

Ecological patterns of relative clutch mass in snakes

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Summary. Data on the relative clutch mass of snakes are summarized for over 100 populations. RCM was significantly lower in live bearing versus egg laying forms. We suggest that the longer reproductive season of viviparous snakes results in higher overall mortality compared to oviparous species; by reducing RCM, viviparous snakes may reduce this risk of mortality. Unlike lizards, no differences in RCM were found between categories of either escape behavior or foraging mode, possibly because detailed information on these behaviors are lacking for most snakes. In four populations examined, RCM did not vary among years. When compared to lizards, snakes demonstrate significantly higher RCM, perhaps owing to a more energetically efficient means of locomotion. Our data support the contention that RCM should be considered a separate and distinctive life-history characteristic of reptiles.

The evolution of life history characteristics is of considerable interest to ecologists. Among the most commonly-reported reproductive traits are clutch size, number of clutches per year, and offspring size. Recently, Vitt and Price (1982) proposed that relative clutch mass or RCM (the ratio of clutch weight to body weight) be considered as an independent and distinctive life history characteristic of lizards. RCM has frequently been used as an indirect measure of reproductive effort in lizards (cf. Tinkle 1969; Pianka and Parker 1975; Martin 1977; Droge et al. 1982), although some authors have objected to such a use on theoretical grounds (Tinkle and Hadley 1975; Hirshfield and Tinkle 1975). In a recent series of papers, L. Vitt and his co-workers (Vitt and Congdon 1978; Vitt 1981; Vitt and Price 1982) convincingly demonstrated that RCM is not necessarily associated with reproductive effort (i.e., the proportion of available resources devoted to reproduction), but is instead highly correlated with a number of ecological and morphological characteristics of lizards. Vitt and Price (1982) suggested that selection acts via differential mortality of gravid females to produce an RCM that is optimal for a particular suite of ecological and morphological traits. For example, high RCM is associated with cryptic escape behavior and the sit-and-wait foraging mode, whereas species which actively flee from predators and are active for-

agers have low RCM. Vitt theorized that species dependent upon speed or agility to find food or avoid predation would be more hampered by a heavy clutch burden than would cryptic or sit-and-wait species. Likewise, a species with a streamlined morphology might be preadapted to low RCM.

Vitt and Congdon (1978) summarized these correlates for lizards and predicted that other organisms might show similar trends. Because snakes are closely related to lizards and because of their distinctive morphology, snakes are a model group with which to test these predictions. In this paper, we test whether the above correlations between ecological traits and the RCM of lizards hold true for snakes and examine several correlations not considered for lizards.

Materials and methods

The primary sources of our data were literature records, although we supplemented these with our own field observations whenever possible. To minimize variation in our samples, we attempted to utilize only those records meeting the following criteria: 1) offspring came from females which were short-term captives (<6 months); 2) offspring and parents were weighed within 72 h of birth or egg-laying; 3) weights came from non-preserved specimens. We relaxed these criteria in occasional instances when no other data sources were available, especially for boids (which were often long-term captives) and for sea snakes, where the available data were derived from preserved specimens.

RCM is defined in this study as total offspring mass/female total mass, including the clutch. This ratio was criticized by Shine (1980) on statistical grounds; however it is used here to facilitate comparisons with lizards. For the purposes of this study, we do not distinguish between the terms viviparous and ovoviviparous; both are combined as "live-bearing". The escape behaviors of snakes were categorized as flight, crypsis, and stand-and-fight. Species that routinely fled from predators were placed in the flight category. Species that usually remained motionless and relied mainly upon background matching to avoid detection and predation were classified as cryptic, and those species that used some form of active defense to deter predators (vibrating the tail, inflating the body, striking) were classified as stand-and-fight. We divided the foraging tactics of snakes into two categories, prey location and prey capture. Snakes locate prey items by either active movements (wide-foraging), or by remaining immobile and waiting for active prey to come within reach (sit-and-wait; Huey and Pianka 1981;

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Table 1. Summary of data on the relative clutch mass (RCM) of snakes

Species	RCM	Reproductive mode	Predator ^a escape	Prey ^b location	Prey ^c capture	Reference for RCM
Family Boidae						
<i>Epicrates cenchria</i>	0.301	Viviparous	S + F	S + W	Ambush	L. Vitt (pers. comm.)
<i>E. gracilis</i>	0.243	Viviparous	Cryp/S + F	S + W	Ambush	Murphy et al. (1978)
<i>Eunectes murinus</i>	0.222	Viviparous	Cryp/S + F	S + W	Ambush	Holmstrom (1980)
<i>Liasis childreni</i>	0.317	Oviparous	Cryp/S + F	S + W	Ambush	Chiras (1982)
<i>Python regius</i>	0.311	Oviparous	Cryp/S + F	S + W	Ambush	Van Mierop and Besette (1981)
<i>P. timorienis</i>	0.269	Oviparous	Cryp/S + F	S + W	Ambush	Murphy et al. (1978)
Family Acrochordidae						
<i>Acrochordus granulatus</i>	0.192	Viviparous	?	Act	Sed	Lemen and Voris (1981)
Family Colubridae						
<i>Chilomeniscus cinctus</i>	0.105	Oviparous	Flee	Act	Sed	Vitt (1978)
<i>Coluber c. constrictor</i>	0.289	Oviparous	Flee	Act	Pursue	Conant (1942)
<i>C. c. flaviventris</i>	0.400	Oviparous	Flee	Act	Pursue	H. Fitch (pers. obs.)
<i>Contia tenuis</i>	0.185	Oviparous	Flee	Act	Sed	Vitt (1978)
<i>Diadophis punctatus arnyi</i>	0.396	Oviparous	Flee/S + F	Act	Sed	H. Fitch (pers. obs.)
<i>Diadophis p. regalis</i>	0.279	Oviparous	Flee/S + F	Act	Sed	Vitt (1975)
<i>Dinodon orientale</i>	0.495	Oviparous	Flee	Act	Sed	Fukada (1963)
<i>Elaphe guttata</i>	0.332	Oviparous	Cryp/S + F	Act	Ambush/Sed	Clark (1953)
<i>Elaphe o. obsoleta</i>	0.338	Oviparous	Cryp/S + F	Act	Ambush/Sed	H. Fitch (pers. obs.)
<i>Elaphe vulpina</i>	0.319	Oviparous	Cryp/S + F	Act	Ambush/Sed	Conant and Downs (1940)
<i>Eridiphas slevini</i>	0.217	Oviparous	?	Act	?	Hunt and Ottley (1982)
<i>Heterodon nasicus</i>	0.410	Oviparous	Cryp/S + F	Act	Sed	Munro (1949)
<i>Heterodon platyrhinos</i>	0.439	Oviparous	Cryp/S + F	Act	Sed	Kennedy (1961)
<i>Hypsiglena ochrorhyncha</i>	0.433	Oviparous	Cryp	Act	Sed	Vitt (1975)
<i>Hypsiglena torquata</i>	0.477	Oviparous	Cryp	Act	Sed	Dundee (1950)
<i>Hypsiglena torquata</i>	0.379	Oviparous	Cryp	Act	Sed	Clark and Lieb (1973)
<i>Lampropeltis c. calligaster</i>	0.375	Oviparous	Flee	Act	Ambush/Sed	H. Fitch (pers. obs.)
<i>Lampropeltis getulus floridana</i>	0.325	Oviparous	Flee	Act	Ambush/Sed	Conant and Downs (1940)
<i>Lampropeltis g. holbrooki</i>	0.402	Oviparous	Flee	Act	Ambush/Sed	J. Collins (pers. obs.)
<i>Lampropeltis g. holbrooki</i>	0.413	Oviparous	Flee	Act	Ambush/Sed	Grimpe and Benefield (1981)
<i>Lampropeltis mexicana</i>	0.375	Oviparous	Flee	Act	Ambush/Sed	Assetto (1978)
<i>Lampropeltis pyromelana</i>	0.387	Oviparous	Flee	Act	Ambush/Sed	Martin (1976)
<i>Lampropeltis triangulum sypila</i>	0.376	Oviparous	Cryp	Act	Ambush/Sed	J. Collins (pers. comm.)
<i>Lampropeltis t. sypila</i>	0.438	Oviparous	Cryp	Act	Ambush/Sed	H. Fitch (pers. obs.)
<i>Leioheterodon madagascariensis</i>	0.288	Oviparous	Cryp/S + F	Act	Sed?	Conant (1938)
<i>Liophis lineatum</i>	0.297	Oviparous	Flee	Act	?	L. Vitt (pers. comm.)
<i>Liophis poecilogyrus</i>	0.178	Oviparous	Flee	Act	?	L. Vitt (pers. comm.)
<i>Liophis viridis</i>	0.258	Oviparous	Cryp	Act	?	L. Vitt (pers. comm.)
<i>Masticophis bilineatus</i>	0.439	Oviparous	Flee	Act	Pursue	Vitt (1975)
<i>Masticophis taeniatus schotti</i>	0.430	Oviparous	Flee	Act	Pursue	Gloyd (1934)
<i>Masticophis t. taeniatus</i>	0.409	Oviparous	Flee	Act	Pursue	Parker and Brown (1980)
<i>Nerodia cyclopion</i>	0.112	Viviparous	Flee	Act	Pursue	Conant and Downs (1940)
<i>Nerodia erythrogaster alta</i>	0.241	Viviparous	Flee	Act	Pursue	Conant (1965)
<i>Nerodia e. transversa</i>	0.265	Viviparous	Flee	Act	Pursue	Conant and Downs (1940)
<i>Nerodia harteri</i>	0.164	Viviparous	Flee	Act	Pursue	Conant (1942)
<i>Nerodia kirtlandi</i>	0.396	Viviparous	Flee	Act	Pursue	Conant (1943)
<i>Nerodia kirtlandi</i>	0.386	Viviparous	Flee	Act	Pursue	Tucker (1976)
<i>Nerodia rhombifera</i>	0.289	Viviparous	Flee	Act	Pursue	R. Seigel (pers. obs.)
<i>Nerodia fasciata</i>	0.201	Viviparous	Flee	Act	Pursue	Conant and Downs (1940)
<i>Opheodrys aestivus</i>	0.372	Oviparous	Cryp	Act	Pursue	M. Plummer (pers. comm.)
<i>Oxybelis aeneus</i>	0.325	Oviparous	Cryp	S + W	Ambush	L. Vitt (pers. comm.)
<i>Philodryas olfersi</i>	0.350	Oviparous	Flee	Mixed	Ambush/Pursue	Vitt (1980)
<i>Pituophis melanoleucus deserticola</i>	0.389	Oviparous	S + F	Act	Ambush/Sed	Parker and Brown (1980)
<i>Pituophis m. melanoleucus</i>	0.250	Oviparous	S + F	Act	Ambush/Sed	Conant and Downs (1940)
<i>Pituophis m. mugitus</i>	0.391	Oviparous	S + F	Act	Ambush/Sed	Lee (1967)
<i>Pituophis m. sayi</i>	0.454	Oviparous	S + F	Act	Ambush/Sed	J. Collins (pers. comm.)
<i>Regina grahami</i>	0.251	Viviparous	Flee	Act	Sed	Kennedy (1964)
<i>Regina grahami</i>	0.328	Viviparous	Flee	Act	Sed	R. Seigel (pers. obs.)
<i>Regina septemvittata</i>	0.315	Viviparous	Flee	Act	Sed	Branson and Baker (1974)
<i>Rhinocheilus leonti</i>	0.374	Oviparous	Flee	Act	Sed	Vitt (1975)
<i>Salvadora hexalepis</i>	0.225	Oviparous	Flee	Act	Pursue	Vitt (1978)
<i>Sonora semiannulata</i>	0.226	Oviparous	Flee	Act	Sed	Vitt (1978)
<i>Sphalerosophis cliffordi</i>	0.348	Oviparous	Flee	Act	Pursue	Dm'iel (1967)
<i>Storeria d. dekayi</i>	0.372	Viviparous	Flee	Act	Sed	Jones (1976)

Table 1 (continued)

Species	RCM	Reproductive mode	Predator ^a escape	Prey ^b location	Prey ^c capture	Reference for RCM
<i>Storeria d. texana</i>	0.359	Viviparous	Flee	Act	Sed	H. Fitch (pers. obs.)
<i>Thamnophis cyrtopsis</i>	0.614	Viviparous	Flee	Act	Pursue	Vitt (1975)
<i>Thamnophis proximus</i>	0.277	Viviparous	Flee	Act	Pursue	D. Clark (1974)
<i>Thamnophis proximus</i>	0.204	Viviparous	Flee	Act	Pursue	R. Seigel (pers. obs.)
<i>Thamnophis radix</i>	0.209	Viviparous	Flee	Act	Pursue	R. Seigel (pers. obs.)
<i>Thamnophis sirtalis parietalis</i>	0.272	Viviparous	Flee	Act	Pursue	H. Fitch (pers. obs.)
<i>Thamnophis s. parietalis</i>	0.244	Viviparous	Flee	Act	Pursue	H. Guarisco (pers. comm.)
<i>Thamnophis s. sirtalis</i>	0.264	Viviparous	Flee	Act	Pursue	Conant and Downs (1940)
<i>Tropidoclonion lineatum</i>	0.426	Viviparous	Flee	Act	Sed	Funk and Tucker (1978)
<i>Virginia valeriae</i>	0.304	Viviparous	Flee	Act	Sed	J. Collins (pers. comm.)
<i>Waglerophis merremii</i>	0.244	Oviparous	Mixed	Act	?	L. Vitt (pers. comm.)
Family Elapidae						
<i>Cacophis squamulosus</i>	0.321	Oviparous	Mixed	Act	Sed	R. Shine (pers. comm.)
<i>Cryptophis nigrescens</i>	0.312	Viviparous	Mixed	Act	?	R. Shine (pers. comm.)
<i>Drysdalia coronoides</i>	0.219	Viviparous	?	Act	?	R. Shine (pers. comm.)
<i>Drysdalia rhodogaster</i>	0.261	Viviparous	?	Act	?	R. Shine (pers. comm.)
<i>Hemiaspsis signata</i>	0.276	Viviparous	Mixed	Act	?	R. Shine (pers. comm.)
<i>Micrurus fulvius</i>	0.554	Oviparous	Cryp	Act	Ambush/Sed	Campbell (1973); Tryon and McCrystal (1982)
<i>Pseudechis guttatus</i>	0.364	Oviparous	Flee	Act	Pursue	R. Shine (pers. comm.)
<i>Suta suta</i>	0.262	Viviparous	S + F	Act	?	R. Shine (pers. comm.)
Family Hydrophiidae						
<i>Aipysurus eydouxi</i>	0.224	Viviparous	Flee?	Act?	?	Lemen and Voris (1981)
<i>Emydocephalus schistosa</i>	0.280	Viviparous	Flee?	Act	?	Lemen and Voris (1981)
<i>Lapemis hardwickii</i>	0.216	Viviparous	Flee?	Act	?	Lemen and Voris (1981)
<i>Hydrophis brookii</i>	0.276	Viviparous	Flee?	Act?	?	Lemen and Voris (1981)
<i>Hydrophis caeruleus</i>	0.247	Viviparous	Flee?	Act?	?	Lemen and Voris (1981)
<i>Hydrophis fasciatus</i>	0.265	Viviparous	Flee?	Act?	?	Lemen and Voris (1981)
<i>Hydrophis melanosoma</i>	0.219	Viviparous	Flee?	Act?	?	Lemen and Voris (1981)
<i>Hydrophis torquatus</i>	0.258	Viviparous	Flee?	Act?	?	Lemen and Voris (1981)
<i>Thalassophina viperina</i>	0.241	Viviparous	Flee?	Act?	?	Lemen and Voris (1981)
Family Viperidae						
<i>Agkistrodon contortrix</i>	0.286	Viviparous	Cryp/S + F	S + W	Ambush	H. Fitch (pers. obs.)
<i>Agkistrodon contortrix</i>	0.308	Viviparous	Cryp/S + F	S + W	Ambush	R. Seigel (pers. obs.)
<i>Crotalus durissus</i>	0.164	Viviparous	Cryp/S + F	S + W	Ambush	Armstrong and Murphy (1979)
<i>Crotalus enyo</i>	0.137	Viviparous	Cryp/S + F	S + W	Ambush	Tryon and Radcliffe (1977)
<i>Crotalus horridus</i>	0.335	Viviparous	Cryp/S + F	S + W	Ambush	J. Collins (pers. comm.)
<i>Crotalus lepidus</i>	0.414	Viviparous	Cryp/S + F	S + W	Ambush	Armstrong and Murphy (1979)
<i>Crotalus polysticus</i>	0.405	Viviparous	Cryp/S + F	S + W	Ambush	Armstrong and Murphy (1979)
<i>Crotalus viridis</i>	0.352	Viviparous	Cryp/S + F	S + W?	Ambush	Conant and Downs (1940)
<i>Crotalus willardi</i>	0.358	Viviparous	Cryp/S + F	S + W	Ambush	B. Martin (1975)
<i>Echis colorata</i>	0.409	Oviparous	Cryp/S + F	S + W	Ambush	Mendelssohn (1965)
<i>Pseudocerastes fieldi</i>	0.310	Oviparous	Cryp/S + F	S + W	Ambush	Mendelssohn (1965)
<i>Sistrurus cateratus</i>	0.247	Viviparous	Cryp/S + F	S + W	Ambush	R. Seigel (pers. obs.)
<i>Sistrurus miliarius</i>	0.276	Viviparous	Cryp/S + F	S + W	Ambush	Carpenter (1960)
<i>Sistrurus miliarius</i>	0.319	Viviparous	Cryp/S + F	S + W	Ambush	Fleet and Kroll (1978)
<i>Vipera berus</i>	0.304	Viviparous	Cryp/S + F	S + W	Ambush	Prestit (1971)
<i>Vipera russelli</i>	0.263	Viviparous	Cryp/S + F	S + W	Ambush	Nalleau and van den Brule (1980)
<i>Vipera xanthina</i>	0.341	Oviparous	Cryp/S + F	S + W	Ambush	Mendelssohn (1963)

^a Cryp = Cryptic defense; S + F = Stand and fight

^b S + W = Sit and wait foraging; Act = active foraging

^c Sed = sedentary prey taken

Vitt and Price 1982). Prey capture may be accomplished by a short chase (pursuit), by striking from hiding (ambush), or by taking sedentary prey species, which probably require neither behavior. Snakes were assigned to various categories using literature references and our own field observations.

Preliminary data suggest that although there is no correlation between female body size and RCM within species,

such relationships may exist for between-species comparisons (Plummer 1984; N. Ford, pers. comm.; Seigel and Fitch in prep.). We therefore tried to use analysis of covariance (ANCOVA) for comparisons of RCM among species whenever possible in this paper, rather than making direct comparisons of RCM ratios as in Vitt and Congdon (1978) and Vitt and Price (1982). RCM ratios are still presented for illustrative purposes, but such ratios should be evaluated

with caution, especially when making comparisons between species. All data used in ANCOVA analysis were transformed to log-normal values before testing. In all ANCOVA results reported, differences among groups were due solely to differences in Y-intercepts, and not in the slopes of the regression lines.

Predictions

The following predictions were made prior to data collection and analysis;

1) Live-bearing species should have a lower RCM than egg-layers.

2) Species that actively flee from predators should have a lower RCM than species using the cryptic or stand-and-fight strategy.

3) Active foragers and snakes using the pursuit tactic to capture prey should have a lower RCM than sit-or-wait foragers, or those species taking prey from ambush. Snakes taking primarily sedentary prey should have RCM intermediate between the above.

4) Yearly variation in RCM may be apparent if either predation intensity or food availability vary among years.

Predictions 2 and 3 are from Vitt and Congdon (1978), Huey and Pianka (1981), and Vitt and Price (1982). Prediction 1 stems from the increased "cost" to viviparous females imparted by the lengthy period that live-bearers must maintain offspring within the body as compared to egg-layers (Tinkle and Gibbons 1977). We hypothesize that viviparous females may circumvent this cost by reducing the magnitude of the burden (i.e., the clutch mass). Prediction 4 rests on the assumption that RCM is determined primarily by differential mortality of gravid females via predation or food availability. Evidence for such temporal variation in RCM was reported for lizards by Ballinger (1977) and Dunham (1982).

Finally, we compared the RCM of snakes and lizards. No a priori predictions were made for this comparison.

Results

We assembled data on the RCM of 97 species and subspecies of snakes, representing 106 populations (Table 1). Although literature records of clutch size are numerous, relatively few investigators reported offspring size, and still fewer recorded the weights of both females and offspring.

Because the traits considered here are likely to be co-evolved, it was necessary to select one trait for initial testing. Owing to the non-ambiguous nature of reproductive mode compared to foraging behavior or escape strategies, this trait was tested first.

Reproductive mode. – The RCM of live-bearing snakes was consistently lower than the RCM of egg-layers (Table 2). There was a significant regression between clutch mass and female body mass (minus the clutch) for both reproductive modes (oviparous; \log clutch mass = $-0.0098 + 0.893 \log$ body mass, $r^2 = 0.944$, $P < 0.001$; viviparous; \log brood mass = $-0.045 + 0.820 \log$ body mass, $r^2 = 0.909$, $P < 0.001$). An analysis of covariance (ANCOVA) using body mass as the covariate demonstrated that on a size-independent basis, live-bearing snakes had a smaller clutch mass than egg-layers (all taxa, $F = 37.8$, $P < 0.001$). This trend held true both within and among taxonomic groups; i.e., the RCM of egg-laying colubrids was higher

Table 2. Relative clutch mass of oviparous versus viviparous snakes (upper) and phylogenetic comparisons of RCM (lower)

Reproductive mode	RCM ($\bar{X} \pm SD$)	Range	N
Oviparous	0.346 \pm 0.086	0.105–0.639	52
Viviparous	0.281 \pm 0.082	0.112–0.614	54

Family	Reproductive mode	RCM ($\bar{X} \pm SD$)	N
Boidae	Oviparous	0.299 \pm 0.026	3
	Viviparous	0.255 \pm 0.040	3
Acrochordidae	Viviparous	0.192	1
Colubridae	Oviparous	0.344 \pm 0.087	43
	Viviparous	0.295 \pm 0.106	22
Elapidae	Oviparous	0.413 \pm 0.124	3
	Viviparous	0.266 \pm 0.033	5
Hydrophiidae	Viviparous	0.247 \pm 0.024	9
Viperidae	Oviparous	0.353 \pm 0.051	3
	Viviparous	0.298 \pm 0.079	14

Table 3. Differences in RCM among snakes using the cryptic/stand and fight strategy vs those fleeing from predators. Separate values are given for oviparous and viviparous species

Escape strategy*	Reproductive mode	RCM ($\bar{X} \pm SD$)	N	P-level (ANCOVA)
Cryptic/S + F Flee	Oviparous	0.367 \pm 0.073	25	0.633
	Viviparous	0.355 \pm 0.098	22	
Cryptic/S + F Flee	Viviparous	0.289 \pm 0.072	18	0.199
	Oviparous	0.281 \pm 0.092	31	

* S + F = Stand and Fight. See text for definition of categories

than that of viviparous colubrids (Table 2). Differences among reproductive modes within the Colubridae were significant (ANCOVA, $P < 0.05$); sample sizes for other families were too small for statistical analysis.

Predator escape and foraging strategies. – Because of the obvious effect of reproductive mode on RCM, differences in foraging and escape behaviors were tested after the data were partitioned for oviparous and viviparous forms. In no case could a significant difference in RCM be demonstrated between categories of escape behavior or foraging mode (ANCOVA, $P > 0.05$), and our predictions concerning which behaviors should have the lowest RCM were rarely verified (Tables 3 and 4). Certain species fit the expected pattern well; for example, hognose snakes (genus *Heterodon*) are rather large-bodied, slow-moving snakes that feed primarily on toads, and have an elaborate defensive display (Conant 1975). Such a species should have relatively high RCM, and this is the case (*H. nasicus* = 0.410, *H. platyrhinos* = 0.439). However, exceptions to predictions 2–3 were equally common. The whipsnakes (*Masticophis*) and racers (*Coluber*) are slim, fast-moving snakes that flee rapidly when approached (Conant 1975), and sometimes at least, actively pursue their prey. RCM should be relatively low in such species, but varied from 0.409 to 0.439 in *Masticophis*, and 0.289–0.400 in *Coluber* (Table 1). Because

Table 4. Differences in RCM among snakes using different foraging strategies. Separate values are given for oviparous and viviparous species. Part I shows differences in prey location tactics, Part II differences in prey capture tactics. See text for explanation of categories. Questionable assignments are not used. SW=sit and wait; SED=sedentary prey

	Foraging mode	Reproductive mode	RCM ($\bar{X} \pm SD$)	N
I	SW	Oviparous	0.326 ± 0.042	7
	Active	Oviparous	0.349 ± 0.093	44
	SW	Viviparous	0.286 ± 0.075	16
	Active	Viviparous	0.284 ± 0.094	30
II	SW/Ambush	Oviparous	0.326 ± 0.042	7
	SW/Pursue	Oviparous	–	–
	Active/Ambush	Oviparous	–	–
	Active/Pursue	Oviparous	0.369 ± 0.074	9
	Active/SED	Oviparous	0.347 ± 0.118	13
	Active/Mixed (SED + Ambush)	Oviparous	0.382 ± 0.067	16
	SW/Ambush	Viviparous	0.286 ± 0.075	16
	SW/Pursue	Viviparous	–	–
	Active/Ambush	Viviparous	–	–
	Active/Pursue	Viviparous	0.276 ± 0.119	15
	Active/SED	Viviparous	0.318 ± 0.073	8
	Active/Mixed	Viviparous	–	–

Table 5. Yearly variation in the RCM of snakes. Data for *Opheodrys aestivus* are from M. Plummer (pers. comm.). Other data from Fitch (pers. obs.)

Species	Year	RCM ($\bar{X} \pm SD$)	N	p-level
<i>Thamnophis sirtalis</i>	1963	0.288 ± 0.049	4	0.699 ^a
	1979	0.277 ± 0.066	9	
<i>Agkistrodon contortrix</i>	1958	0.301 ± 0.072	5	0.100 ^b
	1964	0.332 ± 0.028	5	
	1972	0.282 ± 0.042	8	
	1974	0.287 ± 0.023	6	
<i>Diadophis punctatus</i>	1977	0.262 ± 0.034	9	0.500 ^b
	1965	0.399 ± 0.071	24	
	1966	0.356 ± 0.059	8	
<i>O. aestivus</i>	1974	0.402 ± 0.069	15	0.250 ^a
	1979	0.381 ± 0.072	30	
	1981	0.363 ± 0.051	29	

^a Mann-Whitney U test

^b Kruskal-Wallis test

Table 6. Comparison of RCM in lizards and snakes. All lizard data are from Vitt and Price (1982). Separate values are given for oviparous and viviparous forms. Geckos are not included, but their exclusion does not change the results

Taxa	Reproductive mode	RCM ($\bar{X} \pm SD$)	N	p-level (Mann-Whitney U)
Lizards	Oviparous	0.224 ± 0.073	83	0.001
Snakes	Oviparous	0.346 ± 0.087	52	
Lizards	Viviparous	0.226 ± 0.084	10	0.054
Snakes	Viviparous	0.281 ± 0.082	54	

we recognized that low sample size for some species might bias our results, we deleted those species with $N < 3$, and repeated the above comparisons. Again, no significant differences were found between categories of escape behavior or foraging strategies (ANCOVA, $P > 0.05$).

Yearly variation. – Yearly variation in RCM was assessed for two egg-laying species (*Opheodrys aestivus* and *Diadophis punctatus*), as well as for two live-bearers (*Agkistrodon contortrix* and *Thamnophis sirtalis*). In no case were significant differences in RCM found among years (Table 5).

Comparisons of lizards and snakes. – Differences in the RCM of lizards and snakes were striking, particularly for oviparous forms (Table 6). For both reproductive modes, the RCM of snakes was higher than that for lizards, although probably owing to small sample size, the differences between viviparous forms was not quite significant (Mann-Whitney U, $P = 0.054$). Because differences in reproductive mode were not considered by either Vitt and Congdon (1978) or Vitt and Price (1982), we utilized data from the latter study to determine whether differences in reproductive mode affected the RCM of lizards as well. The mean RCM of oviparous lizards (0.208 ± 0.077 , $N = 102$) was actually less than the mean RCM for viviparous lizards (0.226 ± 0.084 , $N = 10$), but the differences were not significant (Mann-Whitney U, $P < 0.52$). If geckos (which demonstrate fixed clutch size) are deleted from the sample, the RCM of oviparous forms increases to 0.224 (SD = 0.073, $N = 83$), virtually identical to that of viviparous lizards.

Discussion

Reproductive mode. – Our prediction that live-bearing snakes should have lower RCM than egg-layers was verified by the data in Table 2. This result is consistent with various models of the evolution of viviparity, which suggest that there is an increased “cost” to the female associated with live-bearing (Tinkle and Gibbons 1977; Shine and Bull 1979). This idea was substantiated by the data of Shine (1980) and Bauwens and Thoen (1981), who demonstrated that there was an inverse relationship between RCM and escape speed in lizards (unfortunately, similar data are lacking for snakes). Furthermore, Shine (1980) found that gravid Australian skinks were more susceptible to predation than were non-gravid individuals (but see Bauwens and Thoen 1981). This implies that increasing RCM (within a species) may be associated with decreasing ability to avoid predators, and consequently, increased predation rates. This effect should be most noticeable for species using flight to avoid predation, or which are active foragers. Species taking prey from ambush, or species using crypsis to avoid predation may avoid this cost, as may species that normally flee from predators, but which switch to crypsis during the reproductive season (Bauwens and Thoen 1981). Models for the evolution of viviparity also assume that egg-laying is the ancestral mode of reproduction in reptiles, with viviparity a derived trait (Neill 1964; Tinkle and Gibbons 1977; Shine and Bull 1979). Our data therefore suggest that RCM decreases in snake lineages evolving viviparity. Decreased RCM should translate into either reduced clutch size, smaller offspring size, or both, traits that should not be favored by natural selection unless there is some corresponding advantage to the female in making the reduction (Williams 1966).

Our model for the reduced RCM of viviparous snakes is as follows. Assume two hypothetical cohorts of snakes (one oviparous, the other viviparous), with the simplifying assumptions that each cohort has equivalent foraging and escape behaviors, that each is subject to the same potential predators, and that the predation rates are constant throughout time. Under this set of assumptions, the instantaneous probability of survivorship for gravid females in each cohort is identical. However, when survivorship is plotted for the entire reproductive season, the net survivorship of the egg-laying cohort will be somewhat higher than that for the live-bearers (Fig. 1), simply as a consequence of the longer gestation period of live-bearers compared to egg-layers (about 100 days for viviparous snakes, 50–60 days for oviparous forms; Tinkle and Gibbons 1977). This argument is similar to that of Shine and Bull (1979), who noted that the “cost” of egg retention was proportional to the duration of the retention. Because the death of a gravid female means not only the loss of the brood, but also of all future reproductive potential, it is difficult to see how viviparity could be maintained in light of potentially increased predation rates.

Reptiles have at least two non-exclusive options to increase net survivorship: 1) decrease the gestation period, or 2) decrease RCM. Decreasing the gestation period has the obvious effect of increasing overall survivorship of the female, but is of limited usefulness, since there is a physiological lower limit to how long embryos must be maintained in the female’s body to insure normal development. The second option is the apparent solution to this dilemma. By reducing RCM, escape speed is increased (Shine 1980), instantaneous predation risk is consequently decreased, and net overall survivorship presumably increased. The effect of a 25% reduction in RCM, paralleling approximately the actual differences between viviparous and oviparous snakes, is shown in Fig. 2. Under this model, net differences in survivorship between the two reproductive modes are minor.

Energetic constraints also could result in lower RCM among viviparous snakes, for three reasons. First, there may be a high daily energetic cost involved in maintaining young within the body of the female, especially for those species which directly provide nutrients for the offspring during development. Secondly, even if the maintenance costs for the two reproductive modes are equal on a daily basis, the longer reproductive season of viviparous species still would result in higher overall energetic costs. Finally, several viviparous species cease feeding during the latter parts of the reproductive season (Shine 1980; Fitch ms.), further increasing energetic constraints on this mode of reproduction. If RCM is related to energetic costs, then a reduction in RCM among viviparous snakes would reduce this constraint. Therefore, in explaining the reduced RCM of viviparous snakes, a model based on energetic costs gives the same result as a model based on survivorship, making it difficult to separate the two.

Tinkle and Gibbons (1977) listed two major drawbacks of viviparity: 1) decreased yearly fecundity (viviparous species are primarily single-brooded, whereas oviparous forms may produce multiple clutches), and 2) increased maintenance costs to the female. For snakes, another factor must be added to these costs, reduced clutch mass. As noted above, reduced RCM per breeding episode should translate into either smaller brood size, smaller offspring size, or

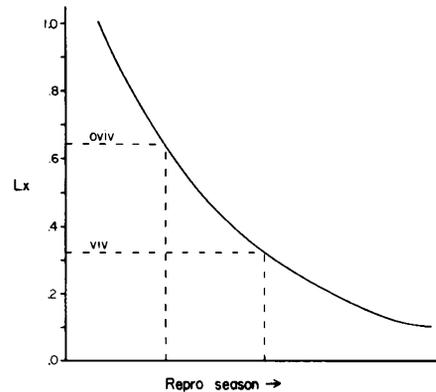


Fig. 1. Graphical representation of survivorship (y-axis) of hypothetical cohorts of gravid oviparous and viviparous snakes, assuming constant mortality throughout the reproductive season (x-axis). Note that even if mortality rates and RCM are equivalent among the cohorts, the viviparous group demonstrates lower over-all survivorship, owing to the longer reproductive season

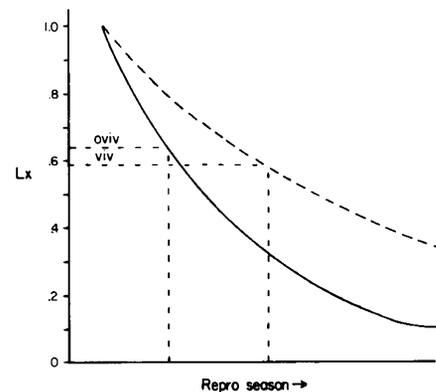


Fig. 2. Effect of a 25% decrease in RCM on the survivorship of viviparous snakes (dotted line). The survivorship curve for oviparous snakes (solid line) remains the same as in Fig. 1. Although viviparous snakes still have a longer reproductive season, overall survivorship increases among this group if decreased RCM translates into lower susceptibility to predation. See text for discussion

some combination of the two. Preliminary information suggests that viviparous snakes produce clutches as large or larger than oviparous species, at some sacrifice of relative offspring size. Iverson (in prep.) examined body size/clutch size patterns in snakes and noted a general trend toward larger brood sizes among viviparous forms. Feaver (1977) reported that viviparous snakes produce offspring that are relatively smaller than young from oviparous species, although his data base was somewhat limited.

In summary, the following “trade-offs” (Stearns 1976) might have occurred during the evolution of viviparity. 1) Female survivorship – given equal RCM, the survivorship of a viviparous female through the reproductive season would be expected to be lower than that of a similar oviparous female (Fig. 1). By reducing RCM, viviparous females trade-off some reproductive output (apparently in the form of offspring size) in the expectation of future reproductive success. 2) Fecundity – Tinkle and Gibbons (1977) suggested that fecundity must be lower in viviparous reptiles, since the long reproductive season precludes multiple broods (but see Iverson, in prep.). There are currently only minimal data to suggest that either oviparous or viviparous

snakes produce multiple broods (Fitch 1970; Aldridge 1979). However, perhaps owing to resource limitations, viviparous snakes tend to skip opportunities for reproduction more frequently than do oviparous snakes (Bull and Shine 1979). Iverson (in prep.) suggested that the increased brood size of viviparous snakes represented either compensation for decreased survivorship of adults, or compensation for decreased number of clutches. Our data indicate that the latter is more likely correct, since the decreased RCM of viviparous snakes may at least partly reduce the mortality risks of gravid females (Fig. 2). 3) Offspring survival – other factors being equal, large offspring may have higher survivorship and fitness than smaller young (Brockelman 1975; Derickson 1976; Ferguson and Bohlen 1978; Swingland and Coe 1979). Given reduced RCM, viviparous snakes apparently trade-off higher fecundity at the cost of offspring size, possibly resulting in lower after-birth survivorship of viviparous offspring, compared to oviparous young. However, demographic data to test this hypothesis are lacking. Finally, before hatching (or birth) survivorship of viviparous young may be higher than among oviparous offspring, because the latter are exposed to environmental pressures (desiccation, overheating, nest predation) from which viviparous young are partially protected (Tinkle and Gibbons 1977).

A note of caution should be inserted here. All data presented in this study represented the end-point of RCM, i.e., the clutch mass at the time of birth or egg-laying. Limited data suggest that RCM in viviparous snakes may increase as the reproductive season progresses (Semlitsch and Gibbons 1978). Additional information on this topic would be useful in assessing the survivorship model presented above.

Escape behavior and foraging mode. – Vitt and Congdon (1978) and Vitt and Price (1982) reported distinct correlations between escape behavior, foraging mode and RCM in lizards. Even after reproductive mode was factored out, we found no statistical difference in RCM among either foraging strategies or escape behaviors of snakes (Tables 3 and 4), although in some cases (e.g., escape behavior) we correctly predicted which strategy should have the lower RCM. We suggest three explanations for the failure of snakes to follow the pattern predicted from lizards: 1) Inaccurate assignment to categories – unlike lizards, which are easily observable in the field, snakes are often quite secretive. Therefore, it is possible that our assignments of some species to categories such as sit-and-wait or active foraging were based on inaccurate or insufficient data. For example, most biologists would classify rattlesnakes of the genus *Crotalus* as sit-and-wait foragers. However, H. Greene (pers. comm.) has carefully followed several *C. viridis* via radio-telemetry, and found that the species was much more active in its foraging patterns than previously believed. Erroneous assignments of certain species might have significantly biased our results. Finally, the possibility that both defensive behaviors and foraging tactics may be dependent on environmental conditions cannot be overlooked. Environmental factors (especially temperature) have been found to influence the foraging tactics of water snakes (Patterson and Davies 1982) and the defensive behaviors of lizards (R. Huey, pers. comm.). The validity of the assignments in Table 1 may therefore be suspect, especially if the behaviors of many species are affected by environmental influences. 2) Failure of snakes to “fit” dichotomous categories

– Pianka (1973) noted that dichotomous categories such as sit-and-wait or active foraging represented only the end points on a continuum of behaviors. If the majority of species considered here actually cluster mainly along the midpoint of such a continuum (rather than near the end points), no major difference in RCM among either foraging or escape behaviors could be expected. 3) Current RCM theory is inappropriate when applied to snakes – despite the phylogenetic relationships among lizards and snakes, they differ in many anatomical and ecological characteristics (most notably in lack of limbs among snakes). The differences in RCM patterns between the two groups (Table 6), suggest that their responses to selection for this life history trait may differ substantially.

Clearly, the first two hypotheses proposed here can only be tested by amassing additional field data on the behavioral ecology of snakes. Careful field studies (such as that for *C. viridis*), are obviously needed.

Temporal variation. – If RCM is determined primarily by differential predation on gravid females, then yearly changes in RCM within a species might be low unless predation intensity varies greatly among years, and unless such variation is predictable. Fluctuating resource availability could also result in variable RCM (L. Vitt, pers. comm.). We analyzed yearly variation in RCM for four species of snakes, with up to five year's of data on RCM (Table 5). For no species tested were significant differences found among years, despite significant inter-annual differences in both clutch size and apparently resources in these populations (Seigel and Fitch, ms). The pattern of inter-annual variation in RCM is mixed for lizards. Significant variation was found among years for both Texas and New Mexico populations of *Urosaurus ornatus* (Ballinger 1977; Dunham 1982), but not for other Texas *Urosaurus* (Martin 1977).

Comparisons with lizards. – Two interesting differences in RCM were found between lizards and snakes: 1) the RCM of snakes is uniformly higher than the RCM of lizards (Table 6), and 2) there is no significant difference in RCM among viviparous compared to oviparous lizards, as is true for snakes. The higher RCM of snakes may be the result of energetic constraints on lizard locomotion. Energetically, it may be more costly to raise an egg-laden body off the ground with limbs, than to spread the weight evenly over the ventral surface as is the case for snakes (L. Vitt, pers. comm.). Hence, we might expect limbless lizards to have higher RCM than other forms. However, such species are often fossorial, which may impose counter-selection to ease the movement through the soil by lowering RCM (Vitt and Price 1982). Interestingly, the terrestrial limbless lizard *Ophisaurus attenuatus* has a mean RCM of 0.278 (Fitch, pers. obs.), which is 1.24 times higher than the mean RCM of other oviparous lizards. Additional data on such forms would be of interest.

The lack of a significant difference between the RCM of viviparous and oviparous lizards is puzzling, particularly since the pattern is so strong for snakes. However, L. Vitt (pers. comm.) points out that most viviparous lizards are sit-and-wait predators, so the cost of high RCM may be reduced in such forms.

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