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REPRODUCTION OF THE CAPE ORANGE-THROAT WHIPTAIL, *CNEMIDOPHORUS HYPERYTHRUS HYPERYTHRUS*

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Abstract. The reproductive cycle of the endemic lizard *Cnemidophorus hyperythrus hyperythrus* at El Comitán, Baja California Sur, México, was determined through the dissection of 42 males and 78 females during 1992 and 1993. Vitellogenesis begins in March and ends in July. Oviductal eggs appeared in June. Mean clutch size was 2.55 eggs and positively correlated with female body size. Maximum testes size was recorded in August. Female fat body depletion was associated with vitellogenesis but in males the fat body cycle was not correlated with an increase in testis mass. The reproductive characteristics of this population are compared to those of other *Cnemidophorus* species and to other Mexican lizards of similar latitudes.

Resumen. El ciclo reproductivo de la lagartija endémica *Cnemidophorus hyperythrus hyperythrus*, en El Comitán, Baja California Sur, Mexico, fué determinado a través de la disección de 42 machos y 78 hembras durante 1992 y 1993. La vitelogénesis comenzó en Marzo y terminó en Julio. Los huevos oviducales aparecieron en Junio. El tamaño de puesta promedio fue de 2.55 huevos y está correlacionado directamente con el tamaño de las hembras. El tamaño máximo testicular se registró en Agosto. La diminución de los cuerpos lipídicos de las hembras, estuvo asociado con la vitelogénesis, pero en los machos no estuvo correlacionada con el incremento en la masa testicular. Las características reproductivas de esta población se compararon con otras especies de *Cnemidophorus* y con otras especies Mexicanas de latitudes similares.

Key Words: Baja California Sur; Cape lizard; *Cnemidophorus hyperythrus hyperythrus*; Reproduction.

One of the least-well studied desert lizards in North America is the Cape orange-throat whiptail, *Cnemidophorus hyperythrus hyperythrus*. It is a small (5–9.4 cm SVL; Stebbins 1985), slender, and active diurnal lizard. The main characteristic of this lizard is the reddish-orange color of its throat, belly, and ventral side of the tail, which becomes more intense and evident in the breeding season (Stebbins 1985). This lizard inhabits washes and other sandy areas where there are rocks and patches of brush, as well as rocky hillsides, coastal chaparral, thornscrub, and riparian habitats (Galina 1994). *Cnemidophorus h. hyperythrus* is endemic to the Cape Region of the southern part of the Baja California peninsula and to 51 adjacent islands (Galina 1994), and it is abundant in our study area, "El Comitán." Although *C. h. hyperythrus* is an abundant and conspicuous diurnal lizard in the Cape Region, and despite the fact that some aspects of subspecies ecology are known (Asplund 1967; Galina 1994; Karasov and Anderson 1984), its complete reproductive cycle has not been studied. For this reason, and because of its endemism, we studied the reproductive cycle of *C. h. hyperythrus* to answer the following questions: (1) Is the reproductive cycle of this endemic subspecies similar to that of other species? (2) Is there synchrony between male and female reproduction cycles? (3) Is there a synchrony among fat bodies and reproductive cycles?

MATERIALS AND METHODS

Study Site

Field work was conducted at "El Comitán" in the northern part of the Cape Region, 20 km north of La Paz, Baja California Sur, México (24°10' N, 110°30' W). El Comitán is a coastal lowland (10 m above sea level) with mud-sandy soils (Romero-Schmidt et al. 1994). The climate of the zone is warm and arid with an average annual temperature of 23.9°C and mean annual precipitation of 62 mm which falls primarily during summer (Fig. 1; Alvarez et al. 1989). Its predominant flora is xerophytic scrub (Léon de la Luz and Troyo 1985).

Reproductive Cycle

During the first three days of each month from April 1992–March 1993, we traversed an area of 50 ha at El Comitán in search of adult *C. h. hyperythrus*. Lizards were collected using rubber bands and by hand and returned to the laboratory within 3 h of capture. We recorded snout–vent length (SVL), tail length, body weight, and fat body mass for all individuals. For females, we recorded the mass, diameter, number of unyolked follicles, yolked follicles and corpora lutea in both ovaries, and oviductal eggs. For males, we recorded the length and

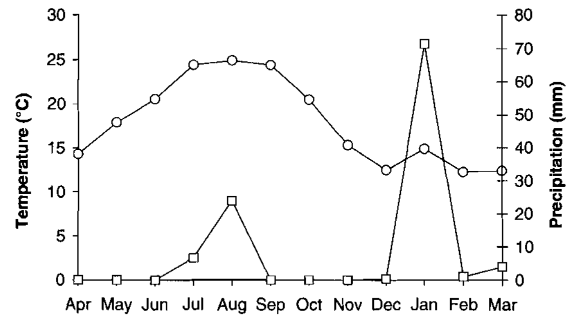

Figure 1. Average monthly temperature (circles) and precipitation (squares) at the El Comitán study site during April 1992–March 1993.

Table 1. Body size and reproductive cycle data for female *Cnemidophorus hyperythrus hyperythrus* collected in 1992 and 1993 (sd = standard deviation).

	1993	1992						
	Mar	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**
n	9	10	10	10	10	10	10	9
SVL (mm)	52.83	54.05	54.59	57.8	57.9	57.94	59.74	48.46
sd	0.33	0.48	0.57	0.41	0.62	0.43	0.44	1.12
Body mass (g)	4.27	4.30	5.00	4.30	4.75	5.21	5.11	3.21
sd	0.18	0.27	0.09	0.04	0.2	0.13	0.12	0.22
Ovary mass (g)	0.002	0.019	0.027	0.037	0.047	0.056	0.021	0.0004
sd	0.0002	0.001	0.0017	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Fat body mass (g)	0.047	0.057	0.033	0.007	0	0	0.005	0.004
sd	0.002	0.001	0.001	0.0003	-	-	0.0002	0.0002
Follicles with vitellum (mm)	0.90	1.60	1.90	1.90	2.60	-	-	-
Oviductal eggs (mm)	-	-	-	3.60	8.60	14.40	15.10	-
Corpora lutea (mm)	-	-	-	2.00	2.80	1.90	0.70	-
% with vitellogenesis	22.20	40.00	60.00	100.00	50.00	-	-	-
% with oviductal eggs	-	-	-	40.00	80.00	100.00	20.00	-
% with corpora lutea	-	-	-	50.00	90.00	100.00	30.00	-

mass of the testes. Linear measurements were made with calipers (to nearest 1 mm) and mass recorded to the nearest 0.001 g with a digital balance (Ohaus Model E4000D).

Reproductive characteristics were averaged to obtain monthly means. Using SVL as a covariate, an analysis of covariance (ANCOVA) and Student-Newman-Keuls (SNK) post-hoc test (Sokal and Rohlf 1969) were used to define significant differences among monthly values and to identify statistically indistinguishable months respectively. The specimens were deposited in the CIBNOR collections.

RESULTS

Female Reproductive Cycle

Seventy-eight females were dissected in total. Most females collected in March ($n = 9$) had undeveloped ovaries, but by late March follicular development began in some (22.2% had yolked follicles). In June, all females showed signs of yolk deposition and by July most contained oviductal eggs (Table 1). The female reproductive season peaked in August, when all females had oviductal eggs and several corpora lutea. In October, reproductive activity had ceased.

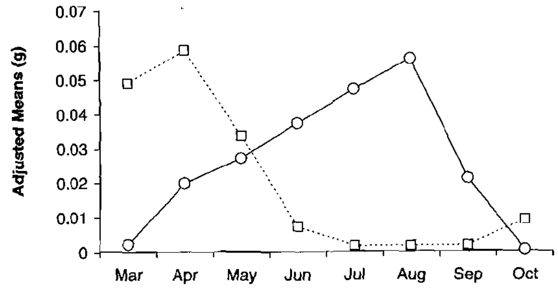

Figure 2. *Cnemidophorus hyperythrus hyperythrus* ovary (circles) and fat body (squares) mass. Means adjusted for SVL.

Analysis of covariance (ANCOVA) with SVL as the covariate was used to statistically remove the SVL-ovarian mass relationship so that the changes in monthly ovarian mass were not influenced by a body-size bias among months. We found that there was a significant difference among the monthly analyzed ovarian masses ($r^2 = 0.56$; $F_{(7,69)} = 77.3$; $P < 0.001$; Fig. 2). Ovary mass increased from March to August, the month when mass is at a maximum, and abruptly declined in September and October. The SNK test revealed that there were significant differences among all pairwise comparisons among months except for March and October.

The relationship between body size and repro-

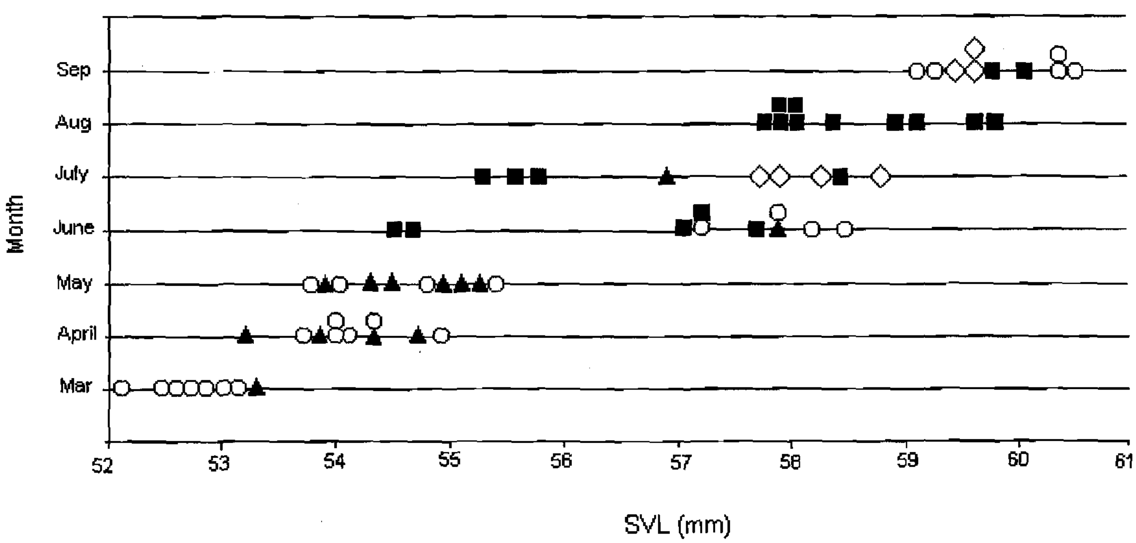

Figure 3. Relationship between body size (SVL), reproductive condition, and capture period of female *Cnemidophorus hyperythrus hyperythrus*. Each symbol corresponds to one animal: circle = nonreproductives; triangle = ovarian follicles; square = oviductal eggs; diamond = postreproductive.

ductive condition is shown in Fig. 3. Body size of dissected females (n = 78) ranged from 46–60 mm SVL. Reproductive females (those with yolked follicles or oviductal eggs) ranged in size from 53–60 mm ($\bar{x}$ = 58.02 ± 0.6 mm)

Prior to reproduction ovaries contained from 4–12 ($\bar{x}$ = 6) transparent to translucent white or gray follicles < 1 mm in diameter. These were indistinguishable from those found in postreproductive females. Yolked follicles were present in females collected in late March and were common until June (range 10–20 follicles; x = 12), ranging from 2.0–2.5 mm in diameter. Ovulation occurred in June as evidenced by the presence of oviductal eggs. Average clutch size was 2.6 eggs (n = 21, SD = 0.89), and ranged from 1–4. Clutch size was positively correlated with female body size (y = 0.75x - 40.99; r^2 = 0.78; P < 0.05; Fig. 4).

The size of the fat bodies in *C. h. hyperythrus* females were small (< 0.001–0.06 g) throughout the year. Fat bodies reached their maximum size in April and were smallest in July and August which coincided with the peak of the reproductive season (Table 1). Maximum mass of fat bodies was 0.06 g (right and left lobe combined) in a female collected in April 1992 which represented 1.3% of her total body mass. The smallest fat bodies were thin membranous sacs (< 0.001 g) and were found in females collected in July and August.

Using ANCOVA we found that there was a significant difference among the monthly means of female fat body masses (r^2 = -0.38; P < 0.001; $F_{(7,69)}$ = 3688.24; P < 0.001). An inverse relationship between ovarian and fat body mass cycles was found from April–August (Fig. 2). The correlation is statistically significant (y = 0.09x - 1.99; r^2 = 0.91; P < 0.05). The female reproductive cycle lasted seven months with the peak of activity occurring during August (Fig. 2).

Male Reproductive Cycle

Male testes developed slowly from April–May and followed by an abrupt increase from May–June (Table 2). Testes of males collected in April ranged from 0.018–0.020 g ($\bar{x}$ = 0.018) which comprised 0.34% of the total body mass. Testis mass increased to 0.028 g (mean) in May when it comprised 0.44% of the total body mass. In June, testes accounted for 0.68% male body mass. Average male SVL was 61.5 mm in April and 64.7 mm in May. In June, it was a SVL of 65.4 mm. Length of testes ranged from 2.95–4.55 mm ($\bar{x}$= 3.78). Maximum testis

Table 2. Mean reproductive characteristics of male *Cnemidophorus hyperythrus hyperythrus* collected in 1992. Standard deviation provided in parentheses.

	Apr	May	Jun	Jul	Aug	Sep	Oct
n	6	5	7	7	8	5	4
SVL (mm)	61.48	64.66	65.4	62.76	63.10	61.25	57.15
	(0.98)	(1.17)	(1.43)	(0.92)	(2.86)	(1.29)	(1.41)
Body mass (g)	5.52	6.33	7.05	6.29	6.35	6.17	5.46
	(0.07)	(0.57)	(0.23)	(0.08)	(0.42)	(0.06)	(0.18)
Fat body mass (g)	0.008	0.003	0.0133	0.0151	0.0153	0.009	0.001
	(0.0006)	(0.0009)	(0.0007)	(0.0012)	(0.0021)	(0.0005)	(0.00009)
Testes length (mm)	3.62	4.18	4.42	4.01	3.74	3.53	2.97
	(0.28)	(0.196)	(0.064)	(0.055)	(0.177)	(0.071)	(0.032)
Testes mass (g)	0.019	0.028	0.048	0.028	0.026	0.023	0.008
	(0.0006)	(0.0019)	(0.003)	(0.0012)	(0.0017)	(0.0005)	(0.0001)
Testes % of total body mass	0.34	0.44	0.19	0.44	0.41	0.37	0.15
Fat body % of total body mass	0.14	0.05	0.19	0.24	0.24	0.14	0.02

mass was recorded in June. Testis mass suggested that males were reproductively active until mid-September. Thereafter, testis size decreased rapidly (Table 2). Analysis of covariance with SVL as covariate revealed that there was a significant difference among monthly testis mass ($r^2 = 0.74$; $F_{(6,32)} = 133.5$; $P < 0.001$; Fig. 5).

Throughout the reproductive cycle male fat bodies never exceeded 0.02 g in weight (Table 2). However, their values were similar to those found in females. The ratio of fat body mass to body mass was 0.14 in April, abruptly decreased in May (0.05%), and slightly increased in June (0.19%), July (0.24%), and August (0.24%).

Male fat body mass values were correlated with SVL ($r^2 = 0.31$; $F_{(6,32)} = 66.27$; $P < 0.001$) and, thus, ANCOVA adjusted means were calculated on a monthly basis to examine seasonality in the amount of energy reserves in the abdominal fat deposits (Fig. 5). Student-Newman-Keuls post-hoc tests revealed that there were two groups of months which were significantly different from each other. The first group has low values of fat body mass and includes April, May, September, and October. The other group, with slightly higher values, includes June, July, and August. Testicular development was not correlated with a decrease in fat body mass (y = 0.186x + 0.006; $r^2 = 0.439$; $P < 0.05$; Fig. 5).

DISCUSSION

While reproductive activity of small lizards from temperate climates is typically seasonal, a wide range of reproductive patterns are known for small tropical lizards (Benabib 1994). Female *C. h. hyperythrus* in this study became reproductively active in March and had oviductal eggs from June–September. The appearance of eggs in oviducts coincides with the peak in precipitation and with the mean temperature maxima of the year when the environmental conditions are more favorable to juveniles. At El Comitán, *C. h. hyperythrus* male and female reproductive cycles are synchronized; both reach their activity peak during the summer (July and August). Synchrony of male and female reproduction cycles is not known for all lizards. Thus, *C. h. hyperythrus* exhibits a reproductive cycle similar to subtropical and temperate lizard species whose reproductive cycles are associated with the rainy season (Barbault 1975, 1981; Ortega 1986).

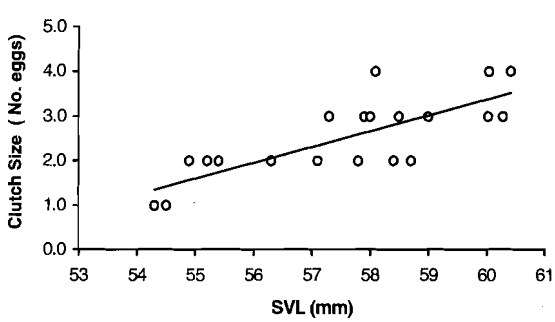

Figure 4. Relationship between clutch size and body size in *Cnemidophorus hyperythrus hyperythrus.*

Our results partly confirm the work of Asplund (1967) and Karasov and Anderson (1984) on *C. h. hyperythrus*. Asplund (1967) reported that individuals of this subspecies collected during August were in reproductive activity. However, his study included only a very short portion of the *C. h. hyperythrus* reproductive period (only August). Karasov and Anderson (1984) reported that individuals of this subspecies collected during the first part of September (1978 and 1979) were in reproductive activity. This was the only month for which they presented reproductive observations. Besides these studies, which included only notes on the reproductive state of few individuals of this subspecies in one particular month, there are no other studies dealing with the reproductive cycle of this subspecies.

Several similarities between subspecies of *C. hyperythrus* exist. For example, SVL of reproductive females and average clutch size of *C. h. hyperythrus* is similar to that recorded by Bostic (1966) for *C. h. beldingi*. Subspecific differences were seen in the period during which eggs were present (June–September in *C. h. hyperythrus*; mid-June to mid-July in *C. h. beldingi*). The reproductive cycle of *C. h. beldingi* females (2 mo) is shorter than that of *C. h. hyperythrus* (7 mo). Maximum testis volume was achieved abruptly in July in *C. h. hyperythrus* while in *C. h. beldingi* this occurred gradually in April (Bostic 1966).

Comparisons between *C. h. hyperythrus* with other *Cnemidophorus* species show conflicting results. We found that females of a southern California montane *C. tigris* population (Goldberg

1976) and a population of *C. sexlineatus* studied in Alabama (Etheridge et al. 1986) both possessed vitellogenic ovarian follicles during May. In contrast, yolk deposition in *C. h. hyperythrus* occurs during March. The possible cause for this difference in timing of egg-lipid deposition is perhaps the more favorable climate of the Cape Region that allows *C. h. hyperythrus* to initiate vitellogenesis earlier in the year than other subspecies. Furthermore, *C. tigris* and *C. sexlineatus* females have oviductal eggs from May–July, whereas *C. h. hyperythrus* possess oviductal eggs from June–September (Fig. 3). All three taxa produce two clutches per year. *Cnemidophorus h. hyperythrus* males exhibit largest testicular size in June, as do *C. tigris* males in southern California (Goldberg 1976) and *C. sexlineatus* males in Alabama (Etheridge et al. 1986). Males of these species exhibit maximum testis size during the same months that females achieve peak reproductive activity.

In comparing the reproductive cycle of *C. h. hyperythrus* with data from other Mexican lizards at El Comitán, such as *Urosaurus nigricaudus* (Romero-Schmidt et al. in press), we found that both sexes reach two reproductive activity peaks: one during the spring (May–June) and a second during late summer (August). Comparing the *C. h. hyperythrus* reproductive cycles with other Mexican lizards of similar latitudes (e.g., "La Michilia," Durango, Mexico), we found that *Sceloporus grammicus* females have oviductal eggs from February–May and *S. scalaris* females from August–September. *Sceloporus grammicus* males exhibit largest testicular size in September and November, whereas *S. scalaris* exhibits largest testis size in April and August (Ortega 1986). In contrast, *C. h. hyperythrus* females exhibit oviductal eggs from June–September and males exhibit largest testicular size in June. This reflects an evident diversity of reproductive patterns existing among species occurring in the same general habitat.

Lipids stored in abdominal fat bodies are important to egg production in many lizard species (Hahn and Tinkle 1965). However, fat body lipids rarely exceeded 50% of the total storage lipids and therefore do not indicate the absolute quantity of storage lipids available (Derikson 1976). Four patterns of lipid storage

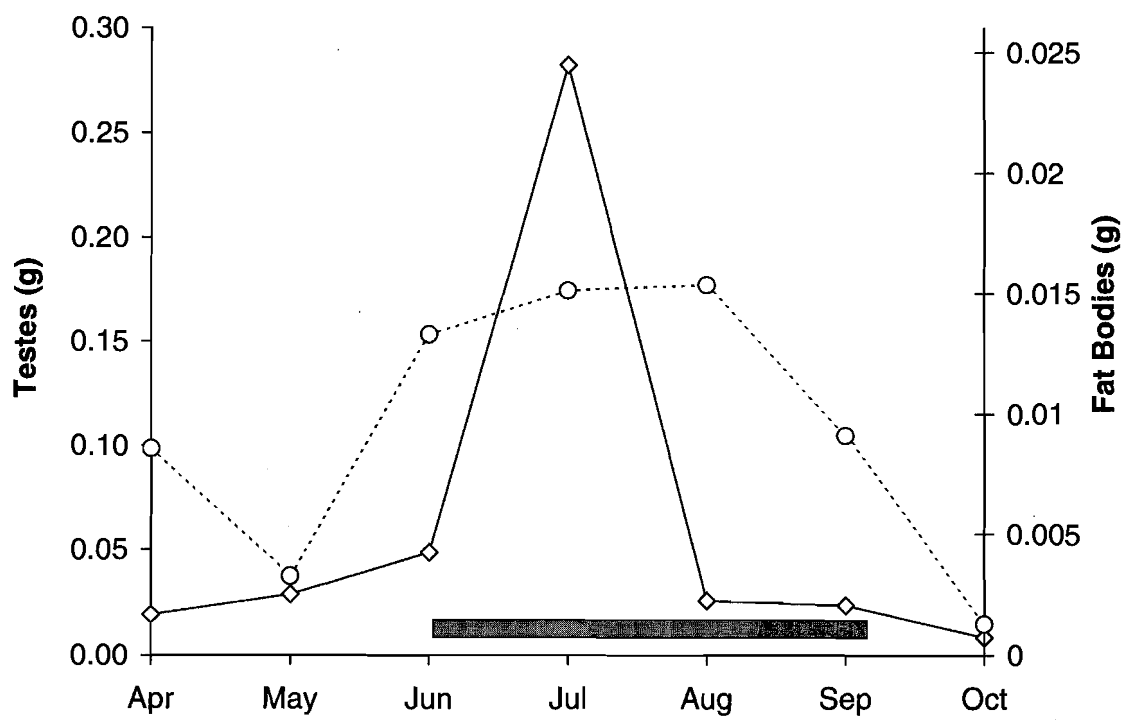

Figure 5. Adjusted means of the male testis (diamonds) and fat body (circles) mass for *Cnemidophorus h. hyperythrus*. The shaded bar at the bottom of the figure corresponds to period when oviductal eggs are present in females.

and utilization among lizards have been observed: (1) no lipid cycling; (2) cycling associated only with winter dormancy; (3) cycling associated only with reproduction; and (4) cycling associated with both winter dormancy and reproduction (Derikson 1976). In this case, the storage lipids in fat bodies were small quantities for both sexes. Fat body depletion by female *C. h. hyperythrus* is clearly associated with ovarian vitellogenesis (Fig. 2), but in males, fat body depletion is not correlated with an increase in testes mass. According to Derikson (1976), it looks as if females have cycling associated with reproduction and males do fit none of the four patterns. Differential use of energy reserves between sexes has been previously documented (Etheridge et al. 1986; Guillette and Casas-Andreu 1981; Marion 1970; Ortega 1986).

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