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A comparative study of the diet of the wedge-snouted sand lizard, *Meroles cuneirostris* (Strauch), and the sand diving lizard, *Aporosaura anchietae* (Bocage), (Lacertidae), in the Namib Desert

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1 INTRODUCTION

The Namib wedge-snouted sand lizard (*Meroles cuneirostris*) and the Namib sand-diving lizard (*Aporosaura anchietae*), are two common lacertids from the Namib Desert of coastal south-western Africa (Fitzsimons 1943, Holm and Scholz 1980). These two lizards are of a similar size and are found in narrow sympatry in the parallel dune-system south of the Kuiseb River in the central Namib. *M. cuneirostris* (5-9 g) is found mainly on the lightly vegetated dune base but is also occasionally found in the sandy interdune areas. *A. anchietae* (3-6 g) occurs mainly on the dune slipfaces but is also occasionally found on the dune base or sandy interdune areas. The micro-habitats of these two species thus overlap slightly in the dune environment.

The diets of these two lizards have been previously examined (Louw and Holm 1972, Robinson and Cunningham 1978, Stuart unpublished) but never in the same area at the same time. The object of this study was to compare the diets of these two sympatric lacertids using material collected in the same area at the same time and to observe the feeding behaviour of *M. cuneirostris*, the less well studied of the two species.

2 MATERIALS AND METHODS

M. cuneirostris and *A. anchietae* were collected from the dunes more than 10 km south of Gobabeb (23° 33'S, 15° 05'E). Lizards were sampled monthly from June 1978 till May 1979. A total of 101 *M. cuneirostris* and 95 *A. anchietae* stomachs were collected and analysed. Between 6 and 12 individuals were captured each month. Stomachs from an additional *M. cuneirostris* were obtained from the same areas during December 1980 and January 1981.

Analysis of the stomach contents was as follows: Number of prey items or segments thereof were counted. Prey items were identified with the aid of a dissecting microscope and a reference collection. The volume (in ul i.e. mm³) of prey in each stomach was estimated by spreading the stomach contents uniformly out on a piece of graph paper in a petri dish and estimating the relative areas covered by each prey item, and visually estimating each item's height.

ABSTRACT

The diets of two sympatric lizards, *Meroles cuneirostris* and *Aporosaura anchietae*, collected in the same areas at the same time, were compared by analysis of the stomach contents. Observations of the feeding behaviour of *M. cuneirostris* were also made.

A. anchietae has an omnivorous diet, with seeds constituting the major portion of the items consumed. *M. cuneirostris* consumes largely arthropods. Although rainfall appeared to influence the relative proportions of the different prey items, prey volumes in the stomachs did not increase significantly after heavy rains.

M. cuneirostris has an active bimodal foraging pattern during the day. However *M. cuneirostris* also employs "sit and wait" tactics, often robbing *Camponotus detritus* ants of food and waiting at newly formed termite mounds. Although there is some evidence of opportunistic feeding, *M. cuneirostris* generally appears to be selective in the type of food taken.

TABLE 1: Monthly stomach analyses of *Merolles cuneirostris*. - Numbers refer to: no. of items and vol. (mm³) respectively (ad = adults; l = larvae).

No. of stomachs	JUL 78 12	AUG 78 11	SEP 78 11	OCT 78 11	NOV 78 6	DEC 78 10	JAN 79 12	FEB 79 9	MAR 79 6	APR 79 7	MAY 79 6	DEC 80 6	JAN 81 4	TOTAL = 111
ORDER SQUAMATA														
Fam. <i>Lacertidae</i> (<i>Merolles juv.</i>)										1 450				1 450
ORDER ARANEAE	1 24	15 42	6 16	7 30	2 44	4 195	- 24	- 6	3 36	2 12	2 2	2 4	7 7	44 435
ORDER SOLIFUGAE			1 30			- 9		1 6					1 104	3 149
ORDER ISOPTERA														
Fam. <i>Termitidae</i>	54 166	2 1	67 1652	20 1500							34 40		17 234	194 3593
ORDER MANTODEA														
Fam. <i>Mantidae</i>	1 1													1 1
ORDER ORTHOPTERA														
Fam. <i>Acrididae</i>			1 105											1 105
Fam. Undetermined				2 2	1 5		6 450				12 29			21 486
ORDER HEMIPTERA														
Sub-order <i>Heteroptera</i>		21 85	18 70			10 40	4 256			1 40				54 431
Sub-order Undetermined	1 10	8 10	7 14	30 197	1 2	2 18		- 12	3 8	- 24				52 293
ORDER NEUROPTERA														
Superfamily <i>Myrmeleontoidea</i> (1)		1 21		1 60			4 59				- 6			6 146
ORDER COLEOPTERA														
Fam. <i>Carabidae</i>	2 4													2 4
Fam. <i>Tenebrionidae</i> (ad)		18 870	11 81	7 60		33 1160	30 128	43 830	22 600				12 720	181 4449
(1)	1 25	4 180		1 90		4 130			1 40	3 80				14 545
Fam. <i>Staphylinidae</i> (1)			1 2							3 3				4 5
Fam. Undetermined (ad)	62 60	37 174	52 375	30 115	24 334	7 122	21 102	66 777	16 210	7 14	23 273	2 4	19 174	366 2734
(1)			1 240	2 10							4 18			7 269
Superfamily <i>Curculionoidea</i>			1 126			29 288	5 50							35 464
ORDER DIPTERA	2 2	5 4		1 4		7 192		1 16		6 40				22 258
ORDER LEPIDOPTERA	1 1													1 1
ORDER HYMENOPTERA														
Superfamily <i>Formicoidea</i>														
Fam. <i>Formicidae</i>														
Sub-fam. <i>Formicinae</i>				1 6	44 150					18 70	5 140		3 4	71 370
Sub-fam. <i>Myrmicinae</i>	19 10				229 343	36 42						8 4	1 2	293 401
Sub-fam. Undetermined			13 35		2 2									15 37
Superfamily <i>Apoidea</i>														
Fam. <i>Apidae</i>			5 4											5 4
Fam. Undetermined			8 14	1 45										9 59
Superfamily <i>Ichneumonoidea</i>														
Fam. <i>Braconidae</i>									9 15					9 15
Superfamily <i>Chrysoidea</i>	1 6													1 6
Superfamily Undetermined	29 14		2 6	46 312	40 103	21 29		1 40	2 2	68 134	4 2		1 80	214 722
UNDETERMINED INSECTS (ad)	12 9	13 28	23 66	3 48			24 33	1 32	- 24	10 78	10 255	3 12		99 533
(1)		8 65	1 3				3 13	8 94	5 90	3 9	1 6			29 280
PLANT MATERIAL	2 5	6 5	1 2	2 10	1 2						4 38	1 4		17 66
UNDETERMINED MATERIAL		- 54				1 81		- 9			- 20	1 8	45	2 217
TOTAL	188 337	138 1539	218 2601	153 2719	346 995	1157 2317	102 1106	118 1818	56 935	122 952	90 820	17 26	51 102	1773 10000

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TABLE 1: Monthly stomach analyses of *Meroles cuneirostris*. - Numbers refer to: no. of items and vol. (mm³) respectively (ad = adults; l = larvae).

No. of stomachs	JUL 78 12	AUG 78 11	SEP 78 11	OCT 78 11	NOV 78 6	DEC 78 10	JAN 79 12	FEB 79 9	MAR 79 6	APR 79 7	MAY 79 6	DEC 80 6	JAN 81 4	TOTAL 111
ORDER SQUAMATA Fam. <i>Lacertidae</i> (<i>Meroles juv.</i>)										1 450				L 450
ORDER ARANEAE	1 24	15 42	6 16	7 30	2 44	4 195	- 24	- 6	3 36	2 12	2 2	2 4	7 7	44 435
ORDER SOLIFUGAE			1 30			- 9		1 6					1 104	3 149
ORDER ISOPTERA Fam. <i>Termitidae</i>	54 166	2 1	67 1652	20 1500							34 40		17 234	194 3593
ORDER MANTODEA Fam. <i>Mantidae</i>	1 1													1 1
ORDER ORTHOPTERA Fam. <i>Acrididae</i>			1 105											1 105
Fam. Undetermined				2 2	1 5		6 450				12 29			21 486
ORDER HEMIPTERA Sub-order <i>Heteroptera</i>		21 85	18 70				4 256			1 40				54 431
Sub-order Undetermined	1 10	8 10	7 14	30 197	1 2	2 18		- 12	3 8	- 24				52 293
ORDER NEUROPTERA Superfamily <i>Myrmeleontoidea</i> (1)		1 21		1 60			4 59				- 6			6 146
ORDER COLEOPTERA Fam. <i>Carabidae</i>	2 4													2 4
Fam. <i>Tenebrionidae</i> (ad)		18 870	11 81	7 60		33 1160	30 128	43 830	22 600				12 720	181 4449
(1)	1 25	4 180		1 90		4 130			1 40	3 80				14 545
Fam. <i>Staphylinidae</i> (1)			1 2							3 3				4 5
Fam. Undetermined (ad)	62 60	37 174	52 375	30 115	24 334	7 122	21 102	66 777	16 210	7 14	23 273	2 4	19 174	366 2734
(1)				1 240	2 10						4 18			7 269
Superfamily <i>Curculionoidea</i>			1 126			29 288	5 50							35 464
ORDER DIPTERA	2 2	5 4		1 4		7 192		1 16		6 40				22 258
ORDER LEPIDOPTERA	1 1													1 1
ORDER HYMENOPTERA Superfamily <i>Formicoidea</i> Fam. <i>Formicidae</i>														
Sub-fam. <i>Formicinae</i>				1 6	44 150					18 70	5 140		3 4	71 370
Sub-fam. <i>Myrmicinae</i>	19 10				229 343	36 42						8 4	1 2	293 401
Sub-fam. Undetermined			13 35		2 2									15 37
Superfamily <i>Apoidea</i> Fam. <i>Apidae</i>			5 4											5 4
Fam. Undetermined			8 14	1 45										9 59
Superfamily <i>Ichneumonoidea</i> Fam. <i>Braconidae</i>									9 15					9 15
Superfamily <i>Chrysoidea</i>	1 6													1 6
Superfamily Undetermined	29 14		2 6	46 312	40 103	21 29		1 40	2 2	68 134	4 2		1 80	214 722
UNDETERMINED INSECTS (ad)	12 9	13 28	23 66	3 48			24 33	1 32	- 24	10 78	10 255	3 12		99 533
(1)		8 65	1 3				3 13	8 94	5 90	3 9	1 6			29 280
PLANT MATERIAL	2 5	6 5	1 2	2 10	1 2						4 38	1 4		17 66
UNDETERMINED MATERIAL		- 54				1 81		- 9			- 20	1 8	- 45	2 217
TOTAL	188 337	138 1539	218 2601	153 2719	346 995	1157 2317	102 1196	118 1818	56 935	122 952	99 829	17 36	54 1363	1773 17637
RAINFALL (mm)	0	0	0	0	0	0	0	2.75	0.1	appr. 4.0	1.6	0	0	8.45

The foraging behaviour of *M. cuneirostris* was observed for 10 days in December 1980 and for 4 days in April 1981 on a 600 m² study area located on the dunes 8 km south of the Kuiseb. Lizard movement and foraging behaviour within this site was recorded by 3 to 7 observers using binoculars. In December the first 3 days were spent observing numerous lizards. From the third day a characteristic female (2 tailed) was observed and her feeding behaviour recorded. A total of 33,2 lizard observation hours were accumulated during this study period. During April, 23 hours of observations were obtained.

Sand surface temperatures were recorded during observation periods using a mercury thermometer. Readings were taken at half hour intervals.

During December, an estimate of total insect activity was obtained by "fixing" the binoculars on a spot on the sand surface about 10 m distant and counting the number of insects passing through the field of vision in 5 minutes.

Samples of the most common ant species were collected, 160 of the common, unidentified myrmicine ant and 1075 *Camponotus detritus* of various sizes. These were weighed and individual ants measured to obtain an indication of their potential energy yields.

3 RESULTS

Analysis of the stomach contents of 111 *M. cuneirostris* (Table 1) indicated that coleopterans were by far the most important food for this lizard species on a volumetric basis. Isoptera and Hymenoptera also figured prominently. In contrast, analysis of 95 stomach contents of *A. anchietae* (Table 2) indicated that seeds were the most common food item both on a numerical and volumetric basis.

When foraging, individuals of *M. cuneirostris* were often observed ascending small tussocks on which they would remain for long periods. From here they apparently preyed upon small myrmicine ants, which constituted the most commonly observed prey consumed by *M. cuneirostris* (Table 3). Termites were the second most common prey type, 68% of which were taken as they moved upward through the sand toward the surface. Whilst the myrmicine ant foraging pattern is indicative of a 'sit and wait' foraging tactic, that of the termites appears to follow an active foraging search.

Sixteen per cent of the total feeding observations involved items robbed from other animals, mainly termites taken from the jaws of *C. detritus*. On more than one occasion, a lizard was observed to lie motionless in the shade of a bush and allow all the solitary *C. detritus* ants to pass. However those ants carrying objects in their jaws were almost always robbed by the lizard. On a few occasions the lizard did not eat the

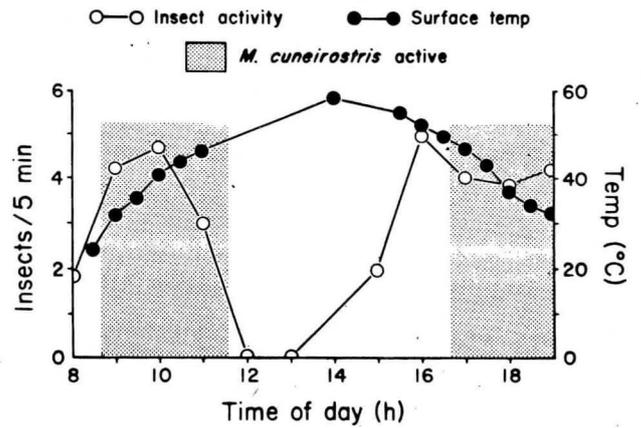


Figure 1: Graph of insect activity and temperatures versus time of day

stolen item which was in each case found to be an inanimate object such as dry faeces.

C. detritus was the most common insect observed in the study area although not often consumed by *M. cuneirostris*. It is much larger than the myrmicine ants commonly preyed upon (*C. detritus* — weight: 41,0 mg, n = 1075, length: $12,7 \pm 1,7$ mm, n = 150; myrmicine ants — weight: 1,5 mg, n = 160, length: $4,2 \pm 0,3$ mm n = 142).

Insect activity and lizard activity, derived from total counts of individuals, were found to be distinctly bimodal with lowest activity during the hottest part of the day and peak activity occurring during the cooler periods of mid-morning and late afternoon, (Fig. 1).

4 DISCUSSION

Our observations on the dietary preferences of *M. cuneirostris* and *A. anchietae*, collected from a dune area south of Gobabeb, suggest that *M. cuneirostris* prefers a more insectivorous diet whilst *A. anchietae* a more omnivorous one. Stomach analyses (Tables 1 and 2) indicate that both these lacertid lizards eat a wide variety of arthropod species, consisting mainly of insects. Although *A. anchietae* forages on insects belonging to orders which are amongst those foraged upon by *M. cuneirostris*, monocotyledonous seeds appear to constitute the largest proportion of the diet of *A. anchietae*.

The diet of *M. cuneirostris* has previously been examined by Robinson and Cunningham (1978), in the Kuiseb River floodplain (near Rooibank 23° 9'S 14° 35'E), and by Stuart (unpubl.) in the low vegetated eastern Namib Dunes (Kamberg Dunes, approx 23° 40'S 15° 40'E). Observed diets in these studies differed considerably from each other and from the current study.

Robinson and Cunningham (1978) found, on a numerical basis, that Lepidopteran larvae, followed by ants (Formicidae), other hymenopterans, tenebrionid lar-

TABLE 2: Monthly stomach analyses of *Aporosaura anchietae*. - Figures in each column refer to no. and vol. (mm³) respectively (ad = adults; l = larvae).

NO. OF STOMACHS	JUNE 78 6	JULY 78 6	AUG 78 12	SEP 78 11	OCT 78 12	NOV 78 6	DEC 78 12	JAN 79 12	FEB 79 6	MAR 79 6	APR 79 6	TOTAL 95
CLASS MONOCOTYLEDONAE												
Fam. <i>Gramineae</i> (seeds)	17 45	192 360	165 270	14 20	184 400	60 100	50 80	180 300	222 750	102 340	239 540	1425 3205
CLASS DICOTYLEDONAE (seeds)	12 14		106 160		112 200	46 40	43 30	186 260		78 100	57 20	640 824
CLASS ARACHNIDA												
ORDER ARANEAE		1 1	1 2		1 20		- 30			1 125		4 178
CLASS INSECTA												
ORDER THYSANURA												
Fam. <i>Lepismatidae</i>											1 3	1 3
ORDER ISOPTERA												
Fam. <i>Termitidae</i>	2 4	2 1		1 2								5 7
ORDER ORTHOPTERA												
Fam. <i>Pyrgomorphidae</i>				1 300								1 300
Fam. undetermined						1 32		1 50				2 82
ORDER HEMIPTERA												
Sub-order <i>Heteroptera</i>												
Fam. <i>Tingidae</i>				2 60								2 60
Sub-order undetermined					- 20					3 9		3 29
ORDER COLEOPTERA												
Fam. <i>Tenebrionidae</i> (ad)			6 25						2 56			8 81
(l)				36 1152	7 350			2 100				45 1602
Fam. <i>Curculionidae</i>	1 400											1 400
Fam. <i>Staphylinidae</i> (l)						4 6				2 1		6 7
Fam. <i>Meloidae</i> (l)			1 81									1 81
Fam. undetermined (ad)				33 200	6 48	- 150	1 24					40 422
(l)							4 24					4 24
ORDER DIPTERA (l)			3 15								1 1	4 16
ORDER HYMENOPTERA												
Fam. <i>Formicidae</i>						5 5						5 5
Fam. <i>Chalcidae</i>					6 8						1 1	7 9
Fam. undetermined	1 1		2 1									3 2
UNDETERMINED INSECTS (ad)			13 30		20 105	- 20			2 4	- 50		35 209
(l)			10 50		2 6				- 9			12 65
(pupae)								6 240				6 240
UNDETERMINED MATERIAL		- 49					- 110	- 200				- 359
TOTAL	33 464	195 411	307 634	87 1734	332 1109	122 251	97 424	376 1174	226 819	184 624	301 566	2260 8210
RAINFALL (mm)	0	0	0	0	0	0	0	0	2.75	0.1	appr. 4.0	6.76

TABLE 3: Observed feeding responses of *Meroles cuneirostris* during the December 1980 and April 1981 study periods. Active, robbed and dead refers to prey individuals that were active at the time of their capture; individuals that were robbed from other organisms and dead individuals respectively

Prey type	Active	Robbed	Dead	Total
Myrmicine ants	51	—	—	51
<i>C. detritus</i>	—	1	3	4
termites	19	9	—	28
dipterans	1	—	—	1
unidentified	—	4	—	4
				88

vae and weevils (Curculionidae), were the preferred dietary items of *M. cuneirostris*. Orthopterans, mantids, and wasps were reported to have been eaten seasonally, but tenebrionid adults and larvae, other Coleoptera, ants, undetermined Hymenoptera and lepidopterans were taken nearly every month.

Stuart's (unpubl.) analyses (Table 4) indicated that isopterans, adult and larval coleopterans and ants were significant prey items, with a high percentage occurrence each months.

The present study revealed that an unidentifiable form of adult coleopteran, other hymenopterans, tenebrionid adults and termites contributed substantially to the diet of *M. cuneirostris*.

Apparent differences (Table 5) in the prey preferences could be related to the faunal and ecological differences between the three habitat types, although the data necessary to confirm this are currently not available.

The study by Robinson and Cunningham (1978) near Gobabeb on the diet of *A. anchietae*, is comparable to the present study. Both studies suggested that this lizard has an omnivorous diet. In both studies, insects

were the largest animal component. On a numerical basis grass seeds, followed by *Trianthema hereroensis* seeds, unidentified bugs (Hemiptera) and thysanurans dominated the diet of the *A. anchietae* examined by Robinson and Cunningham (1978). Grass seeds, dicotyledonous seeds, adult tenebrionids, undetermined adult coleopterans and undetermined adults insects were numerically dominant prey items in the present study. Both studies thus indicate graminous seeds to be important in the diet of *A. anchietae*. According to Robinson and Cunningham (1978) seeds of several species of grass (*Stipagrostis gonatoschys*, *S. ciliata*, *S. sabulicola* and *S. cf. namaquensis*), are available at all times of the year and constitute an important energy resource for *A. anchietae*.

Availability of some of the prey items noted by the 3 studies may reflect responses to climatic factors. The rainfall that was recorded during Robinson and Cunningham's (1978) study (87mm) was much higher than that recorded for the Kamberg or Gobabeb studies (although 107,5 mm of rain had fallen prior to the commencement of the 1980 study.) Heavy rain may produce an expansion of the niches occupied by certain animals and plants to the extent that overlap occurs in specific instances (Seely and Louw, 1980).

Differences in foraging behaviour, i.e. active foraging versus a 'sit and wait' type foraging tactic, has been suggested by Huey et al (1984) to reflect differences in locomotor capacity or even differences in potential activity levels. However, both the physiology and morphology must be expected to affect the locomotor abilities of lizards. *M. cuneirostris* and *A. anchietae* seem well adapted to living in narrow sympatry in the Namib Desert. They are morphologically similar and have a very similar diurnal activity pattern, but they differ markedly in their diet, reproductive activity and habitat (Goldberg and Robinson 1979). Differences in

TABLE 4: Monthly stomach analyses of *Meroles cuneirostris* from the kamberg dunes during 1974. (C. Stuart unpubl.). Numbers refer to % occurrence — calculated using number of prey items. (ad = adults; l = larvae).

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	TOTAL	MONTHLY
No. of Stomachs analyzed	11	0	13	15	13	16	12	16	8	21	15	10	151	13,73
Order Scorpiones			8								7		15	1,36
Order Solifugae				7	8			6		5			26	2,36
Order Isoptera	9		85	73	23	37	67	62		9	13	10	388	35,27
Order Orthoptera					8	6			11	5			30	2,73
Order Hemiptera	9				8				22		7		46	4,18
Order Neuroptera									33				50	4,55
Order Coleoptera (ad)	9		8	27	23	25	8	37	33	38	33	70	373	33,91
(l)	27				23	12			44	43	13		162	14,73
Order Diptera				13		6					20		39	3,55
Order Lepidoptera				7	8					5	7		27	2,45
Order Hymenoptera														
Fam. Formicidae	18		15	60		44	8	6	22	29	20	20	242	22
Undetermined	9				23	6	16	6		5			65	5,91
Rainfall	----- 14,0 -----						----- 10,5 -----							

may therefore be a reflection of the relative abundance and preferred dietary alternatives present within each habitat type.

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