

REPRODUCTIVE BIOLOGY OF THE SECRETIVE MEDITERRANEAN COLUBRID *MACROPROTODON CUCULLATUS* IN THE SOUTHERN IBERIAN PENINSULA

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We examined 150 museum specimens of *Macroprotodon cucullatus* from the southern portion of the Iberian Peninsula to determine size at sexual maturity, reproductive and fat body cycles, clutch size and hatching period. Males mature at a smaller absolute and relative size than females and, as in Moroccan populations, show a postnuptial spermatogenic cycle. The mating period occurs earlier than that of any other Mediterranean snake species. Females reproduce every two years and there is no correlation between body size and clutch size. The tendency for *M. cucullatus* to have a biennial reproductive frequency and a fixed clutch size is discussed in relation to some features of the ecology of this species, including its burrowing habit, its likely low range of preferred temperatures in relation to epigeous species, and its low feeding frequency.

INTRODUCTION

In European temperate and subtropical areas oviparous female snakes are monoestrous with a rather uniform reproductive cycle. Ovulation occurs in late spring and early summer, and hatching in late August or September (e.g. Bourlière & Petter-Rousseaux, 1955; Saint-Girons, 1982; Naulleau, 1992; Luiselli, Capula & Shine, 1997). Male reproductive cycles of snakes in the same areas, however, are not so uniform. Most of the species demonstrate spermatogenesis during aestivation, with multiplication of spermatogonia beginning in the spring, and spermiogenesis ending in early autumn (e.g. *Coluber viridiflavus*: Bourlière & Petter-Rousseaux, 1955; *Elaphe longissima*: Saint-Girons, 1963; and *Coronella girondica*: Bons & Saint-Girons, 1982). Some species from Mediterranean and arid zones of the southern Palearctic, however, have prenuptial spermatogenesis which begins in late winter or early spring and ends in early summer (*Malpolon monspessulamus*: Cheylan, Bons & Saint-Girons, 1981; *Coluber hippocrepis*: Bons & Saint-Girons, 1982; Pleguezuelos & Feriche unpub. data).

Macroprotodon cucullatus, the sole species of the genus and the smallest Palearctic colubrid, is distributed from southern Palestine to western Morocco, relictually in central (Hoggar) and western (Río de Oro) Sahara, some western Mediterranean islands, and across the southern half of the Iberian Peninsula (Busack & McCoy, 1990). Known details of its natural history are very peculiar: this species displays the lowest feeding frequency among Mediterranean colubrids, and feeds mostly on long-bodied and burrowing prey; it is secretive and fossorial, with skeletal modifications correlated with its fossorial habit (Rasmussen, 1979; Wade, 1988; Pleguezuelos, Honrubia & Castillo, 1994; Pleguezuelos, 1997).

An aestival reproductive pattern, with spermatogenesis from March to October, and spermatozoa overwintering in the vas deferens until the

following spring, has been found in male specimens from Morocco (Saint-Girons, 1963; Bons, 1967). Why spermatogenesis occurs one to two months before other Palearctic colubrids with aestival spermatogenesis (see Saint-Girons, 1982) is unclear and, apart from occasional reports of specimens in captivity (González de la Vega, 1988) or in the field (Escarré & Vericad, 1981), little is known about the female reproductive cycle and its relationship to the male reproductive cycle.

Here we record body size, ontogenetic and seasonal change in gross gonadal morphology, fat body level, and clutch size of *M. cucullatus* in the Iberian population, and present data concerning size at maturity, reproductive cycle in both sexes, fat body cycling, and certain morphological traits of hatchlings.

MATERIAL AND METHODS

We studied 150 specimens of *M. c. ibericus* (84 males, 64 females and two juveniles of undetermined sex) from the southern Iberian Peninsula (36° 00'-39° 40' N, 1° 25'-7° 23' W). The climate in this area is typically Mediterranean, with mild and rainy winters in the west, cool and less rainy winters in the east, and hot, dry summers throughout (Montero & González-Rebollar, 1982). Specimens were obtained from: Museo Nacional de Ciencias Naturales (Madrid), Estación Biológica de Doñana (Seville) and Departamento de Biología Animal y Ecología (Univ. Granada). Data from preserved material were combined with field observations of mating behaviour and hatching data obtained during standardized searches (1988-1993) throughout the eastern portion of the study area.

Snout-vent length (SVL, ± 1 mm) and total body mass (± 0.1 g) were measured. Lengths and body masses were mainly taken from fresh specimens or obtained from labels of museum specimens that were measured fresh; in ten cases (6.7% of the sample size) the measurements were taken from well-preserved mu-

seum specimens. All specimens were dissected. Testis size (longest, median, and shortest diameter, ± 0.1 mm) was recorded in males. Testicular volume (TV) was calculated using the formula for volume of a flattened ellipsoid, $TV = 4/3 \pi abc$, where a = longest radius, b = median radius and c = shortest radius. Because TV increases significantly with SVL, we used the ratio of organ:body size (SVL^3 as measure of body size) as an indicator of male reproductive activity (Seigel & Ford, 1987; Whittier & Limpus, 1996). In this way, the resultant ratio is independent of body size, although at the limit of significance ($r = 0.253$, $n = 55$, $P = 0.057$). To calculate size at maturity in males, we related the volume of the right testis (always anterior and normally the largest) to body size.

The presence and number of oviductal eggs, diameter of the largest ovarian follicle or oviductal egg (± 0.1 mm), and fat body development in females were recorded. We were not able to remove the fat bodies from some museum specimens and scored fat bodies from zero (no traces of fat) to four (a continuous fat layer in the ventral part of the abdominal cavity). Reproductive condition of each female was established by presence of vitellogenic follicles, oviductal eggs, and internal signs of recent oviposition (widened oviducts). For clutch size, we made conservative estimates by counting only shelled oviductal eggs or well-developed vitellogenic follicles. The proportion of gravid females in the sample during the reproductive period served to estimate frequency of reproduction. Appearance of neonates in the field and collection dates for the smallest specimens in collections served to approximate time of hatching. To calculate size at hatching, we consider only young seen or collected during this period with fresh vitellogenic scars. Specimens were sexed in the field following Feriche, Pleguezuelos & Cerro (1993).

RESULTS

Apparently the relative testicular volume (RTV) does not increase with body size in specimens with $SVL < 240$ mm. Beginning at 240 mm SVL, there is a testicular growth that implies an 8- to 12-fold increase in RTV (Fig. 1). Therefore, we considered males exceeding this size to be sexually mature. The largest male *M. cucullatus* recorded in the Iberian Peninsula measured 475 mm SVL (present data), and males mature at about 50% of maximum length. Largest specimens ($SVL > 370$ mm) have a lower RTV (mean \pm SD = 0.55 ± 0.26 , $n = 6$) than smaller mature specimens ($240 < SVL < 370$ mm; mean \pm SD = 1.24 ± 0.64 , $n = 39$; Mann Whitney *U*-test, $P = 0.002$; Fig. 1). This testicular involution is only apparent, because four out of the six largest specimens were collected outside the testicular recrudescence season.

Testicular recrudescence began in early May with peak volume being achieved by late September. Testis volume decreased sharply during October and regressed testes were observed during autumn and late winter, and presumed, but not observed, during mid-

winter (RTV in September versus October + November + December; *t*-test, $t = 3.95$, $P = 0.01$; Fig. 2). Copulation was observed in the field as early as 15 March. In captivity, mating also occurs in March in specimens from the south-western Iberian Peninsula (J. P. González de la Vega, pers. comm.). The male reproductive cycle is seasonal and annual progression of the RTV indicates that *M. cucullatus* has an aestival spermatogenic cycle.

The smallest *M. cucullatus* female that showed signs of reproductive activity (vitellogenic and well-developed follicles with high fat body level) was 280 mm SVL (Fig. 3). A female of 302 mm SVL from the south-west of the Iberian Peninsula deposited two eggs (González de la Vega, pers. comm.). Therefore, we consider that females mature at about 280-300 mm SVL. No female with a $SVL < 280$ mm collected during the period of reproductive activity (late spring or early summer, $n = 5$) contained either enlarged vitellogenic follicles or oviductal eggs. Each of the small group of females with a SVL between 255-275 mm collected during early summer and autumn with follicles 1.1-6.6 mm in length (Fig. 3) was non-reproductive. The largest female *M. cucullatus* recorded in the Iberian Peninsula measured 409 mm SVL (present data), and females mature at about 70% of maximum length.

As expected, the female reproductive cycle is also seasonal. Vitellogenesis begins in late March, in follicles 4 mm in diameter. Ovulation occurs from April to May, and females are gravid between early May and early July (Fig. 4). Post-reproductive females (distended oviducts) were observed from early July. We estimate oviposition in the field to occur between June and early July. We found a few specimens with follicles > 4 mm in length in summer (Fig. 4), but do not interpret this as post-reproductive vitellogenesis, because they were atretic.

The mean number (\pm S.D.) of oviductal eggs was 4.16 ± 0.75 (range = 3-5, $n = 6$), and we found no correlation between female SVL and the number of oviductal eggs ($r = 0.26$, $n = 6$, $P = 0.62$). Six out of the twelve (50%) sexually mature females in the reproductive period (May to early July) contained oviductal eggs or enlarged follicles. In order to test any bias by the effect of body size, we compared SVL in mature but

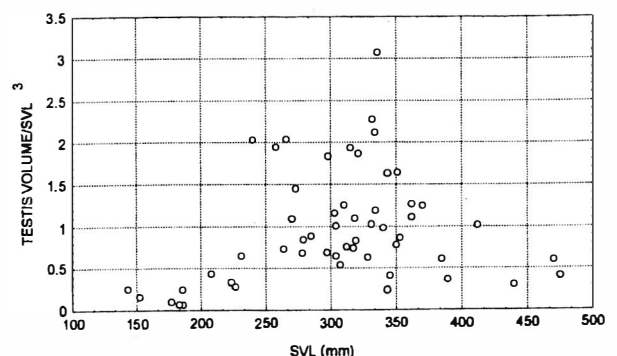


FIG. 1. Gonadal activity of male *M. cucullatus* as indicated by relative testicular volume versus body length ($n = 55$).

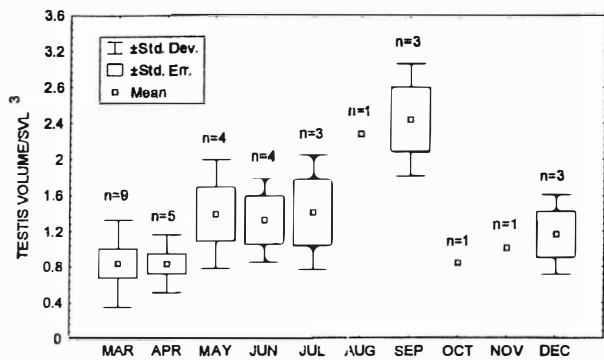


FIG. 2. Relative testis volume of sexually mature male *M. cucullatus* (SVL > 240 mm, n = 34) in relation to calendar year.

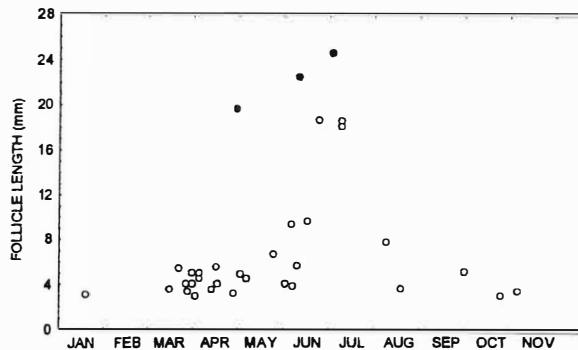


FIG. 4. Length of the largest follicle (open circle) and oviductal egg (solid circle) of sexually mature female *M. cucullatus* (SVL > 280 mm, n = 34) in relation to calendar year. The two females from early June with follicles about 9 mm in length were non-reproductive (very low level of abdominal fat).

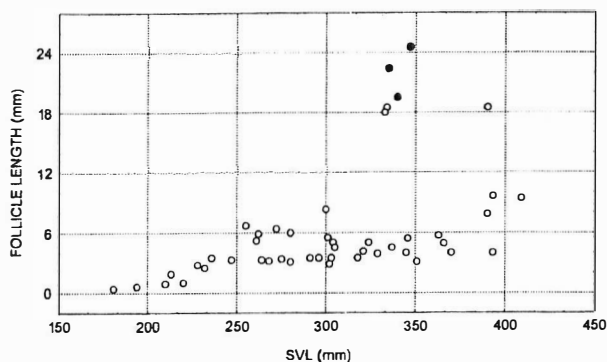


FIG. 3. Gonadal activity of female *M. cucullatus* as indicated by length of the largest previtellogenic follicles (< 3-4 mm; open circle), vitellogenic follicles (open circle) and oviductal eggs (solid circle) versus body length (n = 48).

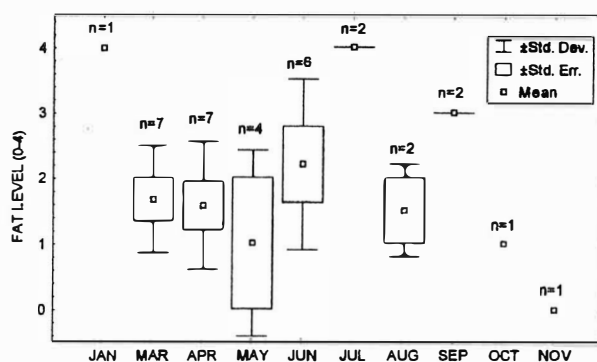


FIG. 5. Abdominal fat level for reproductive female *M. cucullatus* (n = 33).

non-reproductive females (mean \pm SD = 350.0 \pm 28.1 mm, n = 6) and reproductive females (mean \pm SD = 358.0 \pm 34.1 mm, n = 6), finding no difference (Mann Whitney U-test, P = 0.4). The low frequency of reproductive females suggests a biennial reproductive cycle.

We noted no significant monthly differences in fat body level in reproductive females (Kruskal-Wallis test, $H_{6,28} = 9.50$, P = 0.15; October to February omitted because of small sample size; Fig. 5).

First hatchlings were recorded in the field on August 15, and more appeared in both field and museum collections toward late September. Hatchling SVL varied from 123 to 166 mm (mean \pm S.D. = 146.5 \pm 11.8; n = 15) and body mass was between 1.4 and 2.5 g (2.0 \pm 0.3 g; n = 15). Taking length at maturity to be 240 mm SVL in males and 280-300 mm SVL in females, there is an increase between 1.6 and 1.9 times the hatching length on reaching maturity for males and females respectively.

DISCUSSION

Male *M. cucullatus* mature at a smaller absolute and relative size (SVL at maturity versus maximum SVL) than females, despite the lack of sexual dimorphism in body size found by Feriche *et al.* (1993) working with the same data set used at the current study. In a recent

review, Parker & Plummer (1987) also found that males of about two-thirds of the temperate snake species analysed (sample size of 58 species) matured at a smaller body size than did females. Cost to males of early maturity is lower than that for females. Moreover, females appear to delay maturity because fecundity is proportional to body size (Shine, 1978; Swaner & Sarre, 1988).

Our data indicate that the reproductive cycle of male and female *M. cucullatus* in the southern Iberian Peninsula begins in spring, as it does in Morocco (Bons, 1967). This pattern appears in females of all snake species from the Western Palearctic (e.g. Goddard & Spellerberg, 1980; Naulleau, 1992; Baron, Ferriere, Clobert & Saint-Girons, 1996; Luiselli *et al.*, 1997). From the geographic distribution of *M. cucullatus*, a prenuptial spermatogenic cycle would be expected (as in *Malpolon monspessulanus* and *Coluber hippocrepis*, Mediterranean colubrids with a similar distribution; Cheylan *et al.*, 1981; Pleguezuelos & Feriche, unpubl. data). However, as in other colubrid species having a more northerly Palearctic distribution (see data in Introduction), this species has a postnuptial spermatogenic cycle (Bons, 1967). A previous study revealed *M. cucullatus* in the western Mediterranean to have the lowest frequency of specimens with gut con-

tents among Mediterranean colubrids (24.6% of individuals contained food remains in the whole gut; Pleguezuelos *et al.*, 1994). In the current data set, only 14.7% of the mature females ($n = 34$) and 14.0% of all females pooled ($n = 50$) had prey in their stomachs. In our previous study we suggested that this species had low energy requirements, as is expected in reptiles that live under rocks or lead a fossorial life style (Kamel & Gatten, 1983). Moreover, if *M. cucullatus* dwells under rocks and burrows (Pleguezuelos, 1997), it follows that it must thermoregulate more slowly than do epigeous species. Thus, this species would have a postnuptial spermatogenic cycle and a lengthy spermatogenesis period because it is likely that low energy specialization precludes it from developing the entire spermatogenic cycle in a short period. This contrasts with other Mediterranean species, normally epigeous and non-secretive, with a prenuptial cycle in which spermatogenesis occurs rapidly (Cheylan *et al.*, 1981; unpubl. data from the authors). Temperature is the main environmental factor related to testicular activity in temperate reptiles (Marrion, 1982) and the onset of the spermatogenic cycle in *M. cucullatus* begins with the warmer temperatures of mid-spring, and extends through the hottest months of the year.

The mating period of *M. cucullatus* occurs earlier (see also González de la Vega, 1988) than in any other Mediterranean snake species (i.e. mid-May in *Coluber viridiflavus*: Saint-Girons, 1982; April-June in *Coronella girondica*: González de la Vega, 1988; June in *Elaphe scalaris*: Blázquez, 1993; May in *Natrix natrix*: Luiselli *et al.*, 1997). In the study region, activity differed between sexes, with a higher peak in male activity detected in early spring, but at the limit of significance (Yate's corrected $\chi^2 = 3.76$, $df=1$, $P = 0.052$; Pleguezuelos & Feriche, unpubl. data). This pattern is probably associated with the mating period. Male specimens from Morocco, on emerging from overwintering (toward mid-March), have reproductive ducts full of spermatozoa (Saint-Girons, 1963; Bons & Saint-Girons, 1982). If *M. cucullatus* proved to be a low energy specialist, copulation would be accomplished early in the year because females would then have a longer period for completing vitellogenesis, ovulation and shelling than other Mediterranean snakes. Although the long period during which we found females with oviductal eggs (75 days; Fig. 4), supports this suggestion, it is only tentative, because the scarcity of mature females during early spring (Fig. 4) precludes us from establishing the real length of the vitellogenesis period.

Breeding frequency is among the most important yet least understood aspects of snake reproductive biology (Seigel & Ford, 1987). Most studies on snake reproductive ecology have used the proportion of gravid females in the population to estimate the frequency of reproduction (see review in Seigel & Ford, 1987). Although interpretations about reproductive cycles based on museum specimens must be treated cautiously, half the *M.*

cucullatus females in collections from the southern Iberian Peninsula had enlarged follicles and oviductal eggs in the appropriate reproductive period. Reproductive frequency, based on percentage of reproductive snakes, could be biennial in female *M. cucullatus*.

This method of estimating the reproductive frequency has recently been criticized (Bonnet & Naulleau, 1996; see also Martin, 1993). Females undergoing vitellogenesis and pregnancy may require body temperatures higher than non-reproductive females, and Bonnet & Naulleau (1996) found that reproductive *Vipera aspis* females basked more frequently than non-reproductive *V. aspis*, resulting in different catchability among females; sampling bias can strongly affect breeding frequency estimates in snakes. Nevertheless, we believe that the difference in catchability found in *V. aspis* does not apply to the species here studied. *M. cucullatus* spend much of the time sheltering under stones, at least in the south-eastern Iberian Peninsula (Pleguezuelos *et al.*, 1994), and only rarely bask, even during the reproductive period (Busack & McCoy, 1990; Pleguezuelos, 1997). Most specimens in collections have been found under stones (from personal observations and notes on the labels of the specimens), and thus the probabilities of finding reproductive and non-reproductive females may be the same. Anyway, if gravid females were selectively collected because they were more sedentary and obvious, then a reduction in reproductive frequency in the sample is likely to reflect a more severe reduction in frequency in the total population (G. Shea, pers. comm.).

In a survey of 38 species and populations of colubrids, Dunham, Miles & Reznick (1988) found that most species reproduced annually, and only 8% of species were distinctly biennial in breeding frequency. Moreover, *M. cucullatus* SVL at maturity and mean SVL of adult females are lower than the mean for the same life history traits for biennially reproducing snakes (613.5 mm and 747.7 mm, respectively, in a review of 30 species; Dunham *et al.*, 1988), and any known colubrid with biennial or triennial reproduction (see Dunham *et al.*, 1988). These traits of its reproductive ecology could be related to the low-energy specialization here suggested for this species. As it seems that female reproductive frequency essentially depends on resource availability (Andren & Nilson, 1983; Seigel & Ford, 1987; Whittier & Crews, 1990), and adult female *M. cucullatus* are food limited (Pleguezuelos *et al.*, 1994; present data set), they may be unable to recoup energy in less than one year following parturition. Constraints on activity and foraging may limit the reproductive capacities of females (Dunham *et al.*, 1988). The presence of non-reproductive adult females in the sample studied could explain our not having found either monthly differences in fat body levels or an association of vitellogenesis with the decline in fat body levels that appears in other temperate snakes (Diller & Wallace, 1984; Hailey & Davies, 1987).

Female fecundity was low, but within the range of other small colubrids from temperate areas (Seigel & Ford, 1987; Dunham *et al.*, 1988). Scattered data on the reproduction of this species indicate a clutch size of three for one female just to the north of the study area (Escarré & Vericad, 1981) and two to six for specimens in captivity from the south-west of the Iberian Peninsula (González de la Vega, 1988). A positive correlation between female SVL and clutch size is common among snakes (Ford & Seigel, 1989; Dunham & Miles, 1985). The lack of correlation in *M. cucullatus* between female size and female fecundity may be an artifact of sample size, and may also be related to the narrow band of body sizes at which females appear to be reproductive. If we pool our data with data gathered by González de la Vega (pers. comm.) from the south-west of the Iberian Peninsula, and data gathered by us in populations from similar climatic areas in north-western Africa, we still fail to find any correlation between female body size and clutch size ($r = 0.38$, $n = 12$, $P = 0.21$). Low correlation between female SVL and fecundity reflect the trend towards a fixed clutch size. Invariant clutch size is normally found in fossorial (H. Saint-Girons, *in* Agrimi & Luiselli, 1994) and prey-limited snakes (Shine, 1988). *M. cucullatus* fits these characteristics because its morphology (Rasmussen, 1979) and ecology (Pleguezuelos, 1997) places it among the most fossorial snakes in the Western Palaearctic, and its likely sit-and-wait foraging habit places it among those terrestrial snakes with the lowest feeding frequency (Pleguezuelos *et al.*, 1994). Moreover, when grouped by reproductive frequency, foraging mode, distribution, etc., the lowest values in a regression analysis of mean clutch size on female SVL at maturity are found in biennially reproducing snakes (Dunham *et al.*, 1988).

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