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ANNUAL VARIATION IN REPRODUCTION IN SNAKES IN A FLUCTUATING ENVIRONMENT

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SUMMARY

(1) We studied annual variation in clutch or litter size in five populations of four species of North American snakes: *Diadophis punctatus* (L.), *Thamnophis radix* (Baird & Girard), *T. sirtalis* (L.), and *Agkistrodon contortrix* (L.), with samples taken over periods ranging from 2 to 15 years.

(2) We found that even after changes in female body size were corrected for, clutch or litter size varied significantly among years in four of five populations.

(3) In three populations, clutch size was higher in years having above-normal rainfall. Furthermore, clutch size in *Diadophis* was significantly correlated with autumn rainfall.

(4) Our data show that clutch size can vary as much among years as it can among populations. We caution investigators that the use of short-term data to compare reproductive traits among geographically separated populations may be misleading.

INTRODUCTION

In a recent review of life-history variations, Ballinger (1983) posed a challenging question for ecologists; are observed life-history variations the result of evolutionary processes, or do these variations reflect non-evolutionary sources? In this review, Ballinger showed that clutch size in the lizard *Urosaurus ornatus* (Baird & Girard) was more dependent on proximate environmental factors than on evolutionary causes, thus supporting the arguments of Gould & Lewontin (1979) that the excessive use of adaptationist explanations for observed life-history variations are potentially misleading.

Detailed information on the frequency and magnitude of intrapopulational variations in life-history traits can be most useful in determining whether the observed variations result from proximate or evolutionary sources (Ballinger 1977, 1983). For example, high variation in reproductive traits such as clutch size or clutch frequency may be correlated with resource availability or environmental conditions, suggesting a proximate basis. Conversely, low variation among years for such traits may suggest a significant adaptive component. Table 1 briefly summarizes data on intrapopulational variation in reproductive traits for a variety of vertebrates. While far from exhaustive, this review suggests that significant variation in reproduction occurs both within and among years for many species, and that this variation is often correlated with either resources or environmental conditions.

Despite a wealth of reproductive data (cf. Fitch 1970; Turner 1977), information on intrapopulational variation for snakes is limited mainly to changes in the proportion of females breeding/year, and then is restricted primarily to the family Viperidae (Aldridge

TABLE 1. Summary of reproductive traits that vary among years in different groups of vertebrates

Group	Parameters varying among years	Critical parameter*	Representative sources
Turtles	Clutch frequency	Clutch frequency	Tinkle <i>et al.</i> 1981 Gibbons, Greene & Patterson 1982
Lizards	Clutch size Clutch frequency Offspring size RCM	Clutch frequency	Ballinger 1977 Dunham 1981 Dunham 1982 Vitt & Price 1982
Snakes	Clutch frequency Offspring size (?) Clutch size (?)	Clutch size (?)	Aldridge 1979 Andren 1982 Blem 1982 Andren & Nilson 1983
Birds	Clutch size Number offspring Fledged	Number offspring Fledged (?)	Lack 1966 Bryant 1975 Murphy 1983

* The parameter contributing most heavily to reproductive success.

1979; Blem 1982). However, Andren (1982) and Andren & Nilson (1983) recently documented that annual changes in the reproductive traits of the viper *Vipera berus* (L.) were a function of changes in prey availability. Contrariwise, Plummer (1983) showed that reproduction in the colubrid *Ophiodrys aestivus* did not vary among climatically distinct years. Because most snakes lack both parental care and multiple clutches (Aldridge 1979), variation in reproductive success in snakes is likely to be a function of either offspring size or more likely, clutch size. Thus, reproductive effort may be more easily quantified in snakes than in lizards or birds, where the situation is complicated by either multiple clutches or parental care. In this paper we document significant annual variation in the reproductive traits of four species of snakes, using data collected over a 30-year period.

METHODS

Data were collected at two localities; the Natural History Reservation of the University of Kansas (NHR), located in eastern Kansas U.S.A. just outside Lawrence, and the Squaw Creek National Wildlife Refuge (SQ), located *c.* 90 km NE of the NHR in western Missouri. Squaw Creek is a 2770 ha refuge consisting of a cordgrass prairie, deciduous woodlands and open marshes. The NHR is mainly second growth deciduous woodland; see Fitch (1960, 1965, 1975) for a detailed description of the NHR.

Snakes at the NHR were collected by hand capture and funnel traps (Fitch 1960) between 1950 and 1982. Snakes at SQ were collected from 1979–82 by either hand capture, trapping, or road collecting. At both localities, clutch size was determined by either dissection, counting enlarged follicles by palpation, or by keeping females in captivity until parturition or egg-laying occurred. Presumably, these methods each might yield slightly different results, since numerous studies have demonstrated that reduction occurs through progressive mortality from ovarian follicles to fertilized ova to neonates. However, field techniques were the same from year to year for each species, and the substantial annual changes that were found to occur in clutch and litter sizes are believed to be real. In addition, one of us (RAS) checked palpation counts by subsequent dissection, and found the error rate for snakes with small to moderate clutch sizes (<25) was low (<5%). A

weather station was maintained on the NHR and precipitation was measured daily. The second author was resident on the area throughout the years covered by our records, with only occasional brief absences. Studies of ecological succession during this period provided information concerning the main resources that sustained snake populations, and the changes that occurred in them. The wire funnel traps used to capture snakes also were effective in sampling certain prey animals, e.g. small mammals and amphibians. Earthworms were not sampled separately, but they were apparently abundant at all times, their availability to snakes depending on soil surface moisture. In times of drought they apparently retreat deep underground, out of reach of the snakes.

Data on annual variation in clutch size were analysed initially using a one-way analysis of variance (ANOVA). However, because there is frequently a strong correlation between body size and clutch size in reptiles (Tinkle, Wilbur & Tilley 1970; Fitch 1970), we tested to see if such relationships existed for our species, then used a one-way analysis of covariance (ANCOVA) to correct for any yearly variation in female body size. Data were transformed to log-normal values before testing to meet the assumptions of parametric tests. In all ANCOVA results reported, differences between groups are due solely to differences in Y-intercepts, and not in the slopes of the regression lines.

RESULTS

Sample size. We collected sufficient data to compare annual differences in clutch size for five populations of four species; the ringneck snake (*Diadophis punctatus*), the red-sided garter snake (*Thamnophis sirtalis*), the plains garter snake (*T. radix*), and the copperhead (*Agkistrodon contortrix*). Table 2 summarizes data on number of individuals examined and number of sample years for each site. In total, we examined 750 gravid females over 42 reproductive seasons.

Clutch size. An ANOVA shows that mean annual clutch sizes differed significantly among years for all populations except *T. sirtalis* from SQ (Table 3). The most extreme variation was demonstrated by red-sided garter snakes from the NHR, where the maximum mean annual clutch size was more than two times the minimum (Table 3).

Clutch size is significantly correlated with body size in all five populations (Table 4). Thus, the differences in mean annual clutch size shown in Table 3 could be a result of yearly variation in female body size. An ANCOVA using female snout-vent length (SVL) as the covariate shows that even after female size is accounted for, significant differences in clutch size exist among years for four of the five populations (Table 5). Using the ANCOVA, significant differences in annual clutch size were detected for *T. sirtalis* from SQ but not for *T. radix*, the opposite of results obtained from the ANOVA in Table 3. The value of using ANCOVA to compare annual differences in clutch size is demonstrated by contrasting the unadjusted minimum and maximum clutch sizes of *T. sirtalis* from SQ in Table 3 to the

TABLE 2. Summary of data collected on clutch size in five populations of snakes

Species	Locality	Total sample size	Sample years
<i>Diadophis punctatus</i>	NHR	389	13
<i>Thamnophis sirtalis</i>	NHR	158	9
<i>T. sirtalis</i>	SQ	19	2
<i>T. radix</i>	SQ	52	3
<i>Agkistrodon contortrix</i>	NHR	131	15

TABLE 3. Comparison of extremes of mean annual clutch size for five populations of snakes. Note that the ANOVA was performed on data from all years, not just on the extremes

Annual clutch size	Yearly variation in clutch size		ANOVA (all years)
	Minimum mean annual clutch size	Maximum mean annual clutch size	
<i>Diadophis punctatus</i>	3.11 ± 0.60 n = 9 (1976)	5.17 ± 2.04 n = 12 (1963)	F = 4.11***
<i>Thamnophis sirtalis</i> (NHR)	11.27 ± 4.24 n = 22 (1963)	23.38 ± 8.41 n = 16 (1978)	F = 7.62***
<i>Thamnophis sirtalis</i> (SQ)	11.00 ± 4.64 n = 5 (1981)	14.29 ± 6.93 n = 14 (1982)	F = 0.95 NS
<i>Thamnophis radix</i>	9.00 ± 2.76 n = 32 (1980)	11.87 ± 4.05 n = 15 (1982)	F = 4.95*
<i>Agkistrodon contortrix</i>	4.00 ± 0.76 n = 8 (1972)	6.00 ± 1.20 n = 8 (1960)	F = 2.14*

*P < 0.05; **P < 0.01; ***P < 0.001.

TABLE 4. Results of linear regression analysis of clutch size on body size (SVL in mm) for five populations of snakes. The low *r* values may be an artifact of combining sample years (Gibbons 1972). CS = clutch size

Species	Regression analysis		
	Regression equation	<i>r</i> ²	<i>P</i> value
<i>Diadophis punctatus</i>	CS = -4.83 + 0.030SVL	0.377	0.001
<i>Thamnophis sirtalis</i> (NHR)	CS = -15.0 + 0.048SVL	0.303	0.01
<i>Thamnophis sirtalis</i> (SQ)	CS = -13.6 + 0.046SVL	0.357	0.01
<i>Thamnophis radix</i>	CS = -4.83 + 0.030SVL	0.223	0.01
<i>Agkistrodon contortrix</i>	CS = -1.28 + 0.010SVL	0.117	0.01

adjusted values in Table 5. Note that once SVL is accounted for, the difference in the number of offspring/year almost doubles. On the other hand, the difference in number of offspring/year in *T. radix* declines using ANCOVA, resulting in an insignificant F-value.

Environmental variables. Several authors (e.g. Mayhew 1966; Martin 1973; Vinegar 1975) have used rainfall as an index of resource availability in lizards. Although not as useful as direct information on resource abundance (Ballinger 1977) such data may be useful in crudely assessing 'good' *v.* 'bad' years. We partitioned the activity seasons of our snakes into 'autumn' and 'spring', defining spring as the time from emergence to oviposition, and autumn as the period from oviposition to hibernation. Thus, we define spring for our oviparous species (*D. punctatus*) as 1 April–31 May and autumn as 1 July–31 October. For the viviparous species, spring = 1 April–31 July and autumn = 1 September–31 October. June was deleted from the oviparous sample and August from the viviparous sample because of variation in the timing of oviposition and birth in those months. Table 6 shows spring, autumn, and combined rainfall totals for the NHR from

TABLE 5. Comparison of mean annual clutch sizes for five populations of snakes after correction for female body size by ANCOVA. Note the differences between these results and the ANOVA for *Thamnophis radix* and *T. sirtalis*

Species	Yearly variation-adjusted group means		ANOVA (all years)
	Minimum mean adjusted clutch size	Maximum mean adjusted clutch size	
<i>Diadophis punctatus</i>	3.04 ± 0.93 n = 33 (1967)	4.85 ± 0.94 n = 12 (1963)	F = 5.88***
<i>Thamnophis sirtalis</i> (NHR)	11.62 ± 4.72 n = 22 (1963)	20.38 ± 4.35 n = 16 (1978)	F = 4.64***
<i>Thamnophis sirtalis</i> (SQ)	9.01 ± 4.87 n = 5 (1981)	14.99 ± 4.78 n = 14 (1982)	F = 5.43*
<i>Thamnophis radix</i>	9.15 ± 2.86 n = 32 (1980)	11.16 ± 2.99 n = 15 (1982)	F = 2.39 NS
<i>Agkistrodon contortrix</i>	4.01 ± 1.16 n = 8 (1971)	6.05 ± 1.17 n = 13 (1969)	F = 2.42*

* $P < 0.05$; *** $P < 0.001$.

TABLE 6. Mean, one standard deviation and range in parenthesis of precipitation data (no. days with rainfall) for oviparous (*Diadophis punctatus*), and viviparous (*Thamnophis sirtalis*, *Agkistrodon contortrix*) snakes from the NHR, 1960–79. See text for definition of categories

	Spring	Autumn	Combined
Oviparous	17.15 ± 3.71 (13–27)	27.55 ± 8.51 (11–40)	44.70 ± 9.47 (25–55)
Viviparous	32.45 ± 7.24 (20–47)	14.20 ± 4.61 (5–23)	46.65 ± 8.19 (28–62)

TABLE 7. Comparison of clutch size in three species of snakes during wet and dry years

Species	Season	Mean clutch size (wet)	Mean clutch size (dry)	F-value (ANCOVA)
<i>D. punctatus</i>	Autumn	4.07 n = 80	3.21 n = 42	4.03*
	Spring	4.13 n = 97	3.55 n = 72	22.5**
<i>T. sirtalis</i> (NHR)	Spring	16.2 n = 31	12.0 n = 31	6.77*
<i>A. contortrix</i>	Both	5.2 n = 26	4.3 n = 22	7.14*

* $P < 0.05$; ** $P < 0.01$.

1960 to 1979. We defined wet and dry years as those ± 1 S.D. above and below the 20-year mean, respectively. Using these criteria we found that seasons with fewer days of precipitation generally translated into smaller clutch or brood sizes (Table 7), but that the season of greatest significance varied among species. For ringneck snakes, lower rainfall in either spring or autumn produced lower clutch sizes, but only lower precipitation in the spring meant lower brood sizes in *T. sirtalis*. The only significant difference in brood size for *A. contortrix* between wet and dry years came when seasons were combined (Table 7).

Because of the relatively large number of seasons over which data were collected, we attempted to correlate directly precipitation and clutch size, using either spring, autumn, or combined precipitation totals as the independent variable. Significant correlations were found between autumn rainfall and clutch size for *D. punctatus* ($r = 0.570$, d.f. = 11, $P < 0.05$); no other significant correlations were found

DISCUSSION

Our data show that, even after annual differences in female body size are accounted for, significant differences in clutch size were found for four of five populations of snakes. Although few years' data (2–15) were available for comparison for some species, the range of variation was found to be great in every case. Indeed, the amount of annual variation is comparable to the amount of difference normally found between remote geographic populations. An obvious conclusion from our findings is that a species' clutch or litter size, even for a local population, cannot be accurately determined from just one season's data. The figure obtained in any such short-term study may be much lower or much higher than that which a more representative sample would show, depending on whether the field study coincided with a 'good' year or a 'bad' year. Investigators concerned with lizard reproduction have already found such year-to-year differences in clutch size, and have cautioned against accepting a single season's figures as representative (Pianka 1970; Martin 1973, 1977; Dunham 1982; Worthington 1982). These lizard studies, in arid regions of the southwestern U.S.A., all showed that reproduction was drastically reduced in years of subnormal precipitation. The sites of our study are likewise subject to extreme weather fluctuations, with the rigours of a continental climate. In more stable environments, such as those of coastal or insular areas, or especially the relatively aseasonal environments of tropical rain forest or cloud forest, clutch and litter sizes might be expected to show less annual variation.

An example of the potential misuse of short-term data is shown by comparing the SQ and NHR populations of *T. sirtalis*. Consider the hypothetical case where each study had lasted but a single year and had been published in that form. Thus, there could have been nine distinct published means for litter size resulting from the NHR and two from SQ, with a total of eighteen potential comparisons between the sites. Using adjusted mean values, our data show that in six of the comparisons, an investigator would conclude that the NHR had a higher brood size than SQ (SNK test, $P < 0.05$), with no difference between the remaining comparisons. There is then a 33% probability that an investigator could conclude that brood sizes in the southern population were higher than those in the north. Without belabouring the point, it is also clear that under current life-history theory, a perfectly plausible adaptive argument could be made to explain such geographic differences in reproduction, when in fact such differences only exist on relatively rare occasions.

In each of the four species that we sampled, female size was variable from year to year in the same locality, and although the differences were larger than might have been anticipated, they were not significant. Age structure of the adult population (and its mean size) changes from year to year, depending especially on the youngest cohort, and whether or not it has been unusually successful as a group in numbers, growth and survival. In a typical snake population, newly-mature individuals may make up as much as half of the total of adult females, but with much change from year to year. When they are unusually numerous, average female size is reduced, and when they become scarce, mean size increases correspondingly. For each of the four species in our study we have adjusted the

data to compensate for year-to-year differences in lengths of females (Table 5). Annual differences are shown not to be based upon female size alone, but instead are highly significant even when adjustment is made for the size of each individual female. Changing food supply is the one most evident factor controlling annual variation in clutch and litter size. However, the relationship is complicated by the fact that gravid females feed sparingly or not at all during late stages of pregnancy or before egg-laying. Development of the clutch is partly controlled by feeding and conditioning that occurs long before ovulation, probably during the preceding year, but conditions as far back as the second year before ovulation may have lasting effects. Even after onset of vitellogenesis the female may respond to deteriorating environmental conditions by reducing her clutch by resorption of the follicles.

Of the five snake populations involved in our study, *Diadophis punctatus* (NHR) is by far the most stenophagous (eating earthworms and little else). The availability of earthworms depends upon soil surface moisture; hence, it was possible to show a relationship between precipitation and clutch size. For *Agkistrodon contortrix* and *Thamnophis sirtalis* the food consists of several or many prey species that differ in their ecology, each fluctuating in numbers independently from year to year, and correlations between weather and litter size could not be identified; probably such relationships are highly complex. Our lack of data on prey abundance made elucidating these relationships more difficult. However, the fact that we could demonstrate significant differences in clutch size among wet and dry years, and that clutch size and rainfall are correlated in *D. punctatus* suggests that such relationships indeed exist for snakes.

Clutch size and RCM

Seigel & Fitch (1984) demonstrated that there were no significant annual differences in relative clutch mass (RCM) among the NHR snakes considered here. RCM is usually defined as offspring mass/female total mass (Vitt & Congdon 1978), but can be further broken down as follows:

$$\text{RCM} = \frac{\text{No. of offspring} \times \text{individual offspring mass}}{\text{female total mass}}$$

Since we have shown (Seigel & Fitch 1984; this paper and unpublished) that neither RCM or female body weight varies significantly among years but that clutch size does, we suggest that females adjust not only the number of offspring produced, but the size of those offspring as well. We recognize that there may be a trade-off between clutch size and offspring size in snakes. In addition, data from lizards suggest that larger offspring may have higher survivorship than smaller young (Derickson 1976; Ferguson & Bohlen 1978; Ferguson, Brown & DeMarco 1982). Andren & Nilson (1983) have recently demonstrated annual changes in the offspring size of the European viper (*Vipera berus*), and we are currently determining if similar changes can be detected in our species as well.

In summary, our data support the ideas of Ballinger (1983) that proximate environmental factors may play an important role in determining the variation associated with reproduction. Long-term studies, such as those urged by Tinkle (1979) are essential if we are to determine how widespread this phenomenon is.

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