Capital Breeding and Allocation to Life-History Demands Are Highly Plastic in Lizards

Robin W. Warne,* Casey A. Gilman,[†] David A. Garcia, and Blair O. Wolf

Biology Department, University of New Mexico, Albuquerque, New Mexico 87131

ABSTRACT: The use of stored resources to fuel reproduction, growth, and self-maintenance in the face of uncertain nutrient availability is a tactic common to many organisms. The degree to which organisms rely on stored resources in response to varied nutrients, however, is not well quantified. In this study, we used stable isotope methods to quantify the use of stored versus incoming nutrients to fuel growth and egg and fat body development in lizards under differing nutrient regimes. We found that the degree of capital breeding is a function of an individual's body condition. Furthermore, given sufficient income, lizards in poor condition can allocate simultaneously to storage, growth, and reproduction and "catch up" in body size and reproductive allocation to better-conditioned animals. Using natural variation in the $\delta^{13}C$ of environmental nutrient pulses, we also found a high degree of variation in capital breeding in a lizard community. These findings demonstrate that capital breeding in lizards is not simply a one-way flow of endogenous stores to eggs but is a function of the condition state of individuals and seasonal nutrient availability. We use our findings to comment on capital breeding in lizards and the utility of the capital-income concept in general.

Keywords: resource allocation, capital and income breeding, lizards, stable isotopes, $\delta^{13}C$.

Introduction

To fuel the competing demands of reproduction, growth, and maintenance, organisms often depend on environmental resources that can vary widely in availability and nutritional quality. A growing body of literature has demonstrated that the storage of energy and nutrients is an integral component of many organisms' strategies to balance these nutrient demands with environmental variation (Derickson 1976b; Perrin and Sibly 1993; Reznick and Yang 1993; Doughty and Shine 1998; Houston and McNamara 1999). For example, through the use of stored resources an animal can allocate nutrients to reproduction at a time when food is scarce but when the potential fitness of its offspring is high (Hahn and Tinkle 1965; Derickson 1976b; Reznick and Braun 1987; Bonnet et al. 1998; Doughty and Shine 1998). While it is clear that adjustment in allocation to reproduction, growth, and maintenance is an integrated response to variation in nutrient availability, the degree to which individuals within a species can vary their use of stored resources to balance these demands with environmental variation remains poorly understood.

In this study, we investigate the extent to which lizards use stored lipids and protein to fuel reproduction and growth in the face of environmental variation. Lizards have been a model organism for studies of resource allocation and life-history trade-offs for decades. They stand in contrast to small endotherms, because their low-energy ectothermic lifestyle facilitates the storage and retention of nutrients over periods of months to years. This trait allows for the accumulation of nutrients during periods of resource abundance and their later use for breeding when resources may be locally scarce (Bonnet et al. 1998). A number of researchers have found that resource availability affects the size of fat stores (Hahn and Tinkle 1965; Derickson 1976a; Doughty and Shine 1997), growth rates (Ballinger and Congdon 1980), and reproductive effort in lizards (Derickson 1976a; Ballinger 1977; Schwarzkopf 1993; Doughty and Shine 1997, 1998). These researchers have documented both seasonal changes in abdominal or caudal fat stores (Derickson 1976b) and shown an inverse relationship between the size of fat stores, muscle condition, and reproductive tissues (i.e., egg and testes development) in many temperate-zone reptiles (Derickson 1976b; Doughty and Shine 1998). Several studies have also directly manipulated fat stores and have shown that while the removal of fat bodies delay and even inhibit follicular growth (Hahn and Tinkle 1965), an increase in fat storage can translate into greater clutch sizes (Doughty and Shine 1998). While these studies demonstrated the strong effects that variation in endogenous stores have on first-clutch provisioning, a recent study by Warner et al. (2008) demonstrated that nutrient stores can be used to provision multiple clutches during a breeding season

* Corresponding author. Present address: Zoology Department, Southern Illinois University, Carbondale, Illinois 62901; e-mail: rwarne@siu.edu.
[†] Present address: Morrill Science Center III, University of Massachusetts, Amherst, Massachusetts 01003.

given sufficient resource abundance. Taken together, these studies demonstrate that nutrient storage is important or perhaps even critical to successful reproduction in squamate reptiles. However, the degree to which lizards can alter their allocation tactics among storage, reproduction, or growth in response to variation in resource availability remains unclear.

Allocation of stored resources to reproduction in response to environmental variation may also covary with longevity (Derickson 1976*a*; Perrin and Sibly 1993; Schwarzkopf 1993; Doughty and Shine 1998). Small, short-lived species generally show high reproductive effort in a given breeding season and produce multiple (2–3) clutches of eggs (Dunham et al. 1988). Short-lived lizards also respond quickly to short-term environmental variation by readily varying clutch size and number within a season (Tinkle 1961; Ballinger 1977; Svensson et al. 2002). Furthermore, because the fitness of offspring is higher in eggs hatched early in a season relative to later hatching clutches (Ferguson and Fox 1984; Sinervo and Doughty 1996), lizards that lay multiple clutches in a season are likely to benefit from using nutrient stores to quickly provision the first clutch of eggs (Hahn and Tinkle 1965). Longer-lived species, with lower annual reproductive effort, appear to make more modest adjustments to reproductive output in order to balance nutrient allocation over a period of one or more years (Schwarzkopf 1993; Doughty and Shine 1998; Tracy 1999; Jordan and Snell 2002). Some researchers have argued (Derickson 1976*a*; Doughty and Shine 1998) that longer-lived species may conserve a greater proportion of their nutrient stores to ensure survival and future reproduction. These findings suggest that an interspecific survey of lizards from the same ecosystem could provide insight into the degree to which capital breeding—the use of stored resources for reproduction—varies with life history.

In this study, we used stable carbon isotopes as tracers to quantify the relative allocation of resources derived from either stored endogenous sources (capital) or recent dietary sources (income) to reproduction and growth in lizards. The use of stable carbon isotopes ($\delta^{13}C$) as tracers of nutrient flow is a proven method for inferring the origin and estimating the allocation of nutrient resources in animals (O'Brien et al. 2000; Gauthier et al. 2003; Warner et al. 2008; Warne et al. 2010*b*) and across ecological compartments (Fry et al. 1978; Warne et al. 2010*a*). We combined a laboratory experiment using the prairie lizard (*Sceloporus undulatus consobrinus*), a moderately lived, medium-sized species, with a field survey of seven species of wild-caught lizards to explore the interactions between environmental variation, life-history tactics, and patterns of resource allocation. Specifically, our goals were to (1) quantify the variation in capital allocation by female lizards when provisioned with pre- and posthibernation diets that

varied in their total nutrient content; (2) examine whether such dietary conditions alter allocation patterns to storage, growth, and reproduction; and (3) survey whether several species with varied life histories allocate stored resources to reproduction in the wild.

Material and Methods

Lizard Capture and Maintenance

For measures of capital breeding in wild lizards, females of seven species were caught during April–July 2008 under the approval of the University of New Mexico Institutional Animal Care and Use Committee (UNM-IACUC 05MCC004). Lizards deemed by palpation to be egg bearing were returned to the lab and euthanized, and reproductive tissues were prepared for stable isotope analysis (see below). For the laboratory study, 32 female prairie lizards (*Sceloporus undulatus*) were caught on Bureau of Land Management reserves near Albuquerque, NM, during the last 2 weeks of July 2007 and maintained in a room at the biology department of the University of New Mexico under the approval of the UNM-IACUC (07UNM007). Two lizards were housed per 20-gal glass terrarium and were provided a sand substrate as well as perch and shelter spaces built with stacked pieces of plywood and rock. Lizards were kept on a 12L : 12D photoperiod, and a temperature gradient was provided by a 100-W heat lamp placed at one end of the terrarium and focused on the wood perch, providing a stable heat gradient that ranged from $39° \pm 1.7°C$ at the perch to $26° \pm 0.8°C$ at the cool end of the tank. Resulting mean daytime body temperatures were $36.3° \pm 6.2°C$ ($n = 18$). An ultraviolet-B fluorescent light (ZooMed UVB 10.0 fluorescent) was also provided for vitamin D synthesis.

Experimental Dietary Treatments and Reproduction

Sceloporus undulatus were captured from a cottonwood woodland field site, paired by snout-vent length (SVL), and then randomly split into either a high- ($n = 16$) or low-nutrient treatment ($n = 16$). The high-nutrient diet consisted of seven crickets and two mealworms per week, similar to an ad lib. diet found by Angilletta (2001). We estimated that a low-nutrient diet reduced by ~30% of ad lib. (five crickets/week and one mealworm every other week) would reduce body condition and reflect the poor conditions experienced by lizards in the wild (see Ballinger 1977, 1979; Ballinger and Congdon 1980; Sinervo and Adolph 1994). These low-diet lizards were switched to the high diet after hibernation, referred to hereafter as the LH treatment ($n = 16$). The high treatment before hibernation was split into a high diet posthibernation (HH, $n = 8$) and a low

treatment (HL, $n = 8$). We did not have an LL treatment because we assumed that they would be in such low body condition that they would not reproduce.

The lizards were prepared for hibernation during November 2007 by gradually reducing the photoperiod to 7L : 17D, and they were fasted for 2 weeks. Lizards were then placed in 27-L plastic containers with a sandy substrate and wood shavings for burrowing on November 17, 2007, and maintained at $10.2° \pm 3.1°C$. The lizards were removed from hibernation on February 2, 2008. To induce reproduction, male prairie lizards that were maintained for a separate study were introduced for 2 weeks to the female terrarium in mid-February of 2008. Reproduction was observed in numerous tanks (mounting and copulation), and signs of reproduction (bite marks) were apparent on all females. The female lizards were then palpated weekly to monitor egg development. When eggs appeared to be nearly shelled or shelled, the lizards were euthanized via an intraperitoneal injection of sodium pentobarbital (using a dose of 60 mg/kg). Two lizards were euthanized in late March following rapid development of shelled eggs. All other lizards were euthanized during the last week of May 2008, at which time most were found to have either large follicles or shelled eggs.

Stable Isotope Treatments

After the lizards were euthanized, liver, fat body, and thigh muscle samples were harvested and freeze-dried, and a 0.5-mg sample was placed into a precleaned tin capsule (Costech, 041074, Valencia, CA) for stable isotope analysis. Eggs and follicles were also harvested, their length and width were measured, and they were freeze-dried. All lipids were extracted from freeze-dried and ground muscle and eggs/follicles by a 2 : 1 chloroform and methanol bath; lizard muscle had undetectable amounts of lipids. The suspended lipids from eggs were pipetted into separate storage vials and air-dried. Lipids and lipid-free egg tissues were then loaded into tin capsules. We measured the $\delta^{13}C$ of each egg and follicle greater than 6 mm in length (one-half the length of shelled eggs and assumed to reflect reproductive allocation). Our stable isotope methodology follows standard methods, and our protocol is described in detail in Warne et al. (2010a, 2010b). We report all isotope values in the standard delta notation ($\delta X = (R_{sample}/R_{standard}-1) \times 1,000$) in parts per thousand relative to the international carbon standard VPDB (Vienna Pee Dee belemnite). Measurements were conducted on a continuous-flow isotope ratio mass spectrometer in the University of New Mexico Earth and Planetary Sciences Mass Spectrometry lab. The precision of these analyses was ± 0.1‰ SD for $\delta^{13}C$ based on long-term variation of the working laboratory standard (valine $\delta^{13}C = -26.3$‰

VPDB), samples of which were included on each run in order to make corrections to raw values obtained from the mass spectrometer.

Essential to this study is the observation that differences in photosynthetic biochemistry inherent to C_3 and C_4 plants produces distinct differences in the $\delta^{13}C$ of their tissues, which can be used to trace the movement of nutrients through consumers (Hobson et al. 1997; O'Brien et al. 2000). *Sceloporus undulatus* lizards were collected from cottonwood woodlands in which their diet was largely composed of C_3-plant-derived carbon, as evidenced by a baseline muscle $\delta^{13}C$ of -25.1‰ ± 0.1‰ VPDB, near that of the mean value for C_3 plants of -27.3‰ ± 0.04‰. Before hibernation, lizards were maintained on a diet composed of crickets (mean $\delta^{13}C \pm$ SEM for lipids $= -22.5$‰ ± 0.1‰ and lipid-free carbon $= -21.7$‰ ± 0.1‰ VPDB, $n = 16$) raised on C_3-plant-derived dog food (Nutro Natural Choice large-breed-puppy lamb and rice formula) and mealworms (lipids $= -26.3$‰ ± 0.1‰ and lipid-free $= -24.35$‰ ± 0.1‰ VPDB, $n = 8$) raised on bran meal. Here we used the mathematical normalization model of Post et al. (2007) to determine the lipid-free $\delta^{13}C$ values for these insects, assuming reported lipid contents of 13.8% for crickets and 32.8% for mealworms (Bernard and Allen 1997). Maintaining lizards on a C_3 diet before hibernation insured that their capital stores of fat bodies and muscle would have consistent carbon isotope values. After hibernation the lizards were switched to a C_4-based insect diet of crickets (lipids $= -16.3$‰ ± 0.1‰, and lipid-free $= -15.53$‰ ± 0.1‰ VPDB, $n = 35$) raised on a C_4-corn-based dog food (Iams Smart Puppy large-breed formula) and mealworms (lipids $= -13.0$‰ ± 0.3‰ and lipid-free $= -10.2$‰ ± 0.2‰ VPDB, $n = 9$) raised on coarse-ground cornmeal, which provided an "income" diet with $\delta^{13}C$ values distinct from the prehibernation C_3 diet.

We used tissue $\delta^{13}C$ values and a standard two-endpoint mixing model ($\delta^{13}C_{eggs} = p(\delta^{13}C_{fat}) + (1 - p) \times (\delta^{13}C_{insects}) + \Delta_{fat}$) to estimate the proportion of endogenous fat or muscle (capital) and incoming insect-dietary sources used to provision eggs. Because crickets and mealworms had different $\delta^{13}C$ values and the dietary treatments imposed on the lizards also consisted of differing quantities of feeder insects (high $= 7$ crickets $+ 2$ mealworms/week; low $= 5 + 0.5$/week), we used a weighted mean to calculate the insect $\delta^{13}C$ for each treatment in this model. The weighted $\delta^{13}C$ value for the high-dietary treatment for C_4 insect lipids was -15.6‰ and -14.3‰ for lipid-free carbon; for the low-treatment C_4 insect, lipids was -16‰ and lipid-free carbon was -15‰. The discrimination ($\Delta^{13}C$) values used in this model for muscle (-1.9‰) and fat bodies (0‰) were experimentally determined for *S. undulatus* (Warne et al. 2010b).

Statistical Analysis

The effect of dietary treatment on the body condition of lizards was analyzed by repeated-measures ANCOVA with treatment and stage of the experiment as fixed effects, individuals as random effects nested within treatment, and SVL as a covariate. Body condition was estimated as the least squares mean of body weight (minus eggs) adjusted for SVL in this ANCOVA model, a method argued to be more statistically sound than other condition indices (Packard and Boardman 1988; García-Berthou 2001). Treatment effects on SVL were similarly analyzed by repeated-measures ANOVA. Mauchly's test was used to confirm that the assumption of sphericity for repeated-measures analysis was valid, and ε corrections to the degrees of freedom were applied when necessary. Dietary treatment effects on growth were measured by the specific growth rate of SVL ($\ln(SVL_2/SVL_1)/\Delta$days) for the pre- and posthibernation periods and analyzed by one-way ANOVA. Dietary treatment effects on reproductive effort, measured as relative clutch mass (RCM = clutch mass/body mass with no eggs) and clutch size, were analyzed by one-way ANOVA. The effect of dietary treatment on tissue $\delta^{13}C$ values was similarly analyzed by one-way ANOVA. Post hoc comparisons of treatment effects during the four experimental stages were conducted using Tukey-Kramer's HSD test. Before all analyses, the data were tested for homogeneity of variance and confirmed to meet model assumptions. These analyses were performed in JMP 8.0 (SAS Institute, Cary, NC). All values are reported as mean $\pm$ SEM.

Results

Treatment Effects on Body Condition, Growth, and Reproduction

Dietary treatment had a statistically significant effect on *Sceloporus undulatus* body condition, estimated by ANCOVA of body weight with SVL as a covariate (fig. 1*A*; $F_{2,22} = 10.61$, $P < .001$). There was also a significant treatment × experimental stage interaction ($F_{5,70} = 3.23$, $P = .01$). Note that because Mauchly's test indicated that the assumption of sphericity had been violated ($\chi^2 = 34.4$, $P < .001$), the degrees of freedom were corrected using the Huynh-Feldt correction ($\varepsilon = 0.852$). Before and after hibernation, lizards from the LH treatment weighed 18% (2.5 ± 0.3 g) less than the high-food treatment lizards, for the same SVL, reflecting lower body condition (Tukey test, $P < .05$). The condition of lizards, however, did not differ at capture or after reproduction (Tukey test, $P > .05$). Although the treatments did not have a detectable effect on snout-vent lengths (fig. 1*B*; $F_{2,27} = 1.17$, $P = .33$) and SVL did not differ between the treatments within any stage of the study (Tukey test, $P > .05$), there was a statistically sig-
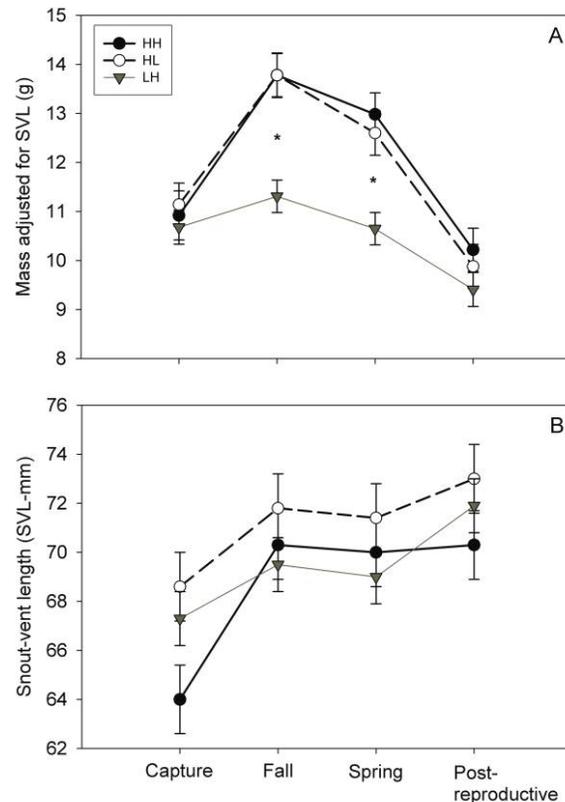

Figure 1: *A*, Treatment effects on body condition (least squares mean mass adjusted for snout-vent length [SVL] in ANCOVA) of *Sceloporus undulatus* at the experimental stages of initial capture, fall (before hibernation), spring, and after reproduction (at dissection). Symbols represent high (H)- and low (L)-nutrient diets imposed before and after hibernation for the treatments of HH (closed circles), HL (open circles), and LH (triangles). *B*, Change in SVL during the study. Asterisks denote a statistically significant treatment effect (Tukey test, $P \leq .05$).

nificant treatment × experimental stage interaction ($F_{6,81} = 5.47$, $P < .001$). This interaction term reflects treatment effects on growth rates during the pre- ($F_{2,26} = 6.91$, $P = .004$) and posthibernation periods ($F_{2,26} = 9.47$, $P = .001$). Before hibernation, the HH lizards grew at a specific growth rate of 0.8 ± 0.1/day, which is faster (Tukey test, $P < .05$) than the HL lizards that grew 0.4 ± 0.1/day or the LH lizards at 0.2 ± 0.1/day. Note that the HH lizards started at a smaller initial size and subsequently grew more rapidly than the HL lizards (fig. 1*B*). By contrast, during the posthibernation period (during reproduction), the LH lizards grew 0.5 ± 0.1/day, which was faster (Tukey test, $P < .05$) than the HH lizards at 0.2 ± 0.1/day and the low-diet HL lizards at 0.05 ± 0.1/day.

During hibernation, 2 of the 32 lizards from the low treatment died; both individuals were emaciated but

showed no signs of disease. During the reproductive period, 21 of the remaining 30 lizards produced shelled eggs or large follicles (>6 mm). Of the 14 lizards in the LH treatment, 4 produced eggs and 4 developed follicles. Of the 8 lizards in the HL treatment, 6 produced eggs, 2 developed follicles, and 1 female developed eggs nearly 2 months earlier (March 28) than the others. Of the 8 lizards in the HH treatment, 2 produced eggs, 6 produced follicles, and 1 also produced eggs 2 months earlier than the others. The 9 nonreproductive females, 3 from the HH and 6 from the LH treatments, either had no follicles or very small follicles (<3 mm). These nonreproductive females did not differ in body condition (ANOVA, $F_{1,27} = 1.42$, $P = .24$) or growth rates ($F_{3,56} = 1.15$, $P = .34$) from the reproductive lizards.

Considering only those lizards that produced shelled eggs, reproductive effort measured as relative clutch mass (RCM = clutch mass/body mass with no eggs) was influenced by dietary treatment, (fig. 2B; $F_{2,9} = 5.6$, $P = .02$). The LH lizards had a mean ($\pm$SEM) RCM of 0.26 $\pm$ 0.02 ($n = 4$), that was lower (Tukey test, $P < .05$) than that of the HH treatment (0.42 $\pm$ 0.03, $n = 2$), but not that of the HL treatment (0.33 $\pm$ 0.02, $n = 6$). Clutch size and clutch mass, however, were not influenced by treatment (clutch size, $F_{2,9} = 0.31$, $P = .74$; mass, $F_{2,9} = 1.61$, $P = .25$). The mean ($\pm$SEM) clutch size for the LH group was 9.5 $\pm$ 0.6 eggs with a total clutch wet mass of 2.7 $\pm$ 0.2 g, the HL clutch size was 9.8 $\pm$ 0.5 eggs with a clutch wet mass of 3.2 $\pm$ 0.2 grams, and the HH clutch size was 9 $\pm$ 1 eggs with a clutch wet mass of 3.1 $\pm$ 0.02 g.

Isotope Composition of Somatic and Egg Tissues

Diet treatment had a statistically significant effect on $\delta^{13}C$ of fat bodies (one-way ANOVA, $F_{2,12} = 21.66$, $P < .001$), liver ($F_{2,18} = 12.13$, $P < .001$), and muscle ($F_{2,18} = 13.2$, $P < .001$) of reproductive *S. undulatus* (fig. 2A). The LH group had more enriched or positive $\delta^{13}C$ tissue values (closer to C_4-income sources) relative to the high-dietary treatments that ranged from an enrichment of 4.4‰ $\pm$ 0.6‰ VPDB in fat bodies to 2.2‰ $\pm$ 0.4‰ VPDB in liver and 1.7‰ $\pm$ 0.3‰ VPDB in muscle (Tukey test $P < .05$). The $\delta^{13}C$ values of these tissues did not differ among the high (HH and HL) treatments (fig. 2A; Tukey test, $P > .05$).

Diet treatment also had a statistically significant effect on the $\delta^{13}C$ of egg lipids (fig. 2A; two-way ANOVA with treatment and egg status as fixed effects, $F_{4,16} = 18.41$, $P < .001$) and egg nonlipid carbon ($F_{4,15} = 17.32$, $P < .001$). The 2 lizards that developed eggs in March (2 mo earlier than all others) were analyzed separately (fig. 2A). Egg status (shelled eggs vs. follicles) did not influence the
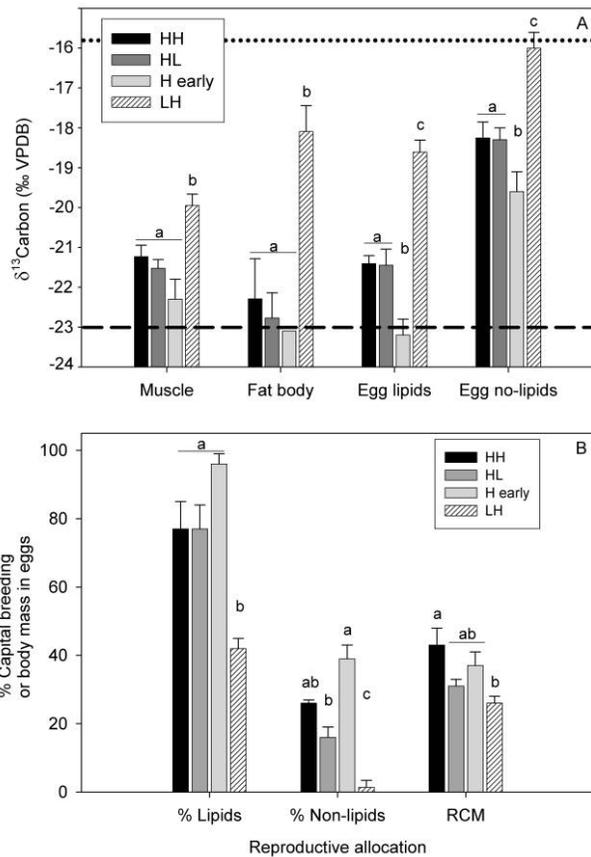

Figure 2: Allocation of dietary nutrients to endogenous storage and reproduction. *A*, Carbon isotope composition (mean $\delta^{13}C \pm$ SE‰ Vienna Pee Dee belemnite carbon standard) of somatic and egg tissues for experimental *Sceloporus undulatus* is shown ($n = 22$). The $\delta^{13}C$ values for the feeder insects are shown as horizontal lines; the C_3-fed insects (whole body = −23.2‰ $\pm$ 0.5‰) were given to the lizards in the fall for endogenous nutrients: capital storage (dashed line); and the C_4-fed insects (−15.8‰ $\pm$ 0.2‰) were provided in the spring for the income diet during reproduction (dotted line). *B*, Mixing model estimates of the degree of capital breeding in which fat body and muscle $\delta^{13}C$ values of individuals ($n = 22$) served as the capital source for allocation to egg lipids and nonlipid carbon, respectively, and the $\delta^{13}C$ value of C_4 feeder insects served as the income source. Relative clutch mass (RCM) for only those lizards with shelled eggs ($n = 12$) is also shown. Letters denote statistically significant treatment effects within each tissue (Tukey test, $P \leq .05$).

$\delta^{13}C$ of either egg component (lipid, $F_{1,16} = 0.05$, $P = .82$; nonlipid carbon, $F_{1,15} = 1.11$, $P = .31$). Egg and follicle $\delta^{13}C$ were thus combined in subsequent analyses. There was also little variation in $\delta^{13}C$ between eggs in any given clutch (SD ranged from 0.1‰ to 0.5‰ for lipids across all clutches; nonlipid carbon, 0.1‰–0.9‰). The LH group again had more enriched $\delta^{13}C$ values than the high-diet lizards for both egg lipids (fig. 2A; 2.7‰ $\pm$

0.4‰ VPDB; Tukey test, $P < .05$) and nonlipid carbon (2.2‰ ± 0.3‰ VPDB; Tukey test, $P < .05$). The two H_{early} reproducing lizards, in contrast, had egg $\delta^{13}C$ values that were much more depleted than those of lizards in the high-dietary treatments (fig. 2A; H_{early} lipids = −2.3‰ ± 0.7‰, and nonlipids = −1.7‰ ± 0.2‰; Tukey test, $P < .05$).

Capital versus Income Resource Allocation

Across all reproductive *S. undulatus* the $\delta^{13}C$ of egg lipids and fat bodies showed a positive correlation with a slope of 0.48 ± 0.08 (fig. 3A; $r^2 = 0.72$); muscle and nonlipid egg tissues also showed a positive correlation with a slope of 0.97 ± 0.19 (fig. 3B; $r^2 = 0.59$). Because the liver integrates dietary and stored nutrients to produce the egg yolk precursors and vitellogenin (Ho et al. 1982; Sheridan 1994; Barboza et al. 2009), we expected a strong positive

relationship between liver and egg $\delta^{13}C$ (see also Gauthier et al. 2003). Liver and egg lipid $\delta^{13}C$ were positively correlated with a slope of 0.99 ± 0.12 (fig. 3C; $r^2 = 0.79$), while liver and nonlipid egg tissues exhibited a slope of 0.74 ± 0.13 (fig. 3D; $r^2 = 0.66$). While these correlations provide an indication of the relationship between endogenous nutrient sources and egg components, mixing models allow for the relative quantification of capital allocation.

Using $\delta^{13}C$ values of C_4 insects as the income source, and the C_3-derived fat bodies of individual lizards as capital sources in isotope mixing model estimates, lizards in the HH and HL treatments were found to have used 77% ± 8% and 77% ± 7% stored lipids to provision eggs (fig. 2B). The 2 early-reproducing lizards from the HH and HL treatments relied almost entirely on stored fat to provision eggs ($H_{early} = 96\% ± 4\%$). The LH lizards, in contrast, used only 42% ± 3% stored lipids to provision their eggs. Muscle was less important as a nutrient source

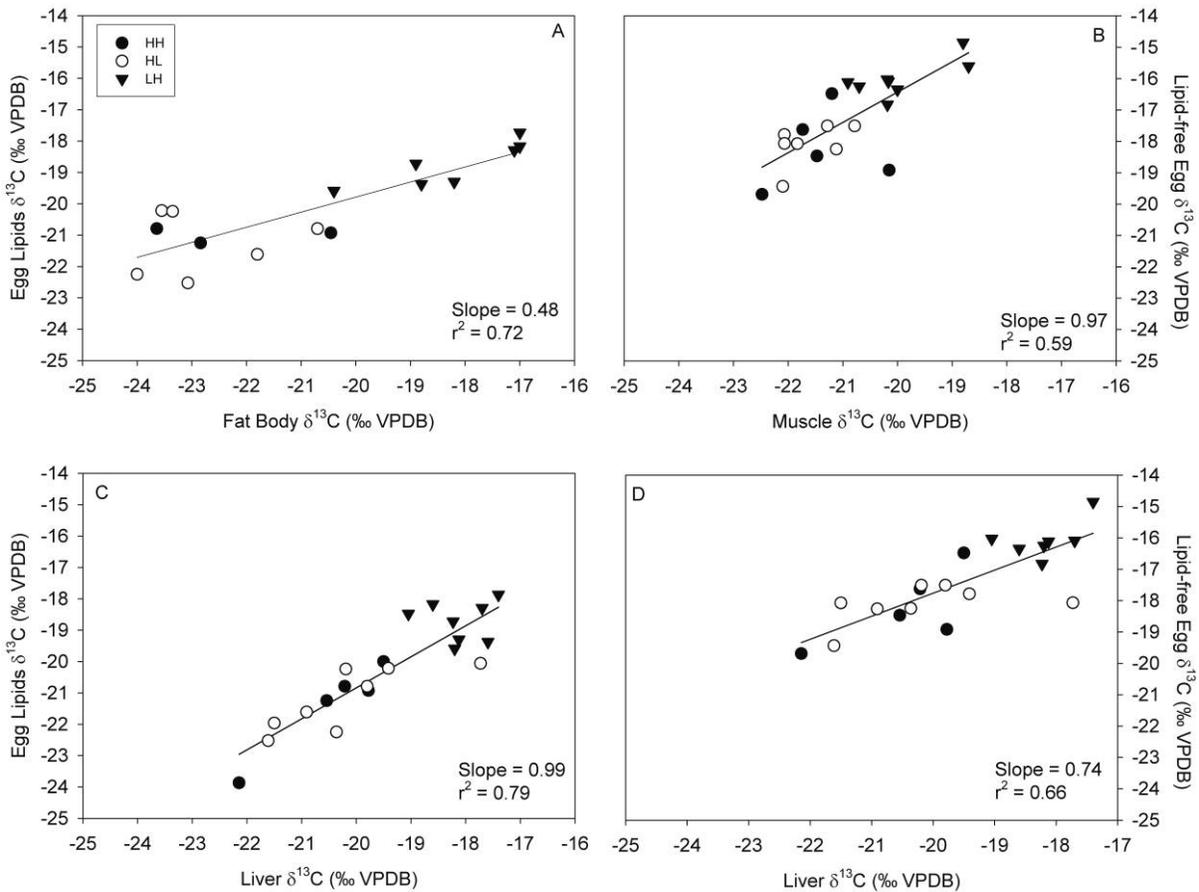**Figure 3:** Relationship between $\delta^{13}C$ values of fat bodies, whole liver, and egg lipids after reproduction in experimental *Sceloporus undulatus*. Symbols represent high (H)- and low (L)-nutrient diets imposed before and after hibernation for the treatments of HH (closed circles), HL (open circles), and LH (triangles). VPDB = Vienna Pee Dee belemnite carbon standard.

for provisioning egg nonlipid carbon (proteins) and contributed 1.4% ± 2% of the nonlipid carbon in the LH lizards and 39% ± 6% in the H$_{early}$ lizards (fig. 2*B*). It is important to note, however, that the estimates for the LH group are of potential allocation because we had to use mean δ^{13}C values for fat bodies (−22.6‰) and muscle (−21.5‰) of the HH and HL animals as their endogenous capital source in our mixing models. We could not use fat body and muscle δ^{13}C values for individuals in the LH group because these tissues were not solely developed before hibernation on C$_3$ resources (as were the H lizards) but instead were substantially derived from the C$_4$-income diet, as shown by more positive values compared with those of the high lizards (fig. 2*A*).

Interspecific Survey of Capital Breeding in Lizards in the Field

Because winter and summer monsoonal rains drive seasonally separated C$_3$ and C$_4$ plant production and resource flux in Chihuahuan Desert food webs (Warne et al. 2010*a*), we hypothesized that we could use natural variation in the δ^{13}C of C$_3$ and C$_4$ resources to examine capital breeding in wild lizards. We predicted that during the late summer and early fall lizards would develop endogenous lipid stores (capital) from C$_4$-derived sources because C$_4$ plants (primarily grasses) comprise the bulk of primary production during this period. We also predicted that reproduction in the spring (the income source) would be fueled by C$_3$ plants associated with winter rains (fig. 4). To test these predictions, female lizards of a variety of species were sampled during April–June to gauge the relative use of capital (C$_4$) versus income (C$_3$) resources for their first clutch of the season. Statistically significant and positive relationships were exhibited between the δ^{13}C of egg lipids and fat bodies (slope = 0.55, r^2 = 0.35) and liver (slope = 0.65, r^2 = 0.43) across seven lizard species (fig. 5). Stomach content δ^{13}C values were not correlated with egg lipids (fig. 5*C*). The relative contribution of fat stores allocated to eggs was estimated with a two-source mixing model (see "Material and Methods"), in which fat body δ^{13}C values of individuals served as the capital source and the mean δ^{13}C value of insects (−26.3‰) feeding on C$_3$ plants (−27.3‰; plus a Δ^{13}C of 1.0‰ when insects feed on C$_3$ resources) served as an income source (see Warne et al. 2010*a*). Estimates for the degree of capital allocation to reproduction ranged from 30% ± 5% in *S. undulatus* to 94% ± 5% in *Crotaphytus collaris* and 93% ± 7% in *Uta stansburiana* (table 1).
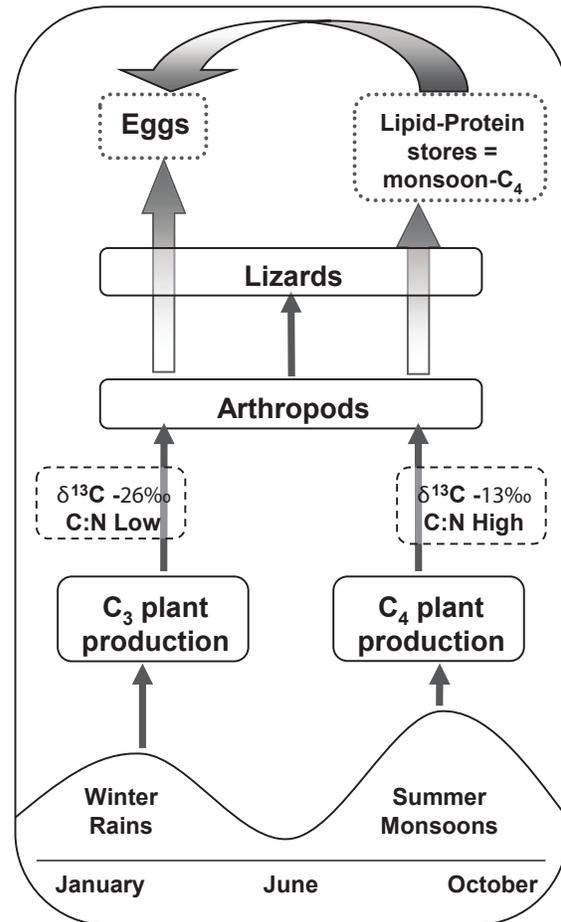

Figure 4: Winter and summer monsoonal rains drive seasonal C$_3$ and C$_4$ plant production and seasonal resource flux (black arrows) in Chihuahuan Desert food webs (Warne et al. 2010). We hypothesized that because lizards develop fat bodies during late summer–fall months, which are used to fuel hibernation and subsequent reproduction, that these endogenous lipid stores would thus be derived from C$_4$ sources (graded arrow). Because C$_3$ plants predominate during the spring reproductive period and thus represent income resources, we predicted that we could then examine the degree of capital (C$_4$) versus income (C$_3$, stippled arrow) resource allocation in lizards of differing life histories.

Discussion

Animals often depend on environmental resources that vary greatly in their quality and availability to fuel growth, reproduction, and self-maintenance. The endogenous storage of energy and nutrients, often called capital resources, is an integral component of the nutritional tactics animals use to buffer against such resource uncertainty (Derickson 1976*b*; Perrin and Sibly 1993; Reznick and Yang 1993; Doughty and Shine 1998; Houston and McNamara 1999). The allocation of capital to breeding is important for many or-
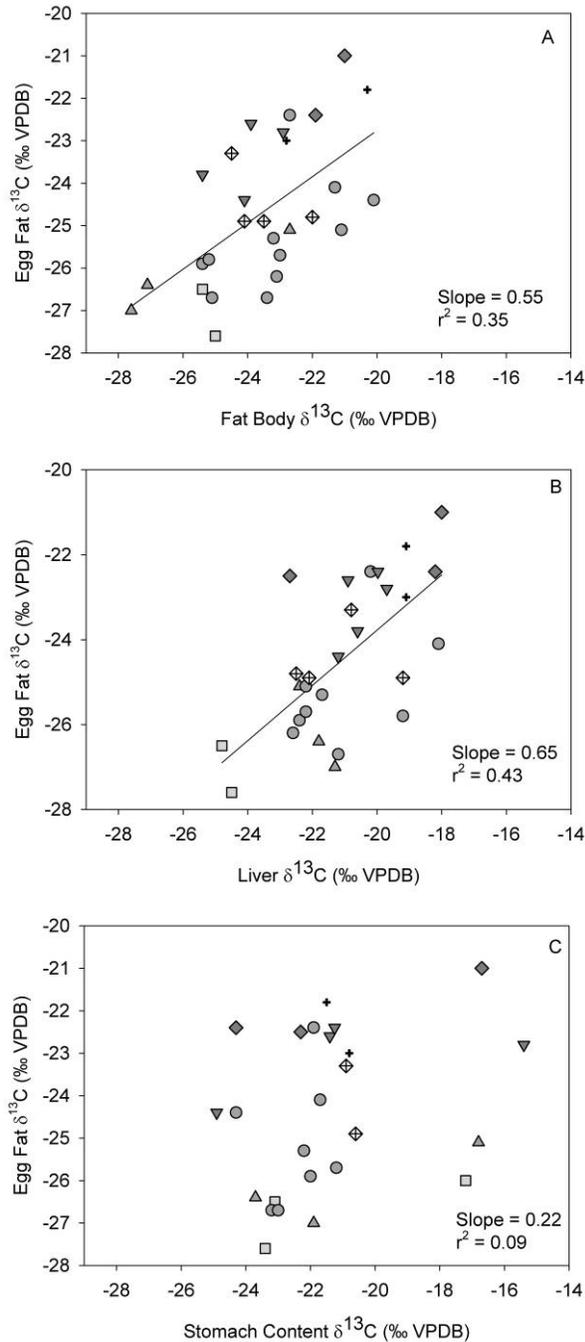
Figure 5: Relationship between $\delta^{13}C$ values of egg lipids and endogenous lipid sources (*A*), liver (*B*), and stomach contents (*C*) for seven species of wild-caught lizards (see table 1 for species). Symbols for each species: *Cophosaurus texanus* (up triangle), *Crotaphytus collaris* (diamond), *Eumeces multivirgatus* (plus), *Phyrnosoma modestum* (square), *Sceloporous undulatus* (circle), *Urosaurus ornatus* (diamond), *Uta stansburiana* (down triangle). VPDB = Vienna Pee Dee belemnite carbon standard.

ganisms because it enables reproduction during periods when food may be scarce but fitness benefits are potentially high (Hahn and Tinkle 1965; Derickson 1976b; Reznick and Braun 1987; Bonnet et al. 1998; Doughty and Shine 1998). Nutrient allocation tactics and their flexibility in response to varying endogenous and exogenous resource availability are not well known or quantified. In this study, one goal was to quantify how resource allocation to reproduction and growth varied under conditions of seasonal resource variation and uncertainty in captive lizards. We were specifically interested in the degree to which lizards could vary their use of capital resources for reproduction and growth. While previous studies have demonstrated that capital breeding is an important reproductive tactic for reptiles (Derickson 1976b; Doughty and Shine 1997; Bonnet et al. 1998; Warner et al. 2008), our laboratory data show that the use of capital resources for breeding in these lizards is quite flexible and is a function of an individual's body condition. Furthermore, given sufficient income resources, even lizards in relatively "poor" condition can allocate simultaneously to nutrient storage, growth, and reproduction at rates that allow them to "catch up" to lizards that were in "better" body condition before reproduction. A second goal of this study was to survey a wild community of lizards and use natural resource signals ($\delta^{13}C$ of C_3 vs. C_4 plant biomass) to estimate the relative use of capital versus income allocation tactics. Our measurements indicate that the degree of capital breeding varies greatly across this lizard community. In the following discussion we provide a more detailed analysis of these results and explore the implications of these findings for our understanding of capital breeding in lizards and the utility of the capital-income concept in general.

Nutrient Availability and Body Condition Effects on Capital Breeding

Our laboratory study showed that female prairie lizards vary to a large degree the sources they use to provision their first clutch in response to seasonal variation in nutrient availability. The lizards that were fed the high-treatment diet before hibernation (good body condition) and either the high- or low-nutrient diets posthibernation both relied on capital resources to provision their first clutch of eggs (77% use of capital) and did not differ in body condition indices. We note, however, that the HH lizards did start out at a slightly shorter SVL and did allocate more nutrients to growth and somewhat more to reproduction, as shown by a higher relative clutch mass (RCM). The HL-treatment lizards were only slightly affected by the lower quantity of income resources available during the development of their first clutch; however, low resource availability during an entire breeding season may affect later clutches (Warner et

Table 1: Carbon isotope composition (mean $\delta^{13}C$ ± SE‰ Vienna Pee Dee belemnite carbon standard) of somatic tissues and egg lipids for seven species of wild-caught lizards

Species	Liver	Stomach	Fat body	Egg lipid	% lipids from fat bodies	Adult survival
Cophosaurus texanus ($n = 3/7$)	−22.2 ± .4	−20.3 ± .9	−25.3 ± .7	−26.2 ± .6	33 ± 12	.30
Crotaphytus collaris ($n = 2/4$)	−19.8 ± 1.1	−21.4 ± 1.6	−21.3 ± .3	−22 ± .5	94 ± 5	.48
Eumeces multivirgatus ($n = 2/2$)	−19.1 ± .0	−21.2 ± .4	−21.6 ± 1.3	−22.4 ± .6	85 ± 10	...
Phrynosoma modestum ($n = 2/3$)	−24.7 ± .2	−21.2 ± 2.0	−25.2 ± .2	−26.7 ± .5	n.d.[a]	.20
Sceloporus undulatus ($n = 11/14$)	−21.1 ± .5	−22.7 ± .4	−22.7 ± .5	−25.3 ± .4	30 ± 5	.20
Urosaurus ornatus ($n = 4/8$)	−21.5 ± .5	−20.9 ± .4	−24 ± .6	−24.5 ± .4	50 ± 8	.32
Uta stansburiana ($n = 4/11$)	−20.1 ± .3	−20.8 ± 1.0	−24.1 ± .5	−23.2 ± .4	93 ± 7	.25

Note: Sample sizes are for the number of reproductive females with both eggs and fat bodies out of the total collected. Estimates of the percentage (±SE) of fat stores allocated to eggs are derived from a two-end-point mixing model, in which fat body $\delta^{13}C$ values of individuals served as the endogenous-capital source endpoint and the $\delta^{13}C$ value of insects (−26.3‰) feeding on C_3 plants (−27.3‰; plus a $\Delta^{13}C$ of 1.0‰ when insects feed on C_3 resources) served as the exogenous-income source endpoint (see Warne et al. 2010). Adult female survival rates were compiled in Charnov et al. (2007).

[a] No data; percentage estimate not applied because egg lipid carbon isotope values were not bounded by insect and fat body values.

al. 2008). The HL lizards, for example, are likely be nutrient limited, which could result in fewer or smaller clutches in a given season as well as later hatching dates leading to reduced fitness compared to animals with high nutrient availability (see Olsson and Shine 1997, 1999). These results (HH and HL dietary treatments) contrast sharply with those for the LH treatment. LH lizards were nutrient limited before hibernation and exhibited poor body condition posthibernation. As a result, when this group was provided with high nutrient levels posthibernation, only 42% of the lipids for their first clutch were derived from capital sources. Despite this lack of capital resources, the proportion of total mass (RCM) that LH lizards allocated to reproduction was only slightly less than those of the HH- and HL-treatment lizards. Thus, prairie lizards rely on income resources to reproduce even with a deficit in endogenous stores. This approach has potential costs, which may include reduced future reproduction or survival—a finding that likely reflects the importance of current reproduction for short-lived animals (Derickson 1976a; Reznick 1985; Reznick and Braun 1987; Reznick and Yang 1993; Schwarzkopf 1993; Doughty and Shine 1998).

Our results show that lizards have great flexibility in the allocation of nutrients to growth and storage, as well as to reproduction. Lizards on the LH regime had sufficient income resources while on the high diet to simultaneously allocate nutrients to reproduction, storage, and growth at rates that allowed them to catch up to the HH and HL lizards. Before hibernation, the LH lizards showed the slowest growth rates due to restricted food availability. After hibernation, however, the LH group had the fastest growth rates and allocated more nutrients to growth dur-

ing the reproductive period than both the HH or HL lizards. This pattern of "catch-up" allocation using income nutrients is reflected in the enriched (more positive) $\delta^{13}C$ values of the LH lizard's muscle, liver, fat, and eggs, which were enriched by the C_4 income diet (fig. 3). These findings demonstrate that lizards can and do allocate incoming nutrients to multiple life-history processes simultaneously in order to rapidly overcome a nutritional deficit (see also Telemeco and Baird 2011).

This simultaneous resource allocation also highlights how resource trade-offs between storage, growth, or reproduction, that are likely prevalent in prairie lizards can be diminished by abundant resources. Life-history theory predicts that in seasonal environments, finite resources lead to trade-offs, and as a result allocation to growth and storage often occur postreproductively (Stearns 1992; Perrin and Sibly 1993; McNamara and Houston 2008). Because we examined only the prairie lizard's first clutch, however, it is possible that such trade-offs could become apparent in later clutches or over the animal's life. Future work using the stable isotope methodology employed here, but with biopsies of fat bodies and egg yolk instead of destructive sampling, could provide a means of quantifying such life-history trade-offs over the course of a lizard's life.

Quantitative Estimates of Capital Breeding in a Wild Lizard Community

Our field study was an effort to quantitatively estimate the degree of capital breeding in a diverse lizard community. Because winter and summer monsoonal rains drive seasonally separated C_3 and C_4 plant production and resource

fluxes in Chihuahuan Desert food webs (Warne et al. 2010a), we hypothesized that we could use natural seasonal variation in the $\delta^{13}C$ of C_3 and C_4 resources to estimate capital allocation in wild lizards (fig. 4). We predicted that fat bodies in lizards developed during the late summer would show enriched $\delta^{13}C$ values reflecting the consumption of insects that were feeding on the monsoon-driven C_4 plant production that is abundant during July to October. We found, however, that fat body $\delta^{13}C$ values in insectivorous lizards were closer to those of C_3 plants than we had predicted, because a weak summer monsoon (the period when these lizards developed their fat stores) reduced C_4 primary production in 2007. Despite this discrepancy, the fat body and egg lipid $\delta^{13}C$ values of the lizard community were still enriched compared to those insects feeding on C_3 plants (table 1). Using these data, our estimates of capital allocation to reproduction ranged from 30% ± 5% in *Scleoporus undulatus* to 94% ± 5% in *Crotaphytus collaris* and 93% ± 7% in *Uta stansburiana* (table 1). These results could suggest that the degree of capital breeding in lizards may not vary with observed survival rates. This is in contrast with findings of previous studies, which suggested that short-lived lizards might rely more heavily on stored lipids to fuel high annual reproductive effort, while longer-lived species may conserve a greater proportion of their nutrient stores to ensure survival and future reproduction (Derickson 1976a; Schwarzkopf 1993; Doughty and Shine 1998). However, even our most long-lived lizard, *C. collaris*, with an annual survival probability of 0.5, used stored fat for 94% ± 5% of the lipids in its eggs; this value is similar to that of *U. stansburiana*, with a survival probability of only 0.25 (table 1). The survival rate of 0.5 in *C. collaris*, however, is not all that high, and it may be that a survival rate greater than 0.5 is needed to detect differences in allocation strategies. Our laboratory study suggests another alternative; seasonal variation in resource availability and thus body condition of lizards may have resulted in simultaneous allocation of resources to fat stores and egg development during the spring, when animals were sampled. Our wild-caught *S. undulatus*, for example, used 30% ± 5% capital resources to provision their eggs, which is comparable to the 42% capital allocation in the LH experimental lizards. These observations support the general claim that reptiles and other ectotherms are capital breeders that span a continuum that ranges from pure income to pure capital breeding strategies (Bonnet et al. 1998; Meijer and Drent 1999; Lourdais et al. 2002; Warner et al. 2008; Telemeco and Baird 2011). Our current data set, however, still provides only modest insight into how longevity affects capital-income allocation strategies, and we suggest that an expanded data set that includes quantitative estimates for capital breeding in longer-lived lizards under varied dietary conditions is needed to resolve how environmental factors and individual life-history tactics underlie patterns of capital breeding.

Macronutrient Routing to Reproduction

Another organism × environment interaction that warrants further exploration is how variation in dietary macronutrient content also affect the routing of nutrients to endogenous stores and capital reproduction (Meijer and Drent 1999; Stephens et al. 2009; Oppel et al. 2010). The concept of nutrient routing describes how macronutrients such as carbohydrates, proteins, and lipids are metabolized and shunted into differing nutrient storage or tissue pools (Tieszen and Fagre 1993; Martínez del Rio and Wolf 2005). This concept can be extended to egg provisioning because lipids have been shown to be preferentially used for metabolism, while protein is important for somatic development in lizard embryos (Thompson et al. 2001; Thompson and Speake 2002). In this study, we found that endogenous lipids are used extensively by prairie lizards to provision eggs, whereas protein carbon appears to come from exogenous (income) sources and not from muscle tissue. Similar results have also been reported for other taxa including a number of birds and one other lizard species (Meijer and Drent 1999; Warner et al. 2008; Oppel et al. 2010). Our observation that muscle is not readily used as a protein source for egg provisioning is not entirely surprising, because muscle carbon turnover in lizards occurs at a relatively slow rate (Warne et al. 2010b), and allocating muscle carbon to reproduction may compromise physical performance and survival (Lourdais et al. 2004). However, other researchers have reported findings that suggest additional research into nutrient routing within a predictive capital-income framework might be profitable. Speake et al. (2004), for example, found that the lipid profile of lizard egg-yolk closely matches that of insect prey. This is an important observation because energy and nutrient density of insect prey can vary seasonally (Chen et al. 2004), and differing insect prey taxa influence conversion efficiency and allocation patterns in lizards (Rich and Talent 2008; Telemeco and Baird 2011). Taken together, these findings suggest that environmentally induced variation in the quality and availability of differing insect prey could alter nutrient routing patterns and the capital and income breeding tactics of lizards.

The Capital-Income Concept as a Predictive Framework

Our laboratory study suggests that lizards do alter their nutrient routing tactics in response to resource availability (e.g., LH lizards). Furthermore, our finding of simultaneous allocation to storage, growth, and reproduction in the LH-

treatment lizards has broader implications for the characterization of capital breeding in animals. The capital-income breeding concept relies on the assumption that stored resources are acquired months, seasons, and even years before their use for reproduction (Bonnet et al. 1998). However, our finding that prairie lizards in the LH treatment simultaneously allocated nutrients to fat stores and egg development suggests that it may not be correct to assume that capital breeding is signified by an inverse relationship between diminishing fat stores and increasing reproductive tissue mass. In other words, during reproduction the flow of nutrients may not always be out of stores toward eggs, and instead, animals may be depositing nutrients to endogenous stores while reproducing, depending on the environmental conditions. Research by Oppel et al. (2010) has also shown that differing foraging patterns among individuals (eider ducks, in this case) can result in large variation in the income sources used for egg provisioning. When combined with the results from our study, Oppel et al.'s (2010) work suggests that both individual foraging patterns and body condition are important determinants of income versus capital allocation tactics. Many of these patterns are unresolved, and thus, we agree with Stephens et al. (2009) that future studies clearly need to focus on quantifying the degree to which endogenous stores are used and how they quantitatively contribute to breeding success. Research in this direction could provide insight into how individuals alter their allocation tactics in response to changing environmental conditions and the concomitant fitness-related effects of such decisions. Such endeavors could expand the value and utility of the capital-income paradigm by providing a predictive framework with testable hypotheses of how animals may respond to global change (Stephens et al. 2009).

Literature Cited

Angilletta, M. J., Jr. 2001. Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). Ecology 82:3044–3056.

Ballinger, R. E. 1977. Reproductive strategies: food availability as a source of proximal variation in a lizard. Ecology 58:628–635.

———. 1979. Intraspecific variaiton in demography and life history of the lizard *Sceloporus jarrovi* along an altitudinal gradient in southeastern Arizona. Ecology 60:901–909.

Ballinger, R. E., and J. D. Congdon. 1980. Food resource limitation of body growth rates in *Sceloporus scalaris*. Copeia 4:921–923.

Barboza, P. S., K. L. Parker, and I. D. Hume. 2009. Integrative wildlife nutrition. Springer, Heidelberg.

Bernard, J. B., and M. E. Allen. 1997. Feeding captive insectivorous animals: nutritional aspects of insects as food. Nutrition Advisory Group, Michigan State University, East Lansing.

Bonnet, X., D. Bradshaw, and R. Shine. 1998. Capital versus income breeding: an ectothermic perspective. Oikos 83:333–342.

Charnov, E., R. Warne, and M. Moses. 2007. Lifetime reproductive effort. American Naturalist 170:129–142.

Chen, X., M. B. Thompson, and C. R. Dickman. 2004. Energy density and its seasonal variation in desert beetles. Journal of Arid Environments 56:559–567.

Derickson, W. K. 1976*a*. Ecological and physiological aspects of reproductive strategies in two lizards. Ecology 57:445–458.

———. 1976*b*. Lipid storage and utilization in reptiles. American Zoologist 16:711–723.

Doughty, P., and R. Shine. 1997. Detecting life history trade-offs: measuring energy stores in "capital" breeders reveals costs of reproduction. Oecologia (Berlin) 110:508–513.

———. 1998. Reproductive energy allocation and long-term energy stores in a viviparous lizard (*Eulamprus tympanum*). Ecology 79:1073–1083.

Dunham, A. E., D. B. Miles, and D. N. Reznick. 1988. Life history patterns in squamate reptiles. Pages 441–522 *in* C. Gans and R. B. Huey, eds. Biology of the Reptilia. Liss, New York.

Ferguson, G. W., and S. F. Fox. 1984. Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana*: its causes and evolutionary significance. Evolution 38:342–349.

Fry, B., A. Joern, and P. L. Parker. 1978. Grasshopper food web analysis: use of carbon isotope ratios to examine feeding relationships among terrestrial herbivores. Ecology 59:498–506.

García-Berthou, E. 2001. On the misuse of residuals in ecology: testing regression residuals vs. the analysis of covariance. Ecology 70:708–711.

Gauthier, G., J. Bety, and K. Hobson. 2003. Are greater snow geese capital breeders? new evidence from a stable-isotope model. Ecology 84:3250–3264.

Hahn, W. E., and D. W. Tinkle. 1965. Fat body cycling and experimental evidence for its adaptive significance to ovarian follicular development in the lizard *Uta stansburiana*. Journal of Experimental Zoology 158:79–86.

Ho, S. M., R. Kleis, R. McPherson, G. J. Heisermann, and I. P. Callard. 1982. Regulation of vitellogenesis in reptiles. Herpetologica 38:40–50.

Hobson, K. A., K. D. Hughes, and P. J. Ewins. 1997. Using stable-isotope analysis to identify endogenous and exogenous sources of nutrients in eggs of migratory birds: applications to Great Lakes contaminants research. Auk 114:467–478.

Houston, A., and J. McNamara. 1999. Models of adaptive behaviour: an approach based on state. Cambridge University Press, Cambridge.

Jordan, M. A., and H. L. Snell. 2002. Life history trade-offs and phenotypic plasticity in the reproduction of Galapagos lava lizards (*Microlophus delanonis*). Oecologia (Berlin) 130:44–52.

Lourdais, O., X. Bonnet, R. Shine, D. DeNardo, G. Naulleau, and M. Guillon. 2002. Capital-breeding and reproductive effort in a variable environment: a longitudinal study of a viviparous snake. Journal of Animal Ecology 71:470–479.

Lourdais, O., F. Brischoux, D. DeNardo, and R. Shine. 2004. Protein catabolism in pregnant snakes (*Epicrates cenchria maurus Boidae*) compromises musculature and performance after reproduction. Journal of Comparative Physiology B 174:383–391.

Martínez del Rio, C., and B. O. Wolf. 2005. Mass balance models for animal isotopic ecology. Pages 141–174 *in* J. M. Starck and T. Wang, eds. Physiological and ecological adaptations to feeding in vertebrates. Science, Enfield, NH.

McNamara, J., and A. Houston. 2008. Optimal annual routines: behaviour in the context of physiology and ecology. Philosophical Transactions of the Royal Society B: Biological Sciences 363:301.

Meijer, T., and R. Drent. 1999. Re-examination of the capital and income dichotomy in breeding birds. Ibis 141:399–414.

O'Brien, D. M., D. P. Schrag, and C. Martínez del Rio. 2000. Allocation to reproduction in a hawkmoth: a quantitative analysis using stable carbon isotopes. Ecology 81:2822–2831.

Olsson, M., and R. Shine. 1997. The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): why early clutches are better. Journal of Evolutionary Biology 10:369–381.

———. 1999. Plasticity in frequency of reproduction in an alpine lizard, *Niveoscincus microlepidotus*. Copeia 1999:794–796.

Oppel, S., A. N. Powell, and D. M. O'Brien. 2010. King eiders use an income strategy for egg production: a case study for incorporating individual dietary variation into nutrient allocation research. Oecologia (Berlin) 164:1–12.

Packard, G., and T. Boardman. 1988. The misuse of ratios, indices, and percentages in ecophysiological research. Physiological Zoology 61:1–9.

Perrin, N., and R. M. Sibly. 1993. Dynamic models of energy allocation and investment. Annual Review of Ecology and Systematics 24:379–410.

Post, D., C. Layman, D. Arrington, G. Takimoto, J. Quattrochi, and C. Montana. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia (Berlin) 152:179–189.

Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos 44:257–267.

Reznick, D., and B. Braun. 1987. Fat cycling in the mosquitofish (*Gambusia affinis*): fat storage as a reproductive adaptation. Oecologia (Berlin) 73:401–413.

Reznick, D., and A. P. Yang. 1993. The influence of fluctuating resources on life history patterns of allocation and plasticity in female guppies. Ecology 74:2011–2019.

Rich, C., and L. Talent. 2008. The effects of prey species on food conversion efficiency and growth of an insectivorous lizard. Zoo Biology 27:181–187.

Schwarzkopf, L. 1993. Costs of reproduction in water skinks. Ecology 74:1970–1981.

Sheridan, M. A. 1994. Regulation of lipid metabolism in poikilothermic vertebrates. Comparative Biochemistry and Physiology B 107:495–508.

Sinervo, B., and S. C. Adolph. 1994. Growth plasticity and thermal opportunity in *Sceloporus* lizards. Ecology 75:776–790.

Sinervo, B., and P. Doughty. 1996. Interactive effects of offspring size and timing of reproduction on offspring reproduction: experimental, maternal, and quantitative genetic aspects. Evolution 50:1314–1327.

Speake, B. K., J. F. Herbert, and M. B. Thompson. 2004. Comparison of the fatty-acid compositions of prey items and yolks of Australian insectivorous scincid lizards. Journal of Comparative Physiology B 174:393–397.

Stearns, S. 1992. The evolution of life histories. Oxford University Press, New York.

Stephens, P., I. Boyd, J. McNamara, and A. Houston. 2009. Capital breeding and income breeding: their meaning, measurement, and worth. Ecology 90:2057–2067.

Svensson, E. I., B. Sinervo, and T. Comendant. 2002. Mechanistic and experimental analysis of condition and reproduction in a polymorphic lizard. Journal of Evolutionary Biology 15:1034–1047.

Telemeco, R. S., and T. A. Baird. 2011. Capital energy drives production of multiple clutches whereas income energy fuels growth in female collared lizards *Crotaphytus collaris*. Oikos 120:915–921.

Thompson, M. B., and B. K. Speake. 2002. Energy and nutrient utilisation by embryonic reptiles. Comparative Biochemistry and Physiology A 133:529–538.

Thompson, M. B., B. K. Speake, K. J. Russell, and R. J. McCartney. 2001. Utilisation of lipids, protein, ions and energy during embryonic development of Australian oviparous skinks in the genus *Lampropholis*. Comparative Biochemistry and Physiology A 129:313–326.

Tieszen, L. L., and T. Fagre. 1993. Effect of diet quality and composition on the isotopic composition of respiratory CO_2, bone collagen, bioapatite, and soft tissues. Pages 123–135 *in* J. B. Lambert and G. Grupe, eds. Molecular archaeology of prehistoric human bone. Springer, Berlin.

Tinkle, D. W. 1961. Population structure and reproduction in the lizard *Uta stansburiana stejnegeri*. American Midland Naturalist 66:206–234.

Tracy, C. R. 1999. Differences in body size among chuckwalla (*Sauromalus obesus*) populations. Ecology 80:259–271.

Warne, R. W., A. D. Pershall, and B. O. Wolf. 2010*a*. Linking precipitation and C_3-C_4 plant production to resource dynamics in higher trophic level consumers. Ecology 91:1628–1638.

Warne, R. W., C. A. Gilman, and B. O. Wolf. 2010*b*. Tissue carbon incorporation rates in lizards: implications for ecological studies using stable isotopes in terrestrial ectotherms. Physiological and Biochemical Zoology 83:608–617.

Warner, D., X. Bonnet, K. Hobson, and R. Shine. 2008. Lizards combine stored energy and recently acquired nutrients flexibly to fuel reproduction. Journal of Animal Ecology 77:1242–1249.