# Lizard herbivory in a sand dune environment: the diet of *Angolosaurus skoogi*

R.D. Pietruszka[1], S.A. Hanrahan[2], D. Mitchell[3], and M.K. Seely[1]     1986

[1] Desert Ecological Research Unit, P.O. Box 1592, Swakopmund, 9000, SWA/Namibia
[2] Department of Zoology, University of the Witwatersrand, Johannesburg 2001, South Africa
[3] Department of Physiology, University of the Witwatersrand Medical School, Johannesburg 2193, South Africa

**Summary.** Early observations of the feeding habits of *Angolosaurus skoogi* (Andersson), a 50 120 g lizard inhabiting the almost vegetationless dunes of the northern Namib Desert, indicated that this species was herbivorous. Less than two percent of living lizard species are predominantly herbivorous and these species tend to have a high body mass (> 100 g). We therefore analysed fecal pellets of *A. skoogi* to obtain dietary details of this relatively rare lizard. Eighteen food taxa were identified: 81 percent by mass was composed of vegetable matter, of which 56 percent was an endemic, perennial cucurbit *Acanthosicyos horrida*. Both spatial and temporal variation in dietary composition were apparent. Ready access to water in the form of *A. horrida* is postulated to have allowed *Angolosaurus* to occupy this extreme habitat and to forage on components of the windblown detritus, a food source that would probably not be usable in other circumstances.

**Key words:** Sand dune - Lizard - Herbivory - Fecal analysis - *Angolosaurus*

Lizard diets often are catholic, but generally limited to insects and vertebrates (Mayhew 1968); few species are herbivorous. Reviewing the literature, Pough (1973) found only about 2 per cent of the 2,500 living lizard species to be predominantly herbivorous, and those tended to have high body mass (> 100 g). Several hypotheses have appeared in the literature concerning the adaptive significance of carnivory or herbivory in lizards. Szarski (1962) posited that herbivorous lizards would be subjected to greater predation pressure because they required a longer time to forage. In contrast, Dawson (1965) suggested that the higher preferred temperatures of herbivorous lizards allowed them to feed on plant material when potential predators could not be active. The prohibitive energy cost which would be experienced by large lizards in capturing living prey was advanced by Wilson and Lee (1974) and Ruppert (1980) as the basis of herbivory in large lizards (but see Pough and Andrews 1985). Pough (1973) suggested that the energetic demands of the larger species cannot be met from a diet of insects and few alternative prey are available. Other factors militate against herbivory in smaller lizards. Ostrom (1963) proposed that few herbivorous lizards exist because

of structural limitations of the lizard jaw. Sokol (1965) suggested that small lizards do not have the physical strength to reduce the particle size of vegetation sufficiently to allow for ingestion.
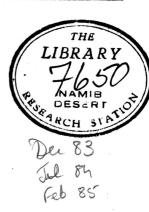
In desert environments lizards are among the most abundant and conspicuous vertebrates. *Angolosaurus skoogi* (Andersson) is a chthonic inhabitant of the northern Namib Desert of southern Angola (Fitzsimons 1953) and Namibia (Steyn 1963). It is one of only two cordylid (= Cordylidae + Gerrhosauridae) species known to be herbivorous (Pough 1973). *Angolosaurus* is the largest Namib Desert dune lizard, but its size (adult range: 50 120 g) puts it on the lower limit postulated for herbivory. Despite being herbivorous, it lives in the vegetationless slipface habitat of the Namib sand dunes (Hamilton and Coetzee 1969).

Details of the ecology of *Angolosaurus* are unknown. Currently, the total knowledge concerning diet is confined to the anecdotal account of Steyn (1963) based on an examination of 12 specimens. A more thorough examination of its diet in relation to habitat may help elucidate how ecological specialization may promote herbivory in lizards despite small size (sensu Pough 1973). We have therefore investigated the diet of *Angolosaurus skoogi* using the technique of fecal analysis and assessed the degree of spatial and temporal variation in dietary composition.

Analysis of fecal pellets (scats) has been used previously to acquire dietary information for a number of reptile species (e.g., *Agama agama*, Harris 1964; *A. stellio*, Mienis 1981; *Physignathus lesueurii*, Hardy and Hardy 1977; *Sauromalus obesus*, Hansen 1974; *Sphenodon punctatus*, Walls 1981). It may be the preferred method with rare or endangered species where it is "unwise or unfeasible" to kill animals for stomach analysis and where a comprehensive "population diet" is the objective (Hansen 1974), a situation which prevails for *Angolosaurus*. *Angolosaurus* scats are easily obtained from dune slipfaces, and it is possible to find study areas virtually devoid of scats from other species.

## Study area

The study area was located on the south bank of the usually dry bed of the Unjab River, approximately 15 km inland on the eastern (inland) side of the northern Namib dunes (20°09′ S, 13°14′ E). Here the dunes are composed mainly of barchanoid ridges 3 10 m high with connected concentric

**Table 1.** Dietary composition of *Angolosaurus skoogi* based on examination of 232 fecal pellets. Contribution (%) = mass of component as percentage of dry weight biomass in scats; Frequency = proportion of scats containing this component

| Food component | Contribution (%) | Frequency |
|---|---|---|
| **NARA** | | |
| *Acanthosicyos horrida* | 55.7 | 0.94 |
| **GRASS** | | |
| *Stipagrostis* sp. | 21.8 | 0.75 |
| **SEED** | 3.8 | 0.31 |
| **ANIMAL** | | |
| Coleoptera | | |
| *Cauricara brunnipes* | 0.3 | 0.02 |
| *Eustolopus octoseriatus* | 6.3 | 0.11 |
| *Lepidochora* sp. | 0.3 | 0.01 |
| *Onymacris bicolor* | 4.2 | 0.08 |
| *O. unguicularis* | 2.6 | 0.03 |
| *Zophosis (Calosis) amabilis* | 1.3 | 0.06 |
| *Z. (C.) lundholmi* | 0.1 | 0.06 |
| *Z. (C.) sp.* | 1.3 | 0.06 |
| Orthoptera | | |
| Grasshopper | 0.6 | 0.03 |
| Arachnida | | |
| Acari | 0.01 | <0.01 |
| Solifuga | 0.01 | <0.01 |
| Unidentified Arthropods | 0.4 | 0.04 |
| Unidentified Material | 0.5 | 0.06 |

**Table 2.** Dietary diversity* in seasonal and total samples for all taxonomic categories and for the four major food groups

| | Diet diversity | |
|---|---|---|
| Sample | All taxa | Major groups |
| February (summer) | 2.83 | 2.76 |
| July (winter | 2.00 | 2.31 |
| Total | 2.71 | 2.53 |

* diversity calculated as $1/\Sigma p_i^2$, where $p_i$ = the proportional representation of component $i$

slipfaces (Lancaster 1982). Climatically the study area is hyperarid but cool and foggy under the influence of the Benguela Current.

Within the study area, the mobile sand surface of the dunes was devoid of vegetation. The dominant plant of the area, a sparsely distributed long-lived cucurbit, *Acanthosicyos horrida*, commonly called nara, is a focal point for sand accumulation. On the interdune areas some persistent plant species are common. However, total vegetative cover over the one km² study area was less than 1%.

Chthonic tenebrionid beetles are the most conspicuous invertebrates in the study area. Diurnal adesmine species occupy the dune slipfaces and the interdune areas. Only three other lizard species were present on the study area, all three much less abundant than *Angolosaurus*.

Dunes from which fecal pellets were collected ranged from ca. 3 m high to over 10 m high; some had nara bushes growing out of the slipface whereas others were bare sand, with the nearest nara 30 m away. In addition, the patchiness of distribution of other plant species resulted in some slipfaces having adjacent succulents and grasses, whereas for others the nearest similar vegetation was up to 50 m distant. Tenebrionid beetles were present on all slipfaces.

**Materials and methods**

Four to more than 50 fresh scats of *Angolosaurus skoogi* were collected from 25 dune slipfaces during December 1983, July 1984 and February 1985. Scats were then returned the to laboratory where they were heated to 70° C for 24 h to kill the larvae of ptinid beetles which live in and feed on the scat material. After drying, scats were individually weighed and measured following the removal of any adhering sand grains. A subsample of pellets reflecting the entire size range collected (13.70–40.92 mm in length) was then selected for further analysis. Under a dissecting microscope each scat was then teased apart and the various components were evenly spread out in a petri dish. Scats were discarded if activity of ptinid larvae was noted. Organic components were identified using voucher plant and insect material; plant and insect species in the study area were very distinctive and their diversity limited. Visible inorganic material was separated out. Per cent composition of each of the organic components was estimated visually to the nearest 1%. The weight-specific fraction of each component was then obtained by multiplying its proportional representation in the scat by scat weight, assuming all components to have the same density.

A random subsample of nara and of scats from the December and July collections was ashed at 1,200° C, in the presence of benzoic acid, to determine the proportion by mass of inorganic material; energy content was measured by bomb calorimetry.

Statistical comparisons were made using the methods of Conover (1980) and Sokal and Rohlf (1981). Spatial variability in scat composition was assessed using a Kruskal-Wallis test. Temporal comparisons were made using Mann-Whitney U tests. The relationship between scat size and composition was determined by Spearman rank correlation. The minimum acceptable level for significance was $P = 0.05$.

**Results**

Eighteen food taxa were identified in 232 *Angolosaurus skoogi* scats examined, although the majority of these taxa made only small contributions to the total diet (Table 1). In general, the components of individual fecal pellets could be allocated to one of four groupings. Dominant among these was nara (*Acanthosicyos horrida*), followed by grasses of the genus *Stipagrostis*, small seeds, and an animal group consisting of one or more of a variety of arthropods, of which tenebrionid beetle species were predominant (Table 1). Whereas other plants, or components of wind-blown detritus, may also contribute to the diet of the lizards, their debris were not apparent in scats nor did our observations of the feeding behaviour of *Angolosaurus* suggest that they were quantitatively very important in the diet. The relatively narrow range of food items consumed is reflected in the

Table 3. Seasonal changes in scat composition. Values are per cent of total dry weight biomass in samples. Numbers of scats examined in ( )

| Food Group | February (96) | July (136) | Total (232) |
|---|---|---|---|
| Nara | 49.5 | 59.9 | 55.7 |
| Grass | 29.6 | 16.5 | 21.8 |
| Seeds | 6.1 | 2.2 | 3.8 |
| Animal | 13.7 | 21.3 | 18.5 |

low values of dietary diversity (Hill 1973) both by season and for the sample as a whole (Table 2).

The percentage of visible inorganic material in the scat samples, as determined by manual separation and weighing, was about 10%. Ashing of a subsample of the scats showed that a much higher proportion of the material, 62.4% ($n = 24$, $SE = 1.7\%$), was inorganic. There was no statistically significant difference between the December and July collections ($t$-test, $t = 0.499$, $P > 0.50$).

The animal component of the diets of individual *Angolosaurus* varied greatly (0–95% animal matter by mass) suggesting the opportunistic use of animal taxa by the lizards. A comparison of the animal component of scats in the July (winter) collection revealed significant heterogeneity in the animal content of the diet among the 13 different slipfaces sampled (Kruskal-Wallis test, $H = 26.389$, $n = 136$, $P < 0.01$). This heterogeneity indicates a significant spatial component to the use and/or availability of animal prey which may be related to the size of the slipface. Notably, scats with the highest percentage of animal matter originated from the largest of the slipfaces sampled.

Seasonal variation in diet was also evident. A shift towards greater dependence on nara and animal components in the diet during winter (July), coupled with a reduction in the grass and seed components (Table 3), was reflected in a lower dietary diversity index for winter (Table 2). Among the four diet groupings, statistically significant seasonal differences in the per cent composition of scats were found for nara ($Z = 2.050$, $P < 0.020$), seed ($Z = 3.183$, $P < 0.001$), and animal content ($Z = 2.590$, $P < 0.005$, large sample Mann-Whitney tests, Conover 1980). These patterns parallel the observation that in summer the lizards generally appeared more robust than in winter.

The energy content of the organic material of the scats, expressed per unit of ash-free dry weight, was 19.2 kJ/g ($n = 24$, $SE = 0.9$ kJ/g). No statistically significant seasonal variation in energy content ($t$-test, $t = 0.336$, $P > 0.50$) was apparent.

In the field, we observed partial segregation of the feeding locations of some *Angolosaurus*. During observations of feeding behaviour spanning a 3-wk period (February and July), we recorded most feeding activity in and about nara plants. Flowers, new shoots and thorns were eaten readily by all lizards, with little apparent preference. Some differentiation in feeding location was apparent, however, among the smallest size class of lizards (snout-vent length $\leq 70$ mm, mass $\leq 10$ g). These individuals often foraged at the base of the slipface, apparently feeding on windblown seeds and detritus in much the same manner as *Aporosaura anchietae* (Louw and Holm 1972), which coinhabits the slipfaces. Seed husking during these bouts was obvious and audible at several meters. In contrast, larger *Angolosaurus*,

particularly subadults and adults, foraged less frequently in this zone and were observed occasionally feeding on succulents and dry grass tufts on the plains near the dune base.

We examined the possibility of ontogenetic change in dietary composition further through Spearman rank correlations (Conover 1980) of the proportions of seeds and animal matter in scats with the length and mass of scats. The seed component showed a highly significant negative relationship to both measures of scat size (length: $r_s = -0.245$, $P < 0.0005$; mass: $r_s = -0.242$, $P < 0.0005$, n = 232). In contrast, the animal component showed no relation to scat length ($r_s = 0.055$, $P > 0.32$) and a weaker although still significant, positive relationship to scat weight ($r_s = 0.160$, $P < 0.02$). Assuming a direct relationship between lizard size and scat size (Harris 1964) in *Angolosaurus*, these results imply a shift away from seeds as lizards get older, presumably as a result of a change in foraging location. For the animal component, however, the relationship to body size is less clear and may be influenced by the spatial heterogeneity of available prey.

## Discussion

As is characteristic of all fecal analyses, the remains in scats of *Angolosaurus skoogi* will be influenced by differential digestability of the dietary components. Nevertheless, because of the limited variety of potential foods available, and because the results agree with our field observations, of foraging lizards, we believe that fecal analysis in *Angolosaurus* provides a reasonable estimate of diet.

Within the families Agamidae, Scincidae, Iguanidae and Cordylidae, lizards smaller than 50–100 g are almost all carnivorous, whereas those larger than 300 g are almost all herbivorous (Pough 1973). Mean weights for a sample of adult male and female *Angolosaurus* were 84.7 g ($n = 27$, $SE = 3.0$) and 59.1 g ($n = 22$; $SE = 3.0$), respectively. Based on size alone, *Angolosaurus* would be expected to be primarily carnivorous. Early reports (Steyn 1963; Hamilton and Coetzee 1969) that *Angolosaurus* was predominantly herbivorous therefore were intriguing.

Using scat analysis, supplemented by field observations of more than 50 animals at each of the seasonal extremes, we have confirmed that *Angolosaurus* is a predominantly herbivorous lizard. Plant debris constituted more than 80% of the mass of organic material in the scats, and 94% of all scats contained the nara plant, *A. horrida. Angolosaurus* also eats a variety of animals, notably tenebrionid beetles. Statistical analysis of body-size and spatial variation in the animal components of the scats indicates that consumption of animal taxa is opportunistic. Nonetheless, the apparent shift away from seeds in the diet with age, coupled with the observed segregation in feeding locations between different age classes of lizards, suggests that foraging opportunities will vary with foraging location.

A remarkable feature of the scat composition of *Angolosaurus* was the very high proportion of inorganic material: almost two-thirds was not combustible. For comparison, about 20% of the dry matter of human feces is inorganic (Lentner 1981), and the inorganic content of the scats of another southern African lizard, *varanus niloticus*, eating a diet of mammals in the laboratory, was 4% (Buffenstein and Louw 1982). The inorganic material was not accreted sand, nor was it obvious under the microscope; it must

have been part of the plant and animal debris. Nara has a moderate inorganic content (Mean = 7.5%, dryweight, $SE = 0.2\%$, $n = 10$) and the intestinal tracts of chthonic beetles contain sand (Seely 1983).

The energy content of the organic material of *Angolosaurus* scats, irrespective of season, was $19.2 \pm 0.9$ kJ/g, surprisingly similar to values for two carnivorous iguanid lizards fed insects in the laboratory (20.8 kJ/g for *Sceloporus virgatus*, Merker and Nagy 1984; 18.2 kJ/g for *Uta stansburiana*, Nagy 1983). Our value for *Angolosaurus* may have been an underestimate, because the high inorganic content of the material resulted in a slow burn in the bomb calorimeter, but is clearly in line with that of other lizards known to be entirely carnivorous.

Assuming the organic material in scats to be composed of protein, carbohydrate, and fat, the relative contribution of each component can be determined from the energy content of the mixture. Using standard energy values for fat, protein and carbohydrate (Ulmer 1983), we calculated that the organic material of scats contained 89% carbohydrate plus protein, and 11% fat. The high carbohydrate and protein component is consistent with the majority of the scat material being undigested plant debris like cellulose, and animal debris like chitin. Nevertheless, the fat content is higher than one finds in human feces, for example (Lentner 1981), and may explain the similarity of energy content to that of carnivorous lizards. We suspect that the fat arises from the lipids from undigested plant and animal cell walls. Also, although the guts of herbivorous reptiles do not normally contain symbiotic microorganisms (Pough 1973), the cell walls of excreted intestinal bacteria may also contribute to fecal fat.

In hyperarid climates such as that of the Namib, water availability is a pivotal ecological factor that can have a large impact on feeding specializations (Louw and Seely 1982). *Angolosaurus* fullfils its moisture requirements through its use of nara which, because of a deep tap root system, is always under positive turgor pressure; nara has a water content that exceeds that of *Angolosaurus's* animal prey (ca. 80%; beetles ca. 40-60%, Seely 1983). The need for and adequacy of this water source is evidenced from several critical field observations. First, it is not uncommon to observe *Angolosaurus* biting off emergent stems only to drink the water which beads on the severed ends. Second, the daily defection by individual *Angolosaurus*, which typifies the terminus of the pre-activity basking period, is accompanied by a rather copious amount of urine (> 3 ml), an unusual characteristic among desert lizards (Cloudsley-Thompson 1971).

Thus, we postulate that it is the ready access to water from nara which allows *Angolosaurus* to utilize vegetable matter that might not be usable in other circumstances. Grass and seeds, for example, constitute over 35% of *Angolosaurus's* total diet, with grass from 5-7 fold more common than seeds. Our observations of foraging in *Angolosaurus* suggest that most grass is obtained from dead tufts, by older individuals, whereas small seeds are more often recovered by juveniles from the detritus. Both sources are characterized by a very low moisture content and an additional water source seems necessary for their utilisation (Hamilton et al. 1977).

Detritus is an extremely common component of the Namib Desert ecosystem and represents a potentially superabundant food resource for those organisms that can take advantage of it. The ready availability of water, in nara, opens up to *Angolosaurus* the use of reliable sources of sustainable food in detrital components and other vegetable matter. Thus, it may well be this relative reliability and abundance of potential food sources in the sand dune habitat which has determined, at least in part, the direction of ecological specialization in *Angolosaurus*.

## References

Buffenstein R, Louw GN (1982) Temperature effects on bioenergetics of growth, assimilation efficiency and thyroid activity in juvenile varanid lizards. J Therm Biol 7:197-200

Cloudsley-Thompson JL (1971) The temperature and water relations of reptiles. Merrow, Watford Herts., England

Conover WJ (1980) Practical nonparametric statistics. 2 ed. John Wiley and Sons, New York

Dawson WR (1965) Interspecific variation in physiological responses of lizards to temperature. In: WW Milstead (ed), Lizard Ecology: a Symposium. University of Missouri Press, Columbia MO pp 230-257

Fitzsimons V (1953) A new genus of gerrhosaurid from Southern Angola. Ann Transvaal Mus 22(2):215-217

Hamilton WJ III, Coetzee CG (1969) Thermoregulatory behaviour of the vegetarian lizard *Angolosaurus skoogi* on the vegetationless northern Namib Desert dunes. Sci Pap Namib Desert Res Stn, no 47:95-103

Hamilton WJ III, Buskirk R, Buskirk WH (1977) Intersexual dominance and differential mortality of Gemsbok *Oryx gazella* at Namib Desert waterholes. Madoqua Ser II,10(1):5-19

Hansen RM (1974) Dietary of the chuckwalla, *Sauromalus obesus*, determined by dung analysis. Herpetologica 30(2):120-123

Hardy CJ, Hardy CM (1977) Tail regeneration and other observations in a species of agamid lizard. Aust Zool 19(2):141-148

Harris VA (1964) The life of the rainbow lizard. Hutchinson and Co Ltd, London

Hill MO (1973) Diversity and evenness: a unifying notation and its consequences. Ecology 54:427-432

Lancaster N (1982) Dunes on the Skeleton Coast, Namibia (South West Africa): geomorphology and grain size relationships. Earth Surface Processes Landforms 7:575-587

Lentner C (1981) (ed) Geigy Scientific Tables Vol 1, Units of Measurement, body fluids, composition of the body, nutrition. 8 Ed. Basle: Ciba-Geigy, pp 151-157

Louw GN, Holm E (1972) Physiological, morphological and behavioural adaptations of the ultrapsammophilous, Namib Desert lizard, *Aporosaura anchietae* (Bocage). Madoqua Ser II, 1:67-85

Louw GN, Seely MK (1982) Ecology of desert organisms. Longman, London

Mayhew WW (1968) Biology of desert amphibians and reptiles. In: Brown GW Jr (ed), Desert biology Vol 1, Academic Press, New York pp 195-356

Merker GP, Nagy KA (1984) Energy utilization by free-ranging *Sceloporus virgatus* lizards. Ecology 65(2):575-581

Mienis HK (1981) Land snails in faecal pellets of *Agama stellio* (Reptilia: Sauria: Agamidae). Salamandra 17(3-4):205-206

Nagy KA (1983) Ecological energetics. In: RB Huey, ER Pianka, TW Schoener (eds) Lizard ecology. Harvard University Press, Cambridge p 24-54

Ostrom JH (1963) Further comments on herbivorous lizards. Evolution 17:368-369