Seasonal Shifts in Clutch Size and Egg Size in the Side-Blotched Lizard, *Uta stansburiana* Baird and Girard

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Summary. There is evidence that the side-blotched lizard, *Uta stansburiana,* and some other organisms of temperate latitudes produce fewer and larger eggs as the reproductive season progresses. There are at least two models that could explain this phenomenon.

Proponents of the parental investment model claim that females are selected to increase egg size, at the cost of clutch size, late in the season in order to produce larger and competitively superior hatchlings at a time when food for hatchlings is in low supply and when juvenile density is high. In this model the selective agent is relative scarcity of food available to hatchlings late in the reproductive season, and the adaptive response is production of larger offspring.

The alternative explanation (bet-hedging model) proposed in this paper is based on the view that the amount of food available to females for the production of late-season clutches is unpredictable, and that selection has favored conservatively small clutches in the late season to insure that each egg is at least minimally provisioned. Smaller clutches, which occur most frequently late in the season, are more likely to consist of larger eggs, compared to larger clutches, for two reasons. Firstly, unlike birds, oviparous lizards cannot alter parental investment after their eggs are deposited, and therefore, in cases of fractional optimal clutch size, the next lower integral clutch size is selected with the remaining reproductive energy allocated to increased egg size. With other factors constant, eggs of smaller clutches will increase more in size than eggs of larger clutches when excess energy is divided among the eggs of a clutch. Secondly, unanticipated energy that may become available for reproduction during energy-rich years will similarly increase egg size a greater amount if divided among fewer eggs.

Introduction

Numerous authors have reported seasonal shifts in mean clutch size in populations of temperate lizards (e.g. Kramer 1946; Tinkle 1961, 1967; Fitch and Greene 1965; Mayhew 1965, 1966; Hoddenbach 1966; Hoddenbach and Turner 1968; Telford 1969; Turner et al. 1970; Tinkle and Ballinger 1972; Ballinger and Schrank 1972; Ballinger et al. 1972; Goldberg 1973, 1975; Parker and Pianka 1975; Derickson 1976; Michel 1976; Nussbaum and Diller 1976; Ballinger 1977; and Schall 1978). In all cases, late-season clutches were found to be smaller than early-season clutches. Similar results have been reported for other groups of animals (e.g., Wolda and Kreulen 1973). There is less information available concerning seasonal shifts in egg size within lizard populations. Ballinger et al. (1972) wrote that small females of *Cophosaurus texanus* Troschel laid larger eggs later in the reproductive season, but that large females did not alter egg size seasonally. Derickson (1976) found that cal/egg increased between the first and third clutches in *Sceloporus undulatus* (Latreille), and that the size (snout-vent length) of hatchlings correspondingly increased between the first and third clutches in this species. Derickson (1976) also reported a seasonal increase in cal/egg for *Sceloporus graciosus* Baird and Girard. Ferguson and Bohlen (1978) cited Tinkle (1967), Turner et al. (1970), Tinkle (1972) and Ballinger and Schrank (1972) as authorities for reported seasonal increase in egg size for *Uta stansburiana, Sceloporus undulatus* and *Cnemidophorus gularis* Baird and Girard. However, I find no data concerning shifts in egg size in these references. Schall (1978) stated that egg weight does not vary seasonally in 5 species of *Cnemidophorus* and no evidence has been found for seasonal shifts in egg size in *Sceloporus merriami* Stejneger and *Urosaurus ornatus* Baird and Girard (A. Dunham, pers. comm.).

Nussbaum and Diller (1976) found an inverse correlation between clutch size and egg volume, which was independent of female size, in a northern population of *Uta stansburiana.* They also found that late clutches were smaller than early clutches, again independent of female size. These two relationships suggested that late clutches consisted of larger eggs compared to early clutches. To examine this possibility, the same population was sampled in a later year with attention to egg weight rather than egg volume. The results are presented in this paper, along with a discussion of two models of shifts in egg size.

Methods and Materials

The study site in north-central Oregon was described by Nussbaum and Diller (1976). Females of reproductive size were collected 15 May 1976 (early sample) and again 13–20 June 1976 (late sample). Snout-vent lengths (SVL) and tail lengths were recorded to the nearest 1.0 mm in the field before preservation. Body weights (BW) and individual wet weight of oviductal eggs (IWWE) were estimated to the nearest 0.05 gm in the field before preservation with a 5.0 g pesola scale. Eggs were then preserved individually in 95% ethanol in scintillation vials.

Dry weights of individual eggs (IDWE) were obtained in the laboratory by first cleaning the external surfaces of the vials in soapy water followed by a rinse and then by a second cleaning in acetone. Vials were handled only with clean forceps after washing. The lids were then removed, and the lid liners rinsed into the vials with fresh 95% ethanol. The lidless vials were placed in a drying oven and dried to constant weight at 80° C. The weight of each vial plus egg residue

was estimated to the nearest 0.001 g on a Mettler balance. Vials were then soaked in baths of xylene, hot soapy water, hot rinse water, and finally acetone to remove egg residues. Empty vials were placed in the oven and again dried to constant weight. IDWE was calculated as (weight of vial and residue) – (weight of clean empty vial). Controls were run by drying vials with alcohol but without eggs. The residue weights of the 10 controls were not significantly different from 0.0 ($P<0.05$), indicating that the preserving fluid did not contribute substance to the dried egg mass, and that the cleaning and taring process did not influence the results. Scrimshaw (1945) and Thibault and Schultz (1978) similarly found that preservation of fish eggs did not affect their dry weight. There remains the possibility that egg substance (volatile lipids?) was lost during drying. Presumably, however, such error would have affected the May and June samples identically.

The amount of time an ovulated egg has been in an oviduct could influence both IWWE and IDWE because water and shell are added in the oviduct. To test for this effect, eggs were staged as (1) freshly ovulated, no shell; (2) shell forming; and (3) shell fully formed or nearly so. These 3 stages were considered in the statistical comparisons.

Egg weights, both wet and dry, were averaged for each clutch, and these averages were used to represent each female's egg weight. Clutch sizes were recorded for all females with late ovarian eggs and with oviductal eggs. Egg weights, however, were recorded only for oviductal eggs. Therefore, the sample sizes in the analyses presented below may vary between comparisons.

Results

Clutch Size. A preliminary, forward, stepwise multiple regression analysis was done in order to determine the correlations between clutch size and the independent variables month, SVL, IWWE and IDWE. The results are shown in Table 1. With the level for inclusion set at $\alpha \leq 0.05$ IWWE was eliminated from the regression. The remaining three variables accounted for 74.3% of the variance in clutch size ($P<0.0001$). Month (May or June) was the most significant factor, accounting for 51.3% of the variance in clutch size. SVL and IDWE were second and third, accounting for an additional 11.9 and 11.1% of the variance respectively. Month and IDWE are inversely correlated and SVL directly correlated with clutch size.

Analysis of variance indicates that the unadjusted mean clutch sizes for May and June are highly significantly different, with the May sample averaging about 1 more egg per female than the June sample (Table 2). A scatter plot (Fig. 1) illustrated that clutch size varies positively with SVL for both the May and the June samples, and that SVL is not equally distributed between the two months. Accordingly, a covariance model (AN-COVA) was used with SVL as a covariate to compare clutch size by month. F-tests indicate that the slope of the relationship between clutch size and SVL is greater than zero ($P<0.0001$) and that the regressions for May and June are different ($P<0.0001$). The slopes for the May and June samples are not significantly different ($P=0.1417$). Therefore the different regressions result largely from different intercepts. The adjusted mean clutch

Table 1. Forward stepwise regression of clutch size versus month, SVL, IWWE, and IDWE[a]

Step	Variable	Partial	r^2	Significance
1	Month	−0.716	0.513	$P<0.0001$
2	SVL	0.495	0.632	$P<0.001$
3	IDWE	−0.549	0.743	$P<0.0001$

[a] Level for inclusion, $\alpha \leq 0.05$; IWWE was not included. Remaining partial for IWWE = 0.205, $P=0.160$. $N=52$

Table 2. Comparison of clutch size by month without adjustment and with adjustment for SVL

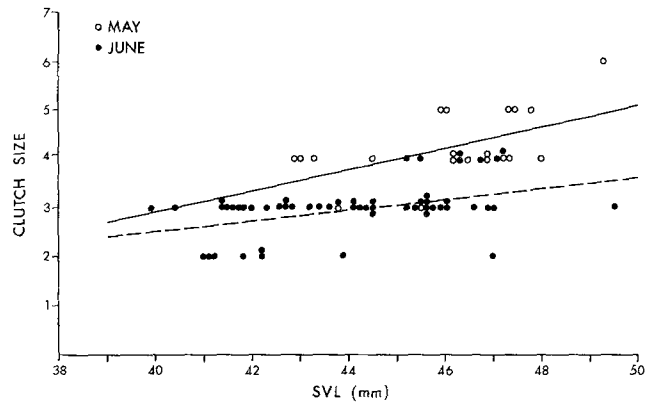|	May	June	Significance (ANOVA F-test)
Clutch size (unadjusted mean)	4.250	2.982	$P<0.0001$
Clutch size (adjusted mean)	4.057	3.052	$P<0.0001$
$N=$	20	55	

Fig. 1. Relationship between clutch size and SVL for early and late clutches, 1976, for a single population of *Uta stansburiana* in north-central Oregon. Lines fitted by least squares regression. Analysis of covariance indicated that the regressions for the two samples were different, but that the slopes were not different (see text). The regression equation for May is CS = − 5.922 + 0.221 SVL with $r^2=0.299$ ($P=0.0125$); for June CS = − 1.919 + 0.111 SVL with $r^2=0.208$ ($P=0.0005$)

size for May is significantly greater ($P<0.0001$) than for June (Table 2).

These results (larger early clutches) agree with expectations for north-temperate iguanid lizards and conform to results obtained for this same population in 1973-4 Nussbaum and Diller, 1976). However, both the May and June clutch sizes were smaller in 1973-4 compared to 1976, indicating annual variation in clutch size for this population.

Egg size. Stepwise regression analysis showed that of the independent variables month (X_1), stage of development (X_2), SVL (X_3) and clutch size (X_4), only stage of development and month influence IWWE at $\alpha \leq 0.05$. Stage of development accounts for 25.81% of the variance in IWWE ($r_{yx_2 \cdot x_1}=0.508$, $P<0.0001$), and month accounts for an additional 17.70% of the variance ($r_{yx_1 \cdot x_2}=0.488$, $P<0.001$).

Stepwise regression of IDWE on the same set of independent variables results in significant regressions only for clutch size and SVL. Clutch size accounts for 9.82% of the variance in IDWE ($r_{yx_4 \cdot x_3}=-0.313$, $P<0.05$), and SVL accounts for an additional 37.45% of the variance ($r_{yx_3 \cdot x_4}=0.644$, $P<0.0001$).

These results indicate that, as expected, water is added to eggs in the oviduct; and that, perhaps unexpectedly, no significant (or detectable) amount of dry matter is added in the oviduct. These results also suggest that the inverse relationship between clutch size and egg size is caused primarily by varying the dry-matter component of egg size rather than the water content of the eggs.

Unadjusted mean IWWE and IDWE were compared between months with a one-way analysis of variance model. Means and significance levels are presented in Table 3. The unadjusted mean IWWE was significantly ($P=0.0239$) greater in the June sample compared to the May sample. The unadjusted mean IDWE was also greater in June ($P=0.0747$). However, the regression analyses described above indicated that comparisons of unadjusted means are not justified because of significant correlation of IWWE and IDWE with other variables. A covariance model was used to account for the effects of significant covariates, and the comparisons (ANCOVA) of the resultant adjusted means are given in Table 3.

Mean IWWE was adjusted (ANCOVA) to account for SVL because the distribution of SVL's was different (Fig. 1) for the two monthly samples. Mean IWWE was also adjusted for stage of development because regression analysis showed that late stage eggs were heavier than eggs in early stages. Both adjustments result in significantly greater IWWE for June compared to May (Table 3).

Mean IDWE was adjusted (ANCOVA) for SVL and clutch size because both were shown by regression to contribute significantly to the variance of IDWE. There is no significant difference between months in mean IDWE adjusted for clutch size (Table 3). This result reflects the inverse correlation between clutch size and IDWE, and suggests that eggs may be larger in June, because of smaller clutches in June (see Discussion).

Larger females have larger clutches in both May and June, and because clutch size and egg size are inversely correlated, it is necessary to adjust for the different distribution of SVL's between the monthly samples. When this is done, the late season (June) sample has a significantly ($P=0.0007$) greater mean IDWE (Table 3).

In summary, both mean IWWE and mean IDWE increase significantly between May and June when SVL is accounted for. This constitutes an 18.40% increase in mean wet weight and a 12.57% increase in mean dry weight per egg between May and June.

Water content of oviductal eggs increased from 44.61% in May to 49.64% in June (percentages based on mean IWWE and mean IDWE adjusted for stage of development by covariance analysis). These percentages are within the range (42.2–62.9) of and on opposite sides of the mean (48.4) % water content of *U. stansburiana* eggs reported by Vitt (1978).

Table 3. Comparison of mean wet weight[a] (IWWE) and mean dry weight (IDWE) of eggs by month

	May	June	Significance (ANOVA F-test)
IWWE			
unadjusted means	0.170	0.189	$P=0.0239$
means adjusted for SVL	0.163	0.193	$P=0.0034$
means adjusted for stage of development	0.165	0.192	$P=0.0003$
IDWE			
unadjusted means	0.0915	0.0967	$P=0.0747$
means adjusted for clutch size	0.0947	0.0954	$P=0.7928$
means adjusted for SVL	0.0875	0.0985	$P=0.0007$
$N=$	16	36	

[a] grams

Discussion

Smith and Fretwell (1974) and Brockelman (1975) discussed theoretical aspects of parental investment. Two important assumptions of their models, which are probably true, are (1) that as parental investment is increased, clutch size must be reduced and (2) that offspring fitness increases as parental investment increases. Their models are further based on the presumption of a functional relationship between expected individual offspring fitness and parental investment which is either convex (Smith and Fretwell 1974) or sigmoid (Brockelman 1975). The curve includes a point of diminishing returns beyond which increased parental investment results in reduced female fitness even though the fitness (survivorship) of individual offspring continues to increase at a reduced rate.

One result of this study, the significant inverse correlation between egg size and clutch size for homogeneous samples of *U. stansburiana*, is consonant with current models of parental investment. Two other results, (1) significantly smaller clutches and (2) significantly larger eggs late in the reproductive season, while perhaps consonant with these general models, are not fully explained by them.

There are at least two reasons why temperate lizards may increase their parental investment as the reproductive season progresses. The obvious, but perhaps erroneous, explanation is that females are adapted by natural selection to increase the size of their late-season offspring. To do so, they must increase egg size, and, because resources are limited, they must also reduce clutch size. This hypothesis, which I will refer to as the "parental investment model", was invoked by Ferguson and Bohlen (1978) to explain larger and more aggressive, but fewer young from late season clutches of *Sceloporus undulatus*. These authors believed that seasonal reduction in food available to hatchlings and increasing hatchling density increased competition and placed a selective premium on large size and aggression. This argument is identical to that offered by Hutchinson (1951, 1967) and Lack (1954) to explain the production of larger and fewer eggs late in the season by some copepods and by Hubbs et al. (1968) and Bagenal (1971) to explain similar phenomena in fishes. A variation on this argument emphasizes predator avoidance rather than competition for food. Thus, Kerfoot (1974) argued that females of the cladoceran, *Bosmina longirostris* (Müller), increase their parental investment late in the reproductive season in order to produce larger offspring that are better able to escape invertebrate predators that become numerous at that time.

In all of these cases there is the assumption that females are selected to produce larger eggs in response to conditions which most often occur late in the reproductive season. At least for lizards, this assumption seems unnecessary, and an alternative explanation, the "bet-hedging model", is offered. The concept of bet-hedging (summarized by Stearns 1976) has been discussed by numerous authors since Murphy (1968) in reference to life history characteristics that apparently evolved in response to environmental uncertainty. Cohen (1967), Boer (1968), and Mountford (1971, 1973) discussed the evolution of clutch size in variable and unpredictable environments. One prediction from their analyses is that if organisms cannot anticipate future conditions then selection will favor conservatively small clutches which will seldom fail, even when relatively poor conditions are realized. In the present context, temperate lizards may produce relatively small late-season clutches as a hedge against clutch failure (Fig. 2), and this may often lead to the production of larger late-season eggs as explained below.

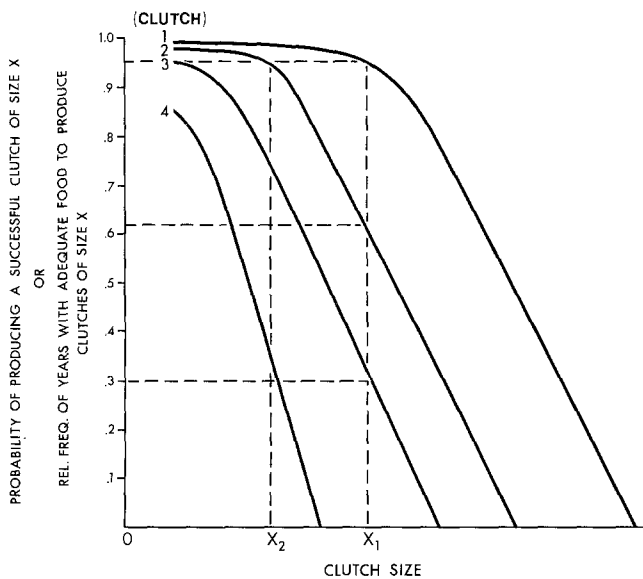Assumptions of the bet-hedging model are (1) that temperate

Fig. 2. Graphical representation of model that may explain selection for seasonally reduced clutch size in temperate lizards. Attempts to produce second clutches of X_1 eggs would fail about 38% of the time according to these hypothetical curves. In a given year, females may allocate a portion of the unanticipated energy which may become available late in the reproductive season to increased egg size

lizards are adapted to utilize food resources that vary considerably in abundance and availability from year-to-year and month-to-month in an unpredictable manner and (2) that only during years of unusually high food abundance would there be enough time to produce late-season clutches that are as large or larger than early-season clutches and (3) that females cannot accurately predict the amount of food that will be available to them for the production of late clutches at the time they begin to develop their late clutches and (4) that females can reduce clutch size by atresia but cannot increase clutch size after some critical early stage in clutch development.

Postulates of the bet-hedging hypothesis are (1) that large offspring are at least as advantageous early in the reproductive season as in the late season and (2) that selection has favored reduced clutch size (not increased egg size) in the late season to insure that each egg is at least minimally provisioned and (3) that unanticipated energy that may become available beyond what is required for minimal provisioning is equally distributed among the eggs of a clutch for maximum utilization of energy available for reproduction and (4) that females are adapted to alter clutch size within and between seasons in such a manner that total energy available for egg production will seldom exceed the amount that would have provided for an additional egg of minimal size.

Predictions of this model are (1) that both large and small clutches will be found to have variable egg size between years, depending upon yearly variation in resource levels (in fact, Ballinger 1977, found yearly variation in egg size in *Urosaurus ornatus* associated with differences in food levels) and (2) that within years, small clutches will have larger eggs than large clutches because unanticipated resources are divided among fewer eggs and (3) that the largest mean difference between egg sizes should occur between eggs of very small and very large clutches sampled at the same time and place and (4) that large-egged clutches

will seldom consist of sufficient surplus yolk, compared to clutches of equivalent size with average-sized eggs, to provision an additional egg of minimal size, and (5) that this model is most likely to apply to species that cannot afford to miss an opportunity to reproduce in the late-season, i.e., those with very high adult mortality, even in the absence of reproduction.

The bet-hedging model incorporates the "fractional egg" principle discussed by Ricklefs (1968), in reference to birds, which is that as clutches become smaller an increasingly higher percentage increase in parental investment is necessary to increase clutch size by one (Fig. 3). Birds have sequential development of eggs in the ovaries and parental care. They can adjust their parental investment to account for optimal clutches of say 2.5 eggs by depositing either 2 or 3 eggs and adjusting the intensity of parental investment during the period when the nestlings are fed. Riclefs (1968) argued that birds will opt to produce the next higher whole egg at the cost of reduced growth rate of nestlings.

Oviparous temperate-zone lizards, however, do not have parental care, and the eggs of each clutch are developed simultaneously. Temperate-zone lizards can respond to an energy shortage after the clutch begins to develop by absorbing one or more eggs, or to an energy flush by increasing egg size. Faced with an optimal clutch size which is fractional, lizards, unlike birds, are likely to opt for the smaller integral clutch size and adjust their investment by increasing egg size, because they do not have the opportunity to alter investment after the eggs are deposited.

Based on the fractional egg principle, Ricklefs (1968) predicted that, among birds, the nestling period would on the average be longer and the variance greater for species with smaller clutches compared to species with larger clutches. He found considerable evidence to support these predictions. Perhaps an analogous prediction for lizards would be a larger average seasonal increase in egg size and greater seasonal and annual variation in egg size among temperate species with smaller clutches compared to those with larger clutches. This prediction stems from the fact that with smaller clutches, adjustment of investment to account for fractional optimal clutch sizes could lead to a
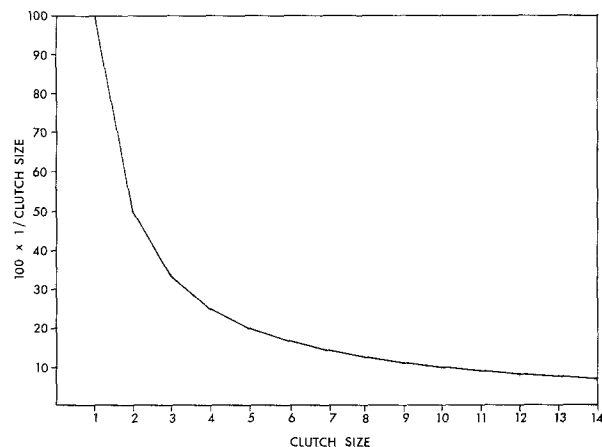

Fig. 3. The relationship between clutch size and the percent of total clutch energy represented by one egg. The shape of the curve allows the prediction that if energy available for reproduction varies across seasons and/or between years, then annual and seasonal variance in egg size should be greater among individuals and populations with smaller clutches. See text for further explanation

higher percentage of remaining energy to be evenly distributed among fewer eggs than would be the case with larger clutches.

Temperate-zone lizards are subjected to time constraints which become increasingly restricted with higher altitudes and latitudes. Late-season clutches will fail if they are deposited too late in the season because of exposure of unhatched eggs to freezing conditions. After the eggs are deposited, lizards cannot increase their parental investment in response to unseasonable weather that could delay embryonic development, because they neither incubate nor feed their young. Therefore, females are likely to be selected to cease investment (deposit their last clutch of the year) rather abruptly on site-specific dates with little variance within populations. The mean date of oviposition of the last clutch should be selected to conservatively allow enough time for development before the onset of cold weather. Female lizards presumably cannot predict the amount of food that will be available to them for development of late clutches. And because, unlike birds, they cannot alter investment or manipulate offspring after oviposition, selection is likely to favor conservatively small clutches that can be adequately provisioned in the ovaries and oviducts even in energy-poor years before the last oviposition date. With this system, females have the opportunity to increase parental investment in good years by increasing egg size, but they cannot increase clutch size.

Some tropical lizards (e.g., *Anolis* spp.) oviposit single eggs that are developed sequentially. Although they too cannot alter investment nor manipulate young after oviposition, they are not subjected to the stringent time constraints of temperate-zone lizards. These tropical species with sequential development are likely to respond to variation in food levels by adjusting the provisioning time of the eggs in their ovaries and oviducts, maintaining constant egg size though time, and altering annual fecundity as a function of yearly variation in food supplies.

The central difference between the parental investment and bet-hedging models is the presumption in the former that hatchlings of larger size are relatively more important to female fitness later in the reproductive season than earlier. Ferguson and Bohlen (1978) tested the parental investment model by measuring the survivorship of hatchling *Sceloporus undulatus* of different sizes in early and late samples. They found that 23.5% (12/51) of the small (20–23 mm SVL) hatchlings marked early in the reproductive season survived until the following spring breeding season, and that 29.4% (5/12) of the large (24–26 mm SVL) hatchlings survived. In the late sample, 21.3% (13/61) of the small and 42.9% (15/35) of the large hatchlings survived. Thus, there was no significant difference in the survival rate between small and large early hatchlings, but large late hatchlings survived at nearly twice the rate of small late hatchlings. Ferguson and Bohlen (1978) therefore concluded that a female gains nothing by producing large hatchlings early in the reproductive season but increases her fitness by producing large late hatchlings. They construed these results as support for their hypothesis.

Unfortunately, their data are troublesome for at least two reasons. Firstly, if greater fitness accrues to larger hatchlings in the late season, and if the authors' samples are representative, then the females are behaving in a curious manner. They are producing 63.5% (61/96) small hatchlings in the late season when they should be producing large hatchlings. This is a higher percentage production of relatively unfit offspring than would be expected from a normal distribution of phenotypes. Secondly, Ferguson and Bohlen (1978) do not claim to have marked every hatchling on the day of hatching. Therefore, they cannot know the exact age of their hatchlings. They list a hatchling size range of 20–26 mm SVL. A 20 mm hatchling growing at 0.2 mm SVL/

day (a reasonable average for iguanid lizards) would require 30 days to reach 26 mm SVL. Because their early and late samples are only 1 month apart, it is conceivable that some of their late large hatchlings actually hatched at much smaller size, perhaps even in the early season, and have been misclassified. A related problem is the potential for rapid growth of superior genotypes. A superior hatchling growing at 0.4 mm SVL/day (twice the average) would grow from 24 to 25 mm in 5 days. If such hatchlings were censused for the first time 2.5–5.0 days after hatching they would be misclassified as large hatchlings. Furthermore, they would almost certainly have high survivorship, but because of superior genotype (rapid growth) rather than because of large hatching size.

Two additional, but perhaps less important problems are associated with Ferguson and Bohlen's (1978) results. If, as the authors claim, the advantage to large size late in the season stems from superior competitive ability at a time when resources are scarce, then a significant reduction in survival of small hatchlings in the late season would be expected. There is a reduction from 24 to 21% survival of small hatchlings between the early and late seasons, but this change is not statistically significant. Lastly, Ferguson and Bohlen (1978) concluded that larger hatchlings are not advantageous in the early season, and yet fully 25% of their early sample consists of large hatchlings, presumably produced at greater cost to the female.

While the data presented by Ferguson and Bohlen (1978) are of great interest, and are perhaps indicative of selection for seasonally increased parental investment, their conclusions are equivocal and their studies should be repeated with attention to the problems presented here.

The bet-hedging model would be falsified for a particular system if a late-season increase in egg size was, on the average, large enough to account for one or more additional eggs of the smaller size. This would constitute clear evidence that clutch size has been sacrificed for egg size. There is no evidence that this occurs in *U. stansburiana*. For an average clutch of 3 late season eggs, the percent increase in egg size must exceed the critical value of 33.3%/egg (Fig. 3). The percentage increase for *U. stansburiana* (12.57%, see results) falls far short of the critical value. There is evidence that clutch size is sometimes sacrificed for egg size in *Sceloporus undulatus*. Derickson (1976) reported an increase of 26.14% in calories/egg for an average of 6 eggs between early and late clutches in this species. The critical percentage for clutches of 6 eggs is 16.67%, a value exceeded by Derickson's results. Presumably, female *S. undulatus* could have laid 1.58 more eggs of smaller size in later clutches rather than increasing egg size. If this situation is normal for *S. undulatus*, then the logical conclusion is that the parental investment model applies for this species. There is direct evidence, however, that at least in some populations of *S. undulatus*, egg size is not always increased seasonally (Marion et al. 1979).

There is no reason to expect that one or the other of these models should explain all cases of seasonally increased egg size. For a given case, unequivocal evidence that larger hatchlings late in the reproductive season increases female fitness would strongly support the parental investment model, as would evidence that late-season eggs are regularly increased in size beyond the respective, critical percentage values. The opposite results would support the bet-hedging model.

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