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Seasonal Variation of Gonadal Development, Sexual Steroids, and Lipid Reserves in a Population of the Lizard *Psammodromus algirus*

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ABSTRACT.—We studied the seasonal variations of reproductive characteristics in a wild population of the lacertid lizard *Psammodromus algirus* by measuring gonadal weight, germinal epithelium height, sexual steroids (testosterone, estradiol, and progesterone), and lipid reserves (in fat bodies and liver) in three phases of the reproductive cycle: early breeding (late April), late breeding (mid-June), and post-breeding season (late July). In males, testis size, germinal epithelium, and testosterone plasma levels were high in the breeding season and decreased dramatically in July. However, spermatogenesis (maximum in June) was slightly delayed with respect to testosterone secretion (peak in April), suggesting that a previous increase in testosterone levels could be necessary to stimulate the initial stages of spermatogenesis. Larger testes and higher testosterone levels were found in larger and more brightly colored males, known to overlap with more females and court them more frequently than their smaller conspecifics. In females, the ovary was previtellogenic in early spring, and showed a rapid growth by mid-June, oviposition occurring in early summer. The increase in 17 β-estradiol levels observed between April and June was coincident with the maturation of previtellogenic follicles. In both sexes fat body cycles were inversely correlated with gonadal cycles. By the end of the breeding season there was a reactivation of hepatic lipogenesis that was coincident with a significant decrease in activity levels.

In reptiles, the best data about gonadal steroids and their cyclicity come from direct measurements of plasma levels by radioimmunoassay, a technique that was fully developed only in the last few years (Kime, 1987). The interactions among these hormones, whose levels are usually measured under laboratory conditions, are of considerable value for understanding the endocrine basis of reptilian reproductive cycles. However, any study of the seasonal variation of endocrine function should at least bear in mind the serious effects of captivity-imposed stress on circulating hormone levels (Licht et al., 1985; Cree et al., 1990). In fact, captive animals usually show significantly lower hormonal levels than free ranging animals under field conditions (reviewed by Greenberg and Wingfield, 1987). Thus, field studies are crucial to evaluate the relevance of the results obtained at the laboratory. Data obtained from free ranging animals are also needed to situate physiological mechanisms within their behavioral and ecological context.

Gonadal cycles of lacertid lizards have received considerable attention in recent years (Bauwens and Verheyen, 1985; Kwiat and Gist, 1987; Braña et al., 1990; Castilla and Bauwens, 1990; Carretero and Llorente, 1991), but relatively few studies have examined seasonal variation of hormonal levels (Courty and Dufaure, 1982; Xavier, 1982; Carnevali et al., 1991; Andó et al., 1992). In addition, data on variations in fat reserves are also needed (Hahn and Tinkle, 1965; Derickson, 1976). Lacertid lipid reserves often show clear cyclicity (Telford, 1970; Braña et al., 1990; Castilla and Bauwens, 1990; Braña et al., 1992). Most of the information available, however, refers to abdominal fat bodies. The lipid contents of the liver, which is an intermediary organ involved in the synthesis, storage, and utilization of lipids, have received much less attention.

Psammodromus algirus is perhaps the most abundant lizard in many regions of the Western Mediterranean (Arnold and Burton, 1978). However, no data have been published concerning reproductive cycles. Moreover, the fact that male *P. algirus* show an orange/reddish sexual coloration developed during the breeding season (Mellado and Martínez, 1974), makes it particularly interesting to study the underlying endocrine mechanisms. This is because the development of the breeding coloration, which is greater in larger (and presumably older) males, is positively related to the activity level, home range area, and intensity of courtship behavior displayed by males (Díaz, 1993). The present study reports seasonal changes in a field population of *Psammodromus algirus* with respect to: (1) gonadal weight; (2) developmental stages of gametogenesis; (3) steroidogenic cycles (levels of testosterone, estradiol, and progesterone, measured from blood samples taken in the field); (4) lipid reserves in fat bodies; and (5) lipid contents of liver. All this information was combined with field data on the seasonal variations of activity. In addition, we explored the relationships between testosterone levels, testis size, and male mating opportunities, using a correlational approach based on differences among males in body size and color pattern (Díaz, 1993).

MATERIALS AND METHODS

Adult females and males were captured in central Spain at a holm-oak (*Quercus rotundifolia*) forest (Soto de Viñuelas, Madrid; 40°35'N, 03°34'W). Captures were made at three distinct times of year: mid-April, early June, and late July. Blood sampling was done immediately after capture in heparinized microtubes by cardiac puncture on lizards anaesthetized with diethyl ether. Blood was kept at 4 C until arrival at the laboratory (maximum 4 h), where plasma samples were obtained by centrifugation, and stored frozen at −25°C until hormonal levels were determined.

The ovaries and oviductal eggs, testes, liver, and fat bodies were removed in the field and kept at 4 C for not more than 4 h. For histological analyses, one testis from each animal was fixed in 10% formalin for 24 h, dehydrated in a graded series of ethyl alcohol, cleared in xylene, embedded in paraffin, serially sectioned at 8 μm, and stained with haematoxylin-eosin. Histometric analysis (germinal epithelium height, given in μm) was performed using an ocular micrometer. Ovarian follicular development was evaluated by measuring the follicular diameters with an ocular micrometer; results are given as relative percentages of three different follicular size classes (<0.5 mm, 0.5–1.5 mm, and >1.5 mm).

Total lipid contents in liver were determined following the method of De la Huerga (1969). After lipid extraction with chloroform-methanol (2:1), the solution of lipids was evaporated to dryness and resuspended in dioxane at 100 C. The quantity of lipids was determined by spectrophotometry at 515 nm, using triolein (Sigma) as a standard.

Steroid plasma levels were measured by radioimmunoassay (RIA) with commercial kits (Sorin) using ^{125}I-testosterone and ^{125}I-estradiol. Plasma levels were quantified without extraction, in duplicate samples from individual lizards. Measurements were made on 25 μl plasma samples. Steroids showing cross-reactivity with the antiserum for testosterone were: testosterone, 100%; 5α-dihydrotestosterone, 7.2%; androstenedione, 0.81%; and other steroids <0.1%. The sensitivity limit of testosterone RIA was 40 pg/ml and the nonspecific binding was 3.5%. The inter- and intraassay coefficients of variation were 9.1% and 5.4%, respectively. Cross-reactivity for estradiol antiserum was: 17β-estradiol, 100%; estrone, 0.9%; estriol, 0.28%; and other steroids, <0.01%. The sensitivity limit of estradiol RIA was 6 pg/ml, and the nonspecific binding was 5%. The inter- and intraassay coefficients of variation were 9.3% and 7.2%, respectively.

Activity was estimated in the field by the number of detected individual lizards per person-hour of search. Censuses were carried out during the course of a study on the spacing patterns and reproductive behavior of *P. algirus* (Díaz, 1993) that covered the whole 1989 activity season. Although our data probably underestimate activity (see Carrascal and Díaz, 1989), due to time spent in the capture and manipulation of animals, the bias was consistent throughout the study year, thereby allowing the detection of seasonal trends.

Nine males from the April sample were arranged according to their development of the red breeding coloration of the head (Mellado and Martínez, 1974; Díaz, 1993). The lower rank was given to the most brightly colored male, and the color sequence was validated by the coincidence among different observers.

TABLE 1. Seasonal variation of the reproductive characteristics of male *Psammodromus algirus*.

	20-25 April		5-9 June		26-31 July	
	x̄ ± SE	N	x̄ ± SE	N	x̄ ± SE	N
Testis weight (mg)	123.2 ± 5.0	15	129.3 ± 5.9	14	6.7 ± 1.3	15
Germinal epithelium height (μm)	37.7 ± 1.5	9	71.7 ± 1.8	5	13.0 ± 2.4	5
Testosterone levels (ng/ml)	15.6 ± 1.1	15	10.2 ± 1.3	11	0.3 ± 0.03	15
Fat bodies weight (mg)	5.2 ± 2.7	15	0.0 ± 0.0	14	106.2 ± 22.8	15
Liver lipids (mg/g tissue)	28.2 ± 2.9	15	95.5 ± 3.3	14	110.7 ± 5.1	15

All statistical analyses were nonparametric due to small sample sizes, heterogeneity of variances, and lack of adjustment to normality in nearly all distributions of the data. We employed Mann-Whitney U tests and Kruskal-Wallis one-way analyses by ranks to examine the seasonal variation of gonadal and fat bodies weight, spermatogenic activity, steroid plasma levels, and liver lipids. The relationships among male breeding coloration, testosterone levels, testis weight, and body size, were explored using Spearman rank correlations. In order to minimize body size effects, statistical tests with organ weights were repeated using residuals from the regression between organ mass and snout-vent length (SVL).

RESULTS

Males.—Testis weight varied significantly throughout the activity season (Table 1: Kruskal-Wallis test, H = 29.1, $P < 0.001$). Such variation was also significant when gonadal weight was adjusted to body size using residual analysis (H = 29.0, $P < 0.001$). The development of testes during the breeding season, already maximal in April but maintained at least until mid-June, was followed by a twenty fold postreproductive regression in late July.

Similarly, spermatogenic activity (Table 1) showed a highly significant pattern of seasonal variation (H = 14.1, $P < 0.001$). The germinal epithelium increased in height between April and June (Mann-Whitney Z = 2.76, $P = 0.006$), reached its highest growth and maturation in this later month, and showed a regressed spermatogenic pattern in the postbreeding season.

Plasma testosterone levels paralleled gonadal changes showing an even greater seasonal variation (Table 1: H = 31.1, $P < 0.001$). In fact, testosterone levels decreased significantly between April and June (Mann-Whitney Z = 2.75, $P = 0.006$) before the one hundred fold postbreeding decrease that took place between June and July.

In April (i.e., at the beginning of the reproductive season), testes were larger, and plasma testosterone levels were higher, in larger males (Table 2). In addition, the development of the red coloration of the head (see Introduction), was positively rank-correlated in April with body size ($r_s = 0.73$, N = 9, $P < 0.05$), testis weight ($r_s = 0.78$, $P < 0.05$), and testosterone plasma levels ($r_s = 0.68$, $P = 0.05$). The relationship between body size and circulating androgen levels vanished in the late breeding season and in the postbreeding season (Table 2). Similarly, the allometric relationship between body and testis size decreased in June but was again highly significant in July when all males had undergone testicular regression (Tables 1 and 2). Testosterone plasma levels were correlated with germinal epithelium height in April (r_s = 0.78, N = 7, $P = 0.054$) but not in June or in July ($P > 0.5$ in both cases).

Lipid storage in fat bodies occurred basically after the cessation of reproductive activity and showed a pronounced seasonal variation (Table 1: H = 29.7, $P < 0.001$; SVL adjusted: H = 29.0, $P < 0.001$) that was inversely related to the cycles of testosterone secretion and testicular development. Liver lipids also varied significantly among sampling dates (Table 1: H = 31.5, $P < 0.001$), though the main increase took place within the breeding season and before the onset

TABLE 2. Relationships between body size and male reproductive cycles: Spearman rank correlations between body size of males (snout-vent length, SVL) and gonadal development (testis weight), and between SVL and testosterone plasma levels.

	SVL vs. testis weight			SVL vs. testosterone		
	r_s	*P*	N	r_s	*P*	N
20-25 April	0.786	0.003	15	0.571	0.032	15
5-9 June	0.427	0.177	11	−0.300	0.343	11
26-31 July	0.819	0.002	15	0.248	0.353	15

TABLE 3. Seasonal variation of the reproductive characteristics of female *Psammodromus algirus*.

	20–25 April		5–9 June		26–31 July	
	x̄ ± SE	N	x̄ ± SE	N	x̄ ± SE	N
Gonadal (ovary + oviduct) weight (g)	0.04 ± 0.00	9	1.68 ± 0.22	9	0.01 ± 0.00	14
% follicles <0.5 mm	28.1 ± 1.8	9	10.0 ± 4.6	4	78.3 ± 4.0	7
% follicles 0.5–1.5 mm	13.8 ± 1.2	9	53.2 ± 18.1	4	16.8 ± 4.5	7
% follicles >1.5 mm	57.2 ± 2.3	9	36.5 ± 13.6	4	4.3 ± 4.3	7
17β-estradiol levels (pg/ml)	99.9 ± 15.4	9	262.8 ± 92.9	5	81.4 ± 14.9	14
Progesterone levels (ng/ml)	5.0 ± 0.8	8	15.6 ± 3.6	3	—	—
Fat bodies weight (mg)	120.3 ± 18.5	9	0.0 ± 0.0	9	96.3 ± 16.1	12
Liver lipids (mg/g tissue)	46.0 ± 6.3	9	96.3 ± 7.3	9	122.5 ± 9.7	14

of testicular regression. The patterns of gonadal and lipid variation in males were roughly consistent with the activity curve shown in Fig. 1. Activity, estimated as number of lizards seen per person-hour, varied significantly between months (H = 16.3, $P = 0.006$), peaking in the reproductive season (May–June) and then decreasing from mid-June until late summer. Similarly, the body condition of adult males, estimated using residuals from the regression between body weight and SVL, followed the same pattern as did abdominal fat bodies (mean deviations of −0.07, −0.37, and 0.42 g from the values expected according to SVL in April, June, and July, respectively: H = 5.52, $P = 0.063$).

Females.—No gravid females were found in April (0 of 9), whereas most females were gravid in June (9 of 11) and only a small number (2 of 16) had oviductal eggs in July. Females without eggs in June and those gravid in July were excluded from subsequent analyses in order to group specimens according to reproductive condition, rather than just a seasonal grouping of animals in different reproductive stages. Gonadal weight (ovary plus oviduct) varied significantly throughout the spring-summer season (Kruskal-Wallis test with the data shown in Table 3: H = 25.2, $P < 0.001$). Such variation was also significant when gonadal weight was adjusted for body size (H = 17.2, $P < 0.001$).

The analysis of ovarian development showed a pattern of follicular production consistent with variations in organ size. The numbers of follicles examined in April, June, and July (x̄ ± SE) were 22.9 ± 1.1, 14.8 ± 3.3, and 15.7 ± 0.7 follicles from N = 9, 4, and 7 females, respectively. In April (Table 3), most follicles were enlarged (>1 mm in diameter) and ready to undergo vitellogenesis, whereas in July, i.e., after oviposition, over 70% of the follicles were small previtellogenic ones (<0.5 mm in diameter). Thus, the proportion of follicles that were small (<0.5 mm), intermediate (0.5–1.5 mm), and large (>1.5 mm) varied significantly throughout the activity season (Table 3: $\chi^2_4 = 141.9$, $P < 0.001$).

Both 17 β-estradiol and progesterone plasma levels (Table 3) showed a significant seasonal variation (estradiol: H = 8.9, $P = 0.011$; progesterone: Mann-Whitney Z = 2.35, $P < 0.02$) that was synchronized with ovarian stages: estradiol levels were highest in mid-June, prior to oviposition, and decreased in July, when most follicles were small (previtellogenic); progesterone levels increased from April (developing follicles but no oviductal eggs) to June (nearly all females with oviductal eggs).

Females with oviductal eggs (N = 11) had an average clutch size (X ± SE) of 5.45 ± 0.39 shelled eggs (range 4–8). No correlation was found between female SVL and clutch size ($r_s = 0.08$, N = 11, $P > 0.75$). Instead, female size was correlated with clutch mass and mean egg mass (r = 0.81, N = 11, and $P = 0.011$ in both cases), which suggests that larger females might lay larger eggs.

The cycle of fat bodies was inversely correlated with ovarian growth, so that their weight varied significantly between sampling dates (Table 3: H = 19.5, $P < 0.001$; we did not adjust for body size effects because the correlation between female SVL and fat bodies weight was not significant, $P > 0.7$). On the other hand, lipid contents of liver were low in April and increased significantly in June and July (Table 3: H = 20.3, $P < 0.001$).

DISCUSSION

In April, larger males had larger testes and higher testosterone levels, and these were associated with a brighter coloration. These results are consistent with behavioral differences suggesting an asymmetry in mating opportunities between large, brightly colored males, and smaller, dully colored ones. Moreover, increased testosterone levels could be directly responsible for the observed increased frequency of courtship in larger males (Díaz, 1993). As demonstrated by Moore and Marler (1987), testosterone-implanted male *Sceloporus jarrovi* are more aggressive than control animals, which suggests a greater degree of success in male-

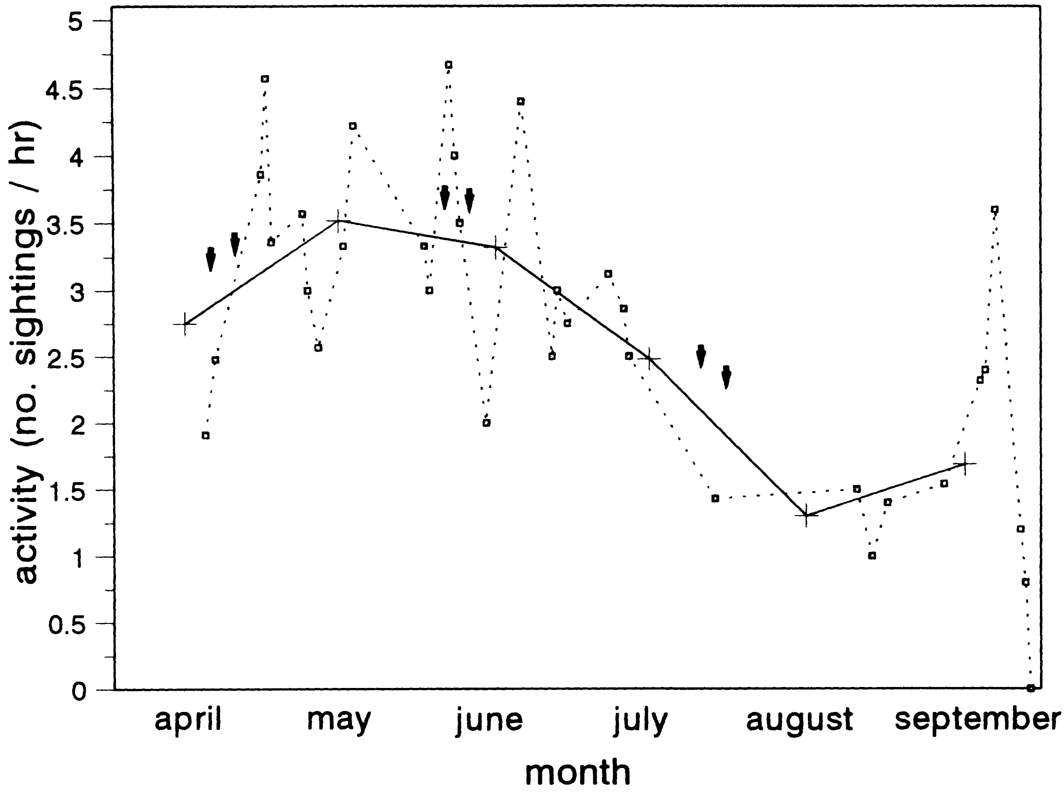

FIG. 1. Monthly variations of activity (number of lizards per person-hour of search) in the *Psammodromus algirus* population studied. Squares and crosses represent one day estimates and monthly means, respectively. The arrows indicate the location of lizard collecting dates.

male competition. Thus, the behavioral effects of testosterone could combine with body size differences (Tokarz, 1985; Vitt and Cooper, 1985) in determining the outcome of hostile interactions. In turn, larger males would have more numerous interstitial cells able to secrete testosterone. Concerning the relationship between testosterone levels and male patterns of sexual coloration, several studies have shown hormonal inductions of color change in both males (Moore and Thompson, 1990) and females (Cooper and Ferguson, 1973; Medica et al., 1973) of several lizard species, as well as an effect of throat coloration in the outcome of aggressive interactions among males (Hover, 1985).

Our results indicate that male *P. algirus* showed a prenuptial spermatogenic pattern, because sperm was produced immediately after hibernation (germinal epithelium height was maximal in June and there were no sperm bundles in April). At this time, i.e., at the beginning of the breeding season, testosterone levels were highest. Nevertheless, the peak of plasma testosterone preceded the spermatogenic wave that was observed between April and June. This result suggests that a previous increase in testosterone levels would be necessary to stimulate spermatogonia multiplication, as has been shown in other ectothermic vertebrates (Delgado et al., 1989, 1992). A similar asynchrony between testosterone secretion and spermatogenesis has been observed in other reptiles (Moll, 1979; Licht et al., 1985; Naulleau et al., 1987), and this duality would be consistent with the existence of two different gonadotropins regulating the endocrine and gametogenic components of testicular function (Licht, 1984).

Psammodromus algirus is a seasonal autochronic breeder (Smith et al., 1973), since follicles develop synchronously in the two ovaries. The vitellogenic cycle of *P. algirus* falls into the most common pattern found among temperate, single-clutched lizards and snakes (review by Licht, 1984); the ovary remained in a previtellogenic condition between midsummer and early spring, and then showed a rapid growth before oviposition (ovarian weight increased by two orders of magnitude within a few weeks).

The coincidence between the increase in 17 β-estradiol levels between April and June and the transformation of previtellogenic to mature follicles during the same time period supported the hypothesis that this hormone is the primary stimulus for hepatic vitellogenesis (Gavaud, 1986; reviewed by Ho, 1987). The low estradiol levels measured in the post-oviposition stage (late July) were consistent with the ovarian status at this time, when only small previtellogenic follicles were present. However, the activity of estrogens may be influenced by other hormones such as progesterone (Ho, 1987). In *P. algirus*, plasma progesterone levels were elevated during gravidity, as it has been found in other reptiles (Licht et al., 1979; Wibbels et al., 1990). High progesterone levels promote egg shelling and help maintain oviductal vascularity and secretion of egg covers (Ho, 1987). Alternatively, progesterone levels were reduced in April, which is consistent with the fact that progesterone inhibits the vitellogenic process and the effects of estrogens on sexual behaviour (Ho et al., 1982; Ho, 1987).

Female fat bodies were minimal in June, during gravidity, probably due to the investment of their lipid contents in vitellogenesis (Smith, 1968; Derickson, 1974, 1976). Liver lipids were high in June, when 17 β-estradiol plasma levels were maximal, probably because of the crucial role played by the liver in the estrogen-induced synthesis of yolk (Carnevali et al., 1991). On the other hand, 17 β-estradiol does not only induce vitellogenin synthesis by the liver, but it also has some lipolytic effect (Hahn, 1967). In July, when nearly all females had laid their eggs and estradiol levels had decreased, liver lipids remained high, showing an active lipogenesis apparently directed towards lipid storage in fat bodies for use in the next season's reproductive cycle (Derickson, 1976). Moreover, the activation of hepatic lipogenesis in the postbreeding season (late July), observed in both sexes, was consistent with the selection of fewer but larger prey (Díaz and Carrascal, 1990, 1993) that probably yielded relatively more energy per capture. It is clear from our results that metabolic resources were intensively used during the breeding season, both by males and females, to support gonadal development and/or to meet the higher energy requirements of increased activity. In fact, activity peaked in the breeding season and was markedly reduced after mid-July (Fig. 1), when most females had laid their clutches and male-male competition was weaker than in previous months.

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