Effects of a Full Stomach on Locomotory Performance of Juvenile Garter Snakes (Thamnophis elegans)

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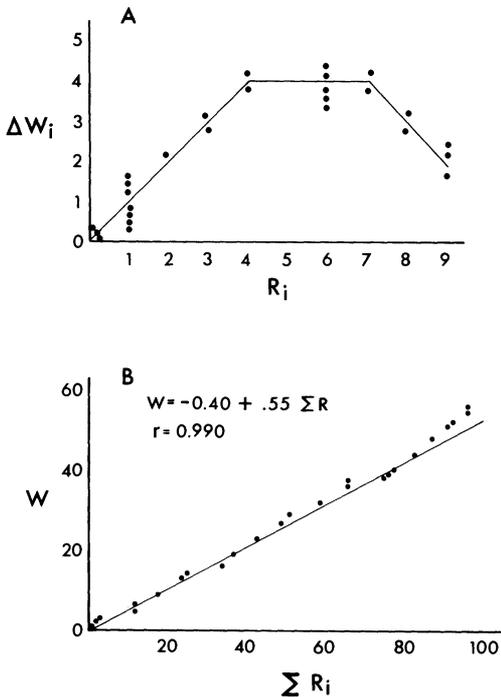Stable URL: https://www.jstor.org/stable/1445117

Fig. 2. A) Hypothetical growth-ration curve (solid line). Each point is a randomly drawn R_i and its corresponding ΔW_i read from the graph. B) Cumulative form with least squares regression and correlation coefficient of the data from A.

tivity of the cumulative procedure, I constructed a non-linear growth-ration relationship (Fig. 2A solid line), drew R_i values from a random number table and read the corresponding ΔW_i from the graph. Like the completely random case, the cumulative regression (Fig. 2B) is highly regular. All traces of the deterministic non-linear relation between ration and growth (Fig. 2A) are eliminated.

The problems of independence and sample size are related. Regression analysis of $\Delta W/R$ data (Fig. 2A) requires independent observations. In practice ΔW is determined as $W_t - W_{t-1}$ so, in serial data on individual animals, each weight determination appears in two successive observations imposing a serial correlation of unknown magnitude. (My artificial data are not subject to this problem since I drew ΔW_i not W_i.) Aside from the mathematical dependence, serial correlation may arise if the feeding and growth history of an animal influence its future responses. The independence problem is exacerbated if the investigator attempts to increase sample size by making observations at

more frequent intervals. Mathur and Silver (1982) discuss inflated sample size and its consequences. Simply stated, 100 data points for one animal are not the same as one observation on each of 100 animals.

Experiments providing independent, replicated observations and analysis (Kitchell and Windell, 1972) eliminate all the problems mentioned in this note.

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EFFECTS OF A FULL STOMACH ON LO-COMOTORY PERFORMANCE OF JUVE-

NILE GARTER SNAKES (*THAMNOPHIS ELEGANS*).—The addition of mass to an animal may be expected to influence its locomotory behavior and capabilities (Coombs, 1978; Taylor et al., 1980). Many snakes experience a large change in effective body mass following feeding. Some venomous species ingest meals that may exceed 100% or even 150% of body mass, and for colubrids (including *Thamnophis*) meals are often 15–30% of body mass (Fitch, 1965; Clark, 1968; Voris and Moffett, 1981). Reduced locomotory performance might therefore be expected in recently-fed snakes.

The aim of this study was to determine whether ingestion of food interferes with the locomotory performance of snakes. Such interference, if it occurs, is representative of a wide class of constraints or tradeoffs among different aspects of fitness (Shine, 1980; Arnold, 1982). In particular, we wished to determine if foraging success (i.e., a full stomach) might reduce a snake's ability to escape from predators.

We employed a paired-comparison design in which the locomotory performance of juvenile garter snakes was scored before and after feeding. Three measures of locomotory performance were recorded: burst speed over one meter, total distance traversed and total elapsed time before snakes assumed stationary defensive behaviors. We hypothesized that all three performance measures would decrease following feeding.

Materials and methods.—The 10 juvenile *Thamnophis elegans* used in the experiment were the laboratory born progeny of four females captured near Eagle Lake, Lassen Co., California. The snakes were 10–12 weeks old during the experiment. Pre-feeding body masses ranged from 2.16–4.20 g ($\bar{x} \pm$ SD = 2.79 $\pm$ 0.62); snout–vent lengths ranged from 165–213 mm (186 $\pm$ 13 mm). The snakes had not eaten for two weeks prior to the experiment.

Locomotory performance was tested by chasing snakes around a rectangular track. The track was constructed of wood with sides 13 cm high and Astroturf covering a 10 cm wide path. The two long sides of the track were 1.0 m; one lap was 3.64 m. A trial was started by introducing one snake into a corner of the track. Snakes were induced to move by gentle tapping on the tail with a cotton-tipped swab, and kept moving by continual tapping at approximately one sec intervals. The time taken for a snake to cover the first 1.0 m was recorded with a hand-held stopwatch to the nearest 0.01 s (inverse = "burst speed" in m/s). Total distance covered before entering defensive behavior was recorded to the nearest 0.01 m as a measure of endurance capacity ("endurance distance"). Total elapsed time to defensive behavior was recorded as another measure of endurance ("endurance time"). Individuals sometimes reversed direction of travel and continued crawling; if a reversal occurred before the initial 1.0 m had been covered, no burst speed was obtained (three of 40 trials). Endurance distance and time were obtained in all 40 trials.

All trials were conducted between 1530 and 1700 hours. Ambient temperature was 25 $\pm$ 2 C. The entire experiment took five days, with snakes being performance tested on days 1, 2, 4 and 5, and fed on day 3. Trial one served to familiarize the snakes with the experimental protocol, and, as reported by Bennett (1980) for lizards, performance generally improved from day 1 to day 2. The performance of each individual on day 2 was recorded as indicative of its before feeding or "empty stomach" performance capability. On day 3, each snake was force fed two fish (*Brachydanio rerio*), which ranged in body mass from 0.22–0.42 g ($\bar{x} \pm$ SD = 0.30 $\pm$ 0.05 g). The total mass of this meal (two fish) ranged from 17.6–26.9% (22.2 $\pm$ 3.1%) of the snake's unfed body mass. Performance on day 4 was recorded as indicative of after feeding or "full stomach" performance ability. Because some digestion occurred between the time of feeding (day 3) and the testing of post-feeding performance (day 4), actual stomach contents were somewhat less than the total mass of the meal. Performance data were also recorded on day 5, but because four individuals regurgitated between day 4 and day 5, these data are not presented. No individuals regurgitated during a performance trial.

Data for the three performance variables were tested for normality with rankit plots (Sokal and Rohlf, 1969). One meter time did not appear to deviate from normality, so a one-tailed t-test for paired samples was used to test the hypothesis that post-feeding (day 4) burst speeds were significantly lower than pre-feeding (day 2) burst speeds. One meter times were obtained for eight of 10 individuals on both days 2 and 4. Both endurance distance and time appeared to deviate from normality in a manner suggesting positive skewness (a few individuals displayed exceptional endurance capacities); however, a $\log_{10}$ transformation was judged to satisfactorily

TABLE 1. PERFORMANCE OF JUVENILE GARTER SNAKES (*Thamnophis elegans*) BEFORE AND AFTER FEEDING (=WITHOUT AND WITH A FULL STOMACH). The data were not normally distributed, so data transformations were employed before statistical comparisons of means with *t*-tests for paired samples. Reported means are in original units as are 95% confidence intervals for means, which are, therefore, asymmetrical.

		Before feeding		After feeding
Burst speed (m/s)	Mean	0.229		0.204
	95% C.I.	0.199 to 0.269		0.183 to 0.229
	Range	0.161 to 0.350		0.153 to 0.290
	N	9		9
	t		−0.565	
	df		7	
	P		>0.10	
Endurance distance (m)	Mean	17.87		11.36
	95% C.I.	12.91 to 24.75		8.09 to 15.95
	Range	7.14 to 45.04		4.04 to 40.39
	N	10		10
	t		2.925	
	df		9	
	P		<0.01	
Endurance time (s)	Mean	156.57		108.04
	95% C.I.	101.20 to 242.22		71.15 to 164.04
	Range	41.77 to 695.16		34.15 to 504.70
	N	10		10
	t		2.908	
	df		9	
	P		<0.01	

normalize the distributions. One-tailed *t*-tests for paired samples were employed to test the hypothesis that endurance distance decreased after feeding and that fed snakes entered their stationary defensive behavior sooner than before feeding. Consistency of performance scores among individuals over the four trial days was tested with Kendall's Coefficient of Concordance, W (Siegel, 1956). Correlations between the three performance measures and body mass were examined with Spearman Rank Correlation Coefficients, r_s, comparing pre-feeding performance scores with body masses as measured on day 3. Intercorrelations among the performance variables were also examined with r_s, correlation coefficients being calculated for each of the four trial days separately.

Results—Burst speed, endurance distance, and endurance time scores of individuals were consistent over the four trial days (W = 0.656, N = 7, $P < 0.01$; W = 0.792, N = 10, $P < 0.001$; W = 0.733, N = 10, $P < 0.01$, respectively). Burst speed was positively correlated with body mass ($r_s = 0.617$, N = 9, $P = 0.041$). Neither endurance measure was significantly correlated

with body mass ($r_s = 0.297$, N = 10, $P = 0.187$ for distance; $r_s = 0.249$, N = 10, $P = 0.288$ for time). Endurance distance and time were highly positively correlated on all four trial days ($r_s = 0.818$ to 0.964, $P = 0.007$ to 0.002). Burst speed, however, was not significantly correlated with either endurance measure on any trial day ($r_s = 0.367$ to −0.383, $P = 0.444$ to 0.139).

There was no significant change in burst speed following feeding ($P > 0.10$, Table 1), and only three of eight individuals exhibited a decrease in burst speed after feeding. Endurance distance and time both decreased significantly ($P < 0.01$) after feeding (Table 1). Endurance distances decreased for nine of 10 individuals and endurance time decreased for eight of 10 individuals following feeding. Mean endurance distance decreased by 36%; mean endurance time decreased by 31%. Qualitatively, locomotion of fed snakes appeared more awkward than before feeding. Also, fed snakes reversed their direction of travel more frequently than before feeding; however, this trend was not significant (one-tailed Sign Test, $P = 0.109$).

The snakes displayed a variety of defensive behaviors that served as markers for terminat-

ing our performance trials. Some snakes coiled their body in a ball over their head, others lunged at the cotton swab with an open mouth attack, and still others simply assumed a linear, rigid body posture. However, defensive behaviors did not appear to differ systematically before versus after feeding. These behaviors will be more fully discussed in a later report.

Discussion.—Feeding had no detectable effect on burst speeds of juvenile garter snakes. However, endurance capacities of recently-fed snakes decreased, and they assumed stationary defensive behaviors sooner than when unfed. R. B. Huey, A. F. Bennett, K. A. Nagy and H. B. John-Alder (pers. comms.) obtained similar results with African lacertid lizards (*Eremias*) following force feeding of termites (up to 30% of body mass). Endurance capacity decreased but burst speed was maintained.

We employed force feeding because not all individuals could be relied upon to feed of their own accord. In addition, force feeding allowed us to limit variation in meal size and in the amount of time between feeding and performance testing. Our methods may be criticized, however, because force feeding can be traumatic on a snake. It is therefore possible that some of the decrease in post-feeding endurance is attributable to the force feeding rather than to the mass of the meal. However, the snakes had 24 hours to recuperate following feeding and all appeared to be healthy and behaving normally the day after feeding. Furthermore, there was no decrease in burst speed. Improvements in future studies would include: 1) allowing animals to feed on their own, 2) on meals of a greater mass range and 3) attempting to correlate mass of meal with the magnitude of decrease (if any) in performance following feeding. It would also be of interest to determine whether force feeding affects performance.

Shine (1980) and Bauwens and Thoen (1981) have demonstrated that gravid female lizards exhibit reduced running speeds as compared with non-gravid females or males. The increase in body mass experienced by gravid animals may or may not be analogous to that experienced following feeding: pregnancy involves many physiological changes beyond simple mass loading.

Burst speed was positively correlated with body weight, as was found by Heckrotte (1967), but our mean burst speed before feeding (0.229 m/s) is greater than the speed indicated by his

Fig. 1 for a 2.8 g garter snake (*Thamnophis sirtalis*) at 25 C ($\approx$0.15 m/s). Endurance capacities were greater in larger snakes in the present study, but the trend was not significant. Pough (1977, 1978) found that adult garter snakes (*T. sirtalis*) and water snakes (*Nerodia sipedon*) possessed greater endurance capacities than did juveniles. Because of the high variability of such performance measures, it is difficult to demonstrate size-related differences in performance (should they exist) within a group of similarly-sized animals (Bennett, 1980).

The two endurance measures were highly correlated, which is not surprising since they measured virtually the same thing. Burst speed, however, was not correlated with either measure. This lack of correlation between different aspects of locomotory performance was also reported by Bennett (1980) for lizards. Performance differences among individual garter snakes were consistent throughout our experiment. This suggests that our protocols for measuring burst speed and endurance capacity would be suitable for the study of intra- or interspecific variation in performance abilities. Bennett (1980) also observed repeatability of performance measures in lizards.

Depending on what aspect of performance is critical for escape from predators, recently-fed juvenile garter snakes might or might not be more susceptible to predation. We suspect that both burst speed and endurance capacity may be important for predator escape, depending on the predator involved (Greene et al., 1978). Although our snakes did not exhibit reduced burst speeds with a full stomach, we think it likely that snakes with larger meals (e.g., 50–150% of body mass) than used in our study (18–27%) might be slower following feeding.

The relationship between meal size and overall fitness is likely complex. Presumably, the larger a meal, the greater the reduction in locomotory performance and ability to escape from predators. On the other hand, snakes that typically take small meals may need to forage more frequently, and the rate at which a snake encounters some predators may be proportional to the amount of time spent foraging (Huey and Pianka, 1981).

versity of Chicago provided office space for TG during this study.

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NATURAL SURVIVAL OF EGGS AND TADPOLES OF THE WOOD FROG, *RANA SYLVATICA.*—Only a handful of studies have monitored the natural survival of anurans from egg-laying to transformation (Herreid and Kinney, 1966; Calef, 1973; Licht, 1974). In each of these studies, mortality was concentrated mainly in the larval stage, and overall survival was low (<10%). Studies that have traced survival in the tadpole stage only, and studies conducted under artificial conditions have generally produced results similar to those noted above, although survival values from field "experiments" tend to be higher than those found under natural conditions (Turner, 1960, 1962; Dumas, 1964; Brockelman, 1969; Cecil and Just, 1979; Woodward, 1982). Howard (1978) reported high mortality among egg masses, but had no data on larval survival.

Most data on anuran survival under natural conditions have been generated under some combination of the following circumstances: 1) the subject species had a prolonged (3–12 month) larval period (Herreid and Kinney, 1966; Calef, 1973; Licht, 1974); or 2) the study was conducted in permanent ponds which contained a wide variety of vertebrate predators (Brockelman, 1969; Calef, 1973; Licht, 1974; Cecil and Just, 1979). Only Turner (1960) reported the survival of anurans breeding in temporary ponds, but his data are limited because egg mortality was not monitored. Thus, complete data on species breeding in temporary ponds with short developmental periods are lacking. In this paper, I report on the natural survival of eggs and tadpoles of the wood frog (*Rana sylvatica*), a species characterized by a short developmental period, at a temporary pond in New Jersey.

Observations on wood frogs were carried out in the springs of 1975 and 1976 at the Great Swamp National Wildlife Refuge, Morris County, New Jersey, mainly at a pond known locally as Hospital Pond. Hospital Pond is a small (surface area ca 150 m²), temporary pond that dries each year by late May or June. The pond usually supports no extensive fish fauna or other vertebrate predators, and the invertebrate fauna is depauperate for the area.

The pond was checked for egg masses every 48 h starting on 28 March 1975. Each egg mass found was numbered and sketched. Survival of