateral dark stripe on head, body or tail.

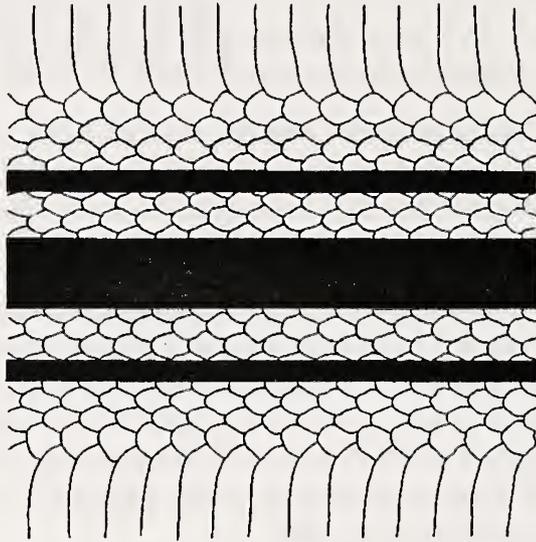


Fig. 1. Midbody pattern of *Liophis lineatus*, MHNG 1368.98, Barranquilla, Colombia, west of the Andes, styled for comparison with figures of the same species in Michaud and Dixon (1987: 6).

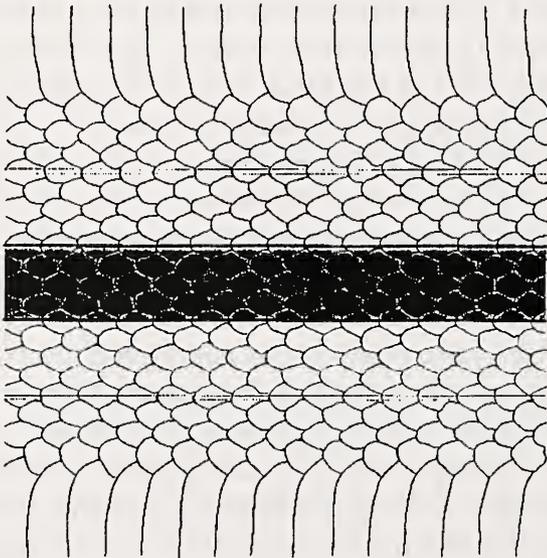


Fig 2. Midbody pattern of *Liophis lineatus*, MHNL 42000566, locality unknown but presumably east of the Andes.

The supralabials are 8-8, 4th and 5th entering orbit; rostral with a narrow, transverse, semicircular ventral prelabial concavity, not reaching even with the lateral edges of mental, and not extending forward more than a third of the median length of the rostral in ventral view; in neither dorsal nor lateral view is the rostral at all protuberant; in lateral view it is much shorter than 1st supralabial, and in dorsal view its posterior edge is semicircular, not pointed, not extended between internasals; latter nearly square, much narrower than prefrontals; latter extending slightly below canthus rostralis, broadly contacting a large, nearly square loreal on each side; loreal contacting 2nd and 3rd supralabials; nasal large, completely divided, butterfly-shaped, naris contacting internasal, narrowly separated from 1st supralabial; preoculars 1-1, half again longer dorsally than ventrally, narrowly separated from frontal, contacting 3rd and 4th supralabials; 2-2 postoculars, upper twice size of lower; temporals 1-1-2, 1-2-3. Infralabials 10-10; anterior chinshields longer than posterior.

Ventrals 169; anal divided; tail complete; 84 subcaudals; 19-19-17 scale rows; scale row reduction at 109th and 110th ventral; scales smooth, without apical pits.

The left maxilla has 18 prediastemal teeth, increasing in size posteriorly; the postdiastemal teeth (two sockets) are half again as large as the preceding tooth, and have a flange but no groove.

The occasional confusion of this species with *Conophis* is due to a remarkable similarity of pattern, especially of *C. vittatus*, which is indistinguishable in pattern from some specimens of *L. lineatus*. There is also a remarkable similarity in the occurrence of a unique ventral concavity on the rostral of *L. lineatus* and all *Conophis*; in the latter genus it appears to be associated with burrowing habits for which the rostral is adapted also by its protrusion in a somewhat conical shape to varying degrees in different species. In addition there are fundamental similarities in scalation (especially scale rows, head scales and number of ventrals), as well as a clinal conformity in northward reduction in number of subcaudals, number of teeth and increase in size and grooving of the fangs.

Of critical importance is the nature of the hemipenis, which on the basis of a fully everted one on a *Conophis vittatus* from El Salvador (KU 183865, Ahuachapán: Barra de Santiago) appears to conform with the dis-

tinctive structure depicted in Dowling and Duellman (1978: 112a.4) for various members of the tribe Xenodontini as of that work. In that specimen the right hemipenis is 14 mm long, the sulcus forks 4 mm from the base; there are two flat apical discs, centrally indented, in contact with each other, without a notable depression between; the calyces on the discs are unornamented; only small spines are present on the sulcate side; large spines are present on the lateral and sulcate surfaces, extending to near the apices, where they are small around the edge of the disc.

Although Dowling (1995) was uncertain of the affinities of *Conophis*, it seems likely that it should be included among the xenodontine genera *Erythrolamprus*, *Liophis*, *Lygophis*, *Lystrophis*, *Umbrivaga*, *Waglerophis* and *Xenodon* (Dixon, 1980; Dowling, 1995), in view of the extensive agreement with some or all of those genera in critical characters.

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## ABUNDANCE AND WATER VOLUME EFFECTS IN AMPHIBIAN LARVAE

*Geoffrey R. Smith*

Density is defined as the number of individuals per unit area or volume. In most studies of intraspecific interactions, the number of individuals is manipulated while area or volume is kept constant. For example, in amphibians, increased densities of larvae have been shown to increase time to metamorphosis, decrease survivorship, decrease size at metamorphosis, decrease growth rate, increase variability and skew in body size, and affect post-metamorphic performance (e.g., Wilbur and Collins, 1973; John-Alder and Morin, 1990; Newman, 1994; Scott, 1994; Tejedo and Reques, 1994). However, in many of these types of studies, both density and abundance change, therefore confounding density effects with abundance effects. The density of individuals could influence encounter rates or behavioral interactions among individuals, such as interference competition, whereas abundance effects could influence food limitation through exploitative competition.

I conducted a short-term experiment to assess the relative importance of abundance and density effects on early growth in bullfrog tadpoles (*Rana catesbeiana* Shaw) by manipulating both the number of tadpoles and the volume of water, while maintaining a constant food ration across treatments. I also conducted an experiment to evaluate the potential influence of water-borne agents by manipulating abundance and water change frequency.

Tadpoles were obtained from field-collected egg masses from ponds in southeastern Michigan in 1995 (Experiment 1) and southwestern Michigan in 1996 (Experiment 2). Only one egg mass was used per experiment to control for potential maternal or genetic effects. Eggs were incubated in aerated pond water, and tadpoles were introduced into the experiment 5 d after hatching. In both experiments, tadpoles were maintained in cylindrical plastic containers (15 cm diameter, 20 cm tall).

Experiment I was a 2 X 2 factorial design (replicated 4 times) with two volume treatments (low: 0.5 L, high: 1 L) and two abundance treatments (low: 3 tadpoles, high: 6 tadpoles). Every 3 d, I changed 3/4 of the

water in each container using unfiltered pond water, and added equal portions of food (algal flakes). Food portions were doubled over the experiment, with the amount of food provided increased when low abundance tadpole treatments fully consumed their food (initial portion = 0.03 g). Experiment 2 was a 3 x 2 factorial design (replicated 4 times) with three abundance treatments (low: 1 tadpole; medium: 2 tadpoles; high: 4 tadpoles), and two water change frequencies (low: changed every 6 d; high: changed every 3 d). All other maintenance was the same as in Experiment 1. At the beginning of each experiment, I randomly assigned tadpoles to treatments, excluding obviously differently sized individuals.

At the end of each experiment (after 30 d), I weighed tadpoles (body mass after blotting dry; BM) to the nearest 0.0001 g using an electronic balance. I used standard parametric analysis after assumptions were checked. Replicate means were used in analyses to avoid pseudoreplication. Means are given  $\pm$  1 SE.

In Experiment 1, tadpoles from low abundance treatments were 2.27 times larger on average than tadpoles from high abundance treatments ( $0.356 \pm 0.026$  g vs.  $0.157 \pm 0.011$  g;  $F_{1,12} = 54.7$ ,  $P < 0.0001$ ). Tadpoles in the low volume treatment were smaller than tadpoles in the high volume treatment; however, the difference only approached statistical significance ( $0.234 \pm 0.040$  g vs.  $0.280 \pm 0.043$  g;  $F_{1,12} = 2.96$ ,  $P = 0.11$ ). There was no significant interaction between abundance and volume ( $F_{1,12} = 0.48$ ,  $P = 0.50$ ). A preplanned contrast between the low abundance, low volume treatment and the high abundance, high volume treatment (i.e., the two treatments with the same density but different abundances of tadpoles) showed a significant difference, with the low abundance, low volume treatment tadpoles being larger than the high abundance, high volume treatment tadpoles ( $0.324 \pm 0.043$  g vs.  $0.171 \pm 0.013$  g;  $F = 16.1$ ,  $P = 0.0017$ ).

In Experiment 2, tadpoles from high abundance treatments ( $0.140 \pm 0.010$  g;  $N = 8$ ) were smaller on average than tadpoles from low abundance treatments ( $0.389 \pm 0.069$  g;  $N = 8$ ), with tadpoles from the medium abundance treatments intermediate in BM ( $0.257 \pm 0.030$  g;  $N = 8$ ) ( $F_{2,18} = 7.94$ ,  $P = 0.003$ ). Water change frequency did not significantly affect BM (low:  $0.228 \pm 0.034$  g vs. high:  $0.295 \pm 0.055$  g;  $N = 12$  in both cases;  $F_{1,18} = 1.73$ ,  $P = 0.20$ ). There was no significant interaction between abundance and water change frequency ( $F_{2,18} = 0.63$ ,  $P = 0.54$ ).

The negative effect of abundance on final BM strongly implicates intraspecific competition. As pointed out above, such a result was not unexpected, and indeed, is not a surprise given the numerous previous studies finding density (abundance?)-dependent growth in amphibian larvae. The lack of water volume effects in this experiment contrasts with the results of several previous studies manipulating the proximity or crowding of tadpoles (both conspecifics and heterospecifics) that found increased physical interaction or increased potential physical interaction decreased various aspects of amphibian larval performance (e.g., John and Fenster, 1975; Breden and Kelly, 1982; Griffiths, 1991). However, Smith (1990) suggested that it may be total space available to tadpoles, and not per capita space that may be important in tadpole performance.

My results suggest that abundance was relatively more important than density in this experiment. First, given a constant and equal food supply among treatments, any increase in absolute numbers of tadpoles per container decreased the per capita food ration. Second, the distribution and nature of the food was such that all tadpoles could have access to the food at the same time if no active interference was occurring (pers. observ.). Third, the preplanned contrast between treatments with the same density (e.g., tadpoles per liter), but different abundances, found that lower abundance tadpoles grew faster on average than high abundance tadpoles. All of these results support the notion that my results reflect an abundance effect, not a true density effect.

What might be the mechanism of the abundance effect? One possibility is exploitative competition (i.e., per capita food availability and consumption was decreased thus resulting in decreased growth). My results are generally consistent with this hypothesis (see discussion above). A second possibility is the presence of water-borne agents (see Beebee, 1995; Griffiths, 1995; Petranka, 1995 for a discussion of water-borne agents in amphibians). While I cannot preclude the second possibility, I think that, given the lack of water volume effects in Experiment 1 and the lack of significant water change frequency effects in Experiment 2, the effect of water-borne agents was relatively minor in my experiments, at least compared to the abundance effect due to food limitation. However, the non-significant trends in the results are consistent with the expected effect of water-borne agents.

In conclusion, abundance effects appeared to influence early-stage bullfrog tadpoles more than true density effects. These preliminary results suggest that additional studies investigating the mechanism of amphibian larval competition, beyond those on water-borne agents, could be very enlightening.

### Acknowledgments

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**Learn to Love Rattlesnakes, Says Author and Photographer**  
**Humans a Greater Danger to Rattlesnakes than the Other Way Around**

Washington, D.C. — Rattlesnakes are among the most feared creatures, so much so that drivers go out of their way to run them over and rattlesnake roundups are organized annually to rid communities of these supposedly menacing reptiles. The phrase “mean as a rattlesnake” is one of the greatest insults you can hurl at an enemy, and a “snake oil salesman” is one of the lowest forms of life.

It is Manny Rubio’s avocation to turn fear into fascination, to encourage people to see the beauty of these majestic creatures and understand their critical role in the ecosystem.

Since his teens, when Rubio lived within walking distance of the Staten Island Zoo and its famed rattlesnake collection, he has searched for rattlesnakes, studied them, photographed them, and written about them. Now Rubio has produced *Rattlesnake: Portrait of a Predator* (Smithsonian, \$39.95), a stunning 272-page book illustrated with more than 250 of his own photographs of rattlesnakes. But it is much more than a picture book: its fourteen chapters are packed with information about rattlesnakes’ evolution, habitat, biology, reproduction, and feeding habits. In addition, Rubio provides a unique glimpse of a snakehandling service in a Pentecostal church and a blunt exposé of rattlesnake roundups.

A longtime sports photographer whose work has appeared in magazines including *Sports Illustrated*, *Time*, and *Newsweek*, Rubio started with the idea of putting together a book of just photographs of rattlesnakes and gradually became convinced that he should write about the snakes as well. Although he was a biology major in college, he considers himself a snake “avocationist.” As such, he says that he has learned a great deal about rattlesnakes because he has had the time to observe them in the field and to read about them widely. And he wanted to pass that knowledge on.

The book was written not for a scientific audience—although scientists reviewed every chapter—but for anyone willing to suspend the inborn human dread of snakes and appreciate their beauty and natural history. It includes a strong message of conservation, because many species of rattlesnakes are endangered. William S. Brown, a leading herpetologist, writes in his foreword, “Rubio’s message may do more to save rattlesnakes than anything yet published.”

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*New Book Releases*

Over a twelve-year period, Rubio photographed almost every one of the approximately 83 living species and subspecies of rattlesnakes. His book includes photos of unusual hybrid snakes and a never-before-recorded sequence of a banded rock rattlesnake eating a large poisonous centipede. He has never been bitten, he says, because he is too aware of the possible danger to take chances, but he has had a few close calls, each of which has made him more cautious in dealing with snakes.

Rubio treats a rattlesnake bite seriously—he says it *must* be treated as a medical emergency—and he offers important emergency procedures to be followed by anyone bitten by a rattlesnake. But he also points out that most snakebites occur when someone is trying to handle, catch, or kill venomous snakes. On average, twelve people are killed by rattlesnake bites each year in the United States.

By contrast, at least 5,000 snakes a year are killed at rattlesnake roundups—highly publicized commercial events that are promoted as a way of controlling rattlesnake populations, ostensibly to prevent the deaths of cattle and people. Snake collectors are paid by the pound for rattlesnakes, so people go so far as to force-feed them sawdust to raise their weight and therefore their value. Many snakes are caught for roundups when their dens are fumigated with gasoline or volatile fertilizers. In addition to driving rattlesnakes above ground, the vapors kill nonvenomous snakes, frogs, toads, lizards, tortoises, and other small animals occupying the underground tunnel.

Thousands more rattlesnakes are killed by cars each year, and drivers go out of their way to run them over. In Florida many years ago, a Cadillac directly in front of Rubio suddenly swerved sharply to try to hit a rattlesnake. When the driver missed, she turned her car full of children around and drove it off the road in an attempt to kill the snake, but she got stuck in the mud instead.

Part of Rubio's mission in writing his book is to educate the people who go to such lengths to kill rattlesnakes. In addition to being beautiful and less harmful than many would like to believe, rattlesnakes are important predators who keep destructive rodents in check. An adult rattlesnake that consumes between 12 and 24 rodents per year is forestalling the eventual birth of thousands of rats and mice.

The key to coexistence with rattlesnakes is respect, Rubio says. If you come across a rattlesnake on a trail, walk on by, giving it a wide berth. If you want to feed birds in your backyard but don't want snakes to prey on them, circle your yard with a snakeproof fence. But above all, Rubio would ask us to remember that "the rattlesnakes were here before us and that they deserve to exist alongside us."

*Rattlesnake* is available at bookstores or from the Smithsonian Institution Press.

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*News and Notes*





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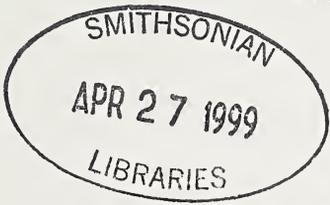
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## Behavioral Resourcefulness in a Striped Whipsnake, *Masticophis t. taeniatus*

Hobart M. Smith, David Chiszar and Kamuran Tepedelen

The anecdotal observations here reported provide a glimpse of a repertoire of ophidian behavior that is almost completely unknown and that could reward intensive investigation.

On 26 July 1992, DC captured an adult (~1 m) Striped whipsnake (*Masticophis t. taeniatus*) on Cross Mountain in Moffat Co., northwestern Colorado. Inasmuch as this species is a noted visual forager, the specimen was kept in captivity for a time in order to compare its feeding behavior with that of the largely ambush-feeding rattlesnakes. It was ultimately released July 1993, at the mouth of Irish Canyon in the Cold Spring Mountains of Moffat Co., some 35 airline km from the point of capture, where the species has frequently been observed and where lizard food (*Uta stansburiana stejnegeri*, *Sceloporus undulatus elongatus*) is reasonably abundant.

In the meantime the snake was kept in a top-lidded wooden cage, 32 cm x 43 cm x 60 cm, with a glass front, maintained at a temperature (with an incandescent bulb) of 28 degrees C during the day, 17 degrees C at night, and provided with a water dish, hide box and a few rock slabs below the light on a newspaper-covered floor. It was hibernated by KT from 1 November 1992 to 15 March 1993, under excelsior in a cage with an ambient temperature of about 10 degrees C, interrupted briefly in January to permit the snake to drink.

During the 6.5 months of activity in captivity, the snake consumed 56 mostly live lizards, predominantly *Sceloporus undulatus elongatus*, but also some *S. g. graciosus* and *Urosaurus ornatus* - all taxa that are moderately abundant in the snake's original habitat. Other lizards eaten were *S. u. erythrocheilus* and *Lepidodactylus lugubris*. *Eumeces obsoletus* (both dead and alive), neonate *Thamnophis radix*, young *Pituophis catenifer* (400 mm TTL) and neonate rats were also offered but not accepted.

Indeed, the snake seldom ate either dead or immobile live lizards. It was extremely quick to chase and attack a moving lizard, but often would crawl right over a stationary live one.

The quantity of food ingested was in sharp contrast with the three or four mice that rattlesnakes consume in the wild in an active season. Correlated with that difference is a sharp contrast in behavior of the two kinds of snakes. Rattlesnakes seldom forage, whereas the whipsnake did so much of the time. It usually emerged from its hide box shortly after the heat lamp turned on, warmed itself for a time under the lamp, then foraged around the cage for a while before returning to rest under the heat source. It would repeat the performance several times a day, and would retire to its hide box shortly before or after the lamp turned off.

The snake was quite efficient in capturing and eating any sceloporine lizard that moved, but had considerable trouble catching the much fleeter geckoes. At times the snake just gave up the attempt when geckoes were in the cage, although in due time it would try again.

The sceloporine lizards quickly became motionless in the snake's cage, in apparent self-protection, allowing the snake to tongue-flick them and crawl right by or even over them. Immobile lizards were rarely attacked - hence dead lizards were not eaten unless they became entangled with a live one that was being consumed.

The *Sceloporus* that feigned death apparently recognized snakes as predators. Although some lizards exhibited what might be interpreted as learning in assuming immobility after several minutes of exposure to the snake, some did so immediately when introduced into the cage; there was little real "learning" time. That there may be an inherent fear of snakes was suggested by the behavior of *S. u. erythrocheilus* observed in the hills near Boulder, Colorado. When most predators appeared in sight there, the lizards would simply dive into the nearest crack in adjacent boulders, where they would be safe from hawks and various mammals. One specimen was observed to spot an approaching racer (*Coluber constrictor flaviventris*) several feet away, whereupon it fled far from the scene, as if aware that a sanctuary in a crevice would be insufficient when faced with a snake predator.

On May 2 the snake exhibited an extraordinary foraging behavior of alertly watching its own probing body movements in an apparent attempt to flush out a lizard that the snake had previously seen but could not find. The snake had been out foraging as usual, after initial warming

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under the lamp. A *S. u. elongatus* was placed in the cage (quickly, because the snake often charged the opened lid at once), but it landed behind the hide box, out of sight. The snake nevertheless was seemingly aware of its presence, and rather frantically began searching throughout the cage without success. It then changed tactics, holding head and fore part of body perfectly still while watching the rear part of body and tail as they energetically felt all around the cage. Twice the snake even charged its own, actively moving tail, before resuming its watch. This behavior continued for two or three minutes, without disturbing the lizard. The snake then gave up the effort, and remained quiet for 10 min., after which it again started foraging, but this time quietly, not frantically as before, interrupted by brief (10-15 secs) episodes of immobility every 2-3 min. It hadn't found the lizard by the time observation ceased a half hour later. The lizard was gone, however, when the cage was checked an hour later.

The body-loop foraging strategy was not observed again. Whether it would ever be utilized in nature is conjectural. It may be a behavior elicited by detection of prey in a relatively closed space. Nevertheless it is indicative of a surprisingly novel attempt to resolve an impasse in feeding.

We encourage others to report observations suggesting comparable sorts of behavioral plasticity in reptiles and amphibians, as such cases will provide a view of the possible range of adjustments the animals may exhibit. Such information can be a source for hypotheses to be tested under controlled conditions.

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## Mudpuppies (*Necturus maculosus*) and Barrier Falls in Wisconsin

Philip A. Cochran

"For zoogeographical purposes *Necturus* should be considered more an ichthyological rather than a typical urodelan problem." - Hecht and Walters (1955)

Since the time of Hecht and Walters (1955), relatively little attention has been paid to the zoogeography of the mudpuppy (*Necturus maculosus*) in the northern part of its range. However, the much greater effort directed at fishes (e.g., Hocutt and Wiley 1986) provides a basis for unraveling how the mudpuppy recolonized glaciated regions from southern refugia after the retreat of glacial ice. For example, Cochran (1991) used previous analyses of fish dispersal routes to explain how the mudpuppy dispersed through Minnesota from a Mississippi River refugium to inhabit drainages now physically isolated from that river system.

The mudpuppy was reported from 29 counties in Wisconsin by Vogt (1981) and has been reported from 22 additional counties since then (Cochran and Lyons 1986, Casper 1996, Casper 1997). Understandably, its range sometimes has been depicted as including the entire state (Bishop 1947, Tynning 1990, Harding 1997), although Conant and Collins (1991) bucked this trend by reducing the Wisconsin range from that shown in the previous edition of the same book (Conant 1975). In any case, examination of distributional data at a finer scale of resolution is necessary to assess the possibility that mudpuppies failed to colonize at least some portions of Wisconsin through a lack of physical access at appropriate times.

Mudpuppies are well known from the Great Lakes bordering Wisconsin (e.g., Reigle 1967, Long 1993) and from the lower portions of Great Lakes tributaries (Gilderhus and Johnson 1980). The Great Lakes drainage in Wisconsin was completely covered by glacial ice during the Pleistocene Epoch. Subsequent access to the Great Lakes from refugia in the Mississippi River drainage was available through several routes at vari-

ous times. These include, in Wisconsin, connections between the present day St. Croix (Mississippi drainage) and Brule (Lake Superior) river valleys and between the Wisconsin (Mississippi drainage) and upper Fox (Lake Michigan) rivers (Greene 1935, Wielert 1980).

Some Great Lakes tributaries pass over falls that are presently barriers to upstream dispersal. The natural occurrence of fishes above such a barrier is an indication that they dispersed into the drainage relatively early, before a combination of isostatic rebound and falling lake levels brought the barrier into effect (Underhill and Mlyle 1968). Cochran (1991) pointed to the lack of mudpuppy records from above barrier falls on tributaries to the north shore of Lake Superior in Minnesota.

Barrier falls occur on tributaries to the south shore of Lake Superior in Wisconsin. The 22 waterfalls listed by Johannes (1974) range in height from 1.5 m to 50 m. Bailey and Smith (1981) suggested that northern pike (*Esox lucius*) colonized the south shore tributaries too late to disperse above their falls, whereas muskellunge (*Esox masquinonge*) occur naturally above the falls and apparently colonized earlier. The purpose of this note is to compare the distribution of mudpuppy records in the Lake Superior drainage of Wisconsin to the position of barrier falls on south shore tributaries.

### Methods

In the modern scientific arena, correlations among geographic variables are typically examined with a computer-driven geographic information system (GIS). In contrast, I used a "poor man's GIS" to compare the geographic distributions of mudpuppy collection sites and barrier falls on Wisconsin's Lake Superior tributaries. The maps supplied by Johannes (1974) and Vogt (1981) provided localities of waterfalls and mudpuppy collection sites, respectively. Although additional Wisconsin localities for mudpuppies subsequent to Vogt (1981) have been documented (see references above), no additional specimens are known from the Lake Superior drainage (Gary Casper, Milwaukee Public Museum, personal communication). An office photocopying machine with a feature permitting specification of percentage enlargement or reduction was used to prepare transparencies of the two maps at equivalent scales. By over laying the transparencies, it was possible to compare directly the locations of mudpuppies and waterfalls.

## Results

Comparison of the maps of Johannes (1974) and Vogt (1981) revealed a single apparent occurrence of a mudpuppy above a barrier fall, a record plotted by Vogt (1981) in central Ashland County just upstream from Copper Falls in the Bad River drainage (Figure 1). Unfortunately, detailed data for records in Vogt (1981) are not available. Copper Falls was described by Johannes (1974) as a 29-foot (8.8 m) drop into a narrow, rock-walled gorge, but a table in the same article listed Copper Falls as a 40-foot (12.2 m) drop. A barrier of either height would be impassible to mudpuppies moving upstream.

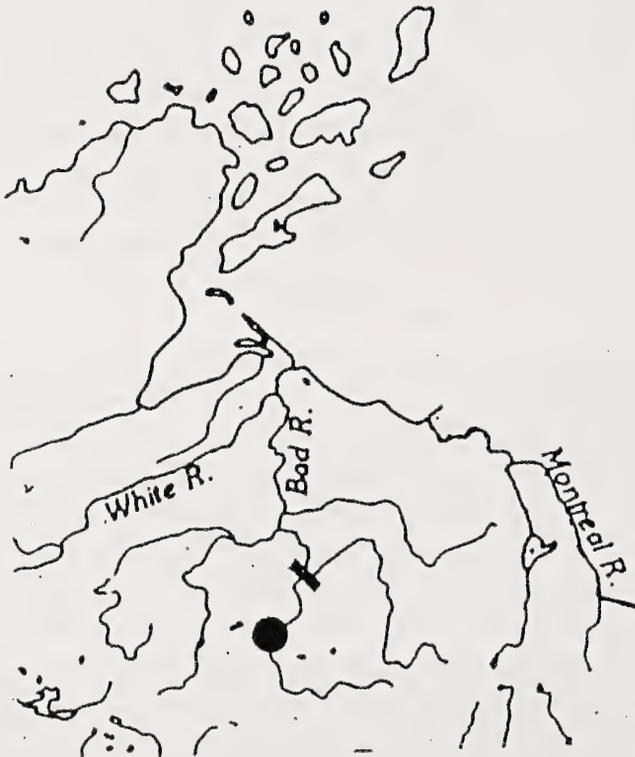


Figure 1. The Bad River drainage in northern Wisconsin, with the location of Copper Falls approximated from Johannes (1974) and the location of a mudpuppy collection site approximated from Vogt (1981).

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Discussion

Although Pleistocene fossils of *Necturus maculosus* have been collected in a few localities, none are known from the Great Lakes or other glaciated regions (Holman 1995). According to Holman's (1992,1995,1998) model of the reoccupation of postglacial Michigan by reptiles and amphibians, the mudpuppy is included among the primary invaders, species whose ecological tolerances include coniferous forests. These species were thought by Holman (1992, 1995,1998) to have invaded Michigan's Lower Peninsula via Indiana and Ohio approximately 12,000 years ago, but not to have reached the Upper Peninsula via Wisconsin until at least 9,900 years ago. Unlike the other primary invaders, however, the mudpuppy does not have a terrestrial stage, and the timing and routes of its dispersal were not necessarily congruent with those of the other species.

The occurrence of a mudpuppy upstream from a barrier on a tributary to Lake Superior's south shore indicates that mudpuppies arrived in the region by the time that Lake Duluth occupied what is now the Lake Superior basin, when lake levels were high enough for fishes (or mudpuppies) to colonize Lake Superior tributaries above their falls (Bailey and Smith 1981). According to Bailey and Smith's (1981) scenario, this occurred approximately 11,600 to 11,500 years ago (see their Fig. 6), but Underhill's (1986) interpretation (see his Fig. 4.7), based on more recent geological studies, would suggest a somewhat later timing (approximately 10,000 years ago). In either case, mudpuppies could have colonized Lake Duluth directly from the Mississippi River drainage via the St. Croix River - Brule River connection.

If the scenario just presented is correct, then additional collections of mudpuppies can be expected above barrier falls on other tributaries to Lake Superior, including both the north shore streams of Minnesota (Cochran 1991) and the south shore streams of Wisconsin. However, it remains possible that mudpuppies are absent above some of these barriers. First, differences in the heights of barriers, coupled with an east-west gradient in rate of isostatic rebound (Larsen 1994), make it almost certain that different barriers came into effect at different times; depending on just when mudpuppies arrived in the basin, they may have had access to some tributaries but not to others. Second, any extinctions of upstream

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populations subsequent to the establishment of corresponding barriers could not have been offset by recolonization.

Hecht and Walters (1955) described *Necturus* as a cold-adapted taxon and suggested that low water temperatures should not have been a limiting factor in its northward distribution. On this basis, it might also be expected that mudpuppies were among the aquatic species that dispersed back into deglaciated regions relatively early. Early recolonization would have permitted mudpuppies greater opportunity to take advantage of temporary routes between drainages and around barriers.

Perhaps, however, mudpuppies are not as cold-adapted as surmised by Hecht and Walters (1955). Their inference was based on the mudpuppy's well known tendency to be active during the winter, as evidenced, for example, by the frequency with which they are caught by anglers fishing through the ice. Subsequent observations have confirmed that mudpuppies forage during the winter (see Vogt 1981 and Cochran 1986 for Wisconsin examples), but it is also well known that mudpuppies reproduce during the summer (Bishop 1926, Cochran and Lyons 1985, Cochran 1995). It is probable that successful completion of egg deposition and embryological development depends on water temperature exceeding some threshold for a minimum length of time. If so, then northward range expansion by the mudpuppy might have been delayed until rivers and lakes shifted from thermal regimes dominated year-round by frigid glacial meltwater to more temperate cycles responding to moderating local climates. Holman (1998) has assumed that the amphibian species of several thousand years ago had essentially the same ecological tolerances and habitat preferences that they do today; if this assumption is valid, then the seasonal cycles in thermal selection (Hutchison and Spriestersbach 1986) and tolerance (Hutchison and Ritchart 1989) displayed by mudpuppies from central Wisconsin may indicate that the aquatic habitats this species invaded in formerly glaciated regions had assumed seasonal cycles in water temperature.

The available evidence concerning the timing of mudpuppy dispersal is somewhat equivocal: (1) A single, problematic record is available from the Mississippi River drainage above St. Anthony Falls (Cochran 1991). (2) A single record from above a barrier falls on a tributary to Lake Superior's south shore was revealed during the present study; details about

this record are unavailable. (3) No specimens are known from above barrier falls along Lake Superior's north shore (Cochran 1991). (4) I am currently investigating the fish fauna above a waterfall on the Devils River, a tributary to the West Twin River in Manitowoc County, Wisconsin (Lake Michigan drainage). Although I have collected several mudpuppies in the nearby East Twin River, I have not obtained any in suitable habitat above the waterfall. A consideration of postglacial drainage changes in this region (Wielert 1980) suggests that mudpuppies could have first colonized the area when Glacial Lake Oshkosh drained into the Wisconsin River valley of the Mississippi River drainage, and this possibility is substantiated by the presence of mudpuppies today in Lake Winnebago, a remnant of Glacial Lake Oshkosh. However, an early presence in Glacial Lake Oshkosh should have permitted mudpuppies to colonize above the Devils River waterfall during the subsequent interval when Glacial Lake Oshkosh drained through the West Twin River valley to Lake Michigan; during this time, the huge volume of water moving through the West Twin River valley should have resulted in a water level high enough to submerge the falls. Alternatively, mudpuppies may first have colonized Glacial Lake Oshkosh after the West Twin River outlet was abandoned by using the subsequent Kewaunee or Ahnapee river outlets to invade from Lake Michigan (see maps in Wielert 1980).

It is hoped that this note will encourage other field personnel in Wisconsin, including fisheries scientists and other aquatic biologists, to document and report the occurrence of mudpuppies in their collections. In light of recent advances in the zoogeography of fishes in other parts of the Great Lakes basin (Legendre and Legendre 1984, Mandrak and Crossman 1992, Stephenson and Momot 1994, Momot and Stephenson 1996), it is also hoped that experts in those regions with access to mudpuppy distributional data will contribute to the analysis of a problem that has lingered since the time of Hecht and Walters (1955).

### Acknowledgments

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## Case Report of an Untreated Human Envenomation by the Western Massasauga Rattlesnake *Sistrurus catenatus tergimimus*

### ABSTRACT

Records were kept on the symptoms following a bite by a western massasauga (*S. c. tergimimus*). Although symptoms included severe swelling from the afflicted hand into the chest area, intense pain, temporary fever and nausea, no medical attention was received. Although documented cases of massasauga bites exist for the eastern subspecies *S. c. catenatus*, no recent case reports exist for this western subspecies.

### INTRODUCTION

Massasauga rattlesnakes occur throughout the state of Texas and are separated into two subspecies (Gloyd, 1955); the desert massasauga *S. c. edwardsi* in the west and southwest and the western massasauga *S. c. tergimimus* in the central and northeastern parts of the state. Though widespread, these snakes are rarely encountered by humans and are typically only observed crossing roads at night during the months of May and June (Knopf and Tinkle, 1961). Werler (1963) reports the western massasauga as docile and reluctant to rattle, but my experience is in agreement with Greene and Oliver (1965). The individuals encountered have been very aggressive; continually rattling and striking repeatedly.

However, due to their reclusive nature, human envenomation by the western massasauga is rare (Tennant, 1998) and well-documented envenomation case reports for this subspecies are presently unavailable. The reports provided by Tennant (1998) give no details or symptoms except that bites are "seldom serious" and in the two cases mentioned, resulted in "no permanent damage." This manuscript describes a different scenario. Case reports available on massasauga bites are from the eastern subspecies and most were documented when popular techniques involved tourniquets and incisions (LaPointe, 1965) which are no longer recommended as treatment.

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REPORT

On September 4, 1997 at 8:45 PM CST, this author (24 years old, 130 lbs., good general health) was bitten by an 43 cm male massasauga while collecting it in Parker County, Texas, west of the city of Fort Worth. Both fangs penetrated the middle finger of the left hand with puncture wounds one centimeter apart. One fang entered on the dorsal side of the medial knuckle, the other on the proximal side of the same knuckle. There was an instant intense burning accompanied by strong throbbing in the bitten finger. Oral suction was immediately applied and continued for five minutes.

At five minutes after the bite, the swelling and throbbing had increased in the finger. There was significant bleeding from the puncture wounds and the finger went numb. At ten minutes, a "tingling" sensation was felt in all fingers on the left hand, numbness, pain, and throbbing continued to increase. At 15 minutes, swelling had increased into the hand and other fingers, lymph nodes in the left armpit became tender, and a dry metallic taste was noticed in the mouth.

At 30 minutes, swelling had continued in both the palm, the dorsal side of the hand to the wrist, and fingers became immovable. At 45 minutes, the taste in my mouth was gone, the puncture sites continued to bleed, swelling had passed my wrist, the pain was almost unbearable and was extremely sensitive to touch or movement.

After one hour, the swelling was into the forearm. The burning sensation was less intense (possibly due to Advil® painkillers at 20 minutes) but the throbbing continued and my arm was immovable beyond the elbow. At 75 minutes, swelling continued toward the elbow, numbness was going in and out of my arm, and tenderness in my left armpit was increasing.

At 1:30 PM, nearly five hours after the bite, I returned home from the field having unadvisedly decided that medical attention would no longer be useful. At this time, swelling had reached the elbow and the pain was significant but bearable. Although slower, the wounds continued to bleed as I managed to go to sleep. At eight hours after the bite, I briefly awoke sweating, shaking uncontrollably with chills, with a fever

of 38.3 C, mild nausea, and was very "lightheaded." The bleeding of the bite wound had stopped and the swelling had slightly increased. At 11 hours, I awoke again with all symptoms from earlier in the morning gone (i.e. my temperature was normal) and took two more Advil for pain. The swelling had rounded the elbow and the throbbing had increased slightly from last night (Figure 1 and Figure 2).



*Figure 1. Photo of the author eleven hours after the bite of a western massasauga rattlesnake. Photo by K. Wray.*

At 14 hours, all of the initial "burning" was gone. The pain was now a dull throbbing ache that I tend to associate with severe bruises. My whole arm was very sore and extremely sensitive to touch and sunlight. Any movement of my arm hairs, even due to my own breath, was extremely painful and the most diffuse sunlight reaching my arm felt like a severe sunburn. At 20 hours, the swelling had reached the midpoint of my left triceps, appearing to have progressed up the back of my arm instead of up the front. The swelling in this area was not tight as in my forearm and hand, but very heavy and sagging. Pain was still considerable.

Twenty-four hours after the bite, I ate for the first time. The swelling had reached my armpit and shoulder. For the following 12 hours, the pain remained unchanged although the swelling progressed through my arm-



*Figure 2. Photo of the author eleven hours after the bite of a western massasauga rattlesnake. Photo by K. Wray.*

pit, into my chest, and down into the left side of my torso. Lymph nodes in my groin and in both armpits became increasingly tender and swollen. At 30 hours, my left wrist measured 24.1 cm in circumference (right wrist = 20.3) and my left elbow measured 33.0 cm (right elbow = 29.2). Estimated elbow movement was constrained to no more than 10-15° either direction of the 130° position.

Between 48-60 hours, swelling in the hand decreased slightly and I regained some finger mobility. Swelling in the arm, pain, and skin sensitivity remained the same with the addition of a slight headache. At 60 hours, the lymph nodes in both armpits were visibly swollen and it was painful to rest my arm next to my body. At 72 hours, the decreased swelling in the hand and forearm enabled the tip of my thumb to touch the tip of my fourth finger with limited wrist mobility. The bitten finger was still immovable.

For the following four days, the swelling that left the hand and forearm drained into the elbow and shoulder and eventually into my torso. Lymph nodes remained very tender and heavy discoloration became apparent in my arm. At one week after the bite, all swelling was gone except

in the bitten finger. All joints and muscles in the left hand, wrist, and forearm were stiff, weak, and sore. At 10 days, stiffness had decreased although I could not completely close my hand into a fist. Except for soreness, the only pain experienced was when contact was made to the arm. Skin was very dry, cracked, and beginning to slough around the bitten knuckle. At 14 days, the entire arm up to the elbow had sloughed at least one layer of skin and discoloration was nearly gone.

At one month, a depression was noticed across each fingernail on the left hand that had slowly grown out and had been cut off through trimming. This depression presumably coincided with the time of intense swelling which had thus affected nail growth.

Seventeen months after the bite, the bitten finger cannot be fully extended and a dull ache is still present at nearly all times, which I expect to be a permanent condition. Any activity that requires a strong grip with my left hand results in increased soreness and even more limited mobility for several days following.

In summary, swelling and pain increased through daily activity and decreased at night during sleep. Bleeding from the puncture wounds continued for five hours. I had no appetite for 24 hours following the bite, but continually drank water. No respiratory or gastrointestinal effects were noted nor was there ever discoloration in urine. The only systemic effects occurred five hours after the bite but did not persist. After two weeks, all visible signs of the snakebite had disappeared. Medical attention was never received and the only medication used was over-the-counter painkillers. I now consider this poor judgement on my part. I greatly underestimated the venom strength of a "pigmy" rattlesnake and an effort should have been made to seek medical attention.

On a more personal note, when this occurred, I was rightfully very concerned as to what I should expect regarding symptoms. However, I could find no literature on a bite from this snake or any *Sistrurus* bite in enough detail to satisfy my anxiety.

Regretfully, I do not have such medical knowledge or the proper equipment available to monitor other attributes (i.e. blood pressure) that may be useful information. Although most of these symptoms are typical

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of pit viper envenomation, should any researcher working with these snakes be as unfortunate as to endure this same experience, I hope this will provide some idea as to what to anticipate. However, I should stress that bites differ in location, amount of venom injected, the reaction by the victim, and variability demonstrated through the seasons of the year and age of the snake (Chippaux, et al., 1991).

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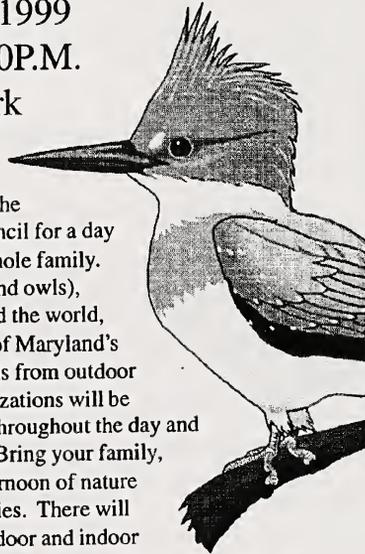
Accepted 20 February 1999

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Directions to Oregon Ridge Park: From the Baltimore Beltway (I-695) take I-83 North to Exit 20-B Shawan Road West. Make a left at the first light onto Beaver Dam Road. Follow signs to Oregon Ridge Park entrance.



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News and Notes

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*News and Notes*

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News and Notes

A New Book from the Society for the Study of Amphibians and Reptiles

# THE LIZARDS OF IRAN

by *Steven C. Anderson*

CALIFORNIA ACADEMY OF SCIENCES AND UNIVERSITY OF THE PACIFIC

IRAN IS A LARGE AND STRATEGICALLY LOCATED country, but few synthetic studies of its herpetofauna have been published. Steven C. Anderson has conducted extensive field work in Iran, beginning in 1958, and has spent a lifetime studying its herpetofauna, a subject on which he is a recognized authority. The lizard fauna of Iran is quite diverse and includes representatives of eight families: Agamidae (20 species), Anguidae (2), Eublepharidae (3), Gekkonidae (39), Lacertidae (42), Scincidae (14), Uromastycidae (3), and Varanidae (2).

This book is the first monographic treatise on the lizards of Iran, and contains sections on the history of herpetological studies in Iran; the biogeography of Iranian lizards; illustrated keys to families, genera, and species; an extensive bibliography of Iranian amphibians and reptiles; and appendices listing specimens examined and a gazetteer of collecting localities. The detailed species accounts include these sections: synonymy, diagnosis, color pattern, size, natural history, habitat, distribution, and remarks.

A major feature of this book is an outstanding group of color portraits of lizards (152 photographs) and their habitats (38). Most of these have not been published previously and many of the species of lizards have never been illustrated before. There are also nearly 150 figures in the text plus 103 spot distribution maps. This book will become the standard reference on the lizards of Iran and adjacent regions.



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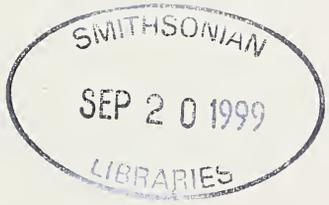
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DEPARTMENT OF HERPETOLOGY

THE NATURAL HISTORY SOCIETY OF MARYLAND, INC.



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## RESTING METABOLISM AND TEMPERATURE SELECTION IN THE DESERT SKINK, *SPHENOPS SEPSOIDES* (REPTILIA: SCINCIDAE)

Talal A. Zari

### Abstract

Resting metabolic rate and temperature selection of the desert *skink*, *Sphenops sepsoides*, were measured during day and night. The resting metabolic rate was low. No significant metabolic differences were observed between night and daytime measurements. The mass exponent  $b$  values ranged between 0.52 and 0.71. Thermal sensitivity ( $Q_{10}$ ) was low at 20-25°C and 30-35°C. Skinks had significantly lower mean selected body temperatures during late scotophase and midphotophase than other times of day over the 24 h period. The adaptive significance of these patterns of metabolism and temperature selection in *S. sepsoides* was discussed.

### Introduction

Oxygen consumption rates of lizards are influenced by many factors including temperature, body mass, season, time of day, sex and phylogeny (Bennett and Dawson, 1976; Andrews and Pough, 1985; Zari, 1987, 1997). Moreover, strong effects of behavior and ecology were observed on the metabolic rate-temperature curves of lizards (Al-Sadoon and Spellerberg, 1985; Zari, 1992, 1996). Behavioral thermoregulation in lizards has been widely studied (Brattstorm, 1965; Avery, 1982). Many factors modify the selected body temperature (preferred body temperature) of lizards such as time of day, light, season, feeding and sexual condition (Spellerberg, 1974; Huey, 1982; Tu and Hutchison, 1994; Zari, 1987, 1998).

Until recently, there were no published studies on resting energy metabolism and temperature selection in *S. sepsoides* (= *Chalcides sepsoides*) during day and night. This skink occurs in North Africa, Senegambia, Arabia and Syria (Khalil and Hussein, 1963; Fuhn, 1975). Do the behavior, ecology and morphology of this desert species affect its energy metabo-

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Key Words: Resting metabolism, temperature selection, skink, *Sphenops sepsoides*, body mass, temperature

lism and temperature selection? To answer this question, resting metabolism and body temperature selection in *S. sepsoides* were measured during day and night.

### Materials and Methods

*S. sepsoides* were imported from Egypt. They were kept in 100 x 60 x 60 cm glass aquaria. A 100 W heat lamp was placed 10 cm above the floor of each aquarium to provide a photothermal gradient. Each heat lamp was switched on between 09.00 and 19.00 h. Each aquarium contained sand, stones and vegetation to simulate a natural habitat. The ambient temperature in the room was around 26°C. Skinks were provided with food (insects and spiders) and water *ad libitum*. They were acclimated to these conditions for at least 2 weeks before any experimental measurements were made.

The resting metabolic rate (RMR) of skinks was measured at different temperatures (20-35°C) as the rate of oxygen consumption ( $\text{ml g}^{-1} \text{h}^{-1}$ ), using constant pressure manometric respirometers having both animal and control chambers as described by Zari (1987). In the morning, the skinks were weighed and placed in the respirometers. The animal and control chambers were immersed in a constant temperature water bath at the test temperature. Measurements of RMR were made on quiescent and postabsorptive skinks of various body sizes during day and night. Consequently, they were deprived of food for 3 to 6 days prior to respirometry.

Body temperature selection by 12 skinks was measured in a linear thigmothermal gradient over a 24 h period. A 120 cm long x 20 cm wide x 40 cm high trough with an aluminium base was heated from below by a subsurface heater to produce a linear 15-45°C gradient when in a room at 15°C. A broad-spectrum fluorescent tube was suspended above the trough to provide light but not heat between 07.00 and 19.00 h. A skink was placed in the trough and allowed to settle for 24 h. A YSI thermistor probe was then inserted about 1.5 cm into the cloaca and taped to the tail. After about 8 h, body temperature was recorded continuously on a chart recorder for 24 h. Mean selected body temperature (MST) was registered at 10-min intervals. All measurements were carried out during the spring (March-May).

Regression analyses of log-transformed oxygen consumption rate and log body mass data were carried out by the method of least squares. Comparisons of regression lines were made using the analysis of covariance (ANCOVA). Statistical comparisons of the mean  $Q_{10}$  values and selected body temperatures were performed using two-tailed *t*-tests and analysis of variance (ANOVA). Differences were considered to be statistically significant when  $P < 0.05$  (Sokal and Rohlf, 1981).

### Results

The relationships between resting oxygen consumption rate and body mass of *S. sepsoides* (0.453 - 7.258 g) were investigated at 20, 25, 30 and 35°C. Regression lines for each temperature were fitted to the data by the method of least squares. The relationship between mass-specific RMR ( $\text{ml g}^{-1} \text{h}^{-1}$ ) and body mass was expressed by the equation:

$$\log \text{RMR} = \log a + (b-1) \log M$$

or the allometric form:

$$\text{RMR} = a M^{(b-1)}$$

where  $\log a$  is the intercept,  $b-1$  is the regression slope (or mass exponent), and  $M$  is the body mass (g). RMR values ( $\text{ml h}^{-1}$ ) are obtained by using  $b$  as the regression slope. The values of RMR at night (scotophase) did not differ significantly than those during day (photophase) ( $P > 0.05$  by ANCOVA); therefore, the data were combined. The values of  $\log a$ ,  $b-1$ ,  $b$  along with correlation coefficients  $r$  and  $P$  values are presented in Table 1. RMR ( $\text{ml g}^{-1} \text{h}^{-1}$ ) decreases with increasing body mass at each temperature (20-35°C). Statistical regression analysis indicates that the regression slopes  $b-1$  were highly significant for all temperatures tested ( $P < 0.001$ ) (Table 1).

Analysis of covariance, ANCOVA, was used to determine whether there are differences in the slopes  $b-1$  and intercepts  $\log a$  of regression equations describing the oxygen consumption rates at different temperatures. There were no significant differences in the slopes of the regressions among the different temperatures ( $P > 0.05$  by ANCOVA). However,  $\log a$  values were significantly distinct from one another only between 25 and 30°C ( $P < 0.001$  by ANCOVA).

Table 1. Regression statistics and ANCOVA for RMR ( $\text{ml g}^{-1} \text{h}^{-1}$ ) of *S. sepsoides* as a function of body mass (g) measured at different temperatures (20-35°C)

T (°C)	n	r	log a	b-1	b	P
20	20	-0.91	-0.962	-0.481	0.519	<0.001
25	22	-0.92	-0.902	-0.485	0.515	<0.001
30	20	-0.87	-0.772	-0.291	0.709	<0.001
35	22	-0.89	-0.687	-0.289	0.711	<0.001

The adjusted mean values for RMR of *S. sepsoides* are shown in Table 2 and Fig. 1. The temperature coefficient ( $Q_{10}$ ) values were calculated from these adjusted mean rates of metabolism over the temperature range 20-35°C (Table 3). The lowest  $Q_{10}$  value was obtained for the temperature range 20-25°C. The highest  $Q_{10}$  value was found to occur in the temperature range of 25-30°C. No significant diel variations existed between the

Fig. 1. The adjusted mean RMR ( $\text{ml h}^{-1}$ ) (ANCOVA) for *S. sepsoides* at different temperatures (20-35°C). Each point represents the mean of different measurements. The vertical lines above and below each mean are standard deviations of that mean.

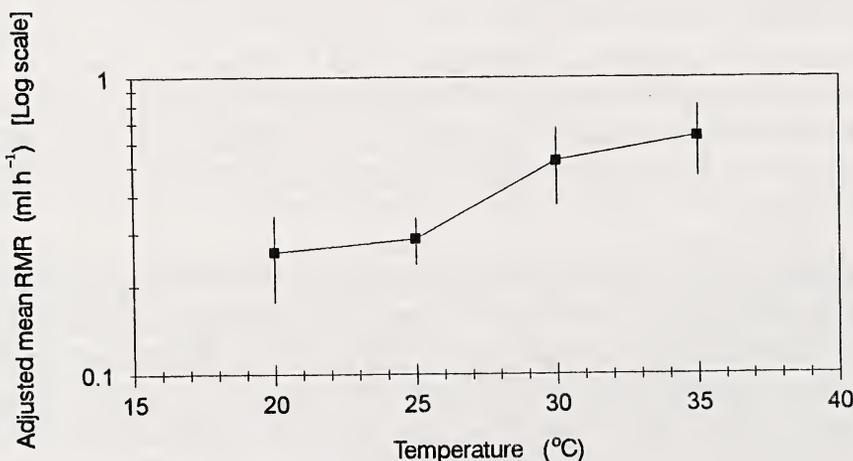


Table 2. Adjust mean RMR ( $\text{ml h}^{-1} \pm \text{SD}$ ) (ANCOVA), mean mass-specific RMR ( $\text{ml g}^{-1} \text{h}^{-1} \pm \text{SD}$ ) and body mass ( $\text{g} \pm \text{SD}$ ) of *S. sepsoides* measured at different temperatures (20-35°C).

T (°C)	n	Adjusted mean RMR ( $\text{ml h}^{-1} \pm \text{SD}$ )	Mean mass-specific RMR ( $\text{ml g}^{-1} \text{h}^{-1} \pm \text{SD}$ )	Mean mass ( $\text{g} \pm \text{SD}$ )
20	20	0.2597 $\pm$ 0.0831	0.0612 $\pm$ 0.0296	4.7078 $\pm$ 1.9530
25	22	0.2874 $\pm$ 0.0509	0.0675 $\pm$ 0.0295	4.6961 $\pm$ 1.8595
30	20	0.5261 $\pm$ 0.1522	0.1173 $\pm$ 0.0377	4.8744 $\pm$ 1.8583
35	22	0.6364 $\pm$ 0.1692	0.1445 $\pm$ 0.0511	4.6961 $\pm$ 1.8595

Table 3. temperature coefficient ( $Q_{10}$ ) values for the adjusted mean RMR (ANCOVA) in *S. sepsoides* within body temperature (T) intervals between 20 and 35°C

T Intervals (°C)	<i>S. sepsoides</i>
20-25	1.22
25-30	3.35
30-35	1.46
Overall	1.82

overall  $Q_{10}$  values over the temperature range 20-35°C ( $P > 0.05$  by ANOVA). The  $Q_{10}$  values at 25-30°C were significantly higher than those at 20-25°C or at 30-35°C ( $P < 0.01$  by *t*-test).

The mean selected body temperature (MST $\pm$ SD) of the twelve skinks was 29.7 $\pm$ 2.5°C (photophase 29.6 $\pm$ 2.3°C, scotophase 29.8 $\pm$ 2.7°C). The selected temperature range was 7.7°C (26.9-34.6°C) during day and 11.7°C (24.1-35.8°C) at night. Skinks chose their lowest MST (27.92 $\pm$ 1.59°C) during late scotophase (02.00 to 05.00 h) over the 24 h period. The MSTs during late photophase (14.00 to 19.00 h), early scotophase (20.00 to 24.00 h) and early photophase (06.00 to 10.00 h) were significantly higher than

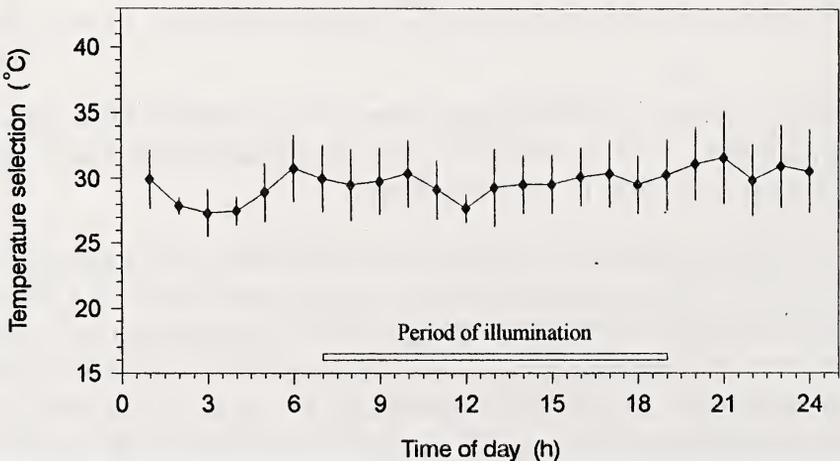
during late scotophase (02.00 to 05.00 h) and midphotophase (11.00 to 13.00 h) ( $P < 0.05$  by  $t$ -test) over the 24 h period (Fig. 2).

### Discussion

The present results show an inversely proportional relationship between the RMR ( $\text{ml g}^{-1} \text{h}^{-1}$ ) of *S. sepsoides* and body mass (g) (Table 1). Mass exponents of *S. sepsoides* ( $b=0.52-0.71$ ) are within the range of values reported for other lizard species (Bennett and Dawson, 1976; Andrews and Pough, 1985; Zari, 1993, 1996, 1997). These intraspecific  $b$  values are lower than the interspecific generalized values reported by Bennett and Dawson (1976), Bennett (1982) and Andrews and Pough (1985). Most mass exponents for comparisons within species are found to be lower than the mass exponent for comparisons among lizard species (Andrews and Pough, 1985). Several studies have differentiated between multi-species and ontogenetic  $b$  values in animals (Taylor and Davies, 1981; Heusner, 1982; Andrews and Pough, 1985).

The observed values of RMRs of adult *S. sepsoides* at different temperatures are lower than the values predicted from the allometric equations of Bennett and Dawson (1976), Bennett (1982) and Andrews and Pough

Fig. 2. Mean selected body temperature of *S. sepsoides* over 24 h in a linear thermal gradient illuminated from 07.00 to 19.00 h. The vertical lines above and below each mean are standard deviations of that mean.



(1985). Similarly, lower metabolic rates have been reported for other fossorial scincid species, e.g., *Acontias meleagris* (Withers, 1981; Brownlie and Loveridge, 1982) and *Chalcides ocellatus* (Bakker and Andrews, 1984; Pough and Andrews, 1984). Andrews and Pough (1985) reported that day-active predators had higher metabolic rates than fossorial lizards. Behavioral, ecological and morphological differences among scincid species are reflected in the variations of their resting metabolism (Withers, 1981; Brownlie and Loveridge, 1982; Al-Sadoon and Spellerberg, 1985; Andrews and Pough, 1985; Zari, 1987) which have been reported for this group. In the present study, low RMR in *S. sepsoides* inhabiting desert environments could be explained by its ecology, behavior and morphology. This specialized burrowing skink is secretive and adapted for burrowing in sand. It has reduced limbs and an elongated body (Fuhn 1975). In the eastern Egyptian desert, the sand-swimming, *S. sepsoides* is always moving from under one bush to another, through the highest layer of the sand. This type of movement produces traces of wavy continuous lines (Khalil and Hussein, 1963). In addition, reduced metabolic rate in desert lizard species was found to be amongst the adaptive means for living in hot deserts (Dawson and Templeton, 1966; Cloudsley-Thompson, 1972; Al-Sadoon and Spellerberg, 1985; Zari, 1996). In the present study, no significant metabolic differences in *S. sepsoides* were observed between night and daytime measurements. This may be due to the fact that the values of  $O_2$  consumption were used only if the skinks did not move during measurements. It is probably that some (and possibly all) of the metabolic differences between night and daytime measurements in the lizards are attributable to spontaneous activity during day (Beaupre *et al.*, 1993) or night (Feder and Feder, 1981). Highest metabolic rates usually occur during active periods and lowest during inactive periods (Cragg, 1978; Mautz, 1979; Feder and Feder, 1981).

The overall  $Q_{10}$  value of *S. sepsoides* is comparatively low throughout the metabolic rate-temperature curve (RT curve) and this is more likely to be related to both thigmothermic and fossorial behaviors of this species. It seems that the RT curve of *S. sepsoides* is rotated to give reduced temperature sensitivity and elevated RMR at low temperature (Fig. 1). This temperature dependent shift may enable the lizards to maintain levels of resting oxygen consumption suitable for activity and locomotion at low temperatures (Tromp and Avery, 1977; Pough and Busack, 1978; Zari,

1996, 1997). Moreover, low thermal dependence is found in *S. sepsoides* at higher temperatures (30-35°C) occurs at its selected body temperature that may assist metabolic homeostasis (Cloudsley-Thompson, 1972; Bennett and Dawson, 1976; Zari, 1993). The MST of *S. sepsoides* is 29.7°C over the 24 h period. Selected body temperatures of skinks are generally lower than those of most other groups of lizards (Brattstorm, 1965; Licht *et al.*, 1966; Avery, 1982). In addition, mean activity temperatures differ widely among scincid species and are correlated with their behavior and ecology (review in Avery, 1982). *S. sepsoides* was fully active at temperatures between 24.4 and 35°C and fully inactive below 18.5°C and above 40°C (Khalil and Hussein, 1963). In the present study, *S. sepsoides* displayed diel cycles of thermal selection. They had significantly lower mean selected body temperatures during late scotophase and midphotophase than other times of day over the 24 h period (Fig. 2). It seems that the timing of the increments in MSTs coincides with normal activity times of this species (Zari, unpublished data). Khalil and Hussein (1963) noted that the activity of *S. sepsoides* is of the arrhythmic type with a nocturnal major period of activity that lies between 19.00 and 23.00 h. Time of day is an important factor in temperature selection in lizards (Sievert and Hutchison, 1989). The highest body temperatures are selected during activity for both diurnal and nocturnal lizards (Regal, 1967; Hutchison and Kosh, 1974; Spellerberg, 1974; Huey, 1982; Bennett and John-Alder, 1986; Sievert and Hutchison, 1988, 1989; Zari, 1998). In Australia, the cryptozoic skinks (*Eremiascincus* spp. and *Hemiergus* spp.) have the lowest preferred body temperatures (PBTs) of all species examined and they show a nocturnal increment in PBTs. *Eremiascincus* are active at dusk and in the early evening. *Hemiergus* have been observed abroad in the late afternoon and early evening and are almost never seen during the day (Bennett and John-Alder, 1986).

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## Emory's Softshell Turtle, *Apalone spinifera emoryi*, in Mexico

Aside from an introduced (since early 1900s), established and widespread population in the Gila-Colorado River drainage in Arizona, Emory's Softshell Turtle, *Apalone spinifera emoryi*, characteristic of the Río Grande (and Pecos River) drainage, is recorded from the Mexican states of Chihuahua, Coahuila, Nuevo León, and Tamaulipas. In Tamaulipas *emoryi* is also known to occur in the Río San Fernando and the Río Soto la Marina/Purificación (Webb, 1962, 1973). Pritchard (1979:633, legend of fig.) provided a good photograph of a softshell readily identified as *emoryi* "from the Rio Verde, San Luis Potosi." Recently, one of us (JAL) acquired two softshells from the Río Balsas, far south of the known range in north-eastern México. These two turtles are deposited in the Colección Herpetologica, Unidad de Biología, Tecnología, y Prototipos, Universidad Nacional Autónoma de México, Campus Iztacala, Tlalnepantla, Edo de México, México.

The two softshells are from about the same place along the Río Balsas, Colonia Valerio Trujano, Guerrero, México. One (JLE 2592) is a young male received from a person working in the river, 15 February 1998; the other (JLE 2593) is a young female (blotched carapace pattern) from the edge of the river below the Mezcala bridge, 23 May 1998. Respective measurements of carapace length and width (curvature) and plastron length [flexible mm tape] and head width [calipers] of the male and female are 96, 148; 87, 123; 77, 107; and 16.5, 21.2 mm. Both are referable to *emoryi* in having (Webb, 1973) the pale rim of the carapace noticeably widened posteriorly, a straight or slightly curved (may be broken) dark line on the forehead between the eyes, low rounded tubercles on the anterior edge of the carapace (female), and the juvenile pattern of white dots confined to the posterior part of the carapace (male). Pattern features of the two Guerrero turtles that vary somewhat from the "norm" are (1) the dark gray carapaces, especially the small male (instead of pale brownish); Webb (1962:511) previously noted some unusual darker individuals of *emoryi*, (2) the mostly complete pale postocular stripes (black borders partly interrupted); stripe variable in *emoryi* (may be complete, UTEP 3385, El Paso), but often only distinct, short postocular stripe with posterior part obliterated, and (3) more bold pattern of larger black spots and barlike marks on

dorsal surfaces of the limbs; pattern variable in *emoryi* but usually reduced with smaller markings.

Thus, the morphological features of the Río Balsas softshell turtles do not suggest any great taxonomic divergence from the known variational parameters of *emoryi*. Further field work is necessary to establish if the two Guerrero turtles are part of a larger interbreeding population, as well as to corroborate occurrence in the Río Verde in San Luis Potosí. Possibly, they represent man-transported introductions. However, local residents at the Río Balsas collection site report having seen these turtles for many years (since about the 1950s). Avise et al. (1992) recognized low levels of genetic variability and differentiation in turtles (reflected in slow evolutionary rate of mitochondrial DNA compared to other vertebrates).

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## SEASONAL VARIATION IN REPRODUCTION IN THE RED-EARED SLIDER (*TRACHEMYS SCRIPTA ELEGANS*)

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### Abstract

Seasonal variation or systematic variation in reproductive life-history traits within a single reproductive season was studied among 1,667 female red-eared sliders (*Trachemys scripta elegans*) over a four year span at two sites in west-central Illinois. Statistically significant seasonal variation was not found in egg mass, clutch size, clutch mass, or maternal mass. However, females nesting in the first half of the nesting season tended to be heavier than those nesting in the second half of the nesting season. Moreover, females found nesting more than once tended to be heaviest prior to laying their first clutches but lighter when laying their second clutches. However, even these differences were slight and were not statistically significant. Variance in clutch size and egg mass within individuals laying multiple clutches and variance in clutch size and egg mass among all individuals sampled did not differ even while holding maternal size constant and removing potential effects of annual and local variation. Environmental and microhabitat influences appear to be controlling factors on reproductive life-history traits.

### Introduction

Seasonal variation can be defined as systematic variation in reproductive life-history traits that occur within a single reproductive season of a given turtle species (i.e., Frazer and Richardson, 1985a). This variation may occur between sequential clutches for species that lay more than one clutch per nesting season (e.g., Gibbons et al., 1982; Iverson and Smith, 1993). Similarly, reproductive traits of turtles nesting early or late in the nesting season may vary (e.g., Frazer and Richardson, 1985a; Rowe, 1994).

The importance of seasonal variation has long been recognized (Iverson, 1978; Moll, 1979). Nonetheless, most studies of turtle reproduction do not examine seasonal variation in detail. Seasonal variation is difficult to study because large numbers of females must be examined to

locate turtles nesting more than once per season (i.e., Iverson and Smith, 1993). Moreover, females must be collected throughout the nesting season (i.e., Frazer and Richardson, 1985a).

An understanding of the magnitude of seasonal variation is needed to accurately define life-history traits such as reproductive effort especially for species known to produce multiple clutches within a single nesting season. Detailed studies of such species find that clutches can vary systematically in traits such as egg size and number (i.e., Gibbons et al., 1982; Frazer and Richardson, 1985b) or that sequential clutches do not vary in any predictable way (i.e., Iverson, 1978; Mitchell, 1985a). Moreover, studies of species such as the painted turtle (*Chrysemys picta*) find variation among successive clutches (i.e., Iverson and Smith, 1993; Rowe, 1994), but others find no evidence of variation between successive clutches (i.e., Gibbons, 1968; Christians and Bider, 1986; Mitchell, 1985b).

Two methods have been used to study seasonal variation. One method divides the nesting season into two or more parts and then compares reproductive life-history traits between or among those parts (e.g., Frazer and Richardson, 1985a; Bjorndal and Carr, 1989; Hayes et al., 1993; Rowe, 1994). The other method compares successive clutches from individual females (e.g., Gibbons, 1968; Mitchell, 1985a, Frazer and Richardson, 1985b; Hays and Speakman, 1992). The first method examines population-wide seasonal variation, whereas the second examines intra-individual variation.

In this study, I use both methods to examine seasonal variation in reproductive life-history traits for female red-eared sliders (*Trachemys scripta elegans*) collected from two populations in West-Central Illinois during 1995-98. Reproduction in these populations have been extensively studied (Tucker et al., 1998a and b), and they are known to show annual and local variation. I further examine whether these two populations show similar patterns of seasonal variation in egg size and clutch size. Mean annual clutch frequency and mean annual fecundity (*sensu* Frazer et al., 1990) will be examined in another study.

### Materials and Methods

I caught turtles either crossing roads adjacent to nesting areas or at nesting areas near Stump Lake in Jersey County and Swan Lake in Calhoun

County, Illinois (see Tucker, 1997). Smaller subsets of the data presented herein were previously published (Tucker and Moll, 1997; Tucker et al., 1998a and b). Turtles have been collected at these two sites from 1994 to 1998. The current study concentrates on those collected between 1995 and 1998 because sample sizes in each of those years are robust.

Gravid body mass (nearest 10 g) and straight-line plastron length (nearest mm) was measured for each female. Eggs were weighed to 0.01 g. Clutch mass was derived by multiplying mean egg mass for a particular clutch by the number of eggs in the clutch (method of Tucker et al., 1998a).

Oxytocin was used to induce oviposition (Ewert and Legler, 1978). Turtles were uniquely marked by drilling holes in the marginal scutes and released at the original collecting area. Hatchlings from eggs collected during this study were released at the collecting sites of their female parents after being overwintered in captivity.

I used SAS for all statistical analyses (SAS Institute, 1988). Spearman's rank correlation ( $Rho$ ) was employed for correlation analysis. Successive clutches from females laying more than one clutch per nesting season were compared with Wilcoxon rank sum test ( $Z$ ). Analysis of covariance (ANCOVA) with maternal plastron length as the covariate was employed to compare reproductive data gathered during the first and second halves of the nesting season for each year from 1995 to 1998. Nesting seasons were divided into equal halves based on the first and last day that nesting females were collected. Means given in the text are accompanied by  $\pm 1$  SD.

This study relied on statistical tests, each of which has an overall 0.05 chance of a type I error (Rice, 1989). I used a conservative approach and employed the sequential Bonferroni procedure to interpret test results on a study-wide basis as opposed to a table-wide basis (Rice, 1989; Amos, 1996). Consequently, I questioned the biological significance of values of  $P$  greater than 0.001.

### Results

Roughly equal numbers of turtles were collected in each half of the nesting season from Stump Lake (Table 1) and Swan Lake (Table 2) in

each year of the study. Once adjusted for differences in maternal size, few comparisons between first and second halves of the nesting season in each of the years examined were statistically different sufficient to exclude type I errors at 0.05 (Table 3).

However, there is evidence of consistent patterns in maternal mass and possibly in egg mass, as well. In every instance, maternal mass adjusted for differences in plastron length was greater among turtles collected in the first half of the nesting season than those collected in the second half of the nesting season (Table 3). In one of eight instances (Swan Lake, 1998), the difference was statistically significant. Except for Stump Lake in 1998, egg mass was greater among eggs collected in the first half of the season than among those collected in the second half of the season (Table 3). However, none of the statistical comparisons were significant and most differences between halves were slight (Table 3).

Because relatively few turtles were found nesting more than once in a particular year, samples from Swan Lake and Stump Lake were combined for analysis (Table 4). None of the comparisons of reproductive traits or maternal mass between sequential clutches were significantly different in any year of the study (Table 4). Nonetheless, maternal mass was greatest for turtles laying their first clutches of the season compared to maternal mass for the same turtles laying a subsequent clutch in each year of the study (Table 4). Clutch size was also greatest in each year among first clutches compared to subsequent clutches. However, in all of these instances statistical comparisons in each year were not significant.

Reproductive traits and maternal mass did not differ between renesting turtles and turtles not found renesting at Stump Lake using ANCOVA. For instance, least squares mean (LSM) for maternal mass for those renesting was greater than those not found renesting (1810 g vs. 1770 g, respectively) but the difference was not significant ( $F_{1,985} = 2.58, P = 0.1082$ ). Similarly, clutch size LSM (14.0 vs. 14.0 eggs, respectively,  $F_{1,846} = 0.00, P = 0.9623$ ), clutch mass LSM (148.3 vs. 142.8 g, respectively,  $F_{1,846} = 1.00, P = 0.3183$ ), and egg mass LSM (10.5 vs. 10.1 g, respectively,  $F_{1,870} = 2.14, P = 0.1437$ ) did not differ between turtles found nesting more than once and turtles not found nesting more than once.

Similarly, Swan Lake turtles found nesting more than once did not

weigh more than those found nesting once (maternal mass LSM 1780 vs. 1820 g, respectively,  $F_{1,765} = 0.99$ ,  $P = 0.3190$ ). Reproductive traits including clutch size LSM (13.5 vs. 12.9 eggs, respectively,  $F_{1,586} = 0.56$ ,  $P = 0.4528$ ) clutch mass LSM (154.7 vs. 140.9 g, respectively,  $F_{1,586} = 1.85$ ,  $P = 0.1744$ ), and egg mass LSM (11.4 vs. 11.9 g, respectively,  $F_{1,600} = 1.52$ ,  $P = 0.2187$ ) did not differ significantly.

*Table 1. Descriptive statistics for reproductive life-history traits and measures of size of red-eared sliders (Trachemys scripta elegans) collected at Stump Lake in Jersey County, Illinois between 1995 and 1998 with the nesting season divided into two equal halves. Measures of length are in mm, and measures of mass are in g.*

Trait	<u>First half nesting season</u>		<u>Second half nesting season</u>	
	N	Mean(SD)/Range	N	Mean(SD)/Range
<b>Stump Lake-1995</b>				
Plastron length	73	214.5(14.8)/167-240	67	214.5(12.4)/184-236
Clutch mass	64	163.6(45.2)/52.5-270.0	67	153.9(47.2)/61.6-292.6
Clutch size	64	15.0(3.61)/6-25	67	14.8(4.19)/7-26
Egg mass	66	10.86(1.37)/6.41-13.42	67	10.42(1.55)/6.50-13.45
Maternal mass	66	1945(377.7)/975-2600	67	1877(310.6)/1200-2475
RCM	64	0.092(0.019)/0.044-0.133	67	0.089(0.022)/0.042-0.137
<b>Stump Lake-1996</b>				
Plastron length	151	213.6(15.1)/170-251	133	215.5(13.7)/179-247
Clutch mass	122	134.0(41.8)/43.0-295.6	128	138.5(38.4)/43.1-221.1
Clutch size	122	13.3(3.22)/6-26	128	13.7(3.24)/6-21
Egg mass	126	10.00(1.64)/6.25-13.26	128	10.06(1.34)/6.54-12.87
Maternal mass	123	1854(384.5)/1000-2850	126	1894(369.2)/1100-2700
RCM	119	0.078(0.017)/0.037-0.140	126	0.079(0.017)/0.037-0.138
<b>Stump Lake-1997</b>				
Plastron length	79	216.6(15.4)/181-251	69	209.3(15.4)/167-245
Clutch mass	64	150.6(46.2)/56.9-301.9	56	143.1(40.5)/46.9-233.1
Clutch size	64	13.8(3.42)/7-26	56	13.7(2.97)/5-20
Egg mass	66	10.76(1.58)/7.11-13.05	58	10.32(1.76)/6.44-14.04
Maternal mass	64	1902(409.8)/1080-2810	53	1781(370.0)/1100-2600
RCM	63	0.085(0.018)/0.037-0.128	53	0.089(0.019)/0.032-0.133
<b>Stump Lake-1998</b>				
Plastron length	231	209.5(15.8)/169-247	187	210.6(15.7)/172-247
Clutch mass	174	140.9(46.4)/29.5-273.8	149	145.1(46.2)/53.8-339.3
Clutch size	174	14.1(3.82)/4-29	149	14.2(3.58)/5-30
Egg mass	185	9.82(1.52)/5.09-13.95	153	10.18(1.51)/5.95-14.56
Maternal mass	215	1705(393.0)/950-2730	184	1673(398.8)/700-2660
RCM	165	0.090(0.020)/0.022-0.161	147	0.093(0.019)/0.034-0.148

Table 2. Descriptive statistics for reproductive life-history traits and measures of size of red-eared sliders (*Trachemys scripta elegans*) collected at Swan Lake in Jersey County, Illinois between 1995 and 1998 with the nesting season divided into two equal halves. Measures of length are in mm, and measures of mass are in g.

Trait	<u>First half nesting season</u>		<u>Second half nesting season</u>	
	N	Mean(SD)/Range	N	Mean(SD)/Range
<b>Swan Lake-1995</b>				
Plastron length	58	214.5(11.4)/190-240	71	208.8(13.3)/181-234
Clutch mass	42	171.6(30.2)/98.9-233.8	52	149.3(35.8)/68.4-224.4
Clutch size	42	14.8(2.50)/8-20	52	13.8(2.95)/8-22
Egg mass	42	11.65(0.84)/9.78-13.23	52	10.87(1.52)/6.91-13.19
Maternal mass	42	1954(268.3)/1300-2550	52	1800(312.1)/1125-2625
RCM	42	0.097(0.013)/0.066-0.123	52	0.091(0.018)/0.047-0.127
<b>Swan Lake-1996</b>				
Plastron length	46	212.8(14.1)/172-241	51	222.9(12.5)/193-248
Clutch mass	40	133.1(28.0)/84.6-219.4	51	153.9(42.4)/64.2-234.5
Clutch size	40	12.1(2.32)/7-16	51	13.7(3.45)/6-23
Egg mass	40	11.08(1.57)/8.35-15.07	51	11.17(1.07)/8.03-13.69
Maternal mass	40	1868(287.8)/1350-2650	51	2058(355.8)/1375-2800
RCM	40	0.077(0.013)/0.047-0.106	51	0.081(0.018)/0.043-0.123
<b>Swan Lake-1997</b>				
Plastron length	112	213.4(13.7)/173-252	167	213.6(13.0)/181-246
Clutch mass	114	133.9(35.2)/61.5-234.5	110	135.9(32.3)/63.4-227.4
Clutch size	114	11.9(2.69)/5-18	110	12.6(2.61)/6-19
Egg mass	115	11.16(1.34)/8.27-14.07	115	10.74(1.44)/7.12-13.75
Maternal mass	115	1829(327.4)/1000-2670	115	1791(346.7)/1000-2630
RCM	114	0.079(0.017)/0.033-0.120	110	0.083(0.018)/0.033-0.120
<b>Swan Lake-1998</b>				
Plastron length	91	215.3(13.9)/168-250	81	214.6(11.4)/188-241
Clutch mass	70	144.4(39.7)/48.2-230.3	64	130.6(31.9)/40.2-224.0
Clutch size	70	13.1(3.11)/6-21	64	12.5(2.50)/4-19
Egg mass	78	10.95(1.31)/7.86-13.	54	66 10.43(1.18)/7.51-13.03
Maternal mass	90	1822(342.5)/960-2600	81	1728(279.3)/1220-2460
RCM	70	0.085(0.018)/0.038-0.133	64	0.082(0.015)/0.022-0.108

Table 3. Results of analysis of covariance for maternal mass and reproductive life-history traits of *Trachemys scripta elegans* collected in west-central Illinois. Measures of mass are in g.

Trait	LSM <sub>1</sub>	LSM <sub>2</sub>	DF	F	P
<b>Stump Lake-1995</b>					
Clutch mass	164.71	152.89	1, 130	3.72	0.0560
Clutch size	15.1	14.7	1, 130	0.35	0.5570
Egg mass	10.88	10.41	1, 132	5.31	0.0228*
Maternal mass	1952	1870	1, 132	10.46	0.0015*
<b>Stump Lake-1996</b>					
Clutch mass	136.1	136.5	1, 249	0.01	0.9278
Clutch size	13.5	13.6	1, 249	0.10	0.7537
Egg mass	10.06	10.00	1, 253	0.16	0.6914
Maternal mass	1877	1872	1, 248	0.07	0.7952
<b>Stump Lake-1997</b>					
Clutch mass	146.4	147.9	1, 119	0.07	0.7882
Clutch size	13.6	13.9	1, 119	0.41	0.5216
Egg mass	10.59	10.52	1, 123	0.13	0.7216
Maternal mass	1862	1829	1, 116	1.29	0.2575
<b>Stump Lake-1998</b>					
Clutch mass	143.2	142.5	1, 320	0.05	0.8296
Clutch size	14.3	14.0	1, 320	0.40	0.7123
Egg mass	9.89	10.09	1, 335	2.30	0.1304
Maternal mass	1712	1664	1, 396	10.55	0.0013
<b>Swan Lake-1995</b>					
Clutch mass	166.2	153.7	1, 93	4.97	0.0283*
Clutch size	14.4	14.0	1, 93	0.53	0.4704
Egg mass	11.53	10.96	1, 93	5.09	0.0265*
Maternal mass	1886	1885	1, 93	1.19	0.2777
<b>Swan Lake-1996</b>					
Clutch mass	143.0	146.1	1, 90	0.28	0.6007
Clutch size	12.8	13.2	1, 90	0.53	0.4674
Egg mass	11.28	11.02	1, 90	0.98	0.3260
Maternal mass	1982	1968	1, 90	0.18	0.6712
<b>Swan Lake-1997</b>					
Clutch mass	133.4	136.4	1, 223	0.64	0.4233
Clutch size	11.9	12.6	1, 223	4.27	0.0399*
Egg mass	11.15	10.76	1, 229	6.15	0.0138*
Maternal mass	1823	1797	1, 229	2.02	0.1566
<b>Swan Lake-1998</b>					
Clutch mass	143.6	131.5	1, 131	6.10	0.0148*
Clutch size	13.1	12.6	1, 131	1.19	0.2777
Egg mass	10.92	10.47	1, 141	6.91	0.0095*
Maternal mass	1815	1736	1, 168	11.56	0.0008

LSM<sub>1</sub> = Least squares mean for first half of nesting season; LSM<sub>2</sub> = Least squares mean for last half of nesting season; \*Values of  $P > 0.0014$  should be viewed with caution due to the number of *post hoc* comparisons.

Table 4. Comparison of sequential clutches for *Trachemys scripta elegans* that were found nesting twice in a single nesting season in west-central Illinois. Measures of mass are in g.

Trait	First Clutch	Subsequent Clutch	Wilcoxon rank sum	
	Mean(SD)/Range	Mean(SD)/Range	Z	P
<b>1995 (N = 3)</b>				
Clutch mass	234.0(6.7)/228.1-241.3	192.3(32.3)/162.9-226.8	1.75	0.0809
Clutch size	19.3(2.52)/17-22	16.0(1.73)/15-18	1.33	0.1840
Egg mass	12.21(1.23)/10.97-13.42	11.98(0.97)/10.86-12.60	0.00	0.9999
Maternal mass	2425(152.1)/2325-2600	2317(137.7)/2225-2475	0.87	0.3827
RCM	0.107(0.01)/0.096-0.116	0.090(0.011)/0.079-0.101		
<b>1996 (N = 12)</b>				
Clutch mass	155.9(19.6)/126.1-183.8	140.4(25.4)/95.4-179.8	1.33	0.1824
Clutch size	14.1(2.19)/11-18	12.8(2.44)/10-18	1.43	0.1519
Egg mass	11.14(0.89)/9.70-12.34	10.96(0.72)/9.54-11.92	0.61	0.5443
Maternal mass	2015(190.4)/1630-2260	1988(227.0)/1600-2300	0.35	0.7287
RCM	0.082(0.012)/0.059-0.100	0.076(0.013)/0.053-0.104		
<b>1997 (N = 5)</b>				
Clutch mass	149.0(27.0)/120.6-193.5	143.5(21.4)/112.0-169.4	0.08	0.9362
Clutch size	14.2(1.92)/12-17	13.4(1.14)/12-15	0.53	0.5936
Egg mass	10.51(1.33)/9.25-12.30	10.72(1.52)/9.33-13.03	0.42	0.6761
Maternal mass	1818(354.1)/1280-2130	1794(326.9)/1270-2150	0.08	0.9362
RCM	0.088(0.012)/0.076-0.104	0.088(0.008)/0.078-0.097		
<b>1998 (N = 14)</b>				
Clutch mass	170.3(48.6)/73.9-273.8	170.4(80.0)/58.2-339.3	0.00	0.9999
Clutch size	15.2(3.62)/8-24	15.1(6.39)/5-30	0.00	0.9999
Egg mass	11.11(1.53)/8.22-13.60	11.38(1.50)/8.80-13.79	0.44	0.6625
Maternal mass	2072(363.8)/1350-2550	1987(409.5)/1300-2660	0.69	0.4905
RCM	0.088(0.012)/0.076-0.104	0.088(0.008)/0.078-0.097		

## Discussion

The primary finding of this study is that seasonal variation among reproductive life-history traits in the turtles that I examined was slight. Turtles nesting early and those nesting late did not differ in any particulars. Similarly, successive clutches also did not vary significantly. The only suggestion of a seasonal "trend" was that females nesting early and females making their first nesting forays were relatively heavy. The desert tortoise (*Gopherus agassizii*) also is heaviest before laying the first clutch of the season than it is just before laying its second clutch of the season (Turner et al., 1984).

Gibbons et al. (1982) suggested that second clutches laid by South Carolina *Trachemys scripta* are smaller than their first clutches. Second

clutches from Illinois *T. scripta* also tended to have fewer eggs like those from South Carolina but the differences among the Illinois clutches are not significant. Gibbons et al. (1982) found that first observed clutches were larger than later clutches in 4 of 12 instances and smaller in 5 of 12 instances. I found that 17 of 36 first clutches of the season were larger than the following clutch in the same year and that 16 of 36 were smaller. Apparently, *T. scripta* from Illinois and South Carolina are able to partition their reproductive output evenly during the nesting season.

Gibbons (1982) pointed out the importance of within and among individual comparisons in the amount of variation in clutch size. If reproductive life-history traits are strongly controlled genetically, then variability in reproductive traits should be greater within the population than within the individual. Gibbons (1982) concluded that for *Trachemys scripta* environmental or microhabitat influences upon the individual are controlling factors. I examined this same problem with the data from Illinois *T. scripta* using ANCOVA to remove the effect of body size (Tucker et al., 1998a) but also accounted for local and annual variation for the years between 1995 and 1998. Main effects were location, year, and turtles with multiple clutch records and the entire sample of turtles. Within individual variance was not significantly different from within population variance for clutch size ( $F_{1,1468} = 1.89, P = 0.1689$ ) and egg mass ( $F_{1,1510} = 2.36, P = 0.1248$ ). The similarity between South Carolina and Illinois turtles is important because both data sets are based on long-term studies and sample size for the Illinois turtles is sufficient to include potential effects of annual and local variation in the examination.

Although I found little indication of seasonal variation in reproduction in the *Trachemys scripta* that I studied, seasonal variation is important for other turtle species. A number of studies of sea turtles find that last-laid clutches tend to have fewer eggs or smaller eggs (Hirth, 1980; Frazer and Richardson, 1985a, b; Hays and Speakman, 1992; Hayes et al., 1993). Similarly, a number of studies of freshwater turtles report seasonal variation. These studies find that the second or last clutch of the season tends to have fewer and sometimes smaller eggs for a number of species (Montevecchi and Burger, 1975; Mitchell, 1985a; Etchberger and Ehrhart, 1987; Iverson and Smith, 1993). Clearly, an understanding of the amount of seasonal variation present is needed before reproductive life-history traits of any turtle species can be properly studied.

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News and Notes

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			1	2	3	4
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12	13	14	15	16	17	18
19	20	21	22	23	24	25
26	27	28	29	30		

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*News and Notes*

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*News and Notes*





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Department of Herpetology, Natural History Society of Maryland, Inc.

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## Reproductive output of *Terrapene carolina*, *Chrysemys picta*, and *Sternotherus odoratus* from west-central Illinois

John K. Tucker

### Abstract

Reproductive life-history traits including egg mass, egg length, egg width, clutch size, and clutch mass were studied in *Terrapene carolina*, *Chrysemys picta*, and *Sternotherus odoratus* collected in west-central Illinois. Clutch size but not egg mass was positively correlated with clutch mass consistent with optimal egg theory. Generally, larger females of each species laid more eggs per clutch. Egg mass increased with maternal size in *C. picta* and *S. odoratus*. Egg mass of *T. carolina* tended to decrease with increasing clutch size and maternal size because egg length was negatively associated with clutch size. Overall, eggs of *T. carolina* were the heaviest, longest, and widest once the effect of maternal size was removed. *Sternotherus odoratus*, the species with the smallest body size, laid more eggs per clutch than the other two species once clutch size was adjusted for differences in maternal size. Turtles of all three species from the west-central Illinois sites laid large clutches and large eggs compared to turtles of these three species elsewhere in the United States.

### Introduction

The study of life-history traits is enhanced when information is available for numerous species from many geographic locations (Iverson, 1992; Iverson et al., 1993). Turtle species in Illinois have been the object of some early studies (Cahn, 1937; Cagle, 1950; Smith, 1961). Turtles from west-central Illinois, particularly the red-eared slider (*Trachemys scripta elegans*) have also been extensively studied (Thornhill, 1982; Tucker et al., 1998a, b). Nonetheless, relatively few data have been published on other species from the Mississippi and Illinois River systems in west-central Illinois. In the current study, I report data collected from 1994-1998 for the eastern box turtle (*Terrapene carolina*), the painted turtle (*Chrysemys picta*), and the stinkpot (*Sternotherus odoratus*).

Herein, I also revisit some of the topics important in understanding turtle reproductive life-history (see Congdon and Gibbons, 1985). Specifically, I examine the influence of maternal body size on egg and clutch size. Moreover, I look at how egg shape varies with respect to maternal body size in these three species (Tucker and Janzen, 1998). Finally, I put data gathered in west-central Illinois into context with data from elsewhere on these same species.

### Materials and Methods

The methods follow those of Tucker et al. (1998a). Turtles were found crossing roads in Jersey and Calhoun Counties. Turtles were palpated to determine their reproductive status. Turtles without oviductal eggs were uniquely marked, measured, and then released at the collecting location within 24 h. Gravid turtles had their gravid body mass (nearest 10 g), straight-line plastron and carapace lengths, maximum carapace height, and maximum carapace width measured to the nearest 1 mm (Tucker et al., 1998b). A smaller subset of the data collected on *Terrapene carolina* was reported by Tucker (1995).

Oxytocin was used to induce oviposition (Ewert and Legler, 1978). Eggs were weighed to 0.01 g with an electronic balance. Egg width and length were measured with vernier calipers to 0.01 mm. Eggs broken by the female during oviposition were included in clutch size. Clutch mass was determined by multiplying mean egg mass for intact eggs by the total number of eggs laid (Tucker et al., 1998a, b). Spent body mass was estimated by subtracting clutch mass from the female's gravid body mass (method of Iverson and Smith, 1993). Relative clutch mass (RCM), relative egg mass (REM), and egg elongation ratio (ELO) were calculated using the method of Iverson and Smith (1993).

Females were released at the original collecting area 48 h after eggs were laid (Tucker et al., 1995). Eggs were incubated to hatching. Hatchlings from eggs collected during this study were released at the collecting sites of their female parents. Hatchling *Chrysemys picta* were overwintered in captivity before being released. Hatchling *Terrapene carolina* and *Sternotherus odoratus* were released within a month of hatching.

I used SAS for all statistical analyses (SAS Institute, 1996). Spearman's rank correlation ( $\rho$ ) was employed for correlation analysis and for par-

tial correlation analysis. I employed the sequential Bonferroni procedure to identify *P*-values that do not exclude type I errors at 0.05 (Rice, 1989).

Because measures of reproductive output are often related to maternal size, I used analysis of covariance (ANCOVA) to compare reproductive traits among species. In order to select the measure of maternal size that explained the maximum amount of variance for all three species, I first performed stepwise multiple regression to find out which measure of maternal size best predicted egg mass and clutch size (Table 1). Carapace width was that measure of maternal size for egg mass, whereas carapace length was best for clutch size. I selected instead, maternal plastron length as the covariate for ANCOVA. This maternal variable was best overall for the two reproductive traits (Table 1). Selection of plastron length has another advantage in that it is nearly universally used as an index of maternal size (but see Jackson, 1988; Tucker et al., 1998b). The plastron of *Sternotherus odoratus* is reduced in length. Carapace length was substituted for plastron length in this species.

### Results

Reproductive traits varied extensively among the three species examined (Table 2). Correlation among reproductive traits varied among

*Table 1. Details from stepwise multiple regression of two measures of reproductive output against six measures of maternal size.*

Reproductive trait:	Egg mass			Clutch size		
	<u>R</u> <sup>2</sup>	<u>F</u>	<u>P</u>	<u>R</u> <sup>2</sup>	<u>F</u>	<u>P</u>
Maternal trait						
Plastron length	0.25	19.22	0.0001	0.20	14.75	0.0003
Carapace length	0.06	3.50	0.0663	0.38	35.53	0.0001
Carapace height	0.34	31.02	0.0001	0.00	0.05	0.8217
Carapace width	0.57	78.49	0.0001	0.00	0.19	0.6676
Gravid mass	0.32	27.37	0.0001	0.17	12.65	0.0007
Estimated spent mass	0.32	27.95	0.0001	0.15	10.15	0.0023

Table 2. Descriptive statistics for three turtle species from west-central Illinois.

Trait	<i>Terrapene carolina</i>		<i>Chrysemys picta</i>		<i>Sternotherus odoratus</i>	
	N	Mean (SD)/Range	N	Mean (SD)/Range	N	Mean (SD)/Range
Platron length	21	135(7.5)/122-151	36	153(8.9)/136-171	12	81(4.6)/74-90
Carapace length	21	132(7.5)/121-145	35	163(9.4)/143-185	13	104(3.6)/98-112
Caparace height	18	67(5.4)/58-76	35	59(4.5)/48-67	12	48(16.1)41-99
Caparace width	18	103(6.9)/92-118	35	117(8.8)/98-134	12	172(2.6)/169-176
Gravid mass	21	550(117)/350-850	34	620(94)/410-810	12	210(52)/100-275
Egg mass	21	10.31(1.12)/B.29-12.45	36	7.16(0.92)/4.81-8.62	13	4.03(0.64)/3.30-5.63
Egg width	20	21.6(0.77)/20.4-22.9	34	18.8(0.96)/16.7-20.1	13	15.6(0.76)/14.5-17.2
Egg length	20	35.9(2.18)/32.4-40.4	34	32.5(1.76)/28.4-36.5	13	26.4(1.71)/23.8-29.7
Clutch size	21	4.9(1.51)/3-9	34	8.0(1.81)/5-13	12	5.8(1.03)/4-7
Clutch mass	21	49.90(13.48)/31.11-80.10	34	57.46(14.22)/34.90-96.98	12	22.98(4.04)/17.00-30.87
Capture date	21	165.0(11.2)/141-194	36	166.0(12.4)/130-192	13	165.5(7.5)/156-181
Egg elongation	20	1.66(0.11)/1.47-1.94	34	1.73(0.09)/1.56-1.98	13	1.69(0.10)/1.54-1.86
REM	21	0.022(0.005)/0.012-0.033	32	0.013(0.002)/0.01-0.016	11	0.023(0.006)/0.016-0.041
RCM	21	0.10(0.02)/0.07-0.18	32	0.10(0.02)/0.06-0.17	11	0.13(0.04)/0.098-0.20

species. For instance, egg length and egg width were positively correlated in *Chrysemys picta* ( $\rho = 0.52, P < 0.0001$ ). Egg width ( $\rho = 0.91, P < 0.0001$ ) and egg length ( $\rho = 0.75, P < 0.0001$ ) were both positively associated with egg mass. Neither linear measure of egg size was significantly correlated with clutch size or clutch mass ( $P > 0.05$ ). Clutch size and clutch mass were also positively correlated ( $\rho = 0.80, P < 0.0001$ ), but egg mass was not significantly correlated with either clutch mass or clutch size ( $P > 0.05$ ).

Similarly, clutch size and clutch mass of *Sternotherus odoratus* were positively correlated ( $\rho = 0.78, P = 0.0027$ ), but egg mass and clutch mass were not significantly related ( $P > 0.05$ ). Both egg length ( $\rho = 0.85, P = 0.0002$ ) and egg width ( $\rho = 0.74, P = 0.0036$ ) were positively correlated with egg mass. No other comparisons were significant.

*Terrapene carolina* mirrored the other two species in having clutch size and clutch mass positively associated ( $\rho = 0.92, P < 0.0001$ ) and in having no significant correlation between egg mass and clutch mass ( $P > 0.05$ ). Again, egg width ( $\rho = 0.65, P = 0.0018$ ) and egg length ( $\rho = 0.77, P < 0.0001$ ) were both positively correlated with egg mass. Interestingly, egg length was negatively correlated with clutch size, but the association only bordered on significance ( $\rho = -0.55, P = 0.0117$ ) given the number of comparisons.

Clutch mass was positively correlated with plastron length ( $\rho = 0.52, P = 0.0018$ ), plastron height ( $\rho = 0.66, P < 0.0001$ ), and gravid mass ( $\rho = 0.61, P = 0.0002$ ) in *Chrysemys picta*. Maternal gravid mass was also positively correlated with egg mass ( $\rho = 0.52, P = 0.0016$ ), egg width ( $\rho = 0.53, P = 0.0018$ ), and egg length ( $\rho = 0.53, P = 0.0017$ ) in *C. picta*. Egg width was positively correlated with maternal plastron length ( $\rho = 0.39, P = 0.0239$ ) and maternal carapace height ( $\rho = 0.47, P = 0.0061$ ). However, the correlations were weak given the number of comparisons made.

In contrast, only egg mass was positively associated with maternal gravid mass ( $\rho = 0.87, P = 0.0003$ ) in the smaller sample of *Sternotherus odoratus*. None of the other comparisons were statistically significant. Possibly, the small sample from a narrow range of maternal sizes (see Figs. 1 and 2) did not allow relationships between maternal size and reproductive traits to be shown.

Reproductive data gathered on *Terrapene carolina* also showed few, correlations with maternal size. Clutch size was positively related to maternal plastron length ( $\rho = 0.67, P = 0.0009$ ) and to maternal gravid mass ( $\rho = 0.65, P = 0.0014$ ). Clutch size was also positively related to maternal carapace height ( $\rho = 0.62, P = 0.0063$ ) but the P-value does not exclude type I error at 0.05 given the number of comparisons. Regardless, the correlation coefficients suggest that clutch size increases as body size increases. In contrast, egg size tends to decrease with clutch size as noted above. Consistent with that observation was the finding that egg mass ( $\rho = -0.34, P = 0.13$ ) and egg length ( $\rho = -0.51, P = 0.0219$ ) but not egg width ( $\rho = 0.12, P = 0.62$ ) were negatively associated with maternal plastron length and other measures of maternal size. Although these associations were not statistically significant, they were consistent with the hypothesis that larger *Terrapene carolina* clutches tend to be laid by larger females and that eggs in those clutches tend to weigh less and be shorter in length but not width than eggs in smaller clutches of smaller females (Figs. 1 and 2).

Egg size-clutch size trade-offs were not demonstrated for any of the three species in partial correlation with the influence of plastron length held constant in the correlation of egg mass and clutch size. Coefficients were negative but not statistically significant for *Chrysemys picta* ( $\rho = -0.21, P = 0.25$ ), *Sternotherus odoratus* ( $\rho = -0.29, P = 0.4150$ ), and *Terrapene carolina* ( $\rho = -0.26, P = 0.26$ ).

Because egg mass was predictable from egg width and length, regression equations were developed for data from each species. The relationship for *Chrysemys picta* (egg mass =  $0.65^* \text{ egg width} + 0.24^* \text{ egg length} - 13.01, R^2 = 0.98$ ) was significant ( $F_{2,31} = 824.68, P < 0.0001$ ). All parameters were significantly different from 0 ( $t > 16.5, P < 0.0001$ ). The same relationship for *Sternotherus odoratus* (egg mass =  $0.48^* \text{ egg width} + 0.20^* \text{ egg length} - 8.79, R^2 = 0.97$ ) was also significant ( $F_{2,10} = 140.74, P < 0.0001$ ), and the regression parameters were also significantly different from 0 ( $t > 7.7, P < 0.0001$ ). Likewise, for *Terrapene carolina* the regression equation (egg mass =  $0.92^* \text{ egg width} + 0.37^* \text{ egg length} - 22.76, R^2 = 0.95$ ) was significant ( $F_{2,17} = 150.80, P < 0.0001$ ) and the parameters were statistically different from 0 ( $t > 11.0, P < 0.0001$ ).

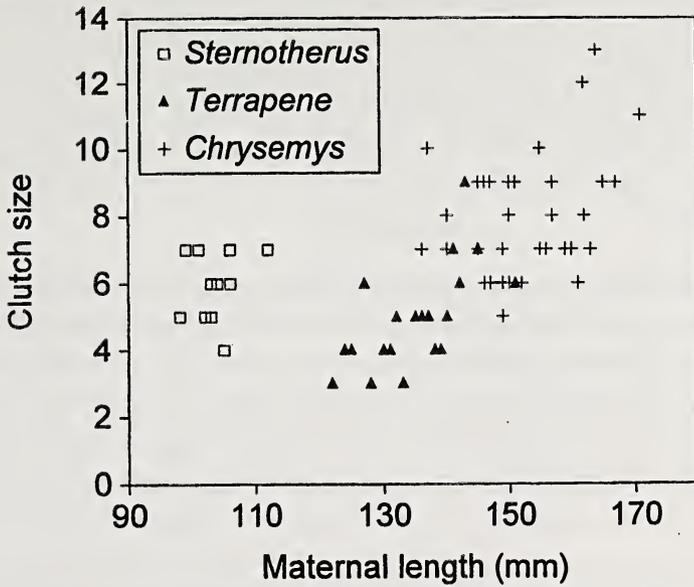


Figure 1. Egg mass as a function of maternal plastron length for *Terrapene carolina* and *Chrysemys picta* and of carapace length for *Sternotherus odoratus*.

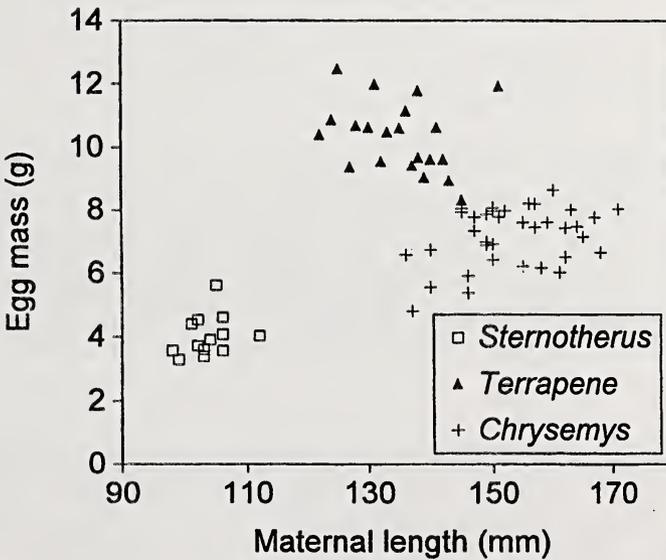


Figure 2. Clutch size as a function of maternal plastron length for *Terrapene carolina* and *Chrysemys picta* and of carapace length for *Sternotherus odoratus*.

Interspecific comparisons of egg mass independent of maternal size using ANCOVA found that LSM for egg mass of *Terrapene carolina* ( $10.37 \pm 0.21$  g) was greater ( $P < 0.0001$ ) than LSM for egg mass of *Chrysemys picta* ( $6.93 \pm 0.27$  g) and *Sternotherus odoratus* ( $4.59 \pm 0.58$  g). The latter two species also differed significantly ( $P = 0.0045$ ). Slopes for egg mass regressed on maternal size for these three species did not differ significantly ( $F_{2,63} = 3.03$ ,  $P = 0.0555$ ).

Eggs of *Terrapene carolina* were also relatively wide when the effect of maternal size was factored out with ANCOVA. Egg width LSM for *T. carolina* ( $21.8 \pm 0.19$  mm) was significantly greater ( $P < 0.0001$ ) than egg width for either *Chrysemys picta* ( $18.3 \pm 0.24$  mm) or *Sternotherus odoratus* ( $16.9 \pm 0.51$  mm). Egg width LSM for the latter two species did not differ significantly ( $P = 0.0623$ ). Slopes of egg width regressed on maternal size did not differ significantly among the three species ( $F_{2,60} = 0.41$ ,  $P = 0.6658$ ).

Slopes varied slightly but significantly among species for egg length regressed on maternal size ( $F_{2,60} = 4.73$ ,  $P = 0.0123$ ). An ANCOVA model for heterogeneous slopes was used to compare egg length among species without the effect of maternal size. All three species differed from each other. *Terrapene carolina* had the longest egg length LSM ( $35.9 \pm 0.43$  mm,  $P < 0.0001$ ), egg length LSM for *Chrysemys picta* ( $32.5 \pm 0.56$  mm) as shorter ( $P < 0.0001$ ) than *T. carolina* but longer ( $P = 0.0004$ ) than egg length LSM for *Sternotherus odoratus* ( $26.4 \pm 1.17$  mm).

Slopes for clutch size regressed on maternal size were homogeneous ( $F_{2,60} = 0.61$ ,  $P = 0.5449$ ). In this instance clutch size LSM for *Sternotherus odoratus* ( $8.8 \pm 0.94$  eggs) independent of maternal size was greater ( $P = 0.0002$ ) than clutch size LSM for *Terrapene carolina* ( $5.2 \pm 0.33$  eggs). Clutch size LSM for *Chrysemys picta* ( $6.8 \pm 0.43$  eggs) was greater ( $P = 0.0095$ ) than clutch size LSM for *T. carolina*. These relationships are particularly well shown in Fig. 2.

Slopes for clutch mass regressed on maternal size did not differ significantly ( $F_{2,60} = 0.28$ ,  $P = 0.7570$ ). Clutch mass LSM for *Sternotherus odoratus* ( $53.92 \pm 6.78$  g), for *Terrapene carolina* ( $52.98 \pm 2.39$  g), and for *Chrysemys picta* ( $43.92 \pm 3.08$  g) did not differ significantly in any pairwise t-tests.

Overall, eggs of *Terrapene carolina* were heaviest, longest, and widest when effects of maternal body size were removed. In contrast, clutch

size was smallest relative to maternal body size for *T. carolina* suggesting that egg size and clutch size are being traded-off in this interspecific comparison. *Sternotherus odoratus*, the species with the smallest body size, was the species that produced the largest clutch mass and clutch size relative to body size.

### Discussion

Congdon and Gibbons (1985) studied reproduction in a number of South Carolina turtle species including the three species that I examined from Illinois. Thus, comparisons of their findings to mine are particularly appropriate. They found that clutch size and clutch mass was positively correlated with maternal size (plastron length) except for *Terrapene carolina* (Congdon and Gibbons, 1985). My findings only agree with theirs with respect to *Chrysemys picta*. I found no relationship between maternal size and egg size in *Sternotherus odoratus*. This finding may reflect the small sample size from a limited range of maternal sizes available to me.

The differences between my findings on *Terrapene carolina* and those of Congdon and Gibbons (1985) are more important. I found a statistically significant positive relationship between clutch size and maternal size in *T. carolina*, whereas this relationship was not detected among the South Carolina *T. carolina*. Moreover, my findings suggest that larger females while laying larger clutches tend to lay lighter and shorter eggs in those clutches. Other studies of *T. carolina* (Allard, 1935) and *T. ornata* (Legler, 1960) also found the largest eggs in the smallest clutches. Reduced egg size in larger clutches that I studied appears to be due to reduction in egg length but not egg width. Judd and Rose (1989) also found that average egg length decreased with increasing clutch size in *Gopherus berlandieri*, another terrestrial turtle but one not closely related to *T. carolina*.

Consistent with optimal egg theories, egg mass was not significantly related to clutch size or clutch mass in any of the three species that I examined. Congdon and Gibbons (1985) made identical findings for South Carolina turtles of these same species. However, a significant negative partial correlation between egg mass and clutch size with maternal size as the partial variable could not be demonstrated for any of the Illinois or South Carolina turtle species. Apparently any egg size-clutch size trade-off is not strong enough to detect given the sample sizes and range of

sizes for the turtles that we each examined (Tucker et al., 1998a).

Nonetheless, large female *Terrapene carolina* from Illinois seem to be trading increased fecundity (i.e., larger clutch size) for smaller eggs and presumably smaller hatchlings (i.e., Packard et al., 1985). This is a remarkable finding given the suspected importance of supplying hatchlings with maximal energy reserves so that they can successfully cope with patchy terrestrial habitats (Wilbur and Morin, 1988; Congdon and Gibbons, 1990). Egg, and thus, hatchling size were actually smallest among the larger box turtles that I studied (Fig. 1).

My findings for these species collected in larger river habitats are consistent with previously published studies of turtles from lakes and ponds in Illinois. Mean clutch size for *Chrysemys picta* from central Illinois was 8.7 eggs in one study (Moll, 1973) and ranged between 5.89 and 9.86 for turtles studied by Tucker (1978). The mean clutch size that I observed (8 eggs) is what would be expected. Mean egg mass unadjusted for maternal body size (7.16 g) is somewhat higher among Illinois *C. picta* than means previously reported from South Carolina (6.17 g, Congdon and Gibbons, 1985), Nebraska (means ranged from 5.4 to 6.66 g, Iverson and Smith, 1993; Rowe, 1994), and Virginia (means ranged from 4.69 to 5.50 g, Mitchell, 1985, 1994).

The Illinois *Sternotherus odoratus* that I observed had larger mean clutch size (5.8 eggs) unadjusted for maternal size than reported for any other population of the species. This value exceeded mean clutch size of 4.6 eggs for northern *S. odoratus* (Tinkle, 1961). Relatively large clutch size for Illinois *S. odoratus* is consistent with the geographic trend for clutch size to increase from north to south (Tinkle, 1961; Fitch, 1985). Mean egg mass (4.03 g) for the Illinois *S. odoratus* that I studied is relatively high and compares to egg sizes for the species from South Carolina (4.04 g, Congdon and Gibbons, 1985) and Alabama (4.2 g, McPherson and Marion, 1981). Findings for Illinois turtles agree with Fitch (1985) who found no evidence of consistent north to south trends in egg size in *S. odoratus*.

Clutch size in *Terrapene carolina* is known to decrease from north to south (Fitch, 1985). Mean clutch size (4.9 eggs) for Illinois *T. carolina* was similar to mean clutch sizes reported from Washington D.C. (4.2, eggs Allard, 1935) and Virginia (4.1 eggs, Mitchell, 1994) even though these

locations are at slightly lower latitudes than the Illinois sites. Mean egg mass (10.31 g) that I observed was greater than egg mass reported for the species from South Carolina (9.02 g, Congdon and Gibbons, 1985) and from Virginia (9.8 g, Mitchell, 1994).

Although I made interspecific statistical comparisons of reproductive life-history traits, I hesitate to statistically compare the ratios that I derived (RCM, REM, and ELO). The geographic and interspecific variation in these was discussed in detail by Iverson (1992) and Iverson et al. (1993). The values I derived for the species that I studied (Table 2) are similar to those listed by Iverson (1992) and Iverson et al. (1993). I do think it is noteworthy that all three of these species lay eggs that have about the same ELO (Table 2). However, REM for *Chrysemys picta* (0.013) was considerably lower than REM for either *Terrapene carolina* (0.022) or *Sternotherus odoratus* (0.023).

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***IXODES SCAPULARIS***  
**(Acari: Ixodidae) Parasitizing**  
**Coal Skink (*Eumeces anthracinus*)**

While *Ixodes scapularis* is known from nearly 125 host species of vertebrates, with Mammalian and Avian hosts being the most common, it has only been recorded from a handful of reptilian species in Southeastern United States. Keirans, et al. (1996) felt that this phenomenon was rare or absent in the Northeast and Mid-west states where the same species of lizards occurred. Studies by Rogers (1953), Oliver, et al. (1996), Apperson, et al. (1993), Durden & Oliver (1996), and Levine, Apperson, Howard, Washburn and Braswell (1998) have shown that various species of skinks, belonging to the genus *Eumeces* and *Ophisaurus* are the most common reptilian host in the Southeast. In Florida, the ground skink (*Scincella lateralis*) has been reported as a host, along with heavy infestations also noted on Broadhead skinks (*Eumeces laticeps*). A single specimen of *E. laticeps* harbored no less than 394 immature ticks, Rogers (1953) and Apperson, et al. (1993). Eads (1949) reported an engorged nymph from a specimens of *Ophisaurus ventralis* in Texas.

In recent years *Ixodes scapularis* has been noted as a primary vector of the spirochete of Lyme Disease (*Borrelia burgdorferi*), and while examining over 300 specimens of *Eumeces anthracinus* from throughout its range four specimens of *Eumeces anthracinus pluvialis* from Arkansas and Missouri harbored larval ticks of *I. Scapularis* behind the forelimb axilla region. This number could possibly be underestimated, as I was concerned with meristic data, and little emphases was giving parasites. MPMC 20812-3 were collected from 3 mi. N. Pickens Chapel, Cleburne County, and 5 miles W. Searcy, White County, Arkansas, while MPMC 15080 was taken from 5 mi. W. Smackover, Union County, Arkansas. Another specimen UK 176549 from Carry Mt. Wildlife Management area, Ozark County, Missouri also harbored ticks. It is noteworthy that all four specimens harboring ticks were collected in the Spring, between April 3 and April 29.

This is the first record for *Eumeces anthracinus* as a host for the *Ixodidae* mentioned above.

I wish to thank Dr. J.R. Levine for verifying the identity of *Ixodes scapularis*.

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## A Major Range Extension of the Yucatecan Blind Snake, *Typhlops microstomus*, (Serpentes, Typhlopidae)

Although the blind snakes of the family Leptotyphlopidae are reasonably common in many parts of Mexico, quite the opposite is true of members of the family Typhlopidae. Concomitantly, whereas five species and 18 subspecies of *Leptotyphlops* are known from Mexico, only three species of Typhlopidae are known (Liner, 1994).

Until recently, the only typhlopoid known from the state of Veracruz was *Typhlops tenuis*, a species known only from scattered localities along Atlantic slopes from central Veracruz to Honduras, excluding the Peninsula of Yucatán (Dixon and Hendricks, 1979: 17). *Ramphotyphlops braminus* has been known for many years from Pacific slopes of Mexico, Baja California to Guerrero, and was first reported on Atlantic slopes in 1975 (Minton de Cervantes and Minton, 1975), in Querétaro, Querétaro. It was for the first time recorded from south-central Veracruz by Mendoza et al., (1993).

The third Mexican species of typhlopoid, *Typhlops microstomus*, has long been assumed to be limited to the Yucatán Peninsula, where records exist for the states of Yucatán, Quintana Roo and Campeche, as well as for Belize and Petén, Guatemala (Lee, 1996: 280). It was thus with considerable surprise that a specimen was taken by GPH shortly after a heavy rain at El Farallón (near Laguna Verde), municipality of Actopán, Veracruz, in March, 1998.

That specimen, UNAM-LT 3501, is 290 mm in total length; scale rows 18-18-18; subocular present; nasal suture complete, contacting rostral. Color pink in life; body scales immaculate, not pigmented.

The present record extends the known range of the species some 600 km northward from previous records in Campeche, and constitutes an addition to the known ophidiofauna of the state of Veracruz. All three species of the typhlopoid snakes of Mexico are now known from the state; no other state is known to harbor more than one.

Whether the apparent discontinuous distribution of the species, with a group of recorded localities in the northern part of the Yucatán Peninsula, another in the southern part of that Peninsula, and a third in central Veracruz, is a sampling artifact or a reality remains to be determined. As secretive as these snakes are they could well have a continuous distribution over the entire area.

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## External Morphological Variation in Hardy's Hooknose Snake *Ficimia hardyi* (Squamata: Colubridae)

*Ficimia hardyi* was described by Mendoza-Quijano and Smith (1993) from four specimens from the Sierra de Zacualtipán, northern Hidalgo. Three additional specimens (Hernández-Ibarra et al., submitted) are from Guadalcázar, San Luis Potosí. Those three include two adult females, one (XR 559, field number of the second and third authors) from San José de las Flores (22° 40' 46" N 100° 24' 52" W) and the other (XR 775) from El Realejo (22° 32' 55" N 100° 27' 46" W), and a hatchling male (XR 767) from San José de los Cervantes (22° 32' 55" N 100° 27' 46" W). They extended the known range of the species about 290 km to the north.

*F. hardyi* occurs in the state of Hidalgo, Mexico, along with its congeners *F. streckeri*, *F. publia* and *F. olivacea* (Hardy, 1990, Mendoza-Quijano and Smith, 1993). Only *F. streckeri* and *F. olivacea* were known from the state of San Luis Potosí (Hardy, 1975, 1990) until *F. hardyi* was reported (Hernández-Ibarra et al., submitted).

Because of the rarity of the species we here report the external morphological variation of all of its seven known specimens. In addition to data from the new material cited above, we include data on the specimens reported by Mendoza-Quijano and Smith (1993), all in the Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México (MZFC 4876-8, 5328, the first a female, all others males).

The supralabials are 7-7 except for two with 6-6, 3rd and 4th entering the orbit, 2nd and 3rd in contact with the single preocular (except for XR 767, only with the 3rd), 2nd with the prefrontal, 1st and 2nd with the nasal. Temporals 1-2, anterior contacting 5th and 6th supralabials, lower secondary the 6th and 7th. Two postoculars, lower contacting 5th and 6th supralabials. No internasals. Dorsals contacting right and left parietals 5-4 in XR 775, 5-5 in XR 559 and MZFC 5328, and 4-4 in XR 767 and MZFC 4878. Infralabials 6-7 in two, 6-6 in three, 7-? in one. Posterior chinshields separated by only one scale in two (XR 539, XR 767), by two scales in one (XR 775), but in contact in all from Hidalgo except MZFC 4878. Scale rows 17-17-17 in all except XR 559 with 17-17-16 and MZFC 5328 with 17-17-15.

Ventrals 140 in all three females, 129-136 in males. Subcaudals 33-40 in three females, 38-46 in four males. Anal divided in all except one with an entire anal (XR 775).

In XR 559 the SVL was 276 mm, tail 43.4 mm; in XR 775, 207.7 mm and 38.5 mm, and in XR 767, 100.8 and 20.4 mm, respectively. Ratios of head measurements are as follows: naris-snout length/eye-snout distance 0.889 in XR 559, 0.0778 in XR 775, 0.667 in XR 767; eye-lip distance/eye diameter 0.714 in XR 559, 0.667 in XR 767, XR 775; rostral length/width, 3.5 in XR 559, 1.4 in XR 775, 0.857 in XR 767, and 1.4 in all Hidalgo specimens except MZFC 5328 with 1.08; rostral length/rostral suture length, 0.875 in XR 559, 1.2 in XR 767, 1.75 in XR 775, 2.77 in MZFC 4876, 2.75 in MZFC 4878, and 2.0 in MZFC 4877; rostral-frontal suture length/frontal length, 1.6 in XR 559, 1.25 in XR 767, 0.364 in XR 775, 0.44 in MZFC 4877, 0.58 in MZFC 4878, and 0.22 in MZFC 5328; frontal width/frontal length 0.8 in XR 559, 0.5 in XR 767, 0.636 in XR 775, 0.823 in MZFC 4877, 0.69 in MZFC 4878, and 0.892 in MZFC 5328; interparietal suture length/frontal length 0.4 in XR 559, 1.5 in XR 767, 0.636 in XR 775, 0.855 in MZFC 4877, 0.677 in MZFC 4978, and 0.75 in MZFC 5328.

Dorsal ground color gray-brown in all specimens; transverse dark blotches on body 47 (XR 775), 49 (XR 559) and 45 (XR 767), but in specimens from Hidalgo 43 in two (MZFC 4876, 4878), 44 (MZFC 4877) and 47 (MZFC 5328); caudal blotches 15 in two (XR 775, MZFC 4878), 17 in three (XR 559, 767, MZFC 4877), 19 in one (MZFC 5328) and 22 in one (MZFC 4876). Width and length (relative to body) of 1st dorsal blotch, 8 and 3 scales respectively (XR 539), 9 and 4 (XR 767), and 7 and 4 (XR 775), whereas the length was 4 scales in all specimens from Hidalgo. The nuchal blotch is separated from the parietals by one scale row in one (XR 767), by two in three (XR 559, 775, MZFC 4878), and by four in one (MZFC 5328).

The most unexpected variation observed was the single anal scale in one specimen. Hardy (1975) recorded an undivided anal scale in only one specimen of the some 155 examined. That one exception was on the lectotype of *F. publia*, of which he saw more specimens (69) than of any other species. It is probably coincidental that *F. publia* is the closest relative of *F. hardyi*.

The new material from San Luis Potosí conforms well with the differential criteria of the species as deduced from the series from Hidalgo and discussed in Mendoza-Quijano and Smith (1993). Especially significant is agreement of the San Luis Potosí material with that from Hidalgo in having one preocular, two postoculars, no internasals, and 45-49 transverse, light-edged dark blotches on body, each blotch separated on each side by a distinct light space from a small dark spot (as in Fig. 1, Mendoza-Quijano and Smith, 1993).

The species' closest relationship remains apparently with *F. publia*. On the other hand, a number of differences between the Hidalgo and San Luis Potosí samples is apparent. There is but a slight difference in mean number of dorsal blotches (44.3 vs 47), but categorical differences in contact vs separation of the posterior chinshields, and in number of subcaudals (40-46 vs 33-38). The samples are not large enough however to justify generalizations, and the differences are not of such magnitude that further material would be unlikely to bridge them. The variation in the San Luis Potosí sample does not tend toward the variational pattern of *F. publia*; the differences from the latter are somewhat greater than in the Hidalgo sample.

All specimens from Hidalgo were collected in a habitat at 1200-1885 m dominated by xerophytic bush or maguey (*Agave*), and submontane bush (*Juniperus*), whereas the habitat where specimens were taken in San Luis Potosí at 1585-2160 m was in chaparral (*Quercus*) and grassland.

### Acknowledgments

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## Strike-induced Chemosensory Searching in the Caucasus Viper (*Vipera kaznakovi*) and the Ocellate Mountain Viper (*Vipera wagneri*)

### Abstract

Three specimens of the Ocellate Mountain Viper (*Vipera wagneri*) and one specimen of the Caucasus Viper (*V. kaznakovi*) were observed after striking rodent (*Mus musculus*) prey and after no-strike presentations of *M. musculus*. Rate of tongue flicking did not rise after no-strike presentations, but exhibited a 10-fold elevation after strikes were delivered. Hence, strike-induced chemosensory searching occurred in these snakes.

Rattlesnakes typically strike and release adult rodent prey, allowing the envenomated animal to wander from the site of attack until venom takes effect (Estep et al., 1981; Kardong, 1986; Hayes & Galusha, 1984). The snakes then exhibit searching movements coupled with a pronounced elevation in the rate of tongue flicking, collectively called strike-induced chemosensory searching (SICS), which facilitates finding and following the chemical trail left by wounded prey (Diller, 1990; Dullemeijer, 1961; Golan et al., 1982). While most recent work on SICS has concentrated on rattlesnakes, there have been a few demonstrations of its presence in non-venomous snakes (Burghardt & Chmura, 1993; Cooper, McDowell, & Raffer, 1989) and a substantial volume of work documenting similar phenomena in lizards (Cooper, 1989, 1994). The only recent paper on Old World vipers showed that SICS occurred in *Vipera ammodytes*, *V. latifii*, *V. raddei* and *V. xanthina* (Chiszar et al., 1982; see Burghardt, 1970, for a review of earlier literature on *V. aspis* and *V. berus*). Hence, it is clear that SICS is a widespread phenomenon, not confined to vipers and pit vipers, but most highly developed in these animals, especially those terrestrial species that ambush rodents using the strike-release strategy (see Halpern 1992, for a review of chemical perception in reptiles).

We now add two relatively rare species of vipers to the list of taxa exhibiting SICS. The Caucasus viper (*Vipera kaznakovi* Nikolsky, 1909) and the Ocellate Mountain viper (*V. wagneri* Nilson & Andren, 1984) are rare in the United States, with only a few zoos exhibiting them. Indeed, when we did our comparative studies of SICS in the 1980's, no specimens of either species were available in American zoos or in any of the western European zoos

with which we were in contact. Consequently, it was with great interest that we studied the present individuals at the Rio Grande Zoo.

### Method

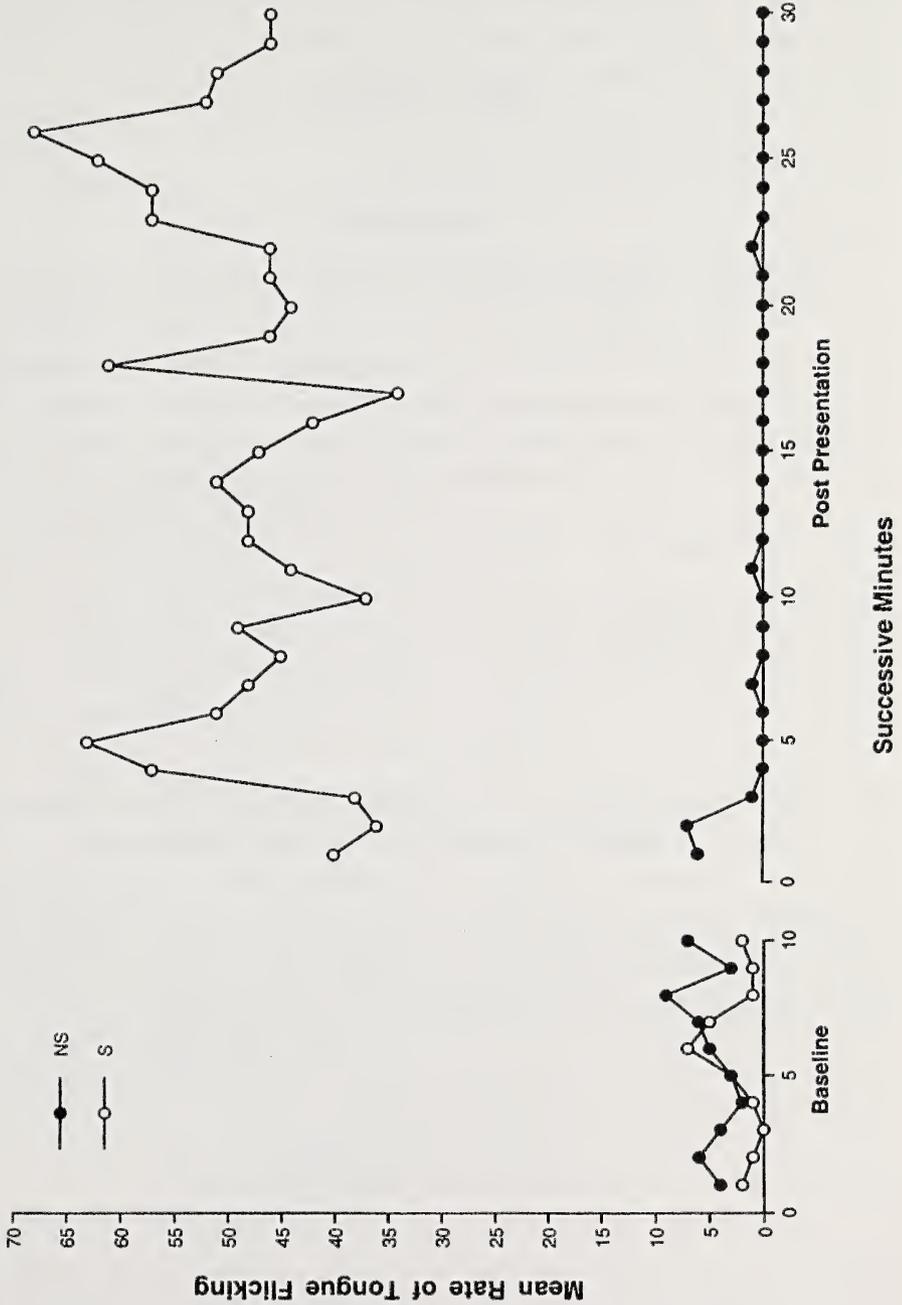
Three adult specimens of *V. wagneri* and one of *V. kaznakovi* in the collection of Rio Grande Zoo were each observed twice during April, 1994. All snakes were maintained in individual glass terraria (51 x 27 x 30 cm). Both observations involved a 10-min baseline period followed by presentation of a mouse (*Mus musculus*, 12-15g) and a 30-min post-presentation period. During each min of observation, we recorded all tongue flicks using hand-held counters. On one trial a freshly euthanized mouse was suspended by forceps into the snake's cage, but held for 3 sec just out of striking range, approximately 15 cm directly in front of the snake's face. The mouse was then removed. This was the no-strike condition (NS). The strike condition (S) was exactly like the NS procedure except that after the 3 sec suspension period, the mouse was moved into striking range. All snakes struck and released the prey, which was then removed.

Temperature was maintained at 26°C and the light cycle was 12:12, centered at noon. All snakes were long-term captives, well acclimated to their current conditions, and accustomed to a feeding schedule that offered one *M. musculus*, freshly euthanized, each fortnight. Cages contained paper substrate, ad libitum water, and a plastic hiding box. Observations were conducted when snakes were 14-days hungry.

### Results

Figure 1 presents the mean rate of tongue flicking over baseline and post-mouse-presentation periods for both NS and S observations. Baseline rates of tongue flicking were low and did not differ significantly between the NS and S trials ( $F = 0.35$ ,  $df = 1,3$ ,  $p > 0.05$ ), indicating that snakes were quiescent prior to mouse presentations. Following NS presentations, the mean rate of tongue flicking did not rise above baseline rate, and it eventually dropped to zero. After S presentations, however, the rate of tongue flicking rose considerably above the baseline rate, and it remained high during the 30 min period. The post-presentation rates of tongue flicking were, therefore, significantly different in the NS and S observations ( $F = 63.24$ ,  $df = 1,3$ ,  $p < 0.05$ ). Repeated-measures analysis of variance showed, in addition, that the interaction between baseline versus post-presenta-

Figure 1. Mean rate of tongue flicking over successive minutes following no-strike (NS) and strike (S) presentations of rodent prey.



tion x NS versus S was significant ( $F = 38.98$ ,  $df = 1,3$ ,  $p < 0.05$ ), indicating that the elevation in rate of tongue flicking beyond baseline was significantly higher after S than after NS presentations. In fact, this interaction accounted for 37% of the variance observed in this experiment. The main effect of NS versus S accounted for 28% of the variance. These two factors, therefore, explain 65% of the variance.

### Discussion

There is no question that SICS occurred in the present eastern species of the genus *Vipera*, agreeing with previous experiments involving mostly western species of that genus (Burghardt, 1970; Chiszar et al., 1982). Hence, we may be reasonably confident that SICS is characteristic of *Vipera* as it is of *Crotalus* and *Sistrurus*. Furthermore, it appears as though SICS is as well developed in *Vipera* as it is in the rattlesnakes, since the post-strike rate of tongue flicking is very high and long lasting in both groups. This leads to the interesting evolutionary issue of whether SICS developed independently in these two groups of solenoglyphs or if SICS was acquired by each through descent from a common ancestor. Our hypothesis is that the latter thought is correct, and we propose that this hypothesis can be tested by studying SICS in relatively primitive viperid genera such as *Agkistrodon*, *Azemiops*, and *Causus* (Liem et al., 1971).

While colubrid snakes and numerous species of lizards exhibit SICS-like behavior, in none of these species does the phenomenon last more than a few minutes. Accordingly, it is unreasonable to hold that *Crotalus*, *Sistrurus* and *Vipera* acquired their highly developed form of SICS directly from saurian or colubrid ancestors. Rather, we think a more likely scenario is that from a colubrid ancestor arose protovipers who evolved a more elaborate form of SICS that was retained by their subsequent descendants, including taxa that are today seen as primitive viperids as well as taxa that represent advanced viperids.

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abroad, as without their cooperation our growing database on the evolution and distribution of SICS in venomous snakes could never have been built.

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## **Amphibia and Reptilia of the high grasslands of the Sierra de Comechingones, Córdoba, Argentina.**

L. J. Avila, M. Morando and J. W. Priotto

### Abstract

Amphibian and reptile fauna of high grassland of Sierra de Comechingones Mountains, the southernmost part of Sierra de Cordoba Mountains, in central Argentina is studied. Distributional data and conservation issues about this fauna is provided.

### Introduction

The present biodiversity crisis, with its quick increase of species extinction rate and accelerated destruction of natural ecosystems, needs immediate biological inventories in such areas as contain an important biodiversity of little-known organisms. These studies are needed to give information, whether for systematic or biogeographic studies or for bio-ecological projects tending to establish proper conservationist measures or sustentable use of natural resources.

The central area of Argentina, more particularly the areas within the province-lines of San Luis and La Pampa provinces, as well as the south of Córdoba province, has a wide variety of environments with a scarcely known diversity of amphibians and reptiles. Studies of this fauna are usually limited to ecological aspects or else are restricted to small geographic areas. In the mountain and hillfoot ("serrana and periserrana") areas in southern Córdoba, the more recent herpetological list based on material deposited in collections is the one made by Martori & Aun (1994), and it is the only one that presents any information on the herpetofauna on the hillfoots of the Sierra de Comechingones; particular data may be found in the descriptions of *Liolaemus saxatilis* (Avila *et al.* 1992) and *Cnemidophorus serranus* (Cei & Martori, 1991), as well as in specific geographic or ecological records (Avila 1994, Avila & Priotto 1995a, b, c, Avila 1997, Avila & Morando 1998).

The highest segment of the Sierra Grande of Córdoba, occupied by high grasslands, called "pastizales de altura," has remained out of reach for herpetologic studies, with the single exception of Pampa de Achala, a

high mountain environment placed about 100 km. north of Sierra Grande, and considered for many years a "faunistic island" (Ringuelet 1961, Di Tada *et al.* 1980, Di Tada *et al.* 1984, Polop 1989, 1991).

The object of the present paper is to record the herpetofauna found in the high grasslands of the central area of the Sierra de Comechingones, and to contribute with some observations on the biology of the species concerned.

### Materials and methods

The survey tasks were performed between 1991 and 1996, in the working stations known as "Cerro de Oro" (1) and "Puesto Gonzalez" (2), situated 2,000 m above sea level on the Sierra de Comechingones, Río Cuarto Department, Córdoba Province, Argentina. The survey was made on these sites, on the area within 2-3 km around, and on the ingress and egress paths. The trips, each one 2 to 5 days in length, were performed during April and June (Fall) 1993, February and March (late Summer) 1994, January and February (Summer) 1995 and January 1996. During these trips, both collecting and observations were performed. Six further trips were made during the Fall and Winter from 1993 to 1994, in which only observations were made. In sundry months of the years 1991 to 1996, 8 trips one to two days in length were made to other areas of the Sierra de Comechingones, affording some sporadic survey of the following tracts: 1) Villa Larca (San Luis) - Quebrada del Tala - Alpa Corral (Córdoba), 2) Villa del Carmen (San Luis) - El Chacay (Córdoba), 3) La Cruz - Quebrada del Rayo - La Cruz (Córdoba), 4) La Cruz (Córdoba) - Cerro Aspero - Carpintería (San Luis) and 5) San Javier (Córdoba) - Champaquí - Villa Alpina (Córdoba). Each trip was undertaken by a group of two or three persons, not always the same, who made captures and observations totaling about 350 man-hours of fieldwork. This afforded data on the presence of species, hours of activity, microambients which they take up and general biological information. Representative series of all the species found were collected (except for *Mabuya dorsivittata*) and deposited in the Herpetological Collection of the Vertebrate Zoology Area (Orientación Zoología de Vertebrados), at the Departamento de Ciencias Naturales, Facultad de Ciencias Exactas, Físico-Químicas y Naturales, Universidad Nacional de Río Cuarto, Río Cuarto (Córdoba) (ZV-UNRC) and also in the Herpetological Collection of the Instituto de Herpetología, Fundación

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Miguel Lillo, Tucumán (FML).

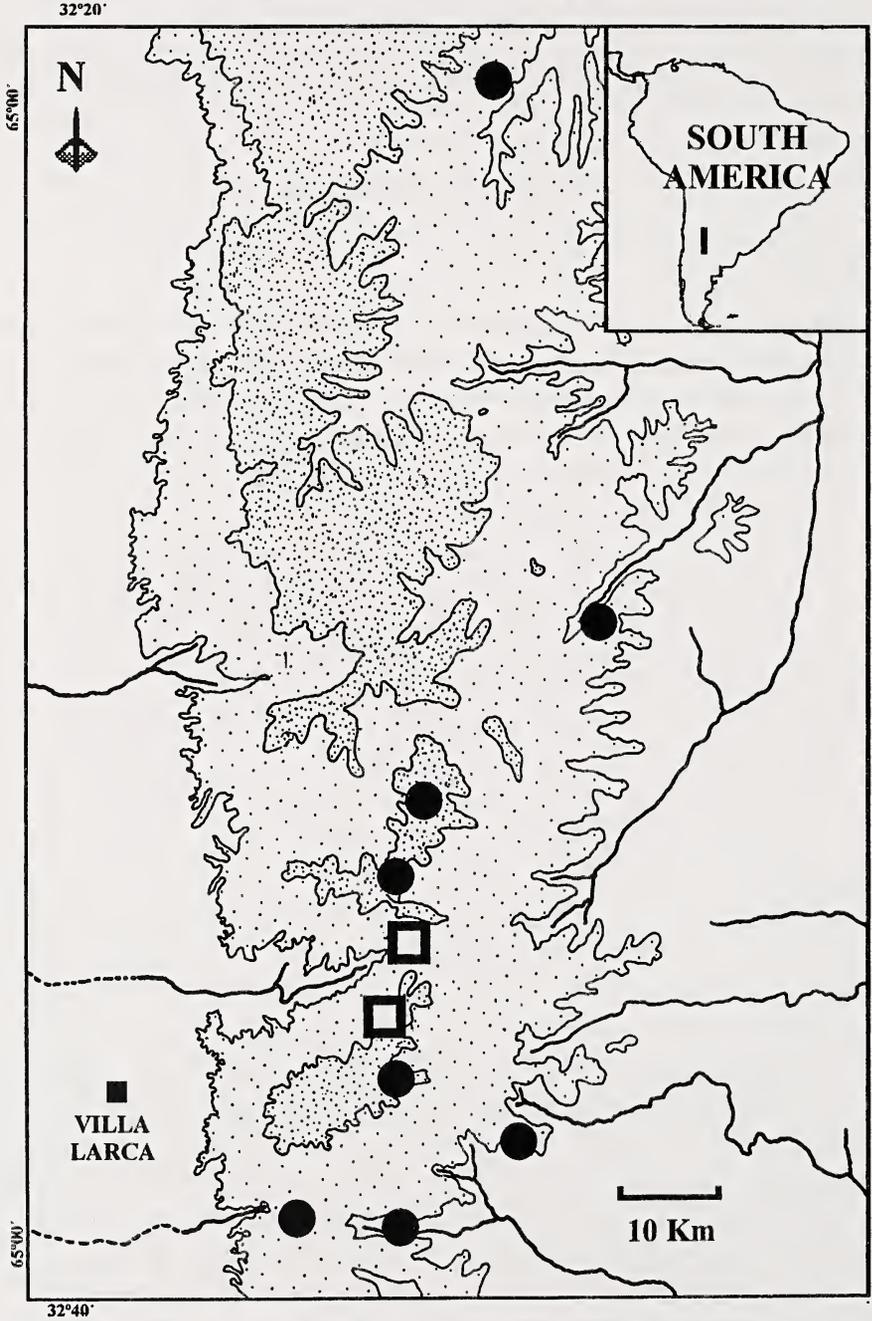
Description of the research area:

Sierra de Comechingones is the denomination given to the mountain chain south of the Cerro (Peak) Champaqui (2790 m.a.s.l.) (32°00'S, 64,58'W), in Calamuchita Department, and which runs approximately up to the locality of Achiras (Cerro La Buena Yerba, 1116 m.a.s.l.) (33°10'S, 64-59'W) in Río Cuarto Department (Map 1). Its north-south length is about 130 km and its width varies, being about 25-30 km at the research area. While the oriental slopes are relatively gentle, the occidental ones are abrupt and cliff-like.

The relief of the research area, restricted to high grasslands, is that of a high mountain plain, or "pampa de altura", remarkable for the mosaic of large rock outcrops and a soil of variable thickness which covers horizontal and depressed areas. Many streams and temporary or permanent watercourses are found all over the area, and these may swell to great spate during rainy spells.

Biogeographically, this area is comprised within the hill-lands steppes (estepas serranas) of the Hilly Chaco District (Distrito Chaqueño Serrano), Chaco Province (Provincia Chaqueña), Chaco Domain (Dominio Chaqueño) (Cabrera & Willink 1973). The physiognomy of the area is described by Bianco et al. (1987) as a Gramineae Steppe, "estepa gramínea" with predominance of "pajas" and "pastos punas", the dominant species being *Festuca hieronymi*, together with other species of the genera *Stipa* and *Aristida*. In wet spots, the so-called "lawns" ("céspedes") appear, dominating species being "sheep's weed" ("yerba de la oveja"), *Alchemilla pinnata*, *Azorella biloba*, *Eryngium agavifolium*, *Stipa flexibarbata*, and stretches of *Poa stuckerti* and *Blechnum penna-marina*. The rock outcrops are bare on parts open to wind or water, but as a rule they are densely colonized by different species of lichens or covered by *Selaginella peruviana*. In fissures, rock cracks and incipient soils, as well as on the creeks, small valleys and sheltered places, generally on slopes with a southern exposition, grow several species of ferns of the genera *Polystichum*, *Ctenopteris*, *Hymenophyllum* and *Lycopodium*, and also "tabaquillo," *Polylepis australis*, more frequent in the Occidental slopes (among those having a southern exposition). Very remarkable are the "moss mattresses" on very humid

Map I: Study area: Squares: working stations, black dots: collection sites, white area: land below 1500 m, more dense dotted: land above 2000 m, black lines: creeks or rivers, Villa Larca: nearest town to study site. South America map: black rectangle is the approximate position of Sierra de Comechingones.



and very sheltered spots, where sometimes different species of amphibians and reptiles are found. As a rule, vegetation is considerably reduced on spots accessible to cattle, and strong erosive processes are observed as a consequence of overpasturing, of grass burning and of the passing of bovine and equine cattle, which are continued by hydric and/or aeolic activity.

The climate of the research area is a cold-temperate mountain climate, with low temperatures in Winter, wide temperature range and strong winds. Maximal absolute temperatures may attain 30° C and minimal absolute may be as low as -15° C. Precipitations begin in Spring and are more abundant in Summer, and almost nonexistent in Winter, when there are only sporadic falls of snow. Mean annual precipitation is about 750 mm; mean relative humidity about 75 %; frosts have been recorded on 9-10 months out of 12. See table I for some observations of amphibians in these areas.

*Table I: Some ecological characters observed in the amphibian fauna of the high grasslands of Sierra de Comenchingones.*

*The four types of environment predominating in the study area are indicated. P = present; r = amphibians in reproductive activity. Time of activity for each species: D = diurnal, C = crepuscular, N = nocturnal. \*Only juveniles.*

SPECIES	ACTIVITY	ENVIRONMENTS			
		Rock Outcrop	Scattered Rocky stretches	Grassland Matresses	Periaquatic area
<i>O. achalensis</i>	C		P		Pr
<i>P. kriegi</i>	C	P			Pr
<i>H. pulchella</i>	DCN				Pr
<i>B. achalensis</i>	C		P		Pr
<i>M. s. steizneri</i>	D		P	Pr	
<i>P. achalensis</i>	D	P		P*	
<i>M. dorsivittata</i>	D				p
<i>L. vanzolini</i>	D				p
<i>B. ammodytoides</i>	D	P			

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## Results

Results of the survey allow to confirm the presence of 4 species of Reptilia (one Polychrotidae, one Scincidae, one Viperidae, one Colubridae) and 5 species of Amphibia (one Hylidae, two Leptodactylidae and two Bufonidae), as detailed in the following commented systematic list:

### **Class Amphibia**

#### **Order Anura**

#### **Family Leptodactylidae Wemer 1896**

*Odontophrynus achalensis* Di Tada *et al.* 1985.

Reference material: ZV-UNRC 1691 to 1695, 2377, 2988 to 2993, 3196, 3516 to 3522.

Presence detected through song and by capture of specimens in several instances. This is the most frequent amphibian species after *H. pulchella cordobae* and *B. achalensis*. Its large tadpoles are found at the bed of the shallower streams, a difference with those of *H. pulchella cordobae*, which are also found at the bed, but in deeper pools. The tadpoles *O. achalensis* also may be found in small temporary courses. Tadpoles were observed along the whole year, but in Winter they seek shelter under stones, or stay motionless in the slime of the bed of permanent streams.

*Pleurodema kriegi* (Müller 1826).

Reference material: ZV-UNRC 2981, ZV-UNRC 3514-3515.

Although its song was heard several times, specimens could be captured only in two instances. In one case, two males were taken while performing the mating song from a small artificial well, in which they floated with the help of their swollen gular sacks. The manner of egg-laying is not known with precision (Di Tada *et al.* 1980), but we agree with what these authors state, namely, that it is a mass laying on flooded areas like the "mallines", since larvae in the earlier stages of development were collected at the confluence of a "mallin" with a stream. In this case, many eggs were also observed; they formed small groups of 10-20 each and were surrounded by gelatinous filaments which adhered to the vegetation around the water. It is not possible to describe the egg-mass adequately, as the place was much altered by the trampling of bovine cattle; however, it may be stated that no evidence was found of a foam-nest, as

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supposed by Duellman & Veloso (1977).

### Family Bufonidae Gray 1825

*Bufo achalensis* Cei 1972.

Reference material: ZV-UNRC 3508 to 3513, 1696 to 1699.

This is the most abundant species after *H. pulchella cordobae*. In Spring-Summer, it shows an intense nocturnal activity and during the day it is found in large numbers under stones of small and medium size, also in cracks under the great rock outcrops and of abandoned humanmade constructions. Its activity increases after the strong Summer precipitation, and extends even to cool periods with ambient temperatures of 10°-15° C.

*Melanophryniscus cf stelzneri stelzneri* (Weyembergh 1875)

Reference material: ZV-UNRC 3194, 3523 to 3538.

This species was collected only in two opportunities, although its song was recorded in several occasions during the day. A single adult specimen was found together with one of *B. achalensis* under a small stone at a considerable distance from any permanent source of water. On another occasion, after a night of heavy rain, many individuals were observed during the day in reproductive activity. Many couples (between 10 and 20 per pool) were found in amplexus in several temporary pools not more than 10 cm deep; most of the latter had formed on small rocky ledges like miniature mesas within the "lawn" of *Alchemilla pinnata*. Several individuals were collected, together with spawn, which produced larvae inside the same container after 24 hs. In this case, more than 80 individuals were observed and the song of a large number was recorded along a transect more than 1 km long. The species appears to be abundant, but its activity is rarely observed.

This is the second species of amphibian found in sympatry with amphibian species endemic to Pampa de Achala: *B. achalensis*, *P. kriegi* and *O. achalensis*. Gallardo (1966) recorded this species for Puesto Pérez, Pampa de Achala, a record repeated by Di Tada *et al.* (1976) but not mentioned in subsequent papers (Di Tada *et al.* 1980, 1996). There is additional material from "Pampa de Achala" in the herpetological collection of the former CENAI, now deposited in the Museo Argentino de Ciencias Naturales (CENAI 3310, 3311, 10914, 10917); this material was collected after

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the record by Gallardo (1966).

The assignation of these specimens to subspecies *M. stelzneri stelzneri* is provisional, since all the collected specimens have chromatic peculiarities which place them apart from the individuals of this subspecies known up to date. A preliminary exomorphologic analysis does not show enough differences to consider the existence of diagnostic characters at this level. *M. stelzneri stelzneri* is found very frequently at lower altitudes on the Sierra (in the "romerillar" and the mountain woods) and also in the high grasslands at the southern end of Comechingones. Its dorsal coloring is dark or even black, with yellow dots placed towards the sides and rarely coalescent; there are small yellow points on the extremities and the ventral coloring is black with red dots on the belly and the femora, and with red feet and hands. In the case of *M. cf stelzneri stelzneri*, the black dorsal coloring is reduced to the middle of the body, yellow coloring predominating towards the sides and extending to the middle part of the head and to the sides of this. The extremities are also yellow with black spots. In ventral view, the black coloring is reduced to the gular area, and the red extends over the whole underside, body and extremities.

At a lower altitude, close to the village of Alpa Corral, three specimens with chromatic characters very similar to those of the high grassland steppe were found, (ZV-UNRC 3832 to 3834). An important point we must stress is that individuals presenting as well coloring patterns similar to those of specimens from high grasslands were collected on the way to Intihuasi ("camino a Intihuasi"), Carolina, Coronel Pringles Department, in the middle of the Sierra de San Luis. These specimens are deposited at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN 35404 to 35420).

More to the south, in an area at a lower altitude situated about 10 Km west of Villa El Chacay, on the peak of the mountain range and on the high grassland immediately adjacent to it, the collected material is similar in coloring to the description of *M. stelzneri stelzneri* (ZV-UNRC 3595 to 3602). At a short distance from this locality, a diurnal mass migration of adults was once observed, a fact not recorded in the literature on this species.

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**Family Hylidae Gray 1825 (1815)**

*Hyla pulchella cordobae* Barrio 1965.

Reference Material: ZV-UNRC 2978 to 2980, 2450 to 2452, 2374 and 2375, 2376, 2037 to 2039, 3319-3320.

This is the species more widespread in the whole area; it was recorded in all the trips and it shows a relatively intense diurnal and nocturnal activity. Its tadpoles, of considerable size, are very frequent in the deep pools of the streams during the whole year. Adult activity was registered, also along the whole year, except in July (mid-winter). In one case, in May (Fall), three adults were observed moving among periaquatic vegetation, with temperature under 0°C., from which it may be inferred that low temperatures do not affect wholly the activity of this species. Its presence was not recorded for the season of the great winter snowfalls, a time where it seeks refuge among the cracks of the stones around the streams or among aquatic vegetation and the streambed stones.

**Class Reptilia**  
**Order Squamata**  
**Suborder Lacertilia**  
**Family Polichrotidae**

*Pristidactylus achalensis* (Gallardo, 1964).

Reference material: ZV-UNRC 2414 to 2416, 2976, 2977.

The species was observed in several opportunities, but reference specimens were not always taken, since nothing indicates a high population density. It is a saxicolous lizard, and on the high grassland steppe the availability of rocky stretches with cracks and large rocky blocks for shelter is not homogeneous.

Until a little time ago, this species was considered endemic to Pampa de Achala, but some records outside the area were given by Cabrera and Bee de Speroni (1984) based on material from the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia": one specimen collected at Mina Clavero, San Alberto Department, and two paratypes (MACN 7877 and 7878) from La Paz, San Javier Department. These specimens correspond, almost certainly, to captures made at the level of the villages mentioned, but on the Sierra Grande, and not near the said villages. Tiranti

(com. pers.) found this species at the level of Merlo, Junin Department, San Luis Province, on the western skirts of the Sierra de Comechingones. The most southern record for this species is the one by Avila (1994). Searching 30 km to the South of this place, at the level of Villa El Chacay, did not yield any specimen of this species, and given the physiography of the area it appears quite dubious that it may be found there; however, there are some mentions of green lizards ("lagartos verdes"), some 10 km to the South of the Cerro de Oro (1), at the level of San Bartolomé.

In the analyzed area, individuals of this species have always been found performing heliothermic heating on large rock outcrops, where they have hiding cracks at their disposal. Only on two opportunities have juveniles been observed in grassland environments, in which burrows excavated into the soil are used as shelter. Although no quantitative records have been made of population density, their abundance appears to be much lower than that observed at Pampa de Achala.

#### Family Scincidae

#### *Mabuya dorsivittata* Cope, 1862.

A single individual, which could not be captured, was observed.

#### Suborder Serpentes

#### Family Colubridae

*Liophis vanzolini* Dixon 1985.

Reference material: FML 02738.

A single specimen was taken 2 km north of the "puesto Gonzalez" (2). According to the local settlers, and to observations of some colleagues (Cantero com. pers.), this species is common in "mallín" areas and among the vegetation along the water courses, but in all the campaigns a single specimen was observed and taken among the periaquatic vegetation.

#### Family Crotalidae

*Bothrops ammodytoides* Leybold 1873.

Reference material: ZV-UNRC 1498.

A single specimen was taken on a rocky stretch surrounded by high grassland. Di Tada *et al.* (1980) consider that this species is "marginal" for

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the formation called "pampa de altura", since, as they point out, the species is found in gorges and peripheral grassland around Pampa de Achala; however, the reference specimen was found in a well-characterized high grassland steppe ("pampa de altura") area.

Comments on the sympatry among "achaleña" and plain species.

Sympatry between altitude species and others which are not typical of the analyzed area, such as *M. dorsivittata* and *Liophis vanzolini*, and most specially the population of *Melanophryniscus* which differs considerably in colouring pattern from the typical specimens of the species *M. stelzneri stelzneri*, present an interesting point. More detailed studies may possibly confirm the presence of *Leptodactylus ocellatus*, a species which was taken, but not collected, at the same place where the presence of *Odontophrynus achalensis* was recorded. This place is the Quebrada del Tala, a gorge separating two mesa-like formations at the level of Alpa Corral (in the west of Córdoba Province), and it shows alteration from pine plantations, because of which it cannot be said to be a characteristic high grassland site. Both *L. ocellatus* and *Bufo arenarum* were found at the Quebrada del Río Seco, one of the access paths to the sampling sites coming by the western skirts, up to some 1,000 m of altitude. Another Leptodactylid species observed on several opportunities in areas near to the high grassland steppe environments, *Leptodactylus gracilis*, was not observed in sympatry with the species from Pampa de Achala, but the possibility of its occurrence cannot be discarded, since it was found in environments quite similar to high grasslands in gorges up to 1,500 m of altitude.

Considerations on the conservation problems of the herpetofauna in the Sierra de Comechingones.

The populations of Amphibia are in a frank decline in many parts of the world, and in some of these they have reached the extinction point; in many cases, this decline is related to obvious modification or destruction of habitats, but in other cases, the causes are still little known (Wake 1991). Sierra de Comechingones has seen human activity since many years ago, with agriculture, cattle-rearing and mining. Some 40 years ago, human presence was greater than nowadays, with many "puestos" where subsistence agriculture was undertaken and low-scale cattle production centered mainly on sheep and goats. A quantification of the effects that this

presence may have had on the native animal populations is difficult to make, since no ancient recordings are available, but we can submit a few considerations about the present and future situations. Cattle exploitation shows a much larger number of bovines than in the past, and in some areas great inversions are being made to fence fields with a view to increase the number of heads of cattle. This increase is due to the fact that the present economic situation has caused many of the small producers to disappear and the large properties must try to maximize their production to obtain an adequate gain. The effect of bovine cattle on hillside areas with delicate soil is studied in several regions of the world and it is known to cause important alterations, among which erosion may be one of the more evidents and dangerous ones.

In the studied area, it was observed that the continued trampling of bovine and equine cattle produces tracks on the slopes and sloping flats, and with the passing of time these, with the action of rain, thaw and winds, turn into large ravines. The material carried away by rain increases turbidity of the water courses where many amphibians are reared, a situation which may extend over several days, and the effects of which on the development of larvae is not quite clear. However, it is known that turbidity in water produces the disappearance of many species of fishes; therefore, it is possible that the same may happen with tadpoles. On the other hand, cattle usually comes to drink at places which are also easily accessible for some species of Amphibians at their reproduction time. This causes death of both adults and tadpoles by trampling, destruction of spawn and also of the vegetation and even of the microambients used as reproduction sites. On several occasions, specimens of *Bufo achalensis* and *Odontophrynus achalensis* were observed trampled to death in pools and stream-margins.

In the past few years, the two provinces which share the Sierra de Comechingones, supported by several Government entities, have been making efforts to enlarge the goat rearing, which is an additional menace for the conservation of this fauna. Indeed, this is quite alarming, as the negative effects of goat pasturing on natural ecosystems are well known and proven the whole world round, and in particular on relatively fragile systems, such as islands and also semidesertic and mountain areas.

The reproduction sites of Amphibia in the streams also are threat-

ened by mining, which usually employs stream water at some point of the process of extraction and returns it directly to the course after use, heavily charged with contaminating sediments, thus causing death of aquatic and periaquatic plants of the invertebrate fauna and of the tadpoles. Also, access to heights is easier along water-courses; therefore, the margins of the latter are chosen to build roads and to deposit residue from the exploitation. This, on addition, produces an important destruction by hydric erosion, particularly in the gorges of the western areas, which run along more abrupt slopes. Fortunately, in the few last years no increase of mining activities has been observed on the highest areas of the high grasslands where the herpetozoa populations are more numerous; for this reason, mining is not considered an immediate danger for these populations. Most of the high altitude mines, in fact, have been abandoned, and these are the ones which used to cause appreciable damage to many altitude streams.

In several regions, a forestation project with exotic conifers has been implemented, together with important plans for promotion and expansion. As it is well known, conifers produce great unbalancing of the soil pH, which turns acid, and afterwards by rainwater washing the alteration is carried to the streams, which usually lose their natural fauna. The sole amphibian species found in streams around these artificial woods is *Hyla pulchella cordobae*, but in the streams within the woods no species of amphibian is found.

Another additional danger is the introduction of the trout (*Oncorhynchus sp.*), an exotic species which usually eliminates from streams all the autochthonous amphibians and fishes. In several streams in the basins of the rivers Calamuchita, Chocancharagua and the closed basins between the last and the river Popopis, trout were released a few years ago and many native species eliminated. It is possible that the upper basins of the local streams, taken up by high grassland, may be safe from their presence because of the small quantity of water which they carry during most of the year and of the abruptness of the streambed slope, but this cannot be predicted at the present moment. However, in mountain areas of San Juan Province (El Pachón), it was observed that specimens of trout manage to enter streams with a very low water-level and with abrupt sloping of the streambed.

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### Discussion

The studied area shelters an herpetofauna of little variety, but very interesting by the presence of species considered endemic to Pampa de Achala until a little ago. The finding in this area of these species of Amphibia and Reptilia, together with several species of birds, mammals (Priotto *et al.*, 1996) and invertebrates, also known previously from Pampa de Achala alone, allows the reconsideration of the character of "faunistic island" frequently assigned to the last, and sustained only by the lack of sampling or observing in adjacent areas.

It is important to try to obtain measures for the protection of the species of Amphibia and Reptilia in high grassland areas. The still incomplete knowledge of their biological characters, their importance from the biogeographic and evolutive point of view, their distribution, restricted to central mountain areas of Argentina and the fragility of the environments in which they are found, all these make the said species deserve to be taken into account in future conservation politics. In a recent paper, Avila and Acosta (1996) consider that at least one of the saurian species, *Pristidactylus achalensis*, and four of the Amphibian species, *Bufo achalensis*, *Odontophrynus achalensis*, *Pleurodema kriegi* and *Melanophryniscus stelzneri stelzneri*, must be considered of maximal priority for conservation, and that *Hyla pulchella cordobae* should be considered with special attention. It is probable that *Liophis vanzolini* may be inside the same category that the first species, in view of its limited distribution, but up to now no study has been made about this species of serpent. The chromatic particularity of the population of *Melanophryniscus* may perhaps reflect a different evolutive history from the rest of the mountain populations, such as may justify its nomination as a new species, which would enhance the importance of the area for conservationist measures.

A very important protection measure would be to exclude from this area the projects of mining and farm exploiting which are encouraged and/or which may be initiated in future, and that protected areas, such as those already established more to the North, at Quebrada del Condorito and Pampa de Achala, are created. Due to the biogeographic and ecological importance of the area, and to the fact that this is the capturing and regulating basin of the waters of a vast area in the south of Córdoba province, these measures and other conservationist policies should be

implemented in a brief space of time to aim at a sustentable use of our biotical wealth.

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**Removal of an Evolutionarily-Reduced Color Signal, and Restoration of the Signal to the Ancestral State, Influence Male-Male Interactions in the Striped Plateau Lizard, *Sceloporus virgatus***

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Abstract

Male *Sceloporus* lizards vary tremendously in the intensity and coverage of blue belly and throat coloration. In the striped plateau lizard, *S. virgatus*, the amount and intensity of blue coloration have been greatly reduced during evolutionary history to only two small, pale throat patches and, in some individuals, a few pale blue belly scales. I examined the influence of male coloration on male-male interactions and female choice in *S. virgatus*. Using paint to manipulate male color, I enhanced the amount and brightness of blue throat and belly coloration to restore the evolutionarily-reduced coloration to the ancestral state. In another experiment, I covered the naturally-occurring blue throat coloration. The presence or absence of blue coloration had no discernible effect on female choice, but I found an influence of coloration on male-male interactions. Resident males tended to win contests against intruders with restored levels of blue belly and throat coloration only when residents were larger than the intruders, suggesting a possible advantage of the restored color for larger intruders but not for smaller intruders. In the presence of a female, males with natural levels of blue coloration tended to exhibit social dominance over males lacking coloration and to lose less weight than males lacking normal levels of throat coloration. In *S. virgatus* the vestigial expression of the suspected sexual signal coexists with no apparent female response but a weak male response to the coloration.

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### Introduction

Darwin (1871) proposed two primary mechanisms by which sexual selection can cause the elaboration of display traits in males: male-male contests for access to females and female choice of mates. Although the mechanism of female choice was not widely accepted at first, current theoretical and empirical research in sexual selection strongly emphasizes the intersexual mode over the intrasexual mode. Many models for the evolution of sexually dimorphic traits are based on female response to male traits (reviews in Kirkpatrick and Ryan, 1991; Andersson, 1994; Møller, 1994; Holland and Rice, 1998). Recently, particular attention has focused on the sensory response of females to male signals (Endler and Basolo, 1998; Ryan, 1998). Sexual selection models based on male response to the traits of other males are far less common (review in Møller, 1994), but male traits under sexual selection can evolve simultaneously as signals for attracting mates and repelling rival males by signalling status (Morris and Ryan, 1996). Studies of within-genus or within-species variation in the coevolution of a male display signal, the female response to the signal, and the male response to the signal are important for evaluating models of secondary sexual character evolution. A few authors have examined the influence of male display signals on both male and female receivers of the signal, using closely related species (or different populations of the same species) exhibiting variation in the male trait (McKinnon, 1995; McKinnon and McPhail, 1996; Morris and Ryan, 1996). More studies of male and female response to male signals are needed, particularly in taxa for which the phylogenetic history is known.

Male lizards of many species have bright coloration, often most vivid during the breeding season (Regamey, 1935; Harris, 1964; Werner, 1978; Schall, 1986; Losos and Chu, 1988; Cooper and Vitt, 1993; Mouton and van Wyk, 1993; Dearing and Schall, 1994; Mori and Hikida, 1994; Galán, 1995). The coloration may aid in species recognition (Losos, 1985) or sex identification (Vinegar, 1972; Cooper and Burns, 1987). In many species variation in male coloration is associated with variation in male reproductive, territorial, or aggressive behavior (Hover, 1985; Madsen and Loman, 1987; Rand, 1991; Thompson and Moore, 1992; Díaz, 1993; Ellingson, 1994; Olsson, 1994a; Carpenter, 1995; Sinervo and Lively, 1996; Baird et al., 1997; Molina-Borja et al., 1998), suggesting a high potential for intrasexual selection on coloration.

Female choice based on male color or other morphological traits has rarely been documented in lizards (reviews in Tokarz, 1995; Olsson and Madsen, 1998). Experiments found no evidence for female mate preference based on male coloration in *Lacerta agilis* (Olsson and Madsen, 1995) or *Eumeces laticeps* (Cooper and Vitt, 1993). When establishing home ranges, female lizards may be more influenced by the distribution of food or other resources than by the distribution of males (Hews, 1993). Only three studies suggest female mate choice based on male color in lizards (Sigmund, 1983; Ellingson, 1994; Baird et al., 1997).

The degree of sexual dichromatism may be associated with the intensity of aggression in some lizards. In Texas populations with strong sexual dichromatism, *Uta stansburiana* lizards of both sexes were highly territorial and aggressive; in Colorado populations with little sexual dichromatism, within-sex home range overlap was extensive and aggressive behavior was rare or non-existent (Tinkle and Woodward, 1967). Comparative studies involving a larger number of taxa would allow evaluation of the co-evolution of aggressive behavior with sexually dimorphic morphological traits.

The lizard genus *Sceloporus* is especially suitable for comparative work on the evolution of sexually dimorphic behavioral and morphological traits and on the response of males and females to those traits. The phylogeny has been well-studied (Wiens and Reeder, 1997), and males of various species differ greatly in the amount and intensity of blue coloration on the belly and throat. Within one subgroup of the genus, for example, the amount of blue ventral coloration ranges from none (*S. exsul*, Dixon et al., 1972) or almost none (a few pale blue belly scales in some individuals, and two small, pale throat patches; *S. virgatus*, Cole, 1963; A. J. Abell, pers. obs.) to bright blue on almost the entire ventral surface (*S. occidentalis taylori*, Camp, 1916). Much of the variation in blue coloration is due to repeated losses of the trait in various lineages, including the lineage of *S. exsul* and *S. virgatus* (Wiens, 1999). The ventral coloration is exposed during aggressive and courtship displays to other individuals (Carpenter, 1978). It is widely believed that the blue coloration functions primarily in aggressive displays (Cooper and Burns, 1987). For *S. undulatus*, Noble (1934) wrote that "the bright colors of the male fence lizard are employed to bluff possible rivals into withdrawing from a fight. The adornment of the male is not wedding finery but a gladiator's vestment." Male

courtship and male-male display behavior is qualitatively similar across species with varying levels of blue ventral coloration (Carpenter, 1978; Fitzgerald, 1982), but variation in color may correlate with variation in the intensity of behavior. Comparing *S. virgatus*, *S. undulatus consobrinus*, and *S. undulatus tristichus*, Vinegar (1975) found the highest levels of male aggressive behavior in the most sexually dichromatic form (*S. u. consobrinus*). The extent of male-male home range overlap reported for *S. virgatus* (74%; Abell, 1999) is considerably higher than for any other *Sceloporus* species (49%, Tanner and Hopkin, 1972; 52%, Ferner, 1974; 33%, Ruby, 1978; 27%, Jones and Droge, 1980; 53%, Ruby and Baird, 1994), possibly indicating reduced levels of male territorial defense in this species with greatly reduced ventral coloration.

Despite the prominence of the blue ventral coloration in many *Sceloporus* species and the belief that it has an important role in male contest, there have been only three studies of sexual selection on male coloration, all considering natural variation in coloration relative to behavior of males in the field. Rand (1991) found that males of *S. undulatus erythrocheilus* with a certain color pattern are socially dominant over other males and spend relatively more time in proximity to females. However, Rand focused on a chin color polymorphism (orange or yellow) rather than the blue ventral coloration. In *S. jarrovi*, Dixon (1993) found no direct sexual selection on blue color traits of males, apart from the correlation of these traits with aspects of male body size under selection. In *S. virgatus*, Abell (1998) found no sexual selection on male throat coloration.

To experimentally examine the correlation between male ventral coloration and the behavioral response of males and females to the coloration, I used protocols and sample sizes similar to those in other recent experimental studies of male secondary sexual traits (Thompson and Moore, 1991; Cooper and Vitt, 1993; Ellingson, 1994; Olsson, 1994a; Morris and Ryan, 1996). Males of *S. virgatus* have retained stereotyped behavioral displays similar to those of more colorful congenics, though these postural displays expose areas of the body that have little or no coloration compared to the extensive bright blue patches of most other species. I predicted that males would likewise retain a behavioral response to the experimentally manipulated coloration of other males, both to restoration of the faint coloration to the large and bright patches typical of close relatives, as well as to the removal of the faint patches normally present.

In addition to behavioral responses, I measured seasonal weight change of males as a possible indicator of longer-term dominance relationships. Males of many squamate species, including *S. virgatus*, lose weight during the breeding season (Nagy, 1983; Merker and Nagy, 1984; Baron et al., 1996; Saint Girons, 1996; Olsson et al., 1997). The amount of weight loss can vary with the level of aggressive behavior (Marler and Moore, 1988). If the color of his opponent causes a male of *S. virgatus* to vary his level of aggressive behavior or his response to the behavior of other lizards, then the degree of weight loss could vary according to male color.

Previous experimental work on male response to the badges or ornaments of other males has generally enhanced or reduced a trait already present in the population, either within or outside the range typical of the population (Rohwer, 1985; Marchetti, 1993; Omland, 1996; Qvarnström, 1997). Restoration of a lost or reduced signal to the level typical of the ancestral state, as I did with one of the experiments reported here, is much less common. In a population of *Anolis carolinensis* lizards that has lost the usual red dewlaps, Christman (1980) reported that grey-throated male anoles responded in the same way to grey-throated and red-throated males, but no quantitative details were provided.

## Methods

### **General Experimental Protocols**

During the spring breeding season, body size has a bimodal distribution in both sexes of *S. virgatus*, with the smaller lizards experiencing their first potential breeding season after hatching and the larger lizards in at least their second potential breeding season (Abell, 1998). All lizards in this study were from the large side of the bimodal size distribution. I captured all experimental males in April and housed them in individual terraria until I set up the experiments. I conducted all experiments during the breeding season, around the time of peak courtship and mating activity (Rose, 1981; pers. obs.).

I extended the range of variation in coloration by painting lizards (Noble, 1934; Cooper and Burns, 1987; Thompson and Moore, 1991). In one experiment (1992) I supplemented the natural level of blue to restore *S. virgatus* to the ancestral levels of bright throat and belly coloration. In another experiments (1994) I covered the little blue that males normally

have. I tested the effect of the restored blue coloration on male-male interactions and the effect of removal of natural blue on male-male interactions and female choice. In the restored color experiment, I presented tethered intruder males (restored or normal color) to resident males in the field (Noble, 1934; Vinegar, 1972; Cooper and Burns, 1987; Thompson and Moore, 1992). In the color removal experiments, I established pairs of males in large outdoor enclosures (Carpenter, 1995; Zucker and Murray, 1996) with an adult female present. I observed interactions between normally-colored and uncolored males and the response of the females to the males. Social relationships that can persist over relatively long periods of time are an important determinant of mating success in males of *S. virgatus* (Abell, 1997), suggesting that response to male color over a period of several days to weeks may be important in this species. For the enclosure experiments, I measured the long-term behavioral response and weight change of receiver individuals to the experimentally-manipulated color signal over at least several days, as well as the initial short-term response.

To manipulate the throat color of males, I used flexible fabric paint (Deka brand) blended to match either the pale blue coloration of an average male *S. virgatus*, the brighter blue coloration of the closely related *S. undulatus consobrinus*, or the off-white background coloration. All paint treatments lasted for the duration of the experiments. In the tethered intruder experiments, I painted some males with bright blue paint (brighter than the normal throat color of *S. virgatus*) on the belly as well as the throat. These males, which I will refer to as Super Blue, resembled males of *S. undulatus consobrinus* in the intensity and coverage of ventral coloration. Populations of *S. undulatus consobrinus* are located within a few kilometers of the study population of *S. virgatus*, but the study population is not part of a contact zone. The Super Blue males did not resemble any species of phrynosomatid lizard found sympatrically with the study population (*S. jarrovi*, *S. clarki*, or *Urosaurus ornatus*). The control treatment (Blue) for the Super Blue males resembled normal *S. virgatus* males, with light-blue paint on the throat and off-white paint on the belly. Clear paint (instead of blue and off-white) was not used for the controls because all available clear paints had strong chemical odors unlike the faint smell of the non-toxic fabric paint. In the enclosure experiments, I painted one male in each pair with white paint to cover the natural blue throat patches. As a control, I painted the other male with pale blue on the natural blue throat

patches. The control males looked the same as they did before I applied the paint. I will refer to these paint treatments as White and Blue, respectively.

Because lizards are sensitive to different parts of the light spectrum than humans (Fleishman et al., 1993), one might ask whether these paint treatments truly mimic blue versus white coloration, from the perspective of a lizard. Other studies using similar paints have shown that *S. virgatus* and the closely related species *S. undulatus* made mistakes in sex recognition when stimulus animals were painted to resemble the opposite sex (Vinegar, 1972; Cooper and Burns, 1987), suggesting that my paint treatments are a reasonable means of manipulating lizard coloration. Also, the patterns reported here mirror those I found in unstaged encounters with *S. virgatus* males varying in natural levels of blue throat coloration (Abell, submitted ms), suggesting that my experimental results are not an artifact of the paint treatment.

#### **Male Contest, Normal Blue and Super Blue Tethered Intruders**

On 10 May 1992 I applied the Blue and Super Blue paint treatments to six stimulus males, which I used as intruders in tethered encounters. For comparison of body size among individuals, I used individual growth rates obtained from repeated measurements (Abell 1998) to estimate the snout-vent length (SVL) of all residents and intruders on a standard day (31 May). The resident population is the same one described in Abell (1998). I chose 12 resident males in this population and presented them with the tethered intruders. I staged tethered encounters during the mating season, from 11 May through 30 May, between about 0930 hr to 1600 hr (excluding the hot midday period around 1200 hr to 1330 hr).

Male traits other than coloration that can influence the outcome of dominance interactions include body size, familiarity with the opponent, and prior experience as a winner or loser (Olsson, 1992, 1994b; Carpenter, 1995; Zucker and Murray, 1996). I controlled for the possible effect of body size by presenting residents with the same intruder twice, once with the intruder painted Blue and once with the same intruder painted Super Blue. The time from one encounter to the next encounter for a given pair ranged from two to 15 days (mean  $6.1 \pm 4.7$  days). I determined which intruder treatment (Blue or Super Blue) a resident received first by flip-

ping a coin. In seven of the 12 paired encounters, the resident met the Blue male first and in the remaining five paired encounters he met the Super Blue male first. In these experiments, the order of presentation did not influence the outcome of the interaction.

During the tethered introductions, I tied the intruder male to the end of a long, thin bamboo pole with heavy thread. The intruder was allowed about 50-70 cm of slack at the end of the tether. Preliminary observations suggested that a strong intrusion (introduction at a close distance) was necessary to reliably elicit a response from the resident, so during the experimental trials I placed the tethered male about 10-30 cm from the resident male, with the long axis of the intruder facing towards the resident. I watched the interaction until one individual retreated from the other (indicated by movement away from the other, usually accompanied by an attempt to seek cover) or for 15 minutes. I noted which individual retreated.

To evaluate the possible influence of both blue color and the size difference between opponents on the aggressive response of the resident, I examined the overall outcome of the trial, as indicated by one of the individuals retreating from the other. Most natural (unstaged) encounters between males of *S. virgatus* involved males differing in body size (Abell, submitted ms), so it is reasonable to examine whether the size difference varied according to the outcome of the trial. For cases where the resident performed better against one color treatment than against the other, I used the t-test to compare the size difference between resident and intruder.

### **Male Contest and Female Choice, White and Normal Blue Males in Enclosures**

For these studies, I chose to examine male-male interactions in the presence of a female. Similar experiments using only a basking site as a resource resulted in extremely low rates of male-male interactions (Abell, unpubl. data), suggesting that the presence of a female was necessary to stimulate male-male behavior in enclosure experiments.

Each outdoor enclosure measured 1.3-1.5 m<sup>2</sup> and was paired with an adjoining space of the same size. Enclosures were considerably smaller than breeding season home range sizes (average 363 m<sup>2</sup>; Abell, 1999) but

were exposed to natural temperature and light conditions and were large enough to allow the expression of courtship behavior and mating (pers. obs.) Each enclosure was furnished with a single cinder block for a perch, and lizards were provided *ad libitum* vitamin-dusted mealworms and waxworms to supplement naturally-occurring insects.

In late April 1994 I established 20 males in the outdoor enclosures. Each enclosure was connected to another of the same size by two doors (one 7.6 cm long and the other 30.5 cm long), kept closed until females were introduced. I matched males in connecting enclosures for tail breakage status and tail length (within a few mm), for SVL (within 1 mm), and for body weight (within 1.1 g; weight difference > 0.4 g for only one pair, established about a week after the others to replace a previously established pair). Males were allowed more than a week to acclimate to the outdoor enclosures. I applied the Blue and White paint treatments on 7 May, using a coin toss to determine which male in a pair would get the control treatment (Blue) and which would receive the experimental treatment (White).

I captured females in early April (13-17 April), prior to the usual onset of courtship in this population, and housed them temporarily in outdoor enclosures with other females. Because female throat color (blue, orange, or mixed) may signal reproductive state (Vinegar, 1972; Weiss et al., 1997), I recorded throat color of females at the time of introduction. I introduced females to males from 8-15 May, with one or two introductions per afternoon. On the day of introduction, I lifted the doors between adjacent males and placed a female in the smaller doorway. I watched enclosures carefully for one hour after the introduction of the female for any instances of courtship or aggressive behavior. I recorded the following male behaviors: approaching the other male (walking or running), head bobbing, and moving away from the other male (walking or running). I also rated the maximal level of aggression of each male according to the ranking system of Moore (1987): 0 = no response, 1 = head bobs or push ups not accompanied by approach, 2 = fullshow with no approach, 3 = shudder with no approach, 4 = approach, 5 = faceoff, 6 = charge or bite. On every subsequent day through 3 June, I scanned enclosures once or twice a day for five minutes each (at approximately 0930 h and 1330 h) to detect the possible presence of aggressive interactions, basking part-

nerships (Abell, 1997) or courtship behavior. I tested for an effect of male color treatment on female response to males and on the initial and long-term interactions between males. I weighed males again at the conclusion of the experiment and compared the rate of weight change of Blue and White males.

## Results

### **Normal Blue and Super Blue Tethered Intruders**

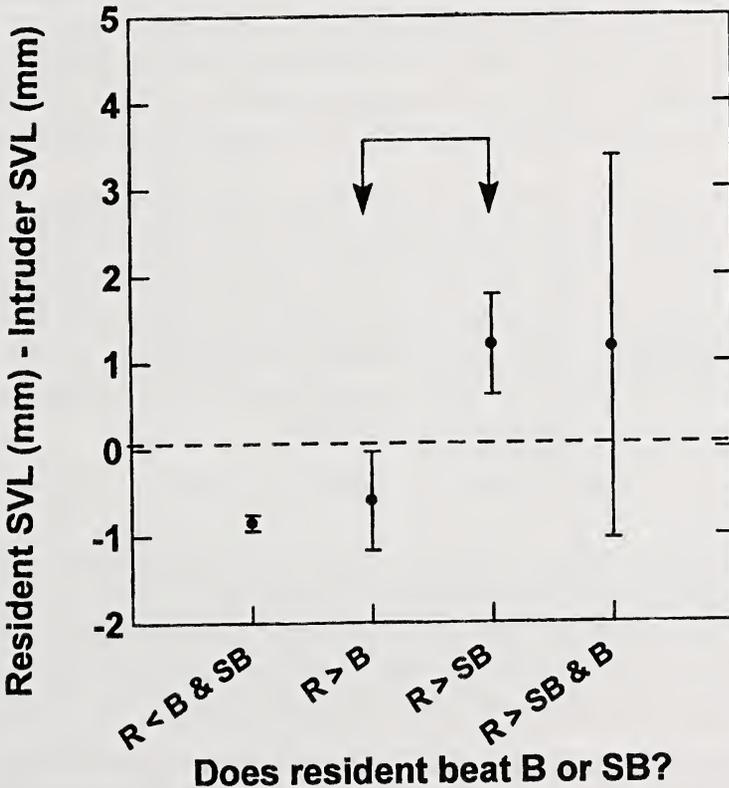
In five of the 12 pairs of trials, the resident either won against both color treatments ( $n = 3$  cases) or lost against both colors ( $n = 2$  cases). In both cases where the resident always performed worse than the intruder, the resident was smaller than the intruder (Figure 1). In the three cases where the resident always performed better than the intruder, there was a wide range of size differences (Figure 1).

Although color did not always influence the outcome of the interactions, there were seven pairs of trials (out of 12) for which the resident performed better (won instead of lost or tied) against one of the color treatments. Overall, residents did not perform significantly better against Blue than against Super Blue (better against Blue in 4 of 7 pairs of trials, exact binomial,  $P=0.500$ ), but the size difference between opponents mediated the influence of color on the outcome of the contest (Figure 1). Considering the seven trials in which a resident won against one color treatment but not the other, the resident size advantage (measured as resident SVL - intruder SVL) was significantly larger when the resident won against Super Blue intruders than when the resident won against Blue intruders ( $|t| = 2.707$ ,  $df = 5$ ,  $P = 0.042$ ). That is, residents won against Super Blue intruders when residents were larger than the intruders but not when residents were smaller than the intruders. This result suggests a possible advantage of Super Blue coloration for larger intruders but not for smaller intruders.

### **Male Contest in Outdoor Enclosures, White and Normal Blue Males**

The presence or absence of male throat color did not influence the outcome of male-male contests during the first hour of contact. In one case the Blue male dominated the White, as shown by the control Blue male chasing the White male, biting him, or supplanting him from a po-

Figure 1. Resident size advantage (resident SVL - intruder SVL; in mm; mean  $\pm$  SE) relative to the outcome of contests between residents and intruders. In 5 of the 12 pairs of trials, residents either lost against both colors ( $R < B$  &  $SB$ ;  $n = 2$ ) or won against both colors ( $R > SB$  &  $B$ ;  $n = 3$ ). In the remaining 7 of 12 pairs of trials, indicated with arrows, residents performed better against one color treatment than against the other.  $R > B$  refers to cases where the resident won over Blue but not over Super Blue ( $n = 4$ );  $R > SB$  refers to cases where the resident won over Super Blue but not over Blue ( $n = 3$ ). The size difference between the males was significantly larger when the resident won against Super Blue intruders than when the resident won against Blue intruders ( $|t| = 2.707$ ,  $df = 5$ ,  $P = 0.042$ ); residents won against Super Blue intruders when residents were larger than the intruders but not when residents were smaller than the intruders.



sition. In another trial, the White male dominated the Blue male, and in two other trials males interacted but neither male demonstrated clear dominance. In another initial trial, the Blue male courted the White male. This Blue male had previously courted the female without success. In

the remaining six of 10 trials, neither male performed any of the behaviors required to assign dominant status (chasing, biting, supplanting).

In the first hour of contact, Blue and White males did not differ in their rate of approaching the other male (Wilcoxon's signed ranks test,  $z = -0.412$ ,  $P = 0.680$ ), number of head bob bouts ( $z = -0.813$ ,  $P = 0.416$ ), rate of moving away from the other male ( $z = 0.422$ ,  $P = 0.673$ ), or maximal aggression score on Moore's (1987) ranked scale ( $z = -0.368$ ,  $P = 0.713$ ).

During the days following the initial introduction of the female, the males exhibited aggressive behavior towards each other in seven of the ten arenas. One male demonstrated dominance over the other in six of these seven cases. There was a nonsignificant trend for males with Blue throat color to dominate males with White throat color (5 of 6 cases, exact binomial,  $P=0.109$ ). The initial dominance relationship did not always predict the long-term dominance relationship. The Blue male eventually achieved dominance in one relationship that was initially unsettled and in another relationship where the White male was initially dominant.

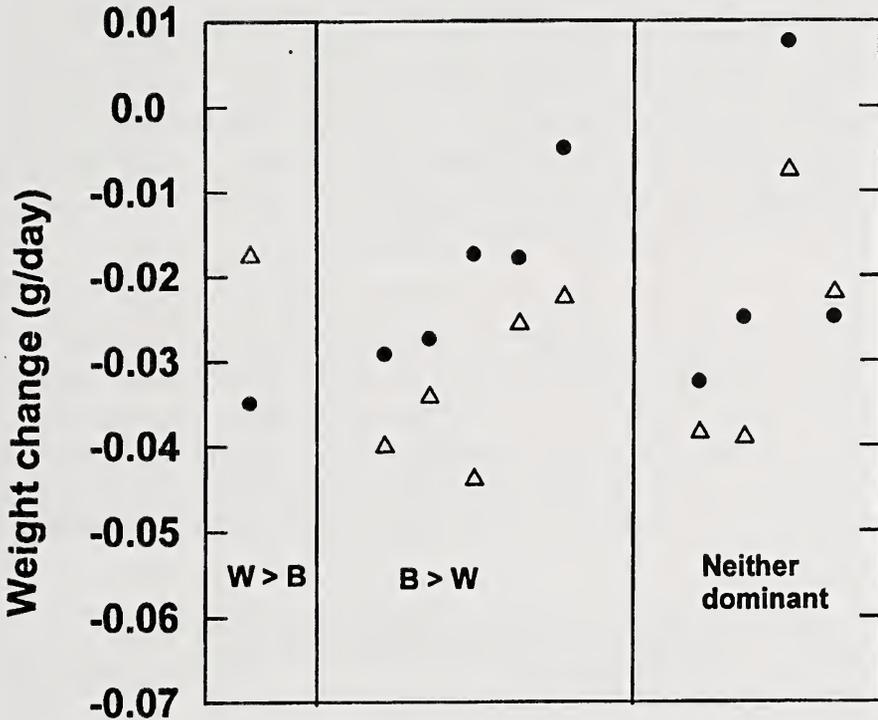
Most males lost weight during the experiment (Figure 2). The magnitude of weight loss was not dependent on initial (April) SVL for either the Blue ( $r=0.181$ ,  $n=10$ ,  $P=0.617$ ) or the White males ( $r=0.0092$ ,  $n=10$ ,  $P=0.801$ ). White males tended to lose weight at a faster rate during the experiment, but this trend just barely missed statistical significance (paired t-test:  $|t|=2.196$ ,  $df=9$ ,  $P=0.056$ ; binomial test: White males lost more weight than Blue in 8 of 10 cases,  $P = 0.055$ ).

### **Female Choice in Enclosures, White and Normal Blue Males**

During the initial encounters, females exhibited little or no association preference. Females always moved from the door to one side of the arena within a few seconds, well before the females could assess the males. In half of the trials, the female moved to the side of the control Blue male first and in the other half she moved first to the side of the White male.

Male response to females did not vary according to female throat color. In half of the ten trials, a male attempted copulation almost immediately upon detecting the female. For these five females, no courtship preceded the copulation or copulation attempt. Instead, the male would approach the female, bite her neck, and attempt to insert a hemipenis, usu-

Figure 2. Weight loss (g/day) of Blue (solid circles) and White (open triangles) males in the enclosures with two males and a female. The two males in each pair are shown one above the other. The order (from left to right) is the pair with the White male dominant in the long term ( $W > B$ ), the five pairs with the Blue male dominant ( $B > W$ ), and the four pairs with no clear agonistic hierarchy (Neither dominant).



ally while the two twirled rapidly in a donut formation. One of these five females had all orange throat coloration, two had all blue, and two had primarily orange with some blue. Two other females were courted but not subjected to a copulation attempt. In all cases where a female was courted in the first hour, she moved away immediately after the male initiated courtship. One of the courted females had predominantly blue throat color with some orange, and the other had mainly orange with some blue. Males neither courted nor attempted to copulate with the remaining three females. One of these females had all blue throat color, one all orange, and the other (the smallest female) lacked throat coloration.

Male throat color treatment was not associated with the sexual behaviors males directed towards females (Table 1). Male throat color also did not influence either female responses to male behaviors or the behaviors that females directed towards males. Of the three females approached by both the Blue and White male, in every case the female either moved away from both males ( $n = 2$  females) or didn't move away from either male ( $n = 1$  female). Of the five females approached by only one of the two males, in three cases the female both moved away and didn't move away, on different occasions, and in two cases the female always moved away (one of these females from a Blue male and the other female from a White male). Behaviors that females were observed to direct toward males were approaching and head bobbing. Three females approached a Blue male and three females approached a White male. Two females head bobbed at Blue males and one at a White male.

During the days following the initial introductions, only two of the ten females exhibited any affiliative preference for one of the males. In both cases, the possible preference was for a Blue, socially dominant male. I saw one female within 45 cm of the Blue male twice but never within that distance of the White male. I saw the other female six times within 35 cm of the Blue male (with the White male at least 80 cm away on each of these occasions) but only once within 35 cm of the White male (with the

*Table 1*

*Number of males performing at least one instance of a behavior directed towards females. The maximum possible value for each entry is 10 (number of pairs of Blue and White males).*

Male Behavior	Male color treatment	
	Blue	White
Attempt copulation	3	3
Bite female's neck (outside of copulation attempt)	4	3
Court female (no copulation attempt)	2	1

Blue male 100 cm away on that occasion). The other eight females were found near the Blue and White males at similar distances and with equal frequency.

### Discussion

In the introductions of tethered males to field residents, there was an interaction between the throat color of intruder males (normal Blue or Super Blue) and the size difference (between intruder and resident) on the outcome of the interaction. Considering only cases where the resident performed better against one or the other of the color treatments, residents won against intruders with restored levels of blue coloration when residents were larger than the intruders but not when residents were smaller than the intruders. The extra coloration in the Super Blue treatment thus conferred no advantage to smaller intruders in contests with larger residents.

Several experimental studies of birds suggest that an enhanced status signal or badge only improves dominance rank if the individual with the enlarged badge can "back up" the signal with real quality (Rohwer, 1975, 1985; Qvarnström, 1997). Similarly, smaller *S. virgatus* intruders with Super Blue coloration may not be able to back up the apparent dominant status signalled by the supplemental coloration. In the present study, the "enhancement" of the coloration is actually a restoration to the ancestral condition rather than enlargement to the level typical of large or dominant males. Natural male-male encounters in *S. virgatus* are most often between individuals of different sizes (Abell, submitted ms). Despite the advantage of large male size, smaller lizards sometimes do dominate in male-male encounters. These experimental studies suggest that restored blue throat and belly patches can confer an advantage in male-male encounters in *S. virgatus* and that the advantage of blue color depends on the size difference between opponents.

In the first hour of interaction in the enclosure experiments, there was no evidence that the presence or absence of throat color influenced male-male interactions. The trends were so weak ( $P > 0.4$  in every case, even unadjusted for multiple comparisons) that I believe the lack of statistical significance represents a lack of biological effect and not a lack of power.

Perhaps because of the relatively low levels of aggression in *S. virgatus*, males in only six of the ten pairs in outdoor enclosures exhibited social dominance hierarchies on the days following the initial introduction. Blue males tended to be socially dominant over the White males and to lose less weight than White males. Neither trend was statistically significant, but the patterns were strong enough to suggest a phenomenon of real biological significance. With one or two additional animals, statistical significance would have been reached with trends of similar magnitude.

Color and dominance status were associated with male seasonal weight loss; White males tended to be subordinate and to lose more weight. When lizards are housed in enclosures, socially dominant individuals sometimes control access to prime feeding sites and reproduce more successfully (Saint Girons, 1977). Subordinate male Turks Island iguanas (*Cyclura carinata*) often failed to eat in captivity, even when abundant food was available (Iverson, 1979). However, I do not believe that differences in food intake can entirely explain the different levels of weight loss of the dominant Blue and subordinate White males of *S. virgatus*. Levels of weight loss in the enclosures were comparable to those in free-ranging *S. virgatus* during the breeding season (Merker and Nagy, 1984; Abell, in press), even though food was available ad libitum in the enclosures. In feeding experiments with free-ranging *S. virgatus* during the breeding season, Rose (1981) and Phelan and Niessen (1989) noted that males often decline offers of supplemental food, even though the males are thin at that time. With the lizard *Anolis carolinensis* in captivity, Bels (1982) likewise observed greater weight loss in socially subordinate males than in dominant males. Greenberg et al. (1984) found higher levels of plasma corticosterone in subordinate captive males of *A. carolinensis* than in dominant males. Laboratory-housed females of *A. carolinensis* had an extra daily peak of corticosterone as well as higher levels of weight loss when housed in dry conditions, even though these females were force-fed the same diet as control females housed under more humid conditions (Summers and Norman, 1988). Glucocorticosteroids have a variety of complex physiological and behavioral effects, including glucose and protein mobilization and changes in foraging behavior (Wingfield, 1994), suggesting a possible physiological mechanism for the greater weight loss of the socially subordinate White males.

There was no evidence that blue coloration of males influenced female mate choice. During the initial introductions, neither female response to male behavior nor female behavior directed towards males varied according to the throat color of the males. On the days after the initial encounters, only two of the ten females tended to associate preferentially with one male or the other. Additional female choice studies are needed to assess possible female preferences in the absence of male-male interactions.

Correlational studies indicated no sexual selection on male ventral coloration in *S. virgatus* (Abell, 1998). However, males with a greater experimental expression of color (Super Blue versus Blue, or Blue versus White) had a weak advantage in staged encounters with smaller or size-matched males. My results are consistent with those of another experimental study of *S. virgatus* (V. S. Quinn and D. K. Hews, pers. comm.), in which large males with painted blue belly patches were more aggressive than size-matched control males. Similarly, males with naturally large blue throat patches exhibited more aggressive behaviors than males with naturally small throat patches, in unstaged encounters with larger opponents (Abell, submitted ms). Additional experimental and correlational work should examine male and female response to coloration and other male traits in a variety of lizards in the genus *Sceloporus*, with an emphasis on subgroups of the genus with particularly large amounts of variation in coloration. The results of the present study also suggest a need for additional studies of relatively long-term effects of variation in male display signals. The influence of the presence or absence of blue color patches was only apparent in the long-term weight loss and social status measurements, not in the short-term behavioral responses. Relatively long-term studies may be especially important in species such as *S. virgatus*, where the overall level of sexual selection on male coloration is so weak as to be undetectable in correlational studies (Abell, 1998).

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## The Challenge of the Plateau and Prairie Lizards (*Sceloporus undulatus*) of New Mexico

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### Abstract

Eight subspecies of *Sceloporus undulatus* occur in New Mexico - twice as many as in any other state. That exceptional diversity reflects a vastly varied topography and ecology. However, the range limits of most subspecies are even yet known as approximations, and although all are allopatric the full extent of their interdigitation is unknown. The species appears to be absent only at high elevations (over about 2750 m) and perhaps in open terrain with inadequate refuges where predation is most intense. More accurate delineation of subspecific ranges opens the door to more critical appraisal of differences in scalation that have been masked in the past by failure to distinguish distinct taxa.

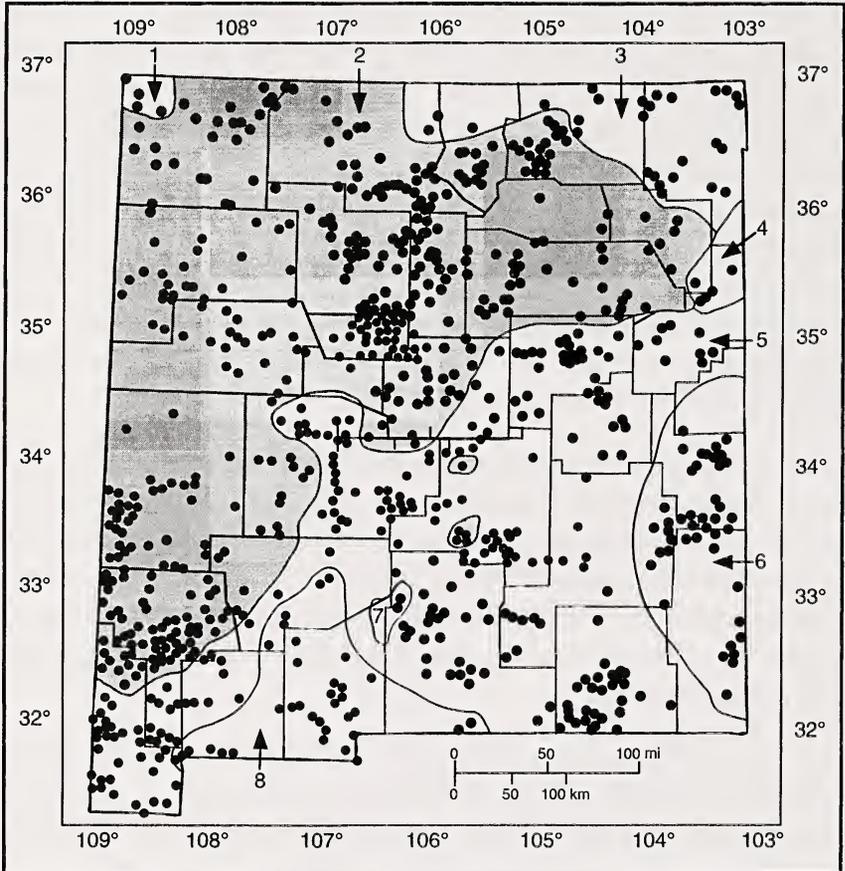
One of the most challenging problems of intraspecific variation in reptiles of North America is found in the ubiquitous *Sceloporus undulatus* of New Mexico, where three subspecies (*S. u. elongatus*, *S. u. erythrocheilus*, *S. u. tristichus*) of the Plateau Lizard (*tristichus*) exerge (subspecies group) occur, along with five of the Prairie Lizard (*consobrinus*) exerge (*S. u. consobrinus*, *S. u. cowlesi*, *S. u. garmani*, *S. u. tedbrowni*), as listed by Smith et al. (1992 submitted a, b).

In their exhaustive monograph of New Mexican herpetology, Degenhardt *et al.* (1996) did not attempt to differentiate or delineate the ranges of these subspecies, which were simply noted as having been recorded from the state. The most recent attempt to map their ranges in New Mexico (Lemos-Espinal *et al.*, 1998) was on too small a scale to depict them with much accuracy.

Our present purpose is to attempt a more detailed approximation to the ranges of the New Mexican subspecies, based on published information and a recent examination of some especially critical material in the Museum of Southwestern Biology (MSB), through the courtesy of Mark A. Jordan, Alexandra Snyder and Dr. William G. Degenhardt.

On those bases we here present (Fig. 1) our best estimates of range

Fig. 1. Distribution of the subspecies of *Sceloporus undulatus*, modified from the spot map in Degenhardt et al. (1996: 182). 1, *S. u. elongatus*; 2, *S. u. tristichus*; 3, *S. u. erythrocheilus*; 4, *S. u. garmani*; 5, *S. u. consobrinus*; 6, *S. u. tedbrowni*; 7, *S. u. cowlesi*; 8, *S. u. speari*.



limits, superimposed on an enlarged version of the detailed spot map for the species in Degenhardt *et al.* (1996). The county names, to which the following discussion frequently refer, are given in Fig. 2, also modified from Degenhardt et al. (1996).

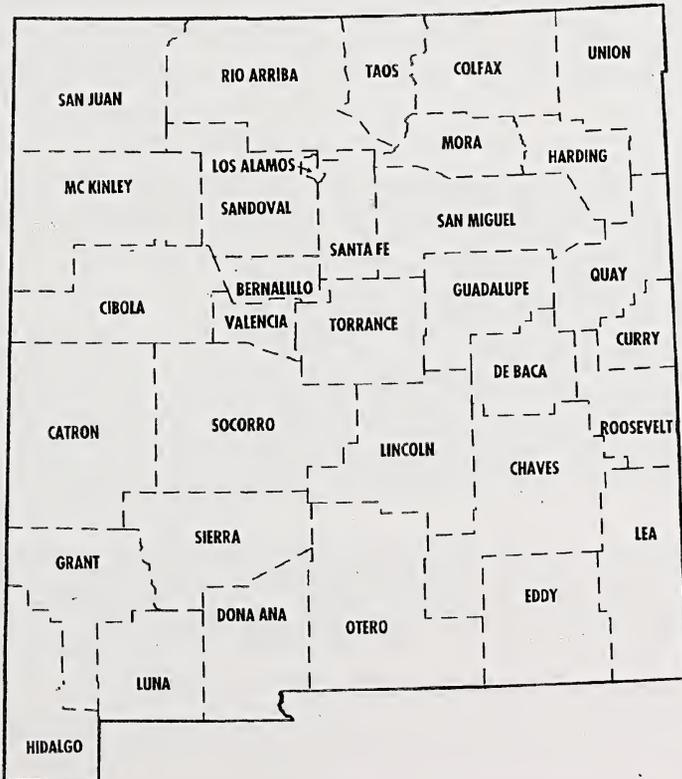
*Sceloporus undulatus tedbrowni*

The greatest surprise of our recent visit to MSB was the discovery of the extensive range of this subspecies throughout the southern half of the

eastern border of the state in the extensive sand dunes and Shinnery oak habitat of that area. The subspecies is also now known along the adjacent western border of Texas, in Andrews, Cochran, Hockley, Lamb, Terry and Yoakum counties (Smith and Chiszar, submitted). It appears (Fig. 1) that the subspecies may even be dichopatric relative to other subspecies of *S. undulatus*, at least in New Mexico.

*S. u. tedbrowni* is also one of the most distinctive races of the species, in size and pattern. It is the smallest, with a maximum known SVL of 59 mm in females, 54 mm in males; the nearest in size is *S. u. garmani*, with a recorded maximum SVL of 68 mm in females, 59 in males (Fitch, 1978). It is most similar to *S. u. garmani*, but their ranges are separated by that of *S. u. consobrinus* (Fig. 1), and the northern subspecies has a very distinct dorsal pattern sharply different from the degenerate dorsal pattern of *S. u. tedbrowni*.

Fig. 2. Names of counties in New Mexico, modified from Degenhardt et al. (1996: xii, fig. 1).



In the 35 specimens examined from Lea Co. (Fig. 2), the dorsal pattern was mostly without dark marks; at most 4 females in 20 showed them, 6 males in 15; where present, the spots were small and confined to the median border of the dorsolateral light stripes. The latter were absent in a few nearly unicolor females, dim and never sharply defined in the others; in males they were usually dim, but sharply defined in 7. In all of both sexes the lateral light stripe was essentially absent, very faint and/or interrupted where present. There was no evidence whatever of either gular or abdominal semeions in females. The gular semeions were essentially absent in males, represented in some by a few black flecks on the extreme posterolateral gular scales; their abdominal semeions were separated minimally by 6-8 scales in a row.

The 23 specimens examined from eastern Chaves and southern Roosevelt counties (Smith et al., submitted b) were essentially the same as those described from Lea Co.

*Sceloporus undulatus cowlesi*

This subspecies, limited to the White Sands, is readily distinguishable from the other arenicolous subspecies, *S. u. tedbrowni*, by its larger size (maximum SVL 69 nun in females, 60 mm in males) and by the presence of both gular and abdominal semeions in both sexes. The presence of abdominal semeions in females suggests derivation from *S. u. tristichus*, which occurs nearby and in which females usually possess abdominal semeions, sometimes indistinguishable from those of males. On the other hand, this subspecies appears to be a member of the *consobrinus* exerge, whereas *S. u. tristichus* belongs to a different exerge bearing its own name (Smith et al., 1992). The exerges differ in evolutionary trends in pattern (striped vs barred), semeion development (weaker vs stronger), size (smaller vs larger) and behavior (cursorial vs scansorial). Biochemical analyses may be useful eventually in confirming the origin of *S. u. cowlesi*.

At present, the White Sands subspecies has been recorded only from Otero Co., but since the Sands extend into Doña Ana and perhaps even into Sierra Co., *S. u. cowlesi* may well occur there also.

*Sceloporus undulatus garmani*

Although occurrence of this subspecies in New Mexico has long been inferred from its distribution in Colorado and Oklahoma, Applegarth (1969) was the first to document it, on the basis of four adult females (MSB 18538-9, 18794-5) he collected 10 mi N, 6.25 mi W Logan, Harding Co. We independently confirmed that identification. Its adjacent subspecies, *S. u. consobrinus*, is readily distinguished by the presence of well developed, often large gular semeions in both sexes. It appears to have no contact with any other subspecies anywhere in its range, although the separation is in some cases only a matter of a mile or so, except for possibly *S. u. tristichus*, narrowly (Fig. 1), in Harding Co. (Applegarth, 1969).

*Sceloporus undulatus speari*

Smith et al. (submitted a) have already recorded this subspecies in the southern Jornada del Muerto Basin (= the Cabeza de Vaca Basin) in southwestern New Mexico, occupying much of Doña Ana Co., southwestern Sierra and Otero counties, and southeastern Luna Co. It had formerly been thought to be limited to the extensive sand dune area of adjacent Chihuahua. It differs from the adjacent *S. u. consobrinus* in its loss or reduction of dark dorsal spots, its uninterrupted dorsolateral light lines, and its reduced gular semeions (absent or small in females, usually separate in males).

*Sceloporus undulatus consobrinus*

This, the remaining subspecies of the *consobrinus* exerge, is the second most widely distributed subspecies of *S. undulatus* in New Mexico (Fig. 1). Only *S. u. tristichus* is more widely distributed. Between the two of them they take up most of the state. It is also apparently the most generalized member of the exerge, and likely has been ancestral to all its members. It is characterized by having dark spots present and well developed, usually distinct dorsolateral light lines that may be interrupted, usually well-developed gular semeions in females, and gular semeions in males usually broadly fused.

In spite of the fact that *S. u. consobrinus* and *S. u. tristichus* are thought to belong to separate exerges, they appear to intergrade throughout their extensive and intricately interdigitating contacts, thus leading to diverse identification of populations in intergrading zones. Intergradation with other members of its exerge also is expected or documented, except for the seemingly isolated *S. u. tedbrowni*.

*Sceloporus undulatus tristichus*

This is a scansorial and predominantly arboreal subspecies living on trees and rocks at relatively high elevation where oaks are dominant or at least prominent (Applegarth, 1969). It is relatively large, has poorly defined dorsolateral light lines interrupted by lateral extensions of the paravertebral dark spots, is of general dark tone dorsally, and has large semeions in both sexes, although usually less well developed in females than in males. Presence of distinct abdominal semeions in females is a notable hallmark of the subspecies; they occur in only a small percentage (11%) of female *S. u. consobrinus*.

As a subspecies of relatively high elevation and cool climate, this subspecies occurs, with the other members of its exerge (*S. u. elongates*, *S. u. erythrocheilus*) farther to the north in the state than the subspecies of the *consobrinus* exerge. Not surprisingly, it is isolated on some higher elevations surrounded by *S. u. consobrinus*, as for example in the Gavilan Mts. of northern Lincoln Co., and the Capitan Mts. in the southern part of the same county (Fig. 1). Still other high altitude populations of the species in Otero Co., might also be more properly referable to *S. u. tristichus* than to *S. u. consobrinus*.

It is of considerable interest that intergradation of *S. u. garmani* with *S. u. tristichus* (Applegarth, 1969) or with *S. u. consobrinus* (pers. obs.), or perhaps with both, is suggested in the contact zones of these three subspecies near the common borders of San Miguel and Quay counties, and extending into adjacent Harding Co. (Fig. 1).

*Sceloporus undulatus erythrocheilus*

Applegarth (1969) devoted much effort to determine the ranges of *S. u. erythrocheilus* and *S. u. tristichus* in northeastern New Mexico, and the limits indicated on our map (Fig. 1) in that area are based on his findings and on those of Hammerson (1986). Like *S. u. tristichus*, *S. u. erythrocheilus* is scansorial, but predominantly petricolous instead of arboreal. Applegarth's data (1969) indicate that the femoral pore total count is usually 34 or more, and the dorsal scale count usually 47 or more, in *S. u. erythrocheilus*, and 33 and 46 or fewer, respectively, in *S. u. tristichus*. The primary chromatic difference he found was the absence of erythritic (yellow, orange and red) colors on the lips and throat of adult *S. u.*

*tristichus* (white instead), and their presence, varying seasonally in intensity, in *S. u. erythrocheilus*.

### *Sceloporus undulatus elongatus*

The range of this subspecies in Colorado (Hammerson, 1986) indicates that it occurs in extreme northwestern New Mexico, as indicated in Fig. 1. In *S. u. elongatus*, 95% have 46 or more dorsals, 80% 18 or more femoral pores on a side, and 92% 7 or more minimal scales in a row between the femoral pore series; in *S. u. tristichus* those figures are 9%, 18% and 18%, respectively (Smith and Chiszar, 1989).

### Discussion

Although approximate ranges of the eight subspecies of *S. undulatus* occurring New Mexico are now reasonably well roughed out as never before, understanding of geographic variation of the species in the state remains rudimentary because of (1) the highly complex topography and climate in the state, with which there is considerable apparent correlation, and (2) the unexplored morphological correlations that may exist in addition to the differences in color, pattern, behavior, size and habitat preferences that largely define the geographic races as now understood. Some attempts in the past to detect morphological correlations with taxonomy have yielded poor or no results through ignorance of what the races are and where they are found. Yet more recent analyses of more discrete populations, as for example of the *tristichus* exerge subspecies (Applegarth, 1969; Smith and Chiszar, 1989) suggest that additional morphological correlations do exist and should be sought.

It is also not unlikely that still other subspecies at present not recognized exist in limited areas of the state, as for example on the vast expanses here and there of black lava, where the populations of *S. undulatus* are especially dark.

These are all derivatives of the *consobrinus* exerge, which in general tend toward the other extreme, of light coloration, hence are of special interest.

There is also the enigmatic Arizona population currently referred to *S. u. consobrinus*, extending into southwestern New Mexico, that has

strange unicolor hatchlings (Smith and Bock, 1990), and at times reaches a rather large size at which a unicolor dorsum appears. At intermediate sizes the dorsal pattern appears more or less normal for the subspecies. That population is but tenuously continuous with more eastern populations of the subspecies, or may actually be isolated from them by contact of the ranges of *S. u. tristichus* and *S. u. speari* (Fig. 1).

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## The Known Distribution in 1998 of the Members of the undulatus Group of the Lizard Genus *Sceloporus* in Chihuahua, Mexico

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### Abstract.

Collections of members of the *Sceloporus undulatus* group in Chihuahua, Mexico, in 1997 and 1998, extend the known ranges of these taxa and permit a more precise estimate of their limits than has been possible up to the present time. Variation is summarized for the newly acquired specimens, and for a series of *S. virgatus* in the University of Colorado museum, and criteria for identification are reviewed.

Three species of the undulatus group of *Sceloporus* are known for the state of Chihuahua, Mexico: *S. belli* Smith *et al.* (1995a), elevated from subspecific (in *S. undulatus*) to species rank by Lemos-Espinal *et al.* (1998); *S. virgatus* Smith (1938), elevated from subspecific (in *S. undulatus*) to specific rank by Cole, 1963; and *S. undulatus* (Bosc and Daudin, 1801). The latter is represented by two subspecies: *S. u. consobrinus* Baird and Girard (1853) and *S. u. speari* Smith *et al.* (1995b).

No other state of either Mexico or the United States has more than two species of the *S. undulatus* group, although New Mexico has by far the greatest number of species-group taxa (9, two species) of that group. No other state exceeds six such taxa (California, one species), and only one other (Colorado) has as many as four (one species). Some member of the group appears likely to occur at any given locality in Chihuahua (Fig. 1), but extensive areas have not been sampled and therefore unknown distributional gaps may exist.

The range of *S. virgatus* was depicted in detail by Cole (1968), and of the others, in less detail, by Smith *et al.* (1995a,b) and in Lemos-Espinal *et al.* (1998). We here review current distributional knowledge, and add to variational knowledge, on the basis of 86 additional specimens of *S. belli* and *S. undulatus* obtained June 2-7, 1997, by all of the authors and Adam Chiszar, and July 8-9 and 14-19, 1998, by JAL-E. All of their catalog numbers are field numbers; those with four digits are in the JAL-E collection,

and those with five digits are at UCM. In addition we record data on 16 previously unreported specimens of *S. virgatus* in the UCM.

*Sceloporus belli*

Thirty-three specimens are in the collections.

Northwestern localities represented are 1 km N Ascensión (36299) ; Rancho La Viuda (31°23'32.3" N, 107°48'20. 3" W) , 1457 m (2902-4, 2907-10, 36300, 36302-3, 36305-12); Rancho El Milagro (36314, 36316-8) ; Rancho Bosque Bonito (31°10'50.0" N, 107°54'54.6" W), 1271 m (36315); km 19 on road to Bismark mine (31°14'2.4" N, 107°41'26.4" W) , 1222 m (2914). Two are from northcentral Chihuahua, at Cerros Colorados (31° 9'15.5" N, 106°22'42.5" W), 1420 m (2828-9), and five from the southeastern part of the state: Rancho Tacubaya (28°19'20.4" N, 104°33'44" W) , 1560 m, km 100 on the Cd. Camargo-Ojinaga Hy (2587-91); and 400 m N military toll, Desviación Santa Elena (28°18'30.8" N, 104°34'24.4" W), 1580 m, fence post next to Cd. Camargo-Ojinaga Hy (2592). The two from Cerros Colorados were on large boulders, the others on large tree trunks or fence posts.

This series demonstrates for the first time an attribute of this species that is rare in *S. undulatus*: a maximum SVL in males (88 mm) exceeding that of females (77 mm); the only exception recorded (Fitch, 1978) is in *S. u. consobrinus* with 74 mm the maximum in 45 males, 71 mm in 46 females. Five males in the present series exceed the recorded maximum for females (Smith et al., 1995a); all, however, are from La Viuda. The maximum SVL in *S. belli* exceeds that of any other member of the *S. undulatus* group, although it is only slightly greater than that of *S. occidentalis* (87 mm.; Fitch, 1978) and of *S. u. undulatus* (86 mm., Conant and Collins, 1998). Furthermore, in most members of the *S. undulatus* group females have greater mean SVL than males (range of M/F mean ratios extending from a low of 87.7 in *S. u. elongatus* to 103.6 in southern *S. occidentalis*, only the latter exceeding 100; Fitch, 1978).

The pattern of these specimens agrees in general with that originally described. The gular semeions in 24 males are separated by the width of one scale in one, two in one, but fused over a length of 1-18 scales ( $M=6.1$ ) in the others. Gular semeions are absent in the two smallest of 7 females (46, 49.5 mm SVL) and one at 63 mm SVL. They are small and weak in two (63, 69 mm SVL), moderately developed in two (58.5, 70 mm

SVL). There is no evidence of abdominal semeions in any of the females.

Pertinent scalation data are as follows. Dorsals 36-42 (M=39.5); femoral pores 13-17, totals 26-33 (M=30.5); minimum scales in a row between pore series 3-7 (M=5.3); prefrontals separated by contact of median frontonasal and frontal in 5, by an azygous scale in 10, and in contact in 15; frontal separated from interparietal in 8, in contact in 23; fewest internasals in a row between median frontonasal and rostral on each side of the median line 3-3 except for two with 2-3, six with 3-4, and one with 4-4; preocular undivided in all except on one side in 5; lorilabials in two complete rows below subocular on 30 sides, reduced to one row at least at one scale in 32.

As indicated in Fig. 1, *S. belli* occurs over most of the state east of the continental divide. Records are lacking or sparse in the southeast and southwest. Peripheral sympatry with *S. u. speari* is known (Lemos-Espinal et al., 1998) at least in the Cerros Colorados area, and may occur elsewhere. The species may possibly occur in extreme southeastern Hidalgo Co., New Mexico, east of the continental divide, which it appears not to cross.

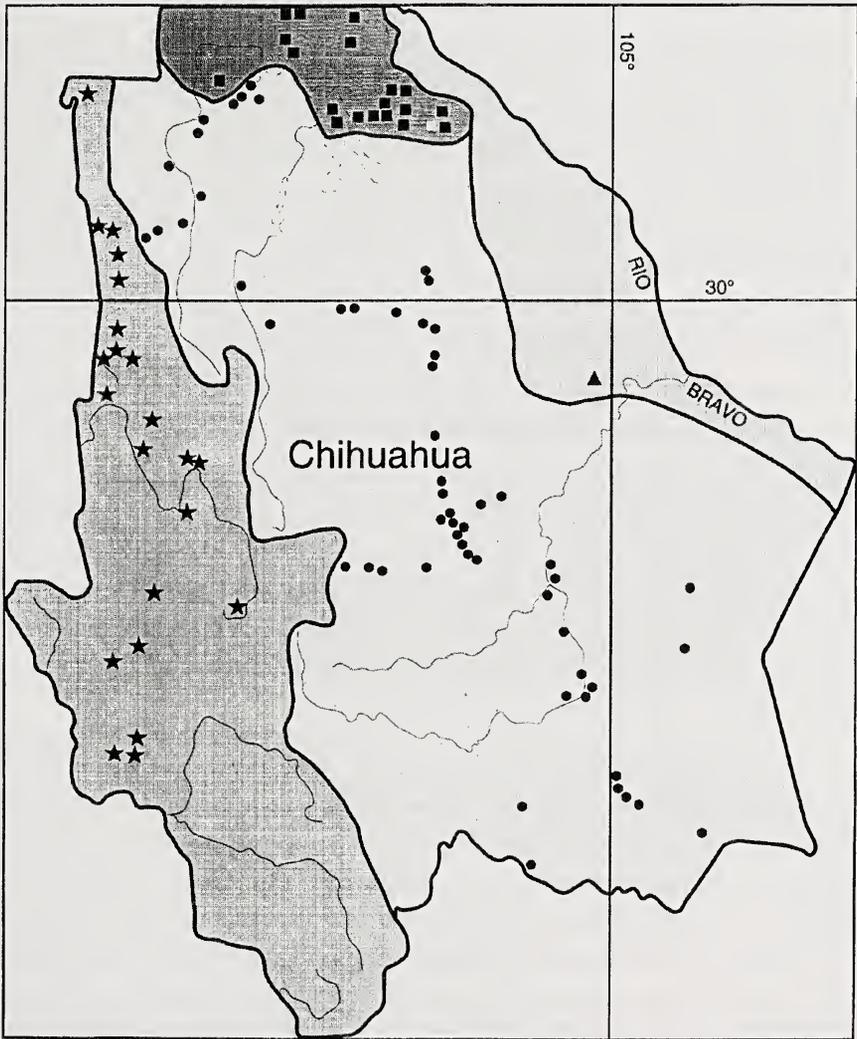
*Sceloporus undulatus consobrinus*

As indicated in Fig. 1, we are aware of only one confirmed locality where this species and subspecies has been taken in Chihuahua. Although there are many records under this name for the state, all actually pertain to *S. belli* or *S. u. speari*. Even our own record (Lemos-Espinal et al., 1998) for 24 airline km NNE Ascensión (UTEP 3568), in the northwestern corner of the state, was in error and pertains to *S. u. speari*.

The locality here reported is at km 140 on the Cd. Chihuahua-Ojinaga highway (México 16), near Coyame (29°27'48.2" N, 105°5'1.2" W), 1270 m (2594, 2596-7), in the central eastern part of the state (Fig. 1). Presumably the subspecies borders the Rio Bravo throughout its length in the state; further documentation is much to be desired.

The specimens from Coyame are all adult males 55-56 mm SVL, but their dorsal pattern is obscured by formalin discoloration. A continuous, broad dorsolateral light line is evident in the lightest example. The abdominal semeions are relatively weak in one, well developed or strong in

Fig. 1. Suggested range limits of members of the *Sceloporus undulatus* group in Chihuahua, Mexico. Circles, *S. belli*; triangle, *S. u. consobrinus*; solid squares, *S. u. speari*; hollow square, locus of sympatry of *S. belli* and *S. u. speari*; stars, *S. virgatus*.



the others. The gular semeions are well developed, in contact over 3-5 scale lengths, each covering 30-43 scales. The dorsals are 39(1)-40; femoral pores 16(2), 17(2) or 18(2); minimum scales in a row between femoral pore rows 6 in all; frontoparietals all 1-1, in contact in one, separated by frontal-interparietal contact in two; prefrontals in contact in two, separated by

median frontonasal-frontal contact in one; minimum internasals in a row on each side of median line between median frontonasal and rostral all 3-3; preoculars single in all; lorilabials in two complete rows below subocular on two sides, reduced to one row at least at one scale on four sides.

*Sceloporus undulatus speari*

This subspecies was originally described on the basis of 69 specimens from the extensive active sand dunes south and southwest of Cd. Juárez, to which it was thought to be confined. Subsequent field work and the present study have revealed that its range extends well beyond the dunes (Fig. 1) northwestward to the U.S. border, eastward at least to Puerto Ventana (31°9'15.3" N, 106°13'25.2" W), 1532 m, and southward to the range of *S. belli*, where the two species are marginally sympatric and syntopic (Lemos-Espinal et al., 1998).

The 52 previously unreported specimens are from km 306, Hy 45, sand dunes near Samalayuca (31°13'34.9" N, 106°30'29.7" W) 1282 m (2778-80); Ojo de Enmedio sand dunes (31°22'45.5" N, 106°35'2.8" W), 1290 m (2838); Rancho El Espejo sand dunes (31°36'46.2" N, 106°53'41.3" W), 1250 m (2852, 2855, 2857, 2863, 2866-7, 2899); El Tule (36331-2); El Ligato (36333-4); 5 km N Hy 2, road to El Espejo (=Los Chontales) (36341); rest stop 11.2 km S Samalayuca, km 307. 65, Hy 45 (31°16'1.1" N, 106°30'16.3" W), 1320 m (36349, 36351-5, 36358); Cerros Colorados (36362-3, 36366); Puerto Ancho (36372-97).

One female (2866) at 70 mm SVL slightly exceeds the previously recorded maximum (69 mm). Color and pattern are much as previously described. In the 18 females, 47.5-70 mm SVL, gular semeions are present in all, but are always separated, usually small and dim; abdominal semeions are completely absent in all but three, in which they are faint; dorsolateral light lines always evident and uninterrupted, but dim in light-colored individuals; lateral light lines always evident, seldom interrupted but often weak; no clearly outlined dark spots bordering the dorsolateral light lines medially, but vestiges usually visible.

In the 25 males, 43-60 mm SVL, for which data are available, the gular semeions are separated in 17, in contact for a length of one scale in 1, two in 3, four in 1, five in 2, nine in 1; they are black-bordered in 2. The

abdominal semeions are well developed in all, and separated by a minimum of 2-6 scales, usually 4; the dorsolateral light lines are broad and uninterrupted in all; the lateral light lines are not evident at all in a few (4), and where present are narrowly and often dimly margined by dark color below.

Dorsals 34-43 (M=37.6), only one exceeding 40; femoral pores 13-19 (M=16.3), totals 28-37 (M=32.8); minimum scales in a row between pore series 3-6 (M=4.4); prefrontals separated by contact of median frontonasal and frontal in 9, by an azygous scale in 14, in contact in 20; frontoparietals 1-1 (30), 1-2 (7), 2-2 (5) or 1-3 (1), separated medially by contact of frontal and interparietal in 31, by an azygous scale in 7, in contact in 5; fewest internasals in a row between median frontonasal and rostral on each side of the median line usually 3-3(29), but 2-2 in 6, 2-3 in 1, 3-4 in 5, 4-4 in 2; preocular usually single (52 of 85 sides), but frequently divided into two (30) or three (3) parts; lorilabials in two complete rows below subocular on 40 sides, reduced to one row at least at one scale in 45.

The range of *S. u. speari* as now understood occupies the southern part of the Cabeza de Vaca Basin (Axtell, 1978), extending a short distance into New Mexico. A specimen (UTEP 3568) from 24 airline mi NNE Ascenci6n, Chihuahua, is typical of the subspecies, and was erroneously referred to *S. u. consobrinus* in Lemos-Espinal *et al.* (1998), before it was realized that *S. u. speari* ranged so widely.

### *Sceloporus virgatus*

Sixteen previously unreported but cataloged UMC specimens are from 11 mi NW El Largo, 7900' (20974-6); 1 mi N Garc3a (20971); 9 mi W Mesa de Hurac3n, 7000' (20977-9); 10 mi SE Mesa de Hurac3n, 3 mi NW Chico, 7000' (20973); 14 mi SW Mesa de Hurac3n (20972); 7 mi SW Natachic (20965-70); 71 mi SW Natachic, 5 mi NE Pinos Altos, 7800' (20964).

All specimens, both males (7) and females (9), exhibit small gular semeions, widely separated by a distance of 5-9 scales (M=7.6). There is no evidence of abdominal semeions in either sex. The dorsolateral and lateral light stripes are prominent on a dark background; especially noteworthy is the broad dark brown line bordering the lateral light line below. Dorsals 35-40 (M=37.5); femoral pores 12-16 (M=13.9), totals 25-30 (M=28); fewest scales in a row between pore series 3-6 (M=4.3); prefrontals sepa-

rated by contact of median frontonasal and frontal in one, by an azygous scale in 15, in contact in none; frontoparietals 1-1 in 9, 1-2 in 3, 2-2 in 3, separated by contact of frontal and interparietal in 11, by an azygous scale in 1, in contact in 2; fewest internasals in a row between median frontonasal and rostral on each side of the median line usually 3-3(8), but 2-2 in 3, 2-3 in 1, 3-4 in 3, and 4-4 in 1; preoculars 1-1 except 2 with 2-2 and 1 with 3-3; lorilabials in two complete rows below the subocular on 17 sides, reduced to one row at least at one scale on 15; median frontonasal separated from lateral frontonasal on 24 sides, in contact on 7 sides.

The entire range of this species is restricted to the Pacific side of the continental divide, where it occurs in oak, pine and mixed oak-pine habitats at elevations of 5000-9600' (Cole, 1968). Its southern distributional limit in Chihuahua remains as uncertain today as it was thirty years ago (Cole, 1968).

### Comparisons

All of the *S. undulatus* group taxa of Chihuahua are allopatric, although marginal sympatry is known to occur at least at one locality (Cerros Colorados) between *S. belli* and *S. u. speari*, and possibly occurs elsewhere between those two taxa and between *S. belli* and *S. u. consobrinus*. Allopatry can aid greatly in identification by locality, but in the extensive areas not yet sampled it can also be fallible because range limits there are at present guesses based on topography.

The most distinctive species of the *S. undulatus* group in Chihuahua is *S. virgatus*. It is the only one occurring west of the continental divide. It is unique, among the taxa of this group in Chihuahua, in completely lacking abdominal semeions in males as well as females; in its combination of bright, continuous lateral as well as dorsolateral light lines, the former bordered ventrally by a broad, continuous, solid brown stripe; by femoral pore scales usually notched both dorsally and ventrally (rather than just ventrally as in most taxa); and by the presence of rugosity and keels on some of the dorsal head scales. (Keels are especially evident on the oculociliaries.) A distinct, median prefrontal concavity is present; the adjacent scales are bulged somewhat, and lateral ridges are present on the anterior moiety of the frontal. Those scales are characteristically flat and smooth in the other species of the group. A weak prefrontal concavity

is present in *S. belli* of all sizes, but is not or scarcely evident in *S. undulatus*.

In addition, as pointed out by Cole (1963), the dorsals and femoral pores average fewer in *S. virgatus* than in the other taxa of the group in the state, and the scales around body average more numerous. In the data on our series, the total femoral pore count is the most distinctive, only 17% of *S. virgatus* having as high as 30, whereas all of *S. u. consobrinus* (3) do, 90% of *S. u. speari* (41), and 65% of *S. belli* (31). An azygous scale separates the prefrontals in 94% of *S. virgatus* (15 of 16), but only 33% of *S. belli* (10 of 30), and of *S. u. speari* (14 of 43), none of the 3 *S. u. consobrinus*. Similarly, the median frontonasal is separated from the lateral frontonasal in 77% of *S. virgatus* (24 of 31 sides), but in only 8% of *S. u. speari* (3 in 40 sides), 10% of *S. belli* (3 in 31 sides), and in none of the 3 *S. u. consobrinus*.

*Sceloporus belli* occupies most of the state east of the continental divide, except near the boundaries of the United States, where *S. u. speari* and *S. u. consobrinus* occur. Mature *S. belli* are readily identified by pattern and size, often exceeding 70-mm SVL - a size rarely reached by *S. u. speari*, and seldom in *S. u. consobrinus*. Mature females lack distinct, continuous dorsolateral light stripes, which area is invaded by relatively large, dark transverse bars; they have no vestiges of abdominal semeions, and have no or weak gular semeions. Mature males have very weak or no dorsolateral light lines, its area bordered laterally by a broad, continuous, uninterrupted dark stripe, bordered in turn by a light area continuous ventrad with the abdominal semeions; no or small, weak dark spots are present in the area between the dorsolateral dark lines. Their gular semeions are commonly (but not always) fused throughout their length, appearing as one, and lack the black edging common in *S. u. consobrinus*.

Immature *S. belli* are less easily distinguished from either adjacent subspecies of *S. undulatus*. No categorical distinctions exist in scalation. The prefrontal concavity is subjectively more pronounced in *S. belli* than in *S. undulatus*. The dorsals in the present specimens are usually (77%) 39 or more in *S. belli* (23 in 30), 32% (13 in 41) in *S. u. speari*. The minimum number of scales in a row between femoral pore series is 5 or more in 77% of *S. belli* (24 of 31), in 39% of *S. u. speari* (16 of 41). We find no other useful distinctions from either subspecies of *S. undulatus*.

The two subspecies of *S. undulatus* in Chihuahua are distinguishable to an acceptable degree in both pattern and scalation, as indicated in Smith et al. (1995b), utilizing exotic material of *S. u. consobrinus*. That same material, plus the three specimens of that subspecies here recorded, is compared as follows with the data on *S. u. speari* here reported. Gular semeions narrowly fused in 28% (8 of 29) of male *S. u. speari*, vs 71% of male *S. u. consobrinus* (89% of those over 49 mm SVL), although rarely is the fusion so extensive as to appear as a single semeion as is common in male *S. belli*; where they are fused, a median black streak commonly separates two blue patches in *S. u. consobrinus*, not in either *S. belli* or *S. u. speari*.

In male *S. u. speari* the abdominal semeions are mostly short; seldom do they reach the groin, whereas they mostly do so in *S. u. consobrinus*.

In female *S. u. speari*, gular semeions are usually absent, and when present are small and faint, whereas they are regularly present and of moderate size in female *S. u. consobrinus*. The latter occasionally have faint evidence of abdominal semeions, never in *S. u. speari*.

The dorsal pattern is brightly striped in both sexes of *S. u. speari*, with no interruptions of the light lines; the lines are evident in *S. u. consobrinus*, but often interrupted and not so distinct.

The most useful distinction in scalation is the more numerous dorsals in *S. u. consobrinus* (84% 40 or more) than in *S. u. speari* (17% 40 or more). In the latter, 61% have a minimum of 3 or 4 scales in a row between the femoral pore series, as opposed to 18% in *S. u. consobrinus*.

Key to the Members of the *Sceloporus undulatus*  
Group in Chihuahua

- 1A. Found west of the continental divide; no abdominal semeions in either sex; a uniformly dark, distinct sublateral line; lateral light line well defined, uninterrupted; free edge of most femoral pore scales notched; head scales microscopically rugose ..... *virgatus*
- B. Found east of the continental divide; abdominal semeions prominent in all males except the youngest; lateral light line less well defined or interrupted, not bordered ventrad by such a

sharply defined lateral dark line; free edge of femoral pores scales not fully notched (notch if present limited to ventral surface); head scales microscopically smooth ..... 2

2A. In females, paravertebral dark spots bar-like, interrupting dim dorsolateral light lines, and gular semeions absent or weak or small; in mature males, dorsum between broad, continuous, very dark lateral dark lines mostly uniform brown, lacking distinct dark spots and dorsolateral light lines; gular semeions with little or no black, BLUE components at least partially fused, in males, except the youngest ..... *belli*

B. In females, paravertebral dark spots, where evident, more nearly rounded, less bar-like, and gular semeions well developed; males with dorsal markings like females, and BLUE component of gular semeions never fused (if the semeions are fused, it is by black borders on the blue); dorsolateral light lines well developed in both sexes ..... 3

3A. Females with no or small, faint gular semeions; abdominal semeions usually short, not reaching groin, in males; dorsals 39 or fewer (83%) ..... *S. undulatus speari*

B. Females regularly with well-developed gular semeions, except in the youngest; abdominal semeions usually reaching groin, in males; dorsals 40 or more (84%) ..... *S. u. consobrinus*

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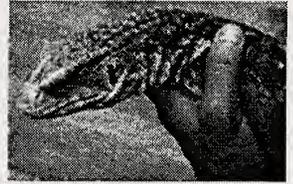
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