The Energetic Costs of Tail Autotomy to Reproduction in the Lizard *Coleonyx brevis* (Sauria: Gekkonidae)

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Summary. Energy reserve utilization and energy budgets were compared in tailed and tailless adult female *Coleonyx brevis*. Carcass, fat body and caudal energy reserves were used for vitellogenesis; mass and energy content (cal/mg and/or cal/reserve) of each were significantly lower at oviposition than at the initiation of vitellogenesis. Total energy reserves accounted for 53% of the reproductive energy investment in tailed females compared to 29% in tailless females. Tailed females had over twice as many reserve calories for egg production than tailless females. Caudal energy reserves represented 60% of the total reserves of tailed females and were one-third greater than the total energy reserves of tailless females. To produce a clutch of eggs both tailed and tailless females supplemented energy reserves with net metabolizable energy that was available after metabolic costs were paid. Tailless females had a significantly greater rate of food ingestion and more net metabolizable energy available for reproduction than tailed females, yet allocated significantly fewer calories/day to reproduction than tailed females, primarily because of the loss of caudal reserves. Reproductive efforts of tailed and tailless females were equivalent. However, the loss of caudal reserves resulted in the production of eggs that were significantly lower in mass and energy content (cal/mg and cal/egg) than when caudal reserves were used. Results empirically support the hypothesis that reproduction has energetic priority over tail regeneration in short-lived, iteroparous species with a low probability of future reproductive success.

Introduction

Autotomy of body parts as a predator defense mechanism has evolved independently in three major animal phyla (Arthropoda, Mollusca and Chordata; Edmunds 1974). Tail autotomy is the mechanism among vertebrates, occuring in 2 of the 8 salamander families (Wake and Dresner 1967; Shaffer 1978) and in 13 of the 20 or so lizard families (Etheridge 1967). In most cases tail autotomy is followed by regeneration of a tail complete with well developed musculature and a calcified rod that replaces the vertebral column (Hughes and New 1959; Moffat and Bellairs 1964). Many species that autotomize the tail also use it as a major site of energy storage (Bustard 1967; Clark 1971). Consequently, it may represent a considerable portion of an

individual's biomass (Maiorana 1977) and energy reserves (Fitzpatrick 1973; Congdon, Vitt and King 1974; Vitt, Congdon and Dickson 1977). Moreover, caudal energy reserves may serve as an important energy source for vitellogenesis (Greene 1969; Smyth 1974; Maiorana 1977). Voluntary loss of such a structure appears paradoxical in evolutionary biology (Clark 1971) and having to regenerate a tail while producing a clutch of eggs represents an energetic conflict between somatic and reproductive interests. Evolutionary trade-offs in resource apportionment to somatic and reproductive recipients have been a central theme in life-history theory for over 50 years (e.g. Fisher 1930; Williams 1966a; 1966b; Cody 1966; Hirshfield and Tinkle 1975; Pianka 1976; Stearns 1976, 1977). However, few studies exist that quantify these trade-offs (e.g. Fitzpatrick 1973; Randolph, Randolph and Barlow 1975; Congdon 1977; Randolph, Randolph, Mattingly and Foster 1977; Brown and Fitzpatrick 1978; Hirshfield 1980).

Although the ecology of tail autotomy has received considerable attention recently (Werner 1968; Vitt 1974; Vitt, Congdon, Hulse and Platz 1974; Johnson and Brodie 1974; Congdon et al. 1974; Vitt et al. 1977; Maiorana 1977; Brown and Ruby 1977; Dial 1978a; Shaffer 1978; Schoener and Schoener 1980), the energetic relationship between reproduction and tail regeneration remains unclear. Vitt et al. (1977) predicted that in lizards the energetic demands of vitellogenesis should have precedence over and reduce energy allocation to tail regeneration. In contrast, Maiorana (1977) demonstrated that in at least one species of salamander tail regeneration has energetic priority over reproduction. Energy budgeting tactics are complex functions of several life-history and environmental parameters, but a dichotomy exists among workers as to the relative importance of each. Williams (1966a, 1966b) proposed that energy allocation between somatic and reproductive recipients is a function of adult life expectancy, or current versus future reproductive expectations. Others (e.g. Murphy 1968; Schaffer 1974; Hirshfield and Tinkle 1975) suggest a more flexible scenario in which adult energy allocation is adjusted relative to life expectations of offspring. By considering longevity and probability of future reproductive success of females, we hypothesized that short-lived, iteroparous species with a low probability of future reproductive success should prioritize energy allocation to reproduction at the expense of other recipients. Because the presence of a tail greatly increases an individual's probability of escape during an encounter with a predator (Congdon et al. 1974; Dial 1978a), energy allocation should shift to tail regeneration once the minimum required reproductive energy investment is paid. On

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Fig. 1. Defensive tail display in adult (SVL = 54 mm) female *Coleonyx brevis*. The tail was raised perpendicular to the substrate and undulated slowly to the left and right. Many captive specimens exhibited this behavior when they were approached by small snakes *(Hypsiglena torquata)*

the other hand, because of the positive value of having a tail during a predator encounter and of the high probability of future reproductive success, long-lived species should prioritize energy allocation to tail regeneration.

In this report, we examine the energetic relations among tail autotomy, tail regeneration and reproduction in *Coleonyx brevis*. Our primary objective was to test the hypothesis that reproduction has energetic priority over tail regeneration in a short-lived, iteroparous lizard species. In addition, we consider the following questions: (i) In a species that utilizes both tail autotomy and caudal energy storage, what is the energetic contribution of caudal reserves to vitellogenesis? (ii) How does the loss of caudal reserves affect a female's energy budget? (iii) What are the effects of the loss of caudal reserves on egg characteristics and reproductive effort?

Methods

We chose the eublepharine gecko *Coleonyx brevis* for this study for several reasons: (i) The species is short-lived and produces several clutches per breeding season (Dial 1975). (ii) Tail autotomy is the primary escape mechanism. The species demonstrates several behavioral characteristics that facilitate escape via autotomy, including body positioning with an arched, waving tail (Fig. 1) that attracts a predator's attention to the tail (Dial 1978a). The importance of autotomy for defense is suggested by the high frequency of regenerated tails in natural populations (males = 68%, females = 80%; Dial 1978a). (iii) Tail regeneration is rapid (authors' unpubl. data). (iv) Empirical analysis of energy partitioning to reproduction is complicated by two variables: clutch size and egg characteristics (Smith and Fretwell 1974; Wilbur 1977; Crump and Kaplan 1979). Clutch size in *C. brevis*

is constant (2 eggs/clutch; Smith 1946). Thus, only variability in egg characteristics need be considered.

Field and Laboratory Analysis

We designed the study to compare changes in compartmentalized energy reserves and energy budgets in an experimental group of lizards in which tail autotomy was induced to a control group of tailed lizards. We collected adult male and female *C. brevis* of equivalent size (no significant difference [$p > 0.05$] among groups in either snout-vent length [= SVL] or mass; Table 1) at the beginning of the reproductive season (March–April) in 1978 and 1979 at Black Gap Wildlife Management Area, Brewster Co., Tx. We randomly divided all lizards into three groups: experimental, control and baseline. Baseline females were frozen immediately and were used to determine reproductive condition and caloric content of tissues at the beginning of vitellogenesis. We induced autotomy in experimental females (all previtellogenic) at the most proximal caudal fracture plane (see Etheridge 1967) and left tails (all original) of control females intact. All lizards were maintained in individual photo-thermal gradients with natural photoperiod and were fed an *ad libitum* diet of mealworms *(Tenebrio molitor)*.

We measured energy budget components, each expressed as cal/d, as follows: (i) Ingestion = I = ($\bar{x}$ dry mass of mealworms ingested/d) ($\bar{x}$ caloric value of mealworm tissue; Johnson and Lillywhite 1979). (ii) Egestion + Excretion = FU = ($\bar{x}$ dry mass of feces and uric acid/d) ($\bar{x}$ caloric value of feces and uric acid). (iii) Net Metabolizable Energy = NME = I − FU. (iv) Metabolic Heat Loss = R. We measured metabolic heat loss indirectly as O_2 consumption in a 10 station Scholander Microvolumetric Respirometer. During the day in the thermal gradient lizards maintained their body temperatures at their preferred temperature of 31° C (Dial 1978b). At night body temperatures dropped to 22° C. We measured O_2 consumption rates at 31° C from 13.00–15.00 h in the light and at 22° C from 22.00–24.00 in the dark. Most geckos became inactive within 5 min of being placed in a test station and rested with eyes closed throughout a trial. (Data from the few active specimens were not used in this analysis). We equilibrated lizards for 30 min and measured O_2 consumption rates at 15 min intervals for 1.5 h. We corrected all gas volumes to Standard Temperature and Pressure Dry (STPD) conditions and converted rates (µl/g/h) to caloric values using the oxycaloric coefficient, 4.825×10^{-3} cal/µl (Brody 1945). (v) Storage = P_s. All individuals had ceased linear growth. Therefore, changes in body and tail tissue mass represented storage or depletion of lipids. P_s = Caloric content of lipid stores in tail and abdominal fat bodies = (change in tissue mass) ($\bar{x}$ caloric value of lipids; Bartholomew 1972). (vi) Reproduction = P_r = (change in follicle mass) ($\bar{x}$ caloric value of follicle tissue). (vii) Tail Regeneration = P_t = (change in tail mass) ($\bar{x}$ caloric value of tail tissue). We froze each female and her eggs at oviposition.

Table 1. Comparison of snout-vent length and mass of adult female and male *Coleonyx brevis*. Mass values for tailless specimens represent mass before tail autotomy

Variable	Baseline females (N = 8)			Tailed females (N = 10)			Tailless females (N = 10)			Tailless males (N = 5)			P[a]
	Mean	Range	SD	Mean	Range	SD	Mean	Range	SD	Mean	Range	SD	
SVL (mm)	53.8	50–58	2.7	53.6	50–58	2.5	54.0	50–57	2.2	52.8	52–55	1.3	NS
Mass (wet, g)	2.57	2.1–3.3	0.4	2.56	1.9–3.2	0.4	2.54	2.0–3.1	0.4	2.43	2.3–2.5	0.1	NS

P[a] = Level of significance; Kruskal-Wallis Test; NS = no significant difference

Table 2. Comparison of carcass, fat body and tail variables in baseline, tailed and tailless female *Coleonyx brevis*. All caloric values are based on AFDM

Variable	Baseline females (N=8)			Tailed females (N=10)			Tailless females (N=10)			P[a]	
	Mean	Range	SD	Mean	Range	SD	Mean	Range	SD	A	B
Carcass											
Mass (dry, mg)	403.9	368.2–473.2	37.5	388.8	345.1–460.2	47.3	385.1	340.4–421.8	43.6	0.05	0.05
H_2O (%)	72.9	70.1–78.6	2.18	74.3	72.5–78.1	2.16	75.2	72.3–77.5	2.39	NS	NS
Ash (%)	15.3	13.8–17.5	1.57	16.9	14.8–17.4	1.76	16.1	12.4–17.4	2.01	NS	NS
Cal/mg	5.05	4.92–5.47	0.12	5.00	4.90–5.21	0.08	4.98	4.71–5.10	0.11	NS	NS
Cal/carcass	2,040	1,974–2,142	82.0	1,944	1,772–2,004	120.7	1,918	1,744–1,990	125.9	0.05	0.05
Fat body											
Mass (dry, mg)	18.8	14.6–21.4	2.6	0.7	0–4.7	1.52	0	0	0	0.001	0.001
Cal/fat body	169	131–192	23.2	6.3	0–42.3	13.7	0	0	0	0.001	0.001
Tail											
Mass (dry, mg)	93.8	74.0–114.1	14.6	38.1	17.4–54.4	9.9	–	–	–	0.001	–
H_2O (%)	71.9	70.8–73.7	1.61	73.6	70.9–78.0	3.07	–	–	–	NS	–
Ash (%)	8.21	6.98–9.79	1.10	7.57	6.58–9.12	0.97	–	–	–	NS	–
Cal/mg	6.04	5.91–6.21	0.10	4.62	4.41–4.87	0.12	–	–	–	0.001	–
Cal/tail	568	440–689	1.7	176	80–265	47.9	–	–	–	0.001	–

P[a] = Level of significance of: (A) Baseline vs. Tailed Females and (B) Baseline vs. Tailless Females
Mann-Whitney U Test; NS = no significant difference

Samples of carcass, ovum and tail tissue of each specimen were dried at 45–50° C in a vacuum oven and cooled to room temperature in a vacuum desiccator containing anhydrous calcium sulfate. Dry mass was measured to the nearest 0.01 mg using an analytical balance. Samples were ground with a mortar and pestle and stored in individual glass vials in a freezer until caloric analysis. We determined all caloric values by combusting two samples (9–15 mg aliquants) per tissue type per specimen in a Phillipson Oxygen Microbomb Calorimeter using standard calorimetric technique (Phillipson 1964). The calorimeter was calibrated at the beginning of each day using benzoic acid. We determined ash content by burning four samples (10–20 mg aliquants) per tissue type at 500° C for 4 h in a muffle furnace (Paine 1971). All caloric data are expressed as ash-free dry mass (AFDM).

We measured SVL to the nearest mm using a millimeter ruler, wet body mass to the nearest 0.01 g using an analytical balance and egg length and width to the nearest 0.1 mm using a Vernier caliper. We determined the remaining variables as follows: (i) Mass-specific caloric content of tissue = total caloric content of sample/dry mass of sample. (ii) Total caloric content of tissue = (cal/mg tissue sample) (tissue mass). (iii) Egg volume was estimated using the formula for the volume of an ellipsoid: $V = 4/3 \pi a b^2$, where *a* equals one-half the longest diameter and *b* equals one-half the shortest diameter at the widest part.

We tested for significant differences in variables with Kruskal-Wallis (among more than two samples) and Mann-Whitney U (between two samples) statistics (Sokal and Rohlf 1969).

Results

Reproduction Versus Tail Regeneration

Each tailed and tailless female *C. brevis* produced two fully developed, shelled eggs. There was no significant difference ($p > 0.05$) between groups in either egg length or egg width (Tailed females: x̄ (SD) length = 12.44 (0.71) mm, x̄ (SD) width = 6.75 (0.37) mm; Tailless females: x̄ (SD) length = 12.52 (0.53) mm, x̄ (SD) width = 6.72 (0.32) mm). The ventral body wall of *C. brevis*

is slightly translucent and ovarian follicles as well as oviductal eggs were visible throughout development. Follicles appeared as yellow masses and changed to white at ovulation. Females in both groups deposited yolk for 30–32 d and oviposited 40–42 d after the initiation of vitellogenesis.

Prioritization of energy to egg production at the expense of tail regeneration is illustrated by comparative rates of energy allocation to tail regeneration. We compared calories allocated per day to tail regeneration in vitellogenic females to a control group of tailless males of equivalent size (no significant difference [$p > 0.05$] between groups in either SVL or mass; Table 1). We assumed that given identical conditions males and females will exhibit the same rate of tail regeneration. Thus, any differences in regeneration rate may be attributed to energy allocation to alternative recipients such as vitellogenesis. Both males and females initiated tail regeneration five-six days after autotomy. However, females allocated significantly fewer ($p < 0.001$) cal/d to tail regeneration than males (Females: x̄ (SD) cal/d = 0.82 (0.20); Males: x̄ (SD) cal/d = 10.83 (0.63)).

Energy Reserves

Female *C. brevis* used energy stored as lipids in carcass, fat body (corpora adiposa) and tail tissue for vitellogenesis; all lipid reserves were virtually depleted at oviposition. Mass-specific caloric content of carcass tissue remained equivalent among females. However, total carcass mass and, therefore, total caloric content of carcass tissue dropped significantly ($p < 0.05$) from the initiation of vitellogenesis (baseline females) to oviposition (tailed and tailless females; Table 2). Percents of carcass tissue that were H_2O and ash were equivalent among groups. We did not determine mass-specific caloric content of fat bodies. However, 95–98% of fat bodies in *C. brevis* is extractable lipid (authors' unpubl. data). We estimated the change in total caloric content of fat bodies during vitellogenesis as (9 cal/mg = caloric value for lipids; Bartholomew 1972) (change in fat body mass). Tailed females had fat bodies significantly lower ($p < 0.001$) in mass and total caloric content than baseline females (Table 2). Fat bodies of tailless females were depleted at oviposition. Mass

Table 3. Estimated contribution of compartmentalized energy reserves to vitellogenesis in tailed and tailless female *Coleonyx brevis*. Values represent mean change in caloric content of each tissue type during vitellogenesis (see Table 2) and are expressed as calories

	Tailed females	Tailless females
Tissue		
Carcass	97	123
Fat body	163	169
Tail	391	–
Total caloric contribution of energy reserves (Ps)	651	292
Ovum energy content (Pr) [a]	1221	993
Percentage of ovum energy supplied by energy reserves	53	29

[a] Taken from Table 5; calculated as $\bar{x}$ caloric value of tailed or tailless female ova $-$ $\bar{x}$ caloric value of baseline female ova

Table 5. Estimated total energy budgets for tailed and tailless female *Coleonyx brevis* during vitellogenesis. Values are expressed as total calories and are for the time period required to produce the first clutch of eggs during a breeding season

Energy budget component	Tailed females	Tailless females
Ingestion (I)	4,538	5,672
Egestion + excretion (FU)	1,452	1,815
Net metabolizable energy (NME)	3,086	3,857
Metabolic heat loss (R)	2,516	3,156
Storage (Ps)[a]	651	292
Reproduction (Pr)	1,221	993
NME needed for reproduction	570	701
Percentage of ovum energy supplied by NME	47	71

[a] see Table 3

and energy content (cal/mg and cal/tail) of tail tissue in tailed females were significantly lower ($p < 0.001$) at oviposition than at the beginning of vitellogenesis (Table 2). Percents of tail tissue that were H_2O and ash were equivalent between tailed and baseline females (Table 2).

We estimated the contribution of each energy reserve to vitellogenesis as follows: (i) Tailed females = $\bar{x}$ caloric value of each reserve in baseline females $-$ $\bar{x}$ caloric value of each reserve in tailed females. (ii) Tailless females = $\bar{x}$ caloric value of each reserve in baseline females $-$ $\bar{x}$ caloric value of each reserve in tailless females. Total energy reserves in tailed females accounted for 53% (651/1,221 cal) of their total reproductive energy investment compared to only 29% (292/993 cal) in tailless females (Table 3). Tailed females had over twice the reserve calories as tailless females. Energy stored in the tail accounted for 60% of the total reserve energy in tailed females and their tail reserves were one-third greater in caloric value than the total energy reserves of tailless females (391 vs. 292 cal, respectively; Table 3).

Energy Budgets

To determine how tail autotomy affects of female's energy budget, we compared energy budget components of tailless females to tailed females. Tailless females had significantly greater rates of ingestion ($p < 0.05$), egestion + excretion ($p < 0.05$), net metabolizable energy ($p < 0.05$) and metabolic heat loss ($p < 0.02$)

than tailed females (Table 4). Tailed females depleted significantly more ($p < 0.001$) lipids (Ps) than tailless females (Table 4), primarily because of the presence of caudal reserves. Although tailless females had higher daily NME, they allocated significantly fewer ($p < 0.001$) cal/d to vitellogenesis than tailed females (Table 4).

We estimated total energy budgets of both groups for the time period required to produce the first clutch of eggs as follows: (i) (cal/d of I, FU, NME or Pr) (42 = $\bar{x}$ number of days from the initiation of vitellogenesis to oviposition). (ii) Total metabolic costs (R) were estimated as the difference between empirically determined NME (= I − FU) and the apparent contribution of NME to reproduction (= Pr − Ps). During vitellogenesis, tailless females consumed 25% more calories than tailed females (5,672 vs. 4,538 cal, respectively; Table 5), had 25% more NME than tailed females (3,857 vs. 3,086 cal, respectively; Table 5), yet allocated 19% fewer calories to reproduction than tailed females (993 vs. 1,221 cal, respectively; Table 5). Total metabolic costs of tailless females were 25% greater than tailed females (Table 5; probably due to the initial stress of autotomy and healing of the intact portion of tail). Total metabolic costs were 1.5 (tailed) and 1.7 (tailless) times the laboratory determined values of standard metabolic rates (see Table 4). These ratios of activity metabolic rate/standard metabolic rate approximate the values suggested for lizards active in the field (Bennett and Dawson 1976; Bennett pers. com.; Bartholomew pers. com). Total NME contributed 47% (570/1,221 cal) of the reproductive

Table 4. Daily energy budgets of a typical tailed (2.56 g) and tailless (2.54 g, with tail) female *Coleonyx brevis*

Energy budget component	Tailed females (N = 10) Cal/d			Tailless females (N = 10) Cal/d			P[a]
	Mean	Range	SD	Mean	Range	SD	
Ingestion (I)	108.1	86.38–124.21	13.01	135.1	103.40–170.24	29.06	0.05
Egestion + Excretion (FU)	34.6	30.96– 41.94	8.82	43.2	39.14– 45.00	8.66	0.05
Net metabolizable energy (NME)	73.5	55.42– 82.27	9.78	91.8	64.26–125.24	11.64	0.05
Metabolic heat loss (R)	39.6	33.28– 41.73	4.80	45.3	35.84– 47.91	4.72	0.02
Storage (Ps)	−15.5	−14.98–(−18.48)	3.38	−7.0	−6.74–(−10.05)	1.17	0.001
Reproduction (Pr)	29.1	27.09– 35.88	3.87	23.7	19.27– 24.48	7.21	0.001

P[a] = Level of significance; Mann-Whitney U Test

Table 6. Comparison of egg characteristics in tailed and tailless *Coleonyx brevis*

Variable	Tailed females ($N=10$)			Tailless females ($N=10$)			P[a]
	Mean	Range	SD	Mean	Range	SD	
Volume (mm^3)	299.1	250.0–345.8	30.1	301.6	265.9–331.0	19.3	NS
Mass (dry, mg)	98.5	75.3–122.5	13.0	82.1	65.8–100.8	11.2	0.01
H$_2$O (%)	57.0	49.8–65.5	3.22	58.3	54.0–62.1	3.30	NS
Ash (%)	5.15	4.61–6.31	1.53	5.06	4.89–6.18	1.87	NS
Cal/mg	6.20	6.15–6.28	0.04	6.05	5.98–6.12	0.05	0.001
Cal/egg	610.7	472.8–757.1	79.0	496.6	393.5–607.8	68.5	0.001

P[a] = Level of significance; Mann-Whitney U Test; NS = no significant difference

energy investment in tailed females compared to 71% (701/993 cal) in tailless females (Table 5).

Egg Characteristics

Characteristics of eggs produced by tailed and tailless females are summarized in Table 6. Although eggs of both groups were comparable in volume, percent H$_2$O and percent ash, they differed strikingly among all other egg comparisons. Tailed females produced eggs that were significantly greater in mass ($p < 0.01$), mass-specific caloric content (cal/mg; $p < 0.001$) and total caloric content (cal/egg; $p < 0.001$) than eggs of tailless females (Table 6).

Reproductive Effort

To determine if differences in egg characteristics between groups represented a comparable difference in reproductive effort (RE), we estimated RE as the proportional contribution of NME used in vitellogenesis (see Williams 1966a). Although tailless females ingested more energy, had more NME and contributed absolutely more NME to egg production (Table 5), their fractional contribution of NME to egg production (= RE) was not significantly different from that of tailed females; RE averaged 18% in both groups (Tailed females = 570/3086; Tailless females = 701/3857; see Table 5).

Discussion

Coleonyx brevis produces 2–3 clutches per season (Dial 1975). Based on several life-history characteristics (iteroparity, rapid attainment of sexual maturity, short-lived; Dial 1975) we presume that its probability of survival to subsequent breeding seasons is low (see Tinkle 1969). If so, selection should favor those individuals that prioritize energy allocation to reproduction at the expense of other energy recipients. Our results support this hypothesis. All tailed and tailless females in our study produced a complete clutch of fully developed eggs at the expense of tail regeneration. Conversely, in long-lived species with a high probability of future reproductive success, other recipients (in particularly those such as tail regeneration that have a positive effect on an individual's future reproductive success) should have energetic priority. Such a relationship was demonstrated by Maiorana (1977) in the salamander *Batrachoseps attenuatus*. This species autotomizes its tail when attacked by snake predators and tail break frequency of a population near Berkeley, California was 48%. Maiorana suggested that in the face of an unpredictable environment selection has favored longevity in *B. attenuatus* and when tail regeneration competes with reproduc-

tion for available energy, selection favors tail regeneration at the expense of reproduction. Virtually all tailless females in Maiorana's study failed to reproduce while regenerating tails.

Congdon et al. (1974) noted that in *Coleonyx variegatus* males regenerate tails at a faster rate than females. They suggested two possible explanations: different selective pressures between sexes and competition for energy by reproductive processes in females. Our results on comparative regeneration rates of male and vitellogenic female *C. brevis* support their second hypothesis.

Production of a clutch of eggs requires a considerable portion of both the energy reserves and net metabolizable energy of an organism. The importance of fat body reserves in lizard reproduction has been demonstrated (Hahn and Tinkle 1965; Licht and Gorman 1970; for a review see Derickson 1976). However, the role of caudal energy reserves has been largely neglected despite the relatively large number of lizard species that stores lipids in the tail. Although carcass and fat body reserves contribute substantially to reproduction in *C. brevis*, caudal reserves represent a much greater initial caloric investment and reproductive energy source. Both tailed and tailless females depleted carcass and fat body lipids at approximately the same rate (see Table 3). However, tailed females had on the average over twice the calories for vitellogenesis than tailless females. The proportion of this additional energy that was represented in the tail and the effects of tail loss on egg mass and caloric content attest to the importance of caudal energy storage to vitellogenesis.

To compensate for the loss of caudal reserves and produce a clutch of eggs, tailless females must increase their rate of food ingestion substantially. The increased rate demonstrated in this study represented an additional 0.53 mealworm/d. When expressed in terms of more natural prey items of *C. brevis* (Dial 1978a), we estimate this to represent ca. 6–8 cicadellid leafhoppers or termite workers/d. Assuming a linear relation between foraging time and calories ingested, we estimate that to produce a clutch of eggs tailless females must forage at least 25% longer than tailed females. Foraging bouts in nature that result in an equivalent net energy gain probably are greater in both area covered and time span. Thus, metabolic expenditure during additional foraging is increased. In addition, tailless females must forage without their primary defense mechanism. Because lizard locomotor efficiency is adversely affected by tail loss (Urban 1965; Ballinger 1973; Smyth 1974; Pond 1978; pers. obsv.), the risks of predation to tailless females are concomitantly greater. Thus, the energetic costs of tail autotomy to reproduction are compounded.

Reproductive effort is the proportion of an individual's energy budget that is allocated to reproduction (Williams 1966a) and is of considerable theoretical interest in the study of life-

history tactics (Williams 1966a; Fitzpatrick 1973; Schaffer 1974; Hirshfield and Tinkle 1975; Tinkle and Hadley 1975; Stearns 1976, 1977; Hirshfield 1980). Although energy budget data are required to accurately estimate RE (Fitzpatrick 1973; Hirshfield and Tinkle 1975; Tinkle and Hadley 1975; Andrews 1979; Hirshfield 1980), most empirical analyses have failed to consider such data, relying simply on size and/or caloric content of eggs. The problems associated with estimating RE in this manner are compounded by including energy reserve contributions to reproduction, which were aquired during feeding activities prior to vitellogenesis and at unknown costs. Production of a smaller egg or an egg of lower caloric value implies a direct change in RE, but, because of the caloric contribution of energy reserves, does not necessarily reflect the proportion of NME allocated to reproduction, as demonstrated in this study. The value of fractional energy budget data in predicting relative levels of reproductive effort has been subject to question (see Andrews 1979).

Relative fitness of an organism is determined by the number of its offspring that survive to sexual maturity. Selection acts on those factors that affect offspring success and primary among them is parental energetic investment (Smith and Fretwell 1974). Energy available to a parent is finite and its partitioning between somatic and reproductive recipients is a complex function of several factors acting synergistically, including predation, competition and environmental uncertainty (Smith and Fretwell 1974; Wilbur 1977). When alternative energy recipients, such as antipredator mechanisms, compete with offspring for energy, selection should result in a compromise of energy allocation that maximizes the parent's genetic contribution to future generations (Wilbur 1977; Congdon, Vitt and Hadley 1978). When faced with an energetic stress, a parent may respond by either a change in the number of offspring or a change in the energetic investment per offspring (Price 1974). Clutch size is constant in *C. brevis*, however our results suggest that selection has favored variation in the amount of energy expended on each offspring.

Our data indicate that the costs of tail autotomy in *C. brevis* include a reduction in egg mass by 17% and a reduction in egg energy content (cal/egg) by 19%. It is generally concluded that larger eggs produce larger, more successful offspring (e.g. correlation between egg mass and hatchling mass and SVL in *Sceloporus undulatus*: Ferguson and Brockman 1980). Kaplan (1980a, 1980b) demonstrated that both mass and caloric content of salamander eggs were direct indicators of hatchling mass and caloric content. Although larger hatchlings represented a greater total number of calories than smaller hatchlings, they used proportionally fewer calories of the initial parental energy investment in the harching process. Hence, larger eggs produced larger hatchlings. We did not measure size or caloric content of hatchling *C. brevis* of either tailed or tailless females; all of the eggs were used to measure egg caloric content. However, data from another study (Dial 1975) suggest a direct relation between initial egg mass (wet, at oviposition) and hatchling mass in *C. brevis*. Assuming a similar relation between egg and hatchling calories, we suggest that hatchlings of tailed females realize a considerable advantage over hatchlings of tailless females in both size and caloric content ($\bar{x}$ cal/egg: Tailed females=610; Tailless females=496). Hatchlings of tailless females begin life with only 81% of the energy of hatchlings of tailed females.

Smyth (1974) examined the effects of tail autotomy on reproduction in two species of Australian lizards (Scincidae). His study demonstrated that in *Morethia boulengeri*, a species with both abdominal fat bodies and caudal reserves, tail loss resulted in reduced egg mass. However, autotomy did not affect egg energy content (measured as fat, % dry mass) as demonstrated

in this study for *C. brevis*. In *Hemiergis peronii*, a species with no abdominal fat bodies but with considerable caudal reserves, tail loss resulted in a reduction in clutch size. Mass and energy content of offspring (the species is ovoviviparous) were not measured.

In competitive, predator rich environments larger hatchlings survive better than smaller hatchlings (Ferguson and Bohlen 1978). By producing larger, more energy rich eggs, tailed females should have more fit offspring than tailless females. Thus, because of the associated costs of tail autotomy, one might predict selection to favor either (i) a shift of caudal reserves to abdominal fat bodies or (ii) tail retention. (i) Although an increase in fat body size may be possible, their size at the onset of vitellogenesis appeared to be maximum; they filled the postabdominal cavity of each baseline female that we examined. The development of caudal reserves in addition to abdominal reserves not only allows for an emergency energy store that can be used during times when food availability is reduced (Bustard 1967), but also permits rapid tail regeneration (Congdon et al. 1974), an important factor for a short-lived, tail autotomizing species. (ii) *Coleonyx brevis* is relatively slow in escape from predators. Relative hind leg length (hind leg length/snout-vent length=HLL/SVL), a measure frequently used to estimate lizard escape speed (e.g. Pianka 1969), is significantly lower ($p < 0.001$) in *C. brevis* ($\bar{x}$ (SD) HLL/SVL=0.37 (0.02), $N=20$) than in such fast moving, mobile species as *Cnemidophorus tigris* ($\bar{x}$ (SD) HLL/SVL=0.73 (0.03), $n=9$) and *Holbrookia texana* ($\bar{x}$ (SD) HLL/SVL=0.86 (0.04), $N=8$). In addition, *C. brevis* lives in a predator rich environment. Besides numerous mammal and bird predators, many species of snakes that are lizard specialists (e.g. *Hypsiglena torquata*, *Salvadora deserticola* and *Masticophis flagellum*) are abundant at Black Gap (pers. obsv.). Thus, the selective advantages of tail autotomy coupled with rapid tail regeneration are considerable.

Utilization of both caudal energy storage and tail autotomy appears paradoxical in evolutionary biology (Clark 1971). However, we suggest that it permits an adaptive compromise in terms of reproductive energy allocation. Caudal reserves not only allow for an emergency energy store (Bustard 1967) and permit rapid tail regeneration (Congdon et al. 1974), but also permit an extra energy reserve that can be used for vitellogenesis. During a reproductive session, size and quality of an egg can vary according to current demands (caudal reserves present or absent; fluctuation in food levels: see Ballinger 1977). The primary mechanism for egg production in *C. brevis* involves utilization of both abdominal and caudal reserves. This allows *C. brevis* to maximize offspring size and quality by increasing mass and energy content of hatchlings with caudal reserves when they are available, yet produce smaller but effective sized offspring when tail autotomy is necessitated. If tail autotomy occurs at the beginning of or during vitellogenesis, abdominal reserves supply the necessary energy for vitellogenesis. Energy allocation shifts to tail regeneration (contribution to the parent's future reproductive value) only after the minimum energy requirement of an egg is paid (contribution to the parent's current reproductive value). Because tail regeneration is rapid, a female can regain her primary antipredator mechanism and still have sufficient time to produce subsequent clutches within the current breeding season.

Energy reserves are probably important only to production of the first clutch of a season. Eggs produced in the second and third clutches of a particular season might not differ significantly in size and caloric content between tailed and tailless females. Therefore, second and third clutch hatchlings may be equal in fitness regardless of the presence or absence of caudal

reserves. Further experimental studies are necessary to examine (i) the relation between tail autotomy of a female and the size and survivorship of her hatchlings, (ii) the relation between tail autotomy and clutch number per season and (iii) the percent of a female's total fitness that is determined by her first clutch.

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