ECOLOGICAL AND PHYSIOLOGICAL ASPECTS OF REPRODUCTIVE STRATEGIES IN TWO LIZARDS

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Abstract. Two lizard species, the northern prairie lizard (Sceloporus undulatus garmani) from Reno County, Kansas and the northern sagebrush lizard (Sceloporus graciosus graciosus) from Washington County, Utah, were used to test four hypotheses and one assumption related to the theory of r- and K-selection. The northern prairie lizard is short-lived, matures early, and has a high reproductive effort (r-strategist) while the northern sagebrush lizard is long-lived, has delayed maturity, and has a low reproductive effort (K-strategist). One of the assumptions of the r- and K-selection theory is that competition for food is more intense for K-strategists than for r-strategists. Given this assumption, greater food availability for the prairie lizard was hypothesized to result in (1) a higher level of body lipids, (2) a higher rate of lipid utilization, (3) a lower percentage of ingested energy available for metabolism, and (4) an expenditure of less energy per offspring than in the sagebrush lizard.

Total lipid levels in the two species collected before and after hibernation indicated that prairie lizards had significantly higher lipid levels than sagebrush lizards during both collection periods. A comparison of the amount of body lipids lost and the amount of egg lipids gained during vitellogenesis of the first clutch suggested that more lipids are being utilized for egg production in prairie lizards than in sagebrush lizards.

Sagebrush lizards apparently are better adapted physiologically to lower food levels since they had lower rates of lipid utilization during starvation studies and they extracted more energy usable for metabolism from ingested food than prairie lizards.

Although both species expended about the same amount of energy on a given clutch of eggs, prairie lizards produced more offspring per clutch and therefore expended less energy per offspring. Prairie lizards produced as many as three clutches per season as compared to two clutches per season for sagebrush lizards, and changes in length-lean weight relationships for the two species over a given season suggested that the additional clutch of eggs produced by prairie lizards may be contributing to the higher mortality observed in this species.

Indirect evidence, based on precipitation levels and insect biomass at the two study sites and mouthgapes of the two species, supported the assumption that more food was available to the prairie lizards than the sagebrush lizard. Higher precipitation levels (indicating greater insect biomass) occurred at the prairie lizard collection site and this species had a smaller mouthgape index, indicating greater specialization in utilization of prey sites.

Key words: Energy, available for metabolism, expended per offspring; Kansas; lipids; prairie swift; sagebrush lizard; strategy, reproductive; Utah.

INTRODUCTION

Although a number of studies have been done on the importance of lipids in the life histories of various animals, no one has attempted to correlate differences in lipid storage and utilization with life history differences. In most seasonal animal species, lipids should be important since lipid storage is a biochemically efficient way to package energy for later usage. A gram of stored lipids represents \( \approx 38 \text{ kJ} \) (9 kcal) of energy, while a gram of carbohydrate or protein, with the higher H,O content, represents only 17-21 kJ (4-5 kcal) of energy. Therefore, more energy can be stored in a smaller package with lipids. In nonseasonal (acyclic) animal species, lipid storage is probably not important since food is always presumed to be limiting but never critically short (e.g., reproduction still occurs at low levels).

Nikolskii (1969) has shown that a correlation exists between lipid levels and fecundity in a number of commercial fishes. Odum (1960), Helms (1968) and King (1970) demonstrated marked increases in lipid storage prior to migration in several passerine bird species. Jameson and Mead (1964) and Davis (1967) indicated that lipids are used during hibernation in several small mammal species. Sawicka-Kapusta (1968) found lipid depletion associated with reproduction in field mice. A vast body of literature on lizards indicates that some species use lipids during hibernation (Dessauer 1955; Mueller 1969, Derickson 1974), while others use lipids during reproduction (Hahn and Tinkle 1965, Licht and Gorman 1970, Telford 1970). Church (1962) could find no evidence of lipid deposition and utilization in...
three species of Jamaican House Geckos which live in a nonseasonal environment.

The literature on life history phenomenon is also bountiful. Several authors (Cole 1954; MacArthur and Wilson 1967; Gadgil and Bossert 1970; Hairston et al. 1970; Pianka 1970, 1972) have put forth arguments to explain variations in life history phenomenon. As a result of work done by these authors it is known that a gradient of life history strategies (strategy being used in a teleological sense) exists, with the two extreme strategies being organisms with short lives, high reproductive efforts, and early maturity and those with long lives, low reproductive effort, and delayed maturity. Tinkle (1969), Tinkle et al. (1970), and Gadgil and Solbrig (1972) have presented empirical evidence on lizards and dandelions, respectively, that supports this dichotomy of life history strategies. This dichotomy has been more popularly referred to as $r$- and $K$-selection (MacArthur and Wilson 1967; Gadgil and Bossert 1970; Pianka 1970, 1972; Gadgil and Solbrig 1972), although Hairston et al. (1970) choose to call it $b$ and $d$ selection. Basically, the theory of $r$- and $K$-selection states that fitness is determined by $r$ (intrinsic rate of increase) in species living in an environment where mortality is unpredictable, while in species living in environments where mortality is more predictable, fitness is determined by $K$ (environmental carrying capacity). In other words, fitness is determined primarily by density independent factors in $r$-selected species and by density-dependent factors in $K$-selected species. For lack of better terminology, $r$- and $K$-selection will be used; however, the independent variable identified as the causative agent is food availability per individual. This includes not only the potential productivity available but also an organism’s access to that productivity. This avoids the issue of whether $r$-selected species are regulated by density-independent factors and $K$-selected species by density-dependent factors. Also, to avoid another problem with the theory it is assumed that the adult and juveniles of the species studied are both utilizing similar resources. Other assumptions are (1) that an optimum size for reproduction exists and that greater food availability will result in reaching this size at an earlier age; (2) that there is a positive correlation between food availability and reproductive effort; and (3) that an inverse relationship between reproductive effort per season and life span exists.

Since differences in life history strategies and in patterns of lipid storage and utilization are known to exist in lizards, it seems logical to conclude that the two may be interrelated. In other words, given the assumption that differences in food availability per individual can result in a variety of life history strategies, it is likely that this same factor may also explain observed differences in lipid storage and utilization.

Differences in food availability per individual should also lead to differences in (1) rates at which lipids are utilized during periods of food shortage, (2) the percentage of ingested energy available for metabolism, and (3) the amount of energy expended on each offspring. An individual of a species that has historically been exposed to low food availabilities should maximize its usage of available food. This may be done by maximizing net energy yield per unit of feeding time, as suggested by Emlen (1966), MacArthur and Pianka (1966), MacArthur and Wilson (1967) and Schoener (1971), through utilization of prey with high caloric values or by utilizing prey that can be captured with a minimum of pursuit and capture time. Given no difference in quality or capturability of prey, a species that has been exposed to lower food levels may maximize energy obtained from ingested energy by (1) reducing losses of ingested energy via respiration, secretions, and excretions, and (2) by conserving stored energy during periods of food shortage. On the other hand, individuals of a species that has historically been exposed to abundant food supplies need to be less stringent in their conservation of stored energy during periods of food shortage and in their utilization of ingested energy.

Food availability to the offspring may dictate how a parent apportions the ingested and stored energy available for reproduction. If the offspring and adults of a given species have both been exposed to low levels of food, a parent may increase its fitness by expending more energy per offspring in the form of parental care or by producing larger offspring (Smith and Fretwell 1974). This assumes that though fewer offspring are produced, their survivorship is enhanced by an increased competitive ability. If, on the other hand, food is abundant to both adults and offspring, the parent may increase its fitness by expending less energy per offspring. This would result in the production of more offspring and it is assumed that survivorship is enhanced by sheer numbers. Harper et al. (1970) indicated that plants under intense competition put more energy into each offspring and produce fewer of them. Dr. Eric R. Pianka (personal communication) compiled a list of various lizard species and indicated that there tends to be a negative relationship between the amount of energy expended per offspring and the number of eggs produced.

By using a $r$- and $K$-selected lizard species, an attempt will be made to verify the following hypotheses:
1) Given greater food availability for the r-selected lizard species, this species should have higher lipid levels before and after hibernation than the K-selected lizard species.

2) Given greater food availability for the r-selected lizard species, this species should have a higher rate of lipid utilization during periods of food shortage than the K-selected lizard species.

3) Given greater food availability for the r-selected lizard species, this species should obtain less energy for metabolism per unit of ingested food than the K-selected lizard species.

4) Given greater food availability for the r-selected lizard species, this species should produce more offspring with less energy expended per offspring, while the K-selected lizard species should produce fewer offspring with more energy expended per offspring.

**Species Studied**

Females of the lizards Sceloporus undulatus garmani and Sceloporus graciosus graciosus were chosen for this study. Some of the reasons for choosing lizards and these particular species were (1) they are easy to study either in the field or laboratory; (2) information related to the theory of the evolution of life history strategies in lizards is available from work done by Tinkle (1969) and Tinkle et al. (1970); (3) a number of studies have looked at the role of lipids in lizards; (4) reproductive effort can be better approximated (since lizards exhibit no parental care, kilojoules per clutch and number of clutches per season should provide a reasonably accurate measure of reproductive effort); (5) these species are similarly sized; thus, effects of body size differences on metabolism are minimized; and (6) in terms of lifespan, age at maturity, and reproductive effort, these two subspecies are known (Ferguson and Bohlen 1973, on S. u. garmani and Tinkle 1973, on S. g. graciosus) to fit the r- and K-selection correlates of Pianka (1970).

*Sceloporus undulatus garmani* is a small iguanid lizard found predominantly in eastern Colorado, Kansas, Nebraska, and Oklahoma. This subspecies, hereafter referred to as the northern prairie lizard, is found in a variety of habitats, including sandy areas, sandstone cliffs, sparse grass, woodpiles, and old trash piles (Smith 1946). At the collection site, located in Reno County, Kansas, they were found in grazed sand prairie around old fallen cottonwood (*Populus* sp.) trees and refuse piles.

Prairie lizards feed on arachnids, Coleoptera, Hemiptera, Diptera, Orthoptera, and Hemiptera (Smith 1946). Their feeding strategy is to sit and wait until prey come within striking distance and then give pursuit. The average lifespan is 1 yr, age at maturity 8–9 mo, and reproductive effort is about three clutches/season (Ferguson and Bohlen 1973). An early age at maturity and production of three clutches results in considerable variation in egg-laying times (Fig. 1). Offspring from the first clutch hatch in mid-July, the second in mid-August, and the third in early September. Lizards from the first clutch will be ready to reproduce the following spring, while those from succeeding clutches will not mature until late spring or early summer. First clutch offspring have the potential for laying clutches in May, June, and July of their first breeding season. Probably, because of this high reproductive effort at such a young age, the first clutch offspring rarely reproduce a second season. Conversely, offspring from the second and third clutches may produce 1–2 clutches in their first breeding season. These offspring from later clutches are more likely to survive a second winter (but most do not) and produce additional clutches of eggs. Therefore, an early age at maturity and the production of three clutches by some lizards results in considerable variation of laying times and size of lizards laying eggs.

*Sceloporus graciosus graciosus* is found predominantly in Idaho, Nevada, Utah, and Wyoming at altitudes > 1,500 m. As the common name, northern sagebrush lizard, suggests, this species is common
Sagebrush lizards have the same general diet and foraging patterns as prairie lizards. They are known to be long-lived, > 6 yr, and mature in 2 yr (Stebbins and Robinson 1946, Tinkle 1973). The number of clutches produced probably varies with altitude and latitude, however, in southwest Utah this species lays two clutches of about four eggs each season (Tinkle 1973). This reproductive schedule will allow an average adult to produce about eight clutches in a lifetime. Unlike prairie lizards, sagebrush lizard hatchlings from first and second clutches reach reproductive maturity at the same time, the beginning of the third season. This results from an extra summer of growth prior to reproduction, which allows all hatchlings to reach reproductive size before their third season (Fig. 1).

**Material and Methods**

Prairie lizards and sagebrush lizard females were collected over a 2-yr period (1972–1973) from Reno County, Kansas and Washington County, Utah, respectively. When possible 10 individuals of each species were collected after hibernation, during the vitellogenic and gravid periods of each clutch of eggs, and about 1 mo after reproduction had ceased. These collection periods were based on observed lipid cycling patterns in other lizard species, such as *Anolis carolinensis* (Dessauer 1955).

**Field samples**

Seventy-eight prairie lizards and 88 sagebrush lizards were collected in the field and kept cool until transferred to the laboratory, where they were quick-frozen immediately and analyzed at a later date for total lipids (simple and complex). The carcass (minus viscera) and eggs of each lizard were weighed and dried to a minimal and constant weight in a thermal vacuum oven at 40°C and 30 psi (Horwitz et al. 1970). Each part was then homogenized in 2:1 vol/vol chloroform-methanol solution in a tissue homogenizer and the homogenates treated according to the Folch method (Folch et al. 1957). Weight of total lipids for each depot were recorded as a percentage of the lean (no lipids) dry body weight (LDBW) to correct for variations in body size. Preliminary studies indicated that complex lipids, those generally not available as storage lipids, represented < 10% of the total lipids. A similar figure for complex lipids was found in *Sceloporus jarrovi* by Hadley and Christie (1974). Since complex lipids represent such a small percentage of the total lipids, no attempt was made to exclude these lipids. Accordingly, all figures are slight overestimates of storage lipids in both species.

Rates of lipid utilization were calculated for both species from field samples by comparing lipid levels in lizards that had come out of hibernation with those ready to lay their first clutch (gravid-initial clutch). Individual lipid levels (mg/g LDBW) of the initial gravid sample was subtracted from the mean lipid level of the posthibernation lizards and this figure was divided by the number of days between these two samples. The same method was used to calculate rates of lipid deposition; only the mean lipid level of the final gravid sample was subtracted from individual lipid levels in the postreproductive sample.

**Experimental studies**

An additional 15 females of each species were collected in 1973 just after the lizards had finished laying their last clutch of eggs (mid-July for both species). Three lizards from each species were analyzed for total lipids to determine initial lipid levels. The remaining lizards of both species were placed in animal cages under similar moisture (watered every other day) and photoperiod regimes (14L:10D) and were studied simultaneously to determine rates of lipid deposition when fed and utilization when starved. An infrared lamp was placed in one corner of the cage to allow the lizards to thermoregulate. Each female was fed a surplus weight of crickets every other day. Feces, urates, and remaining crickets were removed and weighed before the next feeding. Feces and urates were frozen to prevent bacterial decomposition until they could be analyzed for energy content. When the lizards had gained 10% of their body weight, six were sacrificed and analyzed for total lipids as described above, to determine rates of lipid deposition for each species. Remaining lizards were starved until they had lost 10% of their body weight, then analyzed to determine rates of lipid utilization. By knowing the initial lipid levels (mg/g LDBW) and the number of days required to gain or lose 10% of the body weight, rates of lipid deposition and utilization could be calculated. The initial lipid level for the fattening study was determined from the initial sample of lizards mentioned above, while the initial level for the starvation study was the lipid level of the lizards that had gained 10% of their...
body weight. In both cases initial values were computed as means and the difference between these mean values and each starved or fattened lizard was determined. This calculation yielded the number of milligrams of lipid per gram LDBW gained or lost, which was then divided by the appropriate number of days to yield rates of deposition and utilization for the two species.

Calorimetry

Both feces and urates collected during the fattening study and crickets and oviducal eggs from the different clutches, were placed in a drying oven at 60°C and dried to a minimal and constant weight. Some fecal and urate pellets, crickets, and oviducal eggs were then placed in a muffle furnace at 500°C for 4 h to measure ash content. Remaining dried feces, urates, crickets, and oviducal eggs were analyzed for caloric value using a Parr Semi-micro Oxygen Bomb Calorimeter (Model 1411)\(^*\) according to techniques described in Paine (1971). All caloric values were corrected for ash. From these data it was possible to calculate calories per clutch of eggs, calories per egg, ingested and egested energy. Calories per clutch was considered the major proportion of energy expended on reproduction since lizards exhibit no parental care. The percentages of ingested energy available for metabolism (ME) and assimilation efficiency (AE) were calculated using the formulae,

\[
ME = IE - (FE + NE) / IE \times 100
\]

\[
AE = IE - FE / IE \times 100,
\]

where IE is ingested calories, FE is fecal calories, and NE is nitrogenous waste calories. It was also possible to calculate what percentage of the ME was being stored as lipids since the ME and fattening studies were run concurrently. This was done by converting the lipid increases in the fattening study to caloric values (a gram of lipid is \(\approx 38\) kJ, or 9 kcal), dividing this figure by the amount of ingested energy available for metabolism, and multiplying by 100.

Statistical analyses

Least squares analysis of variance was used to compare lipid levels, calories per clutch, calories per egg, eggs per clutch, ME, AE, and the proportion of the energy available for metabolism that was converted to lipids. Rates of lipid deposition and utilization represented deviations from the mean value of the initial samples and these deviations were also compared using least squares analysis of variance. Regression analyses were used to assess relationships between any of the above parameters and LDBW. If relationships existed regression lines were compared both within and between species to determine statistically significant differences. Chow’s (1960) technique was used to compare residual sums of squares of the individual regressions with that of the data combined into a single regression line. If weight was correlated with a given parameter in both species, this parameter was expressed on a per gram basis from the regression equations. If no relationship existed between LDBW and a given parameter in either species, the raw data were compared. The rationale for seeking a relationship between LDBW and each of the above parameters was based on observed relationship of clutch size and body weight in a number of lizard species.

Evidence for the assumption that food level differences exist between prairie lizards and sagebrush lizards

In order to provide some support for this assumption the following comparisons were made: (1) precipitation levels in the two study areas over the past 30 years using U.S. Weather Bureau data; and (2) mouthgape (head length \(\times\) mouth width) vs. snout-vent length for the two species. Insect biomass is correlated with precipitation (Janzen and Schoener 1968) and mouthgape with prey sizes utilized (Schoener 1968). At low food levels a species should use a wider array of prey sizes.

RESULTS

Hypothesis 1

This hypothesis stated that \(r\)-selected lizard species (prairie lizards) should have higher lipid levels prior to and after hibernation than \(K\)-selected lizard species (sagebrush lizards). My results support this hypothesis (Fig 2A). Total body lipids per gram LDBW, pooled over the two collection years, were higher prior to and after hibernation in prairie lizards than in sagebrush lizards.

In prairie lizards, minimal lipid levels reached during production of the middle clutch were lower than in sagebrush lizards. In sagebrush lizards, lipid levels were minimal during production of the final clutch. Neither species apparently depleted their storage lipids since minimal levels (6%–7% of LDBW) were higher than polar lipid levels (2% of LDBW). However, prairie lizards utilized more of their stored lipids during reproduction than sagebrush lizards.

Lipid levels changed more in prairie lizards than in sagebrush lizards during egg production. The loss of lipids from posthibernation to the initial gravid sample was approximately 200 mg/g LDBW in prairie lizards \(versus\) about 60 mg/g LDBW in sagebrush lizards. Simultaneously, there was an increase of about 210 and 220 mg of lipids in the eggs of...
FIG. 2. Seasonal variation of mean lipid levels (per gram lean dry body weight, LDBW) in Kansas northern prairie lizards (open bars) and Utah northern sagebrush lizards (solid bars). Samples are posthibernation (PH), vitellogenesis (V), gravid-initial clutch (01), gravid-middle or initial clutch (02), gravid-final clutch (03). Horizontal bars represent the means; vertical lines the ranges; and vertical bars one standard error. Numbers above bars indicate sample sizes. (A) total body lipids; and (B) egg lipids.

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prairie lizards and sagebrush lizards, respectively (Fig. 2B). The relationship between body lipids lost and egg lipids gained in both species is expanded upon in Fig. 3. Body lipid loss was equivalent to egg lipid gain in prairie lizards, while egg lipid gain far surpassed body lipid loss in sagebrush lizards.

Presumably, sagebrush lizards had to rely more on other sources of energy (i.e., ingested) to produce egg lipids than did prairie lizards. In fact, some prairie lizards had 30,125 J (7,200 cal) in stored lipids which seems more than enough to produce an initial clutch of eggs with a mean energy value of 22,175 J (5,300 cal). In sagebrush lizards maximum lipid levels were equivalent to 15,062 J (3,600 cal), less than a 21,338 J (5,100 cal) clutch of eggs.

Table 1 further emphasizes that sagebrush lizards had to rely more heavily on external sources of

| TABLE 1. Mean rates of body lipid loss (negative value) or gain and mean rate of egg lipid deposition in field and laboratory samples of Kansas prairie lizards (PL) and Utah sagebrush lizards (SL). LDBW = Lean Dry Body Weight; * = 0.05 level of significance; ** = 0.01 level of significance; NS = not significant |
|---------------------------------------------------------------|-----------------|-----------------|
| Period of lipid loss in field                                      | Body (mg/g LDBW · day) | Eggs (mg/g LDBW · day) |
| Posthibernation to gravid-initial clutch                          | PL | −4.5 | 4.0 | **
|                                                               | SL | −0.6 | None |
| Period of lipid gain in the field                                 | Gravid-second clutch to postreproduction | PL | 2.3 | None |
|                                                               | SL | 2.3 | None |
| Laboratory samples                                               | Starvation experiment | PL | −17.0 | None |
|                                                               | SL | −6.5 | None |
| Fattening experiment                                             | PL | 3.2 | None |
|                                                               | SL | 3.6 | None |
TABLE 2. Mean assimilation efficiency (AE), percent of ingested energy available for metabolism (ME), and percent of ingested energy available for metabolism stored as lipids (SF) in Kansas prairie lizards and Utah sagebrush lizards during fattening experiments. * = 0.05 level of significance

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<th>Sagebrush lizards</th>
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<tr>
<td>ME</td>
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<td>76.17%</td>
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<tr>
<td>SF</td>
<td>n = 4</td>
<td>12.51%</td>
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energy than prairie lizards for egg production. The rate of body loss (in milligrams per gram LDBW) exceeded the rate of egg lipid deposition in prairie lizards. In sagebrush lizards the rate of body lipid loss was < 10% of the rate of egg lipid deposition.

**Hypothesis 2**

Based on this hypothesis, r-selected lizard species (prairie lizards) should have higher rates of lipid utilization than K-selected lizard species (sagebrush lizards) during starvation. Data from the starvation study supported this hypothesis (Table 1). The rate of lipid utilization was almost three times greater in prairie lizards than in sagebrush lizards. This difference suggests that sagebrush lizards were better adapted to conserve lipids at lower food levels than prairie lizards.

There was no significant difference between the two species in the rate of lipid deposition in either field or experimental samples, although rates of deposition were higher in the laboratory than in the field. This suggests that food is not unlimited for either species in the field. Since both species have roughly the same amount of time to store lipids prior to hibernation there is no reason to suspect differences in rates of lipid deposition between the two species.

**Hypothesis 3**

According to the third hypothesis, prairie lizards should have a lower percentage of ingested energy available for metabolism than sagebrush lizards. Both assimilation efficiency and percentage of ingested energy available for metabolism were higher in sagebrush lizards (Table 2). Not only were sagebrush lizards absorbing more of the ingested energy across the intestine, but a higher percentage of this assimilated energy was retained and not lost as nitrogenous waste (urates). This higher assimilation efficiency and percentage of ingested energy available for metabolism suggests that sagebrush lizards are better adapted for lower food levels than prairie lizards.

**Hypothesis 4**

This hypothesis stated that sagebrush lizards should expend more energy per offspring than prairie lizards. Regression equations of calories per clutch versus LDBW were significant for both species (Fig. 4). However, regression lines did not differ significantly (Table 3). Therefore, lizards of both species put about the same number of calories into eggs per clutch. The regression of number of eggs per clutch versus LDBW also was significant for both species (Fig. 5). Regression lines did differ significantly between species. A prairie lizard produced significantly more eggs per clutch than an equivalent-sized sagebrush lizard (Table 3). Since the number...
of calories per clutch was the same for both species and the number of eggs per clutch was different for the two species, calories per egg should and did differ (Table 3).

In both species the calories per egg increased with successive clutches. Thus more energy was expended on offspring in later clutches. Egg quality (calories per gram of eggs) also increased seasonally in both species, but did not differ between species.

The number of calories per clutch per gram LDBW and egg calories per body calories provide estimates of the cost per clutch of reproduction to the parent (Table 3). While the cost per clutch was about the same for both species, prairie lizards produced three clutches versus two for sagebrush lizards. Thus, prairie lizards put considerably more energy into eggs than sagebrush lizards each season (Table 4). This additional expenditure of energy on egg production by prairie lizards resulted in nonlipid tissue loss (Fig. 6A). Comparing the regressions of LDBW versus snout-vent length for posthibernation and gravid-final clutch samples in both species revealed the prairie lizards lost more nonlipid tissue during reproduction than sagebrush lizards (Fig. 6B). If there is no net nonlipid catabolism, neither the slopes nor the elevations of these lines should change throughout the season, since lean dry body weights were used. Therefore, any decrease in slope or elevation represents nonlipid tissue loss. The greater nonlipid tissue loss in prairie lizards may render this species more vulnerable to predation or harsh climatic conditions, which would in part explain the shorter

<table>
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<th>Parameters</th>
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Assumption

The higher precipitation levels in Kansas than in Utah (Fig. 7) suggests that potentially more food was available to the $r$-selected lizard species (prairie lizard) than the $K$-selected lizard species (sagebrush lizard). Sagebrush lizards also had a larger mouthgape than equivalent-sized prairie lizards suggesting that they were able to utilize a wider array of prey sizes than prairie lizards (Fig. 8).

**DISCUSSION**

The results of this study suggest general models to explain observed differences in patterns of lipid storage and utilization of various lizard species. Specifically, the $r$-selected lizard (prairie lizards) stored more lipids than the $K$-selected lizard (sagebrush lizards). Greater lipid stores resulted in more lipids being available after hibernation in the $r$-selected species, and these were apparently used in the production of the first clutch of eggs. Because of the lack of total dependence on ingested food to produce the first clutch of eggs, the $r$-selected species is able to start reproducing earlier in the season which resulted in a higher reproductive effort. This higher reproductive effort appeared to have a negative feedback on lifespan. Lower lipid levels in the $K$-selected lizard species resulted in this species being more dependent on ingested energy for egg production. Egg laying occurred later in the season and fewer clutches were laid. This lower reproductive effort had less of a negative feedback on life span than in the $r$-selected species. The $r$-selected species also had a higher rate of lipid utilization when starved, a lower percentage of ingested energy available for metabolism, and expended less energy per offspring than the $K$-selected lizard species. To test the generality of these findings, lipid storage and usage, rates of lipid...
utilization, percentage of ingested energy available for metabolism, and energy expended per offspring in other lizards will be examined.

**Supporting evidence from studies on other lizard species**

It is difficult to compare lipid usage data available on other lizard species with data in the present study. Most of the data available on lipid usage is anecdotal, and does not look at all potentially available lipids, or at seasonal cycling of lipids. However, some data support my hypothesis that lizards with r-strategist characteristics may have more lipids available for reproduction. Based on limited data, Parker and Pianka (1973) observed no correlation between reproductive activity and fatbody length/snout-vent length in female *Sceloporus magister*. They indicated that this species requires at least 2 yr to reach maturity, produces 1–2 clutches/season, and is probably long-lived (K-strategist). Hahn and Tinkle (1965) and Telford (1970) found a significant decrease in fatbody lipids during reproduction in female *Uta stansburiana* and *Takydromus tachydromoides*, respectively. According to Tinkle (1969) and Tinkle et al. (1970), these two species are short-lived, mature early, and have a high reproductive effort (r-strategists). Based on seasonal cycling of carcass, fatbody, and liver lipids in female *Cnemidophorus tigris*, Gaffney and Fitzpatrick (1973) estimated that >3,000 calories of lipid go into egg production, as compared to 1,500 calories for hibernation. These authors collected their *C. tigris* from western Texas, where they mature in 1 yr and produce two clutches/season (r-strategist; Tinkle 1969). Female *Ameiva festiva* and *A. quadrilineata* (Smith 1968) and *Cnemidophorus sexlineatus* (Hoddenbach 1966) also showed decreases in fatbody size during reproduction. These three species can be classified as r-strategists (Tinkle 1969, Tinkle et al. 1970). Licht and Gorman (1970), Ruizal et al. (1972), and Gorman and Licht (1975) found an inverse relationship between reproductive activity and fatbody size in a number of tropical anoles. Those species that reproduced throughout the year either had no fatbodies or very small ones, while those that exhibited reproductive cycles had large fatbodies during the nonreproductive phase (dry season) and lacked fatbodies while reproducing (wet season). Licht (1974) also found that fatbodies in *Anolis cristatellus* would increase during reproduction via supplemental feeding in the field. Apparently, egg production and deposition in many of these anoles creates too much of an energy demand to allow lipid storage from available food. All of the anoles studied by these authors could be classified as r-strategists.

*Anolis carolinensis* (an r-strategist; Tinkle 1969, Tinkle et al. 1970) may be an exception to the hypothesis that r-strategists use lipids primarily for reproduction. According to Dessauer (1955), this species is active most of the year in New Orleans, but only reproduces from April to August. During the months of November and December they are inactive and lipid levels decreased markedly during this period of time. Mean air temperature (and presumably body temperature) in these 2 months is relatively high (15°C) which may account for utilization of large amounts of lipids. A higher hibernation temperature than that of the other lizards mentioned above would result in greater metabolic demands and hence greater utilization of lipid. Dessauer (1955) also stated that *A. carolinensis* feeds little if at all during November and December. Lack of feeding activity plus high winter body temperature may impose a heavy drain on lipid reserves so that lipid levels are too low to use for reproduction in the spring.

Little or no data from the literature support my results on rates of lipid utilization, percentage of in-

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**Fig. 8.** Mouthgape (head length x mouth width) versus snout-vent length in Kansas prairie lizards ( - ) and Utah sagebrush lizards ( - - - - ). Both regressions were significant at the 0.01 level. Comparisons between regression lines were also significantly different at the 0.01 level.
gested energy available for metabolism (ME), and energy expended per offspring. This is the only study of rates of lipid utilization in lizards, so more empirical data on a number of species are needed to determine whether a low rate of lipid utilization is common to K-strategists. Some comparative data are available on assimilation efficiencies and ME, but it is difficult to draw conclusions from these. Mueller (1970) found a ME of 83% for the sagebrush lizard which is consistent with my results (82%). He also found a ME of 83% for Sceloporus occidentalis. This lizard requires 2 yr to reach maturity; however, it is intermediate to sagebrush lizards and prairie lizards regarding lifespan and clutch number (Tinkle 1969, Tinkle et al. 1970, Goldberg 1973). It is difficult to predict whether S. occidentalis should have a high or low ME. Mueller (1970) felt a ME of 83% was an overestimate, because S. occidentalis was studied much of the time at body temperature below the optimum for this species. Sagebrush lizards, however, were studied at their optimum temperatures. If there is an inverse relationship between temperature and ME, S. occidentalis should have a lower ME than sagebrush lizards. However, it is still difficult to categorize S. occidentalis as a r- or K-strategist.

Avery (1971) found that the lizard Lacerta vivipara, a viviparous K-strategist with delayed maturity and low reproductive effort (Tinkle et al. 1970), had an assimilation efficiency (AE) of 89%. In the present study, the sagebrush lizard had an AE of 90%. Finally, Johnson (1966) assumed an AE of 67% for S. undulatus, S. magister, and C. tigris when he measured the number of calories of energy assimilated per gram per day. However, these efficiencies are probably not accurate since my study shows variation in ME between species, and both my data and Pough’s (1973) indicate that an AE of 67% is low for insectivorous lizards. Most insectivorous lizards have high efficiency percentages (from the low 70s to > 80), which may be due to the relatively high energy value of insects, 5,400 calories/g (Golley 1961).

Although data on calories per egg are generally lacking, egg weight data for S. undulatus support my findings on energy expenditure per offspring. Tinkle and Ballinger (1972) calculated egg weights for four populations of S. undulatus and found that, generally, longer-lived populations produced heavier eggs than shorter-lived populations. In Texas S. undulatus matured in < 1 yr, produced about 27 eggs/season, and each egg weighed 0.22 g. Conversely, Colorado S. undulatus matured in ~ 2 yr, produced about 16 eggs/season, and each egg weighed 0.45 g. Ballinger and Clark (1973) showed that relative clutch weight is a good estimator of relative calories per clutch. From Ballinger and Clark (1973) and Tinkle and Ballinger (1972) one can conclude that Colorado S. undulatus are putting more energy into each egg than Texas lizards. In fact, if one uses the caloric and percent water content values estimated by Ballinger and Clark for S. undulatus eggs (6,195 calories/g of egg and 54%), calories per egg can be estimated for each of the S. undulatus populations studied by Tinkle and Ballinger. Such calculations yield an estimate of 1,168 calories/egg for Colorado lizards and 612 calories/egg for Texas lizards. These figures are surprisingly close to those found for sagebrush lizards and, prairie lizards respectively, in the present study.

Data from Tinkle and Hadley (1975) support my conclusion that the higher reproductive effort by prairie lizards results in a shorter lifespan. These authors examined a number of demographic variables and measures of reproductive effort in 11 lizard species and found that the only significant correlation was an inverse relationship between clutch calories/body calories and annual adult survivorship. Interestingly no correlation was noted for clutch weight/body weight, frequently used as an index of reproductive effort, and annual adult survivorship. As seen in Table 4 the clutch calories/body calories index was 2.53 and 1.45 for prairie lizards and sagebrush lizards, respectively. Based on Tinkle and Hadley (1975), prairie lizards would be expected to have the lower annual adult survivorship that it does. A comparison of this index with reproductive energy/total energy budget in these authors’ study indicates that clutch calories/body calories may not be a good index of reproductive effort. For example, while U. stansburiana had a clutch calories/body calories index of 2.54 the calculated reproductive energy/total energy budget was 19%. In S. graciosus, on the other hand, these values were 1.45 and 24%, respectively. This discrepancy is readily resolved when looking at differences in age-at-maturity. Uta stansburiana is essentially an annual species and does everything (matures, reproduces, and dies) in ~ 1 yr, while S. graciosus requires 2 yr to reach maturity. Therefore, for the comparisons to be meaningful, total energy budgets of U. stansburiana and S. graciosus would have to be weighted to account for this difference. This weighting should indicate that clutch calories/body calories is a reasonable index of reproductive effort.

In summary, evidence in the literature parallels the findings of this study. There are correlations of reproductive strategies with lipid levels, percentage of ingested energy available for metabolism, and energy expended per offspring. Higher posthibernation lipid levels are correlated with higher reproductive effort, while percentage of ingested energy available for
metabolism and energy expended per offspring are inversely related to reproductive effort.

More energy per egg and fitness

Based on demographic data on prairie lizards (Ferguson and Bohlen 1976) and sagebrush lizards (Tinkle 1973) and my data on egg energy values, I conclude that higher energy content per egg results in large hatchlings with higher survivorship. Tinkle and Ballinger (1972) indicated that survivorship of offspring from larger eggs (greater energy) was higher. Fourteen percent of Colorado S. undulatus hatchlings survive to the next spring compared to 5% for Texas hatchlings. In sagebrush lizards first clutch (4,431 J, or 1,059 cal/egg) hatchlings were larger (x snout-vent length = 26 mm) than first clutch (2,833 J, or 677 cal/egg) hatchling prairie lizards (x snout-vent length = 23 mm). As mentioned earlier, this larger size in sagebrush lizards is adaptive for using a wider array of food items at lower food levels.

That selection is favoring larger size for lower food levels is further supported by comparing successive clutches of prairie lizards. The mean number of joules (or calories)/egg was 2,833 (677), 3,071 (734), and 3,573 (854) for the first, second, and third clutches, respectively. This suggests that the hatchlings from these clutches should differ in size. Indeed, hatchlings from the first clutch were significantly smaller than those from the third clutch, 22.8 and 24.1 mm (Table 3). If food is critical at all for prairie lizard hatchlings it should be when the last clutch is hatching, late August to early September. During this period hatchling density is highest and insect productivity should be declining which should result in less food per individual.

Even within a given clutch larger-sized prairie lizard hatchlings can be shown to have a survival advantage to the next spring. Ferguson and Bohlen (1976) found that third clutch hatchlings with a snout-vent length > 24 mm had a significantly higher survivorship than those ≤ 24 mm (43% and 21%, respectively). He found no significant difference in survivorship for different-sized hatchlings of the first clutch. These data suggest that larger hatchling size is less important in the first clutch than in the third clutch. Besides the advantage to larger hatchlings of using a wider array of food, larger size confers a dominance advantage during social contests which could be related to food territories (Rand 1967).

Comparable data are not available on sagebrush lizards. However, since joules (calories) per egg are significantly higher in the second clutch than in the first, 5,832 (1,394) and 4,431 (1,059), respectively, the above data would suggest that second clutch hatchlings are larger than first clutch hatchlings. If hatchlings from both clutches are competing for food in sagebrush lizards, then survivorship should be higher for the larger hatchlings in both clutches.

Evidence for food competition

A basic assumption underlying the hypotheses tested in this study was that differences in the degree of competition for food existed between the two species. Additionally, it was assumed that the offspring of each species were exposed to the same degree of competition for food as the adults. Although no attempt was made to look at food levels in the field, data on precipitation levels in the two study areas and mouthgapes for both species suggest that these may be valid assumptions.

Analysis of weather data over the past 30 yr for the two study areas, indicates that precipitation levels are predictably lower in Utah than in Kansas (Fig. 7). Janzen and Schoener (1968) showed that insect productivity increases with precipitation levels. Higher precipitation levels, typically, resulted in greater insect diversity and abundance. Therefore, a lower precipitation level suggests that there should lower food in Utah. Interestingly, there is a greater density, 208/ha, of sagebrush lizards (Tinkle 1973) than prairie lizards, 42/ha (Ferguson and Bohlen 1973). Less potential food and a greater density of lizards strongly suggest that there was less food per individual for sagebrush lizards than for prairie lizards with their low density and more potential food. Mid-July until late October should be a critical time for both the parents and offspring of the two species, since during this time they grow and store lipids for hibernation. Mean precipitation levels at this time are 8.71 cm and 2.79 cm for Kansas and Utah, respectively. Lower precipitation levels should result in less food being available for sagebrush lizard adults and offspring. In sagebrush lizards, low adult mortality during the breeding season results in large numbers of adults surviving (65/ha) during, at least, the early part of the mid-July to October period to compete with offspring for food. High adult mortality in prairie lizards during the breeding season results in fewer adults (22/ha) to compete with offspring. Data from Sexton et al. (1972) and Parker and Pianka (1973) suggested that there is a great deal of overlap in food resources of adult and offspring lizards. Competition among the adults and offspring may further reduce the amount of food available to sagebrush lizard offspring, although this may be mitigated by the juveniles utilizing smaller prey due to their smaller mouths. Differences in precipitation levels and adult mortality during the breeding season, therefore, may result in differences in food availability for the two species after reproduction has ceased.
Additional data suggesting food competition was greater for sagebrush lizards were mouthgape and snout-vent length relationships for the two species (Fig. 8). Regression lines showed that given a prairie lizard and a sagebrush lizard of equal size, the latter had a larger mouth. Schoener (1968) found that average prey size and variance of prey size increased with head length in Bimini anoles. Presumably, longer heads resulted in larger mouths in anoles. Since sagebrush lizards had a larger mouthgape than prairie lizards they should be able to utilize not only larger prey but also a wider range of prey sizes. Species that are food limited should be generalists in their food habits (Emlen 1973). The capacity to handle a wider array of prey sizes suggests that sagebrush lizards may be less specialized in their food habits than prairie lizards.

Finally, Licht (1974) suggested that differences in lipid levels are indicative of different food availabilities. Licht was able to increase lipid levels in Puerto Rican anoles by supplemental feeding in the field. Lizards that were not given additional food in the field had much lower lipid levels, suggesting that a limited amount of food is available. My own laboratory experiments (Table 2) demonstrated that with ad libitum feeding, both species deposit lipids faster than field animals. Also, the discrepancy between lipid deposition rates in the field and laboratory were greater in sagebrush lizards (1.3 mg/g LDBW · day) than in prairie lizards (0.9 mg/g LDBW · day). Therefore, these data suggest that a positive correlation exists between lipid levels and food availability and that prairie lizards may have more food available than sagebrush lizards.

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ADDITIONAL LITERATURE CITED


