SCHOENER, T. W., AND A. SCHOENER. 1982. The ecological correlates of survival in some Bahamian *Anolis* lizards Oikos 39:1–16.

SHUSTER, S. M., AND M. J. WADE. 2003. Mating Systems and Strategies. Princeton University Press, Princeton, NJ.

SMITH, D. D., P. T. SCHELL, R. POWELL, AND J. S. PARMERLEE JR. 1994. Pharyngeal myiasis by sarcophagid larvae (Diptera) in *Ameiva chrysolaema* (Sauria: Teiidae) from the Dominican Republic. Caribbean Journal of Science 30:148–149.

THOMAS, E., F. RENAUD, AND J. F. GUEGAN. 2005. Parasites and Ecosystems. Oxford University Press, London.

ZAMUDIO, K., AND B. SINERVO. 2003. Ecological and social contexts for the evolution of alternative mating strategies. *In* S. Fox, J. McCoy, and T. Baird (eds.), Lizard Social Behavior, pp. 83–106. John Hopkins University Press, Baltimore, MD.

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# Gastrointestinal Fermentation in Greater Sirens (*Siren lacertina*)

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ABSTRACT.—**The nutritional ecology and digestive physiology of salamanders in the Family Sirenidae remain poorly understood. Although the intestinal contents of these salamanders include herbivorous dietary items, the nutritional significance of such ingested matter is unknown. In this study, we examined gut contents, gastrointestinal structure, and microbial fermentation in wild-caught Greater Sirens (*Siren lacertina*). Ingested items included aquatic invertebrates, vascular plants, and algae. The guts of these amphibians were not as voluminous or morphologically specialized as in many herbivores, but the posterior intestine was enlarged and exhibited a distinct folding pattern and an ileocolonic valve that may help maintain a symbiotic microbial population. An active microbial fermentation was indicated by relatively high levels of short-chain fatty acids in the medial-posterior and posterior gut regions. This is the first account of gastrointestinal fermentation in the Family Sirenidae and only the second account in the Class Amphibia.**

It has only recently been determined that some herbivorous amphibians (i.e., larval *Rana catesbeiana*) exhibit a microbial fermentation similar to that of other herbivorous vertebrates (Pryor and Bjorndal, 2005a,b). It remains unknown whether any other amphibians benefit from gastrointestinal fermentation of an herbivorous diet. Considering the diversity of feeding strategies employed among amphibians (Duellman and Trueb, 1994), it would be surprising if anuran larvae were the only herbivorous members of this class with an active gastrointestinal fermentation that contributes to their nutritional requirements.

One group of amphibians worth investigating in these regards is the Family Sirenidae, which includes the Greater Siren (*Siren lacertina*). The diet of *S. lacertina* includes vascular plants, plant-based detritus, filamentous algae, and phytoplankton (Dunn, 1924; Ultsch, 1973; Hanlin, 1978; Conant and Collins, 1991; Behler and King, 1997). Hanlin (1978) reported that plant debris and algae were the two most commonly ingested items in these aquatic salamanders, and Ultsch (1973) found that nonanimal material represented at least 75% of ingested biomass. Despite the predominance of such plant- and algae-based dietary items in the gastrointestinal tracts of *S. lacertina*, some authors have reported that mollusks are an important component of the diet (Moler, 1994 and references therein), and others have questioned whether the ingestion of herbivorous dietary items is incidental to feeding on invertebrate and vertebrate prey (Scroggin and Davis, 1956; Conant and Collins, 1991). However, Ultsch (1973) and Hanlin (1978) provide anecdotal accounts that suggest *S. lacertina* feeds actively and deliberately upon some aquatic vascular plants.

Regardless of the mechanism or intent with which herbivorous food items are ingested, an investigation is warranted to determine whether *S. lacertina* have the gastrointestinal specializations and symbiotic gut communities that would allow them to digest such foods. In many herbivores, symbiotic microbes living in the gut ferment the structural carbohydrates that the host cannot digest enzymatically (e.g., cellulose), and release byproducts such as short-chain fatty acids (SCFA). These metabolic byproducts can be absorbed through the gut wall and used as an energy source by the herbivorous hosts (reviewed in Stevens and Hume, 1995). Accordingly, high levels of SCFA within the gut of an herbivorous host are indicators of microbial fermentation.

The objectives of this study were to investigate the gastrointestinal tract contents, gross gut morphology, and relative concentrations of SCFA within the gut of *S. lacertina*.

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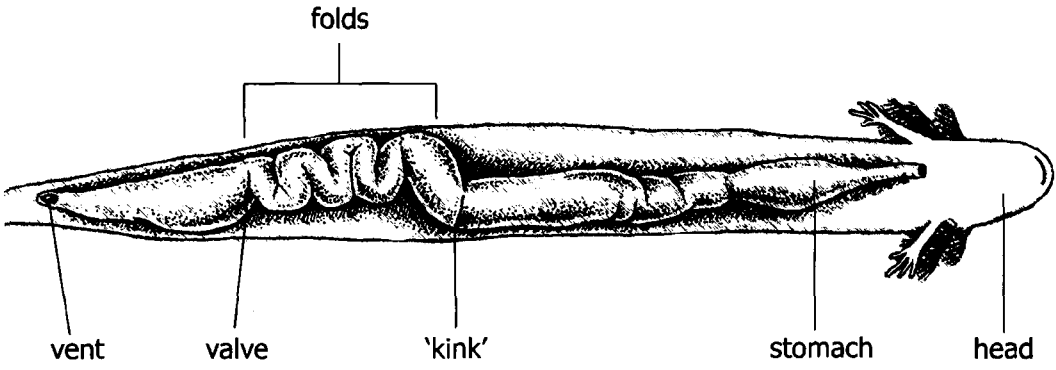


FIG. 1. Gastrointestinal tract of the Greater Siren (*Siren lacertina*). See text for descriptions of the morphological features shown. Illustration by G. Pryor.

## MATERIALS AND METHODS

On 7 March 2004, five Greater Sirens (*S. lacertina*) were collected from the Rodman Reservoir in Putnam County, Florida. The salamanders were killed immediately after capture by placing them in sealed plastic bags that were kept on ice. They were then brought back to the lab, frozen, and maintained at –80°C. The animals were studied in compliance with the Institutional Animal Care and Use Committee at the University of Florida (IACUC D389).

Total body length (TBL), snout–vent length (SVL), and body mass were measured before the five animals were dissected. After dissecting away the accessory organs and gently straightening the full gastrointestinal tract, total gut length (TGL) was measured to the nearest millimeter. Mass of the gut contents, on a wet matter (WM) basis, was measured from each of four gut regions (i.e., anterior intestine; anterior-medial intestine; medial-posterior intestine; and posterior intestine) after the intestinal contents were squeezed from each gut region into a vial. For each animal, the length of each gut region was determined by dividing the total gut into 4 equal sections.

After the samples were processed for fermentation analyses and the gut fluid was separated from the intestinal contents (see details below), the remaining solids were examined under a dissecting microscope. The identity and appearance of dietary items were recorded for each gut region. After microscopic examination, solids were dried completely in a ceramic crucible at 60°C for 48 h to determine mass on a dry matter (DM) basis.

Measurements of symbiotic fermentation activity were based on the methods of Pryor and Bjorndal (2005a). Fermentation activity was indicated by relative concentrations of short-chain fatty acids (SCFA) in the fluid contents among gut regions at the time of death.

As gastrointestinal tracts were dissected, contents from each of the four gut regions were emptied into separate microcentrifuge vials, weighed, and frozen. After all sirens were processed, the gut samples were thawed, homogenized with a vortex mixer, and centrifuged under refrigeration (4°C) at 16,000 g for 10 min. For each of the gut regions, the supernatant was then pipetted into a new, sterile vial. To remove fine particles from the gut fluid (including bacteria, which could potentially further ferment the gut contents), samples were purified using 0.22 μm cellulose acetate centrifuge tube filters (Costar Spin-X gamma sterilized centrifuge tube filters, Corning, New York 14831). These samples were centrifuged under refrigeration at 13,000 g for 15 min and the filtrates were frozen until they were analyzed for SCFA.

Concentrations of SCFA in the gut fluid samples were measured using gas chromatography. Samples were hand-injected into a Shimadzu GC-9AM gas chromatograph equipped with a flame ionization detector (Shimadzu Scientific Instruments, Inc., Columbia, Maryland 21046) and a Perkin Elmer LC-100 integrator (Perkin Elmer, Inc., Connecticut 06484-4794). Two μL of each sample were injected onto a 2 m-long glass column (3.2 mm ID) packed with 10% SP-1000 and 1% $H_3PO_4$ on 100/120 Chromosorb W AW (Supelco, Inc., Bellefonte, Pennsylvania 16823). Carrier gas was $N_2$, at a flow rate of 30 mL $min^{-1}$. Temperatures of the inlet, column, and detector were 180°, 155°, and 200°C, respectively. An external standard containing 90 mg $L^{-1}$ each of acetate, propionate, butyrate, valerate, and isovalerate and 100 mg $L^{-1}$ of isobutyrate was used for calibration. The SCFA concentrations were expressed in several ways: as the millimoles per L (mM) of gut fluid, as micromoles per g dry matter (μmol $g^{-1}$ DM) of digesta, and as a molar ratio of the three predominant SCFA (acetate:propionate:butyrate).

Linear regression was used to test for correlations between wet mass of gut contents and total body mass (i.e., body mass with gut contents included), and between TGL and total body mass. Mean concentrations of total SCFA among gut regions were compared using One-way Repeated Measures ANOVA with LSD multiple comparisons. Alpha values were set a priori at 0.05, and all statistical analyses were conducted using SPSS software (SPSS Inc., Chicago, Illinois 60611).

## RESULTS

The gastrointestinal tracts of *S. lacertina* were linear and uniform in diameter along their lengths, with the exception of several distinct features (Fig. 1). The stomach was discernible as a bulging region of the anterior intestine. A sharp turn ("kink") was located in

TABLE 1. Gastrointestinal tract characteristics of Greater Sirens (*Siren lacertina*) examined in this study.

| Body mass (g) | Total body length (mm) | Snout–vent length (mm) | Total gut length (mm) | Relative gut length (TGL/SVL) | Total gut contents (g)[a] |
|---|---|---|---|---|---|
| 7.6 | 160 | 95 | 145 | 1.53 | 0.442 |
| 9.3 | 165 | 105 | 200 | 1.90 | 0.355 |
| 12.0 | 190 | 120 | 170 | 1.42 | 0.531 |
| 12.8 | 190 | 120 | 155 | 1.29 | 0.525 |
| 70.0 | 323 | 198 | 323 | 1.63 | 4.140 |

[a] Mass of gut contents presented on a wet matter basis. Mean dry matter content of the digesta = 13.4% (range: 10.3–18.4%; standard error: 1.0%).

the medial-posterior intestine, at a point that was approximately four-fifths of the way down the total length of the gut. Posterior to this kink was a series of 4–5 turns in the intestine, which created a folding pattern near the junction of the medial-posterior and posterior intestine. The colon was an enlargement of the posterior intestine, and upon dissection revealed a distinct internal valve (i.e., ileocolonic valve; Guard, 1980) at its proximal end.

Total gut length and mass of gut contents (on a wet matter basis, WM) were strongly correlated with total body mass (i.e., $Y = 2.59X + 140.63$; $R^2 = 0.912$ and $Y = 0.06X - 0.18$; $R^2 = 0.997$, respectively). The ratio of TGL to SVL was 1.55 ± 0.05 (mean ± SE). Total gut contents (WM) represented 4.8 ± 0.4% of total body mass. Gastrointestinal tract measurements for all sirens used in this study are provided in Table 1.

In all sirens, the anterior intestine contained intact filamentous algae and whole amphipods (*Gammarus* sp.). The anterior-medial intestine contained intact and fragmented algae and the exoskeletons of amphipods, and in one siren, an undigested tipulid larva. Amphipod exoskeletons and fragmented algae were also found in the medial-posterior intestine, as well as intact duckweed (*Lemna* sp.) in one individual. The posterior intestine contained the same materials as the medial-posterior intestine, although the algae strands were not as structurally intact or as green as in the previous gut region. Nematodes were also observed in the posterior intestine and were identified as *Falcaustra* sp. (E. Greiner, pers. comm.; see McAllister et al., 1994).

Active microbial fermentation within the guts of sirens was indicated by elevated concentrations of total SCFA in the medial-posterior and posterior intestine relative to the other gut regions (Table 2). The highest concentrations occurred in the posterior intestine and the second highest concentrations occurred in the medial-posterior intestine, whether expressed as μmol $g^{-1}$ DM of digesta (RM ANOVA; $F_{1,3} = 44.23$, $P < 0.001$), or as mM of gut fluid ($F_{1,3} = 20.86$, $P < 0.001$; Table 2). When the SCFA were considered individually, concentrations of acetate among gut regions were much greater than the concentrations of any other SCFA (Fig. 2). The molar ratio of the predominant SCFA (acetate:propioniate:butyrate) in the posterior intestine was 83:8:9.

## DISCUSSION

The oral morphology of *S. lacertina* apparently contributes little to the mastication of food and does not rupture or finely grind ingested invertebrates, filamentous algae, or aquatic vascular plants (i.e., duckweed). This is atypical for many herbivores, which possess shearing or grinding mouthparts (Stevens and Hume, 1995). The gastrointestinal structure of *S. lacertina* is also inconsistent with those of many vertebrates that benefit from fermentative digestion, including other herbivorous amphibians (reviewed in Pryor and Bjorndal, 2005a). For example, the relative gut length of sirens in this study (i.e., TGL/SVL) was approximately 8–10 times shorter than that of herbivorous bullfrog tadpoles (Pretty et al., 1995; Pryor and Bjorndal, 2005a).

The gut structure and relative gut length of sirens in this study were similar, however, to those of some herbivorous marine fishes (Klumpp and Nichols, 1983; Rimmer and Wiebe, 1987; Stevens and Hume, 1995; Clements, 1997), including the Stichaeid fishes *Xiphister mucosus* and *Cebidichthys violaceus* (D. German, unpubl. data). These slender, elongate, and eel-like Stichaeids are benthic herbivores that bear a remarkable resemblance to the sirens examined in this study. The guts of many other herbivorous fishes are also relatively short and straight and function as plug-flow reactors (Horn and Messer, 1992; Stevens and Hume, 1995). Nonetheless, the plants and algae fed upon by some herbivorous fishes with comparatively simple guts are effectively digested by an active microbial gastrointestinal fermentation (reviewed in Clements, 1997). It remains uninvestigated whether sirens also rely upon acid lysis and high intake, as described for some marine fishes that exhibit a fermentative digestive strategy (Horn, 1989; Zemke-White et al., 2000).

TABLE 2. Short-chain fatty acid (SCFA) concentrations within the gastrointestinal tracts of Greater Sirens (*Siren lacertina*). Concentrations expressed as means ± standard errors. Different superscripts within a column represent significant differences between means. Ranges (minimum to maximum) are provided in parentheses.

| | SCFA concentration | |
|---|---|---|
| Gut region | μmol $g^{-1}$ DM | mmol $L^{-1}$ |
| Anterior intestine | 33.0 ± 16.7[a] (5.0–97.3) | 4.47 ± 2.18[a] (0.86–12.83) |
| Anterior-medial intestine | 40.8 ± 10.8[ab] (8.8–66.2) | 5.61 ± 1.47[ab] (1.02–9.43) |
| Medial-posterior intestine | 75.6 ± 21.1[b] (27.0–145.1) | 11.97 ± 3.30[b] (4.73–24.00) |
| Posterior intestine | 108.3 ± 16.3[c] (78.8–151.0) | 22.87 ± 4.62[c] (13.13–37.26) |

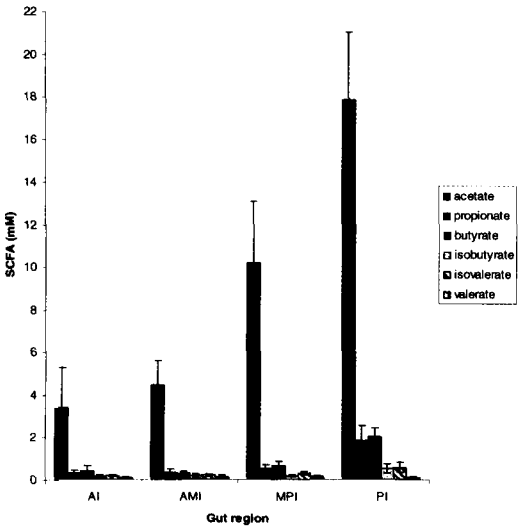


FIG. 2. Concentrations of short-chain fatty acids (SCFA) acetate, propionate, butyrate, isobutyrate, isovalerate, and valerate among gut regions of Greater Sirens (*Siren lacertina*). Gut regions: AI = anterior intestine; AMI = anterior-medial intestine; MPI = medial-posterior intestine; PI = posterior intestine. Concentrations expressed as mean molarity of SCFA in gut fluid, as millimoles per liter (mM). Bars represent standard errors.

Besides a lengthy gut, most herbivores also possess a voluminous gut (Stevens and Hume, 1995). As calculated from prediction equations derived from nonruminant herbivores (Parra, 1978), the total gut contents of a 70 g siren are expected to equal 5.8 g (8.2% of total body mass). In this study, neither the 1.7 g of gut contents collected from a 70 g siren (i.e., 5.9% of total body mass), or the average gut contents from all sirens (4.8 ± 0.4% of total body mass) agreed with such predicted values.

The slender, vermiform body shape of sirenids might preclude the development of anatomical specializations that provide a lengthy, voluminous, convoluted gut (e.g., colonic spirals in herbivorous tadpoles: Pryor and Bjorndal, 2005a). However, other mechanisms such as antiperistalsis, mucous entrapment, colonic partitioning, and the folding pattern observed near the junction of the medial-posterior and posterior intestine might allow for the maintenance of symbiotic populations and the time required for microbial fermentation within the guts of *S. lacertina*. The larger diameter of the posterior intestine and the proximal valve in the colon might help maintain bacterial symbionts in the hindgut of sirens, as they do in some herbivorous reptiles (Guard, 1980).

Occupation of the fermentative hindgut regions by host-specific nematodes, as observed in *S. lacertina* in this study, has also been described in other ectothermic, herbivorous vertebrates (reviewed in Pryor and Bjorndal, 2005a). Several researchers have suggested a mutualistic relationship between these symbiotic nematodes and their hosts (Nagy, 1977; Iverson, 1982; Bjorndal, 1997; Pryor and Greiner, 2004), and Pryor and Bjorndal (2005b) demonstrated that fermentation activity is significantly improved and developmental rates are dramatically increased in herbivorous tadpoles when nematodes are present in the hindgut. The role of nematodes inhabiting the posterior intestine of *S. lacertina* remains to be investigated.

Microbial fermentation in the guts of sirens was indicated by relatively high levels of SCFA (Table 2). This is the first reported account of gastrointestinal fermentation in the Family Sirenidae, and only the second account among amphibians. Concentrations of SCFA in the posterior intestine of *S. lacertina* exceed those of some herbivorous species (reviewed in Pryor and Bjorndal, 2005a), including other amphibians (larval *Rana catesbeiana*), reptiles (*Iguana iguana*), fish (*Kyphosus cornelii*), and birds (*Dromaius novaehollandiae*). Despite the ingestion of invertebrates by *S. lacertina*, the mean concentrations of total SCFA among their gut regions (i.e., 4.5–22.9 mM) are closer to those of herbivorous fishes (7–40 mM) than for fishes feeding upon invertebrates (0.3–2 mM; Clements, 1997).

In most herbivorous vertebrates, significant levels of fermentation occur in a single gut region, such as the hindgut or foregut (Stevens and Hume, 1995). In sirens, high levels of SCFA were observed in the posterior half of the intestine (i.e., the medial-posterior and posterior intestine), relative to the anterior and anterior-medial gut regions. Such an extensive range of fermentation within the gut has also been described in tadpoles (*Rana catesbeiana*) and Florida Red-Bellied Cooters (*Pseudemys nelsoni*), and may represent a fermentative digestive strategy for coping with morphological gut constraints (Bjorndal and Bolten, 1990; Pryor and Bjorndal, 2005a). The mass of gut contents (WM) from the medial-posterior and posterior intestine combined represented 2.7 ± 0.4% of total body mass.

The molar ratio of the three predominant SCFA (acetate:propionate:butyrate) produced in the posterior intestine of *S. lacertina* (83:8:9) is similar to that of a diversity of herbivores feeding upon high fiber diets (Bjorndal, 1979; Bergman, 1990; Clements, 1997; Hume, 1997). It is identical to the ratio of SCFA in the gut of an algae-eating marine fish (*Odax cyanomelas*; Clements, 1997). Although the general ratio of SCFA in mammalian herbivores is near 70:20:10, the ratio shifts towards a greater production of acetate as the proportion of insoluble fiber in the diet increases (Bergman, 1990; Hume, 1997). Such a shift results from alterations in symbiotic microbe populations, which can occur in response to changes in food composition, rates of digesta passage, gastrointestinal pH, food particle size, and other factors (Owens and Goetsch, 1988; Van Soest, 1994). A high proportion of acetate also indicates that the soluble components of the diet are thoroughly digested in the anterior regions of the gut, leaving refractory fiber residues to be fermented in the hindgut (Hume, 1997). Such a pattern is consistent with the appearance of dietary items in the different regions of the siren gut.

The levels of fermentation in the gastrointestinal tracts of *S. lacertina* suggest a possible nutritional gain from ingested plants and algae. Determining the energetic contributions and nutritional importance of such fermentative digestion in sirens, however, would depend upon further research in which in vitro rates of SCFA production are related to their energetic re-

quirements (see Pryor and Bjorndal, 2005a). Closer examination of the fermentative biochemistry and community structure of the gastrointestinal microbiota would provide additional insights into the digestive processes of these poorly studied amphibians.

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LITERATURE CITED

BEHLER, J. L., AND F. W. KING. 1997. National Audubon Society Field Guide to North American Reptiles and Amphibians. Alfred A. Knopf, New York.

BERGMAN, E. N. 1990. Energy contributions of volatile fatty acids from the gastrointestinal tract in various species. Physiological Reviews 70:567–590.

BJORNDAL, K. A. 1979. Cellulose digestion and volatile fatty acid production in the Green Turtle, *Chelonia mydas*. Comparative Biochemistry and Physiology 63A:127–133.

———. 1997. Fermentation in reptiles and amphibians. *In* R. I. Mackie and B. A. White (eds.), Gastrointestinal Microbiology: Volume 1, Gastrointestinal Ecosystems and Fermentations, pp. 199–230. Chapman and Hall, New York.

BJORNDAL, K. A., AND A. B. BOLTEN. 1990. Digestive processing in a herbivorous freshwater turtle: consequences of small-intestine fermentation. Physiological Zoology 63:1232–1247.

CLEMENTS, K. D. 1997. Fermentation and gastrointestinal microorganisms in fishes. *In* R. I. Mackie and B. A. White (eds.), Gastrointestinal Microbiology: Volume 1, Gastrointestinal Ecosystems and Fermentations, pp. 156–198. Chapman and Hall, New York.

CONANT, R., AND J. T. COLLINS. 1991. A Field Guide to Reptiles and Amphibians: Eastern and Central North America. Houghton Mifflin Company, Boston, MA.

DUELLMAN, W. E., AND L. TRUEB. 1994. Biology of Amphibians. Johns Hopkins University Press, Baltimore, MD.

DUNN, E. R. 1924. *Siren*, an herbivorous salamander? Science 59:145.

GUARD, C. L. 1980. The reptilian digestive system: general characteristics. *In* K. Schmidt-Nielsen, L. Bolis, C. R. Taylor, P. J. Bentley, and C. E. Stevens (eds.), Comparative Physiology: Primitive Mammals, pp. 43–51. Cambridge University Press, Cambridge.

HANLIN, H. G. 1978. Food habits of the Greater Siren, *Siren lacertina*, in an Alabama coastal plain pond. Copeia 1978:358–360.

HORN, M. H. 1989. Biology of marine herbivorous fishes. Oceanography and Marine Biology Annual Review 27:167–272.

HORN, M. H., AND K. S. MESSER. 1992. Fish guts as chemical reactors: a model for the alimentary canals of marine herbivorous fishes. Marine Biology 113:527–535.

HUME, I. D. 1997. Fermentation in the hindgut of mammals. *In* R. I. Mackie and B. A. White (eds.), Gastrointestinal Microbiology: Volume 1, Gastrointestinal Ecosystems and Fermentations, pp. 84–115. Chapman and Hall, New York.

IVERSON, J. B. 1982. Adaptations to herbivory in Iguanine lizards. *In* G. M. Burghardt and A. S. Rand (eds.), Iguanas of the World: Their Behavior, Ecology, and Conservation, pp. 60–76. Noyes Publications, Park Ridge, NJ.

KLUMPP, D. W., AND P. D. NICHOLS. 1983. Nutrition of the Southern Sea Garfish, *Hyporhamphus melanochir*: gut passage rate and daily consumption of two food types and assimilation of seagrass components. Marine Ecology Progress Series 12:207–216.

MCALLISTER, C. T., S. R. GOLDBERG, S. E. TRAUTH, C. R. BURSEY, H. J. HOLSHUH, AND B. G. COCHRAN. 1994. Helminths of the Western Lesser Siren, *Siren intermedia nettingi* (Caudata: Sirenidae), from Arkansas. Journal of the Helminthological Society of Washington 61:234–238.

MOLER, P. 1994. *Siren lacertina* (Greater Siren) diet. Herpetological Review 25:62.

NAGY, K. A. 1977. Cellulose digestion and nutrient assimilation in *Sauromalus obesus*, a plant-eating lizard. Copeia 1977:355–362.

OWENS, F. N., AND A. L. GOETSCH. 1988. Ruminal fermentation. *In* D. C. Church (ed.), The Ruminant Animal: Digestive Physiology and Nutrition, pp. 145–171. Prentice Hall, Englewood Cliffs, NJ.

PARRA, R. 1978. Comparison of foregut and hindgut fermentation in herbivores. *In* G. G. Montgomery (ed.), The Ecology of Arboreal Folivores, pp. 205–229. Smithsonian Institution Press, Washington, DC.

PRETTY, R., T. NAITOH, AND R. J. WASSERSUG. 1995. Metamorphic shortening of the alimentary tract in anuran larvae (*Rana catesbeiana*). Anatomical Record 242:417–423.

PRYOR, G. S., AND K. A. BJORNDAL. 2005a. Symbiotic fermentation, digesta passage, and gastrointestinal morphology in Bullfrog tadpoles (*Rana catesbeiana*). Physiological and Biochemical Zoology 78:201–215.

———. 2005b. Effects of the nematode *Gyrinicola batrachiensis* on development, gut morphology, and fermentation in Bullfrog tadpoles (*Rana catesbeiana*): a novel mutualism. Journal of Experimental Zoology 303A:704–712.

PRYOR, G. S., AND E. C. GREINER. 2004. Expanded geographical range, new hosts, and observations of the nematode *Gyrinicola batrachiensis* (Oxyuroida: Pharyngodonidae) in tadpoles. Journal of Parasitology 90:189–191.

RIMMER, D. W., AND W. J. WIEBE. 1987. Fermentative microbial digestion in herbivorous fishes. Journal of Fish Biology 31:229–236.

SCROGGIN, J. B., AND W. B. DAVIS. 1956. Food habits of the Texas Dwarf Siren. Herpetologica 12:231–237.

STEVENS, C. E., AND I. D. HUME. 1995. Comparative Physiology of the Vertebrate Digestive System. 2nd ed. Cambridge University Press, Cambridge.

ULTSCH, G. R. 1973. Observations on the life history of *Siren lacertina*. Herpetologica 29:304–305.

VAN SOEST, P. J. 1994. Nutritional Ecology of the Ruminant. 2nd edition. Comstock Publishing Associates, Ithaca, NY.

ZEMKE-WHITE, W. L., K. D. CLEMENTS, AND P. J. HARRIS. 2000. Acid lysis of macroalgae by marine herbivorous fishes: effects of acid pH on cell wall porosity. Journal of Experimental Marine Biology and Ecology 245:57–68.

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# Reproduction in the Arenicolous Mexican Lizard *Uma exsul*

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ABSTRACT.—***Uma exsul* is a restricted, vulnerable, and rare Mexican lizard that occurs only in fine aeolian sand deposits of the central Chihuahuan Desert. The reproductive cycle of this oviparous lizard was determined using monthly samples of both sexes collected throughout 1992 in the dry Laguna de Mayran in southwestern Coahuila, México. Females reached sexual maturity at a smaller snout–vent length (SVL; 60 mm) than males (73 mm). Reproductive activity of both sexes was synchronous and similar to other oviparous lizards. Mating and courtship occurred from March to June. Males exhibit testicular recrudescence during late winter (February and March) and maximum testicular volume occurred during June. The period of maximal testicular volume was positively correlated with increasing ambient temperature. Testis volume began to decrease in July, reaching minimum volume from August to October. Similarly, females began vitellogenesis during March and contained oviductal eggs from April to July. Females on average laid one or two clutches per breeding season. Mean clutch size based on oviductal eggs was 3.0 ± 0.1 SE (range = 3–5). Clutch size was positively correlated with female SVL. Hatchlings occurred during summer and early fall, when most of the annual rainfall occurs. *Uma exsul* and Mexican *Uma paraphygas* mature early and are short lived, consistent with an *r*-selected life-history strategy. In contrast, the North American species *Uma scoparia*, *Uma inornata*, and *Uma notata* exhibit *K*-selected characteristics.**

Phrynosomatid lizards of the genus *Uma* are found only in aeolian sand deposits of the southwestern United States and northern Mexico (Mosauer, 1935; Carpenter, 1963). The reproductive patterns of several taxa belonging to this genus have been previously reported (Smith, 1946; Shaw, 1952; Mayhew, 1960, 1961, 1964, 1965, 1966a,b; Gadsden et al., 1993). However, little is known about the Mexican species *Uma paraphgas* and *Uma exsul* (Gadsden et al., 1993). These endemic species show extremely low levels of genetic variation, and they are restricted to dune systems of the central Chihuahuan Desert (Adest, 1977; Morafka et al., 1992). Although these species attributes strongly parallel those of more western *Uma* that also inhabit sand dunes, reproductive cycles have been reported only for *Uma paraphygas* in Mexico (Gadsden et al., 1993). Mayhew (1965, 1966a,b) suggested that the three Californian species: *Uma notata*, *Uma inornata*, and *Uma scoparia*, reach peak reproductive activity in May. However, seasonal differences in environmental conditions, such as precipitation and temperature, appear to regulate food diversity and abundance and, thereby, influence the reproductive cycle of these lizards (Mayhew, 1966a; Whitford and Creusere, 1977; Ballinger and Ballinger, 1979). Therefore, an understanding of local environmental conditions as they relate to reproduction is important for any species of *Uma*. The purpose of our study was to describe the reproductive cycle of male and female *U. exsul*, a Mexican endemic species from the central Chihuahuan Desert, and relate these cycles to environmental variables.

## MATERIALS AND METHODS

In 1992, adult *U. exsul* were noosed or shot with BB rifles ($N$ = 88, 47 females and 41 males). Lizards were collected monthly, immediately placed on ice, and subsequently preserved in 10% formalin (Gadsden and Palacios-Orona, 1997; Gadsden et al., 2001a, 2004). We conducted fieldwork in the sand dune systems within the Mapimian subprovince of the Chihuahuan Desert (25°23′N, 103°30′W), in the dry Laguna de Viesca of southwestern Coahuila, Mexico (1100 m a.s.l.). Lizards collected in this study were deposited in the herpetological collection of the Instituto de Ecología, A. C.-Centro Regional Chihuahua, México.

The vegetation was dominated by *Larrea tridentata* and *Suaeda nigrescens* (Gadsden et al., 2001a). Average monthly temperature ranges from 14°C in January to 28°C during June. The average annual precipitation is 187 mm (Fig. 1), but there is strong variation between years (Schmidt, 1979).

For each animal, we measured (1) SVL (mm); (2) number of nonvitellogenic and vitellogenic follicles and/or oviductal eggs; and (3) the longest and shortest testicular axes. All measurements were taken to the nearest 0.1 mm with calipers. Testicular volume (V) was calculated using the formula for the volume of an ellipsoid:

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