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Summer field energetics of the Namib desert dune lizard *Aporosaura anchietae* (Lacertidae), and its relation to reproduction

Michael D. Robinson* 1990 b.

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Doubly-labeled water ($^3H_2{}^{18}O$) was used to quantify the summer field energetics of the omnivorous Namib Desert dune lizard, *Aporosaura anchietae* (Lacertidae). A male expends 824 joules per day, more than twice the energy used by the smaller female (382 J day^{-1}). An analysis of covariance of CO_2 production, mass and sex determined that differences in field metabolism are due to mass and not sex. Most individuals of both sexes lost body mass and were in negative water balance during the summer experimental period. Feeding experiments demonstrated that seed-eating and fasting lizards lose weight at similar rates. The Assimilation Efficiency is lowest for seeds (0·52) and highest for beetle larvae (0·87). The energetic advantages of small female body size are discussed in relation to the Namib dune environment and the reproductive biology.

Introduction

Sand dunes comprise a large proportion of the world's arid regions. Because of prolonged rainless periods, high environmental temperatures, persistent winds and low primary productivity, the vast dune deserts of Africa and Arabia are among the most stressful terrestrial ecosystems inhabited by animals. Yet we know comparatively little about how organisms have adapted to live in these environments.

Various authors have emphasized that adaptation to desert conditions is often related to the acquisition and conservation of energy and water (e.g. Maloiy, 1972; Hadley, 1975; Crawford, 1981; Louw & Seely, 1982). The use of doubly-labeled isotopic water ($^3H_2{}^{18}O$) has enabled researchers to quantify rates of metabolism and water flux in unrestrained animals. Field experiments employing doubly-labeled water have generated many new ideas about the ecological energetics of the Sauria.

For example, energetic differences inherent to foraging modes (Anderson & Karasov, 1981; Karasov & Anderson, 1984; Nagy, Huey & Bennett, 1984), reproduction (Nagy, 1983; Merker & Nagy, 1984), living in different environments (Karasov & Anderson, 1984) and general daily activities (e.g. Nagy & Shoemaker, 1975; Bennett & Nagy, 1977; Nagy, 1977; Nagy, 1982*b*; Congdon & Tinkle, 1982) have been quantified. With a single exception (Nagy *et al.*, 1984), these studies were conducted in North American arid and semi-arid regions with iguanid or teiid lizard species.

Aporosaura anchietae (Bocage) is a small, omnivorous, lacertid lizard endemic to the sand dunes of the coastal Namib Desert of south-west Africa. Several aspects of the biology are reported in Louw & Holm (1972), Goldberg & Robinson (1979), Robinson & Cunningham (1978) and Robinson (1987). The physical and biological environments of Namib sand dunes are discussed by Holm & Edney (1973), Holm & Scholtz (1980) and

*Department of Zoology, Kuwait University, P.O. Box 5969, Safat 13060, Kuwait.

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Robinson & Seely (1980). In terms of biomass, *Aporosaura* is a dominant vertebrate in the southern dune region, and is therefore a key species in the trophic structure. Understanding its energetics is fundamental to developing a more comprehensive energy flow model of this ecosystem.

Materials and methods

Field experiments and behavioural observations were conducted in sand dunes adjacent to the Namib Desert Research Station, Gobabeb, South West Africa/Namibia during the austral summer from November to December 1976, January to February 1977, and January to February 1978.

Fourteen male and 12 female lizards were captured and taken to the laboratory where they were marked by amputation of digits, weighed, and injected with doubly-labeled water ($^3H_2{}^{18}O$) with a dosage of 3 ml kg^{-1} mass. The mean body mass of the males was 5·10 g (range 6·32 to 3·82 g), and females averaged 2·93 g (range 3·60 to 2·28 g). The isotopic water contained 0·3 mC/l of tritium (^3H) and 95 atoms percent ^{18}O. After equilibration of 3–4 h, blood samples were taken by cardiac puncture and collected in 25 μl capillary tubes. The samples were flame sealed, individually labeled and stored at −5°C. Lizards were released at their capture site and subsequently recaptured after 13–17 days, except for one, which was recaptured after 31 days. A second blood sample was taken from recaptured animals and treated as described above. Dry carcass weight and percent body water were determined by oven-drying sacrificed lizards at 65°C until mass was constant. Blood samples were shipped by air to the Laboratory of Biomedical and Environmental Science, University of California, Los Angeles, where they were analyzed. These samples were microdistilled and the fluid portions were counted for ^3H activity by liquid scintillation (Beckman LS 230) and for ^{18}O activity by the proton activation method (Wood *et al.*, 1975). Water fluxes and field metabolic rates were calculated using the equations of Nagy (1975). Details of these procedures are described by Nagy (1980) and Nagy & Costa (1980).

The resting metabolism was measured from 42 lizards that had acclimatized at 35°C and fasted from 2–4 days. Animals were placed in closed-chamber respirometers at a constant temperature of 35°C. A natural light regime was maintained (13 L, 11 D). Air samples were withdrawn with a syringe and analyzed in a Beckman oxygen analyzer. An energy equivalent of 19·9 joules per ml O_2 was used to estimate the energy expended at resting (Table 3). This conversion is appropriate when metabolic substrates are unknown. The maximum error possible is 5% (Hainsworth, 1981). Field energetics were calculated by converting CO_2 production to energy by the relationship 25·7 joules per litre CO_2. This equivalence was determined by Nagy (1983) for an insectivorous lizard and assumes respiratory exchange ratio of 0·75.

The lizard's digestive efficiency of seeds and insects and their ability to maintain body mass when eating each food type were determined by feeding trials. Lizards in the feeding experiments were maintained outdoors in individual cages 35 × 20 × 25 cm. Fifteen centimeters of sand covered the bottom, and the daily cycle of sand temperatures simulated their natural environment (30–35°C at 10 cm, 12–53°C at the surface). Feeding trials continued for 9 to 26 days, following a 5–8-day fasting to eliminate any previous digesta. Food was replenished every second day, and lizards were weighed every fourth day. Diets consisted of tenebrionid larvae (*Tenebrio molitor* and *Onymacris* sp.) and grass seeds (*Stipagrostis* sp. and commercial finch seed). Uneaten prey and faeces were collected by sieving. Energy content, corrected for ash, was quantified for the food and faeces using a Phillipson microbomb calorimeter. Moisture content of the prey was determined by allowing them to dry at 65°C until mass was constant. Assimilation efficiency was calculated as energy ingested–energy excreted/energy ingested. The mean energy content of the larvae and the seeds used in the feeding experiments was 29·5 and 20·6 kilojoules per

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gram dry weight, respectively. The average moisture content of larvae was 74·6% and of seeds 12·8%.

Results

The physical environment

The diel range of summer temperatures in five dune microhabitats frequented by *A. anchietae* are: surface of the leeward slope, 15·1 to 58·6°C; slipface 10 cm deep, 28·7 to 39·7°C; slipface 20 cm deep, 32·8 to 35·9°C; surface of windward slope, 13·7 to 57·5°C; surface at the dune base, 14·3 to 61·2°C.

Except for selection of activity periods, behavioural thermoregulation by *A. anchietae* is rather limited; therefore, body temperature often closely approximates the sand temperature (M.D.R. unpublished; *see also* Huey, 1982). The mean summer activity body temperature is 34·2°C and the daily range is between 22 and 40°C. Lizards emerge in the morning when body and sand surface temperatures are 22–25°C. For the next hour or so body temperature rises gradually to near 36°C, whereupon a lizard will either thermoregulate for a short period or bury in the sand. Body temperature rarely exceeds 40°C during the brief thermoregulatory period. The next 6–8 h are passed beneath the surface at temperatures of approximately 33 to 36°C. The afternoon emergence usually occurs when surface temperatures fall below 37°C. As the dune cools, body temperature decreases to 27 to 30°C, and activity ceases as dusk approaches. The 12 or more nocturnal hours are spent buried at sand temperatures between 33 and 36°C.

Activity periods
thru the day.

Field energetics

Male lizards whose body mass was nearly twice the female's expended an average of 824 joules per day. Females used 382 joules (Table 1). An analysis of covariance of $\log_{10}$ body mass and $\log_{10}$ field metabolic rate (FMR) of all male and female lizards was used to determine if differences in the FMR resulted from mass or sex. According to the analysis of variance, all differences in the FMR of males and females are attributable to mass ($F = 87{\cdot}47, p < 0{\cdot}001$) and not sex ($F = 0{\cdot}087$,NS). However with one notable exception, the plotted data (Fig. 1) suggest females may have a higher FMR than males of equal mass. Table 2 summarizes the regression analyses of body mass and metabolic rate for males and females together as well as separately, and females without the outlying data point. A test for equality of regression coefficients shows that the regression lines of males and females do not differ significantly ($F = 1{\cdot}451$ $p = 0{\cdot}240$), but do when the outlying point is

Table 1. *Mean ($\bar{x}$) and standard deviation(s) of the body mass, summer field metabolic rate, mass change and water flux of* Aporosaura anchietae

	Males			Females		
	$\bar{x}$	s	*n*	$\bar{x}$	s	*n*
Body mass (g)	5·10	0·72	14	2·93	0·52	12
Field metabolic rate						
ml Co_2/day	32·1	7·7	14	1·49	5·1	12
joules/day	824·2	199·0	14	381·90	129·9	12
Mass change (%/d)	− 0·59	0·47	14	− 0·033	0·34	12
Water flux						
ml H_2O in (kg/d)	17·31	7·41	14	2·034	8·78	11
ml H_2O out (kg/d)	20·39	7·69	14	2·379	7·32	11

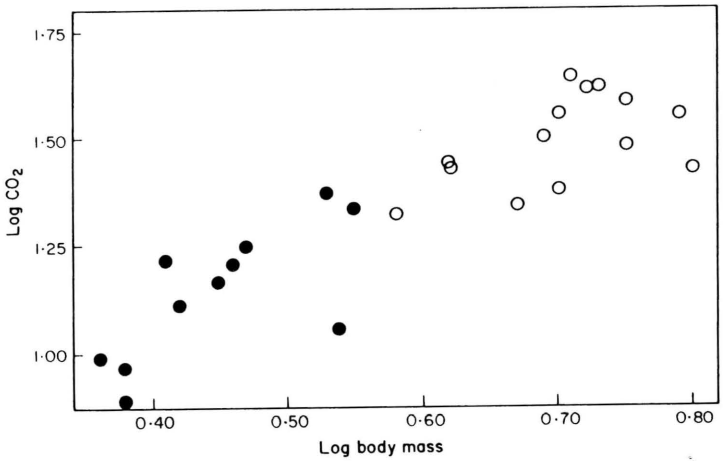

Figure 1. Scatter plot of $\log_{10}$ daily field metabolic rate (CO_2 production) and $\log_{10}$ body mass of male (○) and female (●) *Aporosaura anchietae*.

eliminated ($F = 5{\cdot}538, p = 0{\cdot}027$). Although that data point can be justifiably eliminated on a statistical basis (Dixon, 1950), there is no compelling biological reason to do so. Male lizards normally have longer activity periods than females (about 4 h and 3 h/day, respectively), and males are normally active daily whereas females may spend several consecutive days buried in the sand (pers. obs.). Thus the unusually low female FMR might result from reclusive behaviour, but the activity patterns of individual lizards was not recorded.

The mean diurnal resting metabolism at 35°C was 0·206 ml O_2 $g^{-1}h^{-1}$ ($s = 0{\cdot}07$, $n = 20$). Nocturnal resting respiration at the same temperature was 0·090 ml O_2 $g^{-1}h^{-1}$ ($s = 0{\cdot}05$, $n = 22$). The average resting metabolism of two Kalahari Desert lacertids at 37°C and 26°C was 246 and 96·5 ml O_2 $g^{-1}h^{-1}$, respectively (Nagy *et al.*, 1984).

About two-thirds of the daily energy costs are used during the brief activity periods (Table 3). The increment in energy spent for activity (Activity costs/Resting costs) is greater for males. Since females may spend one or more days inactive, their total resting metabolism is probably more than is budgeted (Table 3).

Ten of the 14 males and seven of the 12 females lost mass during the experimental period, and they were also in negative water balance. Thus, two-thirds of the lizards sampled were unable to obtain sufficient energy and/or moisture from their prey to offset the energy expenditures and water losses accrued under summer conditions.

Assimilation efficiency and energy balance

Feeding experiments were carried out to determine *Aporosaura's* efficiency in digesting seeds and insect food, and to quantify the effect of each food type on maintenance of body

Table 2. *Comparison of regression statistics of the field metabolic rate and body mass of samples of male and female lizards, males, females and females without one outlying data point*

	n	a	b	r^2	F	p
Males & females	26	0·54	1·35	0·792	91·13	> 0·005
Males	14	0·87	0.89	0·264	4·29	0·05 < > 0·10
Females	12	0·40	1·67	0·542	11·83	> 0·01
Females	11	0·17	2·24	0·846	49·61	> 0·005

Table 3. *Summary of summer energy expenditures of* Aporosaura anchietae

	Males	Females
Body mass (g)	5·10	2·93
Resting costs (joules/day)		
Day (6·5 h)	135·9	78·1
Night (13 h)	118·7	68·2
Total	254·6	146·3
Activity costs (joules/day)		
Total field—resting	527·9	216·3
Activity/resting	2·1	1·5

mass during summer conditions. Female lizards fed very irregularly, and their data are therefore omitted from Table 4.

Two male lizards in the feeding experiments were injected with doubly-labeled water. Their metabolic rates, 1024 and 957 joules/day were higher than average but within the range of field values. Therefore, energy expenditures of all lizards in the experiments were estimated using the mean field rate. The total energy assimilated during the feeding trial is the biomass of prey eaten × the energy content × the assimilation efficiency. The average assimilation efficiency of lizards eating tenebrionid larvae, tenebrionid adults, and grass seeds was 0·87, 0·67 and 0·52, respectively.

The relation between diet and change in body mass is summarized in Table 4. Five of the 11 seed-eating lizards consumed sufficient energy but still lost weight, presumably from water loss. Four of the nine lizards feeding on beetle larvae lost mass. Their energy consumption was from 6 to 11% less than required. Those eating larvae and gaining weight ate between 1·3 and 1·9 times the energy required. Starving females lost less mass per day than males, probably because the intensity of their activity was less. Starving and seed-eating lizards lost body weight at similar rates.

The energy and moisture content of several dune arthropods and seeds commonly eaten by *A. anchietae* are enumerated in Table 5. The mean metabolizable energy (energy content × assimilation efficiency) derived from dune arthropods would be about 18·2 kilojoules per gram dry weight, assuming an average assimilation efficiency of 0·77; seeds would yield 10·9 kJ g^{-1} with an assimilation efficiency of 0·52. The field feeding rate necessary to satisfy daily energy costs of male lizards would be 169 mg fresh weight of arthropods or 89 mg of seeds. Females would have to ingest 77 or 41 mg of each prey type.

Table 4. *Results of summer feeding experiments. Values are the mean* ± *S.D.*

	n	Change in mass	
		mg/day	percent/day
Starvation			
Males	6	− 48·7 ± 11·39	− 1·58 ± 0·36
Females	9	− 33·6 ± 13·11	− 1·23 ± 0·43
Seed-eaters			
Males	11	− 41·0 ± 12·17	− 1·23 ± 0·31
Larvae-eaters			
Males	5	33·3 ± 18·76	0·72 ± 0·40
Males	4	− 14·1 ± 11·10	− 0·45 ± 0·41

Table 5. *Mean percent moisture and energy content (ash corrected) of some common prey of* Aporosaura anchietae

	Percent moisture (range)	*n*	Energy content (kJ g^{-1})	*n*
Adult Tenebrionidae (*Dactylocalcar caecus*)	58·3 (51·3–63·4)	8	18·0	4
Tenebrionid larvae (*Onymacris* sp.)	72·9 (54·5–83·5)	5	26·9	2
Thysanura	78·6 (67·2–90·2)	7	23·4	2
Dune cricket (*Comicus* sp.)	75·6 (74·1–77·9)	3	26·7	2
Solfugidae	74·1 (66·6–81·1)	5	27·3	2
Termites (*Hodotermes mossambicus*)	76·8	1*	19·4	2
Grass seeds (*Stipagrostis ciliata*)	17·6 (15·1–20·2)	3	20·6	3
Dune succulent seed (*Trianthema hereroensis*)	9·8 (9·5–10·1)	2	21·3	2

* Determination from one sample of 16 individuals.

Discussion

Small animals inhabiting extremely arid deserts normally acquire energy and water from the prey they ingest. Energy and water balance are therefore tightly linked, and dependent upon the predator's success in obtaining sufficient food. *A. anchietae* is an omnivore that eats a variety of dune arthropods and seeds. Prey selection should depend upon the individual's state of hydration and energy balance, prey availability, and the energy and moisture content of each prey.

Many lizards suffered high rates of mass and water loss during the brief experimental period (Table 1). However, these short-term loss rates could not be sustained for more than several months and must be balanced by periods when sufficient energy and water are obtained from the food.

Generally more seeds are consumed in the summer months (Robinson, 1987), and although a granivorous diet can supply adequate energy, the moisture content would be insufficient to offset water losses. A male ingesting 89 mg of seeds would derive 0·009 ml of water, whereas one *Onymacris* larva could provide as much as 0·21 ml. Nevertheless, seeds are an important source of energy, given their regularity in the diet and the fact that they have twice the metabolizable energy of an equivalent fresh weight of arthropods. Contrary to Nagy's (1982*a*) suggestion, the feeding experiments indicate that *Aporosaura* could not survive on dry plant food without drinking water.

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When rainfall is normal, reproduction decreases towards mid-summer as stored lipids are depleted and the relative proportion of seeds increases in the lizard's diet (Goldberg & Robinson, 1979; Robinson, 1987). Egg formation may be inhibited at this time by less available energy and by insufficient body water. A fresh oviducal egg of *Aporosaura* contains 45 to 55% moisture, or about 0·4 ml of water. Cessation of reproduction in a North American desert iguanid *Sauromalus obesus* (Baird), during a drought year was attributed to water stress (Nagy, 1973).

The mean mass of male *A. anchietae* is greater than the female. Moreover the male's daily activity period is normally longer, and the proportion of time spent at the diurnal resting rate is usually less. Consequently, the male's daily cost of living is more than twice a female's. Size dimorphism and metabolically related behavioural differences may have evolved in response to the selective regimes associated with each sex's distinct energy requirements and utilisation patterns.

Growth rates of adult lizards begin to diverge as they near the age of sexual maturity; thereafter, females grow more slowly (M.D.R., unpublished). A female's greater energy allocation to reproduction (Nagy, 1983; Ryan, Bartholomew & Rand, 1983) may retard growth. However, slow female growth might be genetically regulated. Although the causal factors are unknown, the small female body size of *Aporosaura* has several energetic advantages that could be adaptive in Namib dune environments.

The Namib dunes have an extremely low standing crop biomass (Seely & Louw, 1980). This coupled with the fact that summer foraging time is very brief, may make obtaining enough moist food a difficult task. The dune slope habitat of *A. anchietae* is elevated by approximately 30° and during much of the day it is oriented perpendicular to the sun's path. In the morning the lizards' primary habitat and foraging area, the east-facing slope, heats rapidly (0·17°C min^{-1}) restricting the potential activity time to less than 2 hours (Robinson & Seely, 1980). The afternoon activity period is slightly longer (2·5 h). Compared with African lizards living in flatter, vegetated, desert habitats (Huey & Pianka, 1977; Pianka, Huey & Lawlor, 1979; Pianka, 1986), *A. anchietae* has about 50% less potential activity time. Since a female's daily energy needs are approximately half those of a male, she should require considerably less foraging time. A lower daily energy commitment would be advantageous for a reproductive female in an environment with low prey abundance and little hunting time.

Body size can also influence the timing of reproduction and the length of the breeding season. Small females have lower maintenance costs, and can accumulate energy for egg production more quickly (Downhower, 1976). This enables them to respond rapidly to the brief and unpredictable flushes of productivity that characterize the Namib and other extreme deserts. Furthermore, if the clutch size is very small, as in the case of *A. anchietae* ($\bar{x}$ = 1·3 eggs), egg laying can be frequent and distributed over an extended period (Goldberg & Robinson, 1979).

Several consequences of small female body size would be counterselective. Clutch size is proportional to female mass in Namib lacertids (M.D.R., unpublished) so the reproductive potential per clutch will be decreased. Smaller females are probably less resistant to starvation and desiccation, and the diversity of prey would be reduced from their inability to subdue some large dune arthropods. Thus, mortality might be greater during extended periods of drought and low prey productivity.

The role of body size as an adaptation to adjust the female's energy requirements and temporal pattern of reproduction to an environment's resource predictability, prey productivity and available foraging time has not been explored. This facet of lizard reproduction merits attention.

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