

REPRODUCTION IN TWO NAMIB DESERT LACERTID
LIZARDS (*APOROSAURA ANCHIETAE* AND
MEROLES CUNEIROSTRIS)

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ABSTRACT: The reproductive cycles of two narrowly sympatric lacertid lizards from the Namib Desert of Namibia (South-West Africa) were investigated. *Aporosaura anchietae* is capable of continuous reproductive activity for prolonged periods (Jan 1976-Feb 1977). Reproductive activity declined sharply in March 1977, but quickly increased in April. Recovery was completed by June 1977, and reproduction continued into December 1977 when the study was terminated. Continuous reproduction for more than 1 yr is typical of tropical lizards, but has not been reported previously for a desert species. Causes of the March 1977 reproductive decline are not totally clear, but appear to be related to decreased rainfall, to lower productivity of insects, and to lower levels of stored fat. The average clutch of 85 females was 1.3 eggs (range 1-2), and 2-4 clutches are produced yearly.

Meroles cuneirostris has a reproductive cycle typical of temperate zone species, with spermiogenesis occurring May-February (spring-summer), followed by autumnal regression (March) and then recrudescence (April). Oviducal eggs were found over a 5-mo period (Sep-Mar). Clutch size of 29 females averaged 2.9 eggs (range 1-4), and females can produce two clutches each year.

Both species have seasonal fat cycles typical of temperate zone lizards, in which fat bodies enlarge in autumn and are depleted by spring, but the relative amounts of fat stored by each species differ considerably.

Key words: Lacertidae; Namib Desert; Reproduction; Squamata

REPRODUCTIVE patterns of North American lizards have become increasingly better known in recent years, but in other areas of the world this information is very limited. The coastal Namib Desert of southwestern Africa is such a region, and studies of the reproductive cycles of any of the approximately 50 species of lizards in this fauna are lacking. The Namib is a cool, coastal desert with a mild, subtropical climate (Logan, 1960; Schultze, 1969).

In a preliminary analysis of the reproduction of *Aporosaura anchietae*, Louw and Holm (1972) examined the gonads from 37 individuals and concluded that reproduction probably is aseasonal. The reproductive pattern of *Meroles cuneirostris* was previously unknown. Here we describe the reproductive cycles of these two related species and discuss some environmental factors that may control the differences noted in their reproductive patterns.

MATERIALS AND METHODS

Our study sites lie approximately in the central portion of the Namib Desert and on the Tropic of Capricorn. At Gobabeb, the mean ambient winter temperature is 18.5°C, and it seldom goes below 10°C. Summer air temperatures average 22.8°C, and very few days are above 40°C. Over three-fourths (77%) of the annual rainfall (\bar{x} = 16.8 mm) occurs during the summer (Dec-Apr), but years with less than 15 mm of rainfall are not uncommon (Seely and Stuart, 1976). All *A. anchietae* were collected in the sand dunes within 8-10 km of Gobabeb, 410 m elevation, Namib Desert, Namibia (23°33'S, 15°05'E). This sand-diving lizard is restricted to the vegetationless slopes of sand dunes from approximately 15-27°S latitude (Louw and Holm, 1972). Except for February 1976, monthly samples were collected from January 1976-December 1977. Adult males averaged larger (4.5 g, 49 mm in

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TABLE 1.—Seasonal distribution of stages in testicular cycle of *Aporosaura anchietae*, January 1976–December 1977. (No sample was collected in February 1976.)

Month	n	Spermiogenesis (%)	Regressing (%)	Regressed (%)	Recrudescence (%)
Jan	9	100	0	0	0
Mar	12	100	0	0	0
Apr	11	100	0	0	0
May	11	100	0	0	0
Jun	12	100	0	0	0
Jul	10	100	0	0	0
Aug	12	100	0	0	0
Sep	12	100	0	0	0
Oct	9	100	0	0	0
Nov	13	100	0	0	0
Dec	10	100	0	0	0
Jan	9	100	0	0	0
Feb	10	90	0	10	0
Mar	9	67	0	33	0
Apr	9	78	0	0	22
May	14	86	0	0	14
Jun	10	100	0	0	0
Jul	14	100	0	0	0
Aug	11	100	0	0	0
Sep	9	100	0	0	0
Oct	12	100	0	0	0
Nov	10	100	0	0	0
Dec	12	100	0	0	0

snout-vent length [= SVL]) than females (3.1 g, 44 mm SVL).

All *M. cuneirostris* were collected in the broad deltaic portion of the Kuiseb River, 5–10 km NW Rooibank (23°9'S, 14°35'E), elevation 100 m. This species lives mainly in flat, sandy, and perennially vegetated interdune valleys or in open plains adjacent to the sand dune regions. Except for July 1976, monthly samples were collected February 1976–January 1977. Adult males averaged larger (8.1 g, 54 mm SVL) than females (4.7 g, 49 mm SVL).

Lizards were preserved in 10% formaldehyde, and gonads were embedded in paraffin. Histological sections were cut at 8 μ m and stained with iron hematoxylin followed by eosin counterstain. Gonads from 250 male and 20 female *A. anchietae* and 97 male and 34 female *M. cuneirostris* were sectioned. Fat bodies were removed from

preserved specimens and weighed to the nearest 0.1 mg. Age at sexual maturity was estimated from animals used in mark-recapture studies and verified from lizards subjected to autopsy. Voucher specimens of both species were deposited in the herpetological collection of the Los Angeles County Museum of Natural History (*M. cuneirostris*, Nos. 128624–128951; *A. anchietae*, Nos. 128952–129593).

RESULTS

Aporosaura anchietae

Male cycle.—This species exhibited continuous spermiogenesis from January 1976 through January 1977 (Table 1), and the epididymides contained sperm throughout this period. Testicular regression occurred in 10% of the males in February 1977 and in 33% of the males in March of that year (Table 1). As Licht and Gorman (1970) reported for several species of *Anolis*, spermiogenesis was in progress in some males even though testes had decreased in size. Recovery was rapid (Table 1), and the percentage of spermiogenic males increased in April (78%) and May (86%). From June through December 1977, all males examined were undergoing spermiogenesis. Most males reach sexual maturity at 40–42 mm in SVL when they are 6–7 mo of age (M. D. Robinson, *unpublished*).

Female cycle.—From January 1976 to February 1977, varying proportions of the female population were reproductively active (vitellogenic follicles to oviducal eggs) (Table 2). In March 1977 no reproductive activity was observed in the 16 females examined. Yolk deposition had started again in April as 2 of the 8 females contained follicles in early vitellogenesis (Table 2). Follicles larger than 3 mm were present in two females in May, and females with oviducal eggs were collected in July. Portions of the population were reproductively active through December 1977 when the study was terminated.

The mean number of eggs or enlarged follicles (> 3 mm) in 85 females was 1.3

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(range 1-2), which is one of the lowest values reported for non-gekkonid lizards (Tinkle et al., 1970). The largest reproductively active female measured 47 mm in SVL, and the smallest was 37 mm in SVL. There is no significant correlation between female body size and number of eggs produced ($r = .12$, d.f. = 83, $P > .1$). Oviducal clutches from 25 gravid females averaged 13.82% of total body weight of the female parent. Females become mature at approximately 4-6 mo in age (M. D. Robinson, *unpublished*), and according to Tinkle's (1969) classification they are early-maturing. As might be expected in an aseasonal reproductive cycle, varying percentages of females were reproductively active (Table 2) each month. This contrasts with the synchronous pattern of ovarian development in several temperate zone lizards from North America (Goldberg, 1975) where more than 90% of the females in the population initiate yolk deposition and ovulate at approximately the same time.

Advanced yolk deposition (follicles > 3 mm) occurred at the same time that oviducal eggs were present; therefore, it is clear that females may produce more than one clutch per year. Weight records and palpation of eight marked females indicate that the number of clutches produced per female each year varied from 2-4 (M. D. Robinson, *unpublished*). *Aporosaura anchietae* hatchlings averaged 26-28 mm in SVL at birth and were observed each month from January 1976-December 1977, with most appearing November-February. This observation indicates that a seasonal breeding peak occurs within this aseasonal reproductive pattern and that most egg laying probably takes place from June to September.

The ovarian cycle of *A. anchietae* is similar to the cycle of *Anolis carolinensis*, which produces single eggs over a prolonged period but not during autumn or winter (Hamlett, 1952). Licht and Gorman (1970), Andrews and Rand (1974), and Somma and Brooks (1976) described a similar pattern in other *Anolis* lizards. In contrast, *A. an-*

TABLE 2.—Percentages of reproductively active female *Aporosaura anchietae* (vitellogenic to oviducal eggs), January 1976-December 1977. (No sample was collected in February 1976.)

Month	n	Reproductively active (%)
Jan	13	8
Mar	13	92
Apr	19	11
May	8	63
Jun	7	100
Jul	7	100
Aug	9	78
Sep	10	90
Oct	12	83
Nov	14	50
Dec	10	70
Jan	14	50
Feb	13	46
Mar	16	0
Apr	8	25
May	5	40
Jun	7	14
Jul	10	70
Aug	5	60
Sep	10	60
Oct	13	31
Nov	12	15
Dec	15	67

chietae produced oviducal eggs or follicles with heavy yolk deposition throughout the year and differed from *Anolis* in that some females had clutches of two eggs (1 in each oviduct which developed at approximately the same rate).

In 1976 and 1977 fat bodies in both sexes increased rapidly in size beginning in April (Table 3). In 1977 fat levels began to decrease earlier (June) than in the previous year, and remained low during winter (Jun-Aug) at a time when 1976 fat bodies were greatly enlarged.

Meroles cuneirostris

Male cycle.—The testicular cycle of *M. cuneirostris* was seasonal (Table 4) with the period of spermiogenesis lasting from May through February and epididymides containing sperm throughout these months. Testicular regression commenced during

TABLE 3.—Percentages of *Aporosaura anchietae* with enlarged fat bodies (> 75 mg) and mean weights of fat bodies (mg) from January 1976–December 1977. (No sample was collected in February 1976.)

Month	Females			Males		
	n	% with enlarged fat bodies	Fat-body wt. ($\bar{x} \pm SE$)	n	% with enlarged fat bodies	Fat-body wt. ($\bar{x} \pm SE$)
Jan	13	0	0.0	18	0	0.0
Mar	13	0	2.6 \pm 2.4	23	0	2.4 \pm 1.5
Apr	19	33.0	65.7 \pm 20.3	15	60.0	103.8 \pm 25.2
May	8	75.0	154.1 \pm 35.4	15	80.0	281.4 \pm 72.2
Jun	7	85.7	213.2 \pm 62.9	27	88.0	268.5 \pm 31.7
Jul	7	85.7	215.7 \pm 44.7	12	100.0	466.9 \pm 67.5
Aug	9	88.8	208.6 \pm 32.5	12	100.0	200.9 \pm 27.2
Sep	10	40.0	78.9 \pm 20.9	14	75.0	154.7 \pm 29.9
Oct	12	33.0	72.0 \pm 18.1	14	64.2	155.0 \pm 35.6
Nov	14	14.2	23.8 \pm 9.4	13	46.1	152.9 \pm 56.6
Dec	10	0	16.1 \pm 5.3	11	18.2	34.0 \pm 13.4
Jan	14	0	4.6 \pm 1.1	10	0	9.5 \pm 4.1
Feb	13	0	25.2 \pm 7.6	11	23.2	48.0 \pm 24.7
Mar	16	0	4.3 \pm 3.1	10	10.0	34.7 \pm 13.6
Apr	8	87.5	145.7 \pm 20.9	9	100.0	211.1 \pm 27.9
May	5	80.0	164.6 \pm 41.2	14	57.1	115.6 \pm 29.1
Jun	7	28.5	41.2 \pm 22.5	11	15.4	87.0 \pm 25.2
Jul	10	40.0	74.6 \pm 26.5	16	18.7	53.1 \pm 9.9
Aug	5	40.0	52.4 \pm 22.1	11	54.5	93.5 \pm 12.6
Sep	10	10.0	36.9 \pm 8.9	9	22.2	51.3 \pm 18.3
Oct	13	0	21.0 \pm 3.9	12	0	26.8 \pm 5.9
Nov	12	0	7.5 \pm 2.6	10	0	11.9 \pm 5.7
Dec	15	0	23.0 \pm 5.2	12	0	21.4 \pm 4.3

March, and recrudescence (renewal) was initiated during April and completed in June. Males mature at approximately 45–47 mm in SVL.

Female cycle.—As shown in Table 5,

females contained oviducal eggs over a 5-mo period (Sep–Mar) which corresponds to the length of time that a variety of North American temperate species are ovigerous (Goldberg, 1973). Yolk deposition began

TABLE 4.—Seasonal distribution of stages in testicular cycle of *Meroles cuneirostris*, February 1976–January 1977. (No sample was collected in July.)

Month	n	Spermiogenesis (%)	Regressing (%)	Regressed (%)	Recrudescence (%)
Feb	9	100	0	0	0
Mar	9	22	22	56	0
Apr	9	0	0	0	100
May	9	78	0	0	22
Jun	9	89	0	0	11
Aug	9	100	0	0	0
Sep	9	100	0	0	0
Oct	8	100	0	0	0
Nov	10	100	0	0	0
Dec	9	100	0	0	0
Jan	7	100	0	0	0

TABLE 5.—Percentages of reproductively active (vitellogenic to oviducal eggs) female *Meroles cuneirostris*, February 1976–January 1977. (No sample was collected in July.)

Month	n	Reproductively active (%)
Feb	13	46
Mar	5	40
Apr	12	0
May	7	0
Jun	4	0
Aug	5	60
Sep	6	33
Oct	11	73
Nov	8	88
Dec	10	80
Jan	10	50

TABLE 6.—Percentages of *Meroles cuneirostris* with enlarged fat bodies (> 75 mg) and mean weights of fat bodies (mg) from February 1976–January 1977. (No sample was collected in July.)

Month	Females			Males		
	n	% with enlarged fat bodies	Fat-body wt. ($\bar{x} \pm SE$)	n	% with enlarged fat bodies	Fat-body wt. ($\bar{x} \pm SE$)
Feb	13	0	5.0 \pm 2.7	15	6.6	44.6 \pm 6.4
Mar	5	0	0.0	9	0	6.6 \pm 4.0
Apr	12	16.6	50.0 \pm 8.2	12	25.0	55.5 \pm 13.5
May	7	42.8	126.0 \pm 29.5	13	46.1	83.6 \pm 19.7
Jun	4	50.0	149.0 \pm 119.0	7	71.4	88.1 \pm 18.9
Aug	5	100.0	141.6 \pm 13.6	10	10.0	22.0 \pm 9.7
Sep	6	0	33.1 \pm 10.5	9	0	5.6 \pm 2.7
Oct	11	22.2	45.6 \pm 14.4	10	0	31.1 \pm 9.7
Nov	8	0	65.0 \pm 3.4	12	0	5.1 \pm 4.1
Dec	10	0	10.4 \pm 6.1	9	11.1	31.3 \pm 9.6
Jan	10	0	16.2 \pm 7.1	7	14.2	46.1 \pm 17.5

during August and was evident in 3 of 8 females examined from this month. Including oviducal eggs and/or follicles greater than 4 mm in diameter, we calculated an average of 2.9 eggs (range 1–4) per clutch for a sample of 29 females. In contrast to *A. anchietae*, there is a positive correlation ($r = .50$, d.f. = 27, $P < .01$) between female SVL and clutch size; this relationship is expressed by the regression equation $Y = -3.57 + 0.1325X$. Clutches from nine females with oviducal eggs averaged 13.65% of total body weight of the female parent. The smallest reproductively active female measured 43 mm in SVL, the largest 55 mm. Females were reproductively inactive (no yolk deposition) from April to June (no sample was collected in July). On the basis of a regressing corpus luteum and early yolk deposition for a subsequent clutch in a specimen from January, it appears that females have the potential for producing two clutches each year. Hatchlings averaged 27–28 mm in SVL at birth and were observed in February, March, and May 1976 and in January and March 1977.

Both sexes have a seasonal fat cycle similar to *A. anchietae* in which fat bodies were enlarged from April through August and then declined in size in September–January (Table 6). However, on an absolute basis, the 1976 levels of maximum fat buildup (Apr–Aug) in female and male *M. cunei-*

rostris averaged 1.4 and 4.4 times less than in *A. anchietae* (Tables 3, 6).

DISCUSSION

It was unexpected to find that two related and narrowly sympatric species living in the same subtropical macroclimate would have such contrasting “tropical” (*A. anchietae*) and “temperate” (*M. cuneirostris*) reproductive cycles. Aseasonal reproductive patterns are common in tropical lizards (Tinkle, 1969), but have not been observed previously in desert species. Prey differences between these two lizards may partially explain these contrasting reproductive cycles. At Gobabeb, *A. anchietae* is omnivorous, feeding on arthropods and windblown seeds of *Trianthema hereroensis* and *Stipagrostis* spp. When insect abundances are low, seeds form the bulk of the diet, and during most of the year more females (20–30%) eat seeds than do males (Robinson and Cunningham, 1978). Possibly the perennial availability of seeds allows *A. anchietae* to obtain enough energy for year-round egg production. *Meroles cuneirostris* is an insectivore that is also active all year. In its habitat there is some insect food available all year, but the relative abundances appear to vary seasonally (M. D. Robinson, unpublished). Therefore, there may be pe-

riods when insect food is insufficient to support a continuous breeding cycle.

Temporal patterns of food availability ultimately determine cycles of lipid storage and utilization in lizards; when food is aseasonal there is no need to store fat, but when prey are seasonal in occurrence lipids are garnered for future use (Derickson, 1976). Following the extraordinary rainfall (121 mm) in 1976, the predominant food eaten by *A. anchietae* included seeds, Coleoptera representing 4 families, plus insects from 6 other orders. Eight invertebrate orders provided 85% of the food taken by *M. cuneirostris*. Rainfall the next year was 12.8 mm, slightly below normal (16.8 mm), and *A. anchietae* ate only representatives of two families of beetles, pentatomid bugs, and seeds (M. D. Robinson, unpublished). Unfortunately, no *M. cuneirostris* were collected in 1977. These rainfall-associated changes in prey diversity and abundance are reflected in the lesser quantities of fat stored by *A. anchietae* in the drier year (Table 3), and this may have caused the decline in reproduction in March 1977 (Tables 1, 2).

There are also distinct differences in the amount of fat stored by these lizards. In 1976, when prey abundances were exceptionally high, female *M. cuneirostris*, whose average body weight is 44% more than in *A. anchietae*, stored approximately 28% less weight in their abdominal fat bodies during peak periods of fat storage (Tables 3, 6). In addition to the usual saurian abdominal fat bodies, *A. anchietae* stores lipids in large subcutaneous fat depots in the pectoral region, which are lacking in *M. cuneirostris* and have not previously been described in lizards. Whether this results from differences in prey abundance in the two habitats or from different efficiencies in lipid conversion by the two lizards is not known.

The role of fat bodies in regulation of the ovarian cycle in other lizards with extended reproduction is not clear. No fat bodies were present in the Javanese house geckos *Cosymbotus platyurus*, *Hemidactylus frenatus*, and *Peropus mutilatus*, which are

aseasonal breeders (Church, 1962). Similarly, there was no cycle in weight of fat bodies in *Anolis trinitatus* which also reproduces year-round (Licht and Gorman, 1970).

Both of these Namib lacertids mobilize and deplete lipids in a manner typical of temperate lizards (see Derickson, 1976), but only *M. cuneirostris* exhibits a temperate reproductive cycle. Some portion of the population of *A. anchietae* is reproductively active at all times (Tables 1, 2) but the majority of egg production is observed in late winter, early spring, and summer, with hatchling densities greatest in late summer (M. D. Robinson, unpublished). Therefore, it is probably more correct to consider the *A. anchietae* reproductive cycle as being a modified temperate one.

Of the two species, *A. anchietae* appears to be better adapted to sequester unusually large quantities of reproductive energy by capitalizing on abundances of ephemeral prey and by exploiting a perennial granivorous food resource, especially when invertebrates become scarce. This stored energy is then gradually allocated to produce a few eggs over an extended period of time. Seasonal reproductive inactivity in *M. cuneirostris* is apparently regulated by predictable periods of low food, which are characteristic of temperate ecosystems. These examples suggest that in this desert environment nutritional factors may be primary regulators of reproductive patterns, and that physical variables such as photoperiod and temperature are secondary.

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