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SELECTION ON LOCOMOTOR PERFORMANCE CAPACITY IN A NATURAL POPULATION OF GARTER SNAKES

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Abstract.—Selection on locomotor performance was determined for a series of marked and recaptured individuals from a population of garter snakes (*Thamnophis sirtalis fitchi*) in Northern California. We measured snake length and mass, burst speed, endurance on a treadmill, and the distance crawled around a stationary circular track. Size-corrected values (residuals) of mass and locomotor performance were generated from the scaling equations of S-V length (SVL). Randomization tests and regressions were used to determine the probability that a trait was a significant predictor of survivorship, and a nonparametric, cubic spline estimate of the fitness function was used to facilitate detection of the patterns of selection. From 275 (“cohort”) snakes measured and tested within 8 days of birth in 1985, 79 were recaptured in the spring-summer of 1986 and subsequent years. Birth SVL was the only significant (randomization $P = 0.022$) predictor of neonatal survival from 1985 to 1986 with directional selection favoring larger individuals. In addition to the lab-born cohort, 382 field-born snakes from all ages in the population were captured, tested, and released during spring-summer 1986. Similar to the 1985 cohort, the survivorship of 37 of 86 neonates from 1986 to 1987 showed no significant relationship with any residual value using any statistical test. Survivorship from 1986 to 1987 for 127 of 250 yearlings (including 32 lab-born cohort snakes) analyzed with the randomization test showed that greater values of both speed ($P = 0.007$) and distance residual ($P = 0.008$) significantly favored survival, whereas intermediate values of mass residual ($P = 0.006$) were significantly more likely to survive. Univariate regressions predicting the survival of yearlings from 1986 to 1987 gave similar results to the randomization test, but in a multiple regression with yearling burst speed residual, distance capacity residual, and a quadratic term of mass residual, distance capacity residual was the least important predictor variable. For the survivorship of 37 of the 113 older snakes, greater burst speed residual significantly favored survival (randomization $P = 0.001$).

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The identification of features of organisms under natural selection has been an elusive goal of evolutionary biologists over the past century (Endler, 1986). With the development of new methods of analyzing data to detect selection and its patterns (e.g., Lande and Arnold, 1983; Mitchell-Olds and Shaw, 1987; Schluter, 1988; Crespi and Bookstein, 1989), there has recently been an increasing interest in such studies. Most selection studies measure easily quantified morphological characters, such as body mass (e.g., Bumpus, 1899; Koenig and Albano, 1987), linear dimensions (e.g., Bumpus, 1899; Lande and Arnold, 1983; Ferguson and Fox, 1984; Koenig and Albano, 1987; Conner, 1988; Gibbs, 1988; Grant and Grant, 1989), or meristic characters, such as scale numbers (e.g., Dunn, 1942; Fox, 1975). Although the functional implications of some of these characters are fairly clear (e.g., Grant and Grant, 1989), more generally they are not. For instance, wing morphology and body size are related to differential survivorship through winter storms

in house sparrows and bugs (Bumpus, 1899; Lande and Arnold, 1983), but the effects of these characters on flight ability, the presumed selective feature (Lande and Arnold, 1983), are unknown and poorly predictable on a priori grounds. For this reason, Arnold (1983) advocated measuring selection with separate analyses of the influence of morphological characters on performance ability (the performance gradient) and of performance on fitness (the fitness gradient). He reasoned that such a division would clarify interpretation of the actual operation of selection. To date, few studies (e.g., Koenig and Albano, 1987) actually analyze the fitness gradient, that is, selection on such physiological or behavioral characters.

This study seeks to analyze the effect of locomotor performance capacity on differential survivorship in a natural population. In essence, the question addressed is rather simple: do animals with relatively great locomotor capacities (e.g., speed, endurance) have a survival advantage that can translate into differential fitness? On one hand, such

a positive association might seem trivially obvious. Snell et al. (1988) found that speed of Galapagos lava lizards was correlated with rates of predation. However, in longitudinal studies of locomotor performance and survivorship it has never been demonstrated; in fact, preliminary analysis of comparable studies on two species of fence lizard by R. B. Huey and co-workers (Bennett and Huey, 1990; R. Huey, T. Garland, F. van Berkum, and J. Tsuji, in prep.) found no detectable relationship between locomotor performance capacity and survivorship. Perhaps such physiological and behavioral features play less of a role in natural populations than our naive expectations suggest (Hertz et al., 1988). Further, the null hypothesis ("the race is not to the swift, nor the battle to the strong . . . but time and chance happeneth to them all.") has considerable historical precedence (Ecclesiastes 9:11).

Locomotor performance capacity of lower vertebrates (maximum speed, endurance, and acceleration) has been studied intensively by ecological physiologists interested in its susceptibility to factors such as temperature (e.g., Brett, 1967; Webb, 1978; Bennett, 1980; Putnam and Bennett, 1981; Hertz et al., 1982), dehydration (Pough et al., 1983; Gatten, 1987), feeding state (Garland and Arnold, 1983; Huey et al., 1984), age (Huey et al., 1990), and reproductive condition (Shine, 1980; Seigel et al., 1987b; Jayne and Bennett, 1990). Interindividual differences in factors such as endurance (Garland, 1985; Garland and Else, 1987) and speed (Gleeson and Harrison, 1988) are large and have been found to correlate significantly with physiology and morphology. These characters are heritable (Arnold and Bennett, 1984; Garland, 1988; Tsuji et al., 1989; Jayne and Bennett, 1990) and repeatable, both over short time periods (e.g., Bennett, 1980; Garland, 1985; van Berkum et al., 1989) and under field conditions for as long as 1 year (Huey and Dunham, 1987; van Berkum et al., 1989; Huey et al., 1990; Jayne and Bennett, 1990). Thus, they possess a suite of features (variability, heritability, repeatability) that make them potentially liable to selection (Bennett and Huey, 1990).

In this study, we examine the differential

survivorship of individuals of measured size and locomotor capacity in a natural population of garter snakes (*Thamnophis sirtalis fitchi*). We have commonly observed active diurnal foraging of these animals, and locomotor performance may be an important feature of their biology. Reptiles have frequently served as useful systems for long-term field studies (e.g., Huey et al., 1983; Seigel et al., 1987b), because they may occur in populations of very high density and have relatively low vagility, permitting repeated longitudinal sampling of individuals. They can be easily captured and manipulated; individuals can be marked and returned to the field or kept in the laboratory for long periods (e.g., Arnold, 1981). We followed a lab-born cohort of snakes for 3 years, and supplemented these data with observations on many other individuals within the same population, recapturing and remeasuring individuals on a yearly basis. We have reported elsewhere (Jayne and Bennett, 1990) data on cross-sectional and longitudinal allometry, repeatability, and heritability of locomotor performance in this population of snakes.

STUDY ANIMALS

Natural History of the Population

Some aspects of the natural history of this population of garter snakes are helpful when considering the findings of this study. Snakes are most active at the site from May through August with temperature and moisture apparently affecting the exact periods of activity. Although snakes at this site may emerge from hibernation as early as April (S. Arnold and C. Peterson, pers. comm.), cold spells in the late spring commonly disrupt activity. For example, only a total of 22 snakes (all of which were inactive and under debris) were captured during a cool period in the first 3 weeks of May 1988, whereas a few hours of collecting in a single day in June could often yield more than 80 snakes. The area of the site with standing water reduces from about 30 × 80 m to a circular remnant pond about 10 m in diameter in August. Although young of the year are easily collected in early August, larger snakes become scarce during this time as the site continues to dry. By mid-October, surface

activity for all ages of snakes is uncommon. Hence, neonates do not experience an entire active season until the second summer of their life, and many neonates recaptured in the early summer have primarily spent their time in hibernation.

To estimate population size, an intense search of the site during 29–30 June 1987 yielded 98 snakes. Using a Lincoln index on the numbers of recaptures and snakes known to be marked and alive in each of the previously used age classes, the population size was estimated as 908. Because birth of young generally occurs from the last week of July until mid-August this figure does not include young of 1987, but the 1985 sample suggests this number of animals exceeds 300. Consequently, this study has sampled a relatively large portion (e.g., about 50% of the yearlings in 1986) of the entire population.

Estimating age of first reproduction of females is facilitated by knowing the size and precise age of individuals belonging to a lab-born 1985 cohort. Of the six females belonging to the 1985 cohort captured during July 1988, none was gravid and the maximum SVL and mass observed were 37.4 cm and 20.8 g, respectively, and the means of these quantities were 35.0 and 16.7, respectively. During 4 years of our studying this population, the smallest SVL and mass (postparturition) ever observed for a gravid female were 44.0 cm and 32.3 g. Thus, at least for animals born in 1985, the females apparently will not reproduce until after they are 3 years old; and, in light of the size difference with known reproductive individuals, females may not reach adult reproductive condition until their fourth year of life. This finding differs from three other studies of *Thamnophis sirtalis* (different subspecies from nonmontane areas) that found that snakes were reproductive after 2 years of age (Fitch, 1965; Stewart, 1968; Gregory, 1977). The greatest time between recaptures gives some indication of maximum longevity, and we captured two snakes 7 years after being marked and released by Kephart (1981). Therefore, the 1-year intervals over which survivorship was monitored during this study represents a sizable fraction of the life span of an individual snake. Further, any selection detected on

yearling animals in this study must have occurred prior to reproduction.

We know very little about the importance of predation on this population of garter snakes, but some sympatric species of vertebrates are potential predators. The only instance of predation observed directly involved a robin (*Turdus migratorius*) that flew away carrying in its beak a small snake that appeared to be yearling size or smaller. Other potential avian predators observed at the site include several species of raptors and sandhill cranes (*Grus canadensis*). Cattle often graze at this site, and on eight occasions crushed, dead *Thamnophis sirtalis* were found in the hoof prints of cattle. Other species of artiodactyls that potentially could trample snakes at the site include deer (*Odocoileus hemionus*) and pronghorn antelope (*Antilocapra americana*). On three occasions, coyotes (*Canis latrans*) were seen at the pond. There also appear to be badger (*Taxidea taxus*) burrows in close proximity to the pond, and badgers were observed directly at another site approximately 10 km away. Although the site is within the geographic range of some predominantly ophiophagous species of snakes (e.g., *Lampropeltis*), the only other snake species collected at the site was *Thamnophis e. elegans*, which never exceeded 5% of a sample, and *T. elegans* are known only rarely to consume snakes as prey (Wright and Wright, 1957; S. Arnold and C. Peterson, pers. comm.). Giant water bugs (Belostomatidae) are also found in the pond, and will capture and kill neonatal snakes in staged encounters (pers. obs.). We found only four additional dead snakes other than the trampled snakes, and these showed no obvious signs of predation.

Study Site

The study population of *Thamnophis sirtalis fitchi* was located approximately 6 km southwest of Eagle Lake in Lassen County, California (40°31'N, 120°51'W) at an altitude of about 1,800 m. This population of *Thamnophis* is one of many in the area that have been studied extensively by Arnold and his colleagues (e.g., Kephart, 1982; Kephart and Arnold, 1982); hence, valuable background information on demography and natural history are available. The site

of collection consists of a small (50 × 100 m) temporary pond in a meadow surrounded by mixed conifers (mainly *Pinus jeffreyi*) and Great Basin sage (*Artemisia tridentata*). Large numbers of snakes could be readily collected around the edge of the pond where the amphibian prey (*Pseudacris regilla* and *Ambystoma macrodactylum*) were most abundant. Most of the meadow appears natural and floods with the spring thaw, but a small portion (10 m diameter) of the flooded area appears to have been artificially deepened. The site is currently grazed by cattle. In the surrounding area, there is a rather patchy distribution of meadows and ponds with which *Thamnophis* is associated. During 4 years of collecting in this study and previous collecting (Kephart, 1981), no immigration or emigration has been detected between this site and the other closest (9 km) ponds with *Thamnophis* populations.

MATERIALS AND METHODS

Collecting Procedures

The first collection of snakes was made from 22 to 30 June 1985. Forty gravid females were held in captivity at U.C. Irvine until they gave birth (29 July to 18 August 1985) to 275 offspring, which will be referred to subsequently as the 1985 cohort. Within 2 days of birth, performance testing was started. Within 8 days of the last performance test, these neonates were released at the study site. From 15 June through 24 August 1986, 449 additional nongravid snakes of various ages were captured, tested for locomotor performance in a lab in Susanville, California, and released. Included in the samples of 1986 and other years were individuals from the 1985 cohort that were recaptured and remeasured. Because of logistical considerations involved with testing locomotor performance of captured snakes, generally no more than 50 individuals were captured and released per week. Numbers of snakes (including recaptures) collected from 28 May to 3 August 1987 and during May and July 1988 were 552 and 292, respectively. Because collecting and recapture success during 1988 was relatively poor, survivorship from 1987 to 1988 was not analyzed. For 1986–1988, all snakes were released within 10 days of their capture.

After testing and before release, all snakes were marked by clipping a unique identification code on the ventral scales. This method of marking is not harmful to the snakes, and it persists for long periods (Brown and Parker, 1976): we have captured *Thamnophis sirtalis* with marks (made by Kephart, 1981) that were more than 7 years old. Snakes also were given a mark to indicate when they had been tested, allowing us to minimize disturbance of recently released individuals during additional collecting. Animals were captured readily by hand (as many as 100 in an hour) as two or more people searched the short grass around the perimeter of the pond and overturned objects. Very few snakes sighted were not captured.

If a snake was not recaptured at any time during the study, we assumed it was dead. We integrated the recapture information from all years of the study to determine the survivors at a given point in time. For example, snakes released during 1985 and recaptured in 1987 but not in 1986 would be counted as surviving during the period from 1985 to 1986. Consequently, in some of the tables that follow, the numbers of animals recaptured and tested during a single season were always less than the number of survivors during that same time interval.

Testing Protocol

Within 3 days of birth or capture we began a series of tests for locomotor performance. Greater detail of testing procedures can be found in Jayne and Bennett (1990). All tests were conducted on snakes with a body temperature of 30°C (range = ± 1.0°C), which approximated the normal field activity temperature of this population (pers. obs.). Cloacal temperatures recorded from 40 active individuals (\bar{x} = 29.99, SD = 1.60, range = 25.0–32.4°C) during July 1987 confirmed that the testing temperature closely matched field active temperatures. On both days 1 and 2 of testing, two trials for burst speed were performed. For each trial, snakes were chased twice along a computerized race track (Huey et al., 1981) and the speed over the fastest 50 cm was recorded. The mean of these four trials was used as the burst speed performance of each individual. Many previous studies of burst speed have used a

single value of maximal observed performance (e.g., Bennett, 1980; Huey, 1982; Garland, 1988). In this study we have analyzed mean values as the best predictor of how an animal will respond at any particular time. Because it is nearly impossible to determine the extent of either measurement error or behavioral variation versus physiological capacity, we used mean values to minimize the potential effects of aberrant response by the animals during performance tests. For example, when we determined the variance component attributable to litter (discussed in more detail later) for the burst speed residuals of the 1985 cohort, a slightly higher value (14.1%, $P = 0.002$ versus 13.1%, $P = 0.005$) was obtained for the mean of the fastest speed from each of four trials versus the value for the single fastest burst speed. In light of this result, and the goal of the project to study the predictive value of heritable variation for survivorship, means rather than single maximum values were used. Hence, although mean values were used for statistical analyses, the tests were designed to determine the performance of animals in response to stimulus that appeared sufficient to prompt maximal performance.

On days 3 and 4 of testing, one trial of endurance per day was conducted. Endurance was measured as the time (to the nearest 0.01 min) snakes crawled on a treadmill moving at a constant speed, and the mean of the two endurance trials was used as the score for each individual. The measures of endurance on neonates during 1985 were made with a tread speed of 0.4 km/hr, whereas all other tests used a tread speed of 0.5 km/hr. On both days 5 and 6 of testing, one trial of distance capacity was performed. Distance capacity was measured as the distance (to the nearest 0.1 m) a snake crawled around a stationary circular track before stopping and assuming a defensive posture. During this test snakes were chased continuously with the experimenter's hand, which tapped the snake's tail and scraped the substrate immediately behind the snake. The mean of these two trials was used for further analysis. In contrast to the endurance test, snakes in the distance capacity test did not generally move with a constant speed. Instead, they usually moved rapidly

at the beginning of the test and then slowed gradually. After the performance tests of each snake, length was determined to the nearest millimeter and mass was determined to the nearest 0.1 g.

Statistical Analysis

Unless otherwise stated, the PC+ version of SPSS was used for statistical analyses, the criterion for significance was $P < 0.05$, and all log transforms were base 10. All measures of locomotor performance were size-dependent, and cross-sectional allometric scaling relationships between performance and snout-vent length (SVL) were calculated using least-squares regressions of log-log transformed data. Regressions relating log mass, endurance, and distance capacity to log SVL were linear, whereas the regression relating log speed to log SVL contained a significant quadratic term (for more detail see Jayne and Bennett, 1990). Residual values were calculated as the difference between an observed log value and the value predicted from the regression with log SVL as the independent variable. Because significant growth of snakes occurred during the protracted periods of sampling necessary to accumulate large samples, residuals were used as a "size-corrected" measure that allowed meaningful comparison of the performance of different size and age snakes. For snakes with SVL < 35 cm measured during 1986, the sex of the snakes did not significantly affect the mass, burst speed, or endurance predicted for a given SVL (Jayne and Bennett, 1990). With only two exceptions, residuals were calculated from the cross-sectional sample of the population made during 1986. Because endurance was measured at a different tread speed in 1985 and distance capacity measurements were done by other experimenters, residuals of these tests were calculated from the 1985 tests of neonates. An analysis of selection on residual values calculated from different scaling equations for each size class of snakes is presented in an appendix.

Because methods of relating survivorship to quantitative traits are still being developed and debated (e.g., Lande and Arnold, 1983; Mitchell-Olds and Shaw, 1987; Schluter, 1988; Crespi and Bookstein, 1989), we analyzed our results using one paramet-

ric and one nonparametric method. For the former, Lande and Arnold (1983) proposed that survivorship could be analyzed as the dependent variable in a multiple regression model with independent variables consisting of the measured quantitative traits. For this regression analysis a value of 1 indicated survivors and 0 indicated nonsurvivors. If an independent variable in the regression has a significant slope, the trait has predictive value for survivorship. A significant slope of a linear term suggests directional selection. Squaring the difference between the mean value of a trait and that observed for an individual yields another quantity that can be entered into the regression model. If this quadratic quantity has a significant negative slope, then stabilizing selection is suggested. To test for stabilizing selection, regressions with a lone quadratic term, as well as a combination of a linear and a quadratic term were calculated. As an exploratory tool to determine the reliability of conclusions regarding the importance of different independent variables for predicting survivorship, several additional multiple regressions were calculated. Because of the multiple comparisons involved in this approach, the individual tests of significance necessarily will be minimally informative.

Because of the reliance on the regression analyses on many assumptions (Mitchell-Olds and Shaw, 1987), we also used a nonparametric procedure. The key question of interest is whether survivors were a random subsample from some initial distribution of a quantitative trait. To address this question most directly, we used a type of a sampled randomization test (Sokal and Rohlf, 1981 pp. 791–794). A computer program was written that drew random subsamples (each with N = number of observed survivors) from a file containing all the scores of a quantitative trait for some initial group of snakes. The mean and variance were determined for each random subsample and compared to the quantities observed for the actual survivors. We assumed a priori that higher values of performance should be more likely to survive (thus, one-tailed probabilities were used). We used 1,000 samples to estimate the probability of a randomly drawn subsample having a trait mean great-

er than that observed for the survivors. A low probability of obtaining the mean observed for survivors suggests directional selection. Because the original distribution was used for generating random samples, no assumptions were made about the normality of the original distribution. Decreased variance combined with no change in the mean of a trait has been used as supporting evidence for stabilizing selection (reviewed in Endler, 1986). Hence, results of the randomization test indicating no change in mean and a low probability of obtaining a variance as small as that observed for survivors suggest stabilizing selection.

When either the regression method or the randomization test suggested that selection occurred, a cubic spline function (Schluter, 1988) was used to estimate the fitness function. Because this method does not calculate the probability that selection has occurred or the probability of directional versus stabilizing selection, we primarily used it to check its congruence with the other two methods of analysis. For all analyses of survival from 1 year to the next succeeding year, measurements made during the first year were used as the initial distribution of the quantitative trait and as the values of the independent variables in the regression equations.

RESULTS

1985 to 1986 Survival: 1985 Cohort Neonatal Traits

Size.—Of the 275 snakes in the 1985 cohort, 79 survived until the summer of 1986 and 45 snakes survived to 1987. Table 1 summarizes the means of traits measured within 8 days of birth, and trait means also are listed for those snakes that did or did not survive until 1986. Table 2 lists the results of the randomization tests and regression analyses that were used to determine if the measured traits had predictive value for survivorship. Table 3 reports correlations among size and performance variables in the original 1985 data.

Snout-vent length (SVL) at birth is strongly implicated as being important for survival during the first year of life, which includes a period of activity during late summer, hibernation from fall to late spring

TABLE 1. Summary of means and standard deviations of measurements made in 1985 on the 1985 cohort within 8 days of birth. Samples include all animals measured and released ($N = 275$), survivors in 1986 ($N = 79$), and nonsurvivors ($N = 196$). Residuals are calculated on SVL. Units for SVL, M, MR, V, E, D, VR, ER, and DR are cm, g, log(g), cm/sec, min, m, log(cm/sec), log(min), and log(m), respectively.

	All		Survivors		Nonsurvivors	
	Mean	SD	Mean	SD	Mean	SD
Size						
SVL	17.824	0.973	18.005	0.745	17.752	1.042
Mass (M)	2.372	0.362	2.403	0.335	2.359	0.372
Mass residual (MR)	0.0574	0.0447	0.0506	0.0423	0.0601	0.0453
Performance						
Speed (V)	33.575	5.447	33.546	4.655	33.586	5.735
Endurance (E)	6.473	3.473	7.004	3.915	6.258	3.254
Distance (D)	25.453	16.724	28.033	19.271	24.408	15.452
Performance residual						
Speed (VR)	-0.0430	0.0808	-0.0488	0.0642	-0.0407	0.0864
Endurance (ER)	-0.0003	0.2423	0.0171	0.2485	-0.0073	0.2395
Distance (DR)	0.0001	0.2228	0.0159	0.2277	-0.0063	0.2205

followed by a summer period of activity of variable duration. The randomization test revealed there was a probability of only 0.022 that a randomly drawn sample of 79 individuals would have a mean greater than that observed for the 79 surviving snakes. Figure 1 shows the frequency distribution of SVL for all of the 1985 cohort and for the 1986 survivors, and these distributions suggest truncation selection occurred against the shortest individuals. None of the nine

shortest snakes ($12.1 < \text{SVL} < 16.1$) survived to 1986. Figure 1E illustrates the fitness functions as estimated both by the (linear) regression method and by the cubic spline method (Schluter, 1988). The variance of the mean SVL for the 1986 survivors was also rather low as indicated by a probability of 0.052 that a randomly drawn sample would have a smaller value of this quantity. The slope of a regression predicting survival from SVL was nearly significant

TABLE 2. Probability of selection on phenotype from 1985 to 1986 for the 1985 cohort measured by two different statistical techniques. For randomization test P = probability (one-tailed) that observed mean of survivors will be exceeded by a random sample of equal size or that random sample will have variance less than observed variance. For the regression method the regression coefficient, its standard error and significance level, and the standardized regression coefficient are given. For regression P = probability (two-tailed) that coefficient is different from 0.

	Statistical test					
	Randomization		Regression			
	P for mean	P for var.	Coef.	SE	P for coef.	Std. coef.
Size						
SVL	0.022	0.052	0.0584	0.0280	0.051	0.118
Mass	0.300	0.186	0.0678	0.0755	0.371	0.054
Mass residual	0.972	0.213	-0.9801	0.6100	0.109	-0.097
Performance						
Speed	0.497	0.135	-0.0003	0.0050	0.958	-0.003
Endurance	0.052	0.859	0.0127	0.0078	0.108	0.097
Distance	0.050	0.872	0.0027	0.0016	0.105	0.098
Performance residual						
Speed	0.725	0.302	-0.2538	0.3388	0.454	-0.045
Endurance	0.243	0.641	0.0853	0.1129	0.450	0.046
Distance	0.191	0.607	0.0919	0.1231	0.456	0.045

TABLE 3. Correlation matrix (Pearson's r) of variables measured within 8 days of birth of the 1985 cohort. $N = 275$ except for correlations involving either distance capacity or its residual ($N = 274$). S86 and S87 indicate survivorship during 1986 and 1987, with values of 1 and 0 indicating survival and death, respectively. Other variables are as listed in Table 1. ', *, and ** indicate two-tailed $P < 0.10$, 0.05, and 0.001, respectively. P values were calculated using a parametric test.

	SVL	M	MR	V	E	D	VR	ER	DR
S86	0.12'	0.05	-0.10	-0.01	0.09	0.10	-0.05	0.04	0.05
S87	0.08	0.03	-0.08	0.03	0.02	0.08	<0.01	<0.01	0.09
SVL	—	0.78**	-0.34**	0.55**	0.29**	0.27**	0.07	-0.01	<0.01
M	—	—	0.31**	0.44**	0.18*	0.21**	0.04	-0.07	0.03
MR	—	—	—	-0.17*	-0.17*	-0.11'	-0.05	-0.07	-0.03
V	—	—	—	—	0.39**	0.34**	0.81**	0.35**	0.30**
E	—	—	—	—	—	0.17*	0.27**	0.85**	0.14*
D	—	—	—	—	—	—	0.21**	0.10'	0.87**
VR	—	—	—	—	—	—	—	0.45**	0.38**
ER	—	—	—	—	—	—	—	—	0.22**

(two-tailed $P = 0.051$), and this P value was much lower than that of any other measured trait. There was no significant slope ($P = 0.17$) for a regression predicting survivorship from a quadratic term of SVL (standardized to mean = 0) and the cubic spline estimate of the fitness function (Fig. 1E) had no obvious mode; therefore, no stabilizing selection was suggested. The initial distribution of SVL of the 275 snakes that were released (Fig. 1A) had highly significant negative skewness ($g_1 = -1.61$, $t = -10.8$, $P < 0.001$), whereas the distribution of SVL at birth of the 79 snakes surviving to 1986 (Fig. 1C) was not significantly skewed ($g_1 = -0.25$, $t = 0.92$, $P > 0.2$), and this change in skewness is consistent with the results expected for truncation selection acting on the negative tail of the distribution. The distribution of SVL at birth of the 45 snakes surviving to 1987 also was not significantly skewed ($g_1 = -0.21$). Neither the randomization test nor the regression method detected significant predictive value of SVL at birth for survivorship to 1987.

Mass was another measure of size at birth, but neither the randomization test nor the regression analysis suggested that this trait had predictive value for survivorship (Table 2). Similar to SVL, the initial distribution of mass had significant negative skewness ($g_1 = -0.35$, $t = 2.36$, $0.01 < P < 0.02$).

The mass residual (MR), predicted from a regression of log SVL, indicates snakes that are relatively heavy (positive value) or relatively light (negative value) for a given

length. Similar metrics have been used as an indication of the "condition" of an animal (van Berkum et al., 1989). Contrary to our a priori expectations that larger values would be favored, the randomization test estimated a probability of 0.028 that the mean of a randomly drawn sample would be less than that of the survivors. The regression predicting survival from MR (Fig. 1F, Table 2) had a negative but insignificant ($P = 0.109$) slope. The cubic spline estimate of the fitness function of MR (Fig. 1F) was nearly identical to that estimated by the regression. As shown in Table 3, there was a highly significant negative correlation between SVL and MR for the 1985 cohort, and this correlation combined with selection against small SVL at birth may account for the low mean of mass residuals observed for the 1986 survivors. Neither the regression predicting survivorship from MR² (with mean MR adjusted to 0) nor from MR + MR² was significant, the cubic spline estimate of the fitness function has no distinct mode, and the randomization test also revealed the variance of MR of survivors was not particularly low, suggesting no stabilizing selection on MR. The initial distribution of MR ($g_1 = -0.05$, $N = 275$, Fig. 1B) was not significantly skewed.

Locomotor Performance.—When examining the predictive value of locomotor performance for survivorship, one should recall that all absolute measures of locomotor performance were significantly correlated with SVL (Table 3). Neither the randomization test nor the regression method revealed

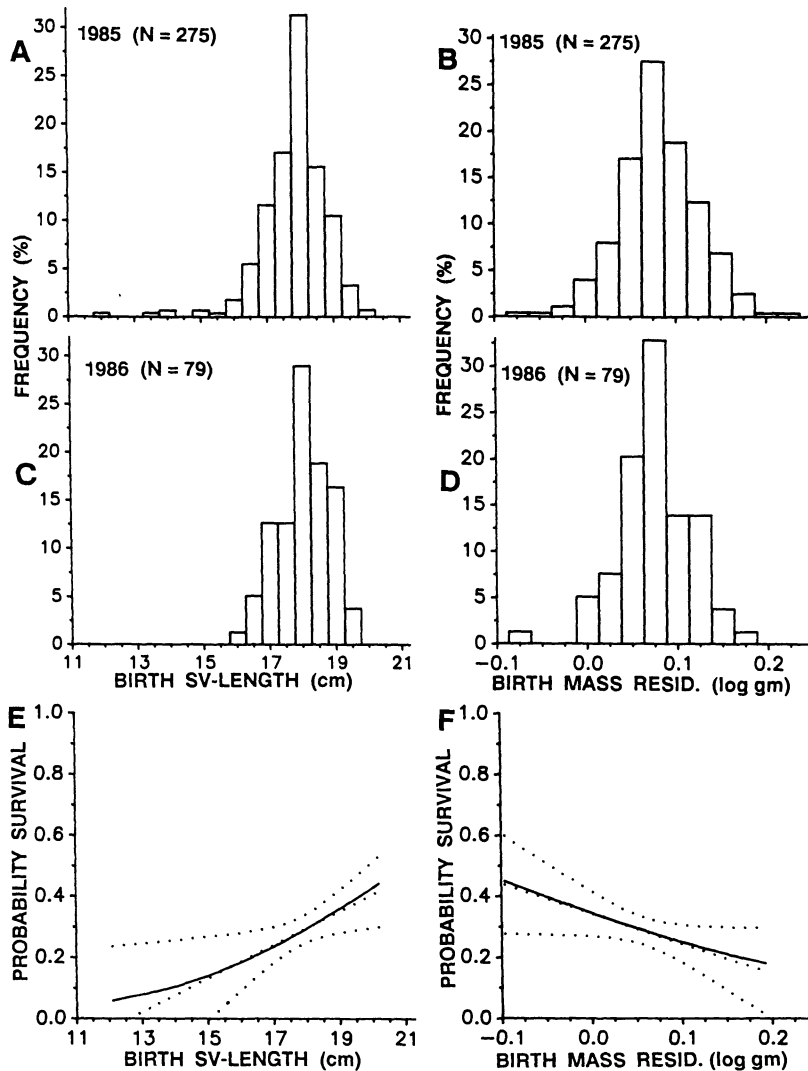


FIG. 1. (A–D) Frequency distributions of snout–vent length and mass residual on S–V length measured within 8 days of birth for the 1985 cohort. A and B are distributions for all snakes that were released in 1985, and C and D are distributions for the individuals that survived to 1986. E and F are estimates of the fitness functions with the dotted lines indicating regression with 95% confidence limits and the solid lines from a cubic spline (Schluter, 1988). (E) The smoothing parameter for the cubic spline was $\ln \lambda = 1$. (F) Note that the regression is not significant, and for the cubic spline $\ln \lambda = 0$.

any significant selection on the absolute measures of locomotor performance (Table 2) of the 1985 cohort, although the probabilities of obtaining the observed means of endurance ($P = 0.052$) and distance capacity ($P = 0.050$) nearly attained significance (randomization test, Table 2). The skewness of the initial distribution of speed for the 1985 cohort was significantly negative ($g_1 = -1.47$, $t = -9.98$, $P < 0.001$; Fig. 2A),

similar to SVL (Fig. 1A). In contrast to speed, the initial distributions of endurance ($g_1 = 1.33$, Fig. 5) and distance capacity ($g_1 = 2.35$) had highly significant positive skewness.

Unlike the absolute measures of performance, the residuals of locomotor performance predicted from SVL showed no significant correlation with either SVL or mass (Table 3). Neither the randomization test

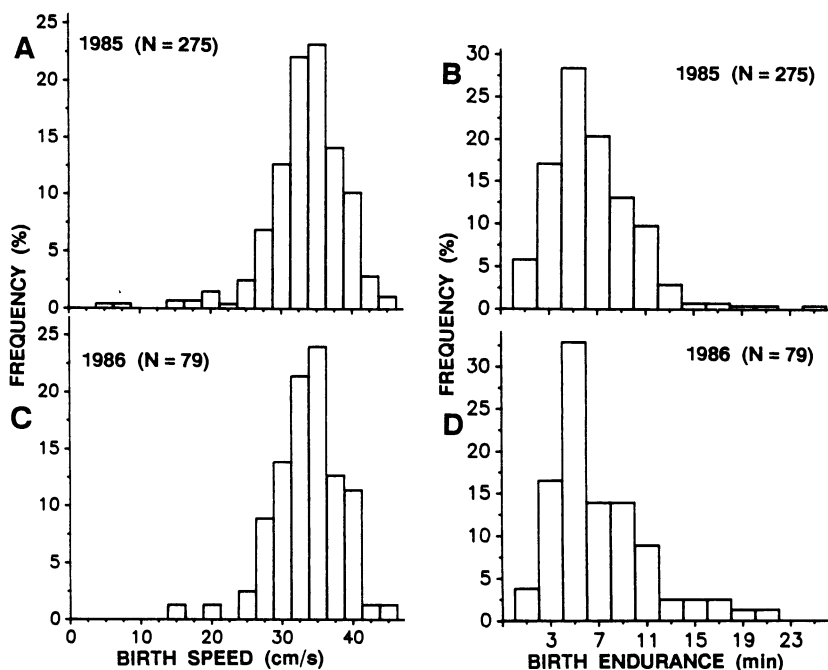


FIG. 2. Frequency distributions of speed and endurance measured within 8 days of birth for snakes in the 1985 cohort. (A, B) Distributions for all snakes released in 1985. (C, D) Distribution of traits for the snakes surviving to 1986.

nor regression analysis detected any significant predictive value of 1985 performance residuals for survivorship to either 1986 (Table 2) or 1987. The initial ($N = 275$) distribution of speed residuals ($g_1 = -4.01$) and endurance residuals ($g_1 = -0.65$, Fig. 3) had significant negative skewness, whereas distance capacity residuals ($g_1 = 0.49$) had significant positive skewness.

No regressions relating 1986 survivorship to any quadratic term (or second degree polynomial) of standardized (mean = 0) neonatal performance or performance residual were significant. Tests of predictive value of the 1985 neonatal locomotor traits for 1987 survivorship were calculated two ways. First, the 45 snakes surviving to 1987 were treated as a subsample of the initial distribution of 275 snakes released in 1985. Second, these 45 survivors were treated as a subsample of the 79 snakes that were alive during 1986. However, none of the measures of lab-born neonatal performance or performance residuals had predictive value ($P < 0.05$) for survivorship to 1987 as indicated by either regression analyses or randomization tests. As shown in Table 3 all

of the correlation coefficients relating survivorship in 1987 to neonatal traits were small and not significant.

Multiple Regressions of Neonatal Traits.— All of the preceding analyses relating neonatal traits to survivorship examined the predictive value of each trait independently. Many of the neonatal traits are significantly correlated to each other (Table 3), and multiple regression is one method for simultaneously evaluating the relative importance of traits that may be correlated (Lande and Arnold, 1983). No consensus exists on how to choose the model for such analysis, and a common occurrence in multiple regression is that several variables entered simultaneously into the equation results in none of them having individually significant coefficients, whereas some subset of all possible independent variables will often have significant partial regression coefficients. For this reason, several different multiple regressions predicting survivorship from neonatal trait were calculated with as many as nine traits (Table 4) as independent variables using a combination of stepwise and forced-fit procedures. However,

TABLE 4. Select multiple regressions predicting 1986 survivorship (1 = survival, 0 = death) from neonatal traits of the 1985 cohort using forced entry of independent variables into the regression. Standardized partial regression coefficients are given for the independent variables. Variables are as listed in Table 1. Below each term of the equation the significance level of the coefficient is given in parentheses and to the left of each equation the overall r^2 value is given with overall significance level of the regression in parentheses.

Equation No.	r^2	Regression				
1	0.027 (0.144)	0.105SVL (0.103)	-0.060MR (0.349)	-0.118VR (0.100)	+0.078ER (0.253)	+0.072DR (0.272)
2	0.039 (0.056)	0.130SVL (0.086)	-0.054MR (0.402)	-0.154V (0.046)	+0.093E (0.160)	+0.094D (0.142)
3	0.017 (0.093)	0.094M (0.140)	-0.126MR (0.047)			
4	0.018 (0.089)	0.096SVL (0.132)	-0.065MR (0.313)			
5	0.018 (0.183)	0.193SVL (0.735)	-0.097M (0.864)	-0.001MR (0.997)		
6	0.029 (0.049)	0.160SVL (0.028)	-0.132V (0.079)	+0.100E (0.129)		
7	0.037 (0.039)	0.148SVL (0.042)	-0.158V (0.041)	+0.098E (0.137)	+0.095D (0.137)	

multiple regression equations are given for only a few of these different models to illustrate the stability (or lack of it) of the importance of an independent variable as a predictor of survivorship (Table 4).

Table 4 lists the standard partial regression coefficients (Sokal and Rohlf, 1981 p. 621) for some of the multiple regressions predicting survivorship to 1986 from neonatal traits of the 1985 cohort. When all of the traits (absolute and residual measures of size and performance) were entered into a regression, none of them had a significant partial regression coefficient. With the exception of SVL, when multiple regressions contained more than four independent variables, none of the partial regression coefficients was individually significant. When two measures of size (SVL and MR) were included as independent variables with either all absolute or all residual values of locomotor performance, none of the standard partial regression coefficients was significant (Table 4, Equations 1 and 2). In fact, when MR was included with any combination of absolute measures of size (SVL or M), none of the partial regression coefficients was ever significant (Table 4, Equations 1-5). The lowest significance level observed for the partial regression coefficient of SVL in any model was $P = 0.028$, and this occurred with SVL, V, and E as inde-

pendent variables (Table 4, Equation 6). When SVL, V, E, and D were in the multiple regression predicting survival (Table 4, Equation 7), both SVL and V had significant ($P < 0.05$) coefficients. Despite the fact that individual regression coefficients were significant in some of the models, the overall F test of the significance of the regression was never significant for any of the multiple regressions without SVL as an independent variable. The low values of the overall r^2 (Table 4) partially result from the fact that the dependent variable is dichotomous, but low values of r^2 may also indicate the low amount of variance in survivorship accounted for by the multiple regression of phenotype. The greatest value of r^2 observed for a multiple regression with five variables was 0.041, and the highest r^2 for a multiple regression with two independent variables was 0.018 (Table 4). Hence, the multiple regressions consistently suggest that SVL at birth is the best predictor for neonatal survival in the first year of life.

1986 to 1987 Survival: Population Analysis

The size of snakes collected and tested during 1986 varied widely (SVL = 18-67 cm). As shown in Figure 4, the SVL of newly caught snakes combined with the size of known age snakes recaptured from the 1985

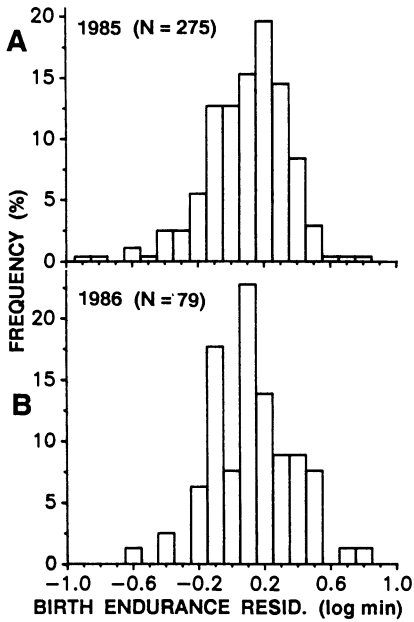


FIG. 3. Frequency distributions of endurance residual measured within 8 days of birth for snakes in the 1985 cohort. (A) Distribution for all snakes released in 1985. (B) Distribution of traits for the snakes surviving to 1986.

cohort facilitated estimating age of the captured snakes based on SVL. Because the importance of traits for survival might be affected by the age of the snake, the 1986 sample was subdivided into three parts: neonatal snakes (born after 30 July 1986), yearling snakes (born during 1985 including those of the 1985 cohort), and older snakes (all remaining).

1986 Neonatal Traits.—Of the 86 snakes that were field-born and tested during 1986, 37 survived to 1987. Table 5 summarizes the means of surviving and nonsurviving neonatal snakes, and Table 6 summarizes the results of randomization tests and regressions predicting survival from single traits. Although the means of nearly all traits of survivors were greater than those of nonsurvivors (Table 5), neither randomization tests nor regressions with single independent variables revealed significant predictive value for survivorship to 1987 (Table 6), results concordant with those for the 1985 cohort during the first year of life. Because of the unknown time between birth and measuring the neonatal snakes captured during 1986, one would expect comparisons

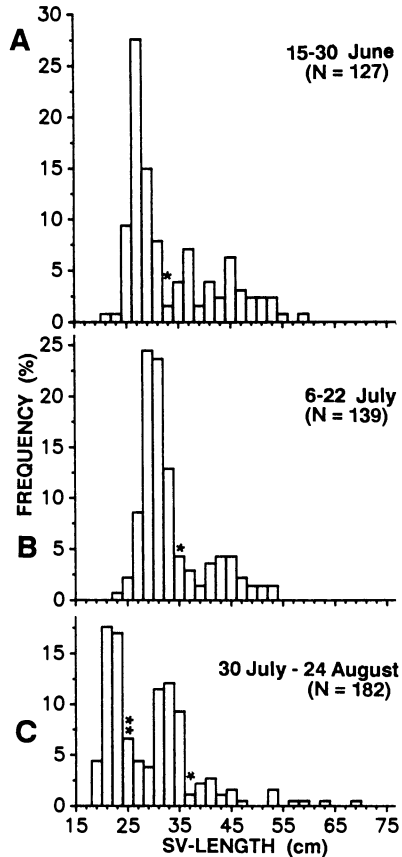


FIG. 4. Frequency distributions of snakes tested and released during the early, middle, and late portions of the 1986 field season. An asterisk indicates approximate division between yearling and older age classes and a double asterisk indicates division between neonatal and yearling size classes. Note that no neonates were collected until 30 July.

of any absolute measures to be minimally informative. The randomization test revealed that the variance of endurance residual was lower than expected by chance (Table 6). Examining the distribution of ER suggested that the low variance of survivors resulted primarily from the death of a single individual with a very low value of ER, and a regression of a quadratic term of ER had no significant slope. Thus, there was no compelling evidence that stabilizing selection was occurring on ER. For all remaining residual traits, neither the randomization test nor a regression of a quadratic term suggested stabilizing selection. Similarly, no multiple regressions of neonatal traits

TABLE 5. Summary of means and standard deviations of measurements for all snakes tested in 1986. N = sample size (1985 cohort animals included as yearlings).

	All		Survivors		Nonsurvivors	
	Mean	SD	Mean	SD	Mean	SD
Neonates						
N	86	—	37	—	49	—
SVL	20.177	1.897	20.376	1.643	20.027	2.055
M	3.321	0.975	3.422	0.881	3.245	1.034
MR	0.0366	0.0524	0.0386	0.0621	0.0352	0.0436
V	45.164	7.407	46.259	5.976	44.337	8.231
E	3.758	1.981	3.754	1.445	3.761	2.305
D	15.969	6.342	16.110	6.577	15.863	6.158
VR	0.0009	0.0605	0.0058	0.0388	-0.0029	0.0725
ER	-0.0180	0.1750	-0.0045	0.1299	-0.0283	0.2019
DR	-0.0017	0.2218	0.0012	0.2193	-0.0039	0.2237
Yearlings						
N	250	—	127	—	123	—
SVL	27.719	2.818	28.131	2.557	27.293	3.006
M	7.529	2.524	7.743	2.263	7.308	2.752
MR	-0.0164	0.0515	-0.0186	0.0459	-0.0141	0.0566
V	68.326	12.040	70.598	11.604	65.980	12.032
E	8.458	5.614	9.074	5.800	7.822	5.340
D	16.128	6.136	16.993	5.865	15.235	6.281
VR	0.0000	0.0513	0.0074	0.0500	-0.0077	0.0515
ER	-0.0081	0.2449	0.0150	0.2399	-0.0319	0.2477
DR	-0.0483	0.1979	-0.0205	0.1730	-0.0769	0.2171
Older						
N	113	—	37	—	76	—
SVL	41.120	6.882	41.835	6.418	40.772	7.070
M	27.081	16.042	28.089	15.589	26.589	16.236
MR	0.0110	0.0522	0.0174	0.0517	0.0079	0.0522
V	87.146	12.316	92.257	9.683	84.658	12.687
E	23.568	19.539	25.341	16.277	22.705	20.890
D	23.404	8.813	25.104	8.875	22.576	8.663
VR	-0.0049	0.0571	0.0168	0.0420	-0.0154	0.0604
ER	-0.0031	0.3098	0.0460	0.2618	-0.0270	0.3281
DR	0.0476	0.1867	0.0819	0.1550	0.0309	0.1982

had significant predictive value for survivorship of the neonates from 1986 to 1987.

1985 Cohort Yearling Traits.—Sixty-seven snakes belonging to the 1985 cohort were captured and retested during 1986 and 32 of these snakes survived to sometime in 1987. Regardless of whether regression or a randomization test was used for analysis, none of the traits measured during 1986 had significant predictive value for the survival to 1987 for this sample (but see 1986 yearling traits below). Speed residual had the lowest significance level of the regression coefficient of any independent variable ($P = 0.18$). No quadratic terms of any of the traits had significant regression coefficients for predicting survival to 1987.

1986 Yearling Traits.—For the field-born

yearlings, 95 of 183 individuals measured during 1986 survived to 1987. Regressions on individual variables of field-born yearlings detected significant stabilizing selection on mass residual ($P = 0.010$), significant directional selection favoring greater absolute burst speed ($P = 0.003$), and burst speed residual was not significant ($P = 0.067$) but it had the greatest predictive value of any of the performance residuals. Using a two-tailed t test on arcsin transformed percentages of survival from 1986 to 1987 indicated no significant differences in the survivorship ($t = 0.91$, $P > 0.20$) of the lab-born yearlings (47.8%) versus the field-born yearlings (52.9%). In addition, when a variable coding for lab-born versus field-born individuals was entered into several mul-

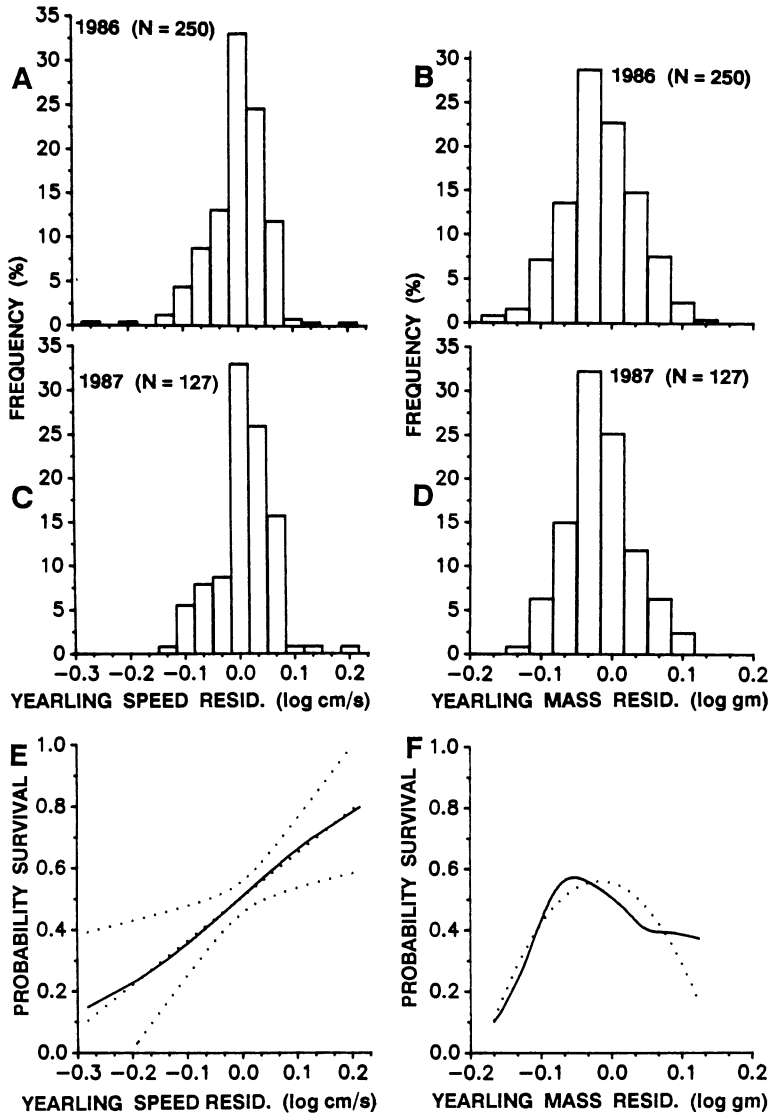


FIG. 5. (A–D) Frequency distributions of speed and mass residuals of yearling snakes measured during 1986. A and B are distributions for all snakes that were released in 1986, and C and D are distributions for the individuals that survived to 1987. (E) Estimates of the fitness functions with the dotted lines indicating a significant regression with 95% confidence limits and the solid line from a cubic spline (Schluter, 1988) with $\ln \lambda = 4$. (F) The dotted line is from a significant regression of a quadratic term of mass residuals (with mean adjusted to 0) and the solid line is from a cubic spline with $\ln \lambda = 0$.

ness function (Fig. 5F) using the cubic spline was very similar to that obtained by using a regression, and this similarity further supports the conclusion that stabilizing selection occurred.

For yearling snakes, residual values of speed and distance capacity appear to have undergone directional selection favoring

greater performance capacity (Table 6). The cubic spline estimate of the fitness function of burst speed residuals (Fig. 5E) suggests directional selection, and it agrees closely with the fitness regression. As shown in Figure 5, the initial distribution of speed residuals had significant negative skewness ($g_1 = -0.90$), and the distribution of VR of sur-

TABLE 8. Select multiple regressions predicting 1987 survivorship from yearling traits of the 1986 sample using forced entry of the independent variables into the regression. Standardized partial regression coefficients are given for the independent variables. Variables are as listed in Table 1. Below each term of the equation the significance level of the coefficient is given in parentheses and to the left of each equation the overall r^2 value is given with overall significance level of the regression in parentheses.

Equation No.	r^2	Regression			
1	0.041 (0.006)	0.137VR (0.030)	-0.138MR ² (0.028)		
2	0.051 (0.005)	0.122VR (0.053)	-0.122MR ² (0.054)	+0.104DR (0.103)	
3	0.051 (0.012)	0.122VR (0.059)	-0.122MR ² (0.057)	+0.104DR (0.128)	+0.001ER (0.981)
4	0.053 (0.010)	0.105VR (0.124)	-0.128MR ² (0.046)	+0.104DR (0.104)	+0.044D86 (0.521)
5	0.042 (0.014)	0.119VR (0.081)	-0.144MR ² (0.023)	+0.045D86 (0.512)	
6	0.022 (0.063)	0.139VR (0.043)	+0.023D86 (0.0736)		
7	0.055 (0.001)	0.181V (0.004)	-0.135MR ² (0.031)		
8	0.055 (0.003)	0.190V (0.072)	-0.135MR ² (0.032)	-0.011SVL (0.916)	

vivors was not significantly skewed ($g_1 = -0.03$). The combined change in the mean (Table 6) and skewness of VR for survivors is consistent with directional selection acting most strongly against the slowest individuals. Regressions predicting survival from VR² and from VR + VR² did not have a significant coefficient for VR², and the randomization test suggested the variance observed for survivors was not unusually small (Table 6). Consequently, stabilizing selection on VR appears unlikely. In addition to the predictive value of VR, absolute speed, V, was significantly correlated ($r = 0.19$, $P < 0.05$) with yearling survival from 1986 to 1987 (Table 7).

Both the randomization test and the regression analysis indicated that selection favored greater values of DR for yearlings from 1986 to 1987. The randomization test found that the variance of DR of survivors was low; however, the regression coefficient of DR² was not significant ($P = 0.09$), suggesting that the reduced variance resulted primarily from directional selection. As with the estimated fitness functions of VR, there was close agreement between the cubic spline and the linear regression.

ER of yearlings just fails to attain signif-

icance ($P = 0.060$) by the randomization test.

Similar to the neonatal measurements of the 1985 cohort, many of the variables measured for the yearlings during 1986 are significantly correlated with each other (Table 7). The date of capture during 1986 (D86, a variable coded for weeks 1-10 of the study) was significantly correlated with some performance variables (e.g., VR and D86, $r = 0.38$, $P < 0.001$) but it was not significantly correlated with 1987 survival (Table 7). MR² had no significant correlation with VR ($r = -0.07$) but did have a significant negative correlation both with ER ($r = -0.20$) and DR ($r = -0.16$), indicating that intermediate values of this morphology were correlated with the greatest endurance capacity. The many significant correlations among performance variables were generally positive (Table 7).

As with the traits of other samples, several multiple regressions were calculated to assess the combined effect of the 1986 traits of yearlings on survivorship to 1987 (Table 8). To determine if the association between measurements and survivorship was obscured by the date of capture, multiple regressions were determined for all possible

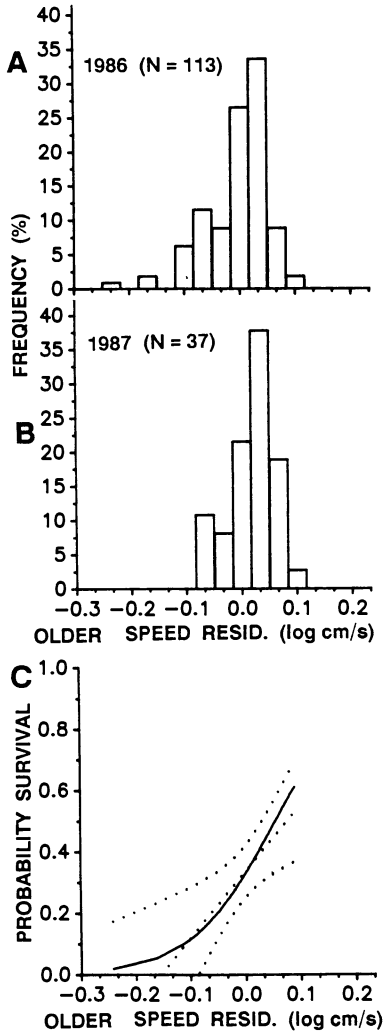


FIG. 6. (A, B) Frequency distributions of speed residuals of older snakes measured during 1986. A is the distribution for all snakes that were released in 1986, and B is the distribution for the individuals that survived to 1987. (C) Estimates of the fitness functions with the dotted lines indicating a significant regression with 95% confidence limits and the solid line from a cubic spline (Schluter, 1988) with $\ln \lambda = -5$.

combinations involving D86 and the four residual variables, but the lack of any significant partial regression coefficient of D86 suggests this variable was not important for predicting survival (e.g., Table 8, Equations 4–6). When all four residual measurements (MR², VR, ER, and DR) were used as independent variables, none of them individually had significant partial regression coefficients but VR and MR² had the lowest (P

< 0.06) and similar significance levels within this regression (Table 8, Equation 3). When only VR and MR² were used as independent variables, they both had significant coefficients (Table 8, Equation 1), and r^2 was higher than that of all but one of the other regressions with two independent variables. Interestingly, the greatest overall r^2 for any two-variable regression involved an *absolute* measure of speed (V) and MR² (Table 8, Equation 7), and this r^2 also was greater than those of many other regressions with more variables (Table 8). When SVL, V, and MR² were entered simultaneously into a regression, the coefficient of MR² was significant, that of VR had a low probability ($P = 0.074$) and that of SVL was not significant (Table 8, Equation 8). Although a univariate regression of DR had some predictive value for survivorship (Table 6), when this variable was entered into regressions with other residual values, it was not significant (Table 8, Equation 2). Thus, multiple regressions indicate that the most important predictors of yearling survivorship were burst speed (or its residual) with greater values significantly favoring survival and mass residual with intermediate values favoring survival.

1986 Older Traits.—Of the 113 snakes measured during 1986 in the older age classes (including all snakes having overwintered twice or more), 37 survived to 1987. As shown in Tables 5 and 6, both the randomization test and a regression suggest there was significant directional selection favoring larger values of VR. Figure 6 illustrates the initial distribution had significant negative skewness ($g_1 = -1.25$), whereas that of the survivors was not significantly skewed ($g_1 = -0.71$), supporting the conclusion that the slowest individuals had a marked disadvantage. The regression and cubic spline estimates of the fitness function were overall similar, but the spline gave a shallower fitness gradient than the regression for the lower values of VR (Fig. 6C). The randomization test indicated that the variance observed for VR of survivors was low (Table 6), but the quadratic regression of VR was not significant, and the frequency distributions suggest that the low variance resulted from directional rather than stabilizing selection. Similar to the yearling snakes, V

was also significantly correlated ($r = 0.29$) with survivorship, and the standardized regression coefficient of V (0.290) was highly significant ($P = 0.002$) when it was used as the only independent variable.

Neither the randomization test nor regressions suggested either directional or stabilizing selection occurred for values of MR, ER, or DR. The date of capture during 1986 was significantly correlated with speed ($r = 0.28$), speed residual ($r = 0.28$), mass ($r = 0.21$), and mass residual ($r = 0.35$), whereas the correlation of D86 and survivorship was not quite significant ($r = 0.17$, $P = 0.06$). Whenever D86 was entered into a multiple regression including V or VR, its regression coefficient was not significant.

DISCUSSION

Selection on Size

In the 1985 cohort, neonatal snakes with small snout-vent length were at a selective disadvantage for survivorship during the first year of their life. General discussions of natural history have emphasized the theoretical importance of size of offspring at birth (reviewed in Calder, 1984), and numerous studies of the reproductive ecology of squamate reptiles have documented significant variation in size of offspring among individuals within a population, among different populations, and among different species (see recent reviews by Seigel and Ford, 1987; Dunham et al., 1988). However, the work of Ferguson and Fox (1984) on the lizard *Uta stansburiana* is the only previous study on a natural population of squamate reptiles that has reported a significant positive relationship between offspring size and early survivorship. They found that experimental removal of predators or supplemental feeding negated the advantage of large body size, and they suggested that large size gave lizards an advantage for securing a high-quality territory that had abundant cover and food. Territoriality is unlikely for our study population of garter snakes. Several individuals were often found in close proximity under a single piece of cover, and during the study foraging behavior of neonatal snakes was commonly observed, but not a single case of territorial behavior was seen. The time span for neo-

natal survival in our study was much longer than the 2-week period of neonatal survival considered by Ferguson and Fox (1984), and our study included a period of hibernation that may have favored larger neonatal size in overwintering snakes (note, however, that neither mass nor mass residual was correlated with survival, Table 3).

Feeding of snakes is characterized by the animals consuming prey whole, and ontogenetic variation in capacity for consuming prey (cranial dimensions) is closely related to SVL. At our study site, neonatal snakes feed almost exclusively on the tadpoles and small frogs of the species *Pseudacris regilla*. Because this species of frog at the study site reproduces only for a brief period during the late spring, most individuals have metamorphosed by the time the garter snakes are born; therefore, the limited range in size of *Pseudacris regilla* does not include the smallest sizes of tadpoles for the snakes to consume. Consequently, extremely small neonatal snakes may be at a disadvantage for capturing prey. As discussed previously in more detail, potential predators of snakes at the site appear to be primarily other vertebrates that are large relative to the neonatal snakes, hence the size difference among neonates would appear to be of little consequence to these animals.

Clearly the size of snakes involves many measurements besides SVL. Interestingly, for the two other measures of size of neonatal snakes belonging to the 1985 cohort, mass did not have significant predictive value for early survivorship, whereas the randomization test indicated that mean mass residual of surviving neonates was significantly less than that of nonsurvivors (Table 2). Discussions of reproductive strategies often consider the constraints of energy availability and female body size on the number and size of offspring per litter. For the garter snake, *Thamnophis butleri*, neonatal mass increased with increased female mass but decrease with the size of the litter (Ford and Killebrew, 1983). We used the data from 34 females that had 2 or more offspring per litter and were captured during the 1985 sample to examine variation in reproductive effort. For this sample the maximum number of offspring per litter was 16, whereas the maximum ever observed

during our study was 27 offspring for a female with an SVL = 70.5 cm. For the 1985 sample, number of young per litter (Y) was significantly related to female SVL (in centimeters) by the regression $Y = 0.35\text{SVL} - 11.40$ ($r^2 = 0.27$, $P = 0.002$). However, for this sample of females, multiple regressions predicting any mean measure of offspring size (SVL, M, or MR) per litter found no significant effect of either female size (mass or SVL) or the number of young per litter. Similarly, for this population Garland (1988) found no significant correlation between log (offspring SVL or mass) and log (litter size). Hence, for our study population no conspicuous trade-offs between size of offspring and litter size are evident. When considering neonatal snakes in the 1985 cohort there was a highly significant negative correlation between SVL and mass residual of individuals (Table 3) and the litter means ($N = 34$) of SVL and MR for 1985 had negative but nonsignificant correlation ($r = -0.21$, two-tail $P = 0.24$). The negative correlation between individual SVL and MR may indicate that if a fixed amount of energy is allocated for a single embryo, either a faster rate or longer duration of embryonic growth will produce a neonate with greater SVL but leaner body composition (lower MR).

For samples of snakes other than the 1985 cohort neonates, the growth that occurs during the protracted period of sampling prohibits meaningful comparisons of the importance of absolute size (beyond the influence on reproductive capacity). However, comparisons of mass residuals among older snakes did reveal some interesting trends. For example, MR of yearlings apparently underwent stabilizing selection from 1986 to 1987 (Fig. 5). Our expectation was that increased MR indicated relatively fat individuals, a condition favoring overwinter survival of snakes which must rely on energy stores during this period of inactivity. Selection against low values of MR in yearlings is consistent with this interpretation, but the selection against high values of MR is not, and factors working against high MR remain unclear. There may be a trade-off between distance capacity and MR as indicated by the highly significant negative correlation between MR and DR in yearlings (Table 7), but the nonsignificant

partial regression coefficient of DR (Table 8) in the equation predicting survivorship from MR, VR, and DR suggests that the simple correlation between DR and survivorship is a correlated response to the stabilizing selection on MR and not the reverse. Because MR also shows a significant positive correlation with the week of the active season (Table 7), it is also tempting to conclude that body composition changes seasonally in these animals. Clearly if everything else is the same for snakes of given SVL, fatter individuals will have greater MR; however, greater MR may also indicate individuals that are lean but relatively stout for a given length. Given the central role that accumulation of fat probably plays in the reproduction and hibernation of temperate snakes (Seigel and Ford, 1987; Lillywhite, 1987), future studies clarifying whether MR results from differential lean growth or fat accumulation will be most informative in light of the correlation between mass residual and survivorship. It is important to bear in mind the stabilizing selection observed on this parameter when a form of mass residual is used as an index of "condition" or health (e.g., van Berkum et al., 1989): animals with a high index may be at a selective disadvantage under natural conditions.

Selection on Performance

For neonates belonging to the 1985 cohort and field-born neonates of 1986, locomotor performance residuals had no predictive value for survivorship to the first year of life. In light of the significant effect of neonatal SVL on survivorship (Table 2) and the high correlation between SVL and absolute measures of performance (Table 3), we have chosen analysis of locomotor performance residuals as the most conservative approach for detecting the relationship between locomotor performance and survivorship. If locomotor performance were important to survivorship, one would expect selection for this trait to operate while the animals were active, and the lack of an entire active season between birth and recapture of the neonatal snakes could have obscured the influence of performance traits on survivorship in this age class.

In the yearling and older age classes of

snakes, faster burst speed residuals were favored (Table 6), and despite the confounding influence of size, absolute burst speed correlates significantly with survivorship (Tables 7 and 8). It seems likely that absolute speed is ecologically more relevant than its residual value because absolute speed will better predict the outcome of escaping the predator or the ability of a snake to chase prey. For lower vertebrates, there are few studies that document the effect of burst speed on the outcome of predator-prey encounters. Taylor and McPhail (1985) compared two populations of coho salmon with different mean size of newly emerged fish and found that one population had significantly greater mean size and burst speed. When these small fish were placed into an enclosure with a predaceous fish, individuals from the faster (and larger) population were significantly more likely to survive; however, one cannot rule out the possibility that larger size by itself increased the chance of escaping a predator. Recent studies of lower vertebrate locomotion have emphasized the importance of initial acceleration in addition to maximal speed for prey to escape predators (e.g., Huey and Hertz, 1984; Webb, 1986), but the extent to which ability to accelerate and attain top speed are correlated is still not well understood for snakes, and this should be a fruitful area for future inquiry.

Another factor relevant to consideration of the importance of burst speed is that the reproductive condition of females influences this measure of performance. Seigel et al. (1987b) found that the speed of pregnant *Thamnophis marcianus* was less than that of nongravid individuals, furthermore, significant variation was found among different stages of pregnancy within individuals. Similarly, Jayne and Bennett (1990) found that gravid females from the study population of *Thamnophis sirtalis* had significantly lower average burst speed (74 cm/sec) compared to similarly sized nongravid females (89 cm/sec). Because of the effects of pregnancy on performance, gravid females were not included in the analysis of survivorship of the older snakes to avoid confounding effects associated with pregnancy itself with effects of performance. For the 497 nongravid *Thamnophis sirtalis*

tested during 1986, MR^2 had a significant negative correlation with VR ($r = -0.105$, $P < 0.02$) suggesting snakes with intermediate mass for a given length have the best burst speed. For the same snakes, there is also a significant negative correlation between (tail length residual)² and VR; however, the results of performance tests after experimental alteration of the tail length suggest this morphological variation was not actually the causative factor for variation in performance (Jayne and Bennett, 1989). Consequently, despite some correlations between performance and morphology, we still know little about the causative morphological characters underlying differences in speed among individuals within this species.

Greater distance capacity of yearlings was correlated with greater chance of survivorship (Tables 6 and 7), although this variable was not significant when considered simultaneously with speed and mass residuals (Table 8). Distance capacity is the distance traveled by the animal while it regulated its own speed as it was pursued by an experimenter, and this variable may indicate the combination of behavior and physiological capacity that allows snakes to evade some predators. As evidenced by variation attributable to different experimenters in the preliminary stages of this study, there appears to be a large behavioral component to this variable. Snakes stopped at the conclusion of a trial and assumed a defensive display (as in Arnold and Bennett, 1984); however, with continued harassment the snakes often resumed crawling. At the conclusion of trials, snakes also maintained their righting response, and loss of this reflex in snakes has been used by other workers to indicate physiological exhaustion (Pough, 1978).

We assume that speed and distance capacity are more likely to facilitate survival of snakes in predator avoidance than by increasing foraging success. Foraging of the snakes was commonly observed, and rather than pursuing prey at high speeds or for long distances, snakes move slowly until the prey item appears to be detected visually and then there is often a quick lunge at the prey when it is less than about one-half SVL away from the snake.

Endurance capacity measured the ability of the snakes to move a particular distance using a constant speed (of the treadmill). Although snakes could still move and possessed a righting response at the end of endurance trials, once a snake failed to match tread speed three times, further harassment could not generally induce the snake to match tread speed, suggesting snakes were closer to a physiological limit than in the distance capacity test. It is interesting to note that neonatal endurance scores were positively skewed, whereas burst speed scores were negatively skewed (Fig. 2), perhaps indicating different extents of physiological constraints on maximal scores of these measures of performance.

The study site has relatively open habitat and few objects to serve as refugia, and for many other snake species travel to a hibernaculum involves considerable distances (Gregory et al., 1987). The endurance test could correlate with the ability to move between successive refugia or to a hibernaculum. About 100 m from the edge of the remnant pond in the site, a pile of boulders serves as a refuge or hibernaculum. A snake moving continuously at 0.5 km/hr would take 6 min to traverse this distance, and this exceeds the average endurance capacity of a small (SVL = 25 cm) snake by about 0.5 min and is about 49% of the average endurance capacity of a (SVL = 35 cm) medium size individual. Although the randomization test showed a low probability of yearling survivors having the observed mean ER ($P = 0.06$), there was not compelling evidence that endurance residuals were significantly correlated with survivorship for any of the different samples.

General Features and Conclusions

As mentioned previously the methodology of analyses for detecting selection is still being refined. Therefore, we have used a variety of approaches and have looked for congruence of results to deduce which traits have predictive value for survivorship. We have used "significant" only for the sake of convenience and have followed common conventions for probabilities that indicate significance. However, rather than rigidly adhering to arbitrary designations of significance level, we feel it is more instructive

to compare probabilities (listed in tables) to determine the relative importance of traits for survivorship. Along these lines one should note that the probabilities listed for the randomization test are similar to one-tailed probabilities, and the probabilities given for regression coefficients are from a test for whether a coefficient is significantly different from zero and are two-tailed: in Tables 2 and 6, for example, regression probabilities are almost always twice those found by the randomization tests. In this study, similar results were obtained with the regression method, the randomization test, and the cubic spline estimates of the fitness functions. False indication of stabilizing selection has been one of the concerns about using the regression approach for analyzing survivorship (Mitchell-Olds and Shaw, 1987; Schluter, 1988). However, no regressions had a significant quadratic term indicating stabilizing selection unless the cubic spline had a distinct mode (Fig. 5F) and the randomization test indicated that the variance of survivors was lower than expected by chance.

The extent to which observed selection is phenotypic or natural selection (as used by Endler, 1986) depends on the genetic basis of the phenotype. Using the data for 34 litters of the 1985 cohort, which had two or more individuals, a one-way ANOVA was used to test for a significant litter effect and estimate the variance component attributable to litter (see Jayne and Bennett, 1990 for more detail on MR, VR, and ER). All measures of neonatal size had highly significant effects of litter ($P < 0.0001$) with SVL, M, and MR having percentage variance components due to litter of 34, 51, and 36%, respectively. All absolute performance variables also had significant litter effects, although the P value (0.015) of the significance test for litter effect on D (litter variance component = 8%), was much larger than that of either V (15%, $P < 0.0001$) or E (31%, $P < 0.0001$). All residual performance scores had a probability of significant litter effect less than 0.0005, and the litter variance components of VR, ER, and DR were 14, 34, and 13%, respectively. Assuming litters consist of full sibs, the maximum value of heritability is estimated as twice the variance component due to litter, and

the above results agree closely with the litter variance components found for speed residual (28.8%) and endurance residuals (34.8%) using a different sample from this same population of snakes (Garland, 1988). Jayne and Bennett (1990) found residuals of mass and locomotor scores for this population were significantly repeatable for up to 1 year between pairs of measurements. However, for a smaller sample of some captive snakes and magnitude of the variance component attributable to litter decreased for values 6 weeks after birth and ER did not have a significant litter effect after this time (Jayne and Bennett, 1990), indicating litter effects on these variables persist for relatively long but not indefinite periods of time. Hence, the performance residuals of yearling and older snakes may undergo natural selection, but realistically we are unable to quantify the genetic basis of performance traits in these older animals.

The intensity of selection of a trait is dependent on both the steepness of the fitness gradient and the distribution of the trait. One method for quantifying the intensity of selection used recently by Schluter (1988) involves using an estimate of the fitness function (whether parametric or nonparametric) to predict fitness for all values of phenotype and then calculate the variance of these predicted fitnesses and divide by the fraction of survivors squared. Table 9 summarizes such intensities of selection on different samples of garter snakes using both regressions and cubic splines as estimates of the fitness functions. These intensities of selection are within the range of values presented by Schluter (1988), which included survival of sparrows (Bumpus, 1899; Schluter and Smith, 1986), Galapagos finches (Boag and Grant, 1981), and human infants (Karna and Penrose, 1951). Intensity of selection was generally very similar comparing values generated by a regression and cubic spline estimates of the fitness function (Table 9). When VR and MR² were used singly to generate a fitness function, the intensities of selection varied little from that of a multiple regression including both VR and MR² (Table 9). For older snakes the standard partial regression coefficient of VR predicting survivorship was less than twice that of yearlings (Table 6), but the intensity

TABLE 9. Selection intensity estimated as the variance in the values predicted by a fitness function for all individuals in a sample divided by the square of mean survivorship. Fitness functions were estimated both by the regression method and by the cubic spline method. Abbreviations for variables are as listed in Table 1. * indicates MR² used for the regression, and MR used for the cubic spline.

Sample	Variable(s)	Selection intensity	
		Regression	Spline
1985 cohort	SVL	0.0339	0.0355
1986 yearlings	VR	0.0209	0.0240
1986 yearlings*	MR	0.0213	0.0217
1986 yearlings	VR + MR ²	0.0186	—
1986 older	VR	0.1446	0.1642

of selection of VR for these groups showed a nearly 3-fold difference. Using regressions on absolute speed, V, to estimate the fitness functions of yearlings and older snakes yielded intensities of selection of 0.0092 and 0.0185, respectively.

None of the analyses in this study establishes the causative factors of selection operating on this population, but some of the measured traits clearly have predictive value. Given the complexity of many natural systems, it is still uncommon even to have quantified the predictive value of traits of animals for survivorship. Physiologically oriented studies of locomotion often emphasize study of maximum performance in the absence of information about the biological relevance of such data (Bennett, 1989), and the present study sheds some light on such a question. The problem of sample size presents a dilemma for obtaining more detailed natural history that may indicate why a particular trait is undergoing selection. For example, in our study 67 yearlings belonging to the 1985 cohort were tested and released in 1986 and 32 of these individuals survived until 1987; however, no significant selection was detected for this sample. In contrast, when all 250 yearlings tested during 1986 were examined, significant correlations with survival were found for two traits. Because of the problems of correlated response and unknown mechanisms of selection, significant correlations between traits and survivorship are often the most open to criticism. However, even in the absence of more detailed natural his-

tory, it is difficult to argue that any trait without a significant correlation to survivorship is important at the population level. Thus, a correlative study such as this can considerably narrow the possibilities for which traits are important to animals in a natural population.

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APPENDIX: ALTERNATIVE METHODS OF SIZE CORRECTION

A variety of approaches could be used to attempt to correct for size differences within a sample of animals. Our primary analysis of “size-corrected” measures was based on the difference between an observed value and that predicted from the cross-sectional allometric equations for the entire sample of snakes measured during 1986. This appears to be the best global correction for size of the snakes. Alternatively one could calculate residuals for each of the subsamples (in this case 1985 measures of the cohort, and 1986 measures of neonates, yearlings, and older snakes). We used the latter approach to examine whether the results would be affected by this alternate means of calculation.

Certain scaling relationships over restricted ranges of the independent variables were different from those obtained by a global calculation of the regressions, and in some cases these differences appeared to obscure meaningful interpretation. For example, one may have noticed that the mean mass “residual” of the neonatal snakes calculated from the population sample of 1986 was greater than zero. Hence, these snakes were unexpectedly heavy for their snout–vent length. This finding corresponds well with the observation that most reptiles are born with substantial quantities of yolk (up to more than 25% of total mass at birth) that often last for several days (Bellairs, 1970). The significant negative correlation between these mass “residuals” and with neonatal SVL may yield additional biological insight by suggesting that longer neonates were relatively lighter than shorter neonates. One expects a priori that mass should scale with the cube of SVL, and for the entire population sample of 1986 this was nearly the case [$\log(\text{mass}) = -3.766 + 2.928 \log(\text{SVL})$, $r^2 = 0.977$, Jayne and Bennett, 1990]. However, for the scaling regressions calculated only using the 1985 measures of neonatal snakes, there was a surprising low slope [$\log(\text{mass}) = -2.540 + 2.327 \log(\text{SVL})$, $r^2 = 0.658$] for which the 95% confidence limits (± 0.200) did not include either 3 or the slope found for the entire population. Of course, the mean of the residuals calculated from the latter scaling equation is equal to zero, and there is no significant correlation with SVL of the neonatal snakes. When the scaling relation of burst speed to SVL was calculated for the population sample of 1986, there was a significant quadratic term in the equation (Jayne and Bennett, 1990). Not unexpectedly with the small range in SVL of neonatal snakes, there was no significant quadratic term in the regression predicting neonatal burst speed from only the 1985 neonatal measurements of SVL. The mean of burst speed “residuals” calculated for the 1985 neonates (VR, Table 1) was negative, but this would seem to make sense mechanically if the neonates were unusually heavy for

their length because of yolk stores. Despite the nonzero mean (Table 1) of these neonatal burst speed “residuals” (from the 1986 population equation), there was no significant correlation between this quantity and neonatal SVL (Table 3). Consequently, the method of calculating neonatal residuals from only the neonatal data appears to obscure some biologically interesting phenomena, and it may be problematic when the scaling relationships are not linear.

One may still argue that a nonglobal method of “correcting for size” is the most appropriate method for analyzing the survivorship data. Hence, for burst speed and mass of the 1985 neonates and for the mass and all performance measures of the neonates, yearlings, and older snakes captured in 1986, residuals predicted from $\log(\text{SVL})$ were calculated from scaling regressions using only the measurements of individuals belonging to the sample that was being analyzed for survivorship. To determine if any of the major conclusions would be affected by this different method of size correction, regressions predicting survivorship from these residuals were then analyzed in the manner as outlined previously. For the measurements of the 1985 cohort, 1986 neonates, and the older 1986 snakes, the conclusions for the predictive value of residuals were identical to those reached by making a global correction for size. For the neonatal measures of the 1985 cohort, regressions did not detect any selection for either the recalculated burst speed residual (VR) or the mass residual (MR), and these recalculated residuals had highly significant correlations with those calculated by using the population sample (VR $r = 0.996$; MR $r = 0.942$). Similarly, all four of the recalculated residuals from the 1986 neonates were highly correlated with those obtained from the global size correction ($N = 86$, $r > 0.95$), and regression analysis did not detect any selection on these variables individually or in multiple regressions. For the older snakes tested during 1986 regression analysis only detected directional selection on burst speed residuals ($P = 0.008$) that favored faster individuals.

Similar to the original analysis (Table 8) of the entire sample of yearling snakes tested during 1986 ($N = 250$), regressions detected stabilizing selection on the recalculated mass residuals ($P = 0.024$), marginally significant ($P = 0.050$) directional selection favoring higher distance capacity residual, and no directional ($P = 0.172$) or stabilizing selection on endurance residual. In contrast to the earlier findings, no significant directional selection was detected on the recalculated burst speed residual ($P = 0.136$). When the recalculated distance capacity residual was entered into various multiple regressions, it did not have a significant partial regression coefficient.

Hence, for the reanalysis of 14 residual variables of four different groups of snakes, the burst speed residual of yearlings was the only variable for which conclusions regarding selection differed between the two methods of correcting for size. When the scaling regressions of burst speed with SVL were recalculated, the neonatal snakes had no significant quadratic term [$\log(V) = 0.045 + 1.231 \log(\text{SVL})$; $r^2 = 0.418$], whereas the scaling of burst speed for both yearlings [$\log(V) = -5.540 + 8.794 \log(\text{SVL}) - 2.552 \log(\text{SVL})^2$; $r^2 = 0.658$] and older snakes [$\log(V) = -6.961 + 10.673 \log(\text{SVL}) - 3.191 \log(\text{SVL})^2$; $r^2 = 0.252$] had both significant linear

and quadratic terms in the equations. The scaling equation of burst speed for the entire population in 1986 [$\log(V) = -3.766 + 6.730 \log(SVL) - 1.975 \log(SVL)^2$; $r^2 = 0.854$, Jayne and Bennett, 1990] has a significant quadratic term and a coefficient of determination greater than any of the 1986 subsamples. In view of this complicated quadratic scaling relationship of burst speed with SVL, it remains an open question whether the population scaling relationship or the scaling regression within a subsample is best suited as a correction for the growth of animals that occurred during a sampling period. The fact that absolute burst speed

did have predictive value for the survivorship of yearling snakes from 1986 to 1987 is suggestive that some measure of burst speed is ecologically important for yearlings. Despite these complications in the analysis of yearlings, absolute burst speed, and its residuals calculated by either of the two methods all had predictive value for the survivorship of the older snakes from 1986 to 1987. Consequently, one would still conclude that burst speed is important for the survivorship of a sizable portion of the population that includes reproductive animals.