Intersexual Differences in Energy Expenditure of *Anolis carolinensis* Lizards during Breeding and Postbreeding Seasons

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ABSTRACT

Although the amount of energy that males and females invest in reproduction is an integral component of theories explaining the evolution of particular mating strategies, few studies have actually determined the amount of energy that each sex allocates to reproduction. We compared how energy is expended by male and female *Anolis carolinensis* lizards during both the breeding and postbreeding seasons. We used laboratory respirometry to determine resting metabolic rates (RMRs) of inactive, freshly captured lizards and the doubly labeled water technique to determine field metabolic rates (FMRs) of free-ranging lizards. Both RMRs and FMRs were influenced by body mass but not by sex. Season did not influence FMRs; however, RMRs of both sexes increased ~40% from the breeding to the postbreeding season. The seasonal increase in RMRs was attributed to a postreproductive increase in feeding rate and specific dynamic action. We used RMRs, FMRs, and thermal profiles of lizards to calculate energy budgets for breeding and postbreeding seasons. Energy budgets partitioned daily field energy (DFE; calculated from FMRs) into daily activity energy (DAE) and daily resting energy (DRE; calculated from RMRs). Energy expended for reproduction was estimated as DAE during the breeding season plus egg production (for females). Despite males having 40% greater body mass, females expended 46% more energy for reproduction than did males (906 and 619 J/d, respectively). Total metabolizable energy (TME = DFE + egg production for females) expended during the breeding season was similar for males and females (1,280 and 1,365 J/d, respectively). Although TME of females decreased 44% from the breeding to the postbreeding season (1,365 vs. 766 J/d), TME of males was similar during both seasons (1,280 vs. 1,245 J/d). There were both seasonal and sexual differences in DRE and DAE. Compared with most lizards from semiarid/desert habitats, *A. carolinensis* in a temperate habitat expends more total energy during the breeding season, allocates more energy to eggs, and appears to have more total energy available for reproduction.

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Introduction

Darwin (1882, p. 224) recognized fundamental differences in the ways that males and females allocate energy to reproduction. He pointed out that "on the whole, the expenditure of matter and force by the two sexes is probably nearly equal, though effected in very different ways and at different rates." Subsequently, differential investment by each sex in gametes (i.e., anisogamy; Bateman 1948) and individual offspring (Trivers 1972) became central concepts in the development of theories explaining the evolution of male and female mating strategies (Williams 1966*a*, 1966*b*; Orians 1969; Arnold and Duvall 1994). In general, reproductive investment by females consists of resources allocated directly to the production of relatively few but energetically expensive gametes. In some species, females also make a substantial investment in gestation and/or care of neonates. Thus, the reproductive output of females is believed to be primarily limited by resources (Bateman 1948; Trivers 1972). In contrast, because males typically invest minimal energy in the production of gametes, male reproductive success is limited by the ability to compete for and successfully mate with females (Bateman 1948). As a result, males may invest considerable energy in activities and traits associated with male reproductive success (e.g., advertisement displays, territorial defense, agonistic encounters, courtship, large body size, structures used for courtship or intermale combat; Bateman 1948; Trivers 1972). The time-intensive reproductive activities of males may also limit time spent in energy acquisition (Congdon 1989). Trivers's (1972) concept of parental investment further suggests how the energy allocated to reproduction by each sex relates to the evolution of particular mating systems. For instance, males that contribute paternal care to offspring and/or provide nuptial benefits to females do not usually have energy

or time to pursue multiple mates, and a monogamous mating system usually results. In contrast, males emancipated from parental care typically invest time and/or energy resources to defend or pursue multiple mates, contributing to a polygynous mating system. In species lacking male parental investment, Trivers (1972) also suggested that the amount of effort invested in reproduction by a male is influenced by the amount of effort invested by other males in the population. When some males invest heavily in reproduction, other males must invest at least the same amount of effort to compete with them and achieve some measure of reproductive success.

Despite the important role that reproductive energetics may have in helping to understand the evolution of mating systems and associated reproductive behaviors, comparisons of the relative amount of energy males and females allocate to reproduction are few (Bennett and Nagy 1977; Congdon 1977). Although many studies have examined costs associated with reproduction, most research has focused on costs in terms of reduced mobility and fecundity or increased predation or mortality rather than direct physiological or energetic costs (studies reviewed by Schwartzkopf [1994]). The lack of studies on reproductive energetics may, in part, reflect the difficulty of measuring energy expended for reproductive activity (e.g., behaviors related to territory, resource or mate defense, and courtship). Although measurement of female reproductive allocation to eggs became relatively easy and inexpensive with the development of bomb calorimetry techniques more than 40 yr ago (Golley 1961; Phillipson 1964), measuring the energy allocated to reproductive activity by free-ranging animals relies on the doubly labeled water technique (using oxygen-18 and deuterium or tritium isotopes; Lifson and McClintock 1966; Nagy 1983*a*), which remains a relatively difficult and expensive procedure.

We chose the green anole (*Anolis carolinensis*) as a model organism for examining the relative energy that males and females allocate to reproduction because (1) both sexes have high site fidelity (Ruby 1984; Jenssen et al. 1995*b*) and provide a high probability for recapture after being captured and released; (2) neither sex uses fat stores accumulated before the breeding season for reproduction (Wade 1981; Michaud 1990) or provides posthatch parental care, simplifying the task of determining the energy expended on reproduction; and (3) the life-history traits and mating system of this species are well documented and provide a basis for relating the energy expended by each sex to their respective reproductive strategies (Ruby 1984; Jenssen et al. 1995*b*, 2001; Jenssen and Nunez 1998).

The female-defense polygyny of *A. carolinensis* is largely an outcome of the distribution of reproductive females in space and time and the response of males to this distribution (Partridge and Endler 1987; Davies 1991; Sutherland 1996). Within stable, small (~8 m^3), overlapping (~20%), and lightly defended (approximately one aggressive encounter per day) home ranges, females are relatively clumped and sedentary (Nunez et al. 1997; Jenssen and Nunez 1998). Small female home ranges and infrequent competitive interactions between neighboring females suggest that resources needed for egg production are not critically limited (Jenssen and Nunez 1998). Iteroparous females lay single-egg clutches at about weekly intervals (Andrews 1985; Michaud 1990) throughout a 4-mo breeding season (Jenssen et al. 1995*b*).

Anolis carolinensis males attempt to monopolize multiple females by means of territorial defense (Ruby 1984; Jenssen et al. 1995*b*; Jenssen and Nunez 1998). Intermale contests for habitat containing females result in a 1 : 3 male : female breeding ratio in a population that has a 1 : 1 adult sex ratio (Ruby 1984; Jenssen et al. 1995*b*). The potential reproductive rate of territorial males is positively correlated with male body size, male territory size, number of resident females, and duration of time a male defends his territory (Ruby 1984; Jenssen and Nunez 1998). Intrasexual selection on males may contribute to prominent sexual dimorphisms. In comparison with females, males are 30%–40% larger in body mass (Jenssen et al. 1995*a*; this study), have eightfold greater territory volume (69 vs. 8 m^3), move sixfold greater distances (27 vs. 4 m/h), display sevenfold more frequently (100 vs. 14 displays/h), and spend a 30-fold greater proportion of the day in consexual dispute (9.2% vs. 0.03%; Jenssen et al. 1995*b*; Nunez et al. 1997; Jenssen and Nunez 1998). That territorial males lose body mass and have an apparent 75% attrition rate by the end of the 4-mo breeding season (Ruby 1984) suggests that males expend a considerable amount of energy on reproductive activity.

The sexually divergent reproductive strategies and behaviors associated with a polygynous mating system suggest the following testable hypotheses regarding the energy that male and female *A. carolinensis* invest in reproduction: males and females allocate about an equal amount of energy to reproduction for an entire breeding season (H_1); during the breeding season, males allocate more energy to activity than do females (H_2); and the total energy expended by both sexes is greater during the breeding season than during the postbreeding season (H_3).

To test our hypotheses, we used an energy budget (Fig. 1) to partition daily energy expenditure to resting and activity energy (Congdon et al. 1982). Thermal profiles and resting metabolic rates (RMRs; mL O_2/h, determined by laboratory respirometry) were used to estimate daily resting energy (DRE). The doubly labeled water technique (Nagy 1983*a*) was used to determine field metabolic rates (FMRs; mL CO_2/d) of free-ranging lizards, which were converted to daily field energy (DFE; J/d). Daily activity energy (DAE) was then calculated as the difference between DFE and DRE (DAE = DFE − DRE). Energy expended for reproduction was estimated as energy allocated to activity during the breeding season for both sexes plus the energy allocated to egg production for females. We assumed that males allocate negligible energy to sperm and ejaculate production. Total metabolizable energy (TME) was

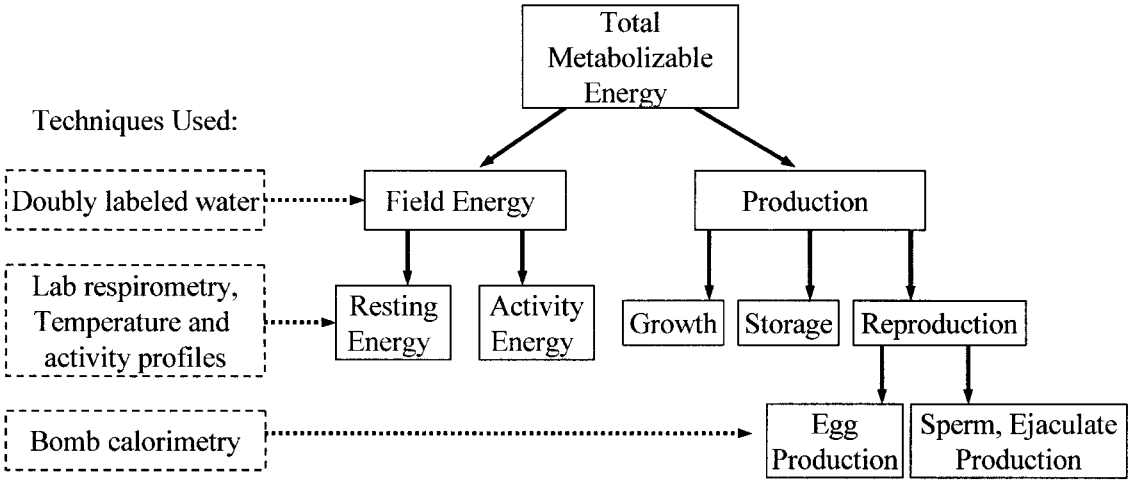

Figure 1. Schematic diagram for the partitioning of an energy budget and techniques used in this study to obtain data

calculated as DFE plus energy allocated to production (e.g., growth, storage, egg production).

The goals for our study were to (1) determine the influence that sex and season (i.e., breeding vs. postbreeding season) have on rates of resting metabolism and daily field energy, (2) use energy budgets to test the working hypotheses, (3) relate energy expenditure to the mating strategy and life history traits of *A. carolinensis*, and (4) compare the energy expended for reproduction by *A. carolinensis* with that previously published for other lizard species.

Methods

The breeding season of *Anolis carolinensis* at our Augusta Canal study site (Augusta, Ga.) begins in early April and is over by the end of July. Breeding season measurements occurred mid-June to mid-July, and postbreeding season measurements began 1–2 wk after reproductive activities (e.g., territoriality, mating) ceased (mid-August). The two seasons had nearly identical temperature profiles. The similar temperature profiles of the two study periods facilitated our comparison of reproductive and postreproductive lizards; that is, because seasonal differences in metabolism were not as a result of different environmental temperatures, they were more likely to be associated with changes in reproductive state and/or behavioral profiles.

Thermal Profiles

A 24-h thermal profile for lizards at the study site was compiled from measured lizard body temperatures (T_B), measured ambient temperatures (T_A), and activity profiles (Jenssen et al. 1995*b*; Nunez et al. 1997). For the 8 h of photophase when lizards maintain T_B by thermoregulation (0900–1700 hours), mean ($\pm$SD) cloacal temperatures of active lizards during the breeding season were measured as 33.4° $\pm$ 1.0°C ($n = 16$). We used Hobo data loggers to record T_A hourly at sunny and shaded locations during breeding and postbreeding measurement periods (June 22–August 19; Fig. 2). To prevent solar heat absorption, data logger temperature probes were suspended in 8-oz metal cans open at both ends and covered in white reflective tape. During the 11-h scotophase (2000–0700 hours), average T_B of lizards was estimated to be the same as average nighttime T_A (23°C; Fig. 2). For the first and last hour of the photophase (0700–0800 and 1900–2000 hours), when lizards could not thermoregulate, average T_B was also estimated to be the same as average T_A (e.g., 23°C). During the 3 h of photophase (0800–0900 and 1700–1900 hours; Fig. 2) when direct sunlight was blocked by tall trees, we assumed that the transition between 23°C and 33°C resulted in an average T_B of 28°C. Because average T_A did not appreciably change from breeding to postbreeding season (Fig. 2), we used the same thermal profile to calculate energy budgets for both seasons.

Resting Metabolic Rates

Because free-ranging lizards are usually digesting prey, we determined resting metabolic rates (volume of O_2 consumed per hour) within 24 h of capturing lizards, while digestion of previously consumed food was still in progress (feces were frequently produced during measurement periods). The RMRs of recently captured lizards should reflect the metabolic cost of digestion (e.g., specific dynamic action [SDA]; Niewiarowski and Waldschmidt 1992) and not the potential effects that long-term laboratory acclimation could have on metabolism (Beyer and Spotila 1994). The RMRs of freshly captured lizards should

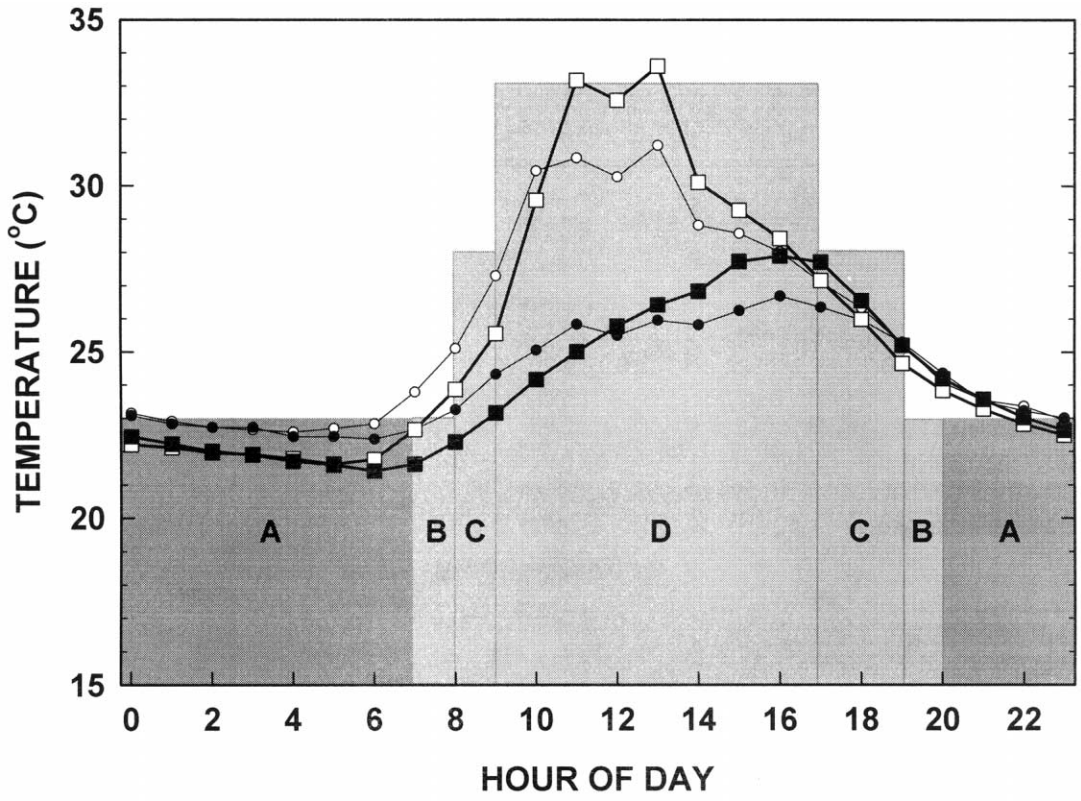

Figure 2. Mean air temperatures recorded hourly at the Augusta Canal study site (Augusta, Ga.) during the breeding season (*thin lines*) at sunny (*open circles*) and shaded (*filled circles*) locations and during the postbreeding season (*thick lines*) at sunny (*open squares*) and shaded (*filled squares*) locations. Areas with gray fill represent the estimated daily thermal profile for *Anolis carolinensis*, which is composed of four periods: *A*, lizards asleep during the scotophase (nighttime, *dark gray*) for 11 h at 23°C (body temperature of lizards estimated to be the same as average air temperature); *B*, lizards alert or active for 2 h during the photophase (daytime, *light gray*) at 23°C (body temperature of lizards estimated to be the same as average air temperature); *C*, lizards active for 3 h during the photophase at 28°C (average body temperature of lizards estimated for the transition from 23°C to 33°C); and *D*, lizards active for 8 h during the photophase at 33°C (body temperature measured in 16 active lizards).

more accurately represent the resting metabolism of free-ranging lizards than standard metabolic rates of fasted, laboratory-acclimated lizards. In addition, because RMRs often exhibit diel variation (Niewiarowski and Waldschmidt 1992; Beaupre et al. 1993), RMRs were measured every 40 min during the scotophase (2000–0700 hours) and then averaged for each lizard. Different lizards were used to determine RMRs for each temperature and season.

Lizards were allowed 2 h of acclimation in clear glass containers (150–360 mL) within a dark chamber, and then rates of O_2 consumption were measured at 40-min intervals with a Micro-Oxymax system (Columbus Instruments, Columbus, Ohio). The Oxymax is a closed system with a reference chamber that recalibrates the sensors after each measurement and normalizes rates of O_2 consumption for standard temperature (0°C) and pressure (760 mmHg; Columbus Instruments 1993). Air in the chambers was refreshed after each measurement to maintain constant O_2 and CO_2 concentrations.

We determined RMRs at 28°C ($n = 17$) and 33°C ($n = 7$) during the breeding season and at 28°C ($n = 31$) during the postbreeding season. We did not determine RMRs at 33°C during the postbreeding season because some lizards at this temperature during the breeding season exhibited signs of stress (mouth gaping), and one lizard died following the measurements.

Additional RMRs required to partition the energy budget at 23°C during the breeding season and at 23°C and 33°C during the postbreeding season were estimated as follows. First, we calculated Q_{10} values (increase in metabolic rate associated with a 10°C increase in temperature) for temperature intervals of 28°–33°C (from scotophase RMRs during the breeding season) and 23°–28°C (from standard metabolic rates measured by

Jenssen et al. 1996). Second, we estimated unknown RMRs on the basis of appropriate Q_{10} values and temperature- and season-specific RMRs. Third, estimated RMRs were multiplied by 1.4 to obtain respective photophase RMRs for alert lizards during the day (on the basis of scotophase and photophase metabolic rates reported for other lizards; Andrews and Pough 1985; Beaupre et al. 1993; van Marken Lichtenbelt et al. 1993; see App. A and Orrell 2002 for more details).

Field Metabolic Rates

The doubly labeled water method (Nagy 1983*a*) was used to determine water influx rates (WIRs; mL H_2O/d) and field metabolic rates (volume CO_2 expired per day) in free-ranging *A. carolinensis* during breeding and postbreeding seasons. The WIRs were used to estimate the amount of free water intake. During the breeding season, subjects were established territorial males and gravid females (i.e., an egg could be palpated).

Lizards (54 males, 43 females) were weighed (± 0.1 g), measured for snout vent length (SVL), toe clipped for identification, and given an intraperitoneal injection of an isotope mixture (3.75 mL of deionized distilled water, 1.25 mL of 95 atom% H_2O^{18}, and 0.34 mL of 99.7 atom% D_2O) at a volume of 7.5 μL/g body mass. On the basis of average body mass of lizards in our study and equilibration times for lizards reported by previous studies (e.g., Nagy 1983*b*; Nagy and Bradshaw 1995), we allowed at least 2 h for isotopes to equilibrate with the body-water pool. Then, a 60–80-μL sample of blood was obtained from each lizard through a 2–3-mm incision in the postorbital capillary bed. Incisions healed within a few days and did not appear to impair eyelid function. Blood was collected in heparinized hematocrit capillary tubes that were capped in the field with critocaps and flame sealed later the same day. Samples were kept on ice in the field and thereafter refrigerated at 3°–4°C until analysis. After initial samples were taken, most lizards were released at their original capture site. In a few cases where high trees or dense vegetation would have interfered with recapture, some females were released into habitats that contained climbable trees and/or moderate undergrowth. On the basis of recapture locations, females tended to remain in the general area in which they were released.

Forty-eight lizards were recaptured 4–12 d after their release (mean = 8.0 ± 1.9 SD), at which time we obtained a second 60–80-μL sample of blood from each and redetermined their body mass. We also obtained 60–80 μL samples of urine (at isotopic equilibrium with blood; Nagy and Costa 1980) from four lizards that yielded inadequate blood (<40 μL) for the second sample. Blood samples were obtained from four unlabeled lizards (two territorial males, two reproductive females) for determination of isotope background levels. The average ($\pm$SD) background concentration of oxygen-18 was 0.200587 ± 0.000519 atom% and of D_2O was 0.01576 ± 0.00015 atom%.

Blood and urine samples were microdistilled under vacuum to obtain pure water (K. A. Nagy, personal communication). Hydrogen isotopes were prepared using the offline Hayes zinc combustion procedure (Coleman et al. 1982) and were then analyzed using the dual inlet technique on a Finnigan Delta S isotope ratio mass spectrometer. Oxygen isotopes were prepared using the guanidine hydrochloride procedure (Wong et al. 1987*b*; R. H. Michener, unpublished data). The carbon dioxide samples generated were again analyzed using the dual inlet of the mass spectrometer. All samples were calibrated to international water samples and normalized to the VSMOW/SLAP (Vienna Standard Mean Ocean Water/Standard Light Antarctic Precipitation) scale (Wong et al. 1987*a*). At least two independent replicates (mean = 2.4 ± 0.7 SD) were analyzed for each sample, and average isotope concentrations were used in calculations. We used data from 36 of the 48 recaptured lizards (17 females, 19 males) to calculate WIRs and FMRs. Twelve recaptured lizards did not provide usable isotope data because of insufficient sample volume, capillary tube leakage, or isotope concentrations that were too low (as a result of complete turnover of isotopes or isotope leakage from the injection site). The maximum sample interval before complete turnover of isotopes was about 12–13 d, with mean ($\pm$SD) initial isotope concentrations of 0.3757 ± 0.0299 atom% O^{18} and 0.0631 ± 0.0074 atom% D_2O.

We calculated WIRs and FMRs according to the equations of Lifson and McClintock (1966) as modified by Nagy (1980). Total body water content was determined by drying the bodies of three postbreeding females and five postbreeding males in an oven at 65°C to a constant body mass. Mean ($\pm$SD) body water content of live body mass was 72.4% ± 0.01% for females, 70.0% ± 0.02% for males, and 70.9% ± 0.02% for both sexes. Rates of FMR (mL CO_2/d) were converted to energy equivalents (DFE) using the value 25.7 J/mL CO_2 (Nagy 1983*b*).

Energy Budget

Daily energy budgets were calculated on the basis of mean ($\pm$SD) body masses of the 47 males (5.7 ± 1.08 g) and 44 females (3.3 ± 0.54 g) in our study. The DRE of males and females during breeding and postbreeding seasons was calculated by multiplying the appropriate RMR (e.g., according to sex, season, temperature, and photophase or scotophase; App. A) by the time that lizards spent at each temperature according to the thermal profile (Fig. 2) and then summing total O_2 consumed over 24 h. Thus, for each sex and season, we calculated total O_2 consumed by resting lizards at night (11 h × scotophase RMR at 23°C) and by inactive, alert lizards during the day (2 h × photophase RMR at 23°C + 3 h × photophase RMR at 28°C + 8 h × photophase RMR at 33°C). Total volumes of O_2 consumption were converted to energy equivalents using the value 20.1 J/mL O_2 (Nagy 1983*b*).

Statistical Analyses

Using $\log_{10}$-transformed body mass as a covariate, $\log_{10}$-transformed WIRs, FMRs, and RMRs were examined for the influence of sex and season using ANCOVA (Kleinbaum et al. 1988; SAS Institute 1989). The ANCOVA compares data independently of the effect that body mass has on metabolism. Tests were considered statistically significant at $P < 0.05$. Residuals for data sets were normally distributed (Shapiro-Wilks statistic, $W = 0.32$–0.74). Statistical analyses were performed with SAS release 6.12 (SAS Institute, Cary, N.C., 1989–1996), and power tests (i.e., the minimum detectable effect for a statistical power of 0.8; Zar 1984) for ANCOVA comparisons were performed with JMP IN version 3.2.1 (SAS Institute, Cary, N.C., 1989–1997).

Results

Resting Metabolic Rates

Within each temperature and season, sex appeared to have no influence on RMRs (ANCOVA; neither slopes nor intercepts significantly differed, $P > 0.90$; Table 1; Figs. 3, 4). Although our data did not include males and females of similar body size (territorial males are always larger than females), it appears that differences in male and female mass-specific RMRs (i.e., mL O_2/g/h; Table 1) are due to males having a 40% greater body mass than females and the allometric effect of body mass on metabolism.

The RMRs measured during the breeding season at 33°C were substantially but not significantly higher than those measured at 28°C (by 15% for males and 29% for females; Table 1; Fig. 3; ANCOVA, data for both sexes pooled: for intercepts $P = 0.07$, for slopes $P = 0.35$). The insignificant statistical result may have been due to the small sample size of measurements at 33°C ($n = 7$). The Q_{10} for the temperature interval of 28°–33°C was 1.3 for males and 1.7 for females (App. A). The RMRs measured during the postbreeding season at 28°C were significantly higher than those measured during the breeding season at 28°C (by 45% for males and 34% for females; Table 1; Fig. 4; ANCOVA, data for both sexes pooled: for intercepts $P = 0.0001$; slopes did not significantly differ, $P = 0.96$).

Because there was a different relationship between body mass

Table 1: Mean snout vent lengths (SVL), body masses, resting metabolic rates (RMRs), water influx rates (WIRs), and field metabolic rates (FMRs) in *Anolis carolinenis* during breeding and postbreeding seasons

	Males	Females
Breeding season at 28°C:		
SVL (mm)	60.5 (8, 3.16)	51.2 (9, 1.13)
Body mass (g)	5.49 (8, 1.21)	3.08 (9, .41)
RMR (mL O_2/g/h)	.242 (8, .05)	.273 (9, .05)
Breeding season at 33°C:		
SVL (mm)	62.6 (5, 3.72)	52.0 (2, 2.00)
Body mass (g)	6.16 (5, 1.46)	2.80 (2, .64)
RMR (mL O_2/g/h)	.279 (5, .07)	.352 (2, .07)
Postbreeding season at 28°C:		
SVL (mm)	62.2 (17, 3.33)	52.5 (14, 3.83)
Body mass (g)	5.76 (17, 1.16)	3.46 (14, .65)
RMR (mL O_2/g/h)	.352 (17, .09)	.365 (14, .08)
Breeding season:		
SVL (mm)	63.1 (7, 3.72)	52.2 (10, 1.72)
Body mass (g)	5.94 (7, 1.30)	3.29 (10, .36)
WIR (mL H_2O/g/d)	.12 (7, .02)	.14 (10, .03)
FMR (mL CO_2/g/d)	8.74 (7, 1.85)	10.30 (10, 1.94)
Postbreeding season:		
SVL (mm)	61.6 (10, 1.96)	53.4 (9, 3.06)
Body mass (g)	5.55 (10, .65)	3.52 (9, .55)
WIR (mL H_2O/g/d)	.12 (10, .03)	.13 (9, .02)
FMR (mL CO_2/g/d)	8.50 (10, 2.64)	9.03 (9, 2.01)

Note. Means are shown with values for n and SD in parentheses.

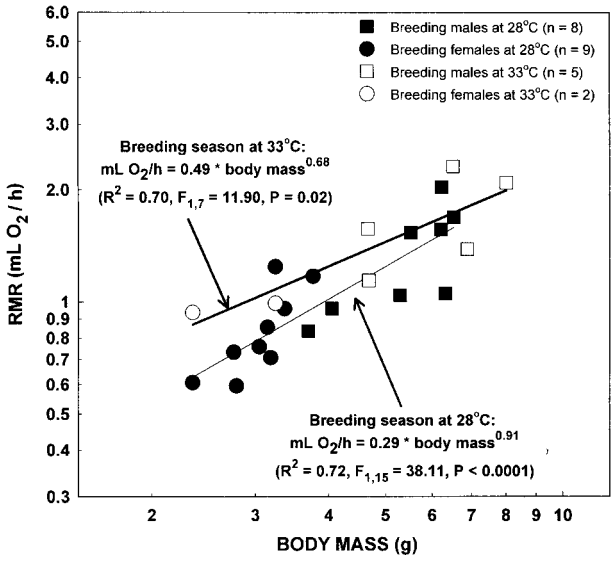

Figure 3. Resting metabolic rate (*RMR*) as a function of body mass in *Anolis carolinensis* measured during the breeding season at 28°C (*filled squares*, males; *filled circles*, females) and at 33°C (*open squares*, males; *open circles*, females). Lines indicate least squares linear regression for the breeding season at 28°C (*thin line*) and at 33°C (*thick line*).

and RMR for each temperature and season, three separate regressions were calculated: (1) for lizards at 28°C during the breeding season (mL O_2/d = 0.29 × body mass$^{0.91}$; $R^2 = 0.72$, $F_{1,15} = 38.11$, $P = 0.0001$; Figs. 3, 4); (2) for lizards at 33°C during the breeding season (mL O_2/d = 0.49 × body mass$^{0.68}$; $R^2 = 0.70$, $F_{1,7} = 11.90$, $P = 0.02$; Fig. 3); and (3) for lizards at 28°C during the postbreeding season (mL O_2/d = 0.39 × body mass$^{0.92}$; $R^2 = 0.54$, $F_{1,15} = 34.35$, $P = 0.0001$; Fig. 4).

Water Influx Rates

Neither sex nor season had a significant influence on WIRs (ANCOVA, for slopes and intercepts all $P > 0.05$; Table 1). Pooling data for both sexes and seasons, a significant relationship between body mass and WIR is described by the equation mL/d = 0.229 × body mass$^{0.58}$ ($F_{1,34} = 27.33$, $R^2 = 0.45$, $P < 0.0001$).

Field Metabolic Rates

Neither sex nor season had a significant influence on FMRs (ANCOVA, for slopes and intercepts all $P > 0.25$; Table 1). However, there was a significant relationship between body mass and FMR, described by the equation mL CO_2/d = 13.49 × body mass$^{0.71}$. After converting FMRs to energy equivalents (25.7 J/mL CO_2; Nagy 1983*b*), the relationship between body mass and DFE is described by the equation J/d = 348 × body mass$^{0.71}$ ($F_{1,34} = 27.10$, $R^2 = 0.44$, $P < 0.0001$; Fig. 5).

Energy Budgets

For both sexes and seasons, DFE was partitioned into DRE and DAE (Figs. 1, 6). For a male, DFE was nearly equal during both seasons, whereas DRE increased 45% and DAE decreased 54% from breeding to postbreeding seasons (Fig. 6). For a female, DFE decreased 12%, DRE increased by 34%, and DAE decreased by 63% from breeding to postbreeding seasons (Fig. 6).

Because most lizards maintained constant body mass during the 4–12-d sample periods (*t*-tests, $P > 0.17$), we assumed that energy allocated to production as growth or fat stores during these periods was zero for both sexes. Given that neither sex allocated energy to growth or fat stores, total metabolizable energy (TME) was equal to DFE for males during both seasons and for females during the postbreeding season. For females during the breeding season, we calculated TME as DFE plus energy allocated to egg production. Energy allocated to eggs was calculated as follows. Although *Anolis* eggs have not been examined, extensive data indicates the energy content of eggs varies little among lizard species (Vitt 1978). Average caloric content of a lizard egg (6.537 cal/mg dry mass; Vitt 1978) was

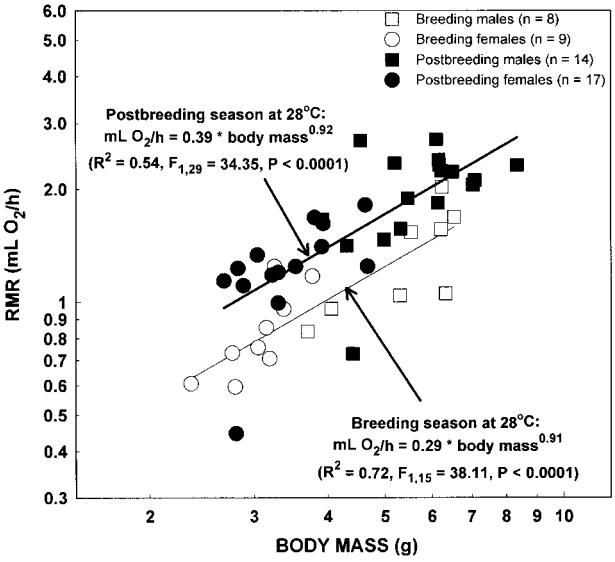

Figure 4. Resting metabolic rate (*RMR*) as a function of body mass in *Anolis carolinensis* measured at 28°C during breeding (*open squares*, males; *open circles*, females) and postbreeding (*filled squares*, males; *filled circles*, females) seasons. Lines indicate least squares linear regression for breeding (*thin line*) and postbreeding (*thick line*) seasons.

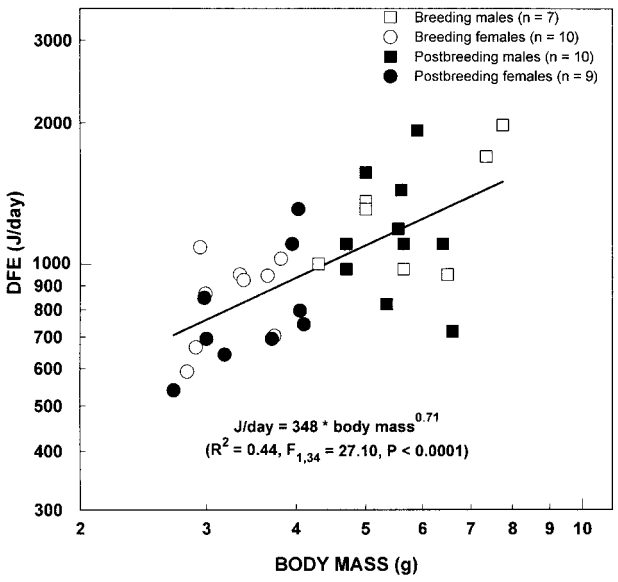

Figure 5. Daily field energy (*DFE*) as a function of body mass in *Anolis carolinensis* during the breeding (*open squares*, males; *open circles*, females) and postbreeding (*filled squares*, males; *filled circles*, females) seasons. Line indicates the least squares linear regression for all data.

multiplied by the mean dry mass of an *A. carolinensis* egg (154 mg mean dry mass, on the basis of a mean wet mass of 293 mg for eggs laid by females collected at our study site; M. Lovern, unpublished data). One egg contains 1,007 cal, or 4.21 kJ, so 14 eggs produced by a 3.3-g (~52 mm SVL) female over the 4-mo breeding season (Andrews 1985; Michaud 1990) equate to 491 J/d, or 58.9 kJ for the entire season.

The majority of energy expended by males for reproduction is for reproductive activity (e.g., territorial advertisement and patrol, competitive consexual interactions, courtship, and mating) because males presumably allocate minimal energy to sperm and ejaculate production. Furthermore, *A. carolinensis* is an ambush predator, so we assumed that energy allocated to foraging during the breeding season was also negligible for both sexes. Males during the breeding season foraged for food only 1% of their day (Jenssen et al. 1995*b*), and females foraged only 1.5% of their day (Nunez et al. 1997). Therefore, the energy males allocate to reproduction was estimated as DAE during the breeding season. A 5.7-g male (~62 mm SVL) would allocate about 619 J/d (Fig. 6), or 74 kJ per season, to reproduction.

Females allocate energy for reproduction to eggs and reproductive activity (e.g., courtship, copulation, competitive consexual interactions). Thus, we estimated the energy females allocate to reproduction as energy contained in eggs (491 J/d) plus DAE during the breeding season (415 J/d; Fig. 6). A 3.3-g (~52-mm) female would allocate about 906 J/d to reproduction, or 108.7 kJ over the 4-mo breeding season.

Discussion

Resting Metabolic Rates

Although the RMRs of *Anolis carolinensis* were not influenced by sex, they were significantly influenced by body mass, temperature, and season. The influence that body mass and temperature had on RMRs was similar to that reported previously for *A. carolinensis*. The average RMR we obtained in freshly captured lizards during the breeding season (0.32 mL O_2/g/h at 33°C) was essentially the same as that of fed *A. carolinensis* during the spring (0.34 mL O_2/g/h at 32°C; Licht and Jones 1967). The increase in metabolism over the temperature interval of 28°–33°C (Q_{10} of 1.5; App. A) was also very similar to that for *A. carolinensis* during the winter (Q_{10} of 1.4; Jenssen et al. 1996). And finally, the influence that body mass (i.e., scaled to an exponent of 0.7–0.9 depending on temperature and season) and temperature had on RMRs was about the same as reported for other anoles (McManus and Nellis 1973; Bennett and Gorman 1979) and other non-*Anolis* lizards (Andrews and Pough 1985).

We found a significant 45% and 34% increase in respective male and female RMRs from breeding to postbreeding season (Table 1; Fig. 4), which we suggest is due to a threefold increase in food intake during the postbreeding season (Jenssen et al. 1995*b*; Nunez et al. 1997). The increase in metabolic rate that is associated with increased food intake is known as specific dynamic action (SDA) and is thought to be due to energetic costs of digestion, transport, and storage of nutrients and protein synthesis (Secor and Phillips 1997). Metabolic rates of lizards digesting food may be as much as 100% higher than postabsorptive lizards (Waldschmidt et al. 1987; Niewiarowski and Waldschmidt 1992; Secor and Phillips 1997). The RMRs of *A. carolinensis* measured at 28°C and within 24 h of capture (while lizards were digesting food) were 32% and 84% higher (breeding and postbreeding season, respectively) than metabolic rates of postabsorptive *A. carolinensis* (0.195 mL O_2/h; Jenssen et al. 1996). Thus, metabolic rates were roughly proportional to food consumption, from 0.195 mL O_2/h in postabsorptive lizards to 0.258 mL O_2/h in lizards consuming 1.2 food items per hour (breeding season) to 0.359 mL O_2/h in lizards consuming 3.6 food items per hour (postbreeding season). In previous studies, increased feeding rates were associated with a 20%–38% increment in *Sceloporous virgatus* RMRs from breeding to postbreeding season (Merker and Nagy 1984) and may have contributed to a 24%–30% increase in *Callisaurus draconoides* FMRs (Karasov and Anderson 1998).

The increase in *A. carolinensis* food intake during the postbreeding season is probably not because of a seasonal difference

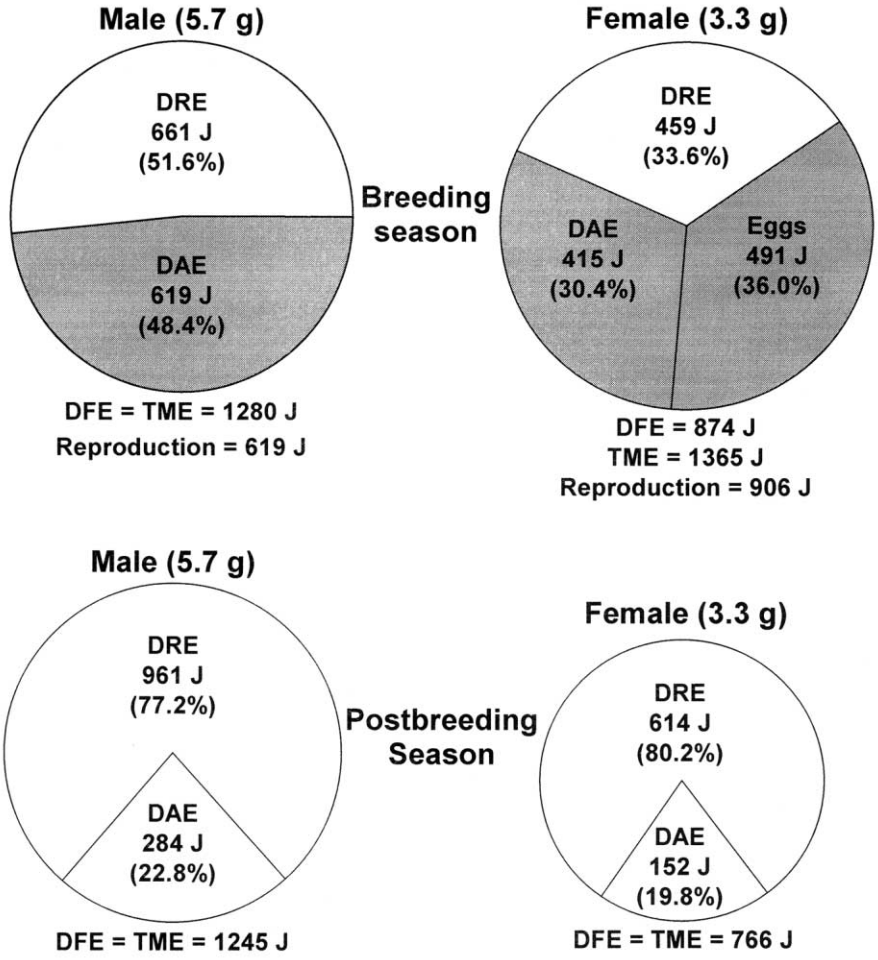

Figure 6. Estimated daily energy budgets for male and female *Anolis carolinensis* during breeding and postbreeding seasons. Pie size reflects the relative amount of total metabolizable energy (*TME*) expenditure for each sex and season. TME = daily field energy (*DFE*; determined by the doubly labeled water technique) + the energy allocated to eggs, storage, and/or growth (energy allocated to storage and growth during the study periods was 0). Daily resting energy (*DRE*) was calculated from resting metabolic rates and a time-temperature profile. Daily activity energy (*DAE*) = DFE − DRE. Proportion of TME allocated to reproduction during the breeding season (DAE for males and DAE + egg production for females) indicated by gray fill. See text for details of calculations.

in food or water availability because insects and water were abundant at our study site during both breeding and postbreeding seasons. Rather, the food intake of males may be limited by the time that they spend in territorial activities (about 70% of the day; Jenssen et al. 1995*b*). During the breeding season, territorial males forage for food only 1% of the day and primarily eat insects encountered during patrol ("eating on the run"; Jenssen et al. 1995*b*). In contrast, males during the postbreeding season spend three times more time foraging, actively search for food more frequently, and feed three times more often than during the breeding season (Jenssen et al. 1995*b*). After 4 mo of reproductive activity, loss of body mass indicates that territorial males may expend energy at rates exceeding their energy intake (Ruby 1984). Increased feeding rates during the postbreeding season would restore energy deficits, provide energy for growth, and provide energy stores for lizards that are inactive and primarily fast during cold winters (Jenssen et al. 1996). During the postbreeding season, both sexes increase glycogen stores and fat body mass (Dessauer 1955; Licht and Jones 1967; Wade 1981).

Because free-ranging females feed at the same rate as males during the breeding season (1.2 items per hour; Nunez et al. 1997), we infer from female postbreeding increases in RMRs, glycogen stores, and fat body size (Dessauer 1955; Licht and

Jones 1967; Wade 1981) that female feeding rates also increase during the postbreeding season. Previous studies have suggested that food intake by females is restricted by the space that eggs take up in the body cavity (Rand 1984; van Marken Lichtenbelt et al. 1993; Weeks 1996). Other studies suggested that gravidity reduces mobility and foraging efficiency and/or increases susceptibility to predators, causing gravid females to forage less often (Sinervo et al. 1991; studies reviewed by Schwartzkopf [1994]).

Water Influx Rates

The WIRs of *A. carolinensis* were primarily influenced by body mass (Table 1). The estimated water content of the amount of food required to support the DFE (App. B) suggests that as much as 70% of water influx was due to lizards drinking water. At the study site, water was available from morning dew or the adjacent Augusta Canal. Consistent with a lizard that has free access to water, the WIRs of *A. carolinensis* (0.12–0.14 mL/g/d) were two- to threefold higher than those of semiarid and desert lizards (e.g., *Urosaurus graciosus*, 0.04 mL/g/d [Congdon et al. 1982]; *Urosaurus ornatus*, 0.03 mL/g/d, and *Uta stansburiana*, 0.05 mL/g/d [Nagy 1982]; *S. virgatus*, 0.04 mL/g/d [Merker and Nagy 1984]) and similar to those of tropical lizards (0.12 mL/g/d for both *Lacerta viridis* [Bradshaw et al. 1987] and *Sceloporus variabilis* [Benabib and Congdon 1992]).

Field Metabolic Rates

The FMRs of *A. carolinensis* were primarily influenced by body mass and did not significantly differ by sex or season (Table 1; Fig. 5). However, it can be difficult to detect sex or seasonal differences in FMRs because of the high variance in doubly labeled water data. Although male FMRs were similar during both seasons, the average female FMR decreased by 12% from breeding to postbreeding seasons (Table 1). A post hoc power test on our data revealed that we had statistical power (0.8) to detect only about a 15% difference in FMRs. Perhaps due in part to low statistical power, several studies have also reported a lack of significant sex or seasonal differences in FMRs (Bennett and Nagy 1977; Nagy and Shoemaker 1984; van Marken Lichtenbelt et al. 1993; Zari and Nagy 1997; Karasov and Anderson 1998).

Although FMRs of *A. carolinensis* (218–265 J/g/d) were within the range of those reported for other lizards (e.g., 58–437 J/g/d; Nagy 1999), they were most similar to those of tropical and temperate lizards (e.g., *L. viridis*, 227 J/g/d [Bradshaw et al. 1987]; *S. variabilis*, 240 J/g/d [Benabib and Congdon 1992]; *Lophognathus temporalis*, 209 J/g/d [Christian et al. 1999]) and 30%–80% higher than most semiarid and desert lizards (reviewed in Nagy 1999). The FMRs of *A. carolinensis* were scaled to body mass with an exponent of 0.71 (Fig. 5), which is similar to the average exponent of 0.78 reported for other Iguanid lizards (Nagy 1999) but lower than the average exponent of 0.93 reported for desert lizards (Nagy 1999).

Energy Budget Hypotheses

Our first hypothesis (H_1), that males and females allocate about an equal amount of energy to reproduction, was not supported. On the basis of the energy budgets we calculated for *A. carolinensis* during the breeding season, a 3.3-g female would allocate about 46% more energy to reproduction than would a 5.7-g male (Fig. 6). For an entire 4-mo breeding season, males would allocate about 74 kJ to reproductive activity, while females would allocate about 109 kJ to reproductive activity and egg production. That female *A. carolinensis* invest 46% more total energy in reproduction than do males is surprising, given that males are 40% larger in body mass and have much greater activity levels than do females. Intense territorial activity leaves males with little time for foraging (1% of their day; Jenssen et al. 1995*b*), and loss in body mass by the end of the 4-mo breeding season (Ruby 1984; Jenssen et al. 1995*a*) indicates that food intake may not meet energy needs. Negative energy balance may contribute to an apparent 75% mortality rate for territorial males by the end of the breeding season (Ruby 1984), which constitutes an additional and important nonenergetic cost of reproduction for males (Trivers 1972; Schwartzkopf 1994).

Our second hypothesis (H_2), that males expended greater DAE than did females during the breeding season, was supported. Energy budgets indicate that males allocated about 50% more energy to daily activity than did females during the breeding season (Fig. 6). That males also expended 44% more daily resting energy than did females during the breeding season (Fig. 6) is due to males having greater body mass than females (i.e., the RMRs of both sexes are similar after adjusting for differences in body mass; Fig. 4). Both sexes expended about the same amount of TME during the breeding season (within 7%; Fig. 6).

Our third hypothesis (H_3), that both sexes would expend greater TME during the breeding season than during the postbreeding season, was supported only for females. Females during the breeding season expended about 80% more TME than during the postbreeding season, whereas males expended about the same amount of TME during both seasons (Fig. 6). The difference in TME for males and females during the postbreeding season was due primarily to males having a 40% larger body mass than females (both sexes had similar rates of DFE after adjusting for differences in body mass; Fig. 5). The seasonal decrease in female TME coincides with the cessation of egg production and decreased DAE during the postbreeding season. Both sexes had a marked seasonal decrease in DAE (54% for males and 63% for females) and a large seasonal increase in DRE from breeding to postbreeding seasons (45%

for males and 34% for females; Fig. 6). The decrease in male DAE is consistent with the shift from territorial activity during the breeding season (100 displays/h, travel 26 m/h) to greatly reduced activity during the postbreeding season (6 displays/h, travel 8 m/h; Jenssen et al. 1995*b*). For both sexes, the increase in postbreeding DRE was a result of the increase in postbreeding RMRs, which we attribute to increased food intake and specific dynamic action.

Comparison with Other Lizard Species

To date, only six studies have examined energy expenditure in reproductive lizards (Bennett and Nagy 1977; Congdon 1977; Nagy 1983*b*; Anderson and Karasov 1988; van Marken Lichtenbelt et al. 1993; Karasov and Anderson 1998), four of which estimated the energy expended by each sex for reproduction. We made standardized comparisons among the four studies by calculating the energy expended for reproduction as male DAE during the entire breeding season and female DAE during the entire breeding season + energy allocated to egg production (Table 2). The amount of energy allocated for reproduction by females exceeded that by males by 44% in *Sceloporus occidentalis*, 110% in *U. stansburiana*, and 234% in *Iguana iguana*. Only males of *Sceloporus jarrovi* expended more energy for reproduction than did females, and that difference was only 11% (Table 2). Thus, despite high activity rates of territorial males, females allocated more energy for reproduction than did males in most lizard species examined.

The amount of energy expended for reproduction is influenced by many factors, including ecology, reproductive strategies, foraging habits, and life-history traits. *Anolis carolinensis* is a temperate species, it has a polygynous and territorial mating strategy, and it is an insectivorous ambush predator. With the exception of *Cnemidophorus tigris* and *I. iguana*, the lizard species included in Table 2 are also polygynous, territorial, and insectivorous ambush predators, but they live in arid/semiarid

Table 2: Daily field energy (DFE), energy allocated to egg production, energy allocated to reproduction, and total metabolizable energy (TME) expended for an entire breeding season by males and females of seven lizard species

Species and Sex	Mass (g)	BSD (d)	DFE J/d	DFE kJ	Eggs (kJ)	Reproduction[a] (kJ)	TME kJ	TME kJ/g$^{0.8}$	References
Anolis carolinensis									This study
Males	5.7	120	1,280	154	…	74	154	38.3	
Females	3.3		874	105	59	109	164	63.1	
Callisaurus draconoides									Karasov and Anderson 1998
Males	10.5	120	1,403	168	…	…	168	25.6	
Females	8		1,100	132	53	…	185	35.1	
Cnemidophorus tigris									Anderson and Karasov 1988
Males	18.8	90	5,628	507	…	…	507	48.5	
Females	15.8		4,009	361	52	…	413	45.4	
Iguana iguana[b]									van Marken Lichtenbelt et al. 1993
Males	713	60	55,329	3,320	…	1,892	3,320	17.3	
Females	1,004		72,188	4,331	3,847	6,317	8,178	32.5	
Sceloporus jarrovi									Congdon 1977 (Turkey Creek population)
Males	23.9	61	2,860	174	…	40	174	13.7	
Females	17.4		1,427	87	43	36	130	13.2	
Sceloporus occidentalis									Bennett and Nagy 1977 (BSD from Stebbins 1985)
Males	11.9	120	1,549	186	…	105	186	27.9	
Females	11.9		1,666	200	32	151	232	32.3	
Uta stansburiana									Nagy 1983*b*
Males	3.7	117	551	64	…	22	64	22.5	
Females	2.4		271	32	18	50	45	24.8	

Note. Values are per season unless otherwise indicated. BSD = breeding season duration. TME = DFE/season + energy allocated to eggs. We calculated TME/body mass$^{0.8}$ to adjust for interspecific differences in body size (Nagy 1999).

[a] Energy allocated to activity by males and energy allocated to activity + eggs for females.

[b] Because oviposition takes place 1–2 mo after the breeding season, females may expend more DFE and TME than indicated.

habitats. *Cnemidophorus tigris* is a polygynous desert insectivore, but both sexes employ a wide-searching strategy for finding food and mates. *Iguana iguana* is a tropical herbivore with a territorial mating strategy and an active-search foraging strategy. To facilitate comparisons, we calculated the total metabolizable energy expended during the breeding season plus energy allocated to eggs by females (Table 2). After adjusting for interspecific differences in body size (energy expenditure/body mass$^{0.8}$; Nagy 1999), the TME of male *A. carolinensis* for an entire breeding season was 37%–180% greater than that of the four ambush predators and 220% greater than the tropical herbivore *I. iguana* but 27% less than the active forager *C. tigris.* Female *A. carolinensis* expended 39%–378% more TME (adjusted for body size) than all six other lizard species and allocated 11%–228% more energy to eggs than all five of the arid/semiarid species (Table 2). However, the proportion of TME that females allocated to egg production was similar for *A. carolinensis* (36%), *C. draconoides* (29%), *S. jarrovi* (33%), and *U. stansburiana* (36%). In contrast, *C. tigris* and *S. occidentalis* females allocated only 13% and 14% of TME to egg production, respectively (Table 2). The proportion of TME that females of *I. iguana* allocated to egg production (47%) may be overestimated. *Iguana iguana* has a 2-mo mating season from March to April (van Marken Lichtenbelt et al. 1993), but oviposition takes place during May or June. Thus, *I. iguana* females may expend energy for reproduction during more than the 2 mo used in our calculations, which would increase the DFE and TME for the breeding season and result in a lower proportion of TME that females allocated to eggs.

Because of plentiful food and water resources in a temperate habitat, *A. carolinensis* appears to have more energy available for reproduction than do lizards from semiarid/desert habitats. Water scarcity in semiarid or desert environments not only limits primary production and prey abundance, but it can also limit the amount of food that can be processed and/or harvested (Congdon 1989). As a result of abundant resources, *A. carolinensis* males and females expend more total energy during the breeding season, and females allocate more energy to eggs than do species from semiarid/desert habitats. The one exception, *C. tigris*, is an active forager that harvests more total energy than any of the other species compared. However, the energy demands associated with searching for food and mates results in *C. tigris* females allocating less energy to eggs than the other six species examined (Table 2).

How males and females allocate energy to reproduction can, in part, help identify the various factors that influence the evolution of mating strategies; however, few studies have actually done so. Several aspects of life history complicate studies that attempt to measure the energy expended for reproduction in lizards. For instance, females of many species, including all the species compared (except for *A. carolinensis*), use at least some energy stored before breeding for reproduction (Jonsson 1997). In contrast, *A. carolinensis* females rely on energy obtained during the breeding season for reproduction. Some species may produce more than one clutch per year, breed for 1 yr only or for multiple years, or may vary the amount of energy expended for reproduction with age (e.g., Congdon 1977; Nagy 1983*b*). Clearly, more studies are needed to determine how various factors impact the energy lizards expend for reproduction and to better understand the relationships among energy expenditure, life-history traits, and mating strategies.

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Appendix A

Table A1: Resting metabolic rates (RMRs) for males and females of *Anolis carolinensis* at three different temperatures during breeding and postbreeding seasons and during the scotophase (sleeping during the night) and photophase (awake and alert during the day)

	RMR (mL O_2/g/h)		
	23°C	28°C	33°C
Males:			
Breeding season:			
Scotophase	.118[a]	.242[b]	.279[b]
Photophase	.165[c]	.339[c]	.391[c]
Postbreeding season:			
Scotophase	.172[d]	.352[b]	.406[e]
Photophase	.240[c]	.493[c]	.568[c]
Females:			
Breeding season:			
Scotophase	.133[a]	.273[b]	.352[b]
Photophase	.186[c]	.381[c]	.493[c]
Postbreeding season:			
Scotophase	.178[d]	.365[b]	.472[e]
Photophase	.249[c]	.511[c]	.661[c]

[a] Rates estimated from the Q_{10} value for the temperature interval 23°–28°C = 4.21 (Q_{10} based on winter standard metabolic rates for *A. carolinensis*; data reported by Jenssen et al. [1996]) and from breeding season RMRs measured at 28°C by this study.

[b] Rates measured in this study using laboratory respirometry.

[c] Photophase rates estimated as 1.4 times the respective scotophase rate (Andrews and Pough 1985; Beaupre et al. 1993; van Marken Lichtenbelt et al. 1993).

[d] Rates estimated from the Q_{10} value for the temperature interval 23°–28°C = 4.21 (Q_{10} based on winter standard metabolic rates for *A. carolinensis*; data reported by Jenssen et al. [1996]) and from postbreeding season RMRs measured at 28°C by this study.

[e] Rates estimated from the Q_{10} value for the temperature interval 28°–33°C = 1.3 for males or 1.7 for females (Q_{10} based on breeding season RMRs for *A. carolinensis*) and from postbreeding season RMRs measured at 28°C by this study.

Appendix B

Table B1: Comparison of daily water influx rates (WIR) with the estimated free water intake (μL/d) for a 5.7-g male *Anolis carolinensis* during the breeding and postbreeding seasons

	Estimated from FMR						
	WIR (μL/d)	DFE (J)	Food Wet Mass (g)[a]	H_2O in Food (μL)	Metabolic H_2O (μL)[b]	Free H_2O Intake (μL)[c]	Season WIR (%)
Breeding	684	1,280	247	73	33	478	70
Postbreeding	684	1,245	241	168	32	484	71

[a] On the basis of an insectivorous diet and assuming that insects contain 70% water (Edney 1977) and 23 J/mg dry mass, 75% of which is metabolized (Harwood 1979).

[b] Metabolic water produced = DFE × 0.026 mL/kJ (Schmidt-Nielsen 1991).

[c] Free water intake = WIR − moisture in food − metabolic water production.

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