
INTERRELATION OF FAT BODY MASS, LIVER MASS, AND ENVIRONMENTAL PARAMETERS ON THE REPRODUCTIVE CYCLE OF THE BROWN ANOLE (*ANOLIS SAGREI*), AN INTRODUCED LIZARD IN TAIWAN

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Abstract.—Reproductive cycle studies are essential because the reproductive biology of a species is a crucial aspect of its natural history. In lizards, stored lipids often provide the energy required for reproduction, and the liver usually plays a vital part in lipid metabolism and storage, so the examinations of the lipid and liver cycles are often important parts of lizard reproductive cycle studies. To develop a better understanding of the interrelation of the fat body mass, liver mass, and environmental parameters on the reproductive cycle of Brown Anoles (*Anolis sagrei*) in Santzepu, Sheishan District, Chiayi County, southwestern Taiwan, we collected 215 male and 204 female specimens in 13 mo. We measured and dissected the lizards to examine the interrelation of the fat body mass, liver mass, and environmental parameters on the reproductive cycle of this exotic invasive species in Taiwan. Our results provide additional support for the conclusion that photoperiods and the associated temperatures determine the reproductive cycles in *A. sagrei*. It also demonstrated that *A. sagrei* most likely combines stored energy and recently acquired nutrients to fuel reproduction, and although reproduction in this species is energetically demanding for both sexes, this species can be highly fecund in areas where suitable prey is abundant.

Key Words.—abdominal fat body mass cycle; invasive species; liver mass cycle; *Norops sagrei*

INTRODUCTION

The biochemical mechanism of storing energy as lipids, which are used for growth, maintenance and/or reproduction, enable animals to accumulate and reserve large amounts of energy in a relatively small space (Derickson 1976). Lipid cycling patterns (i.e., the storage and use of lipids) in lizards differ and can entail (1) no lipid cycling, (2) lipid cycling associated only with winter dormancy, (3) lipid cycling associated only with reproduction, (4) lipid cycling associated with reproduction and winter dormancy, or (5) lipid cycling that only takes place when sufficient food is available (Derickson 1976; Cheng 1987). Because it is unlikely that lipid cycling patterns are fixed genetically and/or determined by external environmental factors such as photoperiods, lipid cycling patterns appear to be regulated by the amount of available food and reproductive demands (Cheng 1987). Furthermore, because lipid storage usually only takes place once the demands for reproduction has been met (Cheng 1987), some spatial and temporal variations in lipid storage patterns may exist among the sexually mature individuals of even the same species.

Reproductive cycle studies are essential because the reproductive biology of a species is a crucial aspect of its natural history. An understanding of the natural history and field ecology of herpetofauna is essential for successful conservation and management programs (Bury 2006). As stored lipids often provide the energy required for reproduction in lizards (Derickson 1976), and because the liver plays a vital part in lipid metabolism and storage (Schaffner 1998), examinations of the lipid and liver cycles are often important components of lizard reproductive cycle studies (e.g., Lin and Cheng 1986; Amat et al. 2000; Ramírez-Bautista et al. 2009). Lizards of the genus *Anolis* store most of their lipids in a pair of visceral abdominal fat bodies (corpora adiposa), and measures of abdominal fat bodies are thus ideal for tracking lipid cycling patterns (Dessaur 1955; Derickson 1976).

The Brown Anole (*Anolis sagrei*) is native to Cuba, the Bahamas and adjacent islands (Rodríguez Schettino 1999; Henderson and Powell 2009) in the Atlantic Ocean. Due to the adaptability and opportunistic nature of this species, *A. sagrei* is a very successful invasive species that has managed to establish populations in parts of the Americas, Hawaii, Taiwan (Kraus 2009), and

Singapore (Tan and Lim 2012). The reproductive cycle (the period during which reproduction takes place) of *A. sagrei* has been studied in Belize (Sexton and Brown 1977), Cuba (Sanz Ochotorena and Uribe Aranzábal 1999), Florida (Lee et al. 1989), Hawaii (Goldberg et al. 2002), Jamaica (Licht and Gorman 1970), and southwestern Taiwan (Norval et al. 2012). In all these localities, the reproductive period of this species was found to be cyclic and long, and usually coinciding with the rainy season. Despite Brown and Sexton (1973) having demonstrated the importance of relative humidity for oviposition, most studies to date suggest that photoperiod and the associated temperatures are the cues that regulate the reproductive cycles of *A. sagrei* (Sexton and Brown 1977; Lee et al. 1989; Goldberg et al. 2002; Licht and Gorman 1970).

The abdominal fat body cycles of *A. sagrei* have been described for populations in Belize (Sexton and Brown 1977), Florida (Lee et al. 1989), and Jamaica (Licht and Gorman 1970) but not for populations in southwestern Taiwan. We studied both the abdominal fat body and liver weight cycles of *A. sagrei* in southwestern Taiwan. We also examined the associations between the reproductive cycles of *A. sagrei* (Norval et al. 2012) and these abdominal fat body and liver weight cycles, and with meteorological factors. This information will contribute to the understanding of the reproductive biology of *A. sagrei* not only in Taiwan, but also as a species, because the liver weight cycle of this species has not been examined in other parts of its distribution range. Such information improves our understanding of the natural history of this species, which is essential for effective management plans.

MATERIALS AND METHODS

We obtained meteorological data for Chiayi City, which is located about 5 km from the study area, for March 2002 to March 2003 from the Taiwanese Central Weather Bureau website (<http://www.cwb.gov.tw/V6e/index.htm>). We calculated the daily photoperiods for Chiayi City with the online sunrise and sunset calculator of the Graduate Institute of Astronomy of the National Central University (http://www.astro.ncu.edu.tw/index_e.shtml?p=outreach/sunriset/index.html). For this study, we only used the 215 male and 204 female *A. sagrei* specimens that were reproductively mature. These specimens were sampled by Norval et al. (2012; see also Norval et al. 2016a) during the first collection period (4 March 2002 to 28 March 2003) of the reproductive cycle. For that study, we collected *A. sagrei* specimens monthly from an area surrounding a plant nursery (23.428464N, 120.482762E, Datum WGS84) in Santzepu, Sheishan District, Chiayi County, southwestern Taiwan. After we euthanized each lizard

with ether, we measured to the nearest 1 mm the snout-vent length (SVL) and tail length (TL) with a transparent plastic ruler, scored the tail as complete or broken, and weighed the lizard to the nearest 0.1g with an electronic scale (YC e68, Shanghai Yong Cheng Scale Company, Ltd., Shanghai, China). We then made a mid-ventral incision and removed the stomach and the abdominal fat body of both sides and the liver. We weighed (wet weight) the abdominal fat bodies and the livers to the nearest 0.01 g with an electronic scale (model FX-1200; A & D Weighing, San Jose, California, USA).

We fixed all the specimens except for the right testes (removed prior to fixation) and the stomachs and stomach contents in 10% formalin for about one day, after which we stored them in vials of 75% alcohol (Norval et al. 2012). We stored the stomachs and stomach contents directly in vials filled with 70% ethanol (Norval et al. 2010). We fixed the right testes in Bouin's solution for about an hour and then prepared microscope slides of sections of them (Norval et al. 2012). To eliminate factors such as inconsistent tail lengths due to caudal autotomy and the weight of stomach and gut contents, we expressed the organ weights of specimens used in this study as a proportionate index (abdominal fat body mass or liver mass/SVL \times 100). We based all the descriptions and analyses on these indices.

In our previous study, we determined the reproductive status of males by examining the histological slides of the testicular tissue samples microscopically, with a compound light microscope at magnifications of 200 or 400 times, and we assigned each sample to one of four stages in the testicular cycle: (1) immature: spermatogonia and spermatocytes are present, but it is not possible to state when spermiogenesis will begin; (2) regressed: seminiferous tubules contained spermatogonia and Sertoli cells only; (3) recrudescing: seminiferous tubules exhibited markedly increased cellularity, with primary spermatocytes predominating; or (4) spermiogenic: sperm, spermatids, and metamorphosing spermatids abundant (Goldberg et al. 2002; Norval et al. 2012). To determine the reproductive condition of females, we visually examined the left ovaries *in situ*, and assigned them to one of four stages of the ovarian cycle: (1) inactive – no yolk deposition; (2) yolk deposition in one or more ovarian follicles; (3) oviductal eggs present and yolk deposition in one or more ovarian follicles; or (4) oviductal eggs present, and no yolk deposition in ovarian follicles (Goldberg et al. 2002; Norval et al. 2012). For this study, we considered males in stages 3 and 4 of the testicular cycle and females in stages 2 to 4 of the ovarian cycle as reproductive and thus classified specimens simply as reproductive or non-reproductive.

In the Norval et al. (2016b) study, we noted no significant variations in the monthly mean abdominal fat body mass index (AFBMI) and monthly mean liver

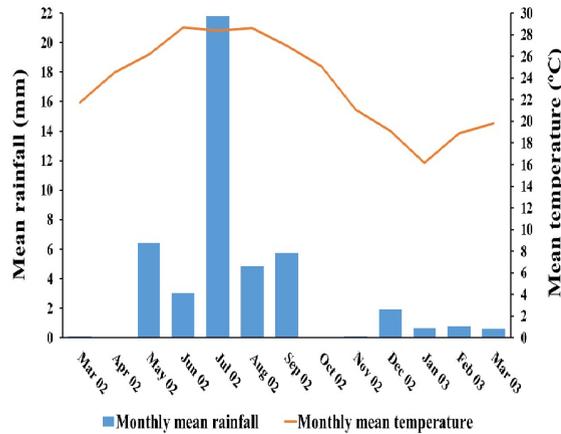


FIGURE 1. The monthly mean rainfall (in mm) and monthly mean temperature (in °C) of the Santzepu sampling area, Taiwan, Republic of China, during the study period.

mass index (LMI) of lizards that had not experienced caudal autotomy and those that had, and therefore we pooled the relevant data of the respective sexes for this study. We tested the normality of data with a one-sample Kolmogorov-Smirnov test and homoscedasticity with Bartlett's tests. Because log data transformation did not normalize the distribution of the SVL, AFBMI, or LMI data of both sexes, we used the Kruskal-Wallis Test to test for significant monthly variations in the medians of these variables, and we used the Dunn's Multiple Comparisons post-hoc test to determine which samples differed significantly from the others. We also compared the SVL, AFBMI, and LMI of males and females sampled in March 2002 and March 2003 in a univariate fashion, using the unpaired *t*-test with Welch correction. We used un-paired *t*-tests with Welch correction if data were normally distributed and homoscedastic. If these assumptions were not met, we used the Mann-Whitney *U*-test to make intersexual comparisons of the monthly mean AFBMI and monthly mean LMI. We used Spearman's rank correlation coefficient (*r*_s) to examine the associations between the monthly proportion of reproductive lizards and monthly mean AFBMI; monthly proportion of reproductive lizards and monthly mean LMI; monthly proportion of reproductive lizards and monthly mean precipitation; monthly proportion of reproductive lizards and monthly mean temperature; monthly proportion of reproductive lizards and monthly mean photoperiod; monthly mean AFBMI and monthly mean LMI; monthly mean AFBMI and monthly mean precipitation; monthly mean AFBMI and monthly mean temperature; monthly mean AFBMI and monthly mean photoperiod; monthly mean LMI and monthly mean precipitation; monthly mean LMI and monthly mean temperature; and monthly mean LMI and monthly mean photoperiod. We analyzed the data with the statistics software package Prism 6 (Graphpad

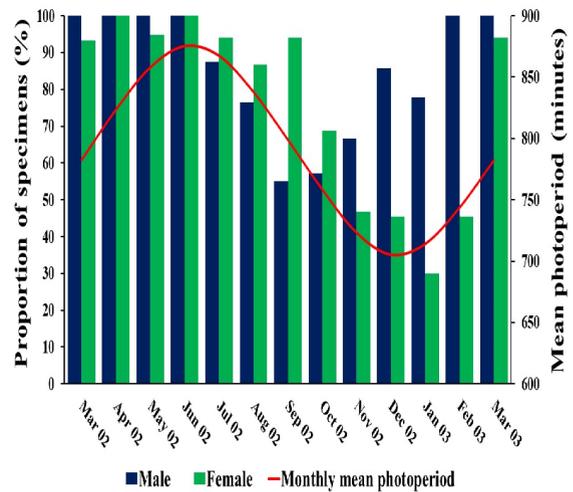


FIGURE 2. The monthly proportion (bars) of male and female Brown Anoles (*Anolis sagrei*) that were reproductive and the monthly mean photoperiod (line) for the study period.

Software, San Diego, California, USA), and we used $\alpha = 0.05$ for all tests.

RESULTS

The mean temperature for the study period was 23.49°C ($\pm 4.25^\circ\text{C}$, SD), with June 2002 the hottest month and January 2003 the coldest. During the same period, 1,419.1 mm of rain was recorded of which 47.6% occurred in July 2002 (Fig. 1). The mean daily photoperiod was $790.18\text{ min} \pm 57.79\text{ min}$, with June 2002 (867.32 min) having the longest mean photoperiod and December 2002 (705.19 min) the shortest.

The mean SVL, TL, and body mass of males were 51.00 mm (± 6.07 SD), 92.03 mm (± 19.97), and 3.86 g (± 1.32), respectively, while that of females were 40.82 mm (± 3.23), 69.28 mm (± 14.49), and 1.88 g (± 0.48), respectively (Table 1). Although all the specimens used in this study were at a sexually mature size (SVL), there were some significant differences between SVLs of males ($H = 51.07$, $df = 12$, $P < 0.001$) in April to June and females ($H = 45.33$, $df = 12$, $P < 0.001$) in March, June, and July (Appendix 1). We found no significant differences in SVLs of either males ($t = 0.955$, $df = 30$, $P = 0.347$) or females ($t = 0.585$, $df = 30$, $P = 0.563$) sampled in March 2002 and March 2003.

Reproductive males and females were present in every month of the study period, albeit in various proportions (Fig. 2). All males collected from April to June, and $> 80\%$ of females collected from March to September were in a reproductive state (Fig. 2). Male reproductive activity was minimal during September and for females during January (Fig. 2). Although there were significant positive correlations between the monthly proportion of reproductively active females and the monthly

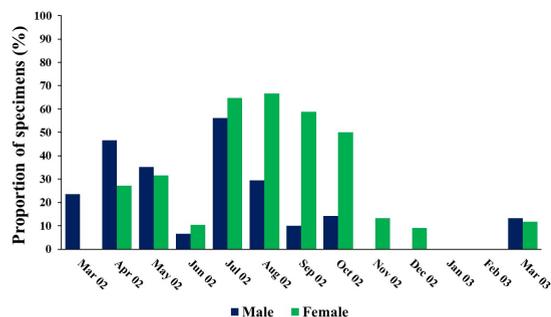


FIGURE 3. The proportion of male and female Brown Anoles (*Anolis sagrei*) from every monthly sample that had no dissectible abdominal fat bodies.

mean photoperiod and monthly mean temperature, we found no significant correlations between the monthly mean values of the climatic variables and the monthly proportion of reproductively active males (Table 2). When we analyzed the stages in the testicular cycle independently, however, there were significant negative correlations between the monthly proportion of males with testicular development stage 3 and the monthly mean photoperiod ($r_s = -0.853$; $df = 11$, $P < 0.001$) and monthly mean temperature ($r_s = -0.678$; $df = 11$, $P = 0.011$). There was also a significant positive correlation between the monthly proportion of males with testicular development stage 4 and the monthly mean photoperiod ($r_s = 0.749$; $df = 11$, $P = 0.003$).

The AFBMI of males ranged from 0 to 0.655, with a mean of 0.163 (± 0.143 SD), while that of the females ranged from 0 to 0.512, with a mean of 0.121 (± 0.119 ; Table 3). Males and females with no dissectible abdominal fat bodies were present in most of the months during the study period, but this condition was more

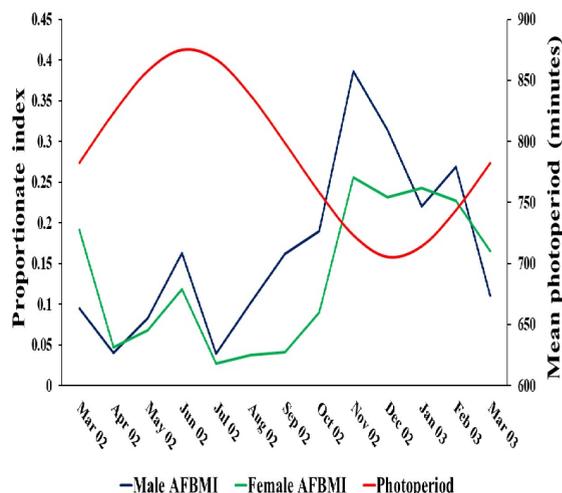


FIGURE 4. The monthly mean photoperiod (Photoperiod) for the study period, and the monthly mean abdominal fat body mass indices of male and female Brown Anoles (*Anolis sagrei*) used in this study.

common in females (Fig. 3). There were significant differences in the monthly mean AFBMI samples of males ($H = 97.88$, $df = 12$, $P < 0.001$) and females ($H = 95.36$, $df = 12$, $P < 0.001$). The intra-sex comparison of the monthly mean AFBMI of the lizards sampled in March 2002 and March 2003 did not differ significantly in males ($t = 0.503$, $df = 30$, $P = 0.619$) or females ($t = 0.740$, $df = 30$, $P = 0.465$). The monthly mean AFBMI of both sexes was lowest in July and highest in November and appeared to follow a similar cycle that had an inverse relationship with the proportion of reproductively active individuals in each monthly sample (Fig. 4). The correlation was, however, only significant in females

TABLE 1. The numbers (n) of male and female Brown Anoles (*Anolis sagrei*) sampled monthly in this study, and the monthly range, mean and standard deviation (mean \pm SD), and median (in parenthesis) of their snout-vent lengths (SVL; in mm).

	Males			Female		
	n	Range	Mean \pm SD (Median)	n	Range	Mean \pm SD (Median)
March 2002	17	36–59	49.71 \pm 7.50 (53)	15	35–46	39.73 \pm 3.17 (39)
April 2002	15	45–60	55.13 \pm 4.07 (55)	22	34–44	41.14 \pm 2.03 (41)
May 2002	17	50–58	54.53 \pm 2.43 (55)	19	36–47	42.42 \pm 2.48 (43)
June 2002	15	50–61	56.67 \pm 3.64 (58)	19	40–47	43.42 \pm 1.54 (44)
July 2002	16	39–63	53.06 \pm 7.53 (55.5)	17	38–47	43.24 \pm 2.31 (44)
August 2002	17	41–60	48.88 \pm 6.84 (46)	15	34–46	39.73 \pm 3.56 (40)
September 2002	20	40–55	48.10 \pm 3.57 (49.5)	17	35–45	40.35 \pm 2.40 (40)
October 2002	21	39–61	48.91 \pm 5.40 (50)	16	34–46	39.50 \pm 3.80 (38)
November 2002	12	44–57	50.58 \pm 4.52 (51)	15	34–46	39.67 \pm 3.52 (39)
December 2002	14	38–62	49.29 \pm 5.77 (49.5)	11	35–44	39.18 \pm 2.60 (39)
January 2003	18	39–54	47.56 \pm 4.46 (48)	10	34–45	38.70 \pm 3.83 (39)
February 2003	18	39–64	51.33 \pm 7.20 (53)	11	34–47	40.55 \pm 3.30 (40)
March 2003	15	40–63	52.07 \pm 6.33 (54)	17	34–47	40.47 \pm 3.86 (40)

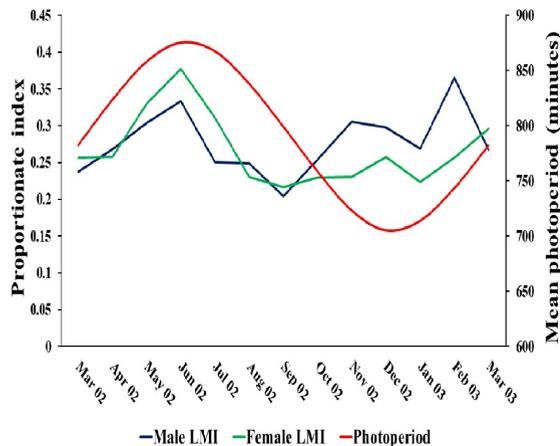


FIGURE 5. The monthly mean photoperiod (Photoperiod) for the study period, and the monthly mean liver mass indices (LMI) of male and female Brown Anoles (*Anolis sagrei*) used in this study.

(Table 2). Even when we analyzed the monthly mean AFBMI and the proportions of males in the different testicular development stages individually, there was only a significant negative correlation between the monthly proportion of males in testicular development stage 4 and their monthly mean AFBMI ($r_s = -0.613$; $df = 11$, $P = 0.026$). The monthly mean AFBMI of males and females differed significantly in March 2002 and the period August 2002 to November 2002 (Table 3). A negative correlation in both sexes between the overall monthly mean AFBMI and the monthly mean photoperiod was found, but there was only a correlation between the monthly mean AFBMI and the monthly mean temperature in females (Table 2).

TABLE 2. The results of the Spearman's rank correlation coefficient analysis between the monthly percentage of reproductive male and female Brown Anoles (*Anolis sagrei*; Repro.), monthly mean abdominal fat body mass indices (AFBMI), monthly mean liver mass indices (LMI), monthly mean precipitation (Prec.), monthly mean temperature (Temp.), and monthly mean photoperiod (Photo.). For each correlation, the number of points is 13. The asterisks (*) indicate a significant correlation.

Variable	Males		Females	
	r_s	P	r_s	P
Repro. and AFBMI	-0.370	0.214	-0.637	0.019*
Repro. and LMI	0.590	0.034*	0.571	0.042*
Repro. and Photo.	0.318	0.290	0.850	< 0.001*
Repro. and Prec.	-0.023	0.940	0.216	0.478
Repro. and Temp.	-0.101	0.742	0.690	0.009*
AFBMI and LMI	0.357	0.231	-0.126	0.681
AFBMI and Photo.	-0.780	0.002*	-0.791	0.001*
AFBMI and Prec.	-0.247	0.415	-0.467	0.108
AFBMI and Temp.	-0.550	0.052	-0.791	0.001*
LMI and Photo.	-0.181	0.553	0.506	0.078
LMI and Prec.	-0.220	0.471	0.297	0.325
LMI and Temp.	-0.363	0.223	0.258	0.394

The LMI of males ranged from 0.111 to 0.574, with a mean of 0.275 (± 0.082), while that of the females ranged from 0.118 to 0.674, with a mean of 0.272 (± 0.087 ; Table 4). There were significant differences in the monthly mean LMI samples of males ($H = 55.94$, $df = 12$, $P < 0.001$) and females ($H = 59.61$, $df = 12$, $P < 0.001$). The intra-sex comparison of the monthly mean LMI of the lizards sampled in March 2002 and March 2003 did not differ significantly in males ($t = 1.259$, $df =$

TABLE 3. The range, mean and standard deviation (mean \pm SD), and median (in parenthesis), of the monthly mean abdominal fat body mass indices (AFBMI) of male and female Brown Anoles (*Anolis sagrei*) used in this study, and the results of the inter-sexual comparisons. The asterisks (*) indicate a significant difference.

	Males		Females		Results
	Range	Mean \pm SD (Median)	Range	Mean \pm SD (Median)	
March 2002	0–0.25	0.1 \pm 0.08 (0.07)	0.09–0.31	0.19 \pm 0.08 (0.20)	$t = 3.335$; $df = 30$; $P = 0.002^*$
April 2002	0–0.13	0.04 \pm 0.05 (0.04)	0–0.15	0.05 \pm 0.05 (0.04)	$U = 147$; $P = 0.589$
May 2002	0–0.41	0.08 \pm 0.11 (0.06)	0–0.24	0.07 \pm 0.07 (0.05)	$U = 157$; $P = 0.897$
June 2002	0–0.32	0.16 \pm 0.1 (0.13)	0–0.28	0.12 \pm 0.09 (0.1)	$t = 1.193$; $df = 31$; $P = 0.242$
July 2002	0–0.15	0.04 \pm 0.05 (0)	0–0.14	0.03 \pm 0.05 (0)	$U = 119.5$; $P = 0.562$
August 2002	0–0.34	0.1 \pm 0.1 (0.09)	0–0.22	0.04 \pm 0.07 (0)	$U = 72$; $P = 0.038^*$
September 2002	0–0.58	0.16 \pm 0.14 (0.14)	0–0.26	0.04 \pm 0.07 (0)	$U = 61.5$; $P = 0.001^*$
October 2002	0–0.50	0.19 \pm 0.14 (0.19)	0–0.39	0.09 \pm 0.12 (0.03)	$U = 91$; $P = 0.019^*$
November 2002	0.09–0.65	0.39 \pm 0.17 (0.34)	0–0.5	0.26 \pm 0.13 (0.29)	$t = 2.264$; $df = 25$; $P = 0.033^*$
December 2002	0.16–0.56	0.31 \pm 0.11 (0.29)	0–0.49	0.23 \pm 0.13 (0.25)	$U = 47$; $P = 0.107$
January 2003	0.04–0.42	0.22 \pm 0.1 (0.21)	0.16–0.39	0.24 \pm 0.07 (0.21)	$t = 0.615$; $df = 26$; $P = 0.544$
February 2003	0.07–0.47	0.27 \pm 0.14 (0.26)	0.1–0.51	0.23 \pm 0.12 (0.24)	$U = 86$; $P = 0.575$
March 2003	0–0.33	0.11 \pm 0.09 (0.11)	0–0.4	0.17 \pm 0.11 (0.16)	$t = 1.542$; $df = 30$; $P = 0.134$

TABLE 4. The monthly range, mean and standard deviation (mean \pm SD), and median (in parenthesis), of the monthly mean liver mass indices (LMI) of male and female Brown Anoles (*Anolis sagrei*) used in this study, and the results of the inter-sexual comparisons. The asterisks (*) indicate a significant difference.

	Males		Females		Results
	Range	Mean \pm SD (Median)	Range	Mean \pm SD (Median)	
March 2002	0.11–0.39	0.24 \pm 0.07 (0.24)	0.15–0.37	0.26 \pm 0.07 (0.24)	$t = 0.753$; $df = 30$; $P = 0.457$
April 2002	0.16–0.4	0.27 \pm 0.06 (0.27)	0.18–0.34	0.26 \pm 0.04 (0.26)	$t = 0.591$; $df = 35$; $P = 0.558$
May 2002	0.14–0.43	0.30 \pm 0.08 (0.32)	0.19–0.50	0.33 \pm 0.08 (0.31)	$t = 0.975$; $df = 34$; $P = 0.336$
June 2002	0.23–0.45	0.33 \pm 0.06 (0.33)	0.23–0.67	0.38 \pm 0.11 (0.36)	$U = 108$; $P = 0.238$
July 2002	0.13–0.4	0.25 \pm 0.09 (0.24)	0.13–0.46	0.31 \pm 0.08 (0.32)	$t = 2.040$; $df = 31$; $P = 0.050^*$
August 2002	0.18–0.48	0.25 \pm 0.08 (0.23)	0.15–0.40	0.23 \pm 0.06 (0.23)	$U = 115$; $P = 0.653$
September 2002	0.14–0.27	0.20 \pm 0.04 (0.20)	0.13–0.33	0.22 \pm 0.06 (0.22)	$t = 0.821$; $df = 35$; $P = 0.418$
October 2002	0.15–0.41	0.25 \pm 0.06 (0.24)	0.12–0.41	0.23 \pm 0.08 (0.21)	$U = 122$; $P = 0.165$
November 2002	0.24–0.44	0.31 \pm 0.07 (0.29)	0.16–0.38	0.23 \pm 0.06 (0.22)	$U = 31$; $P = 0.004^*$
December 2002	0.16–0.46	0.30 \pm 0.10 (0.30)	0.13–0.48	0.26 \pm 0.10 (0.24)	$t = 1.033$; $df = 23$; $P = 0.312$
January 2003	0.15–0.37	0.27 \pm 0.07 (0.26)	0.15–0.33	0.22 \pm 0.06 (0.21)	$t = 1.7266$; $df = 26$; $P = 0.096$
February 2003	0.21–0.57	0.37 \pm 0.10 (0.37)	0.18–0.37	0.26 \pm 0.07 (0.24)	$t = 3.105$; $df = 27$; $P = 0.004^*$
March 2003	0.18–0.37	0.27 \pm 0.06 (0.28)	0.15–0.49	0.30 \pm 0.08 (0.30)	$t = 1.155$; $df = 30$; $P = 0.257$

30, $P = 0.218$) or females ($t = 1.436$, $df = 30$, $P = 0.161$). In both sexes the monthly mean LMI was at its lowest in September, but in males it was at its highest in February and in females in June (Fig. 5). The monthly mean LMI of males and females differed significantly in July 2002, November 2002 and February 2003 (Table 4). The monthly mean LMI cycle of both sexes resembles their respective reproductive cycles, and there were positive correlations between the monthly mean LMI of the respective sexes and the monthly proportions of reproductively active individuals (Table 2).

DISCUSSION

The results of this study indicate that in southwestern Taiwan, although *A. sagrei* males and females have annual reproductive cycles, they are not completely synchronized. The reproductive cycle of males is initiated earlier than that of females, whose cycles consequently end later than that of males. The observed timing differences are most likely related to the respective reproductive roles of the sexes and their different responses to the photoperiod and/or temperature cues that regulate reproduction (Licht and Gorman 1970; Sexton and Brown 1977; Lee et al. 1989).

Although findings from studies involving the congener species *Anolis carolinensis* need not necessarily apply to *A. sagrei* exactly, due to similarities in the biology of these species, some inferences can be made based on the results of studies pertaining to *A. carolinensis*. Studies on *A. carolinensis* males found that these lizards become photoperiod sensitive towards the end of the reproductive cycle at the end

of summer, and as day length decreases regression of their testicular activity is triggered (Licht 1971). After a brief period of quiescence, during which testicular development is most likely inhibited by photoperiod (Licht 1969), testicular recrudescence is initiated in autumn, possibly by some endogenous trigger, and lizards then become thermally sensitive (Licht 1967a). The testes develop during autumn and winter, but the cool temperatures prior to spring prevent the completion of the testicular development (Licht 1967b). In spring, shortly before the onset of the breeding season, higher ambient temperatures stimulate the completion of spermatogenesis enabling them to breed (Licht 1967b; Licht 1969). The strong negative correlation between monthly proportion of sexually mature males in stage 3 of the testicular development and the monthly mean photoperiod and the monthly mean temperature suggests that a similar process takes place in *A. sagrei* males from this study. In other words, males that reach sexual maturity at the end of the reproductive period (March to August) are photoperiod and/or thermally sensitive and that the decreasing photoperiod and/or associated cooling temperatures inhibit the complete development of the testes. As photoperiods and temperatures increase, however, testicular development is completed so that most of the sexually mature males are in a maximal stage of spermatogenesis at the onset of the high reproductive period (March to August). The importance of the influence of photoperiod on the reproductive cycle of males is not that apparent because once males reach the maximal stage of spermatogenesis they usually remain in this state, even if it is at the end of the breeding season (Licht and Gorman 1970; Sexton and Brown 1977).

The observed decline in the proportion of males in the maximal stage of spermatogenesis during the period August to December is likely due to mortality among the large males reaching the end of their life expectancy, rather than an actual decrease in reproductivity.

The monthly proportion of reproductively active females had a significant positive correlation with the mean monthly temperature and photoperiod (Table 2). Similar results were noted in reproductive cycle studies involving *A. sagrei* females in Belize (Sexton and Brown 1977), Florida (Lee et al. 1989), Hawaii (Goldberg et al. 2002), and Jamaica (Licht and Gorman 1970). A study involving *A. carolinensis* from Louisiana found that a combination of photoperiodic and thermal cues initiated reproduction in spring and regression in autumn (Licht 1973). The results of the study described herein suggest that this is also the case in *A. sagrei* females. Temperature plays an important role in the development of reptilian eggs, which tend to develop faster at higher temperatures within an acceptable temperature range wherein successful development can take place (Birchard 2004). Considering that higher temperatures are associated with longer photoperiods, it is not surprising that there was a strong positive correlation between the photoperiod and the reproductive cycle of the *A. sagrei* females in this study.

In *A. sagrei*, either in the absence of competition or with an overabundance of prey, males grow larger as a result of more available food (Schoener and Schoener 1978; Campbell 1999). This suggests that once the demands for reproduction have been met, *A. sagrei* males can be expected to direct available energy towards growth, (Schoener and Schoener 1978; Cox et al. 2009), and the depositing of lipids in the abdominal fat bodies. At the onset of the high reproductive period, males experience a reduction in stored abdominal fat body mass (Licht and Gorman 1970; Sexton and Brown 1977; Lee et al. 1989; Tokarz et al. 1998; Sanz Ochotorena and Uribe Aranzábal 1999). This indicates that in addition to spermatogenesis, the expenditure of energy during territorial conflicts and territorial displays, combined by the loss of possible foraging opportunities during these activities, are energetically costly for males. The lack of a correlation between the monthly mean abdominal fat body mass index (AFBMI) and the monthly proportion of reproductively active males in this study is thus more than likely due to the fact that lipids are not only utilized for reproduction and that aspects such as growth also greatly contribute to the depletion of energy reserves. The correlation between the monthly mean AFBMI of males and the monthly mean photoperiod is likely because during the periods of relatively long photoperiods the lizards are in a high reproductive activity period, during which males expend most energy

on growth, spermatogenesis, territorial conflicts, and territorial displays.

As female *A. sagrei* reach a size at which egg production rates can be increased, reproduction becomes a priority and growth rates decline dramatically as more energy is allocated to reproduction (Schoener and Schoener 1978; Cox et al. 2009; Norval et al. 2014; Warner et al. 2015). Because energy is thus evidently primarily allocated to reproduction, it is not surprising that we found significant negative correlations between the monthly mean AFBMI and the monthly proportion of reproductively active females, as well as between the monthly mean AFBMI and the monthly mean photoperiods and monthly mean temperatures, which determine the period of high reproductive activity. Although lizards of the genus *Anolis* store lipids in various parts of their body, lipid contents of the abdominal fat bodies and liver undergo the most seasonal changes (Dessauer 1955). Dessauer (1955) found that in *A. carolinensis*, changes in glycogen, lipids, protein and water caused the seasonal variations in liver sizes, and of these, lipids caused the greatest change. This is most likely also the case in the livers of *A. sagrei* specimens used in this study. The reptilian liver plays a vital role in the metabolism of bile acids, bile pigments, carbohydrates, hormones, lipids, and proteins (Schaffner 1998). In females, the liver is stimulated by estrogen to convert lipids from the abdominal fat bodies into vitellogenin, which is then selectively absorbed from the bloodstream by the ovarian follicles during vitellogenesis (Schaffner 1998; DeNardo 1999; Zug et al. 2001). As a result, the liver enlarges dramatically during the reproductive period (DeNardo 1999), and likely functions as an intermediary organ during the storage and use of lipids (Dessauer 1955; Derickson 1976). The study described herein supports this assumption because not just females, but also males, experienced a decrease in abdominal fat body weights and increase in liver weights during the period of high reproductive activity, when greater energetic demands are expected. Additional support for this is the positive correlation between the monthly mean LMI and the monthly proportion of reproductively active lizards noted in both sexes.

From the dietary study involving the same specimens used in this study (Norval et al. 2010), it is apparent that foraging takes place throughout the year, which suggests that prey availability does not appear to be a limiting factor for *A. sagrei* in southwestern Taiwan. Anoles (species belonging to the genera *Anolis* and *Norops*) in general tend to be opportunistic feeders (Losos 2009) and are capable of rapid fattening at any time of the year if the opportunity exists (Licht 1974). We found, however, that 7–67% of specimens used in this study had no dissectible abdominal fat bodies

during the period of high reproductive activity. It has been noted that most anoles tend to be relatively lean during the high reproductive period and fatter during the low reproductive period (Licht and Gorman 1970). This indicates that fat from the abdominal fat bodies, one of the two main fat storage depots in anoles (Dessauer 1955), is an important source of energy for reproduction, suggesting that these lizards are capital breeders. If the abdominal fat bodies were the only source of energy during reproduction, however, it would be expected that they would gradually decrease and/or remain low in weight. As can be seen by our data, as well as in other studies (Licht and Gorman 1970; Sexton et al. 1971), this is not the case, indicating that *A. sagrei* and most (if not all) other anoles are to a certain extent also income breeders, i.e., they expend parts of their acquired energy from foraging for reproduction soon after that energy is acquired (Jönsson 1997). Warner and Lovern (2014) found that females provided with a large amount of food produced larger eggs and offspring than females that received a lesser amount of food, providing additional support for this conclusion. It can thus be concluded that *A. sagrei* most likely combines stored energy and recently acquired nutrients to fuel reproduction.

Although no correlation was found between the monthly proportion of reproductive lizards, monthly AFBMI, or monthly LMI of both sexes, the importance of precipitation should not be ignored. In some other anole species, year to year variations in the timing of reproduction is evident, and the changes are correlated with the onset of the dry and wet seasons (Licht and Gorman 1970). As in Belize (Sexton and Brown 1977), Cuba (Sanz Ochotorena and Uribe Aranzábal 1999), Florida (Lee et al. 1989), and Jamaica (Licht and Gorman 1970), the period of maximal reproductive activity in females in this study coincided with the rainy season. In contrast, the period of maximal reproductive activity of females in Hawaii is during the dry season (Goldberg et al. 2002), although *A. sagrei* females have been found to prefer nest sites with a relatively high humidity (Brown and Sexton 1973). When compared to hatchlings from eggs that are deposited in relatively dry nests ($\leq 50\%$ moisture), hatchlings from eggs that are deposited in nests with about 75% moisture, have greater hatching success, tend to be larger, and have overall increased survival rates (Warner et al. 2012; Reedy et al. 2013). A study involving *Anolis aeneus* also found that moisture was crucial for juvenile growth and that even when food was abundant, juveniles could not grow rapidly when water was limited (Stamps and Tanaka 1981). Moisture is also important for many insects (i.e., potential prey) because in dry periods their eggs become quiescent, while at optimum moisture levels the larvae develop quickly (Smith 1996). It has also been found that in tropical areas, during the drier seasons, insect

abundance tends to be higher in moist localities (Janzen and Schoener 1968; Janzen 1973), and many ant species are relatively intolerant of desiccation and therefore prefer moister environments and usually increase in abundance during the rainy season (Kaspari and Weiser 2000). Therefore, although it does not regulate the reproductive cycles of *A. sagrei*, precipitation plays direct (e.g., nest environment) and indirect roles (e.g., abundance of potential prey) in the reproduction of this species.

Precipitation may however also impact on reproduction negatively. The abdominal fat body masses of both sexes in this study were minimal in July, after May and June, in which the fat bodies were increasing in mass. As opposed to most years, in which August is the month with the highest recorded rainfall, July was the month with the highest recorded monthly mean rainfall during our study, which was a result of typhoons Rammasun and Nakri that affected Taiwan. This suggests that during the period of high reproductive activity, environmental conditions such as prolonged periods of rainfall, which is unfavorable for *A. sagrei* foraging (Schoener 1968), can cause rapid decreases in the abdominal fat body masses (i.e., energy reserves), and thus potentially negatively influence the reproductive output of these lizards.

The reproductive strategies of lizards usually entail either maturing early, having relatively short lives, and being highly fecund (often as a result of producing multiple clutches per breeding season) or maturing later, having relatively long lives as reproductive adults, reproducing less often during the reproductive season, and producing few offspring per reproductive session (Tinkle 1969; Tinkle et al. 1970). Both sexes of *A. sagrei* have a life expectancy of < 2 y (Schoener and Schoener 1982; Schwartz and Henderson 1991), and although females produce clutches consisting of a single egg, under favorable conditions they are able to produce a clutch at one to two-week intervals (Cox and Calsbeek 2010), making these lizards potentially highly fecund.

In conclusion, this study provides additional support for the conclusion that photoperiods and the associated temperatures determine the reproductive cycles in *A. sagrei*. The observed fattening during the low reproductively active period suggests that lipid cycling in *A. sagrei* is primarily associated with reproduction. This study also demonstrated that *A. sagrei* most likely combines stored energy and recently acquired nutrients to fuel reproduction, which is energetically demanding for both sexes of this species.

Acknowledgments.—The research presented here adhered to the legal requirements of Taiwan, R.O.C. Because the research was not done within a national park or other conservation area, no permits or other documenta-

tion was required. Clearance for the research presented herein were granted by the College of Agriculture and Environmental Sciences (UNISA) Research Ethics Review Committee (Ref. Nr.: 2013/CAES/022), and the National Ilan University Animal Research Ethics Committee (Animal Research Application and Approval No.: 100-26). We deposited the lizards and their organs in the herpetological collection of the Department of Forestry & Natural Resources, National Ilan University, Yilan, Taiwan (Catalogue numbers NIU-FNR-GN0067 to NIU-FNR-GN0504).

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Herpetological Conservation and Biology



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APPENDIX 1. The Dunn's multiple comparisons test result of the differences in the snout-vent length (SVL), monthly mean abdominal fat body mass indices (AFBMI), and monthly mean liver mass indices (LMI) of male and female Brown Anoles (*Anolis sagrei*) used in this study. The asterisks (*) indicate a significant difference (* $P < 0.050$; ** $P < 0.010$; *** $P < 0.001$).

	Male			Female		
	SVL	AFBMI	LMI	SVL	AFBMI	LMI
March 2002 vs. April 2002	-49.594	33.441	-25.049	-27.491	73.215 *	-3.386
March 2002 vs. May 2002	-44.529	11.382	-53.471	-52.268	65.481	-47.421
March 2002 vs. June 2002	-64.594	-36.225	-76.549 *	-73.926 *	35.954	-68.895
March 2002 vs. July 2002	-31.794	33.754	-10.351	-68.312	94.916 ***	-39.529
March 2002 vs. August 2002	12.971	-1.353	-1.235	-4.267	88.633 **	21.000
March 2002 vs. September 2002	29.506	-28.759	31.468	-10.665	85.710 **	30.559
March 2002 vs. October 2002	18.682	-44.011	-11.168	-0.9938	61.940	23.406
March 2002 vs. November 2002	1.206	-104.14 ***	-56.174	-1.400	-13.233	22.300
March 2002 vs. December 2002	15.027	-95.987 **	-41.132	9.873	-5.603	3.000
March 2002 vs. January 2003	33.373	-62.614	-25.577	11.200	-19.967	29.150
March 2002 vs. February 2003	-9.183	-74.809 *	-81.188 **	-15.036	-7.421	1.136
March 2002 vs. March 2003	-15.861	-8.992	-25.549	-16.518	17.004	-26.706
April 2002 vs. May 2002	5.065	-22.059	-28.422	-24.778	-7.734	-44.035
April 2002 vs. June 2002	-15.000	-69.667	-51.500	-46.435	-37.261	-65.508 *
April 2002 vs. July 2002	17.800	0.3125	14.698	-40.821	21.701	-36.143
April 2002 vs. August 2002	62.565	-34.794	23.814	23.224	15.418	24.386
April 2002 vs. September 2002	79.100 *	-62.200	56.517	16.826	12.495	33.945
April 2002 vs. October 2002	68.276	-77.452 *	13.881	26.497	-11.276	26.793
April 2002 vs. November 2002	50.800	-137.58 ***	-31.125	26.091	-86.448 ***	25.686
April 2002 vs. December 2002	64.621	-129.43 ***	-16.083	37.364	-78.818 *	6.386
April 2002 vs. January 2003	82.967 *	-96.056 ***	-0.5278	38.691	-93.182 **	32.536
April 2002 vs. February 2003	40.411	-108.25 ***	-56.139	12.455	-80.636 *	4.523
April 2002 vs. March 2003	33.733	-42.433	-0.5000	10.973	-56.211	-23.320
May 2002 vs. June 2002	-20.065	-47.608	-23.078	-21.658	-29.526	-21.474
May 2002 vs. July 2002	12.735	22.371	43.119	-16.043	29.435	7.892
May 2002 vs. August 2002	57.500	-12.735	52.235	48.002	23.153	68.421
May 2002 vs. September 2002	74.035 *	-40.141	84.938 **	41.604	20.229	77.980 **
May 2002 vs. October 2002	63.211	-55.394	42.303	51.275	-3.541	70.827 *
May 2002 vs. November 2002	45.735	-115.52 ***	-2.703	50.868	-78.714 **	69.721 *
May 2002 vs. December 2002	59.557	-107.37 ***	12.338	62.141	-71.084	50.421
May 2002 vs. January 2003	77.902 *	-73.997 *	27.894	63.468	-85.447 *	76.571
May 2002 vs. February 2003	35.346	-86.191 **	-27.717	37.232	-72.902	48.557
May 2002 vs. March 2003	28.669	-20.375	27.922	35.751	-48.477	20.715
June 2002 vs. July 2002	32.800	69.979	66.198	5.615	58.961	29.365
June 2002 vs. August 2002	77.565 *	34.873	75.314 *	69.660 *	52.679	89.895 ***
June 2002 vs. September 2002	94.100 ***	7.467	108.02 ***	63.262	49.755	99.454 ***
June 2002 vs. October 2002	83.276 **	-7.786	65.381	72.933 *	25.985	92.301 ***
June 2002 vs. November 2002	65.800	-67.917	20.375	72.526 *	-49.188	91.195 ***
June 2002 vs. December 2002	79.621 *	-59.762	35.417	83.799 *	-41.557	71.895
June 2002 vs. January 2003	97.967 ***	-26.389	50.972	85.126 *	-55.921	98.045 **
June 2002 vs. February 2003	55.411	-38.583	-4.639	58.890	-43.376	70.031
June 2002 vs. March 2003	48.733	27.233	51.000	57.409	-18.950	42.189

Herpetological Conservation and Biology

APPENDIX 1 (CONTINUED). The Dunn's multiple comparisons test result of the differences in the snout-vent length (SVL), monthly mean abdominal fat body mass indices (AFBMI), and monthly mean liver mass indices (LMI) of male and female Brown Anoles (*Anolis sagrei*) used in this study. The asterisks (*) indicate a significant difference (* $P < 0.050$; ** $P < 0.010$; *** $P < 0.001$).

	Male			Female		
	SVL	AFBMI	LMI	SVL	AFBMI	LMI
July 2002 vs. August 2002	44.765	-35.107	9.116	64.045	-6.282	60.529
July 2002 vs. September 2002	61.300	-62.513	41.819	57.647	-9.206	70.088 *
July 2002 vs. October 2002	50.476	-77.765 *	-0.8170	67.318	-32.976	62.936
July 2002 vs. November 2002	33.000	-137.90 ***	-45.823	66.912	-108.15 ***	61.829
July 2002 vs. December 2002	46.821	-129.74 ***	-30.781	78.184 *	-100.52 ***	42.529
July 2002 vs. January 2003	65.167	-96.368 ***	-15.226	79.512	-114.88 ***	68.679
July 2002 vs. February 2003	22.611	-108.56 ***	-70.837	53.275	-102.34 ***	40.666
July 2002 vs. March 2003	15.933	-42.746	-15.198	51.794	-77.912 **	12.824
August 2002 vs. September 2002	16.535	-27.406	32.703	-6.398	-2.924	9.559
August 2002 vs. October 2002	5.711	-42.658	-9.933	3.273	-26.694	2.406
August 2002 vs. November 2002	-11.765	-102.79 ***	-54.939	2.867	-101.87 ***	1.300
August 2002 vs. December 2002	2.057	-94.634 **	-39.897	14.139	-94.236 **	-18.000
August 2002 vs. January 2003	20.402	-61.261	-24.342	15.467	-108.60 ***	8.150
August 2002 vs. February 2003	-22.154	-73.456 *	-79.953 *	-10.770	-96.055 **	-19.864
August 2002 vs. March 2003	-28.831	-7.639	-24.314	-12.251	-71.629 *	-47.706
September 2002 vs. October 2002	-10.824	-15.252	-42.636	9.671	-23.770	-7.153
September 2002 vs. November 2002	-28.300	-75.383	-87.642 **	9.265	-98.943 ***	-8.259
September 2002 vs. December 2002	-14.479	-67.229	-72.600	20.537	-91.313 **	-27.559
September 2002 vs. January 2003	3.867	-33.856	-57.044	21.865	-105.68 ***	-1.409
September 2002 vs. February 2003	-38.689	-46.050	-112.66 ***	-4.372	-93.131 **	-29.422
September 2002 vs. March 2003	-45.367	19.767	-57.017	-5.853	-68.706 *	-57.265
October 2002 vs. November 2002	-17.476	-60.131	-45.006	-0.4063	-75.173 *	-1.106
October 2002 vs. December 2002	-3.655	-51.976	-29.964	10.866	-67.543	-20.406
October 2002 vs. January 2003	14.690	-18.603	-14.409	12.194	-81.906 *	5.744
October 2002 vs. February 2003	-27.865	-30.798	-70.020 *	-14.043	-69.361	-22.270
October 2002 vs. March 2003	-34.543	35.019	-14.381	-15.524	-44.936	-50.112
November 2002 vs. December 2002	13.821	8.155	15.042	11.273	7.630	-19.300
November 2002 vs. January 2003	32.167	41.528	30.597	12.600	-6.733	6.850
November 2002 vs. February 2003	-10.389	29.333	-25.014	-13.636	5.812	-21.164
November 2002 vs. March 2003	-17.067	95.150 **	30.625	-15.118	30.237	-49.006
December 2002 vs. January 2003	18.345	33.373	15.556	1.327	-14.364	26.150
December 2002 vs. February 2003	-24.210	21.179	-40.056	-24.909	-1.818	-1.864
December 2002 vs. March 2003	-30.888	86.995 *	15.583	-26.390	22.607	-29.706
January 2003 vs. February 2003	-42.556	-12.194	-55.611	-26.236	12.545	-28.014
January 2003 vs. March 2003	-49.233	53.622	0.02778	-27.718	36.971	-55.856
February 2003 vs. March 2003	-6.678	65.817	55.639	-1.481	24.425	-27.842