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VARIATION IN RELATIVE CLUTCH MASS IN SNAKES AMONG AND WITHIN SPECIES

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ABSTRACT: We examined the relationship between relative clutch mass (RCM) and female body size (SVL) both within and among different species of snakes. In 10 of 12 within-species comparisons, RCM varied independently of SVL; only viviparous elapids showed a significant regression between these two variables. We suggest that the independence of body size and RCM is explainable on ecological grounds alone. RCM decreased with increasing body size in both viviparous colubrids ($n = 16$ species) and viviparous viperids ($n = 7$ species), but only the colubrid sample was statistically significant. In 20 egg-laying colubrids, RCM increased slightly (but not significantly) with increasing female SVL. We suggest that the differences in the SVL/RCM relationship between reproductive modes is related to the increased costs of viviparity resulting from long gestation times. In addition, small viviparous species may be able to bear a greater RCM because of differences in either longevity or habitat utilization.

Key words: Snakes; Reproduction; Relative clutch mass; Body size; Reproductive mode

THE ratio of clutch weight to body weight, known as relative clutch mass or RCM, has drawn increasing attention over the past decade (see Cuellar, 1984, for a literature review). Originally proposed by Tinkle (1972) as an easily-obtainable measure of reproductive effort, theoretical ob-

jections quickly led Tinkle and Hadley (1975) and Hirshfield and Tinkle (1975) to recommend against such a usage for this ratio. More recently, several investigators have determined that RCM is well-correlated with such ecological parameters as foraging mode and body shape in

lizards (Vitt, 1981; Vitt and Congdon, 1978; Vitt and Price, 1982), and reproductive mode in snakes (Seigel and Fitch, 1984). Despite its correlation with these factors, many authors have continued to use RCM to approximate reproductive effort, especially in lizards. Cuellar (1984) usefully summarized both sides of this argument, but he left unanswered the question of how RCM is best utilized.

One of the major considerations in the use of RCM for ecological or evolutionary comparisons concerns variation in the ratio (Cuellar, 1984). Of particular importance are changes in RCM associated with season, clutch size and, especially, age and body size. Many models of reproductive effort (e.g., Williams, 1966) predict that effort should increase with increasing age or size (but see Congdon et al., 1982). However, RCM tends to remain stable or to decrease with increasing age and body size in several oviparous lizards (Ballinger, 1974; Cuellar, 1984; Vinegar, 1975). Conversely, RCM increases with increasing body size in the oviparous *Iguana iguana* (Fitch and Henderson, 1977) and the viviparous *Lacerta vivipara* and *Sceloporus jarrovi* (Pianka and Parker, 1975; Pilorge et al., 1983). Data from snakes show equally disparate results (Clark, 1970; Ford and Killebrew, 1983; Pianka and Parker, 1975; Plummer, 1984; Shine, 1977). Our understanding of the relationship between these variables and RCM is limited, making direct comparisons of RCM among species or populations difficult. In this paper, we attempt to clarify the role of body size by examining the RCM of snakes among and within a variety of species. Specifically, we ask the following questions: (1) Does RCM change with increasing body size within species? (2) When compared among species, does RCM vary as a function of body size? (3) How does reproductive mode affect these patterns?

MATERIALS AND METHODS

Data for within-species comparisons were collected primarily at the University of Kansas Natural History Reservation (by HSF) and at the University of Texas-Ty-

ler (by NBF). Snakes at the Natural History Reservation were collected and handled as described by Fitch (1960, 1965, 1975) and by Seigel and Fitch (1985). Briefly, all snakes were collected by hand or in wire-mesh funnel traps, and females were maintained in captivity for brief periods until egg-laying or parturition occurred. Snout-vent lengths (SVL) and body weights of females and their offspring were measured on fresh specimens to the nearest 0.1 cm and 0.1 g, respectively. Snakes at the University of Texas-Tyler were collected and maintained as described by Ford and Killebrew (1983), and essentially the same methods of handling were used.

Data for among-species comparisons utilized both the data set described above, and the literature records compiled by Seigel and Fitch (1984). In order to avoid some of the methodological problems associated with RCM (Cuellar, 1984), we limited our use of literature records to those that met the criteria listed in Seigel and Fitch (1984): i.e., data were obtained mainly from short-term captives (<6 m), and body weights and SVL were measured on fresh individuals that were processed within 72 h of birth or egg-laying. In this study, RCM refers to wet clutch mass/total female wet mass, including the clutch.

All data used in regressions in this study were transformed to log-normal values prior to testing. Except where indicated, differences among groups in ANCOVA analyses are due solely to differences in Y-intercepts and not in the slopes of the regression lines. We used SVL as our measure of body size in order to minimize the statistical problems caused by having the same term (female weight) on both sides of the regression equations. The level for statistical significance in this study was $\alpha = 0.05$.

RESULTS

Within-Species Comparisons

There was no significant relationship between female SVL and RCM for any of the nine species or populations we tested

(Table 1). Although most of our data were from viviparous colubrids, data from two oviparous colubrids (*Opheodrys aestivus*, *Diadophis punctatus*) and a viviparous viperid (*Agkistrodon contortrix*) suggest that these patterns are similar regardless of reproductive mode (at least for colubrids and viperids). There was no significant difference in the SVL/RCM relationship among years in *O. aestivus* (ANCOVA, $F = 1.66$, $df = 1,56$, $P < 0.20$), but we lacked sufficient data to test temporal differences for our other species. Finally, we found no significant difference in the SVL/RCM relationship between the two populations of *Thamnophis sirtalis* available (ANCOVA, $F = 1.82$, $df = 1,24$, $P < 0.20$). However, these two populations did differ significantly in RCM (ANCOVA, $F = 4.39$, $df = 1,24$, $P < 0.05$).

Among-Species Comparisons

Table 2 lists the 43 species or populations for which accurate and acceptable data were available for both female size and RCM. In many instances, otherwise excellent records had to be discarded because authors used total length rather than SVL, or because they did not indicate which measurement was taken. Because of the difficulties caused by tail breakage, we suggest that SVL is preferable to total length.

Data taken from Table 2 suggest that the relationship between SVL and RCM is strongly dependent upon reproductive mode (Fig. 1). Both viviparous colubrids ($n = 20$ species) and viviparous viperids ($n = 7$ species) show strongly negative regressions among these variables; however, only the colubrid regression was statistically significant. Conversely, there was no significant relationship between size and RCM among oviparous colubrids ($n = 16$). Because there is a significant difference in slopes among egg layers and live-bearers (ANCOVA, $F = 5.78$, $df = 2,38$, $P < 0.05$), RCM cannot be adjusted for SVL and compared directly among groups without violating the assumptions of ANCOVA. However, at all but the smallest SVL's, the RCM of oviparous snakes tends to be higher than that of live-bearers, and

TABLE 1.—Regression of female body size (SVL) versus RCM in a variety of snakes. All equations are transformed to log_e. Data for different years are shown separately, where available.

Species	Regression equation	r ²	F	n	P	Source
Oviparous species						
<i>Diadophis punctatus</i>	RCM = -2.58 + 0.486SVL	0.049	2.47	50	0.25	H. Fitch (personal observation)
<i>Opheodrys aestivus</i>						
1979	RCM = -0.517 - 0.122SVL	0.003	0.08	30	0.80	M. Plummer (personal communication)
1981	RCM = 1.07 - 0.550SVL	0.126	3.92	29	0.10	M. Plummer (personal communication)
Viviparous species						
<i>Agkistrodon contortrix</i>						
	RCM = 0.279 - 0.375SVL	0.022	0.901	43	0.50	H. Fitch (personal observation)
<i>Regina septemvittata</i>	RCM = 2.57 - 0.918SVL	0.289	3.24	10	0.25	Branson and Baker (1974)
<i>Thamnophis butleri</i>	RCM = -1.29 + 0.019SVL	0.002	0.06	25	0.50	N. Ford (personal observation)
<i>T. radix</i>	RCM = -0.26 - 0.290SVL	0.050	0.05	11	0.50	N. Ford (personal observation)
<i>T. sirtalis</i>	RCM = 1.42 + 0.186SVL	0.000	0.001	16	0.75	H. Fitch (personal observation)
<i>T. sirtalis</i>	RCM = 1.36 - 0.660SVL	0.150	1.57	11	0.25	N. Ford (personal observation)

TABLE 2.—Data on mean RCM and SVL for a variety of snakes. One standard deviation is given after mean values, where available. Except where indicated, sources for RCM and SVL are those listed in Seigel and Fitch (1984). (O) = oviparous; (V) = viviparous.

Species (reproductive mode)	RCM	SVL (cm)	n
Family Colubridae			
<i>Clonophis kirtlandi</i> (V)	0.396 ± 0.023	37.0	2
<i>Clonophis kirtlandi</i> (V)	0.386	38.7	1
<i>Coluber constrictor flaviventris</i> (O)	0.400 ± 0.044	89.5 ± 14.9	4*
<i>Diadophis punctatus arnyi</i> (O)	0.396 ± 0.076	29.0 ± 2.5	46
<i>Diadophis p. regalis</i> (O)	0.279	60.0	1
<i>Dinodon orientale</i> (O)	0.495	59.0	1
<i>Elaphe guttata</i> (O)	0.332 ± 0.003	87.0	2
<i>Elaphe o. obsoleta</i> (O)	0.338 ± 0.010	87.6	3
<i>Eridiphas slevini</i> (O)	0.217	37.2	1
<i>Heterodon nasicus</i> (O)	0.410	53.0	1
<i>Heterodon platyrhinos</i> (O)	0.439 ± 0.062	67.8	4
<i>Hypsiglena ochrorhyncha</i> (O)	0.433	39.1	1
<i>Hypsiglena torquata</i> (O)	0.379	33.8	1
<i>Lampropeltis c. calligaster</i> (O)	0.375 ± 0.015	82.2	2
<i>Lampropeltis getulus holbrooki</i> (O)	0.413	63.0	1
<i>Lampropeltis mexicana</i> (O)	0.375	91.5	1
<i>Lampropeltis triangulum sypila</i> (O)	0.438 ± 0.104	57.6	2
<i>Masticophis bilineatus</i> (O)	0.439	89.0	1
<i>Masticophis t. taeniatus</i> (O)	0.409 ± 0.063	89.5 ± 9.5	10
<i>Nerodia fasciata</i> (V)	0.201	75.0	1
<i>Opheodrys aestivus</i> (O)	0.372 ± 0.063	45.3 ± 4.3	59
<i>Philodryas olfersi</i> (O)	0.350 ± 0.012	83.1	9
<i>Pituophis melanoleucus deserticola</i> (O)	0.389 ± 0.047	101.0 ± 9.0	4
<i>Regina grahami</i> (V)	0.251	52.0	1
<i>Regina grahami</i> (V)	0.328 ± 0.032	64.1 ± 6.7	5
<i>Regina septemvittata</i> (V)	0.315 ± 0.050	59.2 ± 6.2	10
<i>Storeria dekayi texana</i> (V)	0.359 ± 0.098	25.4 ± 2.8	6
† <i>Thamnophis butleri</i> (V)	0.362 ± 0.037	38.3 ± 4.0	25
† <i>Thamnophis marci</i> (V)	0.224 ± 0.052	56.3 ± 7.3	12
<i>Thamnophis proximus</i> (V)	0.277 ± 0.009	57.1	2
† <i>Thamnophis proximus</i> (V)	0.256 ± 0.062	67.4 ± 9.0	4
<i>Thamnophis radix</i> (V)	0.209 ± 0.031	53.6 ± 2.7	4
† <i>Thamnophis radix</i> (V)	0.283 ± 0.045	49.7 ± 7.3	12
<i>Thamnophis sirtalis parietalis</i> (V)	0.272 ± 0.055	67.9 ± 9.6	18‡
† <i>Thamnophis sirtalis semifasciata</i> (V)	0.320 ± 0.067	58.8 ± 8.1	11
<i>Tropidoclonion lineatum</i> (V)	0.426	32.9	1
Family Viperidae			
<i>Agkistrodon contortrix</i> (V)	0.286 ± 0.049	60.9 ± 3.8	43
<i>Crotalus lepidus</i> (V)	0.414	40.0	1
<i>Crotalus polysticus</i> (V)	0.405 ± 0.016	59.7 ± 3.2	2
<i>Sistrurus catenatus</i> (V)	0.247	58.5	1
<i>Sistrurus miliarius</i> (V)	0.276	52.5	1
<i>Sistrurus miliarius</i> (V)	0.319	35.5	1
<i>Vipera russelli</i> (V)	0.263	107.0	1

* n for SVL = 3.

† Neil Ford (personal observation).

‡ n for SVL = 16.

the difference among the two groups accelerates as body size increases.

DISCUSSION

Within-Species Comparisons

We found no significant regression between SVL and RCM for any of the nine

species or populations tested. Pianka and Parker (1975) and Naulleau and Saint Girons (1981) found similar results for *Masticophis taeniatus* and *Vipera aspis*, respectively. These data suggest that body size and RCM vary independently in most colubrids and viperids tested. Clark (1970)

reported that RCM increased with SVL in the colubrid *Carphophis vermis*, but a close examination of his data suggests that this may be a statistical artifact. Using combined samples, Clark failed to demonstrate a significant regression between RCM and SVL. Using very small samples divided by locality and season, Clark demonstrated statistical significance in only one of four comparisons. Although RCM may be associated with SVL in *C. vermis*, the trends are not consistent, nor are the available data convincing. Only in two species of Australian elapids are these variables highly correlated. Shine (1977) showed an inverse relationship between SVL and RCM in the viviparous elapids *Notechis scutatus* and *Pseudechis porphyriacus*. This raises the interesting possibility that the relationship between body size and RCM varies with phylogeny. However, additional data on the RCM of elapids and other snakes is necessary before such patterns can be confirmed.

Several authors (Pianka and Parker, 1975; Plummer, 1984; Shine, 1977) have used the relationship (or lack thereof) between body size and RCM in snakes to test the hypothesis of Williams (1966) that reproductive effort should increase with age and/or size. We suggest that the lack of correlation between RCM and body size is explainable on ecological grounds alone. Vitt and Congdon (1978), Vitt and Price (1982), and Seigel and Fitch (1984) have argued that selection should operate on RCM as a distinctive life history trait, and that the RCM of a given species should be determined by a suite of life history correlates such as reproductive mode, escape behavior, and foraging strategy. Unless these traits change temporally, the RCM for a given population should be relatively constant. Changes in these ecological characteristics appear unlikely for snakes. In other words, a viviparous, sit-and-wait species that uses crypsis to avoid predators is likely to use the same tactics during its entire reproductive lifetime (but see Bauwens and Thoen, 1981). In support of this hypothesis, we cannot demonstrate that either RCM or the SVL/RCM relationship varies temporally in the few snakes for

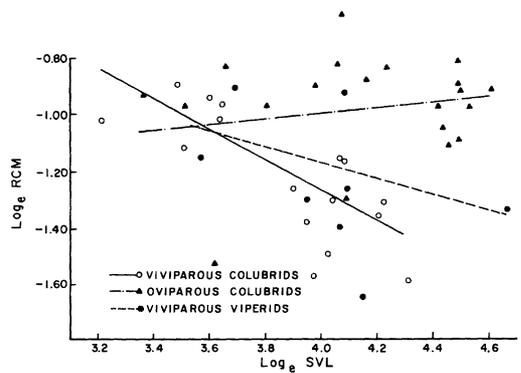


FIG. 1.—The relationship between $\log_{10} \text{SVL}$ and $\log_{10} \text{RCM}$ for different families and reproductive modes of snakes. The regression equation for oviparous colubrids is: $\log_{10} \text{RCM} = -1.249 + 0.067 \log_{10} \text{SVL}$ ($r^2 = 0.02$, $n = 20$, $P > 0.05$); for viviparous colubrids: $\log_{10} \text{RCM} = 0.916 - 0.544 \log_{10} \text{SVL}$ ($r^2 = 0.507$, $n = 16$, $P < 0.05$); and for viviparous viperids: $\log_{10} \text{RCM} = -0.062 - 0.276 \log_{10} \text{SVL}$ ($r^2 = 0.226$, $n = 7$, $P > 0.05$).

which adequate data are available (Seigel and Fitch, 1984; this paper).

In comparison with snakes, lizards appear to show considerable variation in the SVL/RCM relationship, although relatively few species of both groups have been examined. Perhaps this results from the seemingly greater diversity of foraging strategies, escape behaviors, body shapes, and habitats utilized by lizards when contrasted to the snakes considered here. Most of our data were obtained from terrestrial or semi-terrestrial species (mainly colubrids) that vary only slightly from each other in body form (e.g., *Thamnophis*, *Masticophis*, *Regina*). Data from only a few unique body forms were available for snakes (*Ophedryx*), whereas the data from lizards were obtained from a wide variety of ecomorphs, such as *Iguana*, *Cnemidophorus*, *Sceloporus* and *Amphibolurus*, which differ greatly from each other in both body shape, escape behaviors, and foraging modes. Conceivably, this has led to increased variability in the SVL/RCM relationship among lizards.

Among-Species Comparisons

We found that the regression of RCM on SVL among species was strongly dependent upon reproductive mode (Fig. 1);

in viviparous species, RCM tended to decrease with increasing body size, whereas oviparous forms showed a slight (but non-significant) positive relationship. Data taken from European vipers (Saint Girons and Naulleau, 1981) also showed a negative but non-significant relationship between body size (total length) and RCM. Seigel and Fitch (1984) demonstrated that viviparous snakes have smaller RCM than egg-layers, and they argued that this represented an increased "cost" of viviparity. ("Cost" in this context refers to a decrease in either survivorship or the amount of energy available for reproduction.) The present results strengthen that argument, especially when applied to larger species. Apparently, the costs of carrying a clutch mass in oviparous snakes are considerably lower than those for an equal-sized live-bearer. We suggest three possible hypotheses to explain why small viviparous species can "afford" a heavier RCM than can larger species. First, body size may be considered a rough indicator of longevity in some species (Shine, 1977; Williams, 1966). If this is true, and if there is a relationship between RCM and escape ability (Seigel and Fitch, 1984; Shine, 1980), then larger, longer-lived species may maximize survivorship by keeping RCM low. The opposite may then be true of smaller, short-lived species, which tend to have high RCM. Second, because gravity becomes increasingly burdensome with larger size, a high RCM may have little effect on small snakes. Finally, habitat utilization and consequent exposure to predation may vary among small versus large snakes. J. B. Iverson (personal communication) suggested that large species that spend much time in open, relatively exposed habitats may have a higher risk of predation than do small, often secretive species. Many of the small species considered here are indeed secretive, semi-fossorial forms that may not often be exposed to visual predators, or which are not dependent on speed for escape (e.g., *Storeria dekayi*, *Tropidoclonion lineatum*). However, larger species such as *Nerodia fasciata* or *Thamnophis sirtalis* inhabit relatively open areas, and speed may be an important factor in avoiding predation.

Such differences may also be related to foraging strategies (e.g., widely-foraging versus sit-and-wait). Unfortunately, adequate demographic data to test these hypotheses are still lacking for snakes.

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ENDOGENOUS CONTROL OF SEASONAL CHANGE OF EGG, HATCHLING, AND CLUTCH SIZE OF THE LIZARD *SCELOPORUS UNDULATUS GARMANI*

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ABSTRACT: Female *Sceloporus undulatus* producing two clutches of eggs under controlled laboratory conditions increased egg and hatchling size but decreased the number of eggs in the second clutch. The females did not increase in length but did increase in mass between the two oviposition periods. Egg and clutch size were inversely related with an r^2 of 0.13. Egg size and day laid (day after first lay date of the season) accounted for 54% of the variance in hatchling size with most variance due to egg size (48%).

Key words: Lizard; Life-history evolution; Endogenous reproductive allocation; Eggs; Hatchlings; Clutch size; Reproduction

CLUTCH size of lizards varies among species, conspecific populations (Ballinger, 1983; Snell et al., 1984; Tinkle, 1969; Tinkle and Ballinger, 1972), and among

season and years within the same population (Ballinger, 1977; Ferguson and Bohlen, 1978; Nussbaum, 1981). Most lizards that produce more than one clutch per season reduce the size of later clutches. In populations of *Uta stansburiana*, *Sceloporus undulatus*, and *Sceloporus graciosus*, increased egg size accompanies

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