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Diet diversity and prey utilisation by the omnivorous Namib Desert dune lizard, *Aporosaura anchietae* (Bocage), during two years of very different rainfall

Michael D. Robinson*

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Various aspects of the diet diversity and prey utilisation of the Namib Desert dune lizard, *Aporosaura anchietae* (Bocage), are compared between an exceptionally wet year (126·5 mm) and a dry one (12·8 mm). The diet usually consists of several species of seeds and a variety of dune arthropods. The monthly volume of arthropod prey exceeded the seed volume in all months of the wet year. During the dry year the seed volume exceeded the arthropod prey in five of the months. Prey diversity was significantly greater during the wet year. Each lizard captures one-fourth or less of the taxa eaten by the sample population. These results are discussed in relation to the dune ecology and the lizard's population biology.

Introduction

Beginning in the first month of 1976 and continuing into March, the central Namib Desert received several unusually heavy rainstorms that totalled 125 mm. Forty-two years earlier, rains of a similar magnitude occurred (140 mm; Walter, 1971) but their biological effects went unrecorded. During 1977 the precipitation was 12.8 mm, less than half the normal amount (Table 1). There existed, then, an exceptional opportunity to quantify the responses of the desert's communities to an unusual and dramatic environmental change.

Fortuitously, several ecological research projects were underway at the Namib Desert Research Station at the beginning of 1976, and some of the many changes were documented. Seely & Louw (1980) estimated that after the rains, the potential energy in the plants, detritus and animals increased nine-, seven- and sixfold, respectively. This paper analyses the monthly composition of the diet of a sand dune lizard, *Aporosaura anchietae*, and compares the patterns of prey utilisation and diversity during these two years of very different precipitation and productivity. These results are then discussed in relation to the population biology of *A. anchietae* and to the ecology of the dune ecosystem.

Aporosaura anchietae (Bocage) is a small (3–5 g) lacertid lizard, endemic to the Namib Desert sand dunes. The species is strictly psammophilous and inhabits the region of the mobile sands of the dune slipface (Louw & Holm, 1972). Windblown plant detritus is the only energy source for this unique heterotrophic ecosystem. Previous studies have shown *A. anchietae* to be an omnivore that consumes a variety of dune arthropods and the seeds of several plants (Louw & Holm, 1972; Robinson & Cunningham, 1978).

* Present address: Department of Zoology, Kuwait University, P. O. Box 5969, State of Kuwait.

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Materials and methods

From January 1976 to December 1977 monthly samples of *A. anchietae* were taken from a study site in the dune habitat adjacent to the Namib Desert Research Station, Gobabeb, South West Africa/Namibia (23°09′S 15°05′E). Nearly all the samples contained 15 lizards, and individuals of each sex were almost equally represented. The smallest sample, January 1977, contained 11 lizards. No collection was made in February 1976. The minimum sample, determined by curves of the cumulative number of prey taxa and sample units (lizards), was 12 or 13 lizards.

The diet was quantified by the following procedure. Contents of the entire digestive tract were examined and the prey identified to the lowest possible taxonomic category, usually the order or family. The volumes of the stomach contents of 20 lizards were measured by water displacement in a graduated cylinder. These 20 samples included the minimum and maximum volumes of food observed in the monthly samples and ranged from 0·2 to 2·7 ml. They were kept in vials and were used as standards to estimate the total volume of each lizard's digestive tract. The contents were uniformly spread over a plastic plate that had a millimetre grid beneath. The prey were identified, counted and their percent of the total volume was estimated by the number of square millimetres occupied by a taxon.

A detailed analysis of the lizard's diet during 1976 was reported previously (Robinson & Cunningham, 1978). The prey consumed in 1977 are tabulated in the Appendix. The long-term precipitation pattern and the amounts that occurred during this study are given in Table 1.

Table 1. *Monthly precipitation in 1976 and 1977 and the 10-year average at Gobabeb, South West Africa/Namibia (Seely & Stuart, 1976 and unpublished data)*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
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
1976	84·9	7·0	33·1	0	0	0	0	0	0	1·5	0	0
1977	0·1	4·2	0	8·5	0	0	0	0	0	0	0	0

Results

The number of prey items ingested, the frequency of occurrence in the diet and an index of the annual utilisation of the plant and arthropod taxa are compared in Table 2. In 1976, when rainfall and the standing crop biomass reached exceptional levels (Seely & Louw, 1980), *A. anchietae* consumed 24 identifiable taxa. During the following year of low precipitation, 18 prey categories were eaten. Sixty percent of the 25 total taxa were common to the diets of both years.

The greater species richness in 1976 resulted principally from the presence of transient insect species from adjacent non-dune habitats, which were eaten opportunistically by the lizards (e.g. Acrididae, Dermaptera, Thysanoptera, reduviid bugs, Neuroptera, calliphorid flies and Apidae). Regular qualitative observations show that these allochthonous prey were present in the dune slipface habitat neither before nor 4–5 months after the rains had ceased (M. Robinson, unpublished notes). Other ephemeral dune insects, such as carabid and curculionid beetles, and Hemiptera were frequent in the diet during and briefly following the rainy period (Robinson & Cunningham, 1978).

Table 2. *Prey utilisation patterns of* Aporosaura anchietae *during two years of very different rainfall. Frequency is the number of predators with prey/total predators in the sample. Annual utilisation is months the prey was consumed/total months*

	1976*			1977†		
	Number of prey	Frequency	Annual utilisation	Number of prey	Frequency	Annual utilisation
Scorpionida	2	0·067	0·182			
Pseudoscorpionida	1	0·067	0·091			
Aranea	10	0·110	0·545	12	0·094	0·500
Solpugida	3	0·067	0·182	2	0·067	0·083
Thysanura	32	0·139	0·636	11	0·106	0·417
Orthoptera						
Acrididae	2	0·133	0·182			
Gryllidae				1	0·067	0·083
Isoptera	1	0·067	0·091	3	0·071	0·167
Dermaptera	23	0·200	0·273			
Thysanoptera	2	0·067	0·182			
Hemiptera						
Reduviidae	4	0·200	0·182			
Pentatomidae	41	0·267	0·455	33	0·196	0·500
Undetermined	41	0·147	0·455			
Neuroptera	1	0·067	0·091			
Coleoptera						
Carabidae	34	0·341	0·273	66	0·289	0·167
Curculionidae	4	0·200	0·182	3	0·071	0·250
Tenebrionidae larvae	32	0·151	0·636	64	0·310	0·583
Tenebrionidae adult	10	0·171	0·273	69	0·166	1·000
Staphylinidae larvae	26	0·124	0·636	5	0·119	0·250
Undetermined larvae	25	0·117	0·364			
Undetermined adult	10	0·110	0·545	11	0·136	0·250
Lepidoptera	11	0·127	0·455	8	0·123	0·500
Diptera						
Calliphoridae	1	0·067	0·091			
Undetermined	7	0·067	0·182	7	0·098	0·333
Hymenoptera						
Apidae	2	0·133	0·091			
Formicidae	10	0·133	0·182	6	0·077	0·083
Undetermined	12	0·095	0·727	19	0·119	0·583
Squamata						
A. anchietae	1	0·067	0·091	2	0·067	0·167
Seeds						
Poaceae	1073	0·438	1·000	447	0·284	0·917
Aizoaceae	810	0·413	0·727	1334	0·426	1·000
Undetermined				276	0·286	0·333

* Calculated from Robinson & Cunningham (1978).
† Calculated from Appendix.

Thus, the immediate effect of the unusual precipitation in January and March was the abnormal appearance of insects from non-dune habitats. In addition, several insects from the vegetated dune areas, which are seen only when rainfall is greater than about 25 mm (Holm, 1970), underwent population flushes (e.g. carabid, curculionid and staphylinid beetles). Many of these prey were taken by the lizards during the first half of the wet year. Arthropods of the vegetationless slipface community and seeds comprised the monthly diet during the dry year (Appendix).

Omnivory has been reported in various lizard species (Greene, 1982) but *A. anchietae* is, apparently, the only omnivore whose vegetative portion of the diet consists solely of seeds. Nevertheless, the degree of granivory practiced by the species has not been clearly defined. Seeds were eaten in all but one month, and the frequency of seed ingestion was moderate in both years (Table 2). Between 35% (1977) and 42% (1976) of the lizards contained seeds.

The monthly consumption of seeds and arthropods and a Granivory Index were used to determine whether the level of granivory fluctuated in relation to the rainfall regime (Table 3). During the months of heavy rainfall (January–March 1976) insects were eaten almost exclusively (Robinson & Cunningham, 1978) and, consequently, the Granivory Index was low. In April, when ephemeral Coleoptera and Lepidoptera disappeared from the environment, the amount of seeds ingested rose abruptly. Thereafter, seed volume and the Granivory Index remained moderately low, except in October when seeds constituted half of the total volume (Table 3).

Table 3. *Monthly comparison of the volume of seed and arthropod prey consumed by* Aporosaura anchietae

	Volume (ml)			Granivory Index
	Total	Seeds	Arthropods	(seeds/arthropods)
1976				
Jan	4·35	0·14	4·21	0·033
Mar	6·19	0·95	5·24	0·181
Apr	5·36	2·28	3·08	0·740
May	4·98	0·70	4·28	0·164
Jun	7·72	1·27	6·45	0·197
Jul	3·94	0·85	3·09	0·275
Aug	6·23	0·98	5·25	0·187
Sep	5·15	1·18	3·97	0·297
Oct	3·92	1·31	2·61	0·502
Nov	4·36	1·10	3·26	0·337
Dec	4·69	0·91	3·78	0·241
1977				
Jan	3·63	0·46	3·17	0·145
Feb	3·74	2·48	1·26	1·968
Mar	3·31	0·30	3·01	0·100
Apr	5·49	0·84	4·65	0·181
May	6·67	1·10	5·57	0·198
Jun	6·50	2·60	3·90	0·667
Jul	5·39	3·34	2·05	1·629
Aug	5·86	3·43	2·43	1·412
Sep	3·32	1·91	1·41	1·355
Oct	4·66	0·86	3·80	0·226
Nov	4·33	0·31	4·02	0·077
Dec	3·34	2·17	1·17	1·855

Precipitation was slight in the first three months of 1977 (Table 1), but only during February did seeds dominate the diet. Carabid beetles were consumed in large quantities in March, and during April, a month with 8 mm of rain, the main prey were tenebrionid beetles and Orthoptera. Starting in June and continuing to September seeds were the most important food item. Seed-eating declined in October and November but was frequent again in December.

In conclusion, the volume of animal prey ingested exceeded that of seeds in every month of the wet year. In the dry year more seeds were consumed in five of the months. Nevertheless, the seed volume did not differ significantly between years (Wilcoxon signed ranks test, $T=24$, $p>0{\cdot}05$). However, one less month was sampled in 1976. Surface seeds were more abundant in 1976 (22·8 seeds/m^2) than in 1977 (5·3 seeds/m^2) (M. Robinson, unpublished data). Thus the degree of granivory was not proportional to seed abundance. Unfortunately, the animal population densities were not quantified.

In ecological studies the trophic niche breadth is commonly estimated by a species diversity index. The diversity measure used here, Hill's N_2 ($1/\Sigma p_i^2$; Hill, 1973), is sensitive to changes in the importance of the most abundant taxa (Peet, 1974). Ecologically, Hill's index can be interpreted as the number of equally common taxa required to produce the same heterogeneity as the prey sample (Hill, 1973; Peet, 1974). In diet studies the differences in this index should reflect changes in the number of nutritionally important (i.e. abundant) prey groups. Diversity was calculated from the numerical and volumetric proportions (Table 4). Of the two, volume is most relevant to prey biomass and predator energetics; therefore, the discussion is limited to those results.

The mean annual prey diversity was significantly greater in the wet year ($t=2{\cdot}888$, d.f.$=19$, $p<0{\cdot}01$), and the greatest heterogeneity occurred during the austral winter and spring months (June–October). In November and December, 7 and 8 months after the last rainfall, the trophic niche breadth decreased. It increased again in January 1977 but then declined sharply and remained low during the remainder of the dry year (Table 4). The prey abundances were more equal in the diet following the wet season but became less balanced in the subsequent dry months.

The final aspect considered is the variability between individuals in the population with respect to the prey that they eat. The average number of taxa consumed by each lizard and the total number of prey categories taken by the sample population are summarised in

Table 4. *Lizard sample size (n), prey taxa consumed and the monthly variation of the trophic niche breadth as estimated by Hill's (1973) N_2 index, $1/\Sigma p_i^2$. Diversity is calculated from the number of prey items (Individual) and the prey volume (Volume) in each prey category*

	Hill's N_2 1976				Hill's N_2 1977			
	n	Taxa	Individual	Volume	*n*	Taxa	Individual	Volume
Jan	11	7	1·890	4·682	16	10	2·902	6·510
Feb					15	5	1·127	2·741
Mar	15	11	1·157	5·967	15	5	1·761	2·155
Apr	15	8	2·300	6·618	15	8	2·967	3·757
May	15	8	3·908	5·099	15	10	5·222	5·600
Jun	15	14	2·176	9·400	14	8	2·436	3·586
Jul	15	8	3·764	5·217	13	10	1·893	3·435
Aug	15	9	3·645	7·710	16	6	1·658	2·311
Sep	15	14	2·436	6·452	15	7	1·117	2·742
Oct	15	12	2·099	10·225	11	11	3·762	4·594
Nov	16	11	1·928	6·333	13	14	5·784	4·354
Dec	15	13	1·362	4·476	14	6	1·885	3·309

Table 5. The average number of prey per lizard did not differ significantly between years ($t=0{\cdot}514$, d.f.$=19$, $p < 0{\cdot}50$). Each lizard ingested only a small portion, between 15 and 25% of the prey species taken by the whole sample. Therefore, it is probable that two lizards will not capture the same kinds of prey while foraging. Several possible explanations for this are considered in the next section.

Discussion

The exceptional precipitation that fell over the Namib Desert in early 1976 brought pronounced changes in the standing crop biomass of the desert plants and animals. Populations of the arthropod prey responded in two distinct manners. Adults of species associated with the riverine habitat and the vegetated portions of the dunes and interdune valleys, appeared soon after the first heavy showers in January. These flying insects are not normally found in the vegetationless dune habitat but were eaten opportunistically by the lizards. In contrast, the arthropods that inhabit the vegetationless dunes became most abundant 8–12 months after the March rains when the biomass of detritus, their only food, was also greatest (Robinson & Seely, 1980). Together, the two ecologically different faunal elements provided a significantly greater diversity of prey through most of the wet year.

Quantitative data are lacking but it seems likely that the lizard population obtained a greater amount of digestible energy and preformed water from their food in 1976. This supposition is corroborated indirectly by comparing the amount of energy stored by the lizards during the two years. In 1976, the mean fat body weight of females was 95·52 mg, and males contained 165·52 mg. During the dry year these values declined to 23·83 mg and 27·59 mg, respectively (Goldberg & Robinson, 1979).

The degree to which *A. anchietae* depends upon seeds as a primary food is probably an important factor limiting the amount of lipids stored. Seeds dominated the diet in the second half of the dry year (Table 3). From October to December of that year both males and females lacked enlarged fat bodies (Goldberg & Robinson, 1979). Seeds of several dune plants contain fewer calories than do six common dune arthropods (20·94 kJ/g and 23·60 kJ/g, respectively). Also, the apparent digestibility of seeds is low (52·2%) compared to insect larvae (86·8%). Furthermore, dune animal prey contain much more moisture (72·7%) than seeds (13·7%) (M. Robinson, unpublished data). This lack of moisture and the reduced amount of digestible energy become critical during the hottest months of low rainfall years, when seeds are eaten in greater proportions (Table 3) and field animals loose between 15 and 35% body mass (M. Robinson, unpublished data). Feeding experiments demonstrated that lizards maintained on natural seed diets lose weight (41·0 mg/day) at rates comparable to fasting animals (39·6 mg/day) (M. Robinson, unpublished data).

Lizards in the monthly samples usually contained only a small portion of the prey fauna captured by the sample population (Table 5). There are several possibilities to explain why this occurs. First, the variability between individuals in the prey they consume suggests that the spatial distribution of the dune arthropods is often discontinuous. Spatial discontinuity results from the considerable microenvironmental heterogeneity within the dune ecosystem (Robinson & Seely, 1980), and the apparent fidelity of various species to certain microhabitats (Hamilton, 1971; Holm & Edney, 1973). Second, daily and seasonal cycles of prey abundance oscillate, especially in periods of low rainfall (*see* Holm, 1970; Holm & Edney, 1973; Holm & Scholtz, 1980). Finally, some dune arthropods are active for brief periods (1–2 hours). Consequently, the prey species that a lizard can expect to encounter while foraging are but a small subsample of the potential spectrum, and they are likely to be different from those found by neighbouring animals.

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Table 5. *Total prey taxa captured by the sample population and the mean and standard deviation of the number of taxa eaten by each lizard in the sample*

	Prey taxa 1976		Prey taxa 1977	
	Population	Lizard	Population	Lizard
Jan	7	1·82 ±0·876	10	1·50 ±1·317
Feb			5	1·80 ±0·947
Mar	11	1·86 ±0·864	5	1·27 ±0·594
Apr	8	1·25 ±0·775	8	1·47 ±0·916
May	8	1·60 ±0·910	10	2·20 ±1·373
Jun	14	2·69 ±0·947	8	1·67 ±1·047
Jul	8	1·53 ±1·192	10	1·80 ±1·014
Aug	9	1·45 ±0·688	6	2·29 ±0·995
Sep	14	2·67 ±0·724	7	1·50 ±0·650
Oct	12	2·87 ±1·126	11	1·27 ±1·033
Nov	11	2·06 ±1·436	14	1·47 ±1·060
Dec	13	2·47 ±1·302	6	1·13 ±0·916

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Appendix

Number and volume (ml) of prey consumed by Aporosaura anchietae *in 1977 at Gobabeb, Namibia*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Aranea	1(0·60)		1(0·10)		6(0·60)	1(0·10)	1(0·10)			4(0·40)	1(0·10)	
Solpugida	2(0·11)											
Thysanura	7(0·31)											
Lepismatidae							1(0·07)			1(0·07)	1(0·07)	
Orthoptera												
Gryllidae				1(0·70)								
Acrididae				1(0·84)								
Isoptera											1(0·07)	
Termitidae					2(0·14)							
Hemiptera												
Pentatomidae					11(1·35)			14(1·71)	7(0·85)	1(0·10)	1(0·10)	
Unidentified				1(0·14)								
Coleoptera												
Carabidae		1(0·28)	65(2·14)									2(0·30)
Curculionidae	1(0·80)				1(1·20)					1(0·80)		
Tenebrionidae (larvae)	9(1·02)			24(2·76)	3(0·34)	10(1·10)	2(0·21)	6(0·65)		18(1·98)		
Tenebrionidae (adult)	1(0·75)	3(0·70)	3(0·70)	2(0·14)	13(1·80)	19(2·63)	6(0·90)	1(0·07)	1(0·07)	4(0·60)		5(0·80)
Staphylinidae										1(0·21)		
Unidentified	3(0·32)								1(0·28)		5(1·10)	
Lepidoptera		1(0·07)			2(0·14)		1(0·07)		1(0·14)	1(0·07)	4(0·30)	
Diptera												
Calliphoridae							1(0·07)					
Unidentified										4(0·30)	1(0·50)	1(0·07)
Hymenoptera												
Formicidae											6(0·14)	
Unidentified	9(0·28)	3(0·21)	1(0·07)	1(0·07)				1(0·07)				
Squamata												
A. anchietae	1(0·26)			1(1·12)								
Poaceae (seed)	77(0·25)	13(0·40)	9(0·24)	7(0·21)	21(0·64)	132(2·06)	98(1·01)		6(0·18)	21(0·43)	9(0·24)	48(1·46)
Aizoaceae (seed)	40(0·21)	335(2·08)	9(0·07)	7(0·21)	21(0·64)	87(0·54)	214(1·33)	69(0·43)	278(1·73)	4(0·03)	10(0·07)	114(0·71)
Unknown (seed)					88(0·21)	11(0·31)	188(1·05)	276(1·35)				