Comparative diet of two Namib Desert sand lizards (Lacertidae)

by

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1978

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ABSTRACT

The diet of two related Namib Desert sand lizards (Lacertidae) was examined by monthly stomach analyses during 1976 – 77. *Meroles cuneirostris*, a species of the sandy vegetated interdune valleys, is strictly carnivorous and consumes a wide variety (13 orders) of arthropods, mainly insects.

The second species, *Aporosaura anchietae*, lives in the sparsely vegetated sand dunes, and its diet varies from omnivory to carnivory, depending on geographic location. Grass and *Trianthema* seeds are an important part of the omnivorous diet, especially during periods of low insect abundance. Differences in the diet of these two lizards are related to the relative prey abundance in their respective habitats. In environments, such as deserts, which experience seasonal and annual fluctuations of prey, omnivory is an optimal feeding strategy, and this may partially account for the broad geographic distribution of *A. anchietae* in the Namib Desert dune system.

1 INTRODUCTION

The numbers and types of prey eaten by lizards are generally poorly known, and this is especially true for southern African species (but see Huey et al, 1974). Furthermore, few lizard diets have been analysed on a monthly or even seasonal basis, and such sampling provides important information on the seasonal abunfance and phenology of prey items. This study, which is part of an ecological investigation of the Namib sand-diving lizard, *Aporosaura anchietae*, is a comparative monthly analysis of the diet between it and another related sand lizard, *Meroles cuneirostris*. The food differences noted between these two species are but one aspect of the adaptive changes that have accompanied the shift from living in a vegetated sandy plains habitat to living in the sparsely vegetated shifting sand dunes.

2 MATERIALS AND METHODS

All *A. anchietae* were sampled from the sand dunes 8 – 10 km from Gobabeb (23° 33′S, 15° 05′E). The *M. cuneirostris* were collected from a site on the Kuiseb River floodplain at 5 – 12 km NW of Rooibank (23° 9′S, 14° 35′E). Both sites border the northern margin of the southern sand dune desert in South West Africa. Lizards were sampled from January 1976 to January 1977. One month is lacking from the *M. cuneirostris* (July 1977) and the *A. anchietae* (February 1976) collections. A total of 359 stomachs were analysed, 185 from *A. anchietae* and 174 from *M. cuneirostris*. During the study period the Namib Desert experienced summer rains six times greater than normal, which undoubtedly altered usual insect abundances.

Fifteen stomachs (7 – 8 males and 7 – 8 females) were examined each month and their contents analysed

by the following procedure. First, the volume of 20 stomachs with various amounts of food was determined by water displacement in a graduated cylinder, and from this an average volume of stomach contents was calculated to be 1.4 cc for *A. anchietae* and 1,6 for *M. cuneirostris*. Each stomach's volume was visually estimated relative to these "average" values. The contents were then uniformly spread out on a piece of plastic and the prey were identified, individuals counted, and a visual estimate of each prey's volume was made. Conclusions about the relative importance of prey items in a diet that are based only on volume or only on numerical abundance may misrepresent the actual contribution of the prey in the overall resource pattern. When these two paramaters are used in combination they give a more accurate outline of how prey are utilized by a species.

3 RESULTS

Aporosaura anchietae is a small monotypic lacertid (3 – 6 g) with several conspicuous morphological specializations (Louw and Holm 1973) for living in high shifting sand dunes that are largely devoid of vegetation (Plate 1). Two dominant plant species that occur in these dunes are *Stipagrostis sabulicola*, a grass, and *Trianthema hererroensis*, a succulent (Aizoaceae); both are dune endemics and their seeds are important food for *A. anchietae*. *Meroles cuneirostris* is larger (5 – 9 g), and lives in the vegetated low sandy flats and hummocks adjacent to the high dunes (Plate 1) and in broad deltic portions of rivers such as the Kuiseb. Common plants in these sandy interdune valleys include grasses (*Eragrostis spinosa*, *Asthenatherum glaucum*, *Stipagrostis sabulicola*, *S. gonatostachys*, *S. namaquensis*) naras (*Acanthosicyos horrida*), and a succulent (*Trianthema hererdensis*). These latter plants may also occur in the riparian habitats along with other annuals and perennials (e.g. *Monsonia*, *Mesembryanthemum*, *Ricinus*, *Nicotiana*). There is a small area of habitat overlap at the dune base, but for the most part the foraging areas of these species are mutually exclusive.

In the study area, which lies in the central portion of the range of *A. anchietae* this lizard has an omnivorous diet of plant and animal food. Animal food consisted almost entirely of arthropods, and by far the largest component of these was insects (Tables. 1. – 3). In decreasing order of volumetric importance, the major identified insect prey items are tenebrionid beetle larvae, lepidopterans, tenebrionid adults, pentatomid bugs, and other beetle larvae (Table 1). Numerically grass seeds were dominant in the diet followed by *Trianthema* seed, pentatomid and unidentified bugs (Rhyncota), and thysanurans (Table 2). One *Aporosaura* hatchling and the tail of another were found in the stomachs of two adult males. In

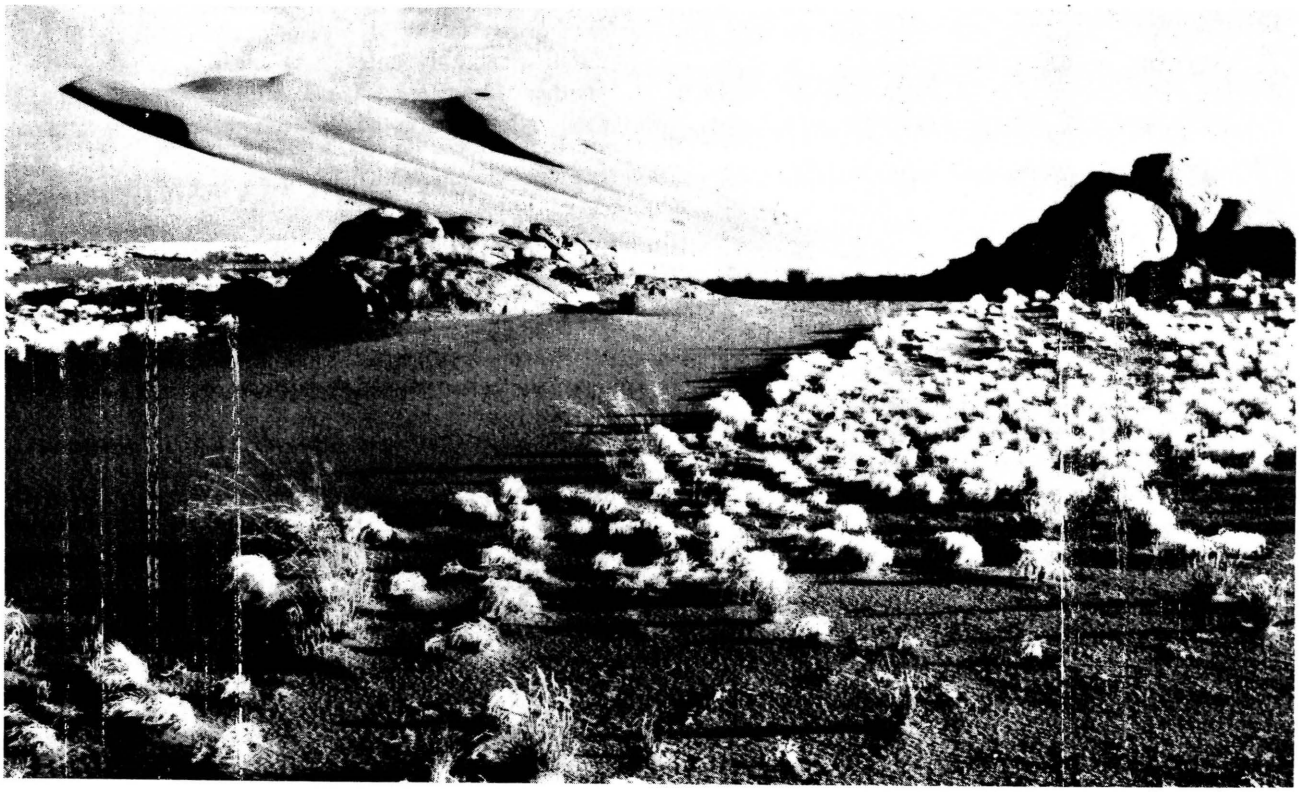

PLATE 1: Dune field in the northern Central Namib Desert showing the vegetated interdune environment of *M. cuneirostris* and the sparsely vegetated dune habitat of *A. anchietae*.

the field, another male was observed eating a juvenile. No reptile species was previously reported (Fox 1974) as cannibalistic. This behaviour may be related to the greater than average densities of young lizards at this time (Robinson, unpublished data).

Seeds of several species of grass (*Stipagrostis gonatostachys*, *S. ciliata*, *S. sabulicola*, and, *S. namaquensis*) and the dune succulent (*Trianthema hereroensis*) constituted 99 % of the plant material in the diet (Tables. 1 – 2). *Aporosaura* is the first lizard reported thusfar to feed exclusively on the seeds of plants, although other species may eat them incidentally. These seeds are non-randomly wind-distributed in the dunes where they collect at the base of the leeward slopes. This food is available at all times of the year and constitutes an important energy resource for *A. anchietae*.

Except for three months, the number of females with seeds in their stomachs was 20 – 30 % higher than for males (Fig 1). During one of these months, January 1976, both sexes fed mainly on the carabid beetles, which flourished after the summer rains. Details of this sexually dimorphic feeding behaviour, the first example in lizards, and its physiological and ecological implications will be discussed elsewhere (Robinson, in prep).

Some animal prey, such as spiders, acridids, earwigs, and curculionid and carabid beetles (Table 3) are eaten seasonally when they are abundant. Tenebrionid larvae, are probably eaten year-round but more larvae were found in stomachs during months when fog is more common (September – December) and this period appears to be a peak breeding time for these beetles. Larvae are often active on foggy mornings just under the surface sand. Bugs (Rhyncota) and various hymenopterans, as well as grass and *Trianthema* seeds are ingested seasonally (Tables. 1 – 3).

Several prey items such as lepidopterans, hymenopterans, thysanopterans, some rhyncotans, neuropterans and dipterans occur as transients in *Aporosaura's* habitat and are therefore infrequently captured, while others like scorpions (low densities) solpugids (too elusive) orthopterans (many too large), isopterans (mainly nocturnal) and adults of several small tenebrionids (crepsular and nocturnal) are dune residents but are seldom eaten.

The summer diet of 17 *A. anchietae* hatchlings was mainly thysanurans and grass and *Trianthema* seeds, with fewer tenebrionid larvae (Table 4). These larvae are smaller than those (*Onymacris* sp.) typically eaten by the adult lizards, and size partitioning of animal food between adult and hatchlings is indicated. Volumetrically animal matter forms the greatest portion of the hatchlings' diet. In a less extensive dietary analysis of *A. anchietae*, Louw and Holm (1972) reported similar results, except fewer insect prey taxa were recorded and grass seeds figured more importantly. During their sampling period, (1968 – 1969) rainfall was lower (6,1 mm) than normal (16,8 mm; Seely and Stuart 1976) and their samples were smaller and less frequent.

West of our study site at two coastal dune localities, where vegetative cover is less and detrital accumulations are fewer, Louw and Holm (1973) found that *A. anchietae* ate only insects, mainly canaceid and coelopid flies and weevils. We analysed a summer (January) sample of 26 individuals from a third coastal site (Sandwich Harbour), and found the main food items were ants, carabid and cicindelid beetles, pentatomid bugs, and four *Lineum* seeds. It appears that throughout its range this lizard is an opportunistic feeder and its diet varies according to local and temporal abundances of seeds and animal prey. However, plant material is probably a minor component in the diet of the coastal populations.

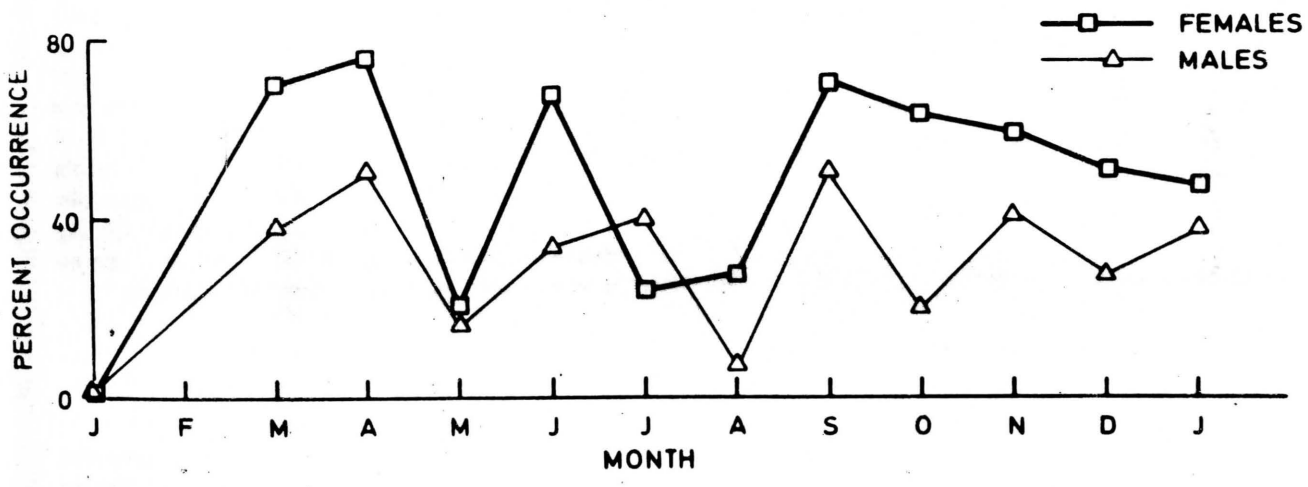

FIGURE 1: Percent occurrence of seeds in stomachs of male and female *A. anchietae* from near Gobabeb, South West Africa/Namibia during 1976.

In contrast to the omnivorous diet of *A. anchietae*, *M. cuneirostris* is strictly insectivorous. The few plant fragments recorded were probably eaten while capturing insects. The insect group representing the largest prey volume in stomachs of *M. cuneirostris* was weevils, followed in decreasing order by tenebrionid larvae, tenebrionid adults, ants, and hymenopterans exclusive of ants (Table 5). Numerically lepidopteran larvae dominated, then ants, other hymenopterans, tenebrionid larvae and weevils (Table 6). Orthopterans, mantids, neuropterans, and wasps were eaten seasonally, but tenebrionid adults and larvae, other coleoptera, ants, undetermined hymenopterans, and lepidopterans were taken nearly every month (Tables. 5 – 7). During our sampling period, the annual availability of several of these insects (e.g. weevils and lepidoptera) may be atypical, resulting from the unusually high summer precipitation (87 mm, unpublished data), but the other prey recorded are abundant at all seasons during normal (15 – 20 mm) rainfall years. No preference in insect prey taxa was noted between males and females.

The bulk of the summer diet of 16 *M. cuneirostris* hatchlings was hymenopterans, neuropterans, spiders, thysanurans, and flies were eaten in lesser quantities (Table 8). Again, the prey eaten by hatchlings was smaller than by adults.

Both of these lacertid lizards eat a wide variety of arthropod species, consisting mainly of insects. Sixteen orders of arthropods were recorded and of these 12 are common to the diets of both lizards. The prey differences noted appear related to the faunal and ecological differences between the two habitat types. For example, no dictyopterans were eaten by *A. anchietae*, and these predatory insects are rarely found in the vegetationless dunes. Ants (*Camptonotus*) are infrequently taken by *Aporosaura* but are a common food item for *Meroles*, a situation that reflects the relative abundance of ants in each habitat type. *Meroles cuneirostris* eats a variety of wasps, cicendelid beetles, and tetragonid orthopterans, all representing families which occur rarely in *Aporosaura's* habitat. Opportunistic shifts to seasonal prey was common in both lizards, but these seasonal prey belong to different insect groups (Tables. 1 – 3, 5 – 7).

4 DISCUSSION

The Namib Desert dune arthropod fauna is extraordinarily rich in species, especially apterous tenebrionid beetles (Koch 1962). These beetles feed directly on the accumulations of plant detritus, and in turn carnivorous arthropods and vertebrates feed on these herbivorous species. The trophic bases of the food chains involving the two lizard species compared here are somewhat different. In the sand dune habitat of *Aporosaura*, the trophic base is windblown plant "detritus" that accumulates on the lee or slipface side of these mobile crests. The identifiable portion of this detrital material is derived from local and nearby plains grassland species (Robinson, unpublished data), and not from distant communities of the escarpment to the east, as was previously suggested, (Louw and Holm, 1973). By comparison, the primary trophic base in the flat sandy plains habitat of *M. cuneirostris* consists mainly of living vegetative cover and some small detriral collections at the base of the plants. In terms of possible insect habitats the latter is more diverse.

Pough (1973) and Wilson and Lee (1974) discussed the relationships of body size, and metabolic rate to the occurrence of herbivory among lizards. They concluded that within several different phyletic lineages of carnivorous species, herbivory has evolved as body weight approaches 100 g. Larger lizards have a lower energy requirement per unit of body weight, and because less time and energy is required to harvest plant foods herbivory is the most economical way to fulfil their greater total energy requirements.

Herbivorous lizards eat leaves, flowers, and smaller stems, and the energy content of these plant parts varies from 15,1 – 17,6 kJ/gm dry wt (Golley 1961). Seeds, however, are the most calorific portion of a plant (21,3 kJ/gm dry wt for millet) and are nearly equal to insects (22,6kJ/gm dry wt) in energy content (Golley 1961). By incorporating seeds in their diet, *Aporosaura* has sacrificed little in terms of energy lost per unit of food, and in fact, a net gain may be realized because of the greater foraging efficiency associated with harvesting seeds instead of insects. Insect food is important however, since it provides much of the water lacking in seeds that is necessary for physiological processes. The lack of seed-eating by *M. cuneirostris* may be partially explained by the absence of seed accumulations in the flat plains habitat, which would require greater expenditures of time and energy to exploit.

Dietary flexibility allows *A. anchietae* to utilize locally and temporally abundant foods, a valuable asset in sparsely vegetated desert environments where food resources may fluctuate widely. This is one possible reason why this species has colonized nearly all of the Namib sand dune systems, from southern Angola to the Northern Cape Province. When possible, omnivory that includes seeds is an optimal feeding strategy for a desert species to obtain sufficient energy and moisture at minimal energetic expenditures.

5 ACKNOWLEDGEMENTS

The C.S.I.R. and the Transvaal Museum provided financial support, and the S.W.A. Division of Nature Conservation and Tourism offered facilities and permission to work in the Namib Desert Park.