ARIEL
Charge
Maxcost: 20.00IFM

(4)

Borrower: IAD

Lending String: *IAI,JNA,UND,SRU,ESR

Patron: Mullin, Stephen

Journal Title: The Southwestern naturalist.

Volume: 53 **Issue:** 3
Month/Year: 2008
Pages: 370+

Article Author:

Article Title: Speed and endurance of thamnophis hammondii...

Imprint: [Lubbock, TX, etc., Southwestern Associa

ILL Number: 46881909

Date Printed: Wednesday, October 08, 2008

Shipping Address:
Booth Library, ILL
Eastern Illinois University
600 Lincoln Ave
Charleston, IL 61920-3099

Fax: 217-581-6066
Ariel: 139.67.69.21

Borrowing Notes;

Searched By / Date: ______________

____

____

Copied By: ______________________

Counted By: ____________________

THE SOUTHWESTERN NATURALIST 53(3):370–373 SEPTEMBER 2008

SPEED AND ENDURANCE OF *THAMNOPHIS HAMMONDII* ARE NOT AFFECTED BY CONSUMING THE TOXIC FROG *XENOPUS LAEVIS*

C. DREW FOSTER* AND STEPHEN J. MULLIN

Department of Biological Sciences, Eastern Illinois University, Charleston, IL 61920
Present address of CDF: Lincoln Park Zoo, Regenstein Small Mammal and Reptile House, 2200 North Cannon Drive, Chicago, IL 60614
**Correspondant: cucdf4@hotmail.com*

ABSTRACT—Toxins of *Xenopus laevis* elicit gaping responses in some snakes, but introduced populations of this species in California provide an additional food source for *Thamnophis hammondii* with no observable ill effects to the snake. This study addresses the locomotor performance of *T. hammondii* after consuming this toxic frog. Endurance and speed of *T. hammondii* were measured along a 2-m long racetrack when subjects were not fed recently, when they were fed sunfish (*Lepomis*, a non-toxic prey), and when they were fed *X. laevis*. Snakes tended to be slower after eating, but ingestion of *X. laevis* did not affect either measure of locomotor performance in *T. hammondii*. Because performance of *T. hammondii* is not compromised, selective pressure against consumption of *X. laevis* probably is absent.

RESUMEN—Toxinas de *Xenopus laevis* provocan que algunas serpientes abran la boca desmesuradamente, pero poblaciones introducidas de esta especie en California proporcionan una fuente adicional de alimento para *Thamnophis hammondii* sin efectos adversos observables en la serpiente. Este estudio se enfoca en el desempeño de movimiento de *T. hammondii* después de consumir esta rana tóxica. Se midieron la resistencia y la velocidad de *T. hammondii* en una pista de 2 metros de largo cuando los sujetos no fueron alimentados recientemente, cuando fueron alimentados con un pez luna (*Lepomis*, una presa no tóxica), y cuando fueron alimentados *X. laevis*. Las serpientes tendieron a ser más lentas después de comer, pero la ingestión de *X. leavis* no afectó ninguna medida de movimiento en *T. hammondii*. Debido a que el desempeño de *T. hammondii* no es afectado, la presión selectiva contra el consumo de *X. laevis* probablemente está ausente.

Amphibian toxins deter many would-be predators, including various species of snakes (Mori, 1989; Brodie et al., 1991). African clawed frogs (Pipidae; *Xenopus laevis*) possess toxins (Daly et al., 1987) that induce oral dyskinesia (yawning and gaping movements) in the North American natricine *Nerodia sipedon* (Barthalmus and Zielinski, 1988) and two species of snakes (*Lycodonomorphus rufulus* and *L. laevissimus*) that are sympatric with native populations of *X. laevis* (Zielinski and Barthalmus, 1989). The toxins are fast acting, triggering oral dyskinesia within 30 s of oral contact in *Nerodia* (Barthalmus and Zielinski, 1988), and often allow the frog to escape from the snake (Zielinski and Barthalmus, 1989). In California, introduced populations of *X. laevis* (Mahrdt and Knefler, 1972; McCoid and Fritts, 1980) provide an additional food source for two-striped gartersnakes (Colubridae; *Thamnophis hammondii*) with no observed ill effects to the snake (Crayon and Hothem, 1998; Ervin and Fisher, 2001). However, no study has examined the effect that ingesting *X. laevis* has on locomotor performance of *T. hammondii*,.

Locomotor performance is a heritable trait (Brodie, 1989, 1993*a*, 1993*b*) correlated with individual survival (Snell et al., 1988) and subject to natural selection (Garland, 1988; Jayne and Bennett, 1990*a*, 1990*b*). Compromised performance might result in an increased risk of predation or a decreased efficiency of finding additional food items (Huey et al., 1984; Brodie and Brodie, 1990). Because maximal locomotion is infrequent during normal activity of squamates (Hertz et al., 1988), mean speed or endurance might provide the most effective illustration of actual performance (Finkler and Claussen, 1999). In this study, we examined the speed and endurance of *T. hammondii* after it consumed *X. laevis*. Additionally, we compared these measures to values obtained when the snake had an empty gastrointestinal track and consumed sunfish (*Lepomis*), a non-toxic prey.

MATERIALS AND METHODS—Eleven *T. hammondii*, five males and six females, were collected in San Diego County, California, 5 June 2001–31 May 2002, and housed in fiberglass cages (30 by 30 by 60 cm) at 22–25°C. Individuals of *X. laevis* were collected from San Diego and Orange counties, California, in June 2003, or purchased from Xenopus 1, Inc. (Dexter, Michigan).

Trials were conducted on a 2-m long, 9-cm wide racetrack. The floor was lined with Astroturf (Brodie and Brodie, 1990; Jayne and Bennett, 1990*b*) and walls, 15 cm high, were painted with semi-gloss paint. Immediately prior to initiating a trial, we randomly chose a subject and determined its mass (±0.1 g). Each trial consisted of four runs down the racetrack with each run separated by 3 min of rest. We measured times of each run from start to finish (±0.01 s) using a digital stopwatch. We defined speed as the mean of the four runs, and the calculated measure of endurance was provided by subtracting the speed of the last run from the speed of the first run (S. J. Downes, pers. comm.). Greater (i.e., less negative) values of endurance indicate less fatigue. Subjects were stimulated to crawl by repeatedly tapping the floor directly behind them, and on the tail if necessary (Brodie and Brodie, 1990). If a subject refused to crawl, however, the trial was discarded (Plummer, 1997), and attempted at a later date. No trial was conducted on subjects in ecdysis.

Trials were conducted 7 August 2003–9 March 2004. Five trials in which snakes had not been fed during the previous 48 h were conducted twice every week prior to, and for comparisons with, feeding trials. Feeding trials were conducted no more than once per week, and were initiated by placing live prey items into the water dish of the snake. Trials began 30 min after consumption of prey following Brodie and Brodie (1990).

We attempted to conduct five trials with *Lepomis* and five trials with *X. laevis* for each subject with trials with *Lepomis* preceding trials with *X. laevis.* Snakes were fed prey at a relative mass of 8–10% (between relative masses of *X. laevis* used by Barthalmus and Zielinski, 1988, at 5% and Zielinski and Barthalmus, 1989, at 15–20%). Keeping mass of prey relatively constant eliminated bias in locomotor performance resulting from varied amounts of gastrointestinal content (Garland and Arnold, 1983; Huey et al., 1984; Ford and Shuttlesworth, 1986).

Speed and endurance were regressed on body mass and snout–vent length (SVL ± 0.1 cm; recorded for each individual upon completion of all trials). Some snakes did not accept *Lepomis* or refused to crawl down the track after consumption of *Lepomis* during all five trials, resulting in an unequal number of trials among types of treatments. To allow for statistical comparisons involving equal sample sizes for each treatment, mean speed and endurance of trials were calculated for all individuals. Differences in speed and endurance were assessed using one-way analyses of variance (ANOVA) and differences among means of treatments were determined using Tukey's post hoc tests. Paired *t*-tests were used to test for fatigue (i.e., a decrease in speeds across the four runs of a trial) in all treatments. To remove any variation created from using the same snakes through all trials, we used a randomized complete-block design with the individual snake treated as the block. Statistical significance was accepted at $P < 0.05$ for all tests.

RESULTS—Neither mass nor snout–vent length differed with respect to sex ($F_{1,31} = 4.08$, $P = 0.05$ and $F_{1,31} = 3.28$, $P = 0.08$, respectively). There was no correlation between speed and body mass ($P = 0.29$) or snout–vent length ($P = 0.33$) of the individual. Similarly, there was no correlation between endurance and body mass ($P = 0.45$) or snout–vent length ($P = 0.34$). Analyzing the first five trials for an effect of experience on performance did not reveal an increase in speed of the subject with repeated runs down the racetrack ($F_{4,40} = 0.73$, $P = 0.58$).

Speed differed among treatments ($F_{2,20} = 5.49$, $P = 0.01$; Table 1). Snakes were faster with empty stomachs than after eating *Lepomis* ($P = 0.01$), but not after consuming *Xenopus* ($P = 0.07$). The speed of snakes fed *Lepomis* did not differ from those fed *Xenopus* ($P = 0.72$). Endurance did not differ among treatments ($F_{2,20} = 1.66$, $P = 0.22$; Table 1). Snakes decreased speed among the four runs of a trial for empty stomach ($t = -5.00$, $P < 0.001$), *Lepomis* ($t = -3.56$, $P < 0.001$), and *Xenopus* ($t = -3.71$, $P < 0.001$; Fig. 1).

DISCUSSION—Greater amounts of gastrointestinal content cause lethargy in snakes (Garland and Arnold, 1983; Huey et al., 1984; Ford and Shuttlesworth, 1986). Snakes of the family Colubridae typically eat meals that are 15–30% of their body mass (Fitch, 1965). By comparison, snakes in this study were fed relatively less, but still tended to be faster on an empty stomach than when fed prey (Table 1, Fig. 1).

Xenopus laevis secretes toxins (Daly et al., 1987) eliciting oral dyskinesia in certain species of snakes (Barthalmus and Zielinski, 1988; Zielinski and Barthalmus, 1989). Many species of *Thamnophis* include toxic amphibians in their diet (Brodie and Brodie, 1990; Brodie et al., 1991), and *T. hammondii* consumes *X. laevis* with no sign of oral dyskinesia (Ervin and Fisher, 2001). We did not observe oral dyskinesia in *T. hammondii* following consumption of *X. laevis,* and toxins

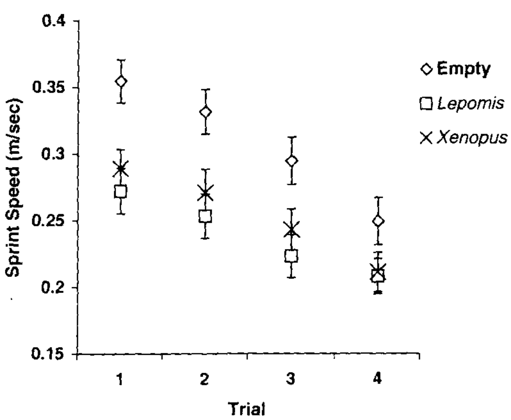

FIG. 1—Mean (±1 *SE*) speed of *Thamnophis hammondii* ($n = 11$) in trials with treatments of empty stomach, *Lepomis*, and *Xenopus laevis* over a 2-m distance, 7 August 2003–9 March 2004.

had no apparent effect on locomotor performance either. Neither speed nor endurance of *T. hammondii* differed between treatments with *Xenopus* and *Lepomis*. Although toxins of *X. laevis* did not affect endurance in *T. hammondii*, snakes were fatiguing consistently within each type of treatment (Fig. 1). Subjects did not increase speed with experience, and therefore, experience on the racetrack could not be masking any effects of toxins from *X. laevis*.

Locomotor performance of *T. hammondii* is not negatively affected after consuming *X. laevis*, suggesting there are no increased risks to snakes that consume this toxic frog. Thus, natural selection should not act against predation on *X. laevis* by *T. hammondii*. While negatively impacting the majority of native aquatic wildlife in California (Bury and Luckenbach, 1976), established populations of *X. laevis* appear to benefit *T. hammondii* as an additional food source. Future studies should attempt to ascertain the long-term effect of consuming *X. laevis* on *T. hammondii*, as well as any resistance to toxins of *Xenopus* in other sympatric species.

Many thanks are due to E. Ervin and R. Fisher of the United States Geological Survey for supplying *Xenopus*, and to A. Hernandez and A. Landeros of the Santa Barbara Zoological Gardens for translating the abstract into Spanish. Thanks also to those who assisted with this study: L. Walston, S. Klueh, J. Florey, and V. Millhoff; these individuals and M. Sikich also provided comments on a previous version of the manuscript. All specimens were maintained following IACUC protocol 04-005. All *T. hammondii* were collected under California Department of Fish and Game permit SC-6239.

TABLE 1—Mean (±1 *SE*) speed and endurance of *Thamnophis hammondii* ($n = 11$) as a function of gastrointestinal content. Means with the same letters are not different at $P < 0.05$; greater values for endurance correspond to less fatigue of the subject.

Treatment	Mean speed (m/s)	Mean endurance (m/s)
Empty	0.308 ± 0.015[a]	−0.105 ± 0.022[a]
Lepomis	0.236 ± 0.013[b]	−0.065 ± 0.010[a]
Xenopus	0.254 ± 0.015[ab]	−0.078 ± 0.015[a]

Literature Cited

BARTHALMUS, G. T., AND W. J. ZIELINSKI. 1988. *Xenopus* skin mucus induces oral dyskinesias that promote escape from snakes. Pharmacology, Biochemistry, and Behavior 30:957–959.

BRODIE, E. D., III. 1989. Behavioral modification as a means of reducing the cost of reproduction. American Naturalist 134:225–238.

BRODIE, E. D., III. 1993*a*. Consistency of individual differences in anti-predator behavior and colour pattern in the garter snake, *Thamnophis ordinoides*. Animal Behaviour 45:851–861.

BRODIE, E. D., III. 1993*b*. Homogeneity of the genetic variance-covariance matrix for antipredator traits in two populations of the garter snake *Thamnophis ordinoides*. Evolution 47:844–854.

BRODIE, E. D., III, AND E. D. BRODIE, JR. 1990. Tetrodotoxin resistance in garter snakes: an evolutionary response of predators to dangerous prey. Evolution 44:651–659.

BRODIE, E. D., JR., P. K. DUCEY, AND E. A. BANESS. 1991. Antipredator skin secretions of some tropical salamanders (*Bolitoglossa*) are toxic to snake predators. Biotropica 23:58–62.

BURY, R. B., AND R. A. LUCKENBACH. 1976. Introduced amphibians and reptiles in California. Biological Conservation 10:1–14.

CRAYON, J. J., AND R. L. HOTHEM. 1998. Natural history notes: *Xenopus laevis* (African clawed frog). Predation. Herpetological Review 29:165–166.

DALY, J. W., C. W. MYERS, AND N. WHITTAKER. 1987. Further classification of skin alkaloids from Neotropical poison frogs (Dendrobatidae), with a general survey of toxic/noxious substances in the Amphibia. Toxicon 25:1023–1095.

ERVIN, E. L., AND R. N. FISHER. 2001. Natural history notes: *Thamnophis hammondii* (two-striped garter snake). Prey. Herpetological Review 32:265–266.

FINKLER, M. S., AND D. L. CLAUSSEN. 1999. Influence of temperature, body size, and inter-individual varia-

eed and endurance of
11) as a function of
s with the same letters
05; greater values for
'atigue of the subject.

Mean endurance (m/s)
−0.105 ± 0.022[a]
−0.065 ± 0.010[a]
−0.078 ± 0.015[a]

:ollected under Califor-
me permit SC-6239.

:ITED

:IELINSKI. 1988. *Xenopus*
skinesias that promote
acology, Biochemistry,

oral modification as a
:ost of reproduction.
–238.

isistency of individual
behavior and colour
Thamnophis ordinoides.
1.

geneity of the genetic
r antipredator traits in
ter snake *Thamnophis*
354.

D. BRODIE, JR. 1990.
arter snakes: an evolu-
rs to dangerous prey.

ND E. A. BANESS. 1991.
is of some tropical
toxic to snake pred-

CH. 1976. Introduced
California. Biological

1998. Natural history
clawed frog). Preda-
29:165–166.

N. WHITTAKER. 1987.
alkaloids from Neo-
idrobatidae), with a
ous substances in the
1095.

2001. Natural history
ii (two-striped garter
Review 32:265–266.

:N. 1999. Influence of
inter-individual varia-

tion on forced and voluntary swimming and crawling speeds in *Nerodia sipedon* and *Regina septemvittata.* Journal of Herpetology 33:62–71.

FITCH, H. S. 1965. An ecological study of the garter snake, *Thamnophis sirtalis.* University of Kansas Publications Museum of Natural History 15:493–564.

FORD, N. B., AND G. A. SHUTTLESWORTH. 1986. Effects of variation in food intake on locomotory performance of juvenile garter snakes. Copeia 1986:999–1001.

GARLAND, T., JR. 1988. Genetic basis of activity metabolism. I. Inheritance of speed, stamina, and antipredator displays in the garter snake, *Thamnophis sirtalis.* Evolution 42:335–350.

GARLAND, T., JR., AND S. J. ARNOLD. 1983. Effects of a full stomach on locomotory performance of juvenile garter snakes (*Thamnophis elegans*). Copeia 1983: 1092–1096.

HERTZ, P. E., R. B. HUEY, AND T. GARLAND, JR. 1988. Time budgets, thermoregulation and maximal locomotor performance: are reptiles Olympians or boy scouts? American Zoologist 28:927–938.

HUEY, R. B., A. F. BENNETT, H. B. JOHN-ALDER, AND K. A. NAGY. 1984. Locomotor capacity and foraging behaviour of Kalahari lacertid lizards. Animal Behaviour 32:41–50.

JAYNE, B. C., AND A. F. BENNETT. 1990*a*. Selection on locomotor performance capacity in a natural population of garter snakes. Evolution 44:1204–1229.

JAYNE, B. C., AND A. F. BENNETT. 1990*b*. Scaling of speed and endurance in garter snakes: a comparison of cross-sectional and longitudinal allometries. Journal of Zoology (London) 220:257–277.

MAHRDT, C., AND F. T. KNEFLER. 1972. Pet or pest? The African clawed frog. Environment Southwest 446: 2–5.

MCCOID, M. J., AND T. H. FRITTS. 1980. Observations of feral populations of *Xenopus laevis* (Pipidae) in southern California. Bulletin of the Southern California Academy of Sciences 79:82–86.

MORI, A. 1989. Behavioral responses to an "unpalatable" prey, *Rana rugosa* (Anura: Amphibia), by newborn Japanese striped snakes, *Elaphe quadrivirgata.* Pages 459–471 in Current herpetology in East Asia ((M. Matsui, T. Hikida, and R. C. Goris, editors). Herpetological Society of Japan, Tokyo.

PLUMMER, M. V. 1997. Speed and endurance of gravid and nongravid green snakes. Copeia 1997:191–194.

SNELL, H. L., R. D. JENNINGS, H. M. SNELL, AND S. HARCOURT. 1988. Intrapopulation variation in predator-avoidance performance of Galapagos lava lizards: the interaction of sexual and natural selection. Evolutionary Ecology 2:353–369.

ZIELINSKI, W. J., AND G. T. BARTHALMUS. 1989. African clawed frog skin compounds: antipredatory effects on African and North American water snakes. Animal Behaviour 38:1083–1086.

Submitted 21 September 2007. Accepted 11 February 2008. Associate Editor was William I. Lutterschmidt.