

The female reproductive cycle of the lizard, *Cordylus polyzonus polyzonus* (Sauria: Cordylidae) in the Orange Free State

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Winter reproductive activity is exhibited by females of the viviparous lizard, *Cordylus p. polyzonus*. Vitellogenesis commences in May (autumn), continuing throughout the winter months with ovulation in October. Females are pregnant during summer and give birth in late summer (February). Clutch size is positively correlated to female body size. During embryonic development, ovarian follicles remain small and translucent and the corpora lutea progressively decrease in size until parturition occurs. Embryonic growth was characterized by a concomitant decline in embryonic yolk mass. Although considerable variation was observed in the fat body mass, maximal fat body mass peaked in winter (June) and in mid-summer (December). The onset of vitellogenesis corresponded to declining photoperiod and environmental temperatures.

Die lewendbarende akkedis, *Cordylus p. polyzonus* toon voortplantingsaktiwiteit gedurende die wintermaande. Dooiermeerlegging begin gedurende Mei (herfs) en duur voort deur die wintermaande tot ovulasie in Oktober. Wyfies is verwagting gedurende die somer en kleintjies word in die laat-somer (Februarie) gebore. Eiergetal is positief gekorreleerd met die liggaamsgrootte van die wyfie. Gedurende embrionale ontwikkeling bly die ovariumfollikels klein en deursigtig en die corpora lutea verklein voor geboorte in Februarie. Embrionale groei gaan gepaard met 'n afname in die embrionale dooiermassa. Alhoewel aansienlike variasie in die massa van die vetliggame voorkom, is maksimum vetliggaam-massa gedurende winter- (Junie) en somermaande (Desember) waargeneem. Die aanvang van dooiermeerlegging val saam met die verkorting van dagliglengte en dalende omgewingstemperatuur.

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Studies examining the reproductive strategies of South African reptiles are uncommon. An examination of the reproductive cycle and the possible proximal factors influencing or controlling this cycle forms the basis of the analysis of the reproductive strategy of a species (Guillette & Casas-Andreu 1987). Information on the reproductive cycles of South African reptiles is anecdotal in nature, consisting primarily of observational data rather than detailed seasonal studies.

Most studies have examined the reproductive biology of North American or European lizard species (see Fitch 1970; Duvall, Guillette & Jones 1982; Licht 1984). These studies have demonstrated that variation in reproductive cyclicity varies among geographically isolated populations of the same species (Guillette & Casas-Andreu 1987). Moreover, field data and laboratory experiments have demonstrated that several environmental factors influence reproductive cyclicity in reptiles (Duvall *et al.* 1982; Licht 1984.) As current life history theory is based on data derived primarily from temperate northern hemisphere reptiles, additional studies are needed examining species inhabiting the tropics and southern hemisphere.

The family Cordylidae is endemic to Southern Africa and Madagascar. All the species included in the six genera of the subfamily Gerrhosaurinae are known to be oviparous. Except for the genus *Platysaurus*, the species of the three remaining genera (*Cordylus*, *Pseudocordylus* and *Chamaesaura*) of the subfamily Cordylinae are known to be viviparous. (FitzSimons 1943; Fitch 1970).

It is widely accepted that separate phylogenies of viviparity must have occurred (Guillette 1981; Shine 1985). Shine (1985) suggested that viviparity evolved only once in the family Cordylidae, however, the specific evolutionary pathway remains to be determined for this group.

Cordylus polyzonus is a rupicolous lizard known from the southern parts of the Orange Free State, westwards throughout the karroo to western Cape Province and southern South West Africa (FitzSimons 1943; Loveridge 1944; De Waal 1978). This species is viviparous, but as for all the other cordylid species, little is known regarding the reproductive cycle of *C. p. polyzonus*. Hewitt & Power (1913) suggested that courtship takes place in September with young born in January. Loveridge (1944) observed fully developed *in utero* young in a female collected in April. Fitch (1970) reported mating in early spring and birth, usually two young, in mid- or late summer. De Waal (1978) found 2–3 well-developed embryos in specimens collected in January and February.

The purpose of this study is to describe the reproductive cycle of *C. p. polyzonus* in the Orange Free State using material housed in the herpetology collection of the National Museum, Bloemfontein. Previous studies have demonstrated that data obtained from museum collections represent an important source of information concerning the reproductive biology of reptiles (see Shine 1980, 1982; Guillette & Casas-Andreu 1987). Because *C. p. polyzonus* is widespread in its distribution,

this study is also the first of a series of investigations throughout the distribution range to eventually analyse geographic variation in reproductive timing in order to understand the role of biogeographic history in shaping the reproductive strategy of this species.

Materials and Methods

Study area

The specimens examined were collected in the southern region of the Orange Free State (O.F.S.) within the boundaries of 28°–31°S latitude and 24°30'–27°E longitude. Vegetation predominantly represents karroo or karroid-veld (Acocks 1975). Dolerite outcrops are a common phenomenon in the study area and De Waal (1978) suggested that *C. p. polyzonus* may occur exclusively on dolerites in the study area. The study area is a semi-arid region with an annual rainfall of 400 mm or less. This region is characterized by summer rains with a distinct dry season during the winter months (Figure 1). Most of the study area falls in the moderately severe frost zone. Weather records were obtained for several weather stations in the region from the South African Weather Bureau. A principal component analysis (PCA) was conducted on the climatic variables whereafter another PCA was conducted on the various weather stations using the environmental variable with the highest PCA score. The Fauresmith weather station (29°46'S / 25°19'E) explained 99,8% of the climatic variation in the study area and was therefore used as the reference weather station. Using daily records, maximum and minimum air temperatures and total rainfall were calculated on a monthly basis for the period 1972–1976 (Figure 1). Photoperiod regimes were calculated using the formula in Van Leeuwen (1981).

Reproductive cycle

The majority of the *C. p. polyzonus* specimens studied were collected during an extensive survey of the reptiles

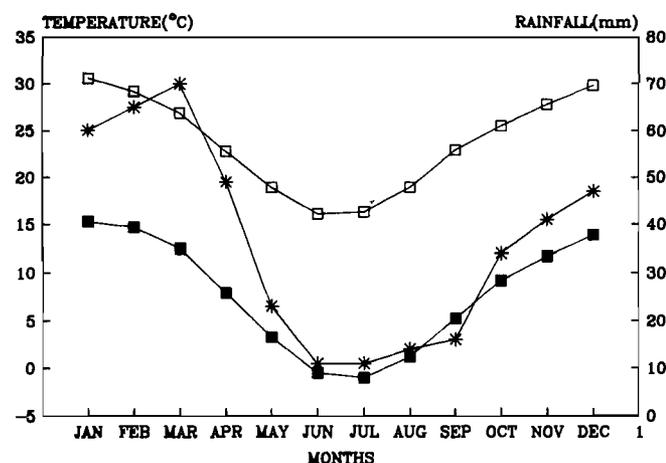


Figure 1 Monthly mean rainfall (★—★) and the maximum (□—□) and minimum (■—■) temperature for the representative weather station in the study area, (Fauresmith, 29°46'S / 25°19'E).

of the Orange Free State region (De Waal 1978) and housed in the collection of the National Museum, Bloemfontein. Additional collecting in the study area was undertaken during 1983 to obtain larger sample sizes. Since the smallest female exhibiting vitellogenesis (therefore sexually mature) had a snout to vent length (SVL) of 87 mm, only lizards larger than 90 mm SVL ($101 \pm 0,54$ mm) ($n = 165$) were dissected. The maximum SVL size reported for this species is 124 mm (FitzSimons 1943; Loveridge 1944; De Waal 1978). Fat bodies, embryo mass, yolk mass and stomach contents were dried to constant mass at 60°C in an oven. The following pertinent measurements were taken during autopsy: SVL (nearest 0,1 mm), diameter of the three largest ovarian follicles (nearest 0,01 mm), diameter of all corpora lutea (nearest 0,01 mm) and longest and shortest diameter of *in utero* eggs (nearest 0,01 mm). Measurements were made either by vernier caliper or an ocular micrometer. Additionally, clutch size was obtained for all pregnant females and embryonic development was staged using the embryonic sequence defined by Defaure & Hubert (1961) for the viviparous lizard *Lacerta vivipara*.

All similar data for a female were averaged and all means for a given month were combined to calculate monthly means and standard errors. Analysis of variance (ANOVA) was performed to determine significant changes in monthly samples. Clutch size was regressed against SVL and linear and exponential models fitted. All means are presented as mean \pm 1SE (standard error). A Student's *t* test was used for comparisons of two groups (BIOSTAT: Pimentel & Smith 1968). Probability values smaller than 0,05 were recognized as significant.

Results

Reproductive cycle

The reproductive cycle of female *C. p. polyzonus* is presented in Figure 2. Females examined during late February and early March contained small translucent ovarian follicles ($1,78 \pm 0,06$ mm). Variability was evident in follicular size during vitellogenesis, indicative of asynchrony among females during this period of follicular growth. However, a significant seasonal trend was observed ($F_{11,151} = 48,96$; $P < 0,0001$). Vitellogenesis began in May (autumn) with 50% of the sample containing follicles larger than 3 mm. During the winter months, June and July, 10% contained follicles larger than 3 mm and 36% had follicles larger than 5 mm. The onset of vitellogenesis and the early part of follicular growth is negatively correlated with decreasing ambient temperatures ($r = -0,9203$; $P < 0,05$), rainfall ($r = -0,9012$; $P < 0,05$) (Figure 1) and photoperiod ($r = -0,8473$; $P < 0,05$) (Figure 3) in the study area. August was characterized by all females having follicles larger than 5 mm. Preovulatory follicles were present in all females towards the end of September. A significant increase in follicle diameter during the period May to September was recorded ($P < 0,0001$) (Figure 2a).

Ovulation occurred during September / October

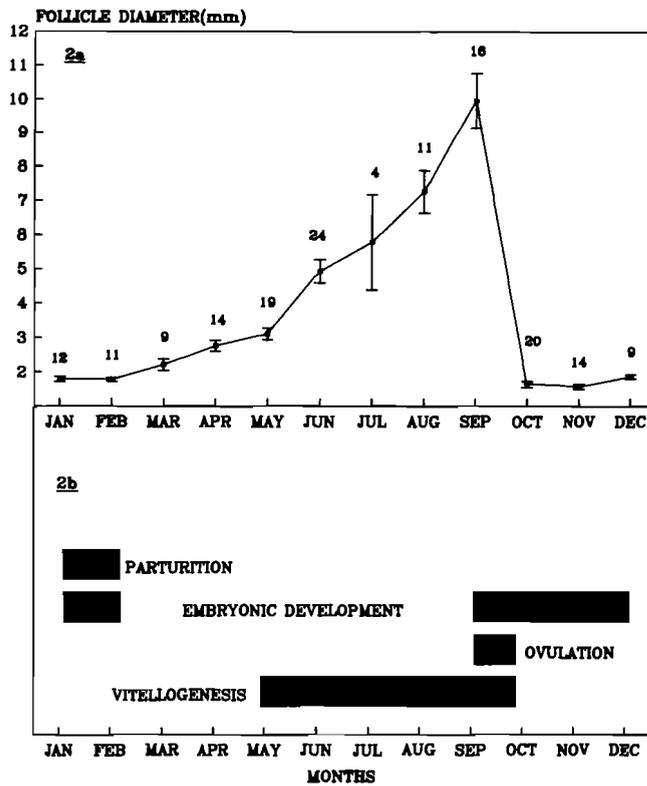


Figure 2 Variation in the mean diameter of the largest follicles of the ovaries during the reproductive cycle of the female *Cordylus p. polyzonus* (Figure 2a) and a summary diagram indicating annual reproductive events (Figure 2b). All monthly values are mean \pm SE. The sample size is given above the bars.

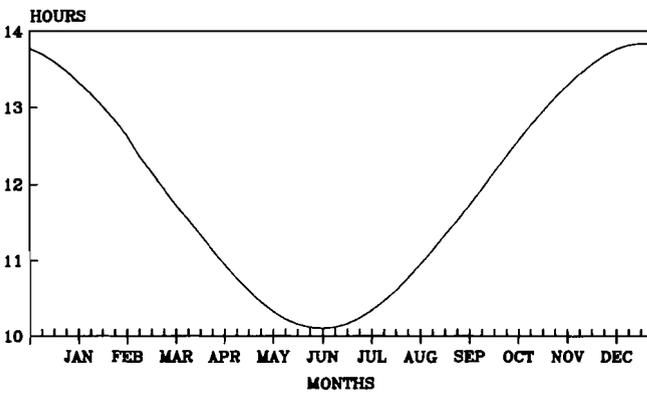


Figure 3 The annual change in the photoperiod for the representative weather station in the study area (Fauresmith, 29°46'S / 25°19'E).

(Figure 2b). The earliest date that a lizard contained oviducal eggs was on 30 September, whereas the latest date that a lizard was collected that had not ovulated was on 28 October. Vitellogenic follicles were observed in the ovaries only during the months May to October, and only non-vitellogenic and atretic or corpora lutea were present during the rest of the year. The corpus luteum just after ovulation appeared large (4,15 \pm 0,46 mm) and sac-like. Luteal size remained relatively constant between embryonic stages 10 and 30 (Figure 4). A

reduction in luteal size was evident following embryonic stage 30.

Following fertilization, embryonic growth commences in October and continues throughout the summer months. Embryonic yolk mass (dry mass) does not change significantly through stages 1-36 ($t = 3,0$; $P = 0,39$). Although not significant, a reduction in yolk mass was observed in large sized embryos (stages 40 & 41) (Figure 5) ($t = 2,846$; $P > 0,05$) and a significant increase in embryo dry mass was only evident after stage 30 (Figure 5) ($t = 4,6387$; $P < 0,0001$). A 13-fold increase was noted between stage 30 and stage 41. Dry mass of the embryos *versus* newly ovulated eggs indicated that a loss of 15,9% occurs during gestation. Embryonic differentiation is rapid during early pregnancy as females examined in October contained embryos from stage 10 to stage 30. However, during the last third of development differentiation was better synchronized.

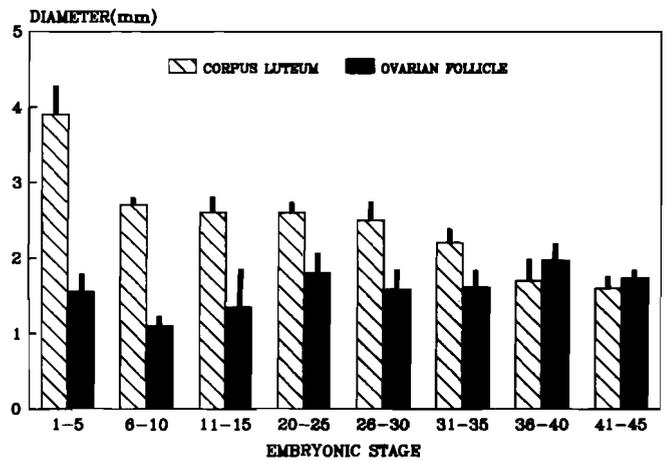


Figure 4 Summary of follicular (dark shaded) and luteal activity (light shaded) during gestation in the lizard, *C. p. polyzonus*. All values are means and SE for the range of selected embryonic stages indicated.

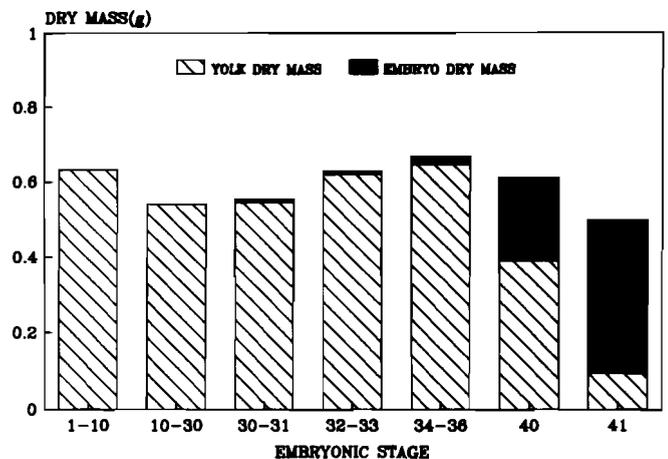


Figure 5 Summary of embryo dry mass (dark shaded) and embryonic yolk dry mass (light shaded) variation during gestation in the lizard, *C. p. polyzonus*. All values are means for the range of selective embryonic stages indicated.

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Ovaries from all females containing *in utero* embryos possessed small translucent follicles (Figure 2).

Parturition begins in February as 50% of the females examined at this time did not contain *in utero* embryos but exhibited stretched oviducts and corpora albicantia. The mean size of neonates close to birth (stage 41) was $41,86 \pm 0,62$ mm. It was of interest that these neonates were not melanistically pigmented like the adults but rather yellow and blotched dorsally like the typical *C. p. polyzonus* pigmentation.

Based on counts of oviducal eggs, clutch sizes vary from 1-5 ($2,85 \pm 0,13$). SVL explained 46% of the variation in clutch size ($r = 0,68$; $F_{1,52} = 44,79$; $P < 0,0001$). The linear model ($y = mx + c$) for this relationship is: oviducal eggs count = $0,132SVL - 10,78$. Both the intercept ($t = -5,285$; $P < 0,0001$) and the slope ($t = 6,693$; $P < 0,0001$) were significantly different than zero (Figure 6). Alternatively, using an exponential model [$y = \exp(mx + c)$], SVL explained 54% of the variation in clutch size ($r = 0,74$; $F_{1,52} = 61,85$; $P < 0,0001$), with oviducal eggs count = $\exp(0,0554SVL - 4,74)$. The intercept ($t = -6,517$; $P < 0,0001$) and the slope ($t = 7,865$; $P < 0,0001$) were significantly different than zero.

Fat body cycle

The mass of the abdominal fat bodies showed considerable individual variation throughout the reproductive cycle (Figure 7). In spite of this variation a significant seasonal trend was evident ($F_{11,143} = 2,713$; $P < 0,05$). A significant increase in fat body mass occurred between March and June ($t = 2,803$; $P < 0,001$). This increase coincided with the onset of vitellogenesis and initial follicular growth (autumn) (Figures 2 & 7). Fat body reserves were gradually depleted during the winter months, reaching a minimum in October (spring) at the time of ovulation. (June vs October, $t = 4,229$; $P < 0,001$). During pregnancy, the fat body mass increased reaching a maximum in January prior to parturition

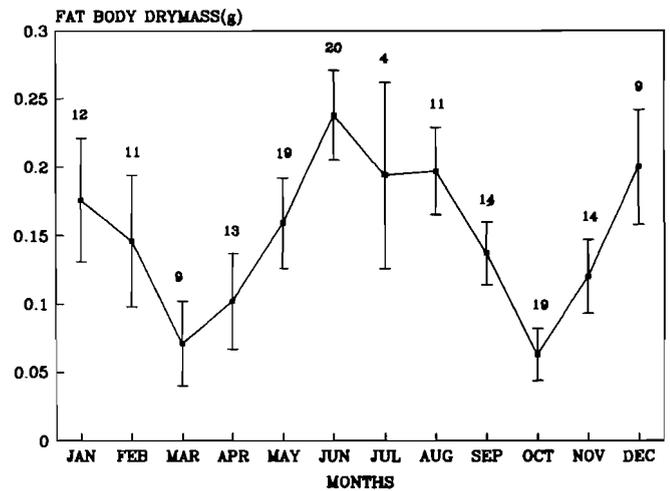


Figure 7 Female fat body cycle of the lizard, *C. p. polyzonus*. All monthly values are mean \pm SE. The sample size is given above the bars.

(October vs January, $t = -2,6568$; $P < 0,05$) whereafter the fat body mass again decreased (January vs March, $t = 2,480$; $P < 0,05$).

Although a detailed stomach content analysis was not conducted, no significant difference was found between the dry mass of stomach contents of specimens examined in June and January / February ($t = 0,384$; $P > 0,1$) suggesting continuous feeding throughout the winter months in the study area.

Discussion

Until recently, it was thought that most temperate zone lizards display reproductive activity during spring and summer months (Fitch 1970; Duvall, *et al.* 1982). For most South African lizards this pattern was also assumed since *in utero* eggs and neonates were usually present in lizards collected in summer by taxonomists (FitzSimons 1943; Loveridge 1944; De Waal 1978). Van Wyk (1983) observed such a classical reproductive cycle for the oviparous lizard, *Agama atra* in the western Cape Province. However, several recent studies suggest that diverse patterns of reproductive activity exist in temperate zone lizards of the northern hemisphere (Guillette & Casas-Andreu 1980; Mendez de la Cruz, Guillette, Villagran Santa Cruz & Casas-Andreu 1988). Some temperate viviparous lizards (*Gerrhonotus coeruleus*, *Xantusia vigilis*) exhibit a typical spring and summer reproductive activity pattern (Steward 1979; Miller 1951). In contrast, Goldberg (1971) reported a reproductive cycle in which gonadal development, courtship and mating were exhibited during the autumn and winter months in the viviparous lizard, *Sceloporus jarrovi*. Vitellogenesis and ovulation took place during autumn and the female retained the fertilized eggs *in utero* throughout winter until spring when parturition occurred. Since the study of Goldberg (1971) several additional reports concerning autumn/winter breeding became available (Guillette & Casas-Andreu 1980, 1987; Guillette 1983; Guillette & Sullivan 1985; Guillette &

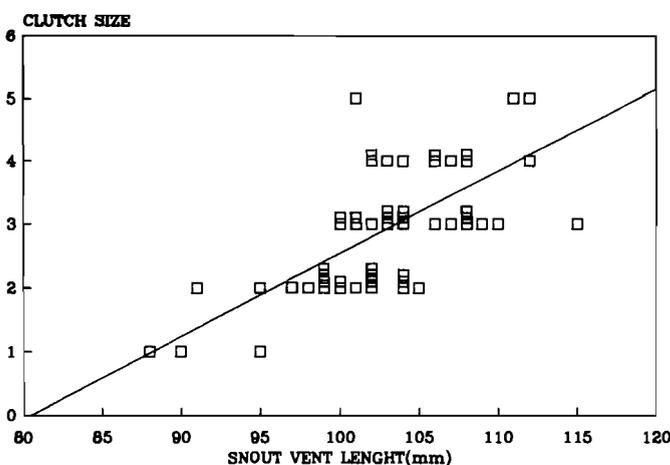


Figure 6 Relationship of clutch size (oviducal embryos) and female size (SVL) in *C. p. polyzonus*. The solid line represents a significant correlation ($y = 0,132x - 10,78$; $r = 0,68$; $n = 54$).

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Bearce 1986; Mendez de la Cruz *et al.* 1988). At first it seemed that autumn/winter reproductive activity in temperate lizards was associated exclusively with high elevations (Goldberg 1971; Guillette 1981). However, autumn / winter breeding is now known to occur at moderate elevations (Guillette & Sullivan 1985) and in lowland species (Guillette & Bearce 1986).

Similar to the autumn / winter breeding cycle, vitellogenesis in *C. p. polyzonus* was observed in late autumn (May) to early winter (June) and continued throughout winter with ovulation occurring in spring (October) and not prior to the winter months. This pattern is similar to that reported for several temperate northern hemisphere lizards, *Sceloporus graciosus* (Woodbury & Woodbury 1945), *Leiopisma zelandia* (Barwick 1959) *Sceloporus a. bicanthalis* (Guillette 1981) although in *C. p. polyzonus* vitellogenesis continued throughout winter to be completed in spring.

Lipids are an important biochemical unit for energy storage which may be utilized at a future time for growth, maintenance or reproduction (Long 1985). As much as 50% of the body lipids in lizards are known to be stored in abdominal fat bodies (Derickson 1976). During oocyte development, vitellogenesis stimulates a drastic reorganization of several metabolic activities (Derickson 1976; Dessauer 1974; Ho, Kleis, McPherson, Heiserman & Callard 1982). This investment in yolk production by female lizards is considered energetically expensive (Nagy 1983) and it is, therefore, not surprising to find a decrease in fat body mass during follicular growth in both oviparous and viviparous lizards (Guillette & Casas-Andreu 1981; Van Wyk 1984; Vitt & Cooper 1985; Guillette & Sullivan 1985). In contrast, the fat body mass in *C. p. polyzonus* increased during autumn, reaching a peak in June. This increase in fat body mass coincided with the onset of vitellogenesis. A similar phenomenon was reported for the viviparous lizard, *Sceloporus g. disparalis* by Guillette & Bearce (1986).

Greenberg & Gist (1985) showed that lipids contained in the fat bodies of the oviparous lizard, *Anolis carolinensis* are part of a pool of lipids which can be utilized in support of reproduction, suggesting that lipids contained in the fat bodies of the lizard *A. carolinensis* were not preferentially utilized for reproduction unless dietary intake is inadequate to meet the accelerated demands of reproduction. The fact that no significant difference could be found between stomach content mass of female *C. p. polyzonus* collected during summer and winter may suggest adequate energy intake to sustain the onset and early part of vitellogenesis as well as building fat reserves. Lipids are also known to be stored in the tail and the carcass of some lizards (Avery 1970; Loumbourdis 1987) and it is not known whether lipids were preferentially utilized from these sites rather than the fat bodies during early vitellogenesis. Derickson (1976), however, indicated that fat body lipids are the most labile and therefore storage or utilization would be apparent in these sites first.

During late winter and early spring at the time of peak vitellogenesis, the fat bodies of *C. p. polyzonus* depleted

until ovulation in October which may be indicative of inadequate energy intake to meet the increased metabolic demand during this period.

In spite of the fact that the material was collected in a large study area and over a period of several years, variation in ovulation time seemed to be limited. Moreover, Guillette & Sullivan (1985) reported that *Sceloporus f. formosus* exhibit reproductive asynchrony of ovulation and follicular development. A similar situation was found in the oviparous female *Agama atra* lizard where several clutches were produced annually (Van Wyk 1984). Apart from variation in the size of vitellogenic follicles, *C. p. polyzonus* did indicate synchronous gonadal activity.

Embryonic growth occurred throughout summer (October–February) with parturition in February in *C. p. polyzonus*. This is in contrast to early spring parturition observed in the autumn/winter breeding lizards (Duvall *et al.* 1982). Fat reserves increased rapidly following ovulation to reach a maximum prior to parturition, suggesting that the energy demands of the growing embryos do not affect the energy balance of the female negatively. The presence of embryonic yolk until just before parturition may suggest that the nutritional function of the placenta may not be important until late in embryonic development (Guillette 1981). The post-partum decline in fat reserves in *C. p. polyzonus* females prior to the onset of vitellogenesis could be attributed to maximum energy assimilation for growth and somatic maintenance.

Several hypotheses have been proposed to explain the seasonal timing of reproduction in reptiles (for review, see James & Shine 1985). It is generally accepted that environmental variables (sources of predictable information) such as temperature, photoperiod, moisture, food availability and several other possible variables are important in coordinating cyclic reproductive processes to maximize maternal fitness by producing young at the time when sources of embryonic mortality could be avoided (James & Shine 1985).

The predicative value of change in ambient temperature for regulation of annual cycles have been questioned because of large day to day variability (Moore, Whittier & Crews 1984). Nevertheless, several studies have suggested that temperature is indeed the most important environmental cue regulating timing of reproduction in temperate zone reptiles (Callard & Ho 1980; Licht 1984). As in the case of autumn/winter breeding lizards, *C. p. polyzonus* became reproductively active during a period of declining ambient temperatures and photoperiod. Although photoperiod is considered to be a more predictable environmental cue, photoperiod probably acts indirectly to facilitate the temperature response. Several examples of combined responses to temperature and photoperiod have been documented (Crews & Garrick 1980; Marion 1982; Licht 1984).

The onset of vitellogenesis in *C. p. polyzonus* coincided with the onset of the cool dry season which may suggest that declining photoperiod and/or ambient temperatures act as possible 'zeitgeber' in controlling the onset of vitellogenesis in *C. p. polyzonus*. Ballinger

(1973) also suggested that decreasing photoperiod may stimulate gonadal activity in *Sceloporus jarrovi* but the mechanism and / or causal agent stimulating reproductive activity has not been determined. Few studies have examined directly the role of decreasing photoperiod and / or temperature as cues for stimulating reproductive activity and research in this regard is needed in autumn-breeding lizards.

The fact that except for the genus *Platysaurus*, all the species of the other genera included in the sub-family Cordylinae are known to be viviparous and inhabiting habitats ranging from montane to xeric lowlands (Loveridge 1944) may be suggestive of strong conservation of reproductive cycles. This would then question the general interpretation of life-history traits, such as reproductive seasonality, as optimal adaptations to the habitat in which we observe at least some lizard species today (James & Shine 1985; Ballinger 1983). Although the synchrony of ovulation in *C. p. polyzonus* between years and collecting sites in the study area corroborates this suggestion, more information regarding geographic variation in the reproductive cycle of this widespread species is needed. Indeed, it is suggested by James & Shine (1985) that because phylogenetic constraints and biogeographic history may have played a major role in shaping the patterns observed today, these aspects should get more attention in future interpretations of a life-history trait, such as reproductive seasonality.

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