A neglected life-history trait: clutch-size variance in snakes

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(With 1 figure in the text)

Most analyses of life-history traits have focused on mean values rather than their associated variances. We review published and original data on snakes, including records gathered over many years on single populations, to examine patterns in clutch-size variability in these animals. Within single populations, the coefficient of variation of clutch size did not vary significantly with maternal body size, or among years. The stability of clutch-size variance through time is consistent with experimental studies showing no significant influence of food intake rates on this characteristic. Clutch-size variances did not differ between viviparous and oviparous snakes, but were dependent upon allometric relationships involving maternal body size and the relationship between clutch size and body size. Clutch-size variability was highest in species with relatively variable female sizes, and with a high rate of increase in clutch size with increasing body size. These two factors acted to magnify the extent of clutch-size variability engendered by variability in maternal body sizes. The relationships among these variables were similar in the two squamate Suborders, but the larger body sizes and mean clutch sizes of snakes resulted in clutch-size variances being higher in snakes than in lizards.

Introduction

The most important attributes of any set of numbers can be summarized by two measures: *a statistic of location* (e.g. mean, mode) and a *statistic of dispersion* (e.g. standard deviation, coefficient of variation) (Sokal & Rohlf, 1981). These two measures are not inevitably inter-correlated—for example, a high mean does not necessitate a high variance—and thus both location and dispersion may convey important information about the data set in question. Mathematical models suggest that both of these parameters may also influence the evolutionary fitness of biological characteristics, leading Stearns (1976) to conclude that "the important life-history traits are both the mean *and the variance* in age at first reproduction, clutch size, size of young, number of clutches per lifetime, and inter-brood interval" (p. 37; our emphasis). Empirical studies, however, have concentrated heavily on the mean values of such traits and generally paid less attention to the evolutionary or ecological significance of the associated variances. Notable exceptions include works on variability in offspring size such as those by Capinera (1979), Kaplan (1987, 1989), Crump (1981, 1984), Kaplan & Cooper (1984, 1988), McGinley, Temme & Geber (1987), and Meffe (1987, 1990). In contrast, variability in clutch sizes has attracted little attention (but see Vitt, Van Loben Sels & Ohmart, 1978; Shine & Greer, 1991). Although life-history tactics of squamate reptiles have been the focus of considerable

TABLE I

Summary of data on means and variances of maternal body sizes (snout-vent lengths) and clutch sizes for snakes. 'Repro mode' = oviparous (1) or viviparous (2); SVL = snout-vent length (mm); CV = coefficient of variation; SD = standard deviation; 'Residuals SD/mean' = residual score from the linear regression of standard deviation of clutch size versus mean clutch size

Family	Genus	Species	Repro mode	Mean SVL	CV of SVL	Mean clutch size	SD of clutch size	Residuals SD/mean	CV of clutch size	Sample size	Source
Pythonidae	Liasis	fuscus	1	1751	8.08	12.96	3.14	-0.89	24.24	116	Madsen & Shine, In prep.
Colubridae	Arizona	elegans	1	660		8.4	1.86	-0.86	22.89	7	Aldridge, 1979
Colubridae	Carphophis	vermis	1	284		2.6	0.88	0.24	34.05	34	Clark, 1970
Colubridae	Cerberus	rhynchops	2	520		3.6	1.43	0.43	39.94	29	Gorman, Licht & McCollum, 1981
Colubridae	Coluber	constrictor	1	633		5.8	1.02	-0.77	17.84	18	Brown & Parker, 1984
Colubridae	C.	constrictor	1	868	9.14	13.6	3.78	-0.80	28.43	11	Fitch, 1963
Colubridae	Diadophis	punctatus	1	281		3.7	1.27	0.23	34.32	379	Fitch, 1975
Colubridae	Elaphe	guttata	1	852		12.0	3.86	-0.14	32.58	21	Ford & Seigel, 1989
Colubridae	Hypsiglena	torquata	1	356	10.16	3.6	1.13	0.13	32.27	9	Clark & Lieb, 1973
Colubridae	Lampropeltis	calligaster	1	822		8.3	1.37	-1.31	16.84	12	H. S. Fitch (pers. comm.)
Colubridae	L.	triangulum	1	576	10.61	6.9	1.13	-1.05	16.91	8	H. S. Fitch (pers. comm.)
Colubridae	Masticophis	taeniatus	1	858	8.56	5.6	2.03	0.31	37.11	10	W. Brown & W. Parker (pers. comm.)
Colubridae	Nerodia	harteri	2	477		14.5	4.31	-0.60	30.32	12	Rose, 1989
Colubridae	N.	rhombifera	2	1200		40.6	9.70	-4.54	24.50	10	Betz, 1963
Colubridae	N.	taxispilota	2	1059	10.52	31.8	12.53	1.43	39.71	32	R. Seigel, pers. obs.
Colubridae	Opheodrys	aestivus	1	400	9.20	6.0	1.07	-0.79	18.36	8	Goldsmith, 1984
Colubridae	O.	aestivus	1	430		6.1	1.84	-0.05	30.28	97	Plummer, 1984 and pers. comm.
Colubridae	Regina	grahami	2	598		11.6	3.06	-1.20	26.40	11	Seigel, 1992
Colubridae	R.	septemvittata	2	592	10.52	12.8	2.57	-1.72	20.60	10	Branson & Baker, 1974
Colubridae	Seminatrix	pygaea	2	328	11.12	8.1	2.87	0.26	35.59	47	R. Seigel & R. Loraine, pers. obs.
Colubridae	Storeria	dekayi	2	230	14.20	9.3	3.30	0.05	35.50	15	Ford et al., 1990
Colubridae	S.	occipitomaculata	2	260		6.9	2.21	0.03	32.10	77	Blanchard, 1937
Colubridae	Thamnophis	butleri	2	381		11.4	3.73	-0.07	32.99	28	Ford & Killebrew, 1983

Family	Genus	Species									Reference
Colubridae	T.	*marcianus*	2	521		9.5	4.58	1.47	49.00	15	N. Ford, pers. comm.
Colubridae	T.	*marcianus*	2	583		13.2	8.61	4.17	65.91	23	R. Seigel, pers. obs.
Colubridae	T.	*marcianus*	2	643		15.3	7.96	2.77	52.93	14	R. Seigel, pers. obs.
Colubridae	T.	*proximus*	2	574		13.0	3.00	-1.36	23.54	13	Tinkle, 1957
Colubridae	T.	*proximus*	2	571		8.4	2.37	-0.35	29.21	7	Clark, 1974
Colubridae	T.	*proximus*	2	525		10.2	2.76	-0.60	27.67	12	R. Seigel, pers. obs.
Colubridae	T.	*radix*				15.8	5.80	0.43	38.54	5	Dalrymple & Reichenbach, 1981
Colubridae	T.	*radix*	2	656		29.5	14.96	4.68	52.81	6	Gregory, 1977
Colubridae	T.	*radix*	2	483	10.63	9.9	3.317	0.06	33.66	52	Seigel & Fitch, 1985
Colubridae	T.	*saurius*	2	667		6.0	1.58	-0.28	27.62	5	Burt, 1928
Colubridae	T.	*sirtalis*	2	616		16.9	6.46	0.69	39.39	8	Burt, 1928
Colubridae	T.	*sirtalis*	2	653	13.49	16.6	7.75	2.10	46.77	158	Fitch, 1965; Seigel & Fitch, 1985
Colubridae	T.	*sirtalis*	2	600		16.4	5.74	0.16	35.63	14	Gregory, 1977
Colubridae	T.	*sirtalis*	2	596		13.4	6.46	1.95	48.83	19	Seigel & Fitch, 1985
Colubridae	Tropidoclonion	*lineatum*	2	260		7.1	2.64	0.39	37.56	26	Krohmer & Aldridge, 1985
Colubridae	Tropidonophis	*mairii*	1	667	9.11	12.0	3.08	-0.92	25.98	23	R. Shine, pers. obs.
Viperidae	Agkistrodon	*contortrix*	2	601	7.10	5.1	1.32	-0.22	25.85	131	Fitch, 1960; Seigel & Fitch, 1985
Viperidae	A.	*piscivorus*	2	747		7.7	1.78	-0.69	23.34	24	Blem, 1981
Viperidae	A.	*piscivorus*	2	768		6.6	2.50	0.43	38.21	31	Allen & Swindell, 1948
Viperidae	A.	*piscivorus*	2	980		5.5	1.50	-0.19	27.48	24	Wharton, 1966
Viperidae	Crotalus	*horridus*	2	987		8.5	2.88	0.13	34.75	10	Fitch, 1985
Viperidae	C.	*horridus*	2	827		6.8	1.72	-0.43	26.57	5	Galligan & Dunson, 1979
Viperidae	C.	*horridis*	2	1002		8.1	1.71	-0.90	21.41	17	Keenlyne, 1978
Viperidae	C.	*viridis*	2	640		9.5	2.88	-0.23	30.63	23	Aldridge, 1979
Viperidae	C.	*viridis*	2	659		5.5	1.40	-0.28	25.55	117	Diller & Wallace, 1984
Viperidae	C.	*viridis*	2	873		8.5	3.01	0.25	36.14	12	Fitch, 1985
Viperidae	C.	*viridis*	2	790		4.6	1.64	0.28	36.02	28	Macartney & Gregory, 1988
Viperidae	Sistrurus	*catenatus*	2	539		6.4	1.88	-0.12	29.83	17	Seigel, 1986
Viperidae	Trimeresurus	*flavoviridis*	1	1226		7.3	2.02	-0.30	28.16	15	Koba et al., 1970a
Viperidae	T.	*okinavensis*	1	502		6.0	2.68	0.82	45.15	25	Koba et al., 1970b
Viperidae	Vipera	*berus*	2	690		7.5	2.20	-0.20	29.71	18	Andren & Nilson, 1983

TABLE I
(cont.)

Family	Genus	Species	Repro mode	Mean SVL	CV of SVL	Mean clutch size	SD of clutch size	Residuals SD/mean	CV of clutch size	Sample size	Source
Viperidae	V.	berus	2	650		10.4	2.70	−0.73	26.65	10	Andren & Nilson, 1983
Viperidae	V.	berus	2			8.8	2.61	−0.25	30.09	19	Nilson, 1981
Viperidae	V.	xanthina	1			14.4	4.93	0.06	35.42	7	Mendelssohn, 1965
Elapidae	Pseudechis	porphyriacus	2	1064	7.73	12.2	2.63	−1.46	21.65	21	R. Shine, pers. obs.
Elapidae	Notechis	scutatus	2	808.9	8.56	23.9	5.98	−2.27	25.26	33	R. Shine, pers. obs.
Elapidae	Austrelaps	superbus	2	713.5	13.43	16.9	6.33	0.56	37.86	36	R. Shine, pers. obs.
Elapidae	Suta	dwyeri	2	299.4	11.97	4.2	1.29	0.07	30.81	28	R. Shine, pers. obs.

interest in recent years, (e.g. Seigel & Ford, 1987; Dunham, Miles & Reznick, 1988), most research has been concerned primarily with means rather than variances. Our intention in this paper is to redress these imbalances by focusing on variability in clutch size among snakes. We review available information on this topic, and use these data to investigate potential determinants of clutch-size variability.

Why study variability in clutch sizes? This characteristic is of interest both because it may constrain evolutionary rates (note that variance of a trait can be used to estimate the opportunity for selection—O'Donald, 1970; Arnold, 1986), and because it may itself be subject to natural selection. Life-history models suggest that natural selection may operate to reduce clutch-size variability under certain conditions, notably in small populations (e.g. Gillespie, 1974, 1975, 1977; Slatkin, 1974; Frank & Slatkin, 1990). Even if low clutch-size variability is not itself the target of selection, biologically important changes in the variability of this characteristic may well arise as a by-product of other evolutionary or ecological processes. For example, we might expect to see low intrapopulational variability in clutch sizes in populations where:

(i) adult females are relatively invariant in body size (Shine & Greer, 1991). This should reduce clutch-size variability because of the widespread correlation between clutch-size and maternal body size among snakes (Seigel & Ford, 1987),

(ii) clutch sizes increase slowly with increases in maternal body size, so that a high level of variability in maternal sizes does not engender a high variability in clutch sizes, or

(iii) adult females are able to reproduce at short intervals and hence are able to adjust their overall reproductive expenditure through variability in clutch interval instead of clutch size. Such flexibility in clutch interval may vary in predictable ways: for example, it may be higher in oviparous snakes than in viviparous species, because of the higher reproductive frequency in the former group (Seigel & Ford, 1987).

Recently, Shine & Greer (1991) analysed the correlates of clutch-size variability in lizards, in the light of these kinds of predictions. These authors found that low clutch-size variability was predictably associated with low mean clutch sizes, and with small and relatively invariant female body sizes. The present paper extends this analysis to snakes. We use a combination of published and original data on body sizes and clutch sizes to examine correlates of clutch-size variability in snakes. Because several very large data sets are available from long-term studies of single populations, we also take the opportunity to investigate the possibility of allometric (size-related) and temporal variations in clutch-size variability.

Methods

Data

We assembled published and unpublished data on clutch-size variability among snakes. Because we were interested in investigating interpopulational differences in clutch-size variability, we used only information from studies of single populations. Thus, data from dissections of museum specimens gathered over broad areas were not included. In most of the cases that we obtained from the literature, insufficient detail was available to determine the actual distributions of clutch sizes. Only means, sample sizes, and standard deviations of this variable could be obtained. Our inclusion of samples of different sizes may be a problem if there is any consistent association between the sample size and the variability in clutch size, but no such correlations are apparent (data from Table I, using Coefficient of Variation as a measure of variance: $n = 60$, $r = 0.11$, $P = 0.42$). We also obtained more detailed information from a subset of species for which data were available on individual clutch sizes and maternal body sizes. Some of these data sets

were from publications, but most came from unpublished data from our own research, and from information kindly provided by Drs H. S. Fitch, M. V. Plummer, W. S. Brown, W. S. Parker, and N. B. Ford. We used the means and standard deviations of these data sets for overall analyses in combination with the other published data, but also analysed these more detailed data sets in other ways described below.

Measures of variation

Most previous analyses of reptilian reproductive biology have not dealt specifically with clutch-size variability. Lizard lineages with totally invariant clutch sizes (e.g. gekkotans and anoline iguanids) have often been considered to be somehow different from other lizards, but most workers have attempted to overcome this problem simply by performing all analyses of trends in mean values of life-history traits twice—with and without the invariant-clutch-size species (e.g. Tinkle, Wilbur & Tilley, 1970; James & Shine, 1988; Dunham *et al.*, 1988). Shine & Greer (1991) have analysed patterns of clutch-size variability among scincid lizards, using the coefficient of variation (CV = standard deviation divided by the mean, and multiplied by 100) as a variance descriptor, but it is important to realise that there is no 'ideal' measure of clutch-size variability. The usual variance measures used in statistical analyses—the variance itself, the standard deviation, and standard error—have the disadvantage that they are often correlated with the mean (Snedecor & Cochran, 1980). Analysis of data in Table I confirms that this is the case with clutch sizes in snakes: the correlation between mean clutch size and the standard deviation of clutch size is 0.88 ($n = 60$, $P < 0.001$; and see Fig. 1). Use of the CV attempts to overcome this problem by simply dividing the standard deviation by the mean, but is based on the assumption that the relationship between the mean and its associated variation is linear with a slope equal to 1.0. The residuals from the general regression of the standard deviation against the mean for all samples offer an alternative measure of variation: one that is less easy to visualize, but which accounts more precisely for any effects of the mean clutch size on the associated variance. Table I lists all 3 of these variance descriptors, and analysis shows that all 3 are highly intercorrelated (CV vs. residual score – $n = 60$, $r = 0.86$, $P < 0.001$; SD vs. residual score – $n = 60$, $r = 0.47$, $P < 0.0001$; SD vs. CV – $n = 60$, $r = 0.60$, $P < 0.0001$). We chose to use SD and CV as our variance descriptors, on the grounds that these are familiar measures which are relatively easy to interpret. The essential difference between these 2 measures is that the SD represents variability in absolute terms, whereas the CV is a standardized score designed to 'correct' for the effect of the mean on the SD. Our calculations of CV also incorporated a correction for sample size (Sokal & Rohlf, 1981).

For analyses of our detailed data sets, where we have information on body sizes and clutch sizes of individual females, we can use more powerful variance descriptors based on the distribution of individual data points rather than an overall variability for the entire sample (see Sokal & Braumann, 1980, for details). We calculated 2 such measures. First, the absolute deviation of each clutch size from the mean clutch size in that sample yields a frequency distribution of the extent to which individual females depart from the mean condition. This measure (our 'uncorrected deviation score') is directly analogous to SD, and mean deviation scores are perfectly correlated with SD among the species for which we have both measures ($n = 19$, $r = 1.00$, $P < 0.0001$). Secondly, we divided each of these deviation scores by the mean clutch size in that sample, to derive a standardized estimate that would tend to correct for allometric effects. This second measure (our 'standardized deviation score') is analogous to the CV, and is significantly correlated with the CV in our data ($n = 19$, $r = 0.54$, $P < 0.02$).

To estimate the rate at which clutch size increases with maternal body size intraspecifically, we used the slope of the reduced major axis regression linking these 2 variables. Reduced major axis (= functional) regression is more appropriate than conventional least-squares regression in this situation, because the errors in measuring the independent variable (maternal body length) are likely to be at least as great as those in measuring the dependent variable (clutch size). Indeed, obtaining repeatable measures of body length in snakes is a difficult proposition (e.g. Fitch, 1987).
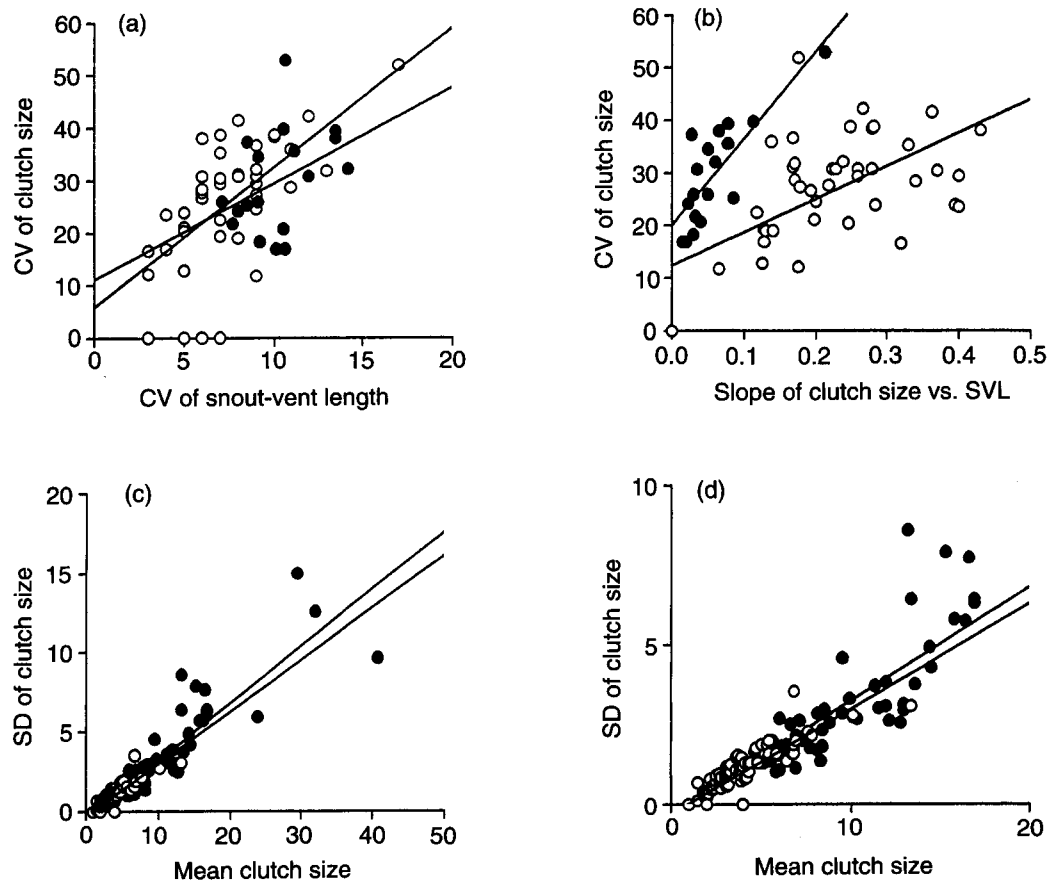
FIG. 1. Correlates of interspecific variability in clutch sizes among snakes (dots) and lizards (circles). Clutch sizes are more variable in species with (a) highly variable maternal body sizes and (b) a high rate of increase in clutch size with maternal body size (reduced major axis slope of regression equation linking clutch size to maternal body size). (c) The standard deviation of the clutch size increases with mean clutch size (detail in d). Snakes (dots) and lizards (circles) follow the same regression lines in most of these cases, but snakes have lower slopes for the rate of fecundity increase with body size (b). Statistical results for snake data and ANCOVAs are given in the text. For lizards: (a) $n = 44$, $r = 0.65$, $P < 0.001$; (b) $n = 44$, $r = 0.62$, $P < 0.001$; (c, d) $n = 103$, $r = 0.87$, $P < 0.001$.

Statistical analyses

We carried out the following kinds of analyses on our data, to examine the relationship between clutch-size variability and:

(i) *Maternal body size*. Within each taxon for which detailed data were available on individual clutch sizes, we examined changes in clutch-size variability with maternal body size by correlating the deviation score (both uncorrected and corrected) with the body length of the female producing that clutch.

(ii) *Time*. Within populations for which more than one year's data were available, we looked at differences in the distributions of deviation scores (both uncorrected and corrected) among years using one-factor ANOVAs with year as the factor (see Sokal & Braumann, 1980 for statistical details).

(iii) *Reproductive variables*. We used the less detailed data set (means and variances for each population, but no records of individual clutches) to look for correlations among attributes such as clutch-size

variability, mean clutch size, and variability in maternal body size. This analysis treated all species as independent units, and thus ignored the possibility that traits may be correlated in occurrence because of common inheritance rather than any functional relationship. In cases where our interspecific correlational analyses identified significant associations between clutch-size variability and other traits, we used one-factor analysis of covariance (incorporating a heterogeneity of slopes test) to examine whether the form of these relationships was affected by reproductive mode. Unpaired 2-tailed t-tests were used to compare average values of traits between oviparous and viviparous species.

We also repeated most of our interspecific comparisons (but not ANCOVAs) within a phylogenetic framework, using the program of Pagel & Harvey (1989). This technique takes values for each character (such as mean clutch size or clutch-size variability) for living species and superimposes these data on to a phylogenetic hypothesis for the group. The program then identifies independent contrasts using monophyletic lineages within the phylogeny, so that evolutionary contrast scores can be calculated for each character across each clade within the lineage. Then, scores for one variable can be compared to scores for another variable across the same clade. If the 2 are functionally related, the magnitudes of their contrast scores should be correlated. This technique is designed to overcome the problem of phylogenetic conservatism in characters, whereby 2 characters may be significantly associated in their occurrence not because of a functional relationship, but simply because both have been inherited from a common ancestor. We used the cladistic hypotheses of Rossman & Eberle (1977), Dowling *et al.* (1983), Mengden (1985), and Lawson (1987) to create an overall phylogenetic hypothesis for the species in Table I.

(iv) *Taxonomy.* Among the taxa for which we had detailed data, frequency distributions of deviation scores were compared interspecifically using one-factor ANOVA with species as the factor, to determine whether species differed consistently from each other in clutch-size variances. Also, we used our less detailed data set (means and variance statistics only) to compare with analogous data for 61 species of agamid, gekkonid, iguanid, phrynosomatid, crotaphytid, lacertid, pygopodid, scincid, teiid, and varanid lizards from reviews by Pianka (1986, Appendix F) and Shine & Greer (1991). We examined these data both for differences in means (using unpaired 2-tailed t-tests) and by using Suborder as the factor in one-factor analyses of covariance as described above for reproductive mode.

Statistical analysis was carried out using the microcomputer software packages SYSTAT (Wilkinson, 1986), SuperANOVA (Abacus Concepts, 1989) and STATVIEW (Abacus Concepts, 1987). All statistical tests were 2-tailed unless otherwise noted. A 95% confidence level was used for all tests, with the significance level corrected for multiple comparisons that would otherwise yield artefactually high numbers of 'significant' results. This correction was carried out using the sequential Bonferroni procedure (Rice, 1989), and results of the Bonferroni procedure are reported as 'corrected' P values.

Results

We obtained values for the means and variances of clutch size from 60 populations of snakes (Table I). These include a wide variety of forms both phylogenetically and ecologically, ranging from tiny colubrid snakes to large rattlesnakes and pythons. Terrestrial, aquatic, and fossorial species are included. Mean clutch sizes ranged from 2.6 in *Carphophis vermis* to 40.6 in *Nerodia rhombifera*, and the CV of clutch sizes ranged from 16.4% in *Lampropeltis triangulum* to 65.2% in *Thamnophis marcianus*. The detailed data sets that we used included the results of several long-term intensive studies of single populations (Table II). The three largest were all from Dr H. S. Fitch's mark-recapture studies on snake populations in the University of Kansas Natural History Reservation, near Lawrence, Kansas. These represented 15 years of data on copperheads (*Agkistrodon contortrix*), 13 years of data on ringneck snakes (*Diadophis punctatus*), and nine years of data on common garter snakes (*Thamnophis sirtalis*). Below, we first consider intraspecific variation in clutch-size variability, using these detailed data sets, before moving on to interspecific patterns based on mean values for each species.

Table II

Temporal changes in clutch-size variance within snake populations. 'CV' = coefficient of variation of clutch size; 'Test statistic' = results of one-factor ANOVA with year as factor; 'P' = probability level from two-tailed test

Species	Number of years	Maximum CV	Minimum CV	Test Statistic	P	Source
Diadophis punctatus	13	39.9	19.3	$F_{12,378} = 1.34$	0.19	Seigel & Fitch, 1985
Opheodrys aestivus	3	30.3	19.3	$F_{2,96} = 2.53$	0.09	M. Plummer, 1983, 1984, pers. comm.
Nerodia taxispilota	2	50.0	36.1	$F_{1,30} = 0.0$	1.00	R. Seigel, pers. obs.
Seminatrix pygaea	2	39.2	31.4	$F_{1,45} = 0.46$	0.50	R. Seigel & R. Loraine, unpubl.
Thamnophis sirtalis	9	47.8	25.5	$F_{8,157} = 1.23$	0.28	Seigel & Fitch, 1985
T. radix	3	34.0	7.9	$F_{2,51} = 1.44$	0.25	Seigel & Fitch, 1985
Agkistrodon contortrix	15	34.0	14.5	$F_{14,130} = 0.49$	0.93	Seigel & Fitch, 1985
Liasis fuscus	2	25.5	23.2	$F_{1,115} = 0.52$	0.47	T. Madsen & R. Shine, unpubl.

Effects of maternal body size on variability in clutch size

The four largest data sets were analysed to determine whether females of different adult body sizes also differed in the variability of their clutch sizes. Significant correlations between the uncorrected deviation scores and body size were evident in two of the four taxa. The uncorrected deviation score increased with maternal body length in both the oviparous colubrid *Diadophis punctatus* ($n = 379$ clutches, $r = 0.17$, $P < 0.001$; with Bonferroni correction, $P < 0.01$) and the viviparous colubrid *Thamnophis sirtalis* ($n = 158$, $r = 0.27$, $P < 0.0008$; with correction, $P < 0.01$), but showed no significant relationship with maternal body length in the viviparous viperid *Agkistrodon contortrix* ($n = 131$, $r = 0.14$, $P = 0.11$) or the oviparous pythonid *Liasis fuscus* ($n = 116$, $r = 0.08$, $P = 0.41$). Even in the case of the two species with highly significant correlations, however, the *standardized* deviation scores showed no relationship with body size (*D. punctatus*, $n = 379$ clutches, $r = 0.08$, $P = 0.13$; *T. sirtalis*, $n = 158$, $r = 0.07$, $P = 0.35$). Thus, the apparent allometry of clutch-size variability with maternal body size in *Diadophis* and *Thamnophis* is simply due to the tendency for larger females to produce larger clutches, and for the absolute deviation score to increase with the mean clutch size.

Temporal changes in clutch-size variability

Does clutch-size variability change from year to year within single populations? Eight detailed data sets were used for this analysis, based on six populations of colubrid snakes, one population of viperids and one population of pythons (Table II). Analysis of variance revealed no significant shifts in clutch-size variability among years in any of the eight populations (see Table II).

Interspecific variation in clutch-size variability

Comparisons of the 18 species for which we have detailed raw data revealed highly significant interspecific differences in absolute clutch-size deviations (one-factor ANOVA with species as the factor, $F_{18,1215} = 31.73$, $P < 0.0001$). The analogous test with standardized deviation scores was also significant, but the F-value was greatly reduced ($F_{18,121} = 3.94$, $P < 0.0001$) and *post hoc*

Tukey-Kramer tests did not detect any significant differences in pairwise comparisons among the taxa. Thus, the sample showed only moderate interspecific differences when clutch-size variances were calculated relative to mean clutch sizes.

Interspecific correlates of clutch-size variability

(i) As expected, the SD of clutch size was significantly correlated with mean clutch size ($n = 58$, r $= 0.88$, $P < 0.0001$, corrected $= 0.001$), but the CV of clutch size was not ($n = 58$, r $= 0.21$, $P = 0.11$).

(ii) Mean female body size was significantly correlated with mean clutch size ($n = 58$, r $= 0.41$, $P < 0.002$, corrected $= 0.02$) but not with clutch-size variability (SD: $n = 58$, r $= 0.24$, $P = 0.07$; CV: $n = 58$, r $= 0.17$, $P = 0.22$).

(iii) Variability in maternal body size was correlated with variability in clutch size, regardless of whether the comparison was based on SD ($n = 19$, r $= 0.48$, one-tailed $P < 0.02$, corrected $= 0.04$) or CV ($n = 19$, r $= 0.54$, one-tailed $P < 0.01$, corrected $= 0.03$).

(iv) This relationship between body-size variability and clutch-size variability was similar in oviparous and viviparous snakes (one-factor ANCOVA with reproductive mode as the factor, using CV as the measure of variability: slopes $F_{1,15} = 0.19$, $P = 0.67$; intercepts $F_{1,16} = 1.47$, $P = 0.24$), and t-tests revealed no significant differences between these two groups in means or variances (SD, CV) of female body sizes or clutch sizes (lowest corrected $P = 0.12$).

(v) Clutch-size variability was significantly correlated with the reduced major axis slope of the regression equation linking clutch size to maternal body length (using CV as the variability measure: $n = 19$, r $= 0.65$, $P < 0.003$, corrected $= 0.02$).

(vi) This relationship between clutch-size variability and the rate of fecundity increase with body size was similar in oviparous and viviparous snakes (one-factor ANCOVA with reproductive mode as the factor, using CV as the measure of variability: slopes $F_{1,14} = 0.89$, $P = 0.36$; intercepts $F_{1,15} = 0.06$, $P = 0.82$).

(vii) Do these two factors (maternal body-size variability and the rate of fecundity increase with size) exert independent effects on clutch-size variability, or are they intercorrelated themselves? Further analysis showed that they are not significantly correlated ($n = 19$, r $= 0.27$, $P = 0.27$), and a stepwise multiple regression (with these two factors as the independent variables, and clutch-size variability as the dependent variable) suggested that both factors contribute independently to the observed clutch-size variability (cumulative $r^2 = 0.57$; $F_{2,18}$ to remove size CV $= 5.39$; to remove the slope of clutch size to body size $= 10.09$, $P < 0.001$, in both cases).

(viii) Most of these correlations were still apparent in phylogenetically-based analyses, but the lower power of these tests (due to decreased degrees of freedom) meant that the results no longer attained statistical significance. Thus, despite relatively high correlation coefficients, contrast scores for the CV of clutch size were not significantly correlated with corresponding scores for the rate of fecundity increase with maternal body size ($n = 18$, r $= 0.49$, one-tailed $P < 0.02$, but corrected $P = 0.06$), the mean clutch size ($n = 15$, r $= 0.40$, one-tailed $P = 0.07$) or the CV of maternal body size ($n = 15$, r $= 0.30$, one-tailed $P = 0.14$).

(ix) Lizards were significantly different from snakes in average values for all of the characteristics tested, including mean snout-vent length of adult females (snake mean $= 669.6$ mm, lizard mean $= 52.7$ mm, $t_{99} = 15.1$, $P < 0.0001$, corrected $= 0.001$), SD of female SVL (snake mean $= 10.2$, lizard mean $= 7.5$, $t_{60} = 3.8$, $P < 0.0003$, corrected $= 0.001$),

CV of female SVL (snake mean $= 10.2$, lizard mean $= 4.1$, $t_{60} = 13.9$, $P < 0.0001$, corrected $= 0.001$), mean clutch size (snake mean $= 10.7$, lizard mean $= 3.5$, $t_{163} = 10.1$, $P < 0.0001$, corrected $= 0.001$), SD of clutch size (snake mean $= 3.5$, lizard mean $= 0.9$, $t_{161} = 9.2$, $P < 0.0001$, corrected $= 0.001$), CV of clutch size (snake mean $= 31.6$, lizard mean $= 21.7$, $t_{161} = 5.0$, $P < 0.0003$, corrected $= 0.001$), and the reduced major axis slope of the regression equation linking clutch size to maternal body length CV of female SVL (snake mean $= 0.06$, lizard mean $= 0.21$, $t_{60} = 5.7$, $P < 0.0001$, corrected $= 0.001$). That is, snakes were longer than lizards, had larger and more variable clutch sizes, and the rate at which clutch sizes increased with female size was lower in snakes than in lizards.

(x) Most of these differences between snakes and lizards in average values of variables are allometric consequences of the differences in mean body sizes of the two groups. When the relationships among variables are examined, rather than mean values, most of the differences between snakes and lizards disappear. Analysis of covariance shows that the two Suborders do not differ in the relationship between clutch-size variability and body-size variability (Fig. 1: using CV as the measure of variability: heterogeneity of slopes $F_{1,58} = 0.55$, $P = 0.46$; intercepts $F_{1,59} = 1.33$, $P = 0.25$) or in the relationship between clutch-size SD and mean clutch size (Fig. 1: slopes $F_{1,159} = 0.35$, $P = 0.55$; intercepts $F_{1,160} = 0.23$, $P = 0.64$). The only significant difference that we detected between the Suborders was in the relationship between clutch-size variability and the rate of fecundity increase with maternal body size: snakes have relatively variable clutch sizes even at relatively low rates of fecundity increase (Fig. 1: slopes $F_{1,58} = 3.89$, $P = 0.53$; intercepts $F_{1,59} = 24.21$, $P < 0.0001$, corrected $= 0.001$).

Discussion

Our analyses suggest that the variability of clutch sizes in snakes is not significantly influenced by female body size within a population, is constant through time within populations, and is similar in viviparous and oviparous species. Among snakes, clutch-size variability tends to be highest in species with a high variability in the body sizes of adult females, and a high rate of increase of clutch size with maternal body size. Clutch-size variability is higher among snakes than among lizards (at least in the samples available to us), and this difference is primarily due to the large differences in adult body sizes (and hence, mean clutch sizes) between the two Suborders.

The observation that clutch-size variability remains relatively constant through time, despite significant fluctuations in mean clutch sizes in most of these populations (Seigel & Fitch, 1985), suggests that changes in food supply modify the population's mean reproductive output but not the variability of reproductive output among females. In keeping with this suggestion, experimental maintenance of female snakes on different levels of food intake modified mean clutch size, but not clutch-size variability, in the colubrids *Thamnophis marcianus* and *Elaphe guttata* (Seigel & Ford, 1992).

The strongest consistent factor to emerge from our analyses is the role of allometry. Body sizes of reproducing female reptiles are correlated not only with the number of offspring that they produce (e.g. Seigel & Ford, 1987), but also with growth trajectories. In reptile species that attain very large adult body sizes, maturation occurs at a lower proportion of maximum size and, hence, the range (and thus, variability) of body sizes of adult females will increase (Andrews, 1982; Shine & Charnov, 1992). Our analyses suggest that both of these factors—high mean clutch sizes and a high variability in maternal body sizes—are likely to increase clutch-size variability, especially if

uncorrected variability measures (e.g. SD, or 'raw' deviations from the mean) are used as the variability descriptor. The rate at which fecundity increases with increasing maternal body size also shows allometry, being higher in smaller species (e.g. in lizards rather than snakes—Fig. 1). Even if a 'corrected' descriptor of variability (e.g. CV) is employed, our results suggest that clutch-size variability will be highest in species with variable female sizes and a high rate of fecundity increase with female size. This result is also consistent with simple logic. Given that clutch sizes increase with female body size, we would expect clutch sizes to be highly variable if: (i) female sizes vary considerably; and (ii) even small differences in female body size produce substantial shifts in clutch size. These results from our analyses are thus not surprising, but offer the first empirical evidence of the existence of such relationships.

In several respects, our results mirror those of previous analyses on other squamates and other life-history traits. For example, Shine & Greer (1991) found a significant correlation of clutch-size variability with maternal body-size variability in lizards, and our analyses show a very similar pattern in snakes (Fig. 1). Also, we have found that the slope of the regression equation linking clutch size and female body size is a significant correlate of clutch-size variability in both of these squamate Suborders (Fig. 1). The difference between snakes and lizards in the exact form of this latter relationship is a consequence of allometry, which influences the rate that fecundity increases with maternal body size. Our overall conclusion concerning the two Suborders—that the relationships between variables are similar but that mean values of traits differ considerably because of allometry—echoes one of the main findings from Shine & Charnov's (1992) review of rates of growth, maturation, and survival in lizards and snakes.

Finally, we end this paper with a caveat and a plea. The caveat is that our data set, although extensive, covers only a tiny fraction of the world's snake species and is heavily biased towards temperate-zone colubroids. More data, on a more ecologically and phylogenetically diverse array of taxa, are needed to establish whether the patterns that we have detected are generally applicable. It is also notable that our phylogenetically-based statistical tests, although showing the same patterns as the more conventional tests, were inconclusive because of low power. It thus remains possible that the patterns we have documented are due to phylogenetic conservatism (shared retention of ancestral characteristics) rather than to functional associations among variables. Our plea is that future analyses of squamate life-histories should give more thought to the variability of the traits that are studied. In combination with earlier work, our results suggest that life-history traits display clear patterns, and that a fuller understanding of the adaptive and ecological significance of these patterns will require attention to the extent of dispersion of the data, as well as to the mean.

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