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BODY SHAPE, REPRODUCTIVE EFFORT, AND RELATIVE CLUTCH MASS IN LIZARDS: RESOLUTION OF A PARADOX

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The concept of reproductive effort, traceable to original thoughts of Fisher (1930), has recently assumed central importance in studies on the evolution of life histories of lizards (Pianka and Parker 1975a; Tinkle 1969; Tinkle et al. 1970; Tinkle and Hadley 1973, 1975). Williams (1966) and Gadgil and Bossert (1970) suggested the ratio of clutch to body weight as an operational estimate of reproductive effort, and Tinkle (1969) and others attempted to explain these ratios in the light of other life-history variables to determine cause and effect relationships. Several recent investigators used ratios of clutch to body calories to estimate reproductive effort (Tinkle and Hadley 1973; Vitt 1974; Vitt and Ohmart 1975), but low variation among species in calories per unit weight of eggs and bodies (Ballinger and Clark 1973; Vitt 1977) rendered these results not much different than simple weight ratios. Tinkle and Hadley (1975) coupled caloric with life-history data to construct energy budgets of several demographically well-known lizards. Reproductive effort was determined as the portion of the energy budget allocated to reproduction. Although Tinkle and Hadley admitted that “data necessary to test fully the various hypothesis concerning the evolution of reproductive effort are still unavailable,” they did present evidence “that the demographic environment may not be of primary importance in determining reproductive effort in a species” (p. 432). Tinkle and Hadley (1975) and Hirshfield and Tinkle (1975) criticized the assumption that clutch-to-body ratios estimate reproductive effort but did not offer alternative explanations as to the adaptive nature of clutch volumes. We contend that ratios of clutch to body or clutch to total (regardless of how measured) are predictable on the basis of body shapes of lizards as related to certain general aspects of their ecology. Thus, we concern ourselves with that portion of the variance in “relative clutch mass” (simple ratios) due to ecological analogy and consider only certain aspects of variance attributable to phylogenetic homology.

MATERIAL AND METHODS

During the reproductive seasons of 1973–1974 (May–June), ovigerous females (containing oviducal eggs) of 26 populations representing 22 species of lizards were collected from a variety of habitats (Vitt 1976). Species were chosen with the intent of cutting across taxa and reproductive strategies. Collection techniques have been described elsewhere (Vitt and Ohmart 1975). Energy content of lizard eggs and bodies was estimated in the same manner as Tinkle and Hadley (1973). The ratio of clutch to total calories (clutch + body) was termed “relative clutch mass” (hereafter RCM). Although

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we recognize that caloric values are not a direct measure of mass, the similarities among species in calories per milligram of eggs and of bodies coupled with high positive correlations of weight to caloric ratios (Vitt 1977) justify this terminology. Other estimates of RCM were calculated for comparisons with literature data (clutch wet weight to total wet weight; clutch dry weight to total dry weight; clutch calories to body calories).

Foraging and predator escape behaviors were observed and recorded for all species studied. Species cryptic in color or form that responded to the presence of the observer by remaining motionless were classed as "cryptic." Those that fled and never attempted to use cryptic behavior were classed as "flight" strategists. There appears to be a continuum of escape strategies between these contrasting behaviors. When confronted by the observer, several cryptic species fled to new positions several meters away and remained motionless. These were classed as "intermediate." Several species appeared to use "known escape routes," moving only short distances to the safety of a burrow. These were similar to cryptic species in that speed was not essential for escape. Several species with complex predator escape strategies were considered separately.

Field observations and limited information from the literature indicate two distinct foraging strategies in lizards (MacArthur and Pianka 1966; Pianka 1973; Schoener 1971). Behavior involving search prior to initial sightings of prey is exhibited by "wide foragers," whereas use of a perch and pursuit of prey items moving within the field of vision comprise the "sit and wait" foraging strategy. As in adaptations for predator escape, a potential continuum of foraging strategies exists, although Pianka (1973) points out that most species are clustered at endpoints of the "continuum."

RESULTS

Table 1 shows that many species displayed paired combinations of "cryptic behavior-sit-and-wait foraging," or "flight escape-wide foraging." Species utilizing "known escape routes" were similar to cryptic species. Species of the first type (cryptic-sit and wait) were arbitrarily grouped in strategy 1, and species of the second type (flight-wide foraging) were grouped in strategy 2.

Although significant differences were apparent in calories per milligram of ash-free dry weight (AFDW) between eggs and between bodies of different species, these differences were insignificant when compared with differences in total clutch or body calories (Vitt 1977). The RCM ranged from 0.287 in *Coleonyx variegatus* to 0.525 in *Sceloporus scalaris* (table 2).

Although variation in RCM exists within species (table 2), a majority of the significant variation was among species (table 3). There was a significant positive correlation ($r = .914$; $Y = 0.683X - 542$; $P < .05$) between total clutch calories and total body calories expressed as species means (fig. 1). The wide variance around the regression is noteworthy and will be considered in detail later.

Species utilizing strategy 1 exhibited higher RCM than species of strategy 2. Species intermediate in foraging and predator escape strategies had intermediate RCM values. Several species with complex predator escape adaptations exhibited substantially different RCM than predicted on the basis of the above arguments.

Information on age at maturity, clutch frequency, and other life-history parameters did not correspond to RCM as r - K theory might predict (Vitt 1976). This suggests that either r - K theory is inadequate or that these ratios are not correlated with the actual apportionment of assimilated energy to reproduction (reproductive effort). For example, short-lived early-maturing species such as *Coleonyx variegatus*, *Callisaurus draconoides*, and *Cophosaurus texanus* had low RCM whereas other short-lived early-

TABLE 1
FORAGING AND PREDATOR ESCAPE STRATEGIES IN VARIOUS LIZARD SPECIES

Family Species	Foraging Strategy	Predator Escape Strategy
Gekkonidae:		
<i>Coleonyx variegatus</i>	Sit and wait, limited foraging	Complex, cryptic, tail display and autotomy
Iguanidae:		
<i>Callisaurus draconoides</i>	Sit and wait	Flight, cryptic, tail display
<i>Cophosaurus texanus</i>	Sit and wait	Flight, cryptic, tail display
<i>Crotaphytus collaris</i>	Sit and wait	Flight, body size, known escape route
<i>Gambelia wislizeni</i>	Sit and wait	Flight, cryptic, body size
<i>Holbrookia maculata</i>	Sit and wait	Cryptic
<i>Phrynosoma cornutum</i>	Sit and wait	Cryptic, morphology ("horns")
<i>P. modestum</i>	Sit and wait	Cryptic, morphology ("horns")
<i>P. platyrhinos</i>	Sit and wait	Cryptic, morphology ("horns")
<i>Sceloporus clarki</i>	Sit and wait	Cryptic, morphology ("horns")
<i>S. magister</i>	Sit and wait	Cryptic, morphology ("horns")
<i>S. scalaris</i>	Sit and wait	Cryptic, known escape route
<i>S. undulatus</i>	Sit and wait	Known escape route, body size
<i>S. virgatus</i>	Sit and wait, limited foraging	Cryptic, known escape route
<i>Urosaurus graciosus</i>	Sit and wait, limited foraging	Cryptic, known escape route
<i>U. ornatus</i>	Sit and wait, limited foraging	Cryptic, arboreal habits
<i>Uta stansburiana</i>	Sit and wait	Cryptic, arboreal habits
Lacertidae:		
<i>Nucras tessellata</i>	Widely foraging	Flight
<i>Eremias lugubris</i>	Widely foraging	Flight
Scincidae:		
<i>Ctenotus pantherinus</i>	Widely foraging	Flight
Teiidae:		
<i>Chemidophorus tigris</i>	Widely foraging	Flight
<i>C. uniparens</i>	Widely foraging	Flight
<i>C. inornatus</i>	Widely foraging	Flight
<i>C. sonorae</i>	Widely foraging	Flight
Xantusiidae:		
<i>Xantusia vigilis</i>	Limited foraging	Known escape route

NOTE.—See text for more complete discussion of these strategies.

TABLE 2
COMPARISON OF VARIOUS RATIOS OF REPRODUCTIVE TO BODY OR REPRODUCTIVE TO TOTAL MATERIALS IN VARIOUS LIZARD SPECIES

Family Species	No.	Wet Clutch Weight		Dry Clutch Weight		Clutch Calories		Total Calories	
		Total Weight		Total Weight		Body Calories		Clutch Calories	Total Calories
Gekkonidae:									
<i>Coleonyx variegatus</i>	6	.211 (.155-.276)		.264 (.218-.316)		.407 (.314-.538)		.287 (.239-.350)	
Iguanidae:									
<i>Callisaurus draconoides</i>	12	.202 (.145-.284)		.293 (.256-.343)		.494 (.412-.656)		.329 (.292-.396)	
<i>Cophosaurus texanus</i>	12	.196 (.155-.232)		.306 (.250-.373)		.543 (.395-.730)		.350 (.283-.422)	
<i>Crotaphytus collaris</i>	5	.217 (.133-.307)		.324 (.253-.359)		.601 (.406-.730)		.372 (.289-.429)	
<i>Gambelia wislizeni</i>	2	.217 (.197-.237)		.338 (.319-.357)		.573 (.502-.645)		.363 (.334-.392)	
<i>Holbrookia maculata</i>	5	.348 (.332-.377)		.429 (.372-.466)		.849 (.663-.980)		.457 (.399-.495)	
<i>Phrynosoma cornutum</i>	4	.366 (.333-.401)		.432 (.366-.471)		.893 (.643-1.043)		.468 (.392-.511)	
<i>P. modestum</i>	6	.310 (.276-.354)		.442 (.401-.486)		.907 (.742-1.151)		.473 (.426-.535)	
<i>P. platyrhinos</i>	6	.277 (.188-.271)		.324 (.264-.398)		.536 (.387-.619)		.345 (.279-.431)	
<i>Sceloporus clarki</i>	2	.322 (.292-.353)		.426 (.410-.442)		.901 (.851-.951)		.474 (.460-.487)	
<i>S. magister</i>	1	.170		.251		.400		.286	
<i>S. scalaris</i>	15	.390 (.277-.506)		.514 (.423-.618)		1.206 (.788-1.811)		.525 (.318-.644)	
<i>S. undulatus</i> (1)	10	.217 (.141-.297)		.321 (.225-.422)		.578 (.335-.874)		.360 (.251-.455)	
<i>S. undulatus</i> (2)	2	.288 (.285-.292)		.418 (.418-.418)		.846 (.830-.862)		.458 (.453-.463)	
<i>S. virgatus</i>	9	.340 (.251-.384)		.471 (.421-.513)		1.088 (.911-1.297)		.519 (.477-.565)	
<i>Urosaurus graciosus</i> (1)	4	.237 (.213-.285)		.345 (.287-.377)		.640 (.473-.716)		.388 (.321-.417)	
<i>U. graciosus</i> (2)	10	.225 (.160-.290)		.353 (.294-.429)		.658 (.507-.835)		.395 (.337-.455)	
<i>U. ornatus</i> (1)	1	.406		.528		1.314		.568	
<i>U. ornatus</i> (2)	1	.277		.408		.861		.463	
<i>U. ornatus</i> (3)	10	.304 (.261-.348)		.435 (.372-.477)		.910 (.683-1.142)		.473 (.406-.533)	
<i>Uta stansburiana</i>	6	.229 (.200-.279)		.374 (.338-.405)		.715 (.593-.828)		.416 (.372-.453)	
Lacertidae:									
<i>Nucras tessellata</i>	1	.158		.237*	268*	
<i>Eremias lugubris</i>	22	.146 (.111-.211)		.222*	252*	
Scincidae:									
<i>Ctenosaurus pantherinus</i>	6	.171 (.129-.224)		.253*	285*	
Teiidae:									
<i>Cnemidophorus tigris</i> (1)	6	.131 (.108-.161)		.239 (.225-.255)		.395 (.368-.420)		.283 (.269-.296)	
<i>C. tigris</i> (2)	7	.164 (.094-.240)		.271 (.178-.355)		.415 (.278-.513)		.291 (.217-.339)	
Xantusiidae:									
<i>Xantusia vigilis</i>	9	.150 (.101-.190)		.260 (.188-.314)		.415 (.278-.513)		.291 (.217-.339)	

NOTE.—Minimum and maximum means in parentheses.

* Calculated from Pianka's data (personal communication) with conversion formulae of Vitt (1977).

† Data on other *Cnemidophorus* included in Congdon et al. (1978).

TABLE 3
ANALYSIS OF VARIANCE MATRIX (F) COMPARING RELATIVE CLUTCH MASS (RCM; See Text) IN 20 GROUPS OF 19 SPECIES OF LIZARDS

Group	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S
B	29.7																		
C	123.1	120.7																	
D	41.5	2.5	132.0																
E	90.4	11.7	207.1	3.7															
F	26.2	6.1	155.6	7.7	32.2														
G	59.5	4.1	168.4	1.6	2.2	17.7													
H	75.9	11.5	188.7	3.7	2.8	21.3	4.7												
I	59.9	17.5	157.1	11.1	15.0	18.0	15.1	5.7											
J	74.4	16.7	196.7	8.2	18.6	17.1	16.2	5.5	2.0										
K	57.7	152.6	216.7	170.2	285.0	169.2	218.1	253.7	201.5	266.6									
L	28.2	16.7	179.3	17.9	49.5	6.6	30.9	29.6	14.8	20.0	164.2								
M	10.5	28.8	184.3	35.2	91.6	17.9	56.9	65.2	40.4	58.7	109.9	9.8							
N	35.7	94.3	246.0	101.5	193.7	99.4	142.0	172.5	147.2	186.2	45.3	110.7	70.2						
O	74.1	174.9	298.7	186.0	348.3	201.5	257.6	308.4	250.9	339.9	24.9	216.9	149.0	15.4					
P	24.1	23.7	159.0	24.4	53.8	11.2	38.4	44.6	16.7	22.5	130.8	2.1	6.8	90.4	170.8				
Q	27.5	48.4	212.5	52.0	122.0	39.1	80.4	82.2	40.9	72.8	125.8	16.4	9.1	106.4	197.0	7.3			
R	5.9	59.6	194.6	71.7	165.2	57.1	107.6	130.4	89.7	133.8	52.5	49.9	16.3	38.4	80.5	34.7	30.4		
S	63.5	48.1	162.3	42.2	69.3	39.5	59.3	43.9	14.8	28.2	183.8	22.9	41.2	159.4	255.0	13.8	27.8	83.1	
T	96.4	31.7	193.2	16.3	41.5	34.6	37.0	29.5	30.8	29.3	301.2	59.3	97.7	179.7	327.6	55.1	135.8	170.4	68.9

NOTE.—F values exceeding 1.7 are significant at $P < .05$. Data indicate that differences exist among most species and between two populations of *Cnemidophorus tigris*. A = *Phrynosoma platyrhinos*; B = *P. modestum*; C = *P. cornutum*; D = *Holbrookia maculata*; E = *Sceloporus scalaris*; F = *S. undulatus*; G = *S. virgatus*; H = *Urosaurus ornatus*; I = *Uta stansburiana*; J = *Urosaurus graciosus*; K = *Crotaphytus collaris*; L = *Cophosaurus texanus*; M = *Callisaurus draconoides*; N = *Cnemidophorus tigris* (1); O = *C. tigris* (2); P = *C. inornatus*; Q = *C. uniparens*; R = *C. sonorensis*; S = *Coleonyx variegatus*; T = *Xantusia vigilis*.

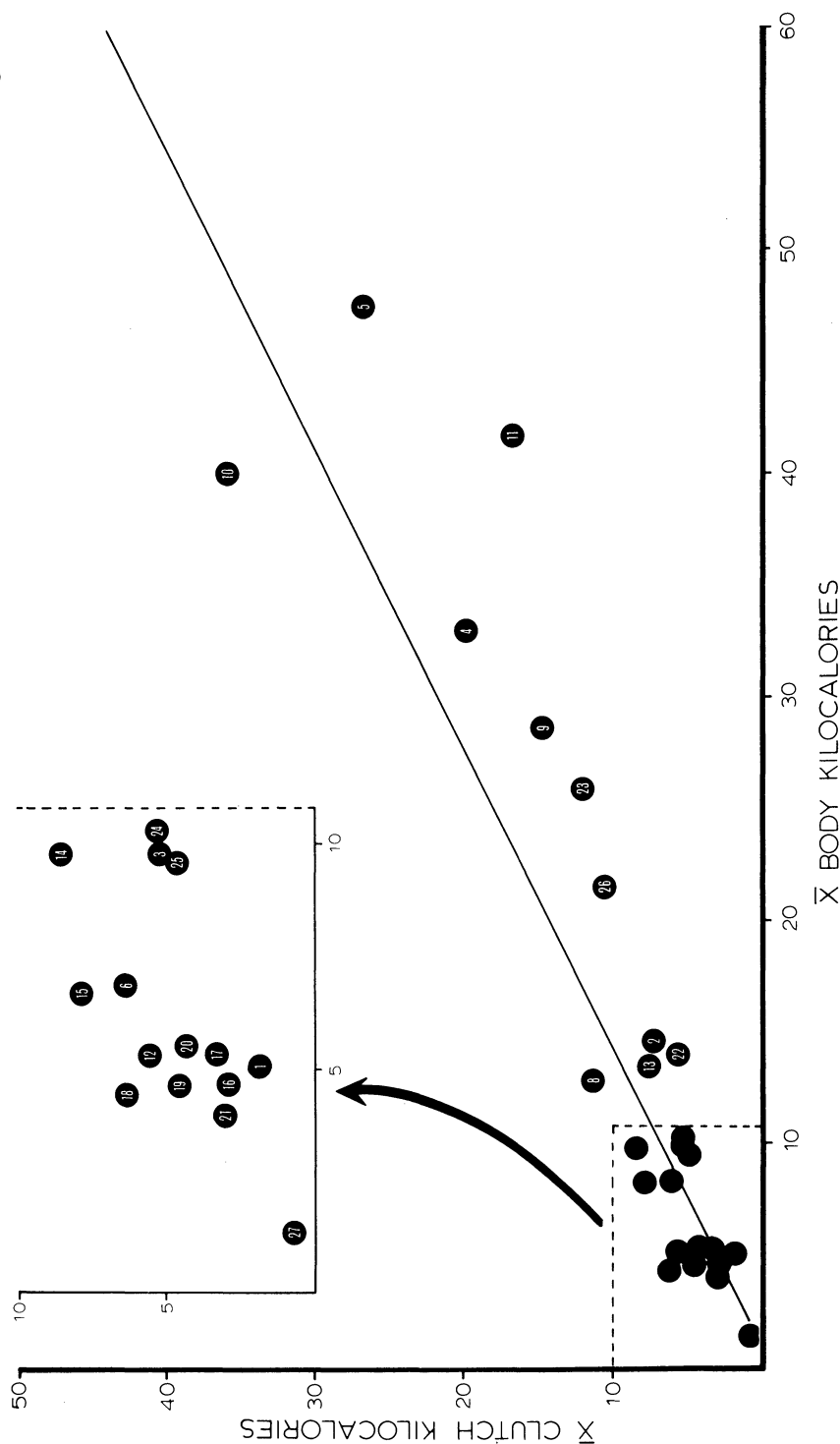


FIG. 1.—Relationship of total clutch calories to total body calories in various lizard species. A high positive correlation is apparent ($r = .914$; $Y = 0.683X - 542$). Numbered points refer to the following: (1) *Coleonyx variegatus*, (2) *Callisaurus draconoides*, (3) *Cophosaurus texanus*, (4) *Crotaphytus collaris*, (5) *Gambelia wislizeni*, (6) *Holbrookia maculata*, (7) *Phrynosoma cornutum*, (8) *P. modestum*, (9) *P. platyrhinos*, (10) *Sceloporus clarki*, (11) *S. magister*, (12) *S. scalaris*, (13) *S. undulatus* (1), (14) *S. undulatus* (2), (15) *S. virgatus*, (16) *Urosaurus graciosus* (1), (17) *U. graciosus* (2), (18) *U. ornatus* (1), (19) *U. ornatus* (2), (20) *U. ornatus* (3), (21) *Uta stansburiana*, (22) *Cnemidophorus tigris* (1), (23) *C. tigris* (2), (24) *C. uniparens*, (25) *C. inornatus*, (26) *C. sonorae*, (27) *Xantusia vigilis*.

TABLE 4

RELATIVE CLUTCH MASS (RCM) AS CALORIC RATIOS (See Text) AND CALORIES PER UNIT WEIGHT OF EGG FOR 22 LIZARD SPECIES

Taxonomic Group	No. of Species	Relative Clutch Mass (Min-Max)	Egg Cal/mg (Min-Max)
Total	22	.384 (.283-.525)	6.540 (6.178-6.852)
Horned lizards	3	.424 (.345-.473)	6.443 (6.406-6.456)
Sceloporines	6	.450 (.360-.525)	6.484 (6.216-6.669)
Copho-Calli-Holbrk	3	.360 (.329-.457)	6.556 (6.450-6.693)
Cnemidophorines	4	.304 (.268-.334)	6.622 (6.370-6.787)

NOTE.—The minimum and maximum values (particularly within sceloporines and the *Cophosaurus-Callisaurus-Holbrookia* group) demonstrate the variability within taxa.

maturing lizards such as *Holbrookia maculata*, *S. scalaris*, *S. undulatus*, *S. virgatus*, *Urosaurus ornatus*, *U. graciosus*, and *Uta stansburiana* had relatively high RCM. Likewise, long-lived late-maturing species such as *Crotaphytus collaris*, *Gambelia wislizeni*, *Cnemidophorus tigris*, and *Xantusia vigilis* exhibited low RCM whereas others, including *Phrynosoma cornutum*, *P. modestum*, *P. platyrhinos*, and *S. Clarki*, had relatively high RCM.

Certain taxonomic trends were apparent in RCM (table 4, fig. 2); however, one family, Iguanidae, had species encompassing the entire range of RCM values reported here and elsewhere. Within this large family, sceloporines had relatively much higher RCM than anolines (Andrews and Rand 1974; see fig. 2); cnemidophorines (Teiidae) had relatively low RCM. Body shapes and associated escape and foraging strategies most likely became limited early in the evolutionary history of each species group, as evidenced by the low variation within and high variation between groups.

RCM and Body Shape in Lizards

In the following we relate body shape of lizards, considered adaptive in the above manner, to RCM values. We assume that any female will fill her body cavity with the maximum amount of reproductive materials that resources (current available food) allow. We also assume that given unlimited resources, females of species with different body shapes, for example horned lizards (*Phrynosoma*) versus whiptails (*Cnemidophorus*), are equally “full” when containing oviducal eggs; they cannot hold any more. Thus differences in RCM reflect differences in body shapes.

The relationship between body shapes of lizards and their general ecologies can be readily evaluated with available data. Referring to table 1, it is apparent that most lizards studied either utilize strategy 1 or strategy 2. Those species utilizing strategy 1 would be expected to have large clutch volumes in relation to body size. This represents a compromise between effective reproductive output and the degree to which this output upsets the effectiveness of the lizard’s cryptic behavior. Horned lizards (*Phrynosoma*) exemplify this strategy. Their predator escape mechanisms, including cryptic behavior and pointed body projections, do not require rapid movement. Thus their morphology complements their behavior. They are short and robust, have appendages not designed for rapid movement, possess occipital horns, and are cryptically colored (Pianka and Parker 1975*b*). As predicted, horned lizards exhibit high RCM.

Species utilizing strategy 2 would be expected to have small clutch volumes relative to their body size, representing a compromise between effective reproductive output and

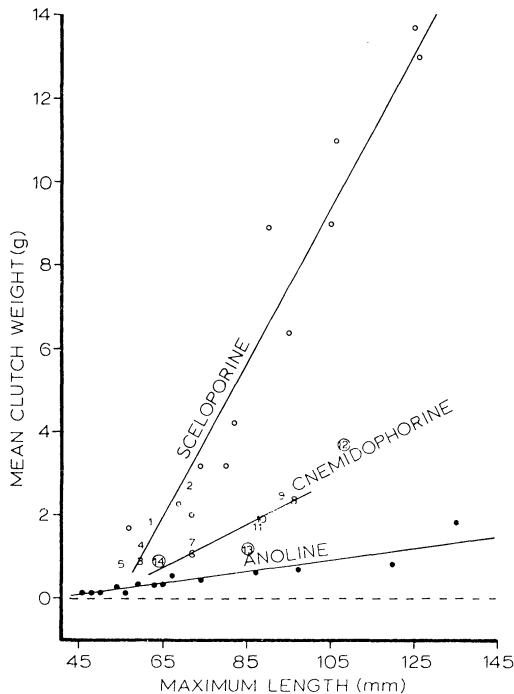


FIG. 2.—Relationship of mean clutch weight (g) to maximum length (mm) for sceloporine, anoline, cnemidophorine, and Old World and Australian “whiptail” lizards. This represents a revision of a figure in Andrews and Rand (1974), and unnumbered open and closed circles correspond to their originals. Numbered points refer to the following (ecological whiptails other than cnemidophorines are designated by circled numbered points): (1) *Sceloporus scalaris*, (2) *S. virgatus*, (3) *Urosaurus graciosus*, (4) *U. ornatus*, (5) *Uta stansburiana*, (6) *Cnemidophorus inornatus*, (7) *C. uniparens*, (8) *C. tigris*, (9) *C. sonorae*, (10) *C. gularis*, (11) *C. velox*, (12) *Ctenotus pantherinus*, (13) *Nucras tessellata*, (14) *Eremias lugubris*.

the degree to which carrying a voluminous clutch increases probability of being preyed upon or reduces foraging efficiency. Thus body shape and clutch volume should coevolve to maximize reproductive success while minimizing adult mortality. It is apparent from this study and others (Andrews and Rand 1974; Tinkle 1969; Tinkle et al. 1970) that as body size increases so does clutch volume (primarily due to differences in number of eggs) within and among species. Even though clutch volume increases with body size, it may not do so proportionally so that the ratio of clutch to body or total may increase, decrease, or remain constant with increase in body size (age). This ontogenetic change in RCM during an individual's lifetime is minimal compared with differences among species that are ecologically dissimilar (table 5). For example, cnemidophorines are ecological analogs to certain Old World lacertids (*Nucras tessellata* and *Eremias lugubris*) and Australian scincids (*Ctenotus pantherinus*). These lizards are wary during their constant search for food (all wide foragers) (Pianka 1969, 1970). Their body shape complements these habits. They are streamlined in form and display a long whiplike tail. Their legs are adapted for rapid surface movement. Coupled with this streamlined morphology are low RCM values (table 2). These low ratios are thus adaptive. Presumably, those individual whiptails (regardless of taxa) which pro-

TABLE 5

RELATIVE CLUTCH MASS (RCM; See Text) AND CALORIES PER UNIT WEIGHT OF EGG FOR LIZARDS

Group	No. of Species	Relative Clutch Mass (Min-Max)	Egg Cal/mg (Min-Max)
Strategy 1	10	.443 (.345-.525)	6.478 (6.216-6.669)
Mixed strategy	3	.350 (.329-.372)	6.579 (6.458-6.692)
Strategy 2	4	.304 (.268-.334)	6.622 (6.370-6.787)
Complex strategies*	2	.289 (.287-.291)	6.522 (6.344-6.700)

NOTE.—Species are grouped ecologically, in accordance with predator escape and foraging strategies. Only species with sample size exceeding three individuals were included. Species in strategy 1 (see text) were significantly different ($P < .05$) from species in strategy 2. The mixed strategy was significantly different from strategy 1 but not from strategy 2.

* See text for description of this category.

duce a more voluminous clutch risk higher mortality. Clearly, individuals successfully producing a larger clutch would have higher relative fitness than individuals with smaller clutches (assuming equal survivorship). This suggests a cost-benefit function and selection should maximize individual fitness, resulting in survival of those individuals that produce clutch volumes compatible with the risks associated with their foraging and predator escape strategies.

Thus the high RCM in horned lizards and the low RCM in whiptails are adaptive in light of the ecological setting each species group is confronted with. These differing RCM values represent evolutionary compromises between benefits of increasing reproductive output and weight and volume limitations imposed by aspects of the ecologies of these animals. Horned lizards can “afford” high RCM whereas whiptails cannot.

For comparative purposes we have chosen two groups of lizards which are presumably ecological extremes. In fact, most species fall between these arbitrary endpoints. The spectrum of adaptive strategies related to clutch volumes may be modeled by depicting the range of RCM values relative to lizard body size. The model will not directly apply to species in which variables other than predator escape and foraging strategies strongly influence the evolution of body shapes. Following presentation of the model, we consider apparent exceptions which, after considering their peculiar ecologies, are explicable by the model.

Figure 3 is a graphic representation of the relationship between clutch volume and body size in lizards. This generally triangular relationship is termed “functional reproductive volume” and refers to the relative range of reproductive volumes prevalent in lizards. Species utilizing strategy 1 are limited in clutch volume only by the degree to which it reduces the effectiveness of cryptic form or behavior, resulting in costs on adult survivorship and future reproductive success. In species utilizing strategy 2, the maximum reproductive volume is evolutionarily limited by the degree to which it reduces foraging or escape efficiency. An individual of any given species or population, or a mean for either (point C in fig. 3, for example), should have a clutch volume or RCM variance as a function of resource availability (Vinegar [1975] has shown such a variance in *S. virgatus*), and this variance should be a subset of the limitations set on RCM by body design.

Ecologically analogous lizards, regardless of taxonomic relationships, should fall along a line of constant slope in this model. Ecological whiptails (*Cnemidophorus* spp., Teiidae; *Ctenotus pantherinus*, Scincidae; *N. tessellata* and *E. lugubris*, Lacertidae) fall on the same regression line (fig. 2) and thus have similar RCM (low). In *Anolis* clutch size is

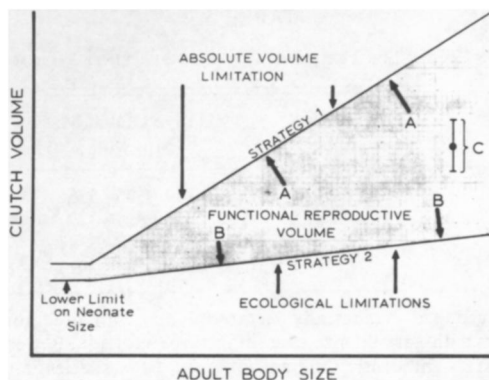


FIG. 3.—Graphic model relating clutch volumes of lizards to adult body sizes. Species utilizing strategy 1 (see text) exhibit high RCM or clutch volumes whereas species utilizing strategy 2 exhibit low RCM (refer to text for definition of terms and complete discussion).

fixed at one egg per clutch (Andrews and Rand 1974, and others), but neonate size among species is correlated with female size. Thus, as female body size increases among species so does clutch volume, but at a low rate due to the clutch size limitation. All *Phrynosoma* have relatively high RCM and fall on a similar regression line relating clutch volume to body size (points 7, 8, and 9 in fig. 1; also see data in Pianka and Parker [1975b]). The lower RCM in *P. platyrhinos* (point 9, fig. 1) and in several other *Phrynosoma* noted by Pianka and Parker (1975b) is attributable to differences in habits of these species and resource levels in habitats occupied by these species.

Ecological factors are suggested for a lower limit on the amount of reproductive materials invested by lizards. This limitation refers to the energy invested by a parent that results in the production of one viable offspring under limitations imposed on neonate size. Although it might be argued that lizards could evolve smaller and smaller neonate size given strong enough selection, we are convinced that ecological factors, including potential competition and predation by invertebrates, and physiological factors, including surface-to-volume ratios and limitations in closed circulatory systems, would counteract this. An upper absolute limitation on clutch volume is described. This limit is approached by species of strategy 1 and presumably represents the optimal compromise between reproductive investment and adult mortality costs.

The following are species with diverse ecologies which support the model. *Cophosaurus texanus*, *C. draconoides*, and *H. maculata* are closely related iguanid lizards. *Cophosaurus texanus* and *C. draconoides* are morphologically similar and have similar cryptic coloration. Both use similar flight behavior and have similar tail displays. When confronted, individuals of each species run a considerable distance then stop and remain motionless, becoming cryptic against the substrate. The model (fig. 3) would predict these to have similar RCM and they do (0.350 and 0.329, respectively). The intermediacy of their RCM was predictable by their mixed escape strategies.

Holbrookia maculata, in contrast, descends from a vantage point and remains motionless when disturbed. Only when threatened at close range does it flee, and then for only a short distance. The model correctly predicts that it should have a high RCM (0.457).

Sceloporines exhibit a diversity of RCM, most of which are relatively high (Andrews and Rand 1974; Tinkle 1969; fig. 2). The observation that all are high when compared

with cnemidophorines (tables 2 and 4) may be attributed to basic differences in foraging and predator escape strategies. Sceloporines use variations of strategy 1 whereas cnemidophorines employ strategy 2. Sceloporine ecology may be used to predict RCM. For example, *S. scalaris* and *S. virgatus* are similar to *H. maculata* in that they do not rely on flight for escape and are limited foragers, tending toward the sit-and-wait strategy. *Sceloporus scalaris* and *S. virgatus* frequently bask and need move only short distances to evade predators. As the model predicts, both have high RCM values (0.525 and 0.519, respectively).

Urosaurus graciosus is an arboreal sceloporine that spends considerable time foraging in the outer canopy of its habitat (Barnes 1974; Vitt and Ohmart 1975), where agility is important. In addition, it uses cryptic coloration and form (Norris and Lowe 1964; Vitt and Ohmart 1975), presumably reducing detection by predators. It is active primarily on thin branches so that cryptic form involves a thin, streamlined body. Unlike *Anolis*, this species uses claws to facilitate foraging on branches with coarse bark. The RCM of *U. graciosus* should be low due to costs of upsetting cryptic form and agility in the outer canopy of vegetation, and it is (0.388–0.395).

Urosaurus ornatus, ecologically quite similar to *U. graciosus*, forages on the trunks and larger limbs of trees in its arboreal habitat (Barnes 1974; Vitt and Ohmart 1975). Under these conditions, cryptic coloration is important but streamlined body form is not. The higher RCM of *U. ornatus* (0.473) was also predictable on the basis of the model.

Several species apparently do not fit the model; their RCM values were not predictable on the basis of variables we identified as most important. However, once factors unique to the ecology of each were considered, we were able to predict RCM values. For example, *Coleonyx variegatus* (Gekkonidae) is a nocturnal terrestrial desert lizard (Parker 1972). Clutch size is restricted to one to two eggs per clutch (Fitch 1970). In addition, the large tail serves as an effective predator distractant, as evidenced by the high incidence of regenerated tails in natural populations (up to 74% in adults [Parker 1972]). Regeneration is rapid (Congdon et al. 1974). Because the large tail is composed of high-energy lipid material (Bustard 1967; Vitt et al. 1977), its regeneration is an energetically expensive event. Individual eggs produced by females are large in relation to parental body size. On the basis of small fixed clutch size and an energetically expensive predator escape mechanism, we predict a low RCM, which is indeed the case (0.287). We further predict that all Eublepharinae should exhibit low RCM for similar reasons.

Xantusia vigilis (Xantusiidae) is a viviparous lizard which exhibits small adult body size and produces proportionately large neonates (Vitt 1976). Clutch size is small (one–three) but similar to other xantusids (Fitch 1970). Individuals inhabit fallen yuccas (Zweifel and Lowe 1966). Movement over short distances among yucca leaves is likely important for predator escape. An excessively robust body while gravid coupled with the long gestation time in these viviparous lizards would restrict movement among the yucca leaves. Based on the above, we predict a low RCM, which is the case (0.291).

As exemplified above, behavioral and ecological data on lizards are necessary to accurately predict RCM. Clearly the ecological factors of predator escape and foraging strategies are of prime importance in many lizards. The RCM values are a function of body shape and relate to selective factors important in determining body shape. There is little indication that demographic components correlate to RCM. Further, our data suggest that use of ratios (RCM) is deceiving in evaluating “reproductive effort” as defined by Fisher (1930). These ratios may not correspond to energetic commitments to reproduction that have been selected for in response to resource availability unless this selection occurred early in the evolutionary history of various lizard groups and

coevolved with body shape, or was a factor in molding predator escape and foraging strategies.

Limitations on the Use of RCM

Tinkle and Hadley (1975), after constructing energy budgets of lizards, concluded that data necessary to test hypotheses related to reproductive effort and its evolution were still unavailable. Gadgil and Bossert (1970), Tinkle (1969), and Tinkle et al. (1970) have applied ratios of clutch to body weight as measures of reproductive effort. In light of present findings, use of such ratios (RCM) as operational estimates of reproductive effort is questionable. We have argued that the body shape of lizards, which in many cases is related to predator escape and foraging strategies, can be used to predict RCM. Our data and the lack of correlation between RCM values and life-history variables (Tinkle and Hadley 1975) suggest that past investigators have relied on inappropriate measures of reproductive effort. Limitations imposed by body shapes and special adaptations of lizards have not previously been considered (but see Pianka and Parker 1975b). Andrews and Rand (1974) indirectly considered restrictions imposed by body shape of *Anolis* but did not present comparative data.

We have shown that unrelated but ecologically analogous lizards have nearly identical RCM because of convergence; RCM is predictable with no knowledge of the demographic environment, resource levels, or energy partitioning. We suggest that RCM need not be correlated with reproductive effort. The use of RCM can be instructive in comparing ecologically similar species and individuals within populations. Where intensity and nature of predation are known for different populations of a species, differences in RCM may be interpreted.

Future investigators studying reproductive effort should be concerned with detailed energy budgets. Given a known energetic commitment to reproduction on an age-specific basis, hypotheses may be adequately tested. Careful consideration of ecological variables that select for body shape in lizards should allow clarification of limitations on RCM imposed on ecologically diverse species. With understanding of RCM, interpretations of the evolution of reproductive effort in all organisms should be facilitated. It is probable that arguments presented here apply to other animal groups. We would expect that predacious mammals that are wide foragers (cheetahs) should exhibit low RCM compared with herbivorous species not relying on flight for escape (water buffalo). Herbivorous species relying on flight for escape (antelope) should exhibit low RCM.

SUGGESTIONS FOR FUTURE STUDY

1. More data on ecologically diverse organisms, particularly in other taxa, should be accumulated to test the applicability of the model presented here.
2. Once comparative data on reproductive effort (based on energy budgets) are available for a variety of lizard species, comparisons with RCM values should be made to determine whether a correlation exists. If a correlation does exist, ecologically similar species should have similar reproductive efforts.

SUMMARY

Lizard body shapes, selected for in the context of predator escape and foraging, serve well to predict the ratios of clutch to body (termed "relative clutch mass") whether in weights or calories. Species cryptic in behavior that employ the sit-and-wait foraging strategy exhibit high relative clutch mass (RCM) whereas species using flight for escape

and the wide-foraging strategy exhibit low RCM. The RCM values for other species with more complex predator escape strategies are predictable once unique aspects of their ecologies are considered. It is concluded that RCM in lizards need not be correlated to reproductive effort, and, if it is, then reproductive effort coevolved with predator escape and foraging strategies and ecologically analogous species should not only exhibit similar RCM values, but also similar reproductive efforts.

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