

REPRODUCTIVE CYCLE AND CHARACTERISTICS OF THE WIDELY-FORAGING LIZARD, *CNEMIDOPHORUS COMMUNIS*, FROM JALISCO, MEXICO

AURELIO RAMÍREZ-BAUTISTA* AND DIANA PARDO-DE LA ROSA

Laboratorio de Ecología, Unidad de Biología, Tecnología, y Prototipos (UBIPRO), FES-Iztacala, Universidad Nacional Autónoma de México. Av. de Los Barrios s/n, Los Reyes Iztacala, Tlalnepantla, Estado de México, C.P. 54090, A. P. 314, México

*Correspondent: raurelio@servidor.unam.mx

ABSTRACT—A 1993–1994 study of the reproductive biology of *Cnemidophorus communis* in the Chamela region, Jalisco, México, revealed that males reached sexual maturity at a snout–vent length (SVL) of 59 mm, and females reached sexual maturity at a SVL of 68 mm. Males exhibited maximum testicular activity from May through October, decreasing in November, and females were reproductive, having vitellogenic follicles or oviductal eggs, from July through October. The mean number of vitellogenic follicles was 6.69 ± 0.59 (2–10, $n = 13$) and mean clutch size of oviductal eggs was 4.8 ± 0.44 (3–9, $n = 17$). Clutch size and egg mass were positively correlated with SVL but relative clutch mass remained constant among females and years. Proximal climatic factors influenced timing and intensity of reproduction in *C. communis*, but the historical effect of foraging mode on teiid lizard morphology constrains relative clutch mass.

RESUMEN—Un estudio de 1993–1994 sobre la biología reproductiva de *Cnemidophorus communis* en la región de Chamela, Jalisco, México, reveló que los machos alcanzaron la madurez sexual a una longitud hocico-cloaca (LHC) de 59 mm, y las hembras a una LHC de 68 mm. Los machos exhibieron la máxima actividad testicular de mayo a octubre, decreciendo en noviembre, y las hembras estuvieron reproductivas, presentaron folículos vitelogénicos o huevos oviductales de julio a octubre. El número medio de folículos vitelogénicos fue de 6.69 ± 0.59 (2–10, $n = 13$) y el tamaño promedio de la puesta de huevos oviductales fue de 4.8 ± 0.44 (3–9, $n = 17$). El tamaño de la puesta y masa de los huevos estuvieron positivamente correlacionados con la LHC, pero la masa relativa de la puesta permaneció constante entre hembras y años. Los factores climáticos proximales influyeron en el patrón temporal y en la intensidad de la reproducción en *C. communis*, pero el efecto histórico de modo de forrajeo en la morfología de las lagartijas teídas restringe la masa relativa de la puesta.

Reproductive activity of temperate and tropical dry forest lizards has been associated with proximal factors such as precipitation (Guillette, 1981; Vitt, 1983; Ramírez-Bautista et al., 1995, 1996; Ramírez-Bautista and Vitt, 1997, 1998), temperature (Ramírez-Bautista and Vitt, 1997, 1998; Ramírez-Bautista et al., 1998), and photoperiod (Marion, 1982; Ramírez-Bautista and Vitt, 1997). In most species inhabiting these habitats, reproductive activity decreases at the beginning of the dry season, and studies have shown that eggs laid in the dry season might die due to desiccation (Andrews and Sexton, 1981). Availability of food resources is another factor potentially limiting lizard reproduction; during the dry season, food is scarce

and lizards may not be able to acquire sufficient energy for reproduction, and lack of food limits the growth rate of hatchlings (Andrews, 1982; Smith and Ballinger, 1994). These hypotheses have been tested in several studies investigating the influence of food availability on lizard reproduction (Dunham, 1981; Ballinger, 1977).

Proximal factors such as rainfall and temperature influence the duration of reproductive period of both females and males, snout–vent length (SVL) and age at sexual maturity, clutch size, clutch mass, relative clutch mass (RCM), and incubation period (Vitt, 1977, 1982; Ramírez-Bautista and Vitt, 1997). Life history characteristics may be associated not

only with environmental factors, but also with phylogeny (Dunham and Miles, 1985), and ecology (Vitt and Congdon, 1978; Vitt and Breitenbach, 1993).

Variability in life histories of *Cnemidophorus* species most often has been associated with variation in food availability, temperature, and rainfall (Ballinger and Schrank, 1972; Goldberg, 1976; Vitt, 1983; Ramírez-Bautista, 1994; Balderas-Valdivia, 1996; Pardo-De la Rosa, 1997). However, clutch size and clutch mass are fundamentally constrained by phylogeny and ecology within this genus (Vitt and Breitenbach, 1993).

Cnemidophorus communis, a conspicuous lizard in the Chamela region, is active from May through October, when food resources (primarily Isoptera and Lepidoptera larvae) are abundant. This species exists in sympatry with conspicuous species such as *C. lineatissimus*, *Anolis nebulosus*, *Urosaurus bicarinatus*, *Sceloporus utiformis*, and *S. melanorhinus* (Ramírez-Bautista, 1994). Its distribution ranges through coastal lowlands of Jalisco, Colima, and Michoacán (Ramírez-Bautista, 1994). To date, only anecdotal descriptions of reproduction of *C. communis* (e.g., Walker, 1982; Ramírez-Bautista, 1994) are available. Here we present data on a population of *C. communis* to address the following questions: 1) are sexually mature males and females the same size; 2) what is the typical reproductive cycle of males and females; 3) is peak reproductive activity associated with variation in environmental factors (temperature, precipitation, and photoperiod); and 4) do clutch size and clutch mass vary with female size?

MATERIALS AND METHODS—Reproductive data were obtained from a population at Chamela, near the Estación de Biología “Chamela” (EBCH). The study area is located 5 km N and 15 km S of the Pacific coast (19°30'N, 105°03'W; elevation from 10 to 584 m) in Jalisco, México. Dominant vegetation is tropical dry forest with rains occurring from June to October. Mean annual temperature is 24.9°C with an average annual rainfall of 748 ± 119 mm (585–961 mm; Bullock, 1986). Data on photoperiod were taken from the Astronomical Almanac of the World (1984). Annual mean temperature and precipitation over a 10-year period during the study were recorded at the Estación Meteorológica of the Estación de Biología “Chamela” and have been reported elsewhere (Ramírez-Bautista and Vitt, 1997). Month-

ly means of precipitation and temperature were used to determine whether reproductive parameters were correlated with weather.

A total of 165 (80 females and 85 males) lizards were collected from August 1993 through November 1994. Because sample sizes for individual months were small, 1993 and 1994 data were pooled by month to describe the annual reproductive cycle. All specimens were killed by cranial alcohol injection, and fixed (10% formalin) in the laboratory, where gonadal analyses were performed. The following linear measurements were taken on necropsied lizards: snout-vent length (SVL; to 1.0 mm), length and width of testes, diameter of oviductal eggs, and diameter of vitellogenic and non-vitellogenic follicles (all to 0.1 mm). The smallest female found to have enlarged vitellogenic follicles or oviductal eggs was used to estimate minimum SVL at maturity. Males were considered sexually mature if they contained enlarged testes (≥8.6 mm³) and epididymides typically associated with sperm production (Goldberg and Lowe, 1966). Testes of males and liver and fat bodies of both sexes were removed and weighed to the nearest 0.0001 g. An egg (oviductal, vitellogenic follicle, or nonvitellogenic follicle) from each side of the body was weighed to 0.0001 g (before preservation) and multiplied by the number of eggs on that side then added to measures from the opposite side to determine female gonadal mass. Because organ mass may vary with body mass, we first calculated regressions of log₁₀ transformed organ mass data with log₁₀ of female mass. For those regressions that were statistically significant (indicating a body mass effect), we calculated residuals from the relationship of organ mass to mass of lizards to produce body mass-adjusted variables. We used these residuals to describe the organ or reproductive cycle of both sexes. For regressions that were not significant (i.e., no body mass effect), we used the actual mass of organs to describe the reproductive or organ mass cycle. We performed ANOVAs on the organ masses with month as the factor, to determine whether significant monthly variation existed, and included only those months for which $n \geq 3$ in the analyses.

To estimate the volume of oviductal eggs, we measured length and width of the largest egg in each oviduct, calculated a mean for the 2 values, and calculated volume as:

$$V = \pi L W^2 (3c^2 + 14c + 35)/210$$

where L is egg length, W is egg width, and the constant $c = \lambda (\sqrt{E} - 1)$, where E was estimated as 2.2 and λ as 0.25 by comparing the shape of *C. communis* eggs with models in Maritz and Douglas (1994).

The number of non-vitellogenic and vitellogenic follicles or oviductal eggs was recorded for females. Clutch size was determined by counting eggs in the oviduct or vitellogenic follicles of adult females dur-

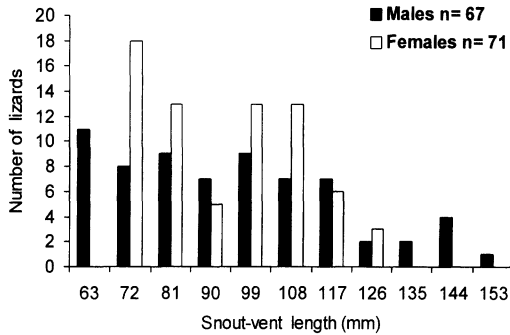


FIG. 1—Size (SVL) distribution of sexually mature males and females of *Cnemidophorus communis* from Chamela.

ing the reproductive season. Mean clutch size was calculated by measuring oviductal eggs from both sides. Incubation period was estimated as the interval between the date on which individual females had their first oviductal eggs of the season (late July), and the date on which first hatchlings appeared in the field (October). We calculated relative clutch mass (RCM; Vitt and Congdon, 1978) as mass of the oviductal eggs/(female mass - clutch mass).

Morphological descriptions were restricted to sexually mature males and females. To examine sexual size differences between males and females, we restricted the data set to the upper 50% of the sample of sexually mature lizards to reduce bias due to sampling error.

Means are presented $\pm 1 SE$ unless otherwise indicated. Standard parametric statistical tests were used when possible, otherwise, appropriate non-parametric tests were substituted. Statistical analyses were performed with the Macintosh version of Statview 4.01 (Abacus Concepts, 1992). Specimens will be deposited at the Colección Nacional de Anfibios y Reptiles, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, in México City.

RESULTS—Body Size and Sexual Maturity—Sexually mature males ranged in size from 59.0 to 152.0 mm SVL ($x = 94.2 \pm 3.0$, $n = 67$) and weighed from 4.0 to 89.9 g ($x = 29.3 \pm 2.6$, $n = 67$). Sexually mature females ranged in size from 68.0 to 128.0 mm SVL ($x = 92.1 \pm 2.0$, $n = 71$) and weighed from 7 to 75 g ($x = 26.6 \pm 2.0$, $n = 71$). Based on comparisons of the largest 50% of sexually mature males and females, males attained a larger size ($x = 111.1 \pm 2.9$, $n = 39$) than females ($x = 104.3 \pm 1.7$, $n = 42$; $t = -2.06$, $P < 0.05$; Fig. 1).

Male Reproductive and Organ Cycles—Sixty-sev-

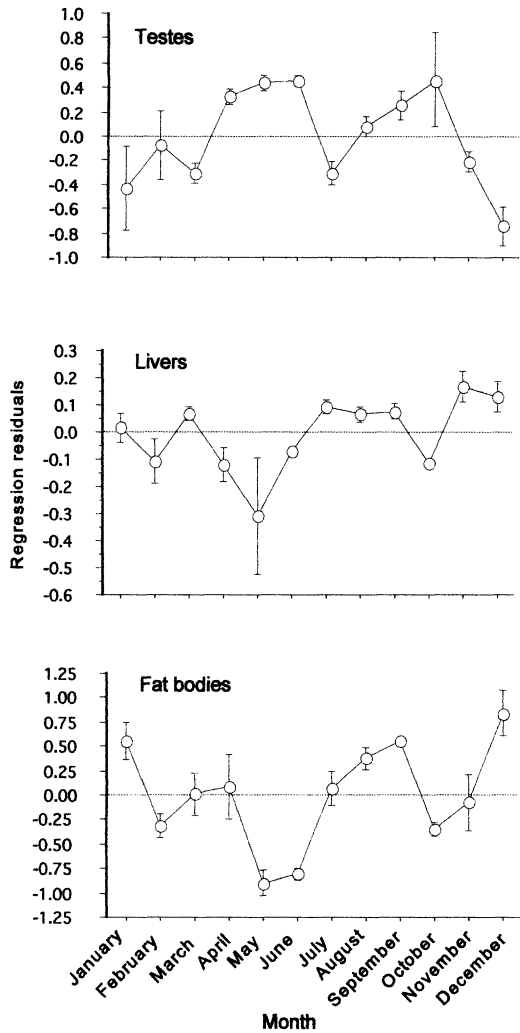


FIG. 2—Testes, liver, and fat body masses of male *Cnemidophorus communis*. Data are mean ($\pm 1 SE$) residuals from a regression of \log_{10} testes mass (g), liver mass (g), and fat body mass (g) against \log_{10} body mass.

en of the males sampled were sexually mature, and there was a significant relationship between \log_{10} body mass and \log_{10} testes mass ($R^2 = 0.69$, $F_{1,65} = 145.2$, $P < 0.0001$), \log_{10} liver mass ($R^2 = 0.68$, $F_{1,65} = 138.7$, $P < 0.001$), and \log_{10} fat body mass ($R^2 = 0.44$, $F_{1,65} = 50.5$, $P < 0.0001$). ANOVAs on residuals of the regressions revealed a significant effect of month on testes mass ($F_{11,55} = 6.8$, $P < 0.0001$), liver mass ($F_{11,55} = 3.69$, $P < 0.001$), and fat body mass ($F_{11,55} = 9.1$, $P < 0.0001$; Fig. 2). Gonadal activity began with an increase of testicular mass

during April, and testes reached their maximum size between May and October (during the wet season). Fat body and liver mass cycles were irregular, mass of liver and fat bodies was smallest when testes began to have their maximum size (April–June), and increased when testes were still large (July–October; Fig. 2). The period of maximal testicular growth of *C. communis* was positively correlated with increasing temperature ($r = 0.57$, $P < 0.05$), precipitation ($r = 0.81$, $P < 0.001$), and photoperiod ($r = 0.64$, $P < 0.05$).

Female Reproductive and Organ Cycles—The annual reproductive cycle is based on a sample of 71 individuals. There were significant linear relationships between \log_{10} body mass and \log_{10} gonad mass ($R^2 = 0.45$, $F_{1,69} = 55.2$, $P < 0.0001$), \log_{10} liver mass ($R^2 = 0.67$, $F_{1,69} = 139.7$, $P < 0.0001$), and \log_{10} fat body mass ($R^2 = 0.42$, $F_{1,77} = 49.4$, $P < 0.0001$). ANOVAs on residuals of the regressions revealed a significant effect of month on gonad mass ($F_{11,59} = 3.7$, $P < 0.005$), liver mass ($F_{11,59} = 3.9$, $P < 0.001$), and fat body mass ($F_{11,59} = 5.4$, $P < 0.0001$; Fig. 3). Average female gonadal mass decreased from March to April, then increased slowly through August, dropped in September, and increased again in October and dropped in November with an increase again in December at the end of reproductive season (Fig. 3).

Females with large vitellogenic ovarian follicles were observed between late spring (June) and late summer (September), with peak reproductive activity occurring during July, August, September, and October. Of 5 females collected in June, 3 (60%) had non-vitellogenic follicles, and 2 (40%) had vitellogenic follicles (Fig. 4). Vitellogenic follicles and oviductal eggs were found during July, August, and September. In October, in a sample of 6 females, 2 (33.3%) had non-vitellogenic follicles, and 4 (66.7%) had oviductal eggs. In November, in a sample of 5 females, 4 showed (80%) non-vitellogenic follicles and 1 (20%) had vitellogenic follicles; however, in a sample of 4 females from December, 2 (50%) had non-vitellogenic follicles and 2 (50%) had oviductal eggs (Fig. 4). Vitellogenesis and follicular growth of females were related to temperature ($r = 0.69$, $P < 0.05$) and precipitation ($r = 0.49$, $P < 0.05$), but not with photoperiod ($r = 0.12$, $P > 0.05$).

Clutch and Egg Size—Mean clutch size of vi-

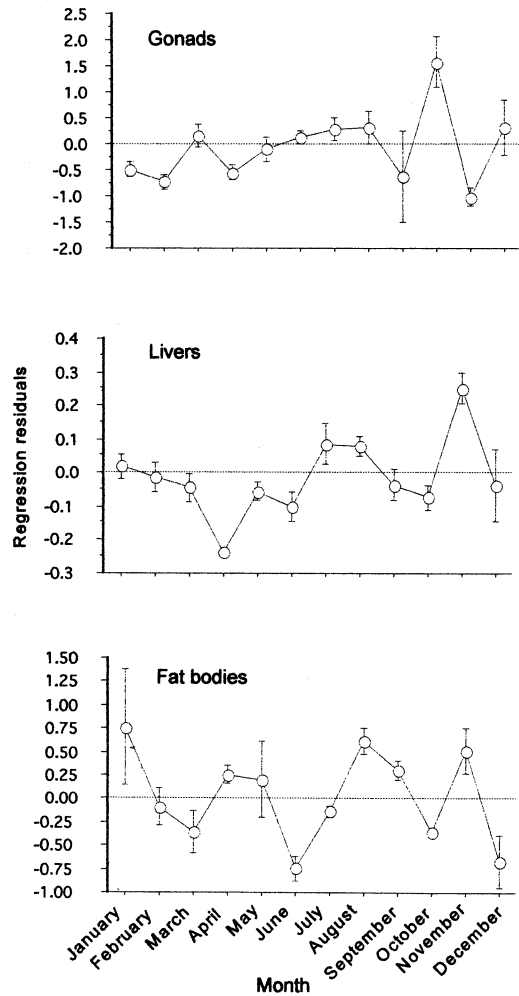


FIG. 3—Gonad, liver, and fat body masses of female *Cnemidophorus communis*. Data are mean (± 1 SE) residuals from a regression of \log_{10} gonad mass, liver mass (g), and fat body mass (g) against \log_{10} body mass.

tellogenic follicles was 6.7 ± 0.59 (2–10, $n = 13$) and oviductal eggs was 4.8 ± 0.44 (3–9, $n = 17$); these results were statistically different (Mann-Whitney U test, $Z = -2.28$, $P < 0.05$). Mean clutch size for 1993 and 1994 was similar ($t = -1.23$, $P > 0.05$) as was clutch mass ($t = -0.77$, $P > 0.05$). Clutch size was correlated with female SVL ($r = 0.45$, $F_{1,15} = 3.76$, $P < 0.05$). Oviductal egg mass was correlated with female SVL ($r = 0.43$, $F_{1,15} = 3.42$, $P < 0.05$). Egg mass during peak egg production (July–October) was not related to female fat body mass ($r = 0.21$, $F_{1,15} = 0.71$, $P > 0.05$) or liver

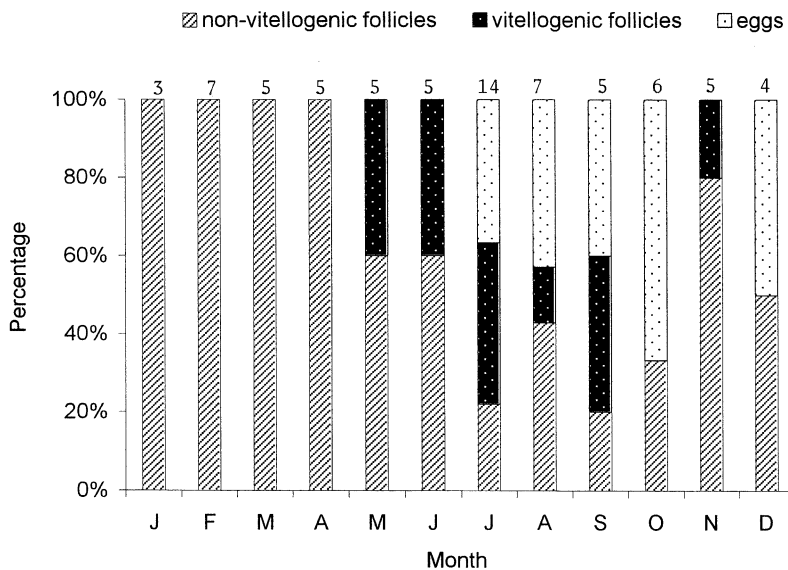


FIG. 4—Seasonal distribution (percent) of female *Cnemidophorus communis* in each of 3 reproductive states; sample sizes appear above bars. Non-vitellogenic follicles were translucent indicating no lipids deposition whereas vitellogenic follicles were yellow indicating that they were developing. Sample size is indicated above the bar for each month.

mass ($r = 0.27$, $F_{1,15} = 1.22$, $P > 0.05$). Mean SVL of females with oviductal eggs from 1993 ($x = 101.8 \pm 5.4$, $n = 8$) was similar to 1994 ($x = 106.8 \pm 5.04$, $n = 9$, $t = -0.68$, $P > 0.05$). Mean RCM for both years was 0.134 ± 0.038 (0.006–0.579, $n = 17$) and did not differ between 1993 and 1994 ($t = -1.53$, $P > 0.05$). RCM was not correlated with female SVL (both variables \log_{10} transformed; $r = 0.09$, $P = 0.731$).

Mean egg length and width were 14.9 ± 0.69 mm (10.5–20.6, $n = 17$) and 10.6 ± 0.46 mm (8.3–14.7, $n = 17$), respectively. Mean egg volume was 954.1 ± 105.4 mm³ (489.7–1840.9, $n = 17$). The first females with oviductal eggs were found in late July, and the first hatchlings were seen in the field in early November. Therefore, the incubation period is estimated to be between 90 and 100 days.

DISCUSSION—Sexual Dimorphism—Males of *C. communis* reached sexual maturity at smaller size but achieved larger body size than females. Males being larger than females among species of this genus is common (Anderson and Vitt, 1990). Although several hypotheses have been advanced to explain the significance of sexual dimorphism in lizards (Anderson and Vitt,

1990), sexual selection is considered to be responsible for sexual dimorphism in several lizard species. Larger body size in males of *C. communis* could be explained in the same way as other lizard species. Large males mate more frequently than smaller ones in *C. tigris* (Anderson, 1986), *Anolis garmani* (Trivers, 1976), *A. carolinensis* (Ruby, 1984), and *Sceloporus jarrovi* (Ruby, 1981). Also larger males are able to win aggressive encounters with other males and are therefore more likely to mate with females (Ruby, 1984; Vitt and Cooper, 1985; Anderson and Vitt, 1990). Males of *C. communis* started reproductive activity (increase in gonadal mass) earlier in the year than females. These data suggest that growth rate is faster in males than females so that they may begin to reproduce immediately at the onset of the reproductive season as occurs in *C. lineatissimus* (Ramírez-Bautista et al., 2000). Yearling males and females began to reproduce at a SVL of 59.0 and 68.0 respectively, suggesting that in yearling lizards (first reproductive period) energy is allocated mostly to reproduction and little to growth during the reproductive season, as has been shown in several studies (Andrews, 1976; Dunham, 1978). Alternatively, it is also possible that size differences between sexes re-

flect differences in growth rate and survival as in some other lizard species (Dunham, 1978).

Male Reproductive Cycle—Reproductive activity in males of *C. communis* is seasonal. Increase in gonadal mass started at the end of dry season (April–May), but testes mass increased when temperature, photoperiod, and precipitation increased. Consequently, these factors, singly or in combination, may stimulate gonadal activity in males as in other species (Licht and Gorman, 1970; Marion, 1982; Lee et al., 1989). However, each species' reproductive activity is influenced by different proximal cues. For example, gonadal activity of *Anolis nebulosus* (Ramírez-Bautista and Vitt, 1997) and *Urosaurus bicarinatus* (Ramírez-Bautista and Vitt, 1998) is affected by temperature and photoperiod, whereas temperature and precipitation produce similar effects in *Sceloporus utiformis* (A. Ramírez-Bautista, pers. obser.) and *Cnemidophorus lineatissimus* (Ramírez-Bautista et al., 2000). These data show that, because *C. communis* is syntopic with these species, reproductive activity is influenced by environmental factors of the region.

Male reproductive activity of *C. communis* began at the same time (May), but ended earlier (November) than that of males of *C. lineatissimus* (Ramírez-Bautista et al., 2000). Male reproductive activity of *C. communis* could be more coincident with the wet season and food availability, because its favored prey (Isoptera and Lepidoptera larvae) are only available during this period. In contrast, *C. lineatissimus* eats insects (Lepidoptera larvae and Coleoptera larvae) that are active throughout the year (D. Pardo-De la Rosa, pers. obser.). Fat body and liver mass were variable during the year, but were lowest during peak reproductive activity. Because *Cnemidophorus* use an active or widely foraging mode (Pianka, 1969), and do not expend energy defending territories, they not only can use energy searching for and courting females (Anderson and Vitt, 1990) but can continue to replenish energy spent in reproductive behavior by continuing to forage widely because they are not constrained by territory defense as occurs with its syntopic species *C. lineatissimus* (Ramírez-Bautista et al., 2000). This reproductive activity pattern is similar to other seasonally (Goldberg and Lowe, 1966; Christiansen, 1971) and aseasonally reproductive species (Sherbrooke, 1975; Vitt, 1983).

Male reproduction ended during November at the end of the rainy season suggesting that male reproductive activity peak could be more closely related to moisture than other proximal environmental cues. A high energetic cost to male reproductive activity is suggested by the negative relationship between testis development and fat body mass during the peak of reproductive season. Liver mass of males varied seasonally similar to fat body mass. The reproductive pattern and relationships of organ mass to reproduction are similar to those observed in other species from the region such as *C. lineatissimus* (Ramírez-Bautista et al., 2000), and in species from other latitudes, *Ameiva ameiva* and *C. lemniscatus* (Magnusson, 1987), and *C. ocellifer* (Vitt, 1983).

Female Reproductive Cycle—Female reproduction also was seasonal. Reproductive activity began in May and decreased in November. Most egg production occurred from July through October, coinciding with the wet season. Timing of reproductive activity is similar to other syntopic species of the region (Balderas-Valdivia, 1996; Ramírez-Bautista and Vitt, 1997, 1998), but different from species from different environments, where female reproductive activity starts in the dry season, but most egg production occurs during the wet season (Magnusson, 1987; Vitt, 1983). The seasonal reproductive pattern is not obvious, but may be explained by environmental conditions in the region. Food is most plentiful (Ramírez-Bautista, 1995) during the wet season, yet hatching occurs at the end of the wet season and early part of the dry season. However, conditions are favorable for hatchling survival during the dry season as moist leaf litter provides both habitat for insect prey and a relatively safe place for hatchlings to forage (Ramírez-Bautista, 1995).

Vitellogenesis in females of *C. communis* began as temperature and precipitation began to increase, and although the correlation with photoperiod was not significant, a combination of the 3 factors could play an important role triggering reproduction such as occurs in syntopic species (Ramírez-Bautista and Vitt, 1997, 1998; Ramírez-Bautista et al., 2000) or in species from other environments (Marion, 1982; Licht, 1984). Although temperature and precipitation influence initiation of reproduction, timing of rainfall could be the ultimate

cue for reproduction through its effects on egg and offspring survival (Andrews and Sexton, 1981; Ramírez-Bautista and Vitt, 1997, 1998). At the beginning of the vitellogenic follicles (May) in 1994, weather was cool and dry and only 2 of 5 females had vitellogenic follicles, but in July, when photoperiod, precipitation, and temperature increased, most females (11 of 14) had oviductal eggs or vitellogenic follicles as do females of *C. lineatissimus* (Balderas-Valdivia, 1996). These data suggest the importance of the 3 environmental factors as proximate cues in initiating the reproductive cycle in this species.

Clutch Size—Clutch size and egg mass of *C. communis* varied with female SVL but not between years, and RCM was consistent among females and between years. The period of egg production by females was from July to December, similar to another syntopic species, *C. lineatissimus* (Ramírez-Bautista et al., 2000), but longer than other species from high latitudes with seasonal reproduction (Christiansen, 1971; Goldberg, 1976). Females likely respond to environmental conditions in the region; during the study, rainfall occurred from July to November, which coincided with peak egg production. As was previously mentioned, rainfall is an ultimate cue through its effect on egg and offspring survival (Andrews and Sexton, 1981; Leon and Cova, 1973; Vitt, 1983).

Clutch size of *C. communis* females was slightly larger than that found for *C. lineatissimus* (Walker, 1970; Ramírez-Bautista et al., 2000) which produces 1 clutch a year, and was similar to the 2 clutches per year typical of *C. exsanguis* (Parker, 1973), *C. gularis* (Ballinger and Schrank, 1972), and *C. sexlineatus* (Fitch, 1958). Clutch sizes in this study were lower than those described for *C. communis* from Colima (Walker, 1982). Clutch size of *C. communis* varied from 3 to 9 eggs. Most small females ($n = 18$; between 68.0 and 108.0 SVL mm) had between 3 and 7 eggs, but a small sample ($n = 12$) of larger females (110.0 to 125.0 SVL mm) had from 6 to 9 eggs, with the exception of 1 female (121.0 mm) who had 3 eggs. Clutch mass was correlated with female body size; this relationship is always found in species with small clutches (Schall, 1978; Vitt and Breitenbach, 1993). In *C. communis* the reduction of the fat bodies is associated with the period of egg production, suggesting that females can-

not harvest enough insects to support egg production during the reproductive season and thus mobilize some of the energy contained in fat bodies to supplement egg production, as has been demonstrated for other lizard species (Hahn and Tinkle, 1965).

The clutch size and RCM of *C. communis* is similar to that of other species of *Cnemidophorus* (Vitt and Breitenbach, 1993; Ramírez-Bautista et al., 2000). Low RCM likely reflects the influence of foraging mode on the evolution of morphology within Teiidae and likely has its origins in an ancient ancestor (Dunham and Miles, 1985; Dunham et al., 1988). The general pattern of low RCM is consistent in this group, and it is related to the active foraging mode and predator escape mechanisms (Vitt and Congdon, 1978; Vitt and Breitenbach, 1993), and to its streamlined morphology (Vitt and Congdon, 1978; Vitt and Price, 1982).

Incubation period occurred from late July to early November, and the first hatchlings were seen during November. The peak of hatchling was between November and December, at the end of rainy season and when insects are most abundant in the litter. This pattern found in *C. communis* is similar to *C. lineatissimus* (Ramírez-Bautista et al., 2000).

Life history characteristics of *C. communis* are similar to those of many other *Cnemidophorus* species from high and low latitudes (Christiansen, 1971; Vitt and Breitenbach, 1993), but this population exhibited some differences in reproductive characteristics. Timing of reproduction was slightly different (May–December) than the syntopic *Cnemidophorus lineatissimus* (June–January; Ramírez-Bautista et al., 2000), but similar to other temperate species (Vitt and Breitenbach, 1993). Clutch size was larger than *C. lineatissimus*, but similar to congeners from high latitude (Parker, 1973; Ballinger and Schrank, 1972). A larger clutch size may be related to a shorter reproductive period, and the fact that during the wet season ample food is available for *C. communis* to acquire the energy necessary to produce a larger clutch. Female SVL at sexual maturity was larger than females of *C. lineatissimus* (Ramírez-Bautista et al., 2000), but similar to that of temperate species (Parker, 1973; Vitt, 1977; Stevens, 1980; Punzo, 1982). In general, like all *Cnemidophorus* species, *C. communis* is oviparous, with a small clutch size and low RCM. Reproductive char-

acteristics shared in species of this genus indicate the influence of the phylogenetic component in the life history evolution of these lizards.

We thank the Estación de Investigación, Experimentación y Difusión Biológica de Chamela, Universidad Nacional Autónoma de México, and the chief, F. Noguera, for making all facilities available during this study. We also thank C. Balderas-Valdivia, for his tremendous help in the field, and L. J. Vitt for his help while ARB was at the University Oklahoma for a Postdoctoral fellowship in 1996–1997. R. Ayala, F. Noguera, L. Oliver, X. Hernández-Ibarra, and A. Borgonio are gratefully acknowledged for their support during the field work. We also thank the anonymous reviewers who provided useful suggestions for improving earlier versions of this manuscript.

LITERATURE CITED

- ABACUS CONCEPTS. 1992. Statview IV. Abacus Concepts Inc. Berkeley, California.
- ANDERSON, R. A. 1986. Foraging behavior, energetics of reproduction, and sexual selection in a widely foraging lizard, *Cnemidophorus tigris*. Unpublished Ph.D. dissertation, University of California, Los Angeles.
- ANDERSON, R. A., AND L. J. VITT. 1990. Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. *Oecologia* 84:145–157.
- ANDREWS, R. M. 1976. Growth rate in island and mainland anoline lizards. *Copeia* 1976:259–262.
- ANDREWS, R. M. 1982. Spatial variation in egg mortality of the lizard *Anolis limifrons*. *Herpetologica* 38:165–171.
- ANDREWS, R. M., AND O. J. SEXTON. 1981. Water relations of the eggs of *Anolis auratus* and *Anolis limifrons*. *Ecology* 62:556–562.
- ASTRONOMICAL ALMANAC. 1984. United States Government Printing Office and Her Majesty's Stationery Office. Washington, D.C., and London, United Kingdom.
- BALDERAS-VALDIVIA, C. 1996. Biología reproductiva de *Cnemidophorus lineatissimus duodecimlineatus* (Reptilia: Teiidae) en la región de Chamela, Jalisco. Tesis de Licenciatura, Facultad de Ciencias, Universidad Nacional Autónoma de México.
- BALLINGER, R. E. 1977. Reproductive strategies: food availability as a source of proximal variation in a lizard. *Ecology* 58:628–635.
- BALLINGER, R. E., AND G. D. SCHRANK. 1972. Reproductive potential of female whiptail lizards, *Cnemidophorus gularis gularis*. *Herpetologica* 28:217–222.
- BULLOCK, S. H. 1986. Climate of Chamela, Jalisco, and trends in the South Coastal Region of México. Archives for Meteorology, Geophysics, and Bioclimatology, series B 36:297–316.
- CHRISTIANSEN, J. L. 1971. Reproduction of *Cnemidophorus inornatus* and *Cnemidophorus neomexicanus* (Sauria, Teiidae) in northern New Mexico. American Museum Novitates 2442:1–48.
- DUNHAM, A. E. 1978. Food availability as a proximate factor in influencing individual growth rates in the iguanid *Sceloporus merriami*. *Ecology* 59:770–778.
- DUNHAM, A. E. 1981. Populations in a fluctuating environment: the comparative population ecology of the iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus*. Miscellaneous Publications of the Museum of Zoology, University of Michigan 158: 1–62.
- DUNHAM, A. E., AND D. B. MILES. 1985. Patterns of covariation in life history traits of squamate reptiles: the effects on size and phylogeny reconsidered. *American Naturalist* 126:231–257.
- DUNHAM, A. E., D. B. MILES, AND D. N. RESNICK. 1988. Life history patterns in squamate reptiles. In: Gans, C., and R. B. Huey, editors. *Biology of Reptilia*, Vol. 16. Ecology B. Defense and life history. Alan R. Liss Inc., New York. Pp. 441–522.
- FITCH, H. S. 1958. Natural history of the six-lined racerunner (*Cnemidophorus sexlineatus*). University of Kansas Publication Museum of Natural History 8:417–476.
- GOLDBERG, S. R. 1976. Reproduction in a montane population of the coastal whiptail lizard, *Cnemidophorus tigris multiscutatus*. *Copeia* 1976:260–266.
- GOLDBERG, S. R., AND C. H. LOWE. 1966. The reproductive cycle of the western whiptail lizard (*Cnemidophorus tigris*) in southern Arizona. *Journal of Morphology* 118:543–548.
- GUILLETTE, L. J., JR. 1981. On the occurrence of oviparous and viviparous forms of the Mexican lizard *Sceloporus aeneus*. *Herpetologica* 37:11–15.
- HAHN, W. E., AND D. W. TINKLE. 1965. Fat body cycling and experimental evidence for its adaptive significance to ovarian follicle development in the lizard *Uta stansburiana*. *Journal of Experimental Zoology* 158:19–86.
- LEE, J. C., D. CLAYTON, S. EISENSTEIN, AND L. PEREZ. 1989. The reproductive cycle of *Anolis sagrei* in Southern Florida. *Copeia* 1989:930–937.
- LEON, J. R., AND L. J. COVA. 1973. Reproducción de *Cnemidophorus lemniscatus* (Sauria: Teiidae) en Cumana, Venezuela. *Caribbean Journal Science* 13:63–73.
- LICHT, P. 1984. Reptiles. In: Lamming, G. E., editor. *Marshall's physiology of reproduction*, Fourth ed., Vol. 1. Churchill Livingstone, Edinburgh, United Kingdom. Pp. 206–282.
- LICHT, P., AND G. C. GORMAN. 1970. Reproductive and fat cycles in Caribbean *Anolis* lizards. University of California Publications in Zoology 95:1–52.

- MAGNUSSON, W. E. 1987. Reproductive cycles of teiid lizards in Amazonian Savanna. *Journal of Herpetology* 21:307–316.
- MARION, K. R. 1982. Reproductive cues for gonadal development in temperate reptiles: temperature and photoperiod effects on the testicular cycles of the lizard *Sceloporus undulatus*. *Herpetologica* 38:26–39.
- MARITZ, M. F., AND R. M. DOUGLAS. 1994. Shape quantization and the estimation of volume and surface area of reptile eggs. *Journal of Herpetology* 28:281–291.
- PARDO-DE LA ROSA, D. 1997. Patrón reproductivo de la lagartija *Cnemidophorus communis communis* (Sauria: Teiidae) en un ambiente tropical estacional. Tesis de Licenciatura, Facultad de Ciencias, Universidad Nacional Autónoma de México.
- PARKER, W. S. 1973. Notes on reproduction of some lizards from Arizona, New Mexico, Texas and Utah. *Herpetologica* 29:703–720.
- PIANKA, E. R. 1969. Sympatry of desert lizards (*Ctenotus*) in western Australia. *Ecology* 50:1012–1030.
- PUNZO, F. 1982. Clutch size and egg size in several species of lizards from the desert southwest. *Journal of Herpetology* 16:414–417.
- RAMÍREZ-BAUTISTA, A. 1994. Manual y claves ilustradas de los anfibios y reptiles de la Región de Chamela, Jalisco, México. Cuadernos del Instituto de Biología No. 23, Universidad Nacional Autónoma de México.
- RAMÍREZ-BAUTISTA, A. 1995. Demografía y reproducción de la lagartija arborícola *Anolis nebulosus* de la Región de Chamela, Jalisco. Tesis Doctoral, Facultad de Ciencias, Universidad Nacional Autónoma de México, México, D.F.
- RAMÍREZ-BAUTISTA, A., AND L. J. VITT. 1997. Reproduction in the lizard *Anolis nebulosus* (Polychrotidae) from the Pacific coast of México. *Herpetologica* 53:423–431.
- RAMÍREZ-BAUTISTA, A., AND L. J. VITT. 1998. Reproductive biology of *Urosaurus bicarinatus* (Sauria: Phrynosomatidae) from a tropical dry forest of México. *Southwestern Naturalist* 43:381–390.
- RAMÍREZ-BAUTISTA, A., J. BARBA-TORRES, AND L. J. VITT. 1998. Reproductive cycle and brood size of *Eumeces lynx* from Pinal de Amoles in México. *Journal of Herpetology* 32:18–24.
- RAMÍREZ-BAUTISTA, A., C. BALDERAS-VALDIVIA, AND L. J. VITT. 2000. Reproductive ecology of the whiptail lizard *Cnemidophorus lineatissimus* (Squamata: Teiidae) in a tropical dry forest. *Copeia* 2000:712–722.
- RAMÍREZ-BAUTISTA, A., Z. URIBE-PEÑA, AND L. J. GUILLETTE, JR. 1995. Reproductive biology of the lizard *Urosaurus bicarinatus bicarinatus* (Reptilia: Phrynosomatidae) from Río Balsas Basin, México. *Herpetologica* 51:24–33.
- RAMÍREZ-BAUTISTA, A., L. J. GUILLETTE, JR., G. GUTIÉRREZ-MAYÉN, AND Z. URIBE-PEÑA. 1996. Reproductive biology of the lizard *Eumeces copei* (Lacertilia: Scincidae) from the Eje Neovolcanico of México. *Southwestern Naturalist* 41:103–110.
- RUBY, D. E. 1981. Phenotypic correlates of male reproductive success in the lizard *Sceloporus jarrovi*. In: Alexander, R. D., and D. W. Tinkle, editors. *Natural selection and social behavior*. Chiron Press, New York. Pp. 96–107.
- RUBY, D. E. 1984. Male breeding success and differential access to females in *Anolis carolinensis*. *Herpetologica* 40:272–280.
- SCHALL, J. J. 1978. Reproductive strategies in sympatric whiptail lizards (*Cnemidophorus*): two parthenogenetic and three bisexual species. *Copeia* 1978:108–116.
- SHERBROOKE, W. C. 1975. Reproductive cycle of a tropical teiid lizard, *Neusticurus ecleopus* Cope, in Perú. *Biotropica* 7:194–207.
- SMITH, G. R., AND R. E. BALLINGER. 1994. Variation in individual growth rates in the tree lizards, *Urosaurus ornatus*: effects of food and density. *Acta Oecologia* 15:317–324.
- STEVENS, P. T. 1980. Notes on thermoregulation and reproduction in *Cnemidophorus flagellicaudus*. *Journal of Herpetology* 14:418–420.
- TRIVERS, R. L. 1976. Sexual selection and resource-acquiring abilities in *Anolis garmani*. *Evolution* 30:253–269.
- VITT, L. J. 1977. Observations on clutch size and egg size and evidence for multiple clutches in some lizards of southwestern United States. *Herpetologica* 33:333–339.
- VITT, L. J. 1982. Reproductive tactics of *Ameiva ameiva* (Lacertilia: Teiidae) in a seasonally fluctuating tropical habit. *Canadian Journal of Zoology* 60:3113–3120.
- VITT, L. J. 1983. Reproduction and sexual dimorphism in the tropical teiid lizard, *Cnemidophorus ocellifer*. *Copeia* 1983:359–366.
- VITT, L. J., AND G. L. BREITENBACH. 1993. Life histories and reproductive tactics among lizards in the genus *Cnemidophorus* (Sauria:Teiidae). In: Wright, J. W., and L. J. Vitt, editors. *Biology of whiptail lizards (Genus Cnemidophorus)*. Oklahoma Museum of Natural History, Norman. Pp. 211–243.
- VITT, L. J., AND J. D. CONGDON. 1978. Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *American Naturalist* 112:596–608.
- VITT, L. J., AND W. E. COOPER, JR. 1985. The evolution of sexual dimorphism in the skink *Eumeces laticeps*: an example of sexual selection. *Canadian Journal of Zoology* 63:995–1002.
- VITT, L. J., AND H. J. PRICE. 1982. Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica* 38:237–255.
- WALKER, J. M. 1970. Morphological variation and

clutch size in a population of *Cnemidophorus lineatissimus* Cope, in Michoacán, México. *Herpetologica* 26:359–365.

WALKER, J. M. 1982. Reproductive characteristics of the Colima giant whiptail, *Cnemidophorus commu-*

nis communis Cope. *Southwestern Naturalist* 27: 241–243.

Submitted 24 March 2000. Accepted 5 April 2001.
Associate Editor was Geoffrey C. Carpenter.