
FAT BODIES AND LIVER MASS CYCLES IN *SCELOPORUS GRAMMICUS* (SQUAMATA: PHRYNOSOMATIDAE) FROM SOUTHERN HIDALGO, MÉXICO

AURELIO RAMÍREZ-BAUTISTA^{1,3}, DANIEL HERNÁNDEZ-RAMOS¹, ALBERTO ROJAS
MARTINEZ¹, AND JONATHON C. MARSHALL²

¹Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, A.P. 1-69 Plaza Juárez, C.P. 42001,
Pachuca, Hidalgo, México

²Department of Zoology, Weber State University, Ogden, Utah 84408, USA

³e-mail: aurelior@uaeh.reduaeh.mx

ABSTRACT.—We describe changes in liver and fat body mass of males and females of the viviparous lizard, *Sceloporus grammicus* from southeastern Hidalgo, México. The changes in the masses of the liver and fat bodies of males and females are usually asynchronous. Typically, reproductively active males and females deplete fat body reserves and experience increased liver mass. However, we observed maximum fat body and liver masses during spermatogenesis (July-August) and vitellogenesis (July-November). In females, the liver and fat body masses decreased while carrying developing embryos. This pattern demonstrates the ability of these lizards to bolster energy reserves during reproductive activity and the high energetic cost associated with embryo development. Also, this response pattern is similar to other populations of this species and to some other species of temperate lizards.

Key Words.—fat body; liver body; Mesquite Lizard; reproductive cycle; *Sceloporus grammicus*.

INTRODUCTION

Fat bodies and liver masses in lizards store energy for use during times of high energetic demand such as the breeding season (Selcer 1987). Amphibians and reptiles have within the peritoneal cavity pairs of solid fat bodies either anchored to the kidneys or near the rectum. These are important resource storehouses needed for hibernation and breeding (Ramírez-Bautista 1995). Although the liver of lizards serves an immunological role, another major function is glucose metabolism (DeMarco and Guillet 1992). The liver removes surplus glucose from the blood and stores it as glycogen (Ramírez-Bautista 1995), and lizards adopt feeding strategies that store energy within these structures in the most efficient manner (Ramírez-Bautista 1995). Lizards with higher foraging success store more energy in their fat bodies and livers than poorly foraging individuals. This promotes faster growth rates and ultimately greater survivorship (Derickson 1976; Ramírez-Bautista 1995).

Studies on fat body and liver glycogen cycling exist for the *Anolis carolinensis* (Dessauer 1955), *Aspidoscelis tigris* (Goldberg and Lowe 1966), *Sceloporus graciosus* (Derickson 1974), and *S. jarrovi* (Goldberg 1972). Seasonal fat body and liver mass cycles generally correspond to seasonal changes in resource demand (Derickson 1976; Ramírez-Bautista et al. 2000, 2002). Several studies on fat-body and glycogen cycling patterns target lizard species in the tropical and temperate environments of México. For example, in

Anolis nebulosus (Ramírez-Bautista and Vitt 1997), *Cnemidophorus* (= *Aspidoscelis*; Reeder et al. 2002) *communis* (Ramírez-Bautista and Pardo-De la Rosa 2002), *C. lineatissimus* (Ramírez-Bautista et al. 2000), and *S. jarrovi* (Ramírez-Bautista et al. 2002), male and female fat body and liver mass cycles correlate negatively with reproductive activity (Ramírez-Bautista and Vitt 1997; Ramírez-Bautista et al. 2000, 2002). In another example, males of *Urosaurus bicarinatus* showed the same pattern as above but females did not (Ramírez-Bautista and Vitt 1998). Rather, vitellogenesis correlated positively with an increase in fat body and liver mass, indicating little energetic costs for female reproduction. Within the species *S. grammicus*, variations of this pattern have even been noted between different populations of the same species (Ramírez-Bautista et al. 2006).

In this study, we expand on the results of Ramírez-Bautista et al. 2006 and describe the fat body and liver glycogen cycles of *S. grammicus* in Hidalgo, Mexico. We use these results to infer how these populations manage resources throughout the year. This kind of life history information is vital for making wise conservation and management decision (Bury 2006).

MATERIALS AND METHODS

We obtained 124 male and 164 female *S. grammicus* from the Colección Nacional de Anfibios y Reptiles (CNAR-IBH, n = 171) and Museo de Zoología, Facultad

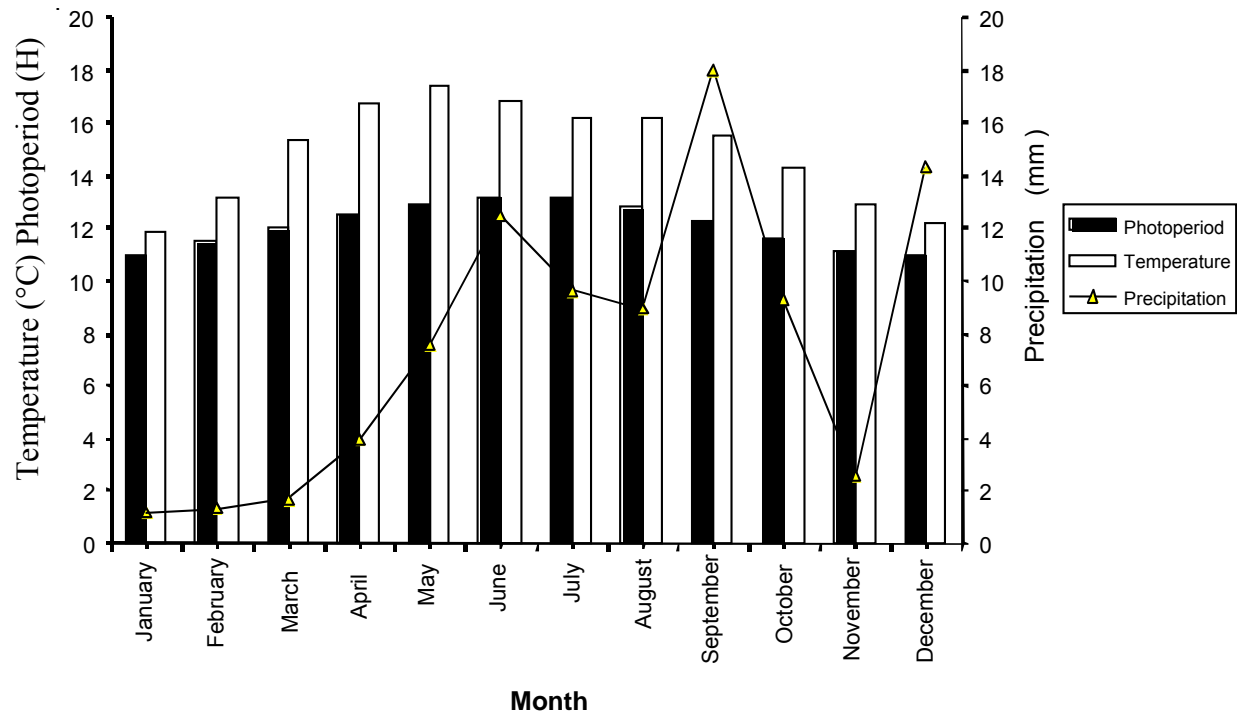


FIGURE 1. Monthly temperature, photoperiod, and precipitation based on 30-yr means recorded at the meteorological station of the Pachuca, Hidalgo, México (García 1981). Photoperiod data were acquired from the Astronomical Almanac (1984).

de Ciencias (MZFC; $N = 117$) both from Universidad Nacional Autónoma de México. Specimens came from localities in southeastern section of the state of Hidalgo, México ($19^{\circ}59'20''N$, $98^{\circ}27'57''W$, elevation = 2000–2648 m) during a 10 yr period from 1985 to 1995.

The climate of the study area is dry and temperate with maximum temperatures and rainfall occurring in the summer (June–August). Mean annual precipitation is 427.4 mm (García 1981; Fig. 1). The dominant plant communities are mesquite, grassland, and oak-pine forest (Rzedowski 1978). We obtained climatic and meteorological data from 1950 to 1980 from the meteorological station of Pachuca. We procured photoperiod data from the Astronomical Almanac (1984).

Because sample sizes were small for individual months, we pooled data from all localities and all years to describe monthly changes of fat body and liver mass and gonads volume of males and females. We recorded snout-vent length (SVL), length and width of testes, length and width of left and right vitellogenic follicles (gonad volume), and width and length of ovulated eggs or embryos (for egg/embryo volume). We recorded all measurements to the nearest 0.1 mm with calipers (Ramírez-Bautista et al. 2002). We removed and took masses of liver and fat bodies to the nearest 0.0001 g on an electronic balance. We used gonadal length and

width to obtain testicular, follicle, and eggs/embryo volumes (V), which we calculated using the formula for the volume of an ellipsoid: $V = 4/3\pi a^2b$, where a is one-half the shorter diameter and b is one-half the longest diameter. Testicular and follicular volumes are indicators of reproductive activity (Ramírez-Bautista et al. 2002, 2006). The smallest females with vitellogenic follicles in their reproductive tracts provided an estimation of the minimum size (in SVL) at sexual maturity. We considered a male to be sexually mature if it had enlarged testes with an enlarged and highly convoluted epididymide (Ramírez-Bautista et al. 2002).

Because organ mass may vary with SVL of the lizard, we first calculated regressions of \log_{10} – transformed organ mass data of males and females SVL (Ramírez-Bautista et al. 2000). For significant regressions, we calculated residuals from the regression of organ mass on SVL to produce SVL-adjusted variables (Schulte-Hostedde et al. 2005). We use these residuals to describe the monthly changes of the fat body and liver mass. We performed ANOVA to analyze statistically monthly variation in organ masses. We included only months for which $n \geq 3$. We used the Bonferroni-Dunn post hoc test to identify differences among months. In addition, we used correlation analysis to identify associations among climate variables such as temperature, precipitation, and photoperiod (Fig. 1) and monthly mean

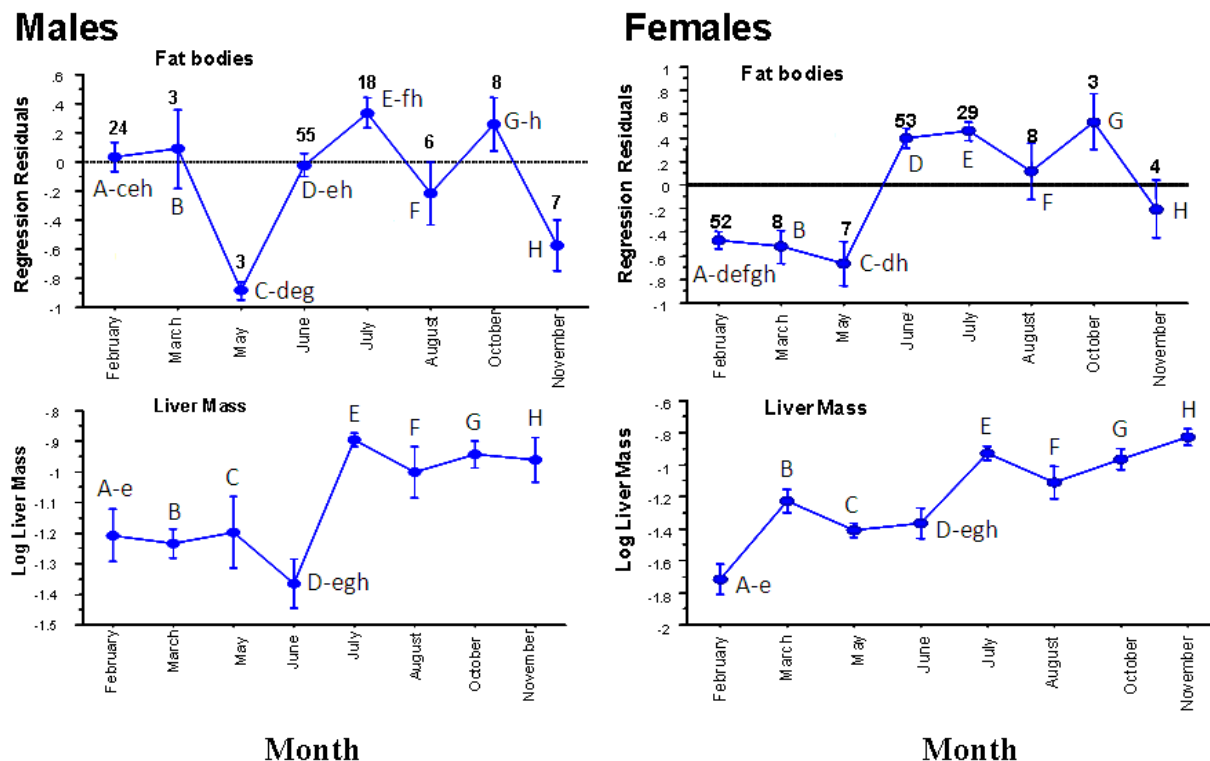


FIGURE 2. Male and female fat bodies and liver cycles of *Sceloporus grammicus* from southeastern Hidalgo, México. Data are mean (± 1 SE) residuals from a regression of \log_{10} fat body mass (g) against SVL, and \log_{10} liver mass (g). Samples sizes are given at each data point in both male and female fat body charts. Upper case characters label the respective month and lower case characters show statistical differences with other months.

mass of fat bodies and livers (Ramírez-Bautista et al. 2002). We presented means \pm SE unless otherwise indicated. We performed all statistical analyses with Statview IV (Abacus Concepts, Inc., Berkeley, CA, 1992). We used $\alpha \leq 0.05$ to assign significance when applying statistical decision theory.

RESULTS

Body Size and Sexual Maturity.—Sexually mature males ranged from 40 to 68 mm SVL (mean = 53.5 ± 0.63 mm, $n = 124$), and females ranged from 40 to 67 mm (51.7 ± 0.47 mm, $n = 164$). Average adult male SVL was significantly larger than for adult females (Mann-Whitney U -test, $Z = -2.44$, $P = 0.014$).

Fat Body and Liver Mass Cycles.—In adult males, the \log_{10} – SVL showed no significant relationship with the \log_{10} – liver mass ($r^2 = 0.15$, $F_{1, 121} = 2.75$, $P = 0.099$) but a relationship was present with the \log_{10} – fat body mass ($r^2 = 0.35$, $F_{1, 122} = 16.92$, $P < 0.001$). Residuals of these regressions revealed significant monthly effects on fat body mass ($F_{7, 116} = 3.92$, $P = 0.0007$; Fig. 2); however, liver mass was only significant when \log_{10} - transformed ($F_{7, 115} = 3.05$, $P = 0.0057$). Liver mass differed significantly (Games-Howell $P < 0.05$) between the

following months: February versus July, and June versus July, October and November (Fig. 2). Liver masses showed slight fluctuations from February to June, but from June to July they increased significantly, and continued to show significant differences until November (Fig. 2).

Fat body mass differed significantly (Games-Howell $P = 0.003$) between the following months: February versus May, July and November; May versus June, July, and October; June versus July and November; July versus August and November, and October versus November (Fig. 2). Male liver mass cycle had a consistent seasonal pattern, whereas the fat bodies cycle was seasonally less consistent (Fig. 2). Liver and fat body masses did not correlate with photoperiod ($r_{liver} = 0.14$, $P = 0.079$; $r_{fat\ body} = 0.15$, $P = 0.087$), temperature ($r_{liver} = 0.31$, $P = 0.207$; $r_{fat\ body} = 0.052$, $P = 0.197$) or precipitation ($r_{liver} = 0.27$, $P = 0.203$; $r_{fat\ body} = 0.35$, $P = 0.206$). There was a significant relationship between \log_{10} – SVL and \log_{10} – fat body mass ($r^2 = 0.05$, $F_{1, 155} = 8.59$, $P = 0.004$) but not with liver mass ($r = 0.108$, $F_{1, 142} = 1.68$, $P = 0.1975$) in females. There was a significant monthly variation in liver mass ($F_{7, 136} = 4.93$, $P < 0.0001$; Fig. 2), whereas residuals of the regressions of fat body mass and female SVL revealed significant monthly variation in fat body mass ($F_{7, 149} = 16.07$, $P < 0.0001$). Liver mass differed

TABLE 1. Monthly mean (\pm 1SE) of the gonads volume changes, liver and fat body mass of the males and females of *Sceloporus grammicus* from southeastern Hidalgo, México. *N* = sample size, SPERM = spermatogenesis, EMDV = embryonic development, VITELL = vitellogenesis, and O = ovulation.

Month	<i>N</i>	Gonad/Embryo* volume (mm ³)	Liver mass (g)	Fat body mass (g)	
Males					
February	24	11.9 \pm 1.8	0.078 \pm 0.007	0.043 \pm 0.007	
March	3	10.5 \pm 2.2	0.059 \pm 0.006	0.031 \pm 0.022	
May	3	38.0 \pm 1.9	0.068 \pm 0.017	0.004 \pm 0.001	
June	55	50.9 \pm 5.2	0.073 \pm 0.008	0.044 \pm 0.008	
July	18	133.2 \pm 23.3	0.130 \pm 0.006	0.071 \pm 0.014	SPERM
August	6	78.9 \pm 11.0	0.109 \pm 0.019	0.024 \pm 0.010	
October	8	37.1 \pm 8.5	0.118 \pm 0.011	0.057 \pm 0.015	
November	7	42.9 \pm 4.	0.120 \pm 0.023	0.014 \pm 0.0	
Females					
February	52	259.5 \pm 22.8*	0.041 \pm 0.005	0.012 \pm 0.004	EMDV
March	8	341.6 \pm 71.9*	0.067 \pm 0.015	0.005 \pm 0.002	
May	7	363.2 \pm 67.9*	0.041 \pm 0.005	0.006 \pm 0.004	VITELL
June	53	1.05 \pm 0.24	0.079 \pm 0.007	0.061 \pm 0.007	
July	29	185.8 \pm 57.5	0.126 \pm 0.009	0.061 \pm 0.012	O
August	8	25.5 \pm 23.2	0.093 \pm 0.025	0.047 \pm 0.023	
October	3	18.7 \pm 5.07	0.110 \pm 0.017	0.034 \pm 0.017	
November	4	143.2 \pm 43.2*	0.152 \pm 0.017	0.012 \pm 0.004	

significantly (Games-Howell $P = 0.005$) among the following months: February versus July; June versus July, October and November (Fig. 2). Liver mass from March to June had small fluctuations, however, females from February had smaller mass. Liver masses increased again between June and July and remained high until November, after which they fell to the minimum mass by February.

Female fat body cycles had a seasonal pattern (June–November; Fig. 2). Fat body mass decreased from February to May and increased from June to November. Photoperiod ($r = 0.22$, $P = 0.078$; $r = 0.62$, $P = 0.062$), temperature ($r = 0.33$, $P = 0.095$; $r = 0.41$, $P = 0.079$), and precipitation ($r = 0.16$, $P = 0.109$) did not influence liver and fat body mass cycles, although precipitation did correlate with fat body mass ($r = 0.84$, $P = 0.009$).

Male and female reproduction.—There was a significant relationship between \log_{10} – SVL and \log_{10} – testes volume ($r = 0.25$, $F_{1, 110} = 7.03$, $P = 0.009$). Residuals of the regression revealed a significant monthly variation in testes volume ($F_{7, 104} = 8.23$, $P < 0.0001$; Table 1). In contrast, there was not a significant relationship between \log_{10} -transformed SVL and gonadal (follicles and egg/embryo) volume ($r^2 = 0.072$, $F_{1, 156} = 0.814$, $P = 0.368$). \log_{10} gonadal volume showed significant monthly variation ($F_{1, 150} = 27.3$, $P < 0.001$; Table 1). Testicular volume positively correlated with liver mass ($r = 0.32$, $P < 0.001$) and fat body mass ($r = 0.17$, $P = 0.05$). In contrast, egg/embryo volume inversely correlated with liver mass ($r = 0.292$, $P < 0.001$) and fat body mass ($r = 0.30$, $P < 0.001$).

DISCUSSION

Studies on the supply and use of energy reserves in relation to environmental demands and reproduction may provide important information on proximate restrictions on reproductive cycles and life history traits of reptiles (Ramírez-Bautista and Vitt 1997, 1998; Doughty and Shine 1998; Wapstra and Swain 2001) and are important for conservation decision-making (Bury 2006). *Sceloporus grammicus* has the typical fall reproductive pattern of viviparous species from temperate zones and high elevations. Fall-pattern species undergo spermatogenesis from July to August, vitellogenesis from July to October, ovulate from November to December, and primary embryo development occurs from December to May (Guillette and Casas-Andreu 1980; Ortega and Barbault 1984; Ramírez-Bautista et al. 2004, 2005). In this study, we observed female and male *S. grammicus* with increased liver mass and fat body volume during periods of both spermatogenesis and vitellogenesis (Goldberg 1974; Derickson 1976; Guillette and Sullivan 1985; Wapstra and Swain 2001). This pattern was similar to most other populations of *S. grammicus* studied so far (Ramírez-Bautista et al. 2006).

The higher liver and fat body masses during these times could indicate that sperm production, yolk deposition, and mating does not represent a high energetic cost compared with survival during other parts of the year, as seen in some other lizard species (Ramírez-Bautista and Pardo-De la Rosa, 2002). Males and females appear to continue foraging and storing energy during this time. However, in female *S.*

grammicus a different pattern of liver and fat body cycles occurred during embryo development. This inverse relationship between egg/embryo volume and the masses of the livers and fat bodies suggests a high energetic trade-off during this period. This is similar to many other temperate and tropical species (Guillette and Sullivan 1985; Ramírez-Bautista and Vitt 1997, 1998; Galdino et al. 2003), and also similar among populations of the same species (Ramírez-Bautista et al. 2006). Several studies on viviparous lizards support that energy for embryonic development comes from the accumulated reserves in the egg yolk (lecithotrophy) and stored energy in the liver (Tinkle and Hadley 1973; DeMarco and Guillette 1992). Our study suggests that in *S. grammicus*, stored lipids in the fat bodies of females provide additional reserves that fuel embryonic development by supplementing those resources from the liver and egg yolk (Weiss 2001; Ramírez-Bautista et al., 2002, 2006).

Adding to the evidence of a high energetic cost of embryo development, we show that after the birth of the neonates the fat bodies and liver masses of *S. grammicus* females begin to increase in size again; this pattern is similar to that which occurs in other lizard species (Castilla and Bauwens 1990; Ramírez-Bautista and Vitt 1997, 1998) and among populations of this species (Ramírez-Bautista et al. 2006). Previous studies demonstrate that the energy in fat bodies influences components of life history such as growth rate, survivorship, litter size, and SVL of neonates at birth (Ballinger 1977; Dunham 1978; Ramírez-Bautista and Vitt 1997, 1998). In this context, these traits remain unstudied in *S. grammicus* populations, but a similar relationship may exist. Understanding how unique life history strategies, such as the unusual energy management schemes, are timed could allow managers to implement actions that minimize interference during key months when demands on foraging and reproduction are at their height (see Bury 2006; McCallum and McCallum 2006).

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AURELIO RAMÍREZ-BAUTISTA is a Titular Professor level “C” at Universidad Autónoma del Estado de Hidalgo in Pachuca City, Hidalgo, México. He received his Doctorate in Biological Sciences from the Universidad Nacional Autónoma de México and he was a postdocal fellow at the University of Oklahoma. He conducted his dissertation research on the demography of *Anolis nebulosus* at the Biological Station “Chamela,” Jalisco, México. Aurelio’s current research interest include: (1) reproductive patterns in lizards from temperate and tropical environments; (2) life-history variation in lizards; (3) demography in tropical lizards; and (4) regional herpetofauna. (Photographed by Anonymous)



ALBERTO ROJAS-MARTÍNEZ is a Titular Professor level “C” at Universidad Autónoma del Estado de Hidalgo in Pachuca City, Hidalgo, México. He received his Doctorate in Biological Sciences from the Universidad Nacional Autónoma de México. He conducted his dissertation research on determination of the movements by elevation of the nectivorous bats from the central region of México. Alberto’s current research interests include: (1) population dynamics of mutualistic vertebrates of plants; (2) determination of carrying capacity of vegetation systems that produce feeding resources for vertebrates; and (3) regional fauna. (Photographed by Anonymous)



JONATHON MARSHALL is an Assistant Professor of Zoology at Weber State University in Ogden, Utah, USA. He received his Ph.D. under Jack W. Sites from Brigham Young University in 2004 and spent two years as a postdoctoral fellow at Yale University. He is now in his first year at Southern Utah University. Jonathon’s current research interests include: (1) methods and philosophical issues of species delimitation; (2) phylo-genetics/geography of *Sceloporus*; and (3) conservation biology. (Photographed by Jason R. Hurst)



DANIEL HERNÁNDEZ-RAMOS was an undergraduate researcher at Universidad Autónoma del Estado de Hidalgo in Pachuca City, Hidalgo, México. He graduated in April of 2005 and is now teaching high school biology in Tabasco City, México. Photograph by Anonymous.