

Reproduction and sexual dimorphism in the montane viviparous lizard, *Pseudocordylus capensis* (Sauria: Cordylidae)

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Received 24 February 1997; accepted 25 March 1998

Pseudocordylus capensis, a melanistic lizard, is regarded as a basal species in the phylogeny of the family Cordylidae and is endemic to the Cape Fold Mountains. Data for this study were obtained from measurements and dissections of museum specimens ($N = 68$). Sexual maturity in both sexes is attained at around 80–90 mm snout-vent length (SVL). Body sizes (SVL) differed significantly between sexes, the mean SVL of adult males being 92.3 mm (range 78.4–104.2) and that of adult females 95.9 mm (range 83.1–108.5). Although the rate of increase in head measurements did not differ significantly between sexes, analysis of covariance (ANCOVA) indicated that head dimensions are marginally, but significantly, larger in males than in females of equivalent SVL. The slight female-plus dimorphism in SVL and male-plus dimorphism in head dimensions is suggested to be related to life in the cold montane environment, and to differential growth to increase female reproductive fitness, rather than to be the result of sexual selection. Males exhibit testicular recrudescence during autumn, with full spermiogenesis during winter maintained through spring (October). The testicular cycle shows characteristics of both 'post-nuptial' and 'pre-nuptial' cycles previously described in Cordylidae lizards. Small testicular volume, associated with testicular regression, was recorded during summer (November/December). Spermatozoa were present in the epididymis from May through to October. In synchrony with the spermatogenic cycle, the onset of vitellogenesis in females starts in autumn, culminating in ovulation during spring (September–October). Females are gravid during summer and give birth to 2–3 young in late summer (December–January). The timing of events during the reproductive cycle of females corresponds to the autumn cycles reported for all other female Cordylidae lizards studied to date, therefore pointing to strong conservatism regarding the timing of female reproductive cycles in this lizard family. Fatbody size in individuals of both sexes is largest during late summer and autumn, and progressively declines during winter to reach smallest sizes during the summer months. The fact that this phylogenetically basal species exhibits well-synchronised male and female autumn gonadal cycles adds to the data that suggest these reproductive traits evolved during the early divergence from the Cordyliformes ancestor and that the evolution of viviparity may be linked to this event or followed soon after.

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Detailed information on the biology of southern African lizard species is restricted to only a few of the approximately 480 species known from the region. The bulk of the information regarding reproductive cycles comes from the family Cordylidae (see van Wyk & Mouton 1996 for review). The family Cordylidae, including four genera (*Chamaesaura*, *Pseudocordylus*, *Platysaurus* & *Cordylus*) is endemic to southern Africa (Branch 1988; Lang 1991) and believed to have originated in the southern Cape region (Mouton & van Wyk 1997).

Apart from members of the genus *Platysaurus*, all other Cordylidae lizards are known to be viviparous (Branch 1988; van Wyk & Mouton 1996). Past studies have shown that female reproductive cycles in members of the Cordylidae, oviparous and viviparous, all exhibit the same basic pattern of autumn/winter vitellogenic activity, with winter/spring ovulation and gestation in the following late summer or autumn (van Wyk 1989, 1991; Flemming & van Wyk 1992; Flemming 1993a; van Wyk & Mouton 1996).

A clear dichotomy, however, has emerged in the timing of testicular cycles in Cordylidae lizards (van Wyk 1990; Flemming 1993b,c; van Wyk 1995; van Wyk & Mouton 1996). In one group, peak spermatogenic activity takes place during late autumn through spring, prior to mating activity in spring (pre-nuptial cycle). Sperm availability decreases as testicular regression sets in during summer, since no meaningful sperm storage in the epididymis or vas deferens occurs. In the other group, spermatogenesis starts much earlier, in summer, after a

spring/summer mating period, with the peak in spermiation in autumn, followed by testicular regression during winter. In contrast to lizards exhibiting pre-nuptial cycles, sperm is stored for extensive periods in the epididymis and vas deferens until mating in late winter or spring through early summer (post-nuptial cycle). Although the definition of a post-nuptial cycle in males accentuates the time when mating occurs (Licht 1984), we shift the emphasis from time of mating to the phenomenon of sperm storage while the testes are in a state of regression (see Bradshaw 1986; van Wyk 1995). It is possible that early matings could occur in autumn with females also storing sperm, which then strictly speaking would make it a pre-nuptial phenomenon rather than post-nuptial.

Associated with the variation in male testicular cycles goes variation in synchronization among male and female reproductive (gonadal) cycles. The autumn breeding phenomenon and the presence of asynchronous reproductive activity in males and females has now been reported for several lizard species inhabiting temperate habitats in Mexico, Argentina, New Zealand and South Africa (see Ramirez-Pinilla 1991, 1994; Guillette & Mendes-de la Cruz 1993; Cree & Guillette 1995; van Wyk 1995; van Wyk & Mouton 1996 for reviews). In several of these studies the phenomenon of asynchronous reproductive activity in males and females has been reported in montane species and Guillette & Mendez-de la Cruz (1993) suggested that autumn reproductive activity may be associated with the evolution of viviparity in certain squamate genera.

Sexual dimorphism, including body size, body proportions, and/or colouration, is another phenomenon/trait that varies interspecifically in the Cordylidae (van Wyk 1992; Mouton & van Wyk 1993; Cordes, Mouton & van Wyk 1995). Dichotomies of male-plus versus female-plus body proportions and brightly coloured males versus dull colouration have emerged in recent studies. Such diversity in the degree and type of sexual dimorphism displayed may be explained by the associated variation in the type of mating system (Mouton & van Wyk 1993; Shine & Fitzgerald 1995; Hews 1996). Although variation in these traits has been explained by adaptationist hypotheses, the described diversity could follow broad phylogenetic lines (Shine & Fitzgerald 1995). It is therefore clear that, without knowledge of the variation in any of the above-mentioned traits within a phylogenetic lineage, and a robust phylogenetic hypothesis, answering questions regarding adaptationist hypotheses or phylogenetic conservatism remains problematic.

The melanistic graceful crag lizard, *Pseudocordylus capensis*, is regarded as a montane species (mostly above 900 m altitude) over most of its range and is endemic to the Cape Fold Mountains (Branch & Bauer 1995). *Pseudocordylus capensis* is an agile, highly rupicolous species that prefers vertical rock faces (Branch 1988). Two races were earlier recognised, but Herselman, Mouton & van Wyk (1992), because of a continuum of variation in several morphological traits, synonymized the races. As one of the most basal species in the Cordylidae clade (Herselman 1991; Mouton & van Wyk 1997), knowledge regarding the reproductive cycle and sexual dimorphism in *P. capensis* will contribute to the understanding of the evolution of these traits within the family Cordylidae. Information regarding the reproductive cycles and sexual dimorphism in members of the genus *Pseudo-*

cordylus is limited to the Drakensberg crag lizard, *P. melanotus* (Flemming 1993b,c; Mouton & van Wyk 1993). *P. melanotus* exhibits pronounced male-plus sexual dimorphism in morphological features, associated with bright male colouration (Mouton & van Wyk 1993). Similar to other Cordylidae lizards, female vitellogenic activity in *P. melanotus* occurs in autumn. Spermatogenetic activity in autumn, and sperm storage in the epididymis and vas deferens through winter and parts of summer, categorise the male cycle as typical post-nuptial, with male and female reproductive cycles not well synchronised (Flemming 1993b, c).

Apart from the important contribution to the understanding of the evolution of Cordylidae reproductive cycles, this study represents the first concerned with the reproductive cycle of a lizard endemic to the Cape Fold Mountains. Studies regarding the biology of the endemic montane fauna, especially the herpetofauna, as part of our natural mountain sanctuaries is long overdue. Since the conservation status of this endemic pseudocordylid lizard remains unknown, we restricted this study to available museum material, and therefore small sample sizes, to provide basic information on sexual dimorphism and seasonal reproduction.

Material and methods

We examined specimens of the graceful crag lizard *P. capensis* ($N = 68$) in the collections of the John Ellerman Museum of the University of Stellenbosch and the Port Elizabeth Museum. These specimens were collected from several localities between Nieuwoudtville ($31^{\circ}33'16''S$, $19^{\circ}07'38''E$) in the west along the Cape Fold Mountains to the Kammanassieberg range in the east ($33^{\circ}36'62''S$, $22^{\circ}52'42''E$; Figure 1). Climatological data from a reference site within the distribution

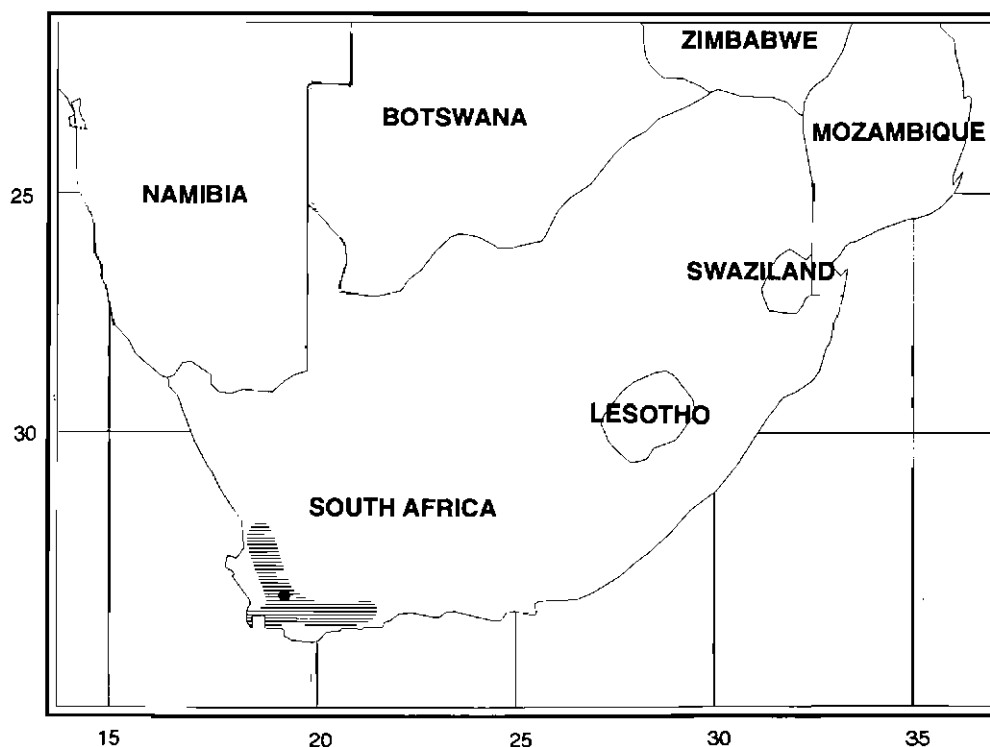


Figure 1 Geographic distribution based on known localities of *P. capensis* (after Herselman *et al.* 1992). Country borders and the Matroosberg Weather Station ($33^{\circ}26'S$, $19^{\circ}49'E$) are indicated (●).

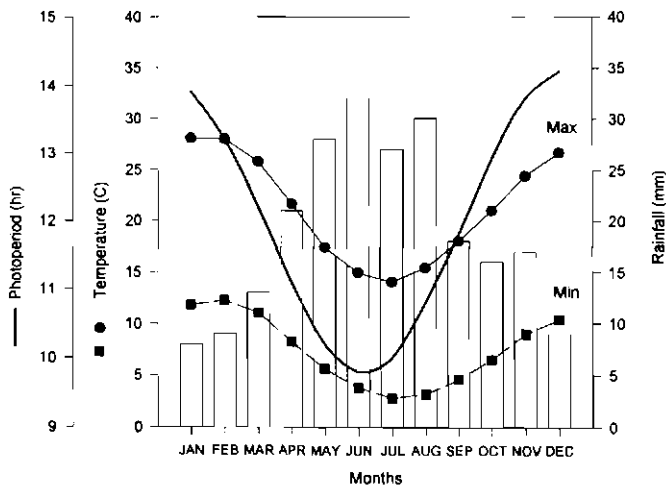


Figure 2 Mean monthly maximum temperature (solid circles), monthly minimum (solid squares), total monthly rainfall (histogram), and photoperiod (solid line) at the Matroosberg Weather Station in the distribution range of *P. capensis* (Figure 1) for the period 1931–1976.

range of *P. capensis*, Matroosberg Weather Station (33°26'S, 19°49'E) (Figures 1 & 2), were obtained from the South African Weather Bureau (WB40-report 1980). These data show that *P. capensis* experiences typical high altitude (1000 m – 2000 m) Mediterranean-type climatic conditions, i.e. hot and dry summers followed by wet and cooler winters (Figure 2). Maximum ambient temperatures during summer range between 25–30°C and during winter between 10–15°C. Photoperiod regimes were calculated using the formula in van Leeuwen (1981).

Data obtained on each preserved museum specimen included: (1) snout-vent length (mm, SVL); (2) head width (mm, HW) (at widest point), (3) head length (mm, HL) (tip of snout to posterior edge of parietals) (4) longest and shortest axes of the testes (mm); (5) number and diameter of the largest ovarian follicles (nearest 0.1 mm); (6) stage of follicular development; (7) presence of oviductal eggs; (8) dry mass (air dried for 24 h; nearest 0.1 g) of fatbodies. Testicular volume (mm^3) was calculated by using the formula of an ellipsoid ($V = 4/3 \pi a^2 b$, where $a = 1/2$ shortest diameter and $b =$ largest diameter). Paraffin sections (10–8 μm) were taken from the middle of the right testis and stained with Harris hematoxylin and eosin. Spermatogenic activity was assessed qualitatively by using an eight-stage classification scheme described in van Wyk (1995). The presence of spermatozoa in the lumen of the epididymis was also noted. Female reproductive activity was classified, based on the appearance of the follicles and the presence of developing embryos, as non-vitellogenic, early vitellogenic, advanced vitellogenic or gravid. Paraffin sections (10–8 μm) were taken from early vitellogenic ovarian follicles in order to establish the seasonal timing of the onset of vitellogenesis.

Data were log-transformed and then subjected to the Kolmogorov-Smirnov normality test and Bartlett's test for homogeneity of variances respectively. One-way analysis of variance (ANOVA) was performed to establish whether significant seasonal variation existed in traits. In cases where the data did not meet the assumptions of normality, Kruskal-Wal-

lis (Kruskal) procedure was employed as a nonparametric analysis of variance and the Mann-Whitney *U*-test for comparing two means. To test whether organ mass was affected by variation in body size, least-squares linear-regression analysis was performed to regress variables on SVL. Neither testicular volume nor mean follicular diameter of the range of adult sizes included in this study was affected by SVL, making it unnecessary to adjust organ masses. We also used least-squares linear-regression analysis to examine relationships between SVL and head measurements (HW, HL). In all cases, the variances passed the normality and homoscedasticity tests, allowing us to proceed with parametric ANOVA. We used analysis of covariance (ANCOVA), with sex as factor and SVL as the covariant, to compare the slopes and intercepts of regressions (head measurements on SVL). In addition, we calculated an index of head dimorphism (D_1) as the female regression slope/male regression slope for the specific parameter (Cordes *et al.* 1995). A size dimorphism ratio (D_2) was calculated as the mean female trait (SVL, HW, HL)/mean male trait. Percentage dimorphism was taken as the absolute value of $[(\text{dimorphism ratio} - 1) \times 100]$ (Cordes *et al.* 1995). Statistical procedures were performed in concordance with Sokal & Rohlf (1985) and Glantz (1992), using the SIGMASTAT (Jandel Scientific) and BIOMSTAT (Rohlf & Slice 1995) statistical software packages.

Results

Size, sexual maturity and dimorphism

Sexual maturity, i.e. signs of vitellogenesis and spermiogenesis, for *P. capensis* was estimated to be at about 80 mm SVL. Although the smallest gravid female measured 83.1 mm SVL, a few females with SVLs smaller than 90 mm were found to be non-gravid during the breeding season. The mean SVL of adult males used in this study was 92.3 mm (range 78.4–104.2; $n = 31$) and for adult females 95.9 mm (range 83.1–108.5; $n = 32$). The female-plus sexual dimorphism in body size (SVL) was found to be statistically significant (ANOVA: $F_{1,61} = 5.90, p = 0.02$). It is obvious from Figure 3 that the frequency distribution of female SVLs in the sample is skewed towards larger SVLs, and therefore possibly affects the mean SVL. The dimorphism ratio (D_2), based on mean SVL, for the

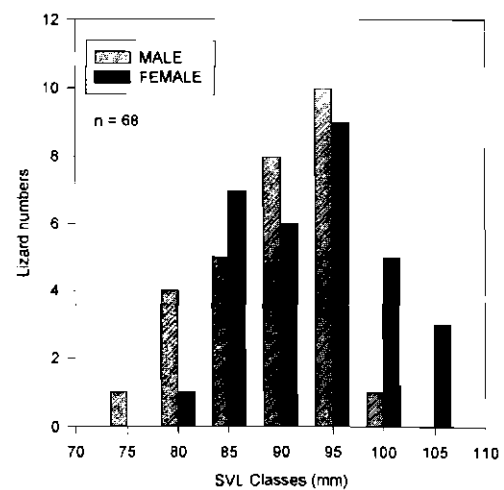


Figure 3 Distribution of body sizes (SVL) for male and female *P. capensis* studied.

P. capensis sample is 1.04, a percentage dimorphism of 4%. Our analyses revealed no significant differences in either mean head width (HW)(ANOVA: $F_{1,61} = 3.11, p > 0.05$) or mean head length (HL)(ANOVA: $F_{1,60} = 2.16, p > 0.14$) between adult males and adult females. However, when comparing ANCOVA adjusted means for HW ($F_{1,61} = 40.13, p < 0.05$) and HL ($F_{1,60} = 27.29, p < 0.05$), head dimensions proved to be marginally, but significantly larger in males.

The head measurements (HL and HW) of *P. capensis* were highly correlated with SVL in juveniles (undetermined sex), adult females and adult males (Figures 4a & 4b). Although the rate of increase in head measurements, HW (Figure 4a; slopes homogeneous $F_{2,62} = 0.001, p > 0.05$) and HL (Figure 4b; slopes homogeneous $F_{2,62} = 0.001, p > 0.05$) did not differ significantly between sexes (common slopes: 0.95 and 0.72 respectively), intercept comparisons further pointed to larger head dimensions in males than females of equivalent SVL. (Figures 4a & 4b: HW, intercepts heterogeneous, $F_{2,62} = 25.8, p < 0.05$; HL, intercepts heterogeneous, $F_{2,62} = 14.3, p < 0.05$). The slightly larger dimensions of male head measurements also showed in the dimorphism ratios, suggesting a percentage dimorphism of 3% towards males. The low number of

juveniles ($n = 5$) in the sample precluded a confident comparison of regression slopes and intercepts among juveniles and adults, but the current data suggest that the HW slope of adult females flattened out when compared to the HW slope of juveniles (Figure 4a).

No obvious sexual difference was noted in adult colouration, both sexes being melanistic. Epidermal glands, femoral and generation glands (Herselman 1991; van Wyk & Mouton 1992) may be present in both sexes. Although indications are that both gland types are more functional in males, detailed studies are necessary to confirm this.

Male reproductive cycle

Significant seasonal variation in testicular volume (ANOVA: $F_{5,22} = 11.8, p < 0.05$) demonstrates an annual spermatogenic cycle (Figure 5). Histological study disclosed testicular recrudescence (stages 3–4, Figure 5) during early autumn (March–April) with associated increments in testicular volume. Metamorphosing spermatids and free spermatozoa in the lumina of seminiferous tubules, epididymis and vas deferens were present in lizards collected during late autumn (April–May, Figure 5) through late spring (October). Testicular volumes decreased during late spring and summer (October–November), and although spermatid numbers were reduced, free spermatozoa were still abundant (stages 7 & 8, Figure 5). Complete testicular regression (stage 1), characterized by involuted seminiferous tubules together with an absence of free spermatozoa in the lumina of the epididymis and vas deferens, characterized males collected during December and January (Figure 5). Lumina of epididymis and vas deferens remained devoid of free spermatozoa from mid-summer (December) through late autumn (April–May) in the following year. Testicular recrudescence in late summer/early autumn (February/March) coincided with decreasing ambient temperatures and decreasing photoperiod, but increasing monthly rainfall (Figures 2 & 5).

Female reproductive cycle

The mean diameter of the largest ovarian follicles varied significantly (ANOVA: $F_{7,22} = 8.81, p < 0.05$) throughout the seasons (Figure 6). Although *P. capensis* females are viviparous, vitellogenesis still contributes to the dynamic changes observed during the ovarian cycle. Histologically, the presence of deutoplasmic droplets in the follicular ooplasm marked the onset of vitellogenesis during autumn (May). Increasing follicular diameter associated with vitellogenic activity continued through autumn and winter to reach maximum pre-ovulatory sizes in spring (September, Figure 6). Gravid females, with embryos in different stages of development, were collected during spring through autumn in the following year (October–April, Figure 6). Clutch size was limited to two young ($n = 14$) produced as a single clutch per annum. Females collected around the same date were generally observed to be well synchronised regarding ovarian development and embryonic development in the oviduct of gravid females (Figure 6), although a single gravid female collected in late summer contained an early developmental stage embryo at a time when most adult females contained well-developed embryos. The onset of vitellogenesis during autumn coincided with decreasing ambient temperature and

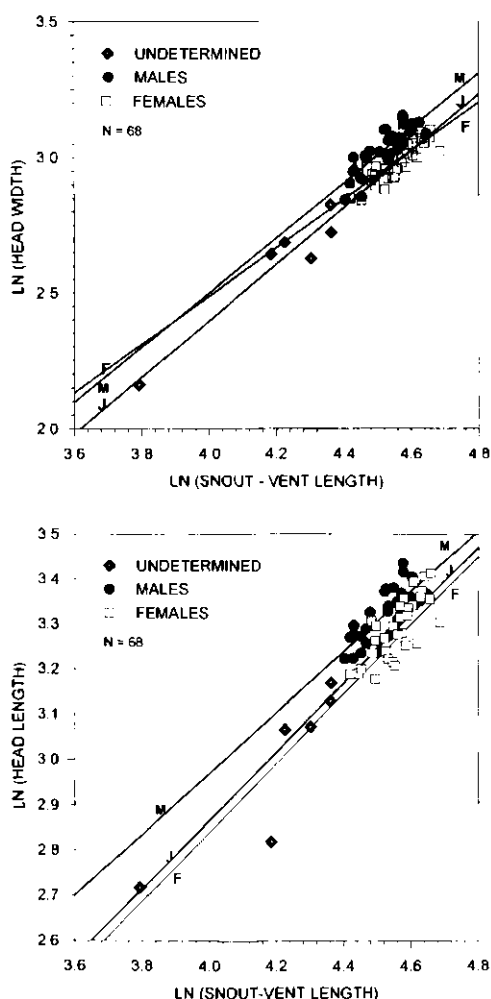


Figure 4 Regression of head dimensions, head width (HW: upper graph) and head length (HL: lower graph) on snout-vent length (SVL) for juveniles, adult males (●) and adult females (□) in *P. capensis*. Lines are fitted by least-squares regression. See text for statistical results.

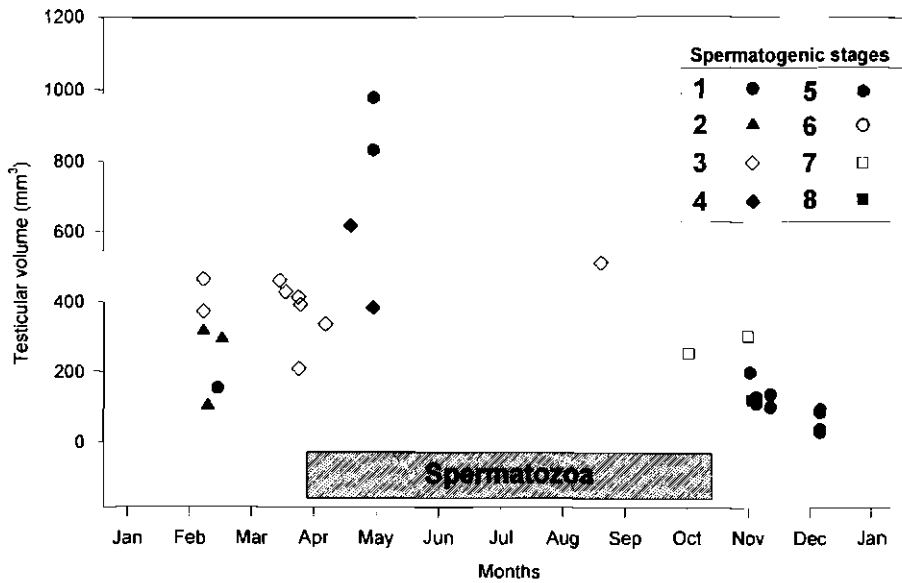


Figure 5 Seasonal variation in testicular volume in *P. capensis*. Each symbol represents one lizard with the specific spermatogenic stage indicated. Classification of spermatogenic stages (van Wyk 1995) are: (1) Seminiferous tubules involuted with spermatogonia; epididymis atrophic with cuboidal epithelium with no spermatozoa; (2) Primary spermatocytes appearing, epididymis atrophic and empty; (3) Secondary spermatocytes with early spermatids abundant, epididymis atrophic and empty; (4) Transforming spermatids with few spermatozoa, epididymis epithelium changing to columnar with few spermatozoa in the lumen; (5) Spermatids abundant and spermatozoa present in seminiferous tubules and epididymus with columnar epithelium; (6) Spermatozoa abundant (maximal level of spermiogenesis), epididymis hypertrophied with many spermatozoa; (7) Spermatozoa abundant, but spermatids and spermatocytes greatly reduced, epididymis epithelium columnar and spermatozoa abundant; (8) Seminiferous tubules involuted with only spermatogonia visible, cuboidal epididymis epithelium, spermatozoa still abundant.

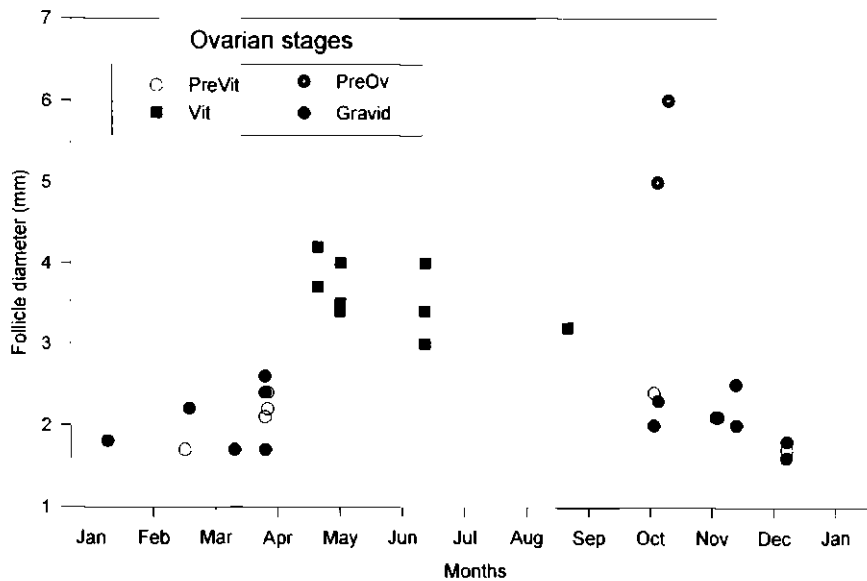


Figure 6 Seasonal variation in mean diameter of largest ovarian follicles in *P. capensis*. Each symbol represents one lizard with one of four female reproductive groups indicated (-○- pre-vitellogenic, -■- vitellogenic, ●- pre-ovulatory, -□- gravid).

photoperiod regimes (Figures 3 & 6), but with increasing monthly rainfall. Embryonic development continued through the warm summer period and birth of young occurred at the onset of the autumn/winter rainy season.

Abdominal fatbody cycles

Although Figure 7 suggests a seasonal pattern in the variation in abdominal fatbody reserves, statistically this variation, in both males (Kruskal; $H = 12.8, 7 \text{ df.}, p > 0.05$) and females (ANOVA; $F_{7,22} = 2.19, p > 0.05$), was not significant, but

proved to be significant when lumping male and female data (Kruskal; $H = 19.16, 9 \text{ df.}, p < 0.05$). Increased abdominal fatbody reserves were observed in males and females during late summer and autumn (Figure 7). Fatbodies were small in both sexes in spring and early summer during the time when the females were gravid and males showed signs of testicular regression (Figure 7).

Discussion

Pseudocordylus capensis, like most other poikilothermic

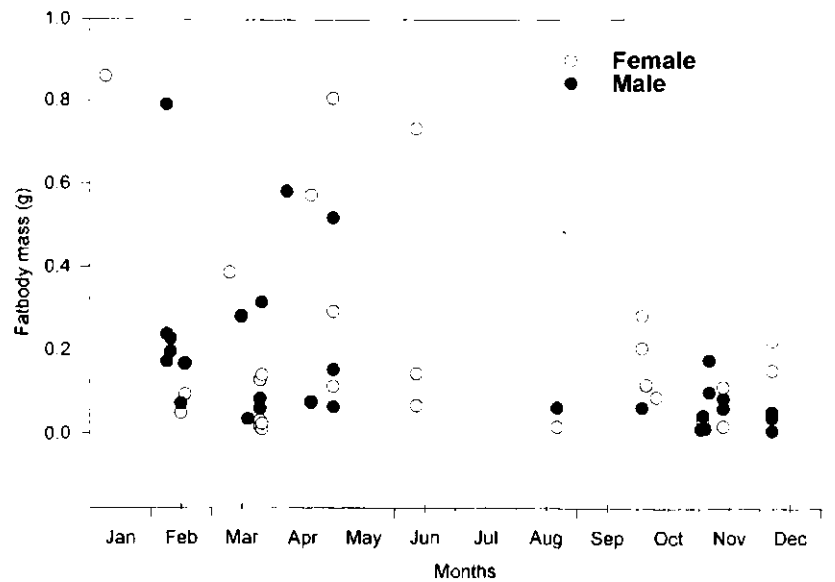


Figure 7 Seasonal variation in male and female fatbody dry mass in *P. capensis*. Each symbol represents one lizard with the sexes indicated (-●- male, -○- female).

squamates (Stamps 1993), matures at a body size less than 80% of asymptotic body size. Meaningful post-maturational growth has also been suggested for other cordylid species *C. cordylus* and *C. niger* (Cordes *et al.* 1995) and *P. melanotus* (Mouton & van Wyk 1993). In the large-bodied cordylid, *C. giganteus*, van Wyk (1992), however, reported that maturity is delayed until close to asymptotic body size. In several other studies and indeed most studies including Cordylidae lizards (see Cordes *et al.* 1995), size at maturity has been determined from cross-sectional data, searching for the smallest individuals indicating gonadal activity in the sample. Apart from *C. giganteus* (van Wyk 1992), all reports including cordylid lizards suggest that size/age at maturity is the same for both sexes (van Wyk 1989, 1991; Flemming & van Wyk 1992; Flemming 1993a,b,c; Mouton & van Wyk 1993; van Wyk & Mouton 1996), thereby, by implication, ruling out the possibility of pre-maturational events contributing to adult sexual size dimorphism (SSD). Shine (1990) presented data for several groups of lizard, snake, and fish taxa, suggesting that sexual differences in body size are set at maturity, with only minor modification after sexual maturity. Therefore, primary determinants of SSD include differential pre-maturational growth or survival rates, or differences in age at maturity. Hews (1996), on the other hand, has shown that Shine's (1990) finding may only hold for differences in overall body size, and not generalise to head traits that exhibit differential growth. Sexual dimorphism in body size and other morphological traits in Cordylidae lizards could therefore indeed be attributed to differential post-maturity influences on growth rates, resulting in differences in asymptotic sizes.

Stamps (1993) pointed out several sampling problems that could erroneously suggest SSD in adults, especially when adult SSD is less pronounced. The difference in body size recorded for *P. capensis* may be a reflection of temporal and spatial variation in the age distribution of the sexes because of differential mortality, therefore resulting in a sexually dimorphic population. Although differences in mean values and the rate of increase of head traits, HW and HL, were non-signifi-

cant in *P. capensis*, ANCOVA (heterogeneous intercepts) and comparisons of ANCOVA adjusted means revealed some degree of morphological dimorphism among sexes. Such differential growth in body size (female-plus) and head traits (male-plus) in *P. capensis* may not be directly related to sexual selection, but rather to different energy related selection pressures on males and females. For example, Cooper & Vitt (1989) suggested that in *Sceloporus undulatus*, after maturity, head size dimorphism results from females increasing body size at a greater rate than head size. The rationale is that females allocate relatively more energy to growth of reproductively significant characters in situations of limited resources such as expected when living in cooler climates, for example at high altitudes (Mouton & van Wyk 1993). It does not necessarily exclude male-plus growth in head traits, resulting in increased male fitness and therefore contributing to sexual dimorphism and maintained by sexual selection (Cooper & Vitt 1989; Mouton & van Wyk 1993; Bull & Pamula 1996).

The association of melanistic cordylid populations with cold-climate situations, such as high altitude, high incidence of fog or increased cloud cover, has recently been pointed out (Badenhorst, Mouton & van Wyk 1993). Cordes *et al.* (1995) reported the absence of pronounced SSD in the melanistic *Cordylus niger*, and attributed the occurrence of the higher frequency of larger sized males in these populations to the impact of the unfavourable climatic conditions on energy allocation in females. Although the lack of pronounced SSD (male-plus) in *P. capensis* may be explained on the same grounds, the higher frequency of larger females seems to be in contrast to the suggested (expected) slower growth in the montane *P. melanotus* (Mouton & van Wyk 1993) and melanistic *C. niger* females (Cordes *et al.* 1995), living under similar cold climatic conditions. Mouton & van Wyk (1993) suggested that pronounced SSD (male-plus) in montane *P. melanotus* could, in part, be the result of differential energy allocation in females (less energy into growth of head traits) which inevitably would effect social structure, i.e. an increase

in the degree of polygyny and the associated pronounced male-plus sexual dimorphism. As in the case of *C. niger* (Cordes *et al.* 1995), *P. capensis* has been recognised as an archaic species (Herselman 1991; Mouton & van Wyk 1997) and although subjected to cool climatic conditions for many years, does not display pronounced SSD (i.e. male-plus) nor a comparable degree of polygyny (unpublished data) when compared to *P. melanotus*. It is clear that research is needed to determine the role of constraining ecological factors, such as low population densities, low visibility and the evolution of melanism to understand the manifestation of sexual dimorphism in Cordylidae lizards. More information is also needed on resource distribution, and its role in determining female spacing, which in turn may affect the ability of a male to monopolize females (Emlen & Oring 1977; Hews 1993). The association of melanistic species, such as *C. niger* and *P. capensis*, with Mediterranean winter rainfall and dry summer conditions (Cordes & Mouton 1996), may indeed reflect the effect of resource distribution on social structure and SSD. On the other hand, the evolution of melanism during cold climatic events some time in the historical past of *P. capensis* could be seen as the most important constraint for SSD to have evolved as part of a suite of traits associated with sexual selection and a polygynous social system. The fact that, in the majority of Cordylidae species studied, larger female body size prevails may point to fecundity selection, which favours large female size when larger females produce larger clutches (i.e. larger reproductive output). As in *Anolis* lizards (Ballinger 1983), clutch size (numbers) in most viviparous members of the Cordylidae are small and do not increase with an increase in female body size. Although this may explain why anole males are larger than females, it does not explain the reverse situation for the majority of gekkonids (Perry 1996) and Cordylidae species. A more likely explanation seems to be that the absence of pronounced male-plus dimorphism or the presence of female-plus dimorphism is under phylogenetic constraint, making a species-specific explanation of SSD unnecessary (Shine & Fitzgerald 1995; Perry 1996). A possibility in this regard is that together with an ancestral monogamous social structure went the selection for a smaller adult male body size, for greater mobility in finding females (van Wyk 1992).

As in most Cordylidae lizards studied (see van Wyk & Mouton 1996) to date, reproduction is a seasonal phenomenon in both sexes of *P. capensis*, with cycles reasonably well synchronised among individuals. Both male and female gonadal cycles are characterized by autumn/winter reproductive activity, culminating in spring at the time of mating, as described for several viviparous members of the Cordylidae (van Wyk & Mouton 1996). The onset of vitellogenesis during the ovarian cycle in *P. capensis* females corresponds to the now general pattern of autumn/winter vitellogenic activity described for all species of the three genera, *Pseudocordylus* (Flemming 1993b,c), *Cordylus* (see van Wyk 1994a, 1995 for reviews) and *Platysaurus* (van Wyk & Mouton 1996) studied to date. This phenomenon of pattern conservatism in the vitellogenic cycles of autumn/winter (fall) vitellogenic activity was also reported for *Sceloporus* (see Guillette & Mendez-de la Cruz 1993) and *Liolaemus* (see Ramirez-Pinilla 1995). Flemming (1993b) reported a few gravid *P. melanotus*

females in late winter (July, August), therefore suggesting that vitellogenic cycles were completed in winter, followed by subsequent ovulation and mating before the onset of the warmer summer months. Whether this phenomenon also occurs in *P. capensis* is not known, since we had limited material available for the winter months. Guillette & Mendez-de la Cruz (1993) suggested that the completion of the ovarian cycle during winter in several montane *Sceloporus* species could be an important adaptation to the success of reproduction at high altitudes in these viviparous lizards, since it will allow for embryonic growth to be completed earlier in summer, thereby ensuring a longer growth season for young which may contribute to their survival in the montane environment. However, in both *P. melanotus* (Flemming 1993b) and *P. capensis* (this study) indications are that ovulation more frequently occurs in spring and early summer and that gestation continues throughout most of summer until autumn.

Compared to other viviparous pseudocordylids, e.g. *P. melanotus* (Flemming 1993b) and *P. microlepidotus* (unpublished data), *P. capensis* showed a longer gestation period. Although limited, our data suggest that parturition in *P. capensis* takes place during late autumn (April–May). In spite of the long gestation period, females seem to reproduce annually. The onset of vitellogenesis before parturition in autumn substantiates this suggestion. This is in contrast to females of the large cordylid, *Cordylus giganteus*, from the Highveld grasslands, known to skip a breeding cycle after a late summer/early autumn gestation period and birth of young during late autumn (van Wyk 1991, 1994a). To date, *C. giganteus* is the only Cordylidae lizard reported to exhibit biennial female reproduction, but also the only member of the Cordylidae family known to stay underground, without feeding, throughout the cold winter months (van Wyk 1991, 1994b). It seems that the birth of young in autumn, prior to the cold winter months, may not affect the survival of young, since van Wyk (1992) reported high survival rates of hatchlings through winter, in spite of aphagy. Mortality of *C. giganteus* hatchlings as a result of predation, however, increased dramatically during the first summer. Although *C. giganteus* hatchlings did not grow during winter (van Wyk 1992), it could be that hatchlings of montane Cordylidae lizards grow through winter because of continued activity and feeding, thereby getting a head start in summer. Activity and feeding throughout winter, together with the available stored fat reserves, probably ensure adequate energy availability for females to continue with vitellogenesis in the cool montane environment.

Although adequate data are lacking, the presence of yolk reserves in late-term *P. capensis* embryos, as in other Cordylidae lizards studied to date (van Wyk 1989; Flemming & van Wyk 1992; Flemming 1993a,b), seems to indicate that most of the nutritional requirements for embryonic development in *P. capensis* are met by yolk reserves deposited during vitellogenesis prior to ovulation. The only cordylid species studied to date that may have meaningful placental transfer, based on indirect evidence, is the large *C. giganteus* (van Wyk 1994b).

The spermatogenic cycle of *P. capensis* starts in late summer/autumn and continues throughout winter and spring, with testicular regression during summer (November–January). The *P. capensis* spermatogenic cycle conforms to the

pre-nuptial spermatogenetic pattern of most temperate lizards with the production of sperm immediately prior to mating, without prolonged sperm storage in the epididymis or vas deferens (see Jameson 1988; van Wyk & Mouton 1996). When considering the onset of spermatogenetic activity in late summer/autumn (Guillette & Mendez-de la Cruz 1993; Ramirez-Pinilla 1995; van Wyk 1995; van Wyk & Mouton 1996), rather than in spring, this variation in the pre-nuptial pattern is clearly different to the well known spring-summer pattern (Fitch 1970; Licht 1984). The onset of spermatogenesis in late summer/autumn is, however, not the rule in males associated with females exhibiting a pattern of autumn/winter vitellogenic activity (Guillette & Mendes-de la Cruz 1993; van Wyk 1995).

The phenomenon of post-nuptial spermatogenesis, i.e. summer–autumn spermatogenesis associated with sperm storage in the epididymis and vas deferens throughout winter until mating in spring, has now been described for several lizard species (see Guillette & Mendez-de la Cruz 1993), including members of the Cordylidae (Flemming 1993c; van Wyk 1995). Associated with post-nuptial spermatogenetic cycles in autumn-breeding species is the phenomenon of asynchronous reproductive activity between males and females (Guillette & Mendez-de la Cruz 1993). The spermatogenetic cycle of *P. capensis* clearly shows characteristics of both seasonal patterns, spermiogenesis completed before winter (typical post-nuptial) but testicular regression associated with the summer period (pre-nuptial), therefore no extended period of sperm storage associated with testicular regression during the winter months (post-nuptial). *P. capensis* exhibits an extended spermiogenic period when compared to the lowland Cordylidae species that exhibit pre-nuptial cycles. Interestingly, the two pseudocordylid species studied to date, *P. melanotus* (Flemming 1993c) and *P. microlepidotus* (unpublished data), both exhibit typical post-nuptial spermatogenetic cycles, i.e. with testicular regression during winter and spring associated with sperm storage during winter through early summer. Because of the early completion of spermiogenesis (i.e. before winter) in *P. capensis*, some degree of asynchrony between male and female cycles is evident. Whether winter matings with sperm storage in females occur is not known and needs further study. The advantages of an extended mating period in low-density populations in an environment where visibility among individuals is low and the breeding season is relatively short seems obvious.

Apart from *Cordylus giganteus*, also exhibiting a post-nuptial cycle (van Wyk 1995), other representatives of the *Cordylus* genus studied to date, *C. polyzonus* (van Wyk 1990; Flemming 1993a) and *C. cordylus* (unpublished data), exhibit autumn pre-nuptial cycles. Regarding a third genus, the oviparous genus *Platysaurus*, van Wyk & Mouton (1996), recently reported pre-nuptial gonadal cycles in two species. Although the phylogenetic position of *Platysaurus* is not certain, in a preliminary analysis Lang (1991) and Herselman (1991) suggested *Platysaurus* to be imbedded within the more advanced *Pseudocordylus* species (*microlepidotus* and *melanotus*), exhibiting the post-nuptial spermatogenetic pattern. Van Wyk & Mouton (1996), at the time concluded that the *Platysaurus* pattern along with the oviparous mode of reproduction could represent a reversal from post-nuptial,

viviparous to pre-nuptial, oviparous, phenomena respectively. However, recent advances regarding phylogenetic relationships within the family Cordylidae suggest that the genus *Platysaurus* may indeed represent a basal stem from the phylogenetic tree (Titus unpublished). The similarity of *P. capensis* cycles to that of the *Platysaurus* species studied corroborates the hypothesis that the *Platysaurus* divergence is closer to *P. capensis*. If the *Platysaurus* divergence proves to be the most basal, then the association of autumn gonadal cycles (van Wyk & Mouton 1996) with the evolution of viviparity in this lineage needs reconsideration. It is clear that only a comprehensive comparative study of gonadal cycles within the Cordyliformes (Gerrhosauridae & Cordylidae) will unravel the evolution of reproductive cycles within the Cordylidae.

In both sexes of *P. capensis*, the fatbody reserves accumulated throughout late summer to reach peak values in autumn at the time of the onset of both gonadal cycles. In *P. melanotus*, the same pattern was reported in both females and males (Flemming 1993b,c). It is noteworthy that *P. capensis* and *P. melanotus* exhibit different spermatogenetic patterns, which suggests that the dynamics of the male fatbody cycle may be unrelated to (uncoupled from) the male spermatogenetic cycle. The fatbody cycle reported here for *P. capensis* is similar to that reported for several other cordylid species studied to date (van Wyk 1989; van Wyk 1994). However, the fatbody cycle of *C. polyzonus* collected from Saldanha, within the same winter rainfall zone as *P. capensis*, was found to peak during early summer (Flemming & van Wyk 1992; Flemming 1993a). The same species was reported to exhibit the typical autumn fat deposition cycle (Derickson 1976) in the Orange Free State province known for its colder winters (van Wyk 1989). It is clear that more data are needed to compare the dynamics of fatbody cycles of cordylid lizards occurring in the Mediterranean and summer rainfall zones in relation to their feeding ecology, before we can hope to understand the variation in cordylid fatbody cycles.

In both *C. giganteus* (van Wyk 1994) and *P. melanotus* (Flemming 1993b,c) collected from the cooler Highveld grasslands, indirect evidence suggested that, prior to the major fatbody build-up in mid-autumn, food abundance and foraging success were high during summer and early autumn. Although the importance of fatbody build-up for male reproduction may not be that clear yet, evidence suggests that fatbody reserves are an important factor determining successful reproduction in females (Greenberg & Gist 1985; Etheridge *et al.* 1986; van Wyk 1991; 1994). If the occurrence of biennial reproductive activity, as reported for *C. giganteus* females (van Wyk 1991; 1994), is an indication of resource stress on reproductive activity, the occurrence of annual reproduction in the montane lizards, *P. melanotus* and *P. capensis*, suggests adequate resource availability in late summer through autumn months for these lizards in the montane environment.

Ambient temperature has been implicated as one of the major factors controlling the onset of reproductive activity in reptiles (Duvall, Guillette & Jones 1982; Licht 1984). In all the cases, including Cordylidae females and other autumn-breeding lizards studied so far (see Guillette & Mendes-de la Cruz 1993), an inverse correlation between autumn/winter

gametogenesis and the main proximal factors has been reported. However, indications are that environmental control is much more complex than anticipated. Species exhibiting different reproductive cycles, i.e. spring/summer and autumn/winter cycles, or the occurrence of asynchronous reproductive activity between males and females, suggest that we need to have a fresh look at the environmental control of reproduction, at least in autumn/winter breeding lizards (Guillette & Mendez-de la Cruz 1993).

It is clear from most studies concerning autumn/winter reproductive cycles that female cycles are relatively invariable (conservative), and therefore under phylogenetic constraint (Guillette & Mendez-de la Cruz 1993). Whether female cycles were fixed during a single evolutionary event, in most cases remains unknown. On the other hand, the reported variation in the timing of spermatogenesis and, especially the occurrence of asynchrony between male and female cycles in species of the same lineage or species of different lineages, call for more comprehensive comparative studies to understand the evolution of reproductive patterns in such groups. To do this, we need a robust phylogeny and historical biogeographic information of the group concerned (Losos & Miles 1994), otherwise the interpretation of such comparative data will remain problematic. The family Cordylidae, with four genera and relatively few species, provides such an opportunity to study the evolution of viviparity, variation in reproductive cycles, synchronization between male and female cycles and ultimately environmental control of reproductive cycles in lizards. The present study suggests that our understanding of the evolution of the reproductive traits in the Cordyliformes lizards is dependent on a robust phylogeny. For example, if the oviparous genus *Platysaurus* is the most basal divergence from the Cordyliformes ancestors, as recently suggested (Titus unpublished), then current knowledge suggests that the shift from a typical spring–summer to autumn–spring gonadal cycle evolved first, without a link to the evolution of viviparity. This hypothesis would then suggest viviparity to have evolved as a second step in the evolution of reproductive traits in the Cordylidae. Alternatively, the hypothesis put forward earlier by van Wyk & Mouton (1996), which suggests that oviparity in the genus *Platysaurus* represents a reversal from viviparity, needs more consideration before being discarded. It is also clear that the lack of knowledge regarding reproductive cycles of the family Gerrhosauridae, the oviparous sister family of the family Cordylidae (Lang 1991), further contributes to the problem of understanding the evolution of reproductive cycles in Cordyliformes lizards.

Acknowledgements

This study was financially supported by grants from the University of Stellenbosch and Foundation for Research Development (FRD) to J.H. van Wyk. We thank the curators of Herpetology collections, W. Haacke of the Transvaal Museum and W.R. Branch of the Port Elizabeth Museum, for allowing us to examine specimens. R.N. Hartzenberg provided us with valuable research assistance. We also thank A. Sadie for her assistance with the statistical analyses and two anonymous reviewers for their constructive comments.

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