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Short Communication

Observations on Diet and Seed Digestion in a Sand Dune Lizard, *Meroles anchietae*

KENNETH A. NAGY, AND DANIELLE R. SHEMANSKI

Department of Ecology and Evolutionary Biology, University of California, Los Angeles, 621 Young Drive South, Los Angeles, California 90095-1606, USA
kennagy@biology.ucla.edu

Abstract.—Shovel-snouted sand dune lizards, *Meroles anchietae*, are reported to include much seed from grasses and fig marigolds in their diets year-round. This diet is quite unusual for a reptile, and invites investigation. We had an opportunity to examine the diet and to measure seed digestibility for *M. anchietae* living on dunes near Gobabeb, Namibia. Stomach contents taken harmlessly via esophageal cannulation in the field revealed that the average diet included 37% (dry mass basis) immature seeds, 61% arthropods and 2% green plant leaves and flowers. Captive lizards fed measured amounts of whole mature (dehisced) grass seeds, both with and without hulls, were unable to digest and assimilate any significant dry matter from them. Microscopic examination of seeds recovered from stomachs along with seed remains found in fresh fecal pellets from free-living *M. anchietae* indicated that most of the "seeds" apparently were soft, moist, somewhat green and immature when eaten, and may be better termed "ovules". This food, perhaps eaten directly from the flowers of the plant, would be much more digestible and nutritious than mature, dry, shed (dehisced) seeds. We suggest that the seed-eating behavior of *M. anchietae* might be better described as herbivory than as granivory.

Key words.—diet, digestibility, nutrition, granivory, seed-eating.

In parts of the Namib Desert, the omnivorous shovel-snouted sand dune lizard, *Meroles anchietae* (previously *Aporosaura anchietae*: Arnold 1991), consumes a substantial amount of seeds (Louw & Holm 1972; Robinson 1987), and it does this year-round (Robinson & Cunningham 1978). The seeds of grasses (mainly *Stipagrostis* spp.) and fig marigolds (family *Aizoaceae*) are the most commonly-eaten seeds in a population near Gobabeb. Although arthropods and occasional fresh plant parts and detritus make up most of the diet annually, individual lizards in this population may have only seeds in their stomachs (Louw & Holm 1972), suggesting dietary specialization on seeds at times and by some individual lizards. Other lizard species are known to eat some seeds on some occasions (e.g. *Angolosaurus skoogi* in the Namib Desert, Pietruszka *et al.* 1986; and *Uma scoparia* in the Mojave Desert, Minnich & Shoemaker 1972), but to date, only *M. anchietae* is known to regularly incorporates seeds in its diet.

Other desert animals that specialize on seeds are typically equipped with specific adaptations for seed processing. Examples are birds with thick beaks that are used for shucking seeds and with gizzards containing pebbles that grind hard seed endosperm, and rodents with large incisors that crack and remove seed hulls along with molars that grind up seeds before they are swallowed (Chambers & MacMahon 1994). Lizards generally have none of these specialized adaptations for preparing seeds for digestion. Thus, we were surprised and intrigued to learn that *M. anchietae* were able to digest and assimilate 52% of the dry matter in the diet of grass seeds and commercial finch seed they were fed (Robinson 1990). During a long-term study of the population ecology of *M. anchietae* living on dunes near Gobabeb (A. Muth & colleagues unpublished), we had the opportunity to examine the diet of free-ranging individuals. Additionally, we re-examined the ability of these lizards to digest grass seeds by conducting a feeding experiment.

Our field study site was on and around Helga's dune, about 2 km south of the Desert Ecological Research Unit in Gobabeb (23° 34'S, 15° 03'E), Namibia. During late mornings in May of 2001, we hand-captured 15 active adult *M. anchietae* for analysis of diet. Upon palpation of their stomachs, six contained little or no food and were released immediately. The stomach contents of each of the remaining nine lizards were gently removed using a polished, lubricated (with saliva) glass tube carefully inserted down the esophagus and into the stomach. All food items were gently massaged into the tube, which was then slowly removed, and the lizard was released where captured. This process took less than 30 seconds and appeared to be harmless. Food items were then blown out of the tube into small, labeled plastic vials which were sealed for subsequent microscopic examination later that day. Food items were identified under a dissecting microscope by comparison with labeled plants and plant parts in the herbarium collection, and with the preserved arthropod collection, both collections being available at the Desert Ecological Research Unit laboratory. After sorting diet items for each individual lizard, separated piles of food types were placed on pre-weighed aluminum pans, and dried to constant mass in an oven at 60° C. Diet components are expressed as percent of total dry mass of food in each stomach.

Digestibility trials.—Seven lizards were captured at dunes near Helga's dune, and flags were placed where the animals were captured so they could be released at the same location when the experiments were over. Lizards were transported to the laboratory, where they were weighed. They were given numbers, and were housed separately in clean rectangular plastic cages (shoe storage boxes), which measured approximately 30 x 15 x 5 cm. Cage lids had a 10 x 10 cm screened hole for ventilation. One end of each cage was shaded and the other end received heat and light from an overhead 200 W floodlight that was on from 08h00 to 18h00 daily. The overnight ambient temperature in the laboratory averaged 25° C, and daytime temperatures in cages ranged from 30° (shaded end) to 36° C (lighted end). These temperatures are comparable to temperatures that the lizards would experience in the sand dunes (Louw & Holm 1972). Preliminary experiments indicated that ingested seeds, when later defecated, were still easily identifiable as seeds. Thus, we gently fed pre-weighed grass seeds (by placing them behind the tongue then waiting for the lizard to swallow), two to four per day, depending on size of the individual lizard, for four days. These seeds still had their hulls intact, as they would be when encountered in the field. To simulate the field diet (see below) by including an arthropod component to the food given, pieces of tenebrionid beetle larvae were also fed. We offered drinking water every day after feeding. The lizards willingly licked and swallowed water from the tip of an eyedropper, so we allowed them to drink as much as they wanted. After a three-day period when only beetle larvae and water were given, another four-day period of seed-feeding was done, this time with seeds that had their hulls completely removed. Following this period, lizards were fed only beetle larvae and watered daily until all seeds fed had been defecated.

We used fresh (untreated) Fescue grass seeds that we purchased from a nursery. The Fescue (genus *Festuca*) grass seeds were a similar size and shape to *Stipagrostis* spp. grass seeds in the herbarium collection at Gobabeb. Seeds with hulls intact and with hulls carefully removed were prepared for measurement of dry mass intake by drying them to constant mass in an oven set at 70° C. Seeds were then divided into four daily portions for each lizard, and weighed while still warm to avoid errors due to hygro-

Table 1: Stomach contents of adult *Meroles anchietae lizards* captured in the sand dunes near the Gobabeb research station, Namibia in May of 2001.

	Dry mass (% of total)		
Animal number	Seeds	Plant parts	Arthropods
18	100	0	0
20	0	0	100
21	81	0	19
23	0	0	100
25	81	0	19
19	37	0	63
29	34.4	17.6	48
30	0	0	100
31	0	0	100
Mean ± SD	37 ± 41	2.2 ± 6.2	61 ± 41

scopic uptake of water vapor. All seeds fed were subsequently recovered from fecal pellets that were voided 2-4 days later. We carefully cleaned each defecated seed under a dissecting microscope using forceps and metal probes. After pooling voided seeds by animal for each four-day trial, seeds were dried to constant mass at 70° C and dry mass voided was recorded.

Calculations.—Percent apparent dry matter digestibility was calculated using the equation: apparent DMD = 100 x [(total dry seed matter ingested - total dry seed matter defecated)/total dry seed matter ingested]. Results are expressed as means with standard deviations (SD). Differences between apparent digestibility values for seeds with and without hulls were tested for statistical significance using a paired t-test.

Natural diet.—We identified three different food types in the stomach contents of nine *M. anchietae* lizards: small seeds, other plant material (stems, leaves, flower parts, etc.), and arthropods (ants, spiders, and small beetles). Only five of nine lizards ate seeds, but three of those five consumed primarily or entirely seeds (Table 1). On average, arthropods accounted for nearly two-thirds of the dry matter in the stomachs, and seeds comprised over one-third. Nearly all the seeds were very small and reniform, unlike local grass seeds but fitting the appearance of seeds from the dune succulent *Trianthema* (Aizoaceae family) in the herbarium collection at Gobabeb. Some seeds appeared green-colored in the dissecting microscope, and many had broken hulls with partially-missing contents. All the small seeds in the stomachs were soft and pliable.

Seed digestibility.—All lizards in the feeding trials maintained or gained body mass during the experiments. The lizards were largely unable to digest dry grass seeds, either with or without hulls. Calculated apparent dry matter digestibilities averaged 0.1% (SD = 2.4%) for the grass seed with hulls intact, and 1.1% (SD = 1.4%) for the grass seed without hulls (Table 2). These DMD values do not differ significantly from each other ($P > 0.05$).

Our results indicate that *Meroles anchietae* did not digest the seeds they were fed. This interesting observation raises several concerns and questions. Was something amiss with our feeding experiment? Why do our results differ so much from the 52% digestibility found by Robinson (1990)? If seeds actually are poor

Table 2. Apparent dry matter digestibility of grass seeds with hulls intact and without hulls. n = number of animals; DMD = dry matter digestibility expressed as a percentage; SD = standard deviation; 95% CI = 95% confidence interval around mean. Lizards were housed indoors during digestion trials.

	Hulled	Hulls removed
n	7	7
Apparent DMD (%)	0.1	1.1
SD	2.4	1.4
95% CI	1.8	1.1

sources of nutrition for *M. anchietae*, why do the lizards eat them?

The results of our digestion experiment are not surprising in view of the literature on digestibility of seeds. The passage of intact seeds through the gut of vertebrates is common, and the presence of seeds in feces from mammals and birds, especially those species that eat fruits, is mentioned in field guides as useful in identifying both the consuming animal species and the food plant species involved (e.g. Kingdon 1997). The indigestibility of seeds is central to the well-known role of vertebrate animals in dispersing seeds away from the parent plant (Levy *et al.*, 2002). Among reptiles, seeds of several plant species show increased germination after passing through the digestive tract of the spur-thighed tortoise, *Testudo graeca*, which also disperse those seeds (Cobo *et al.*, 1998). Galapagos tortoises accomplish a similar service for the endemic tomatoes they eat (Rick & Bowman 1961), as do common green iguanas, *Iguana iguana*, in a tropical forest (Benitez-Malvido *et al.* 2003). Preliminary results from feeding experiments done with the small, omnivorous desert lizard *Uta stansburiana* also indicate low or negligible digestibility of dry grass seeds, with or without hulls (zero to 10% digestibility in six separate trials; N. Huard, S. Yu, M. Hajjar & K. Nagy unpublished results). Birds and mammals that specialize on eating seeds (the granivores) have morphological and physiological specializations for hulling and grinding seeds. Granivorous rodents and birds remove seed hulls using incisors and thick bills, respectively, and rodents pulverize seeds with their molars, whereas the birds grind seeds in their muscular, gravel-containing crop (Withers 1992; Chambers & MacMahon 1994). *M. anchietae* have none of these structures, and apparently cannot, or do not, break up dry seeds prior to enzymatic digestion. Mechanical limitations in the jaw bones and muscles of lizards restrict their ability to chew food items, and most reptile species simply swallow large chunks of food whole (Ostrum 1963; Sokol 1965).

We were careful to house our lizards in clean plastic containers where any regurgitated seeds and all voided urine and feces could be easily seen, collected and measured quantitatively. In Robinson's (1990) feeding trials on *M. anchietae*, where beetle larvae, *Stipagrostis* seeds and commercial finch seed (a mixture of several kinds of grains) were offered every other day, and where lizards fed voluntarily and their cages were outdoors and had sandy floors. Uneaten prey and feces were collected by sieving the sand in each cage. We feel that this procedure may incorporate more opportunities for errors in quantitative collection, weighing, and sand contamination of feces and uneaten foods. Such errors would be detectable in the data because they should cause relatively high variances around measured values. Unfortunately, details of food intake and feces loss measurements and digestibility calculations were not reported, nor were variances (SD, SE or CI) for mean energy assimilation efficiency values (Robinson, 1990).

The puzzling question about possible benefits of seed-eating by *M. anchietae* may have a reasonable answer. Our observation of small, greenish, soft "seeds" (actually ovules?) in fresh stomach contents, rather than the mature, hard seeds we expected to find, suggests that *M. anchietae* were eating immature, unripened seeds directly from flowers in the interdune areas. Microscopic examination of fresh fecal pellets revealed empty or partly empty hulls or seed coats from these unripened seeds, suggesting that the immature seeds were relatively digestible. Unripened seeds, such as green peas and green beans in human diets, are tender, succulent, and nutritious, but as the seeds mature while still attached to the plant, they dehydrate, harden, reduce their metabolic activity, develop tough capsules and enter a relatively impervious, inactive and stress-resistant phase of the plant's life cycle, a phase well-suited to endure long periods of extreme temperatures and desiccation. That is when they are shed (dehisced from the plant) into the environment. If the grass (*Stipagrostis*) and dune succulent (*Trianthema*) seeds identified in diets of *M. anchietae* in earlier studies (Louw & Holm

1972; Robinson & Cunningham 1978) were actually ovules taken by lizards directly from the flowering structures, they may have been identified microscopically as seeds (as we did in this study) rather than as nutritious ovules. This question could be addressed directly by observing feeding behavior and feeding locations of the lizards in the field, and then by examining any plants the lizards visited. If *M. anchietae* are largely consuming ovules rather than dehisced seeds, this dietary preference should be labeled herbivory rather than granivory, and *M. anchietae* should not be included in the list of specialized species that predate on the soil seed bank in deserts.

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