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Comments on the Reproductive Biology of the Namib Desert Dune Lizard, *Aporosaura anchietae,* During Two Years of Very Different Rainfall

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Michael D. Robinson
Department of Zoology, Kuwait University, P. O. Box 5969, Safat 13060, Kuwait

Aporosaura anchietae maintained continuous reproduction over a 24-month period during which rainfall, prey diversity and prey abundance changed greatly. Lizards responded rapidly to improved environmental conditions by accumulating large quantities of fat. Females utilized the fat body to produce various clutches of one or two large eggs over a prolonged period. The annual egg production declined by approximately 50 % when rainfall decreased from 125 mm to 12 mm. The average clutch was 1,52 and 1,19 eggs in the wet and dry years, respectively. Territorial males used stored energy to offset caloric imbalances caused by restricted foraging. The advantages of small female body size and a large hatchling are discussed in relation to the Namib dune habitat. Environmental conditions favouring aseasonal reproduction in extreme deserts are described, and aspects of the reproductive behaviour and polygynous breeding system are related to the dune ecology.

INTRODUCTION

Much of our knowledge about the reproductive biology of desert lizards is derived from studies of species living in temperate habitats and having well-defined seasonal cycles (Ballinger, 1983; Dunham, Miles and Reznick, 1988). With few exceptions (Hoddenbach and Turner, 1968; Vinegar, 1975; Ballinger, 1977; Vitt, Van Loben Sels and Omart, 1978; Dunham, 1980; Van Loben Sels and Vitt, 1984), reproductive cycles have been analysed for a single season. Thus, limited information exists on how changing levels of rainfall and productivity affect lizard reproduction.

Outside tropical latitudes aseasonal reproduction in lizards is uncommon, and in desert species it is rare. To my knowledge, besides *Aporosaura anchietae,* only two small lacertids (*Acanthodactylus pardalis* and *Eremias olivieri*) in the northwestern Sahara Desert are reported to have continuous spermiogenesis (Saint Girons, 1984).

Previous research on the reproductive biology of *A. anchietae* has shown that males and females undergo gametogenesis throughout the year, but fat bodies have distinct seasonal cycles. The proportion of reproductive females varies monthly, and the average clutch size, 1,3 eggs, is one of the lowest known for non-gekkonid lizards (Dunham *et al.,* 1988). Lizards mature in 4 to 7 months, and females can produce a maximum of 4 clutches per year (Goldberg and Robinson, 1979).

Eighty-two months before the initiation of this research (March 1969 to January 1976) the study site (Gobabeb) did not receive one month with effective rainfall (i.e., 20 mm, Lancaster, Lancaster and Seely, 1984). In January 1976 and continuing to March, 123,6 mm of rain fell at Gobabeb (Table 1). In 1977 rainfall was 12,9 mm.

The purpose of this paper is to analyse how changing levels of rainfall and prey abundance affected the amount of energy stored and the number of eggs produced; to determine how different fat reserves are utilized for reproduction and maintenance; to describe the reproductive behaviour of *A. anchietae;* and to briefly consider under what environmental conditions aseasonal reproduction is possible in extreme deserts.

MATERIALS AND METHODS

The results reported here are derived from analyses of collections of lizards taken in the sand dunes near Gobabeb from January 1976 to December 1977. Sample sizes and collection periods are indicated in the relevant tables.

The histological techniques used to determine the reproductive and fat body cycles of males and females are described in Goldberg and Robinson (1979). Total fat was quantified by the Soxhlet total fat extraction procedure. The ash-free dry weight was determined by incinerating carcasses in a muffle furnace at 550 °C. Behavioural and demographic data are from a long-term study of a marked population near the Namib Research Institute, Gobabeb. The monthly rainfall (1975–1979) was provided by the Desert Ecological Research Unit of Namibia, Gobabeb.

RESULTS

Lipid cycles and reproduction

Lipids were stored in a single, visceral, abdominal body and in paired, lateral, subcutaneous fat bodies. Monthly changes in the total fresh weight of the two fat depots are summarized in Table 2 and illustrated for females in Fig. I. Fat body weights increased rapidly following the unusually heavy rains during the first months of 1976. No sample was taken in February 1976, but it is assumed that fat accumulated, eggs developed,

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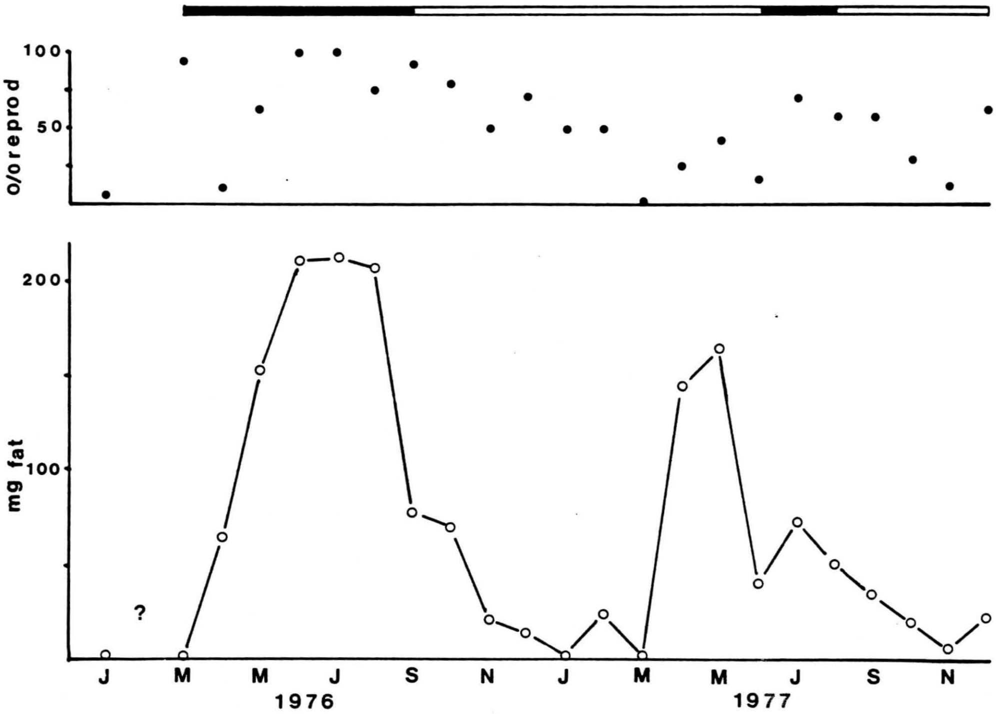

Fig. I

Fresh weight (mg) of female fat body and percent of the females with oviducal eggs. Solid and clear bars indicate periods when two- and one-egg clutches were produced, respectively.

and lipids were depleted, as occurred from January to March 1977. Beginning in March 1976 the fat bodies grew continuously, reaching maximum mass after approximately 120 days. By July males had stored an average of 109,1 mg fat/gm lean body weight (3,89 mg/day), and females 67,2 mg/gm lean body weight (1,80 mg/day). Depletion of the fat bodies required about 180 days. Males used 2,54 mg fat/day and females 1,17 mg/day.

From January to April 1977 the desert received 12,8 mm of precipitation (Table 1), and the lizards responded opportunistically to the January rainfall by accumulating fat and reproducing. As in the previous year, fat body mass began to increase rapidly in March. However, maximum mass was attained by males in 30 days and was 55 % less than the year before; females reached peak fat body weights after 60 days, and the mass was 23 % less. Females had larger fat bodies than males (47 mg fat and 36 mg fat per gram lean body weight), a reversal of the previous year's trend. Fat body lipids were depleted by November.

Females were sampled in January, April, June and September of 1977 to determine how the reproductive cycle was related to storage and utilization of lipids contained in the fat bodies and the carcass tissues (Table 3). Tissue lipids accumulated rapidly from January to April, but then more slowly through the winter. The fat body mass increased gradually from January to April, then quickly rose to the maximum level in June. Most of the fat body had been used by September. In general, there was an inverse relationship between the

Table 1

Monthly rainfall (mm) at Gobabeb, Namibia, during the period 1975–1978. Data for the 10-year mean are from Seely and Stuart (1976).

	J	F	M	A	M	J	J	A	S	O	N	D
1975	0,9	0,0	0,9	0,0	1,0	0,0	2,1	0,0	0,0	0,0	1,8	0,0
1976	84,0	6,5	33,1	0,0	0,0	0,0	0,0	0,0	0,0	1,5	0,0	0,0
1977	0,1	4,3	0,0	8,5	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
1978	1,0	49,3	41,3	17,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
10-year mean	2,2	1,8	5,7	1,2	1,2	0,2	0,4	1,8	1,4	0,7	0,7	0,6

Table 2
Fresh weight (mg) of the fat bodies and proportion of reproductive male and female *Aporosaura anchietae* (Goldberg and Robinson, 1979). Eggs refers to the number of females in the sample with one or two oviducal eggs.

	Males			Females				
	n	mg fat	% sperm	*n*	mg fat	% reprd.	eggs one	eggs two
1976								
Jan.	9	0,0	100	14	0,0	8	0	0
Mar.	12	2,4	100	13	2,6	92	3	2
Apr.	11	103,8	100	18	65,7	11	0	1
May	11	281,4	100	8	154,1	63	0	0
June	12	268,5	100	8	213,2	100	0	7
July	10	466,9	100	7	215,7	100	0	2
Aug.	12	200,9	100	9	208,6	78	2	3
Sept.	12	154,7	100	10	78,9	90	3	3
Oct.	9	155,0	100	12	72,0	83	7	0
Nov.	13	152,9	100	13	23,8	50	4	0
Dec.	10	34,0	100	9	16,1	70	5	0
1977								
Jan.	9	9,5	100	15	4,6	50	2	0
Feb.	10	48,0	90	13	25,2	46	4	0
Mar.	9	34,7	67	16	4,3	0	0	0
April	9	211,1	78	8	145,7	25	0	0
May	14	115,6	86	5	164,6	40	0	0
June	10	87,0	100	7	41,2	14	1	0
July	14	53,1	100	10	74,6	70	2	4
Aug.	11	93,5	100	5	52,4	60	1	1
Sept.	9	51,3	100	9	36,9	60	4	0
Oct.	12	26,8	100	12	21,0	31	3	0
Nov.	10	11,9	100	12	7,5	15	1	0
Dec.	12	21,4	100	14	23,0	67	4	0

Table 3
Distribution of lipids in the tissues and fat bodies of female *Aporosaura anchietae* in 1977. Lipid mass in mg dry weight and body mass is ash-free dry weight (AFDW). Values are mean and standard deviation (below).

	n	Tissue	Fat body	Total fat	Body mass	Fat/ AFDW
January	10	45,6	41,6	87,2	436,8	0,182
		27,8	64,9	81,1	67,9	0,152
April	16	98,5	63,2	161,7	584,9	0,262
		46,8	48,5	95,7	97,1	0,122
June	17	115,6	138,0	253,6	625,1	0,385
		38,0	105,9	127,8	130,1	0,136
September	17	120,6	43,2	163,8	588,7	0,280
		35,3	16,0	47,6	61,8	0,086

Table 4
Frequency distribution of the number of females in various standard length classes (and approximate age) in relation to the number of oviducal eggs.

Length (mm)	38–39	40–41	42–43	44–45	46–47	> 47	*n*
Approximate age (months)	4–6	6–12	12–18	18–36	> 36	> 36	
Two eggs	0	6	21	4	2	0	33
One egg	5	6	18	12	1	1	43

proportion of reproductive females in a sample and the fat body mass (Fig. 1, Tables 2 & 3).

This suggests that energy stored in the fat bodies is primarily allocated to vitellogenesis. Apparently, females mainly use tissue lipids for maintenance during the hottest season (September to January), a time when reproduction is less and many lizards suffer from negative energy and water balance (Robinson, *in press).*

In 1976 females produced two-egg clutches over a period of seven months, during which time the fat body mass was increasing, remained constant and then declined (Fig. 1, Table 2). For the next five months females in the samples contained one egg. In March 1977 fat bodies were very small and no reproductive females were collected. During April and May the fat body mass was at peak levels, but no female in the small samples was ovigerous, probably due to chance. It seems likely that two-egg clutches were produced during that period. Generally, females developed two eggs synchronously when lipid reserves were greatest; otherwise, single-egg clutches were most common. In the wet year 42 % of the females had double-egg clutches, but only 20 % developed two oviducal eggs in the dry year (Table 2). The number of eggs that would have been laid by the females sampled decreased 47 % as a result of the ten-fold decrease in precipitation. The loss in fecundity resulted from less stored energy and a shorter period when two eggs were matured. The average clutch size was 1,52 in 1976 and 1,19 in 1977.

Recapture data of marked females were insufficient to clearly establish how rainfall, energy and seasonality affected the frequency of egg laying. Two females produced four clutches in twelve-month periods following the January 1976 rains. One female had three clutches from May 1976 to April 1977. Six females laid two clutches in 1977. None of these females was captured every month; therefore, oviposition was probably more frequent.

A sample of 76 females that contained oviducal eggs and were collected at various seasons of 1976 and 1977 was analysed in relation to their standard length and clutch size (Table 4). Seventy-five percent of the females bearing two eggs were 42–45 mm, or about 1–2 years old (M.D.R. unpublished data). Most females with a single egg also belonged to this age (size) group. No recently matured female (< 40 mm, 4–6 months old) had two oviducal eggs. Thus, recently matured females are less fecund.

Reproductive behaviour

Male *A. anchietae* maintain territories that persist from several months to more than two years. Juvenile lizards and mature females reside in a male's territory for variable periods. The breeding system is polygynous and territorial males were observed mating with up to four different females. Recapture records show that two types of females live in a territory: resident females remain for periods of up to 23 months, whereas transient individuals are present from several days to three or four weeks.

During spring and summer, territorial males spend a considerable amount of the activity period (73 % to 92 %) observing their area from various vantage points on the dune slipface. In addition to repelling intruding males from neighbouring areas, males concern themselves with vigilating females. After emerging from the sand, a female is approached by the territorial male. As he nears, the female faces and halts the male by touching rostra (Fig. 2). This is usually followed by tongue flicking. At this point a 'receptive' female turns 180 degrees and with her tail arched over the back presents the cloaca. As the male advances she jumps ahead preventing his contact. This routine may be repeated from few to many times before the male attempts copulation by rushing the female and securing himself in the coital position by biting the nape of the female and entwining their tails. Sometimes the female avoids the male by running ahead and burying herself in the sand, only to be excavated by him. This behaviour may be repeated several times until the female escapes or is mated by the male. Nineteen of the 41 'receptive' females observed, escaped from the male. Two of these females copulated with the same male one and three days later.

When in the face-off posture (Fig. 2) a female may also reject the male, which she accomplishes by aggressively biting the male's shoulder and pushing him in front of her. Males normally return to face the female and must be rejected several times before leaving.

Fourteen females that were observed repelling or accepting a male were captured and autopsied to determine their reproductive status. Six females that had repelled males had yolked follicles or oviducal eggs greater than 4 mm diameter. The eight females that appeared receptive all contained small follicles (< 2 mm) without yolk.

DISCUSSION

The exceptional rains that fell over the central Namib Desert from January to March 1976 had profound effects on the flora and fauna. Seely and Louw (1980) estimated that plant detritus and animal biomass in the dune ecosystem increased seven- and six-fold, respectively. On the dune slipface, the primary habitat of *A. anchietae*, detritus biomass was 104 times greater in the wet year, and animal biomass increased 71 times (Seely and Louw, 1980).

Pronounced changes also occurred in the diet of *A. anchietae*. In 1976 the diet was more diverse and prey were more abundant. Qualitative estimates of the arthropod populations indicated that the elevated prey densities persisted throughout most of the wet year (Robinson, 1987). The rainfall-induced increases that occurred in the temporal availability and productivity of the prey were reflected in the energy storage and reproductive patterns of the lizards.

During the wet year male and female lizards accumulated lipids over a four-month period. In the dry year fat storage was limited to one (males) or two (females) months. The difference in the maximum mass of the fat body between the two years was greatest in males. During periods of fat accumulation females were simultaneously diverting lipids to egg production. Had the lipids contained in the eggs been accounted for, the amount of energy stored by each sex would not have been so disparate.

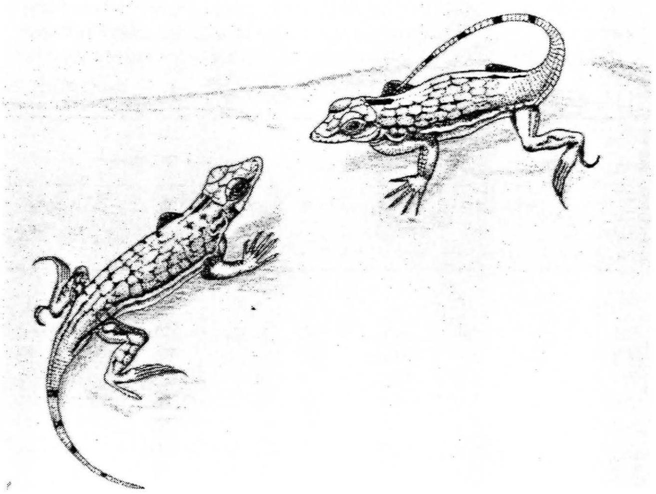

Fig. 2

Male (left) *Aporosaura anchietae* testing the receptivity of a female. From this position the female will accept or repel attempts by the male to copulate.

In 1976 approximately 40 % of the females sampled contained two eggs, but the following year only 20 % developed eggs synchronously (Table 2). Thus, the ten-fold decrease in rainfall and the concomitant decline of prey reduced the egg crop by almost 50 % and the average clutch size by 22 %. Vitt *et al.* (1978) noted that the proportion of reproductive females and the timing and frequency of reproduction in the Sonoran Desert iguanid, *Urosaurus graciosus*, changed during two years of different rainfall. Clutch size and frequency of a Chihuahuan Desert lizard, *Urosaurus ornatus*, increased in response to greater rainfall and prey abundance (Ballinger, 1977).

In both years females were reproductive except when the fat body was almost completely depleted. Concurrent reproduction and lipid accumulation are possible because excess food is available, and only one or two eggs are developed. Licht (1974) was able to increase the fat body weight of *Anolis cristellatus* during reproduction by supplemental feeding. In contrast, temperate desert lizards that lay larger clutches abstain from reproduction until a large energy reserve is obtained (Derickson, 1976; Ballinger, 1983).

Aporosaura anchietae responds quickly to improved environmental conditions. After the January 1977 rains, females garnered sufficient energy to oviposit, depleting the fat body by March. Although no sample was taken in February 1976, a similar pattern was evident (Fig. I). *Aporosaura's* opportunistic reproduction is probably facilitated by the small female mass ($\bar{X}$ = 3,0 g). I have suggested that in extreme deserts where productivity is normally low, small body size could be advantageous because maintenance costs are low, enabling females to rapidly sequester energy for small clutches (Robinson, *in press*).

When food and water are present, the tropical iguanid lizard *Anolis* produces a single egg every seven to 14 days (Andrews and Rand, 1974). The minimal time between oviposition is not known for *Aporosaura,* but several factors indicate that it is longer, perhaps around 30 days. First, the egg and hatchling size (length or mass) of *Aporosaura* is about 45 % greater than that of an *Anolis* species of similar adult size (Andrews and Rand, 1974). Second, synchronous egg development probably lenghtens the time between clutches.

The exceptionally large hatchling is one of the distinctive features of *Aporosaura* reproductive biology. Eighty-four hatchlings averaged 0,62 g (range 0,56–0,77) and their standard length was 25–27 mm, or approximately 20 % of the female's mass and 60 % of her length. A large hatchling would have several advantages. A greater mass reduces the surface to volume ratio, and consequently dehydration is slower. Most hatchlings are born when environmental temperatures are highest (January to March). Large neonates would also have a wider potential prey spectrum. Finally, larger propagules reduce the time needed to reach maturity (Sibly and Calow, 1986).

Seasonal changes in mass of the female fat body and tissue lipids suggest that each depot is used primarily for reproduction and maintenance, respectively. The abrupt decline in the fat body weight coincides with a greater proportion of reproductive females in the population and with a greater frequency of egg development (Table 2). Female *Anolis* asynchronously mature two eggs when their fat body is largest; single eggs are produced as energy reserves become depleted (Licht and Gorman, 1970; Sexton, Ortleb, Hathaway, Ballinger and Licht, 1971).

Tissue lipids began to decline in September after most of the fat body had been used, and reproduction had decreased. Energy from tissue lipids is probably used mainly for metabolism during the hottest months when many lizards are in negative energy and water balance (Robinson, *in press).*

Autumnal fat storage appears to result from lower metabolic costs due to decreased environmental temperatures and from increased prey availability. Some arthropod prey (e.g., Thysanura and Coleoptera) are most abundant in pitfall traps from April to August (Holm and Scholtz, 1980). Other species (carabid, tenebrionid and curculionid beetles) become abundant following rains of 20 mm or more (Holm, 1970; Robinson and Seely, 1980).

The territorial behaviour and polygynous breeding system of *A. anchietae* are related to the ecological characteristics of the sand dune habitat. Detritus, seeds and arthropods are not randomly distributed on the dune slope (Robinson and Seely, 1980). Seeds concentrate along the base of the slipface and arthropods are attracted to the patches of detritus. Lizards preferentially forage at these sites. Thus, the uneven distribution of food and the attraction of females to these areas permits males to monopolize mates and to defend a portion of the slipface against subordinate males. The asynchronous nature of the females' ovulatory cycles further enhances the probability that one male can defend and breed with several females. Under these circumstances the potential is great for territoriality and polygyny based on the male's ability to defend renewable resources essential to the female (Emlen and Oring, 1977). By maintaining frequent contact with the resident females, a territorial male constantly receives behavioural stimuli relating the females' reproductive status, thereby increasing the probability that he will be present when they are receptive.

What ecological conditions favour aseasonal reproduction in desert environments? Several recent reviews of the physical factors regulating lizard reproductive cycles have concluded that spermiogenesis, and to a lesser degree androgenesis, are inhibited by low temperatures (Duvall, Guillette and Jones, 1982; Saint Girons, 1984). The importance of the fat body for ovarian follicle development was demonstrated by Hahn and Tinkle (1965), and fat body cycles are regulated by seasonal patterns of food availability (Derickson, 1976).

Freezing temperatures are uncommon in the subtropical Namib Desert. Winter maximum air temperatures frequently exceed 20 °C to 25 °C (Lancaster *et al.,* 1984), and sand surface temperatures are even warmer (Robinson and Seely, 1980). Therefore, many dune arthropods are active throughout the year, although their relative abundances do vary seasonally (Holm and Scholtz, 1980).

Seeds, an important food of *A. anchietae,* are continuously present, as is detritus, the basic energy resource of the heterotrophic slipface community (Robinson and Seely, 1980; Louw and Seely, 1982). Consequently, environmental temperatures are conducive to aseasonal reproduction, and food resources are normally sufficient throughout the year.

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