On the biology of the lizard *Angolosaurus skoogi* in the Namib Desert

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ABSTRACT

Angolosaurus skoogi, a cordylid lizard, inhabits the sand dune slipfaces of the northern Namib Desert. Aspects of its biology, including characteristics of its habitat, morphology, population, feeding, predation, surface behaviour, locomotion, thermoregulation, and metabolic rate, were studied over four years and are reported here. Possible explanations for its sympatic occurrence with the common slipface dwelling lacertid, *Aporosaura anchietae*, in the northern Namib but not in the southern Namib dunes are discussed.

1 INTRODUCTION

Angolosaurus skoogi (Plate 1), a cordylid lizard (Mertens 1971), is the most conspicuous diurnal dune lizard of the northern Namib Desert of SWA/Namibia and southern Angola. A single specimen from Angola was described as *Gerrhosaurus skoogi* by Andersson (1916). Fitzsimons (1953) described two specimens from southern Angola, but it was not until 1963 that a sample of fourteen lizards was first collected and described from South West Africa (Steyn 1963).

Angolosaurus skoogi inhabits an unusual and relatively restricted habitat, the vegetationless slipfaces of the northern Namib Desert dunes. Apart from the few descriptions of its morphology, little is recorded of the biology of *A. skoogi*. Before we began studying these lizards there had been only one paper which dealt with live animals, namely the paper of Hamilton and Coetzee (1969) on thermoregulatory behaviour. More recently the diet of this lizard was studied by faecal pellet analysis (Pietruszka *et al.* 1986). We have now studied a population of *A. skoogi* at one site in the northern Namib dune sea on nine occasions at different seasons spread over four years. We paid particular attention to the behaviour of the lizards while they were active on the sand surface, partly through interest in their social behaviour, but primarily to analyse their unusual habitat. The vegetationless slipface appears superficially to be a uniform environment but, in actuality, is a thermal mosaic strongly influenced by solar radiation and wind. In addition, wind-blown plant detritus, an especially important food for the smaller individuals of *A. skoogi*, is distributed by wind across the bare slipface but accumulates at the avalanche base. Hence we should expect differential use of the various parts of the slipface by the different sized lizards during different parts of the day and under varying weather conditions as they pursue various social
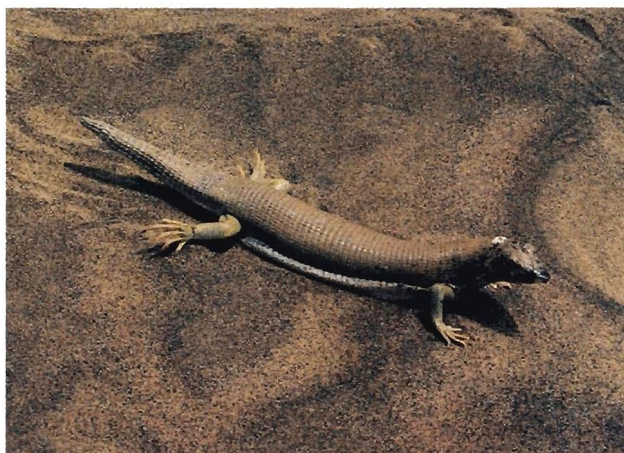
PLATE 1: Male (left) and female (right) adults of *Angolosaurus skoogi* (Andersson). The female has a regenerated tail.
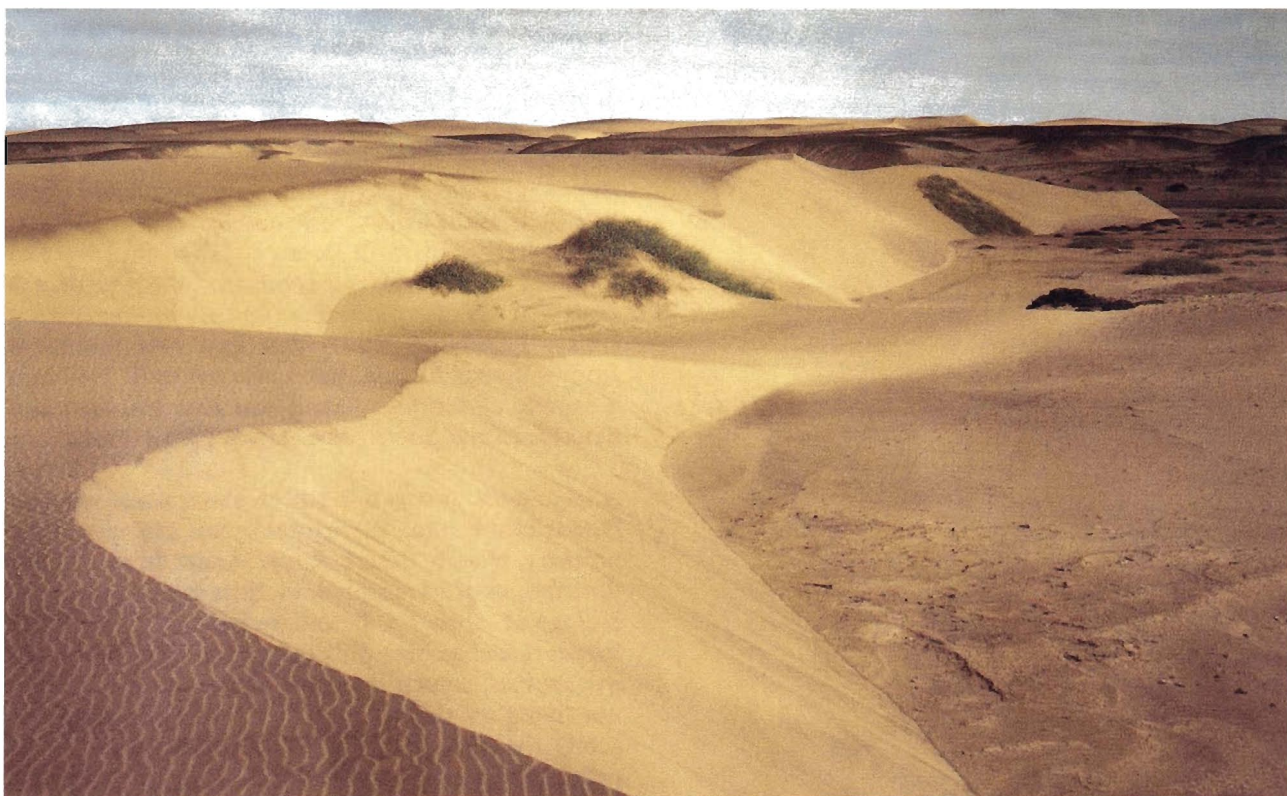

PLATE 2: A typical sand dune slipface with associated nara plant *(Acanthosicyos horrida)* in our study area on the Unjab River in the northern Namib Desert.

and feeding activities, and that is what our study revealed.

2 STUDY SITE

The Namib is a long, narrow desert on the western coast of southern Africa (Fig. 1), lying parallel to the northward flowing Benguela Current of the South Atlantic Ocean, with its associated cold-water upwelling (Meigs 1966). Although relatively cool and foggy, the Namib is hyperarid even by desert standards (Robin-

son and Seely 1980) Our study site was located at 20° 19' S, 13° 14' E, about 15 km inland, on the south bank of the usually dry Unjab River, in the northern Namib dune sea.

Around the study area the sand dunes (Plate 2) consist mainly of barchanoid ridges 3 - 10 m high with connected concentric avalanche forms (slipfaces) (Lancaster 1982). The dominant winds result in the dunes having south-westerly windward slopes of 10° - 12° composed of relatively compact sand, and north-easterly slipfaces of 31°-34° slope. The interdune plains
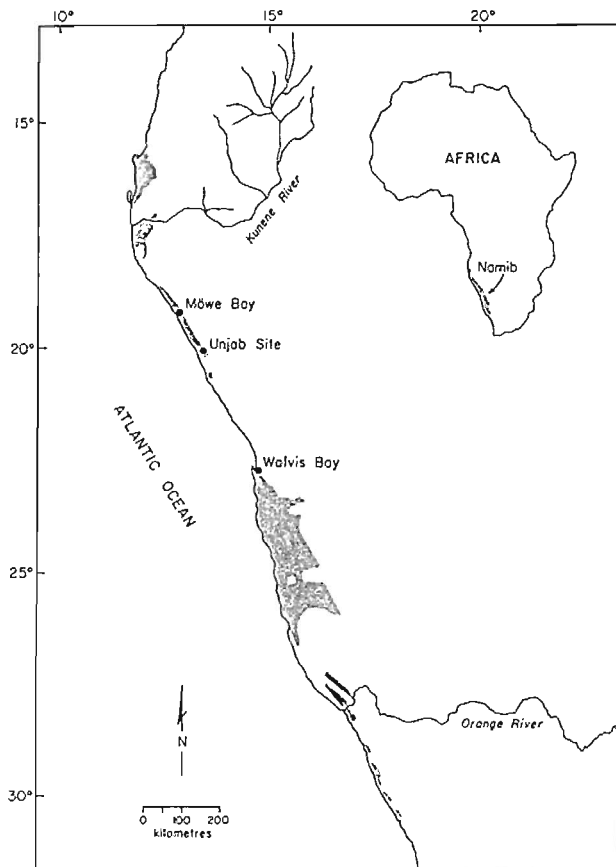
FIGURE 1: The Namib Desert on the southwestern coast of Africa is shaded on the inset; the sand dunes of the Namib Desert are shaded on the enlargement. Our study site on the Unjab River and the nearest weather station at Möwe Bay are indicated.

consist of riverine deposits of basaltic gravels which also underlie the dunes themselves. The Unjab river is usually dry, but floods occasionally leave isolated small pools within the river bed between the dunes, which we encountered only once, in December 1985.

The permanent meteoroglogical station nearest to our study site, on the coast at Möwe Bay (see Fig. 1), recorded rainfall of 22-25 mm per year for the period 1974-1977, and fog on 11-25 days per month.

Mean daily maximum dry-bulb temperatures ranged from 13° to 24°C and minima between 9° and 15°C, but sand surface temperature, under the influence of the strong solar radiation, regularly reached 60°C or more during our visits. The dominant winds are S to SW, and capable of moving sand (>4 m/s) on about half of the days (Lancaster 1982). In winter, high pressure over the interior may cause the wind to switch direction, producing easterly hot berg wind conditions; air temperatures consequently can fluctuate widely between one day and the next.

The interdune plains support a sparse vegetation of persistent plant species including *Suaeda plumosa* and *Merremia guerichii*. Following rain, succulents, such as *Sesuvium sesuvioides* and *Zygophyllum simplex*, ap-

pear and may persist for a few years, as may some grasses of the genus *Stipagrostis*. The dunes support only isolated nara plants, *Acanthosicyos horrida* (Plate 2), and on occasional grass, *Brachiaria psammophila*. Nara is a leafless cucurbit which has a dense root and stem network and which survives the constant movement of the surrounding sands. Indeed, nara bushes frequently are the focal points for sand accumulation. The density of nara was higher in our study area than it was in other areas in the dune sea further from the river. Nevertheless, the nara on the dunes and the other plants in the interdune plains in our study area provided a ground cover of less than 1% (see Plate 2).

For the greater part of any day, and at night, the sand surface appeared to be devoid of any animal life. However, during the limited daily surface activity periods, a profusion of chthonic animals emerged. Most conspicuous and abundant amongst these were the tenebrionid beetles, *Onymacris bicolor* on the dunes and *Zophosis amabilis* and *Z. lundholmi* on the interdune areas. Other diurnal adesmine tenebrionids, including *Onymacris unguicularis*, *O. marginipennis*, *O. langi*, *Eustalopus octoseriatus*, *Cauricara brunnipes*, and *Stenocara gracilipes* were present. Up to 25 *A. skoogi* could be seen on any one slipface during their activity periods. Other lizard species were observed during the day: a few *Aporosaura anchietae* occurred on most slipfaces, and isolated individuals of *Rhoptropus afer* and *Meroles reticulata* (as well as occasional *A. skoogi*) were encountered on the interdune plains. The sinuous tracks of the legless lizard, *Typhlacontias brevipes*, commonly observed were on the vegetated parts of the dune and on dune hummocks. The palmatogecko, *Palmatogecko rangei*, was the most frequently encountered nocturnal reptile in the study area.

The study area received occasional visits from larger birds, especially crows, *Corvus albus* and *C. capensis*, pale chanting goshawks, *Melierax canorus*, and greater kestrels, *Falco rupicoloides*, but some smaller species, such as the grey-backed finch lark, *Eremopterix verticalis*, and tractrac chat, *Cercomela tractrac*, were observed more frequently. Ostriches, *Struthio camelus*, also were observed sporadically in the area, but did not visit the site during our study. The most conspicuous mammal in the area was the pygmy gerbil, *Gerbillurus paeba*. The diurnal striped mouse, *Rhabdomys pumilio*, was encountered amongst the nara plants. On the gravel plains *G. setzeri* was common, and the small-eared elephant shrew, *Macroscelides proboscideus*, and the short-tailed gerbil, *Desmodillus auricularis*, occurred less abundantly. Larger mammals such as gemsbok *Oryx gazella*, springbok *Antidorcas marsupialis*, black-backed jackal *Canis mesomelas*, brown hyaena *Hyaena brunnea*, and the Cape hare *Lepus capensis*, also occurred in the vicinity and occasionally were observed on the study site; only

the antelope and rarely the jackal and hare were sighted sporadically by day.

3 MORPHOLOGY AND POPULATION CHARACTERISTICS

Angolosaurus skoogi is the largest of the Namib dune lizards. Adult males reach a total length of almost 300 mm. Figure 2 shows a plot of snout-vent length (SVL), measured using vernier calipers, against body mass, measured by spring balance (Pesola), for a sample of 229 live individuals freshly caught in the field. The animals were caught at random throughout the activity period. Our heaviest animal weighed 120 g, in agreement with the upper limit reported by Hamilton and Coetzee (1969). Between the smallest hatchling and the largest adult, SVL increased 3.7 fold, and mass increased 50 fold.
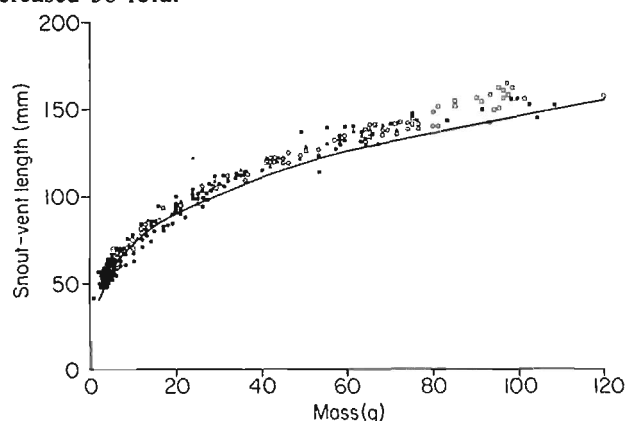

FIGURE 2: Snout-vent length (SVL) and mass of 229 specimens of *Angolosaurus skoogi* measured in the field. An additional 14 male hatchlings (SVL 65.9 ± 1.1 mm, mass 4.3 ± 0.3 g) and 26 female hatchlings (SVL 56.7 ± 0.7 mm, mass 4.2 ± 0.2 g) were not plotted.

Males: Jan/Feb ☐   July/Nov ■
Females: Jan/Feb ○   July/Nov ▲
Unsexed: July ●

The line corresponds to Pough's (1973) relationship between SVL and mass for lizards of ten different families: the ontogenetic development of *Angolosaurus* follows the phylogenetic relationship remarkably well.

On the basis of their appearance in the field, and of the data of Fig. 2, we divided the animals into three size ranges: adults (snout-vent length (SVL) > 115 mm), juveniles (70mm > SVL < 115 mm) and hatchlings (SVL < 70 mm). That these animals also fell into three distinct mass categories is shown by the analysis of a subsample of 171 individuals (Table 1).

TABLE 1: Masses of *A. skoogi* (n = 171) in three different snout-vent (SVL) length categories.

Category	SVL (mm)	n	Mass (g) (mean ± SD)	Significance of difference
Hatchlings	< 70	61	4.7 ±1.6	
				t = 11.5, p < 0.001
Juveniles	70-115	28	19.3 ±9.5	
				t = 12.6, p < 0.001
Adults	> 115	82	68.3 ±19.9	

Of 101 hatchlings, 7 were caught in Jan/Feb, 11 in Oct/Nov, and 83 (or 82%) were caught in the winter (July), whereas 68%, of all animals were caught in July. Coupled with the observation (see below) that courting behaviour took place in February, the high prepoderance of small individuals in July led us to believe that such animals were hatched between February and July.

Adult males were sexed easily by virtue of their striking black throat colouration (Plate 1). It was not straightforward to sex adult females, subadult males, juveniles and hatchlings. We sexed them on the basis of a spectrum of external features (scale characters, vent shape, genital swelling) which one of us (RDP) identified and confirmed by inspection of internal organs of animals which died accidently in the field, and preserved specimens from the State Museum, Windhoek. Although we attempted to catch randomly, there was a preponderance of females caught (1.4 F : 1 M), which was statistically significant (X^2 = 4.74, n = 190, p < 0.05). There was no significant difference between the masses of males and females of the same snout-vent length.

Observations in the laboratory and the remains of eggs found in the field indicate that *A. skoogi* is oviparous. From an examination of 13 gravid females from the field, clutch size appeared to be two. In the laboratory, however, the clutch size was as large as 4 (range 2 - 4, n = 5); although two females with large clutches died during attempts at oviposition. Average size for a clutch of 4 eggs retrieved from one of these females was 22.9 ± 1.5 mm length, 12.0 ± 0.9 mm width, 1.96 ± 0.26 g (female SVL = 140.0 mm; mass = 62.5 g). Incubation period and size at hatching are unknown. The smallest hatchling that we have caught in the field was 2.5 g, 49.0 mm SVL, 101.0 mm total length; it still had an obvious egg scar indicating fairly recent hatching.

We estimated growth rate in *A. skoogi* on the basis of SVL measurements of 22 lizards given permanent marks and then recaptured at least once at periods of from 39 to 339 days (Table 2). Maximum growth rates

TABLE 2: Growth rates of *A. skoogi* in three snout-vent length (SVL) categories, over a period of 39 - 339 days.

Category	SVL	n	Growth rate (mm/day)
Hatchlings	< 70	5	0.052 - 0.121
Juveniles	70-115	3	0.031 - 0.084
Adults	> 115	14	0 - 0.061

were attained in small individuals. A plot of the data shows a growth rate generally decreasing with increasing SVL (Fig. 3).

Like many cordylids, *A. skoogi* has a robust tail. A few individuals lost their tails when we handled them, but

we observed only one tail break in a natural incident, namely a fight between two males. Of subsample of 175 lizards we examined carefully for evidence of tail breakage, 43 animals (24.6%) showed either regrowth or evidence of recent breakage (mean length of regenerated portion = 30.6 mm, SD = 19.4, n = 30). The female lizard in Plate 1 shows typical tail regrowth.

As Hamilton and Coetzee (1969) noted, *A. skoogi* is a wary animal. Except during the breeding season in February, their behaviour was patently guarded whenever an observer was visible to them, even 100 m or more away. To record the natural behaviour of the lizards, therefore, we set up semi-permanent hides near the slipfaces and made sure we entered the hides early in the morning, before the animals were active. Observations then were made using binoculars, with observers working usually in pairs.

We established from field observations that not all animals emerged from the sand every day. To estimate the proportion of animals emerging in any activity period, we colour-coded a subsample of 56 animals (19
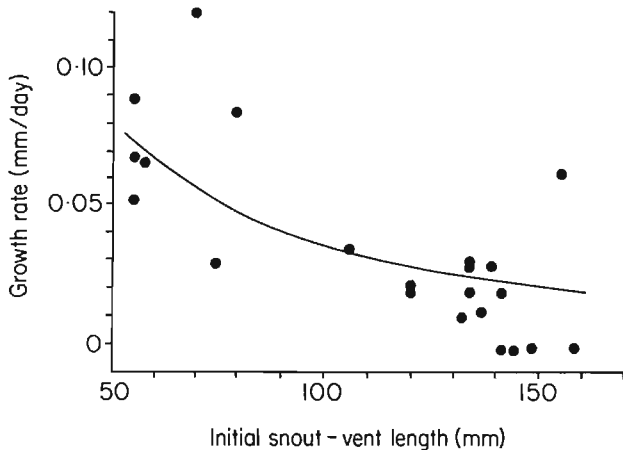

FIGURE 3: Growth rates (change of SVL per day) of 22 *Angolosaurus skoogi* recaptured over periods of 39-339 days: power curve fit (r^2 = 0.5031).

hatchlings, 28 juveniles, 9 adults) in July using water-soluble paint, and released all these animals on the slipface near our hides. Some animals originated from this slipface but most were captured on nearby slipfaces. We released the animals shortly before or after an activity period, and all animals buried immediately.

Eleven of the marked animals (20%) did not re-emerge during our study period of seven days. Table 3 shows the number of resightings as a percentage of possible resightings. About half the marked animals emerged in the first activity period available and about one-third of the lizards present emerged each day for the first four days of observation. The proprotion declined rapidly as lizards left our slipface.

We conclude tentatively that about one-third of the *A. skoogi* on a slipface will emerge in any one day. This

TABLE 3: Resightings of marked animals as a percentage of possible resightings. Day 1 refers to the first activity period available after release. Residents are lizards which remained on the slipface for at least two days.

Day	1	2	3	4	5	6	7
Resightings (%) (total)	49	25	35	22	6	6	4
Resightings (%) (residents)	40	29	40	31	14	14	7

value is the same as that obtained by Medica et al. (1971) for a population of *Cnemidophorus tigris*, although our calculations were confounded by emigration from the slipface. We do not know whether the emigration was a normal phenomenon, or whether it was induced because we introduced intruders. A few of our marked animals were treated aggressively by unmarked lizards (presumably long-term residents). Nor do we know whether the proportion of animals emerging varies with season.

We attempted a crude estimate of the population density of *A. skoogi* in our study area (in December 1983), in the following way. The maximum number of lizards sighted at one time on a large slipface from which no animals had been captured, and to which no intruders had been introduced, was multiplied by three to take account of submerged animals. We measured the length of this slipface, and determined the total length of available slipfaces in the study area from aerial photographs. We then calculated the total number of lizards in the area by simple proportion. Our conservative estimate was 3000 animals/km². This rough estimate takes no account of variations between slipfaces or seasons.

4 FEEDING

We have analysed the diet of *A. skoogi* at the Unjab study site in detail using the technique of faecal pellet (scat) analysis, and reported the results elsewhere (Pietruszka *et al.* 1986). In summary, as Steyn (1963) first reported, *A. skoogi* is a predominantly herbivorous lizard. Herbivory is unusual in a lizard as small as *A. skoogi* (Pough 1973). The staple food at the study site is nara, the remnants of which constituted 56% of the organic material in the scats. *A. skoogi* also takes animal food opportunistically; animal remnants constituted 19% of the organic material in the scats. The animal component of the diet varied with season, and consisted mainly of the diurnal tenebrionid beetles, which were common in the study area.

Here we report on some additional aspects of feeding by *A. skoogi* which were revealed by observation and scat analysis. The most conspicuous feeding behaviour was the grazing of nara on or near the slipface. Lizards of all size categories would travel to the nearest available nara plant throughout the activity period. The lizards preferred nara flowers, when avail-

able, and growing shoots, but also consumed the tough, sharp, nara thorns, as the scat analysis confirmed. Few, if any, other vertebrates are known to eat nara thorns. In order to reach preferred parts of the plant, the lizards would climb clumsily up the network of nara stems. Neither their feet nor tail are prehensile, and lizards frequently fell out of the nara from heights up to 400 mm without apparent harm. Another method of grazing nara was to place the forelegs on a stem with the hindlegs on the sand, and sometimes lizards would rear on the hindlegs without supporting the forelegs. Small individuals often twisted their entire bodies to break off pieces of nara.

We also observed all but the smallest lizards taking vegetation from the interdune plains. They plucked at flowers and leaves of the succulent *Sesuvium sesuvioides* and were seen to swallow the flowers. Other vegetation they were seen to take from the plains was *Suaeda plumosa* and *Stipagrostis hermannii*. Juveniles and hatchlings frequently foraged at the base of the slipface, apparently feeding on windblown seeds and detritus: seed remnants were evident in the scats. Adults were observed less frequently at the base of the slipface.

If body size is a factor determining diet choice between different lizard species (Pough 1973), then, within a species known to be omnivorous, one might expect an ontogenetic shift in diet choice. We were unable to detect any relationship between the size of the faecal pellet (and presumably age of the lizard) and the proportion of animal matter in the diet of *A. skoogi*; the utilization of animal prey, at least, may be highly opportunistic and body size considerations may be of only secondary importance. An apparent shift away

from seeds in the diet as the animals aged (Pietruszka et al. 1986), on the other hand, probably means that shifts in foraging location can and do influence diet. Foraging of seeds, rather than other plant material, by juveniles may well facilitate growth; seeds have an energy content almost as high as that of animal tissue (Pough 1973).

Although beetles were abundant on the slipface, and beetle fragments appeared in the scats, we have only rarely seen an *A. skoogi* lizard actually eat a beetle. The lizards will eat moths and mealworm larvae *(Tenebrio molitor)* voraciously in the laboratory, particularly if the larvae wriggle. On the slipface, lizards often were harassed by tenebrionid beetle adults, particularly *Onymacris bicolor*, and appeared to be bitten by the beetles occasionally; the lizards always conceded.

We have analysed the composition of some of the observed and potential food sources of *A. skoogi*, and the results are shown in Tables 4, 5 and 6. Plant samples were clipped, placed immediately in sealed plastic bags, and refrigerated until analysed. Only green, new shoots, leaves and thorns were collected (because that is what we observed the lizards to take), with the exception of the *Merremia*, where all available plants were partially withered. Beetles were collected from the same area.

Water content was determined as the mass loss following drying at 80° for four days. Concentrations of selected electrolytes were measured by atomic absorption spectroscopy. Osmolarity of nara sap was measured with a Wescor osmometer. Protein content was

TABLE 4: Water and electrolyte composition (mean ± SD) of selected food items available to *A. skoogi*, expressed as proprotion of wet mass.

Plant	n	Water content (%)	Electrolyte concentration (mmol/kg)					K:Na ratio
			Na	K	Ca	Mg	PO⁴	
Acanthosicyos horrida	9	83.6	26	121	31	34	18	4.7
		±0.6	±21	±64	±13	±15	±10	
Merremia guerichii	4	83.2	200	1700	720	620	80	8.5
		±2.5	±180	±890	±490	±370	±50	
Sesuvium sesuvioides	10	91.7	790	57	36	37	8	0.072
		±1.3	±310	±25	±19	±20	±4	
Stipagrostis hermannii	10	49.3	38	17	57	23	10	0.45
		±6.6	±23	±7	±15	±6	±3	
Stipagrostis spp.	9	49.3	46	66	12	31	25	1.4
		±4.2	±26	±86	±7	±12	±11	
Zygophyllum simplex	10	92.0	300	80	450	50	10	0.27
		±2.0	±190	±40	±190	±30	±6	
Tenebrionid beetles								
Cauricara brunnipes	5	66.8	-	36	11	12	12	
		±1.3		±24	±6	±2	±6	
Onymacris bicolor	10	65.2	-	21	9	15	18	-
		±5.6		±10	±2	±2	±6	
Onymacris unguicularis	10	68.0	-	24	6	11	18	-
		±3.1		±8	±1	±3	±3	

determined for three of the plant species using the Kjeldahl technique.

With regard to water content (Table 4) the plants fell into three categories: the succulents *Zygophyllum* and *Sesuvium* consisted of more than 90% water by mass, nara and *Merremia* about 83%, and the *Stipagrostis* grasses about 50%. Thus the lizards had ready access to plants with high water content, even in the hyper-arid dune environment. Also, two-thirds of the mass of the beetles in the diet of *A. skoogi* consisted of water.

The beetles had a uniformly low concentration of the electrolytes we measured, but the plants varied greatly in electrolyte concentration (Table 4). *Merremia* was remarkably rich in electrolytes, especially potassium (1700 mmol/kg wet mass), calcium (720 mmol/kg) and magnesium (620 mmol/kg), and any consumption of *Merremia* would impose a serious electrolyte load. At the other end of the spectrum, the *Stipagrostis* and the preferred nara had low electrolyte concentrations. *Sesuvium* was characterised by a very high sodium concentration (790 mmol/kg) and *Zygophyllum* by high sodium (300 mmol/kg) and calcium (450 mmol/kg). None of the plant species aproached the 20 : 1 potassium to sodium ratio found by Nagy (1972) and Nagy and Shoemaker (1975) in North American desert plants eaten by herbivorous lizards. Indeed, half the species imposed a greater sodium load then potassium load on *A. skoogi*.

Table 5 shows the protein content of three of the plant species, determined from samples taken in January. The values are at the low end of the normal range for mesic leafy vegetable plants, and much lower (up to ten-fold) than the protein content of animal tissue or seeds (Diem 1962). The opportunistic use of animal prey, and the foraging of seeds by young animals, therefore enhances not only energy uptake but also protein uptake.

TABLE 5: Protein content of three plant species eaten by *A. skoogi* (mean ± SD, n - 3 for each species)

| | Protein content (%) | |
	of wet mass	of dry mass
Acanthosicyos horrida	2.38	14.54
	±0.03	±0.17
Merremia guerichii	2.30	13.72
	±0.05	±0.31
Sesuvium sesuvioides	0.62	7.46
	±0.02	±0.20

A. skoogi generally does not have access to free water. However, the lizard excretes copious amounts of fluid urine, a phenomenon unusual in a desert reptile; as we have said, *A. skoogi* has peculiar access to water in the plants it eats. Nevertheless, the reptilian kidney generally is unable to cope adequately with elevations in plasma electrolyte concentrations, and, as Table 6 shows, all the plant species we investigated had electro-

lyte concentrations which indeed would have elevated plasma electrolyte concentration. Herbivorous lizard species often employ a nasal salt gland to dissipate excess electrolytes (Bartholomew 1977, p. 343-4), but we could find no evidence for such a gland in the external morphology of *A. skoogi*, nor did we observe the formation of electrolyte crusts at potential gland sites. A more thorough search for a cryptic gland, and a systematic investigation of kidney function in *A. skoogi*, clearly are warranted.

TABLE 6: Estimated electrolyte-dependent osmolarity of plant species eaten by *A. skoogi*.

Species	Osmolarity (mmol/l)
Acanthosicyos horrida	510*
Merremia guerichii	5630
Sesuvium sesuvioides	2010
Stipagrostis hermannii	550
Stipagrostis spp.	630
Zygophyllum simplex	1910

Note: calculated assuming electrolyte neutrality and complete dissociation, as ([Na] + [K] + [Ca] + [Mg]) x 2 x (% water)/100

*Measured osmolarity of sap: 563 ± 6 mmol/kg, n = 10.

5 PREDATION

The dominant predators on *A. skoogi* appear to be birds. Lizards buried themselves immediately if a bird was visible, even several hundred metres away. The most frequent avian visitors to the dunes were crows, *Corvus albus* and *C. capensis*. Crows sometimes patrolled the dune tops, approaching from the windward side, out of sight of the slipface. We saw crows land on the slipface at sites where lizards had buried and attempt to excavate the lizard. The only other bird we saw attempt to catch a lizard, by swooping down on the slipface, was the greater Kestrel, *Falco rupicoloides*. Other observers have seen the pale chanting goshawk, *Melierax canorus*, and the black harrier, *Circus maurus*, capture *A. skoogi* near our study site (S. Braine, personal communication).

Although jackals visited the study area at night, and seem a likely potential predator (Hamilton and Coetzee 1969), we saw no evidence of any attempts by jackals to excavate the lizards.

We saw one juvenile *A. skoogi* captured near a nara by the sand snake, *Psammophis leightoni*. Peringuey's adder, *Bitis peringueyi*, which preys upon *Aporosaura anchietae* in the dunes of the southern Namib (Robinson and Hughes 1978), and *Bitis caudalis* occur in the area, and ought to be able to capture *A. skoogi* hatchlings.

6 GENERAL SURFACE BEHAVIOUR

A. skoogi is a chthonic animal: all individuals spend most of their existence buried in the superficial layers

of the dune sand. They do not employ burrows, but swim through the sand in a way characteristic of Namib fauna (Coineau et al. 1982, Seely 1983, 1984). Undisturbed individuals which buried of their own accord usually were found under the position of submergence indicating that they did not usually undertake appreciable lateral movement in the sand, an observation we confirmed using individuals fitted with radiotelemetry transmitters. When we excavated buried lizards we generally found them to be within 300 mm of the surface. However, we did fail to retrieve some individuals fitted with radiotelemeters at the greatest depth we could excavate in the soft, sloping sand, about 1 m, although we were not certain that they were buried at the depth. The failure to recover the lizards also may indicate extensive lateral movement through the sand on occasion. In particular, lizards that dived in response to predators (including humans) sometimes moved laterally or upwards, for at least 0.5 m, beneath the sand. In the laboratory also, A. skoogi moved some distance under ground.

Burying was accomplished through a horizontal sinusoidal motion, in which the lizards twisted their bodies into an S-shape by alternating contralateral curving of the head and thorax as one unit and the tail as another, around a vertical axis approximately at the border of thorax and abdomen (see Steyn 1963). The writhe usually was preceded by a short sprint of a few paces, and downward flexion of the neck to submerge the head below the sand surface. The writhing motion, aided by the forward momentum, was sufficient to cause immersion in the quasi-fluid sand without excavation with the front limbs. The great strength of the abdominal muscles used in this writhing could be felt whenever the animals were in hand. We were unable to confirm the observation of Hamilton and Coetzee (1969) that there is a preferred 'burrowing zone' near the top of the slipface: from the hide we observed undisturbed animals burying at all heights on the slipface, and sometimes even in the firmer sand on the windward side of the dune.

We observed four patterns of burying behaviour. When the lizards were agitated they buried using a 'plunge', a rapid energetic writhe almost too fast for the body curvature to be seen. The lizards disappeared entirely within 1 - 2 seconds. The second type 'normal' burying, such as that which usually terminated a day's activity period, was much more leisurely: the lizards executed two or three successive writhes to immerse. We described the third form of burying as 'slow burying'. Here the lizard would tap the ground with its head, or immerse its snout below the surface as if testing the sand, before entering the writhing behaviour. The fourth behaviour we called 'two-part burying', in which the animal immersed its entire head below the sand for several seconds or minutes before writhing. Other than the 'plunge', which was clearly an escape, we could not attribute any specific function to the

burying behaviours. If animals buried by any movement other than the 'plunge', they did not emerge at least until the next activity period. The 'corkscrew' motion mentioned by Hamilton and Coetzee (1969) never was observed.

The surface behaviour of A. skoogi depended markedly on season. In February, that is in late summer, breeding behaviour dominated social interactions, with frequent aggressive encounters between males, sometimes culminating in fights during which physical damage occurred. At other times of the year, notably in July, there was no apparent breeding behaviour. In July the lizards on our observation dune appeared to constitute a socially unstructured tolerant society. There was no evidence of territoriality: up to five adult males were present simultaneously on the slipface without being confined to one area and without interacting aggressively. Lizards of all sizes appeared to avoid physical contact with each other. There were very few encounters and individuals only occasionally approached within 0.2 m or less. An exception occurred in nara plants, where several grazing lizards could be in close proximity to each other. Sometimes lizards in transit along the slipface would make detours to avoid encounters but there was no evidence of any rank hierarchy based on size or sex, except near concentrated food sources.

The absence of the over-riding influence of breeding behaviour in July allowed us to analyse systematically the occupancy of various dune regions (Robinson and
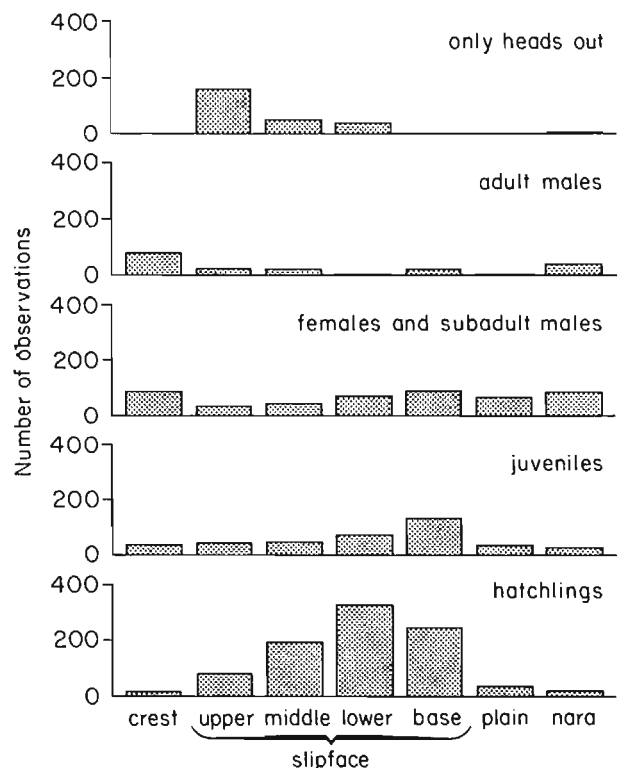
FIGURE 4: Total sightings of Angolosaurus skoogi from five minute scans over six days in July, partitioned into different age groups (and heads only exposed) occupying seven locations on a single dune slipface and its surroundings.

Seely 1980, Seely et al. ms) by lizards of various sizes. For six days we scanned all surface activity at five minute interval on a slipface area of approximately 2000 m². We found that 37% of a total of 2208 sightings were of hatchlings, 18% juveniles, 22% females and immature males, 9% mature males, 12% exposed heads only; the age of 2% of the lizards could not be distinguished. Of these lizard sightings 12% were observed on the crest area, 16% on the upper third of the slipface, 17% on the middle third, 24% on the lower third, 17% at the avalanche base, 9% within the nara bush on the slipface and 6% on the plain away from the dune.

To examine possible differential occupation of different parts of the dune, we combined all sightings of lizards from our scans during the course of the six days. The pattern of use of the different regions of the dune by the different age groups of lizards is shown in Fig. 4. We also wished to examine the effect of time of day and of temperature and wind speed on the differential occupation of the various regions of the dune. By examining the proportion of lizard sightings in each region during each hour of observation, we detected
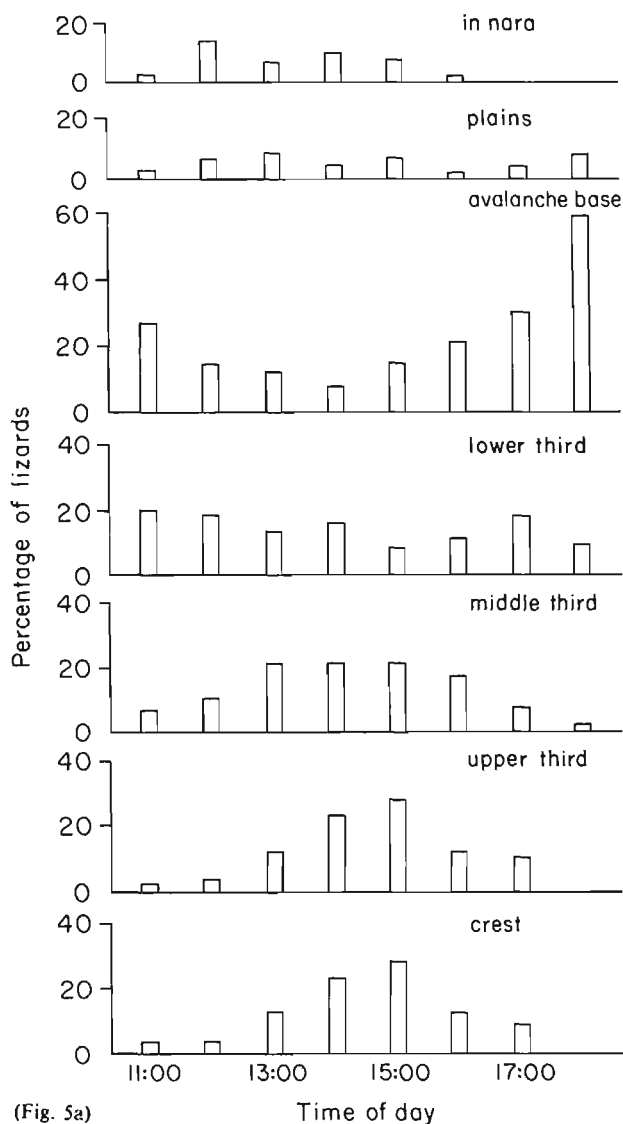
an apparent preference for the lower regions of the slipface, the avalanche base and the lower third of the slipface, during the ends of the day. During the middle of the day the preference was for the higher regions of the dune, the upper third of the slipface and the crest area (Fig. 5a). This observation suggested that the higher parts of the dune were preferred during the presumed warmer parts of the day whereas the lower parts were occupied when conditions were cooler.

Contrary to expectations, there was only a weak association between location and temperature (Fig. 5b). At the lowest globe temperatures at which lizards were

(Fig. 5a) Time of day

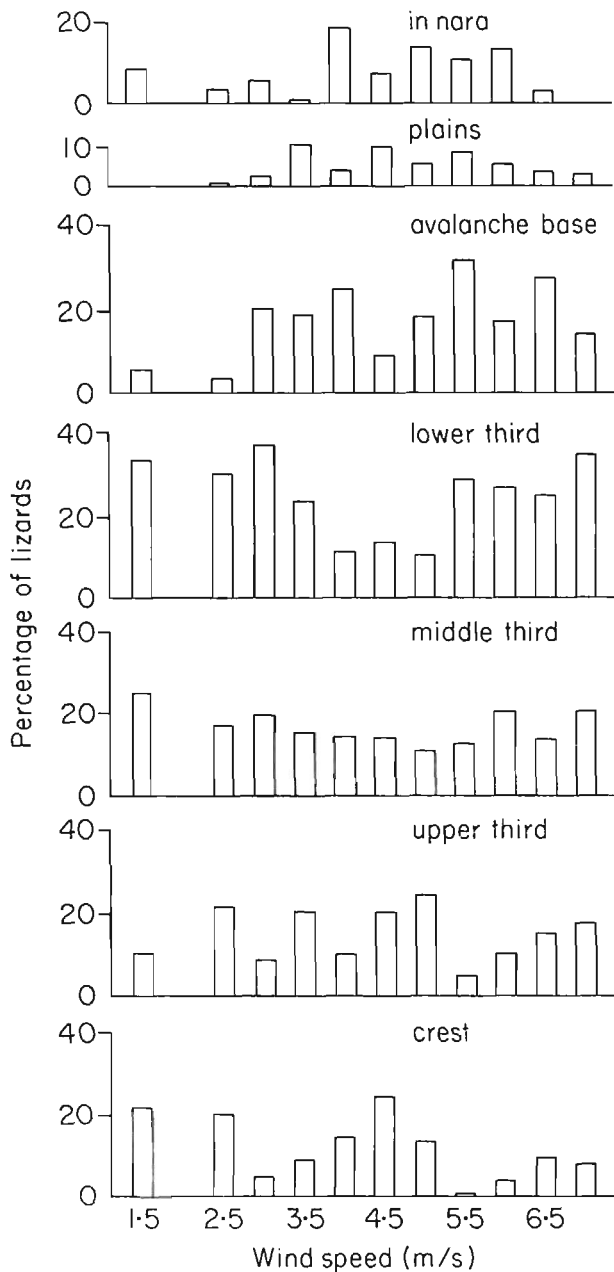(Fig. 5b) Globe temperature (°C)
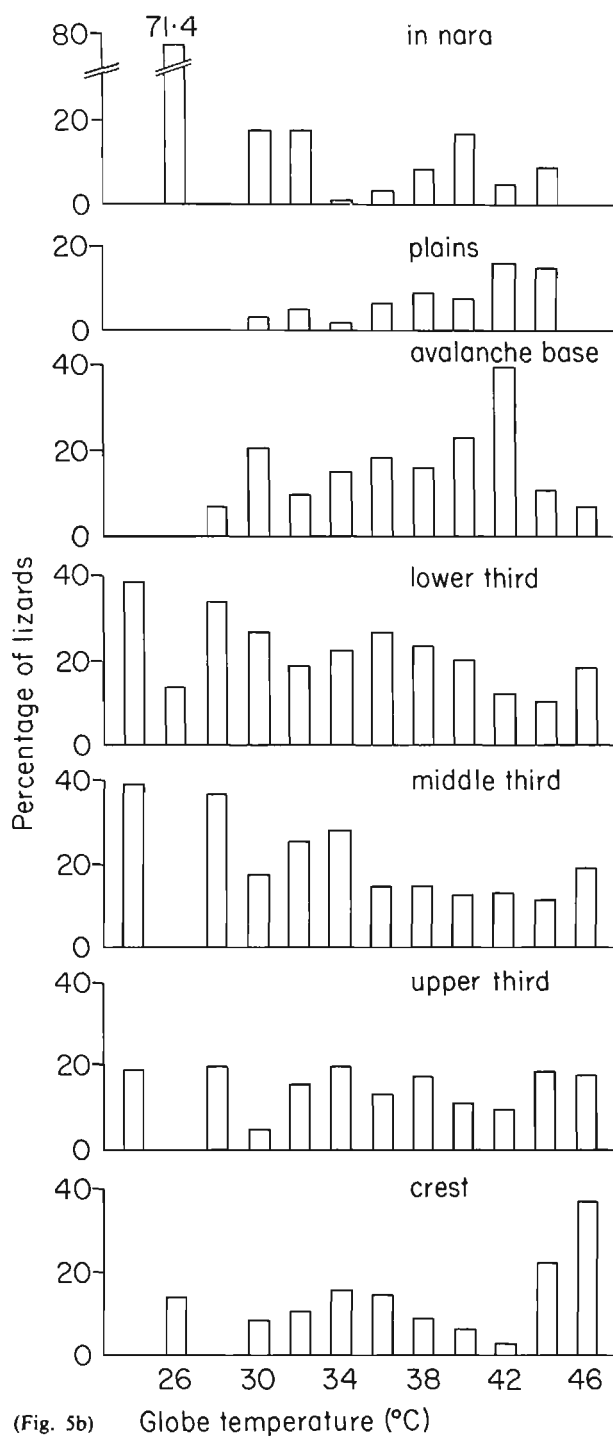
FIGURE 5: Total sightings of *Angolosaurus skoogi* from five minute scans over six days in July partitioned into number occupying seven localities on a single dune slipface and its surroundings. Number of sightings during any one hour (Fig. 5a), at intervals of temperature (2°C) (Fig. 5b), and at intervals of wind speed (0.5 m/sec) (Fig. 5c) are plotted as a percentage of total sightings in each category.

active on the sand surface, 22°-24°C, all sightings were confined to the slipface, where the lizards presumably were somewhat sheltered from wind while fully exposed to solar radiation. At the highest globe temperatures at which lizards were active on the sand surface, 44°-46°C, a greater proportion of sightings was of lizards on the crest, although the slipface also was well represented. In addition to the crest, the upper regions of the slipface should be windier and therefore cooler, but there was no preferential occupation of the upper regions during higher temperatures. We also examined hourly mean values of lizard sightings with respect to

wind speed (Fig. 5c). The patterns of response were even more difficult to interpret, but we conclude that there is no preferential occupation of various parts of the dune in response to varying wind velocity. There is therefore no simple microclimatic explanation for the preferential occupation of different slipface regions at different times of the day.

7. LOCOMOTION

Individual lizards moved around the dunes in a number of different patterns. We categorized locomotion into four modes: walking, walking accompanied by an occasional 'tap' of the head on the sand, walking while rhythmically 'bobbing' the head against the sand surface, and running or sprinting. Travel between two points, for example the point of emergence and a nara plant, usually was accomplished by short runs or walks of about 1 m each, interrupted by interludes in fixed stationary postures. Occasionally some individuals, particularly large adults, would sprint to the dune top, sometimes plunging briefly along the way. Another movement pattern consisted of short excursions in random directions accompanied by tapping of the snout on the sand surface. This behaviour seemed exploratory. Sometimes, lizards would make short random movements, or stand still, and bob their heads up and down clear of the surface in a regular rhythm. This movement was particularly prevalent among smaller individuals in July and also may have been exploratory in nature. In February, however, larger individuals also engaged in this movement. Similar behaviour also has been observed in other lizard species and sometimes has been interpreted as a means of gaining depth perception (Mayhew 1968).

General movement of the lizards around the dune was at a much lower speed than the animals could attain if attacked or chased. When chased, large males could sprint for 50 - 100 m at more than 10 km/hr, after which they became completely fatigued, presumably because, as for other lizards (Bennett 1983), intensive exercise depends predominantly on anaerobic metabolism which is self-limiting.

During two days in July we analysed in detail the movements of single *Angolosaurus skoogi* that were continuously on the surface for periods of at least five minutes. The duration of a mode of locomotion or a posture within the five minute period, the age of the individual and its location on a dune were noted for eight adult lizards, nine juveniles and six hatchlings. Figure 6 indicates the relationship between mode of locomotion used by *A. skoogi* and position on a dune. Identification of a particular mode of locomotion sometimes was difficult, for example, when several of our designated categories of motion were used in rapid succession.
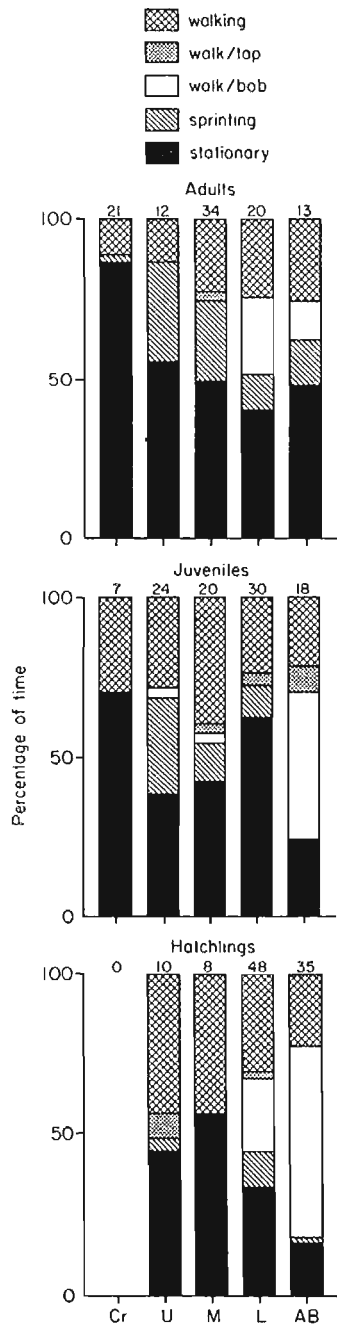
walking
walk/tap
walk/bob
sprinting
stationary

FIGURE 6: Percentage of time the lizards used each of four types of locomotion (see text for explanation) and stationary while in five locations on a slipface (Cr - crest; U, M and L - upper, middle and lower third of slipface; AB - avalanche base).
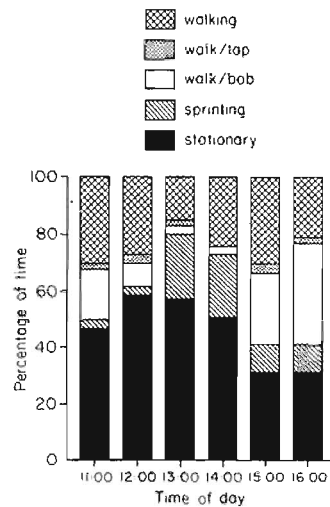

FIGURE 7: Percentage of time 23 lizards, active for at least five consecutive minutes, spent using the four types of locomotion and stationary, during different times of the day.
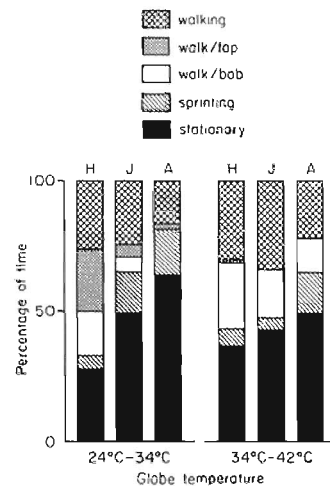

FIGURE 8: Percentage of time 23 lizards, active for at least five consecutive minutes, spent using the four types of locomotion, and stationary, as a function of globe temperature.

The lizards on the surface were sedentary almost half the time except during the late afternoon, when they were more mobile (Fig. 7). At that time walking, especially with 'bobbing', was used most often. Some increased activity also occurred at the beginning of their day. Such movement as did occur in the middle of the day mainly was in the form of sprinting.

Hatchling, juvenile, and adult lizards used the various modes of locomotion differently. We examined their locomotion at a higher and a lower range of globe temperatures (Fig. 8). Overall, adult lizards were the

most sedentary, moving only 43% of the time that they were on the surface. However, when they did move, they engaged in more sprinting, 42% of the time that they were moving across the sand. Juveniles were mobile 53% and hatchlings 68% of the time that they were observed. Walking and rhythmic bobbing was more important for all three size groups at the higher temperatures, whilst there was a higher percentage of sprinting and tapping in the lower temperature range. The fact that sprinting occurred more frequently at lower temperatures does not support Hamilton and Coetzee's (1969) view that it is a thermoregulatory behaviour aimed at achieving a position where body cooling is enhanced.

8 THERMOREGULATION

Angolosaurus skoogi is strictly diurnal in its surface activity. It is also thermophilic, as Hamilton and Coet-

zee (1969) observed, rather similar to the smaller (35g) North American desert iguana *Dipsosaurus dorsalis* (Pough 1973), and various other herbivorous lizards (Dawson 1965). The surface activity period encompassed the hottest part of the day. Sometimes the lizard population on the slipface would exhibit 6 - 8 hours of uninterrupted activity (though single animals never were active for that long), but on particularly hot days surface activity was bimodal: all lizards would bury for a time when ambient temperatures were at their highest. We have extended the earlier study of Hamilton and Coetzee (1969) on thermoregulation in *A. skoogi* in two ways. First, we have related surface behaviour of a natural population on the slipface to prevailing microclimatic conditions (Seely et al. ms). Secondly, we have monitored the body temperatures of individual lizards in a thermal gradient chamber in the laboratory, using indwelling thermocouple thermometers. Here we summarize our main conclusions.

As an inhabitant of dune slipfaces, *A. skoogi* is exposed to surface temperatures that frequently exceed 60°C. Its comparatively large thermal inertia relative to the only other slipface-dwelling lizard in the region, *Aporosaura anchietae* of 4 - 9 g body mass, may be one of the factors which allows *A. skoogi*, but not *A. anchietae*, to maintain surface activity at such temperatures. The relative advantages and disadvantages of being active at high ambient temperatures are similar to those proposed for *Dipsosaurus dorsalis* but the parallel is by no means complete. Whereas *Dipsosaurus dorsalis* (Pough 1973) and other herbivorous lizards (Dawson 1965) may escape most or all of their predators through their thermophilic activity, the same is not true for *A. skoogi*, as its principal predators, both avian and reptilian, are active at the same temperatures. Also, the activity periods of the insect prey which could be taken by *A. skoogi* are not identical to those of the lizard's because of differences in the thermal constraints (Robinson and Seely 1980).

As a chthonic animal, *A. skoogi* has the thermal microclimate of the sand surface and of the sand itself to exploit. The surface microclimate is characterized by cool to moderate air temperatures, variable humidity depending on the presence or absence of fog, variable winds reaching speeds capable of moving sand, and intense solar radiaton at all times of the year. Figure 9 shows the microclimatic conditions prevailing on randomly chosen days in July and February. Air temperature is not uniformly higher in summer than in winter: rather air temperature is determined primarily by wind direction irrespective of season. There is a seasonal variation in subsurface temperature, which Fig. 9 shows, with the temperature 300 mm below the surface about 10°C higher in summer than in winter. However, irrespective of season, a benign thermal environment exists below the sand surface, which can be exploited by animals capable of diving to about 300

mm, well within the capacity of the *A. skoogi*. *A. skoogi* indeed spends most of its existence in this environment. In contrast to the equable temperature at depth, sand surface temperature varied over a 40°C range on both days.

As we have said, individual lizards do not necessarily emerge from the sand every day. When they did emerge, it was at a time of day (usually between 10.00 and 13.00) apparently determined predominantly by an inherent circadian rhythm. Animals captured in the field and kept in the laboratory in a constant-temperature environment with uniform 24 hour lighting continued to bury during the night and to emerge at about the same time as they had emerged in the field. The exact timing of the emergence and reburying was modulated by the prevailing microclimatic conditions, and animals of different size classes behaved in different ways: adults were more thermophilic than hatchlings and juveniles (Seely et al. ms). Even the adults would bury in the middle of the day, however, if the temperatures rose sufficiently.

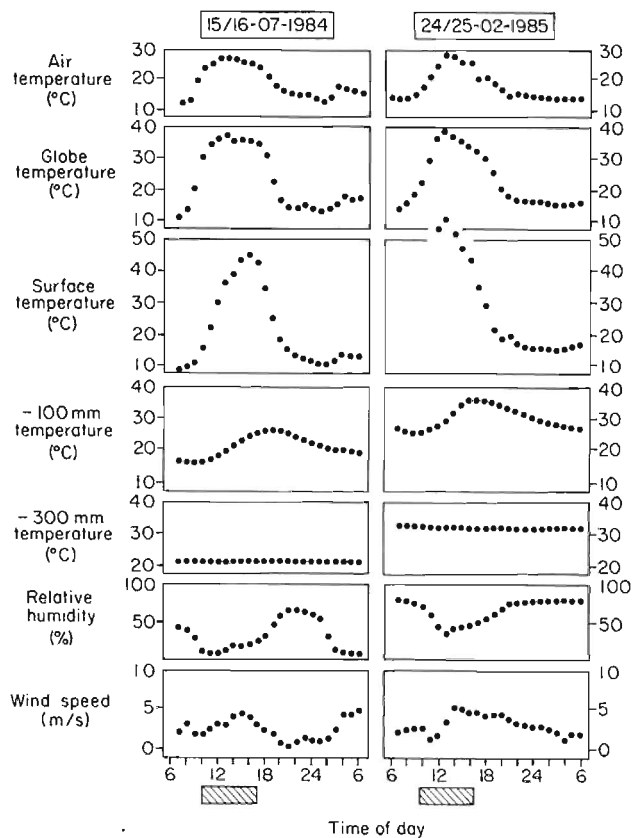In a thermal gradient chamber in the laboratory, a sample of seven lizards of various sizes (SVL 61 - 138

FIGURE 9: Microclimatic conditions on randomly chosen days in winter (July) and summer (February). Striped bars below the time of day show period for which at least two *Angolosaurus skoogi* were present on the surface. Air temperature was measured by sling psychrometer, globe temperature by thermistor in 150 mm diameter hollow black globe on dune top, surface temperature by white thermistor in most superficial sand, subsurface temepratures (-100 mm and -300 mm) by thermocouple, relative humidity by lithium chloride sensor, wind speed by cup anemometer.

mm, mass 5 - 84 g) had a selected body temperature, measured by an indwelling thermocouple in the colon, of 36.8°C (SE 0.4°C). This mean value is below the range of 38° - 42°C proposed by Hamilton and Coetzee (1969), but is consonant with the values quoted by Avery (1979) for the selected body temperature (as distinct from the maximum tolerated body temperature) for the most thermophilic of lizards. The selected body temperature of another southern African cordylid, *Cordylus cataphractus,* measured using a similar technique, was 32° - 33°C (Laburn *et al.* 1981); *C. cataphractus* is rupicolus and does not occur in the Namib dunes.

Hamilton and Coetzee (1969), in support of their proposed selected body temperature of 38 - 42°C for *A. skoogi,* reported that body temperatures of 40°C or more had been measured in other thermophilic lizards in the field. As Fig 10 shows, such temperatures would place a heavy additional energy demand on *A. skoogi:* metabolic rate almost doubled between the preferred body temperature, 36.8°C, and 40°C. We doubt whether any obvious benefit, for example enhanced mobility at the higher body temperature, would compensate completely for the increased energy costs, but one would expect mobility to be improved somewhat. Whereas the rate of formation of lactic acid, during the anaerobic metabolism important for all reptiles, is independent of body temperature, its rate of removal after activity increases directly with body temperature (Bartholomew 1977, p387). Thus recovery from debilitation and exhaustion following activity would be more rapid at higher body temperatures. Improvement of fecundity at the higher body temperature, if it indeed occurs, may also provide benefits (Hamilton 1973).

Angolosaurus skoogi can reach its selected body temperature during the warm part of the day by positioning itself at the appropriate depth in the surface layers of the sand (see Fig. 9). Thermoregulation therefore is not the primary reason for emergence. Rather, other behaviours, like feeding and reproductive behaviours, require the lizards to be on the surface, and we believe they will remain on the surface as long as thermal conditions allow execution of these activities. A similar situation prevails for Namib dune beetles (Seely and Mitchell 1987). Thus we expect that surface thermoregulatory behaviour in *A. skoogi* will be directed towards achieving acceptable, rather than preferred, body temperatures.

In general, the surface thermoregulatory behaviour we observed conformed to that described by Hamilton and Coetzee (1969). The animals used postural variations which could alter rate of heat exchange with the environment. Some postures could enhance heat gain, as in the case of lying flat on the sand surface. Others, such as raising of the hind legs, presumably enhanced heat loss.

In July, we never saw lizards dash for the dune top, a behaviour we saw frequently in February. Hamilton and Coetzee (1969) attributed this behaviour to thermoregulation. We question whether it is only thermoregulatory, because some of our July observation days, when the east wind blew, were as hot or hotter than any of the summer days. Also, as we have said, sprinting generally took place in the cooler parts of the day. We suggest that the dash for the dune top, and the subsequent patrolling, are primarily associated with social behaviour during the breeding season rather than thermoregulation.

In all seasons we observed the 'head out' behaviour which Hamilton and Coetzee (1969) attributed to sub-surface basking. Some adults and large juveniles (but apparently not hatchlings) preceded their surface activity periods by a period of up to 30 min during which they positioned themselves just below the sand surface, with their heads, and sometimes shoulders, protruding from the sand. We do not know what angles their bodies adopted below the surface. In this position, the lizards could take advantage of the heat in the surface layers of the sand (see Fig. 9) while being less visible to predators and other lizards, until their temperatures had risen sufficiently to allow full mobility on the surface. Other lizards, and beetles, frequently would investigate lizards in the 'head out' position, often resulting in the 'head out' lizard reburying temporarily. Because of the effects of solar radiation, we assume that head temperature of lizards in the 'head out' position would be higher than body temperature, as has been noted for several desert species (refs. in Mayhew 1968, p 240-1), a phenomenon which warrants further examination.

9 METABOLIC RATE

We measured the resting aerobic metabolic rate of a small subsample of *Angolosaurus skoogi* in the laboratory. The animals were maintained in dune sand in a terrarium, with a permanent heat source. They were fed *ad libitum* on a diet of lettuce and mealworm larvae, and were given access to water. *A. skoogi* adapted well to captivity, and we have kept individuals for over a year in similar conditions, in good health as evidenced by body condition and the continued production of eggs by mature females.

Lizards used for metabolic rate determination were juveniles (mass = 15.6 g, SE = 5.2, n = 5). A single animal was placed in a metabolic chamber, in a well-ventilated but closed system, the volume of which was measured by nitrogen dilution. The partial pressure of oxygen was measured by an electrochemical sensor (Applied Electrochemical Industries) and the partial pressure of carbon dioxide by infrared analyser (Morgan); carbon dioxide concerntration did not exceed 1%. The lizard remained in the system between 1.5 hrs
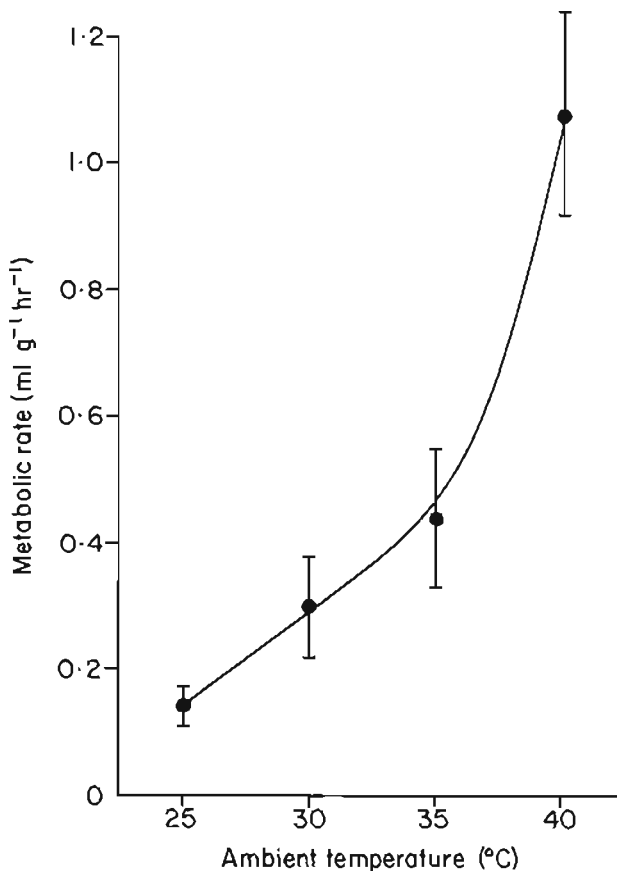
FIGURE 10: Aerobic metabolic rate (ml O_2 g^{-1}. h^{-1} at STP) for a subsample of 5 juvenile lizards (mass 15.6 ± 5.2 g) determined at different ambient tempertures.

and 24 hours, depending on size of the lizard and the ambient temperature. The measurements were conducted at ambient temperatures between 25°C and 40°C.

Figure 10 shows the mean metabolic rate of the animals as a function of ambient temperature. Metabolic rate varied exponentially with ambient temperature, increasing significantly at temperatures greater than 35°C (1 way ANOVA with multiple comparisons, MSD > 5.9, p < 0.001). At 30° there was a statistically significant variation in metabolic rate between individuals (1 way ANOVA, F-test ratio 2671.9, p < 0.001), presumably as a result of differences in size. The mean metabolic rate at 30°C (0.30 ± SE = 0.08 ml O^2 g^{-1} hr^{-1}) was not significantly different (t_1 test$_1$, t = 0.1, p > 0.05) from the value of 0.30 ± SE = 0.04 ml O^2 g^{-1}O hr^{-1} calculated from the Bartholomew and Tucker's (1964) metabolic rate prediction formula: ml O^2 g^{-1} hr^{-1} = 0.82W$^{-0.30}$(where W is mass in grams).

Metabolic rate increased 7.7-fold (corresponding to a Q of 3.9) over the temperature range 25 - 40°, a range well within that likely to be experienced by a lizard emerging from the sand. From the point of view of energetics, therefore, the sand surface on a hot day is

a highly unfavourable place for a lizard to be, even at rest.

One should bear in mind that our measurements were carried out on juveniles. Specific metabolic rate decreases with increasing mass; so, although adults would have higher total energy expenditures, juveniles have higher energy requirements per unit body mass (Pough, 1973). Adults can afford, therefore, to be more thermophilic than juveniles. A. skoogi juveniles as expected, were found to be active at cooler times of the day, together with the adults of the much smaller slipface lizard Aporosaura anchietae.

10   DISCUSSION

Because it is confined to the sand dunes of the northern Namib Desert, Angolosaurus skoogi must be considered a rare lizard. Because its habitat is so remote, it has attracted little scientific attention. Because it has adapted successfully to the apparently harsh environment of the mobile dune slipfaces of one of the driest deserts in the world, and because it is one of only two cordylid lizards known to be herbivorous (Pough 1973), as well as one of Africa's few herbivorous lizards, A. skoogi is particularly interesting to the biologist.

Within its habitat, A. skoogi is not rare: it is the dominant diurnal reptile. It is much more abundant, for example, than the lacertid Aporosaura anchietae, which is the dominant diurnal slipface lizard of the central Namib (Brain 1962, Louw and Holm 1972). It is instructive to consider possible ecophysiological explanations for the numerical dominance of A. skoogi over A. anchietae in the north, but its absence from a superficially similar habitat 300 km further south. Both lizards are chthonic, spending most of their existence buried in the sand; both are adapted morphologically for sand swimming; both are thermophilic and ultrapsammophilous. They have adopted essentially the same approach for coping with their thermal environment, that is to exploit, whenever possible, the benign thermal conditions which persist below the sand surface, emerging only when behaviour such as feeding and reproduction requires; this burying behaviour also reduces the opportunities for predation in both. Both use postural adaptations to maintain body temperature within acceptable limits when on the surface, though the thermoregulatory postures of A. skoogi, confined to hind legs and tail, are less obvious than the thermoregulartory 'dance' of A. anchietae (Louw and Holm 1972). The body size of adult A. anchietae (4.9 g) is equivalent to that of the smallest A. skoogi, so A. anchietae lacks the thermal inertia of A. skoogi adults. The few A. anchietae which were co-resident with A. skoogi in the northern Namib dunes (somewhat larger on average, up to 9 g, than individuals from the southern dunes, 4 g) were active at the

cooler boundaries (early morning and late afternoon) of the activity period of *A. skoogi,* along with the smallest of the *A. skoogi.*

The two lizard species have evolved different solutions to the problem of water supply in the absence of free water. In our Unjab study site, *A. skoogi* uses the high fluid content of nara, the staple component of its diet, as a continuous supply of water, and maintains a sufficiently positive water balance to produce fluid urine routinely. *A. skoogi* does not appear to use the advective fog as a water source, whereas *A. anchietae* in inland dunes does so. *A. anchietae* has a specialized gut which holds water within the lumen for eight weeks after drinking (Louw and Holm 1972), an adaptation which allows it to take advantage of an intermittent water supply; the gut of *A. skoogi* has not been investigated.

The diets of the two lizards differ. *A. skoogi* is predominantly herbivorous, with nara constituting the major part of its diet throughout the year at the Unjab study site. It also eats seeds, and other fresh and dry vegetable matter, and will take animal food opportunistically, including the larger tenebrionid beetles like the *Onymacris sp. A. anchietae* is a preferential insectivore, and in coastal regions, where insects are abundant, eats insects only. In the drier inland dunes, *A. anchietae* will still take arthropods when available, but adds grass seeds and other detritus to its diet. Although tenebrionid beetles are abundant in the central Namib, *A. anchietae* is too small to eat the adults of the larger beetle species. *Onymacris* sp., for example, are absent from its stomach contents (Louw and Holm 1972, Robinson and Cunningham 1978). Its small size and apparent inability to climb preclude *A. anchietae* from exploiting nara. Nara appears to be relatively more abundant throughout the northern Namib than in the southern Namib dunes; we suspect that the relatively greater abundance of nara in the northern Namib makes it a more favourable habitat for *A. skoogi.* However, *A. skoogi* and *A. anchietae* do not appear to compete in any way, so we cannot account for the relative scarcity of *A. anchietae* in the northern Namib relative to the central Namib. Many other Namib desert organisms show a differential distribution between the northern and the southern dune fields (e.g. Penrith 1975, Seely 1978) and historical as well as ecological explanations have been invoked. From our data it is not possible to conclude unequivocally which, if either, of these two possibilities applies to *Angolosaurus.*

Angolosaurus skoogi occupies a relatively simple habitat, the vegetationless slipfaces of sand dunes, which are an important habitat for a variety of small vertebrates and invertebrates. The data we have presented here should serve as a framework for further study of *Angolosaurus skoogi* and, in addition, have raised a number of pertinent questions concerning the biology of dune organisms in the Namib's extreme desert environment.

11 ACKNOWLEDGEMENTS

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