THERMOREGULATORY BEHAVIOUR OF THE VEGETARIAN LIZARD *ANGOLOSAURUS SKOOGI* ON THE VEGETATIONLESS NORTHERN NAMIB DESERT DUNES

by
WILLIAM J. HAMILTON III
University of California,
Davis, California
and
CORNELIUS G. COETZEE
State Museum,
Windhoek.

(With 4 figures)

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INTRODUCTION

The purpose of this paper is to describe the thermoregulatory behaviour of the desert lizard, *Angolosaurus skoogi*.

Details of the discovery and distribution of this lizard are described elsewhere (FitzSimons, 1955; Steyn, 1963). A single specimen was found in 1912 in southern Angola by Skoog and described by Andersson. In 1952 C. Koch found a second and third specimen, also in Angola. Subsequently, a sizable population was located by Steyn (1963) in the dunes near the mouth of the Unjab River, South West Africa, where he collected 30 specimens. More recent expeditions to the Northern Namib in South West Africa have regularly encountered this lizard, and its range now appears to coincide with the vegetationless sand dunes of that desert. No specimens have been secured in the Southern Namib and its occurrence in this much larger and better explored tract of dunes seems improbable. Several competent herpetologists have given considerably more attention to the herpetofauna of this desert than to the Northern Namib and have secured no specimens.

The habits of *Angolosaurus* are little known, and the brief comments concerning the thermoregulatory behaviour of this species now in the literature are referred to in the appropriate subsections of this paper.

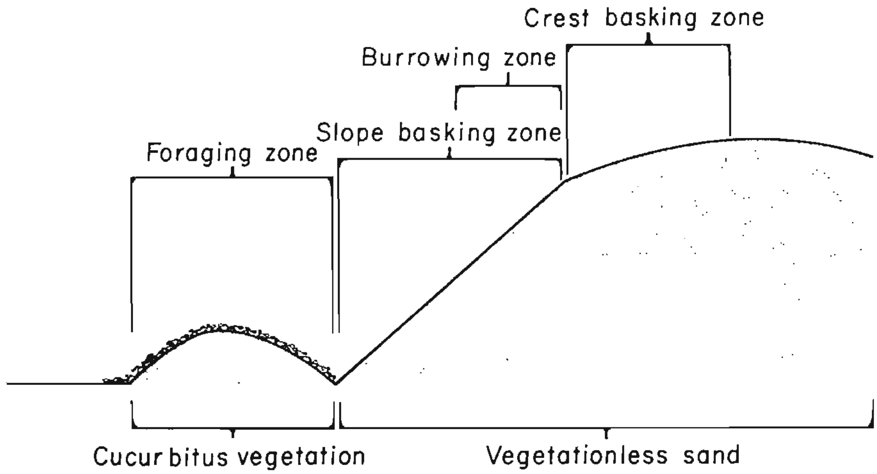


Figure 1: A sample profile of a dune in the Unjab River mouth area of the Northern Namib Desert, South West Africa, showing the regions where various behavioural activities are performed.

DESCRIPTION OF *ANGOLOSAURUS*

Angolosaurus is a large heavy-bodied lizard. The males attaining a total length of nearly 30 cm (five adult males averaged 29.1 cm) and weigh as much as 120 grams. Females are considerably smaller, being not over 26 cm in length (eight adult females averaged 24.1 cm). The body is heavy and cylindrical, the tail thick and rounded, the legs stumpy. Both sexes and all age classes are essentially alike in body proportions, but in addition to the size dimorphism there is a striking sexual colour dimorphism. Adult males have a shiny black chin and throat. In the female these parts are white. The belly of all females and young is shiny white. This part is also white in some males but in many individuals the black part extends the full length of the underside. In addition the dorsal surface of the male is evenly marked with small orange spots on a light brown background. The females and young are this colour across the entire dorsal surface of the head, body, and limbs. Finally, although both sexes have a row of pore bearing scales on the trailing part of the femur, the females lack the bright orange substance found on the males.

Much of the lives of these lizards, over 20 hours a day on most days, is spent beneath the sand surface. Squat stature and shortened legs may seem poor adaptation to this subsurface existence, but the subterranean life is apparently passive, involving little or no lateral movement. In their diving movements they operate as a screw, the powerful thoracic musculature and hind legs rapidly twisting them to a considerable depth. This movement, generally through loose sand, is enhanced by their spade-like snout.

THERMOREGULATORY BEHAVIOUR

Because of the unique arrangement of its environment *Angolosaurus* offers an exceptional opportunity to analyze thermoregulatory adaptations. This peculiarity is that the space where most thermoregulatory activities take place, on sand dunes and crests, is exclusively devoted to this activity and social interactions. Feeding occurs elsewhere, in and about the Narras bushes, *Acanthosicyos horrida,* and cucurbit clumps, *Citrullus echirrosus,* or at the base of the slipfaces of these dunes (Figs. 1 and 2). Thus, behaviour patterns observed on the open sands may be assigned either to thermoregulation or social interactions (Fig. 1). There is no difficulty distinguishing the two.

The thermoregulatory activities can be best understood in the context of a hypothesis. This is that they are attempting to attain and maintain body temperatures in the vicinity of 38° C to 42° C while above the surface, and that they attempt to remain on the surface as long as possible. Details of the evidence relating this hypothesis to a considerable number of lizards and other animals of diverse phyletic affinity is considered elsewhere (Hamilton, 1969). In summary, this evidence is that maximum body temperatures of field captured animals of the most heat tolerant species tend to approach a maximum just above 40° C. Some examples are 40.5° C for *Uma notata* of the Sonoran Desert (Licht, *et. al.*, 1966), 41.0° C for *Gerrhosaurus flavigularis* of South Africa (Stebbins, 1961), 41.0° C for *Dipsosaurus dorsalis* in the Sonoran Desert (DeWitt, 1963), 41.5° C for *Scapitra suborbitalis* and *Eremias lineo-ocellata* in South Africa (Stebbins, 1961), and 43.0° C for *Amphibolurus inermis* from Australia (Licht, *et. al.*, 1966). Norris, (1953) has recorded the highest voluntarily tolerated temperature, 46.4° C for *Dipsosaurus dorsalis* (but see this same species, above, determined by DeWitt, 1963). Since these temperatures represent the one extreme value in each study, they naturally depend upon sample size. For this reason the extreme figure for *Angolosaurus* reported here, 40.9° C in a sample of 15 measurements, will undoubtedly be raised as more measurements become available.

In spite of the maximum normally encountered extremes, many lizards tend to approach these levels and then maintain nearly constant temperatures. This applies in spite of the fact that in the case of naturally living animals there is no

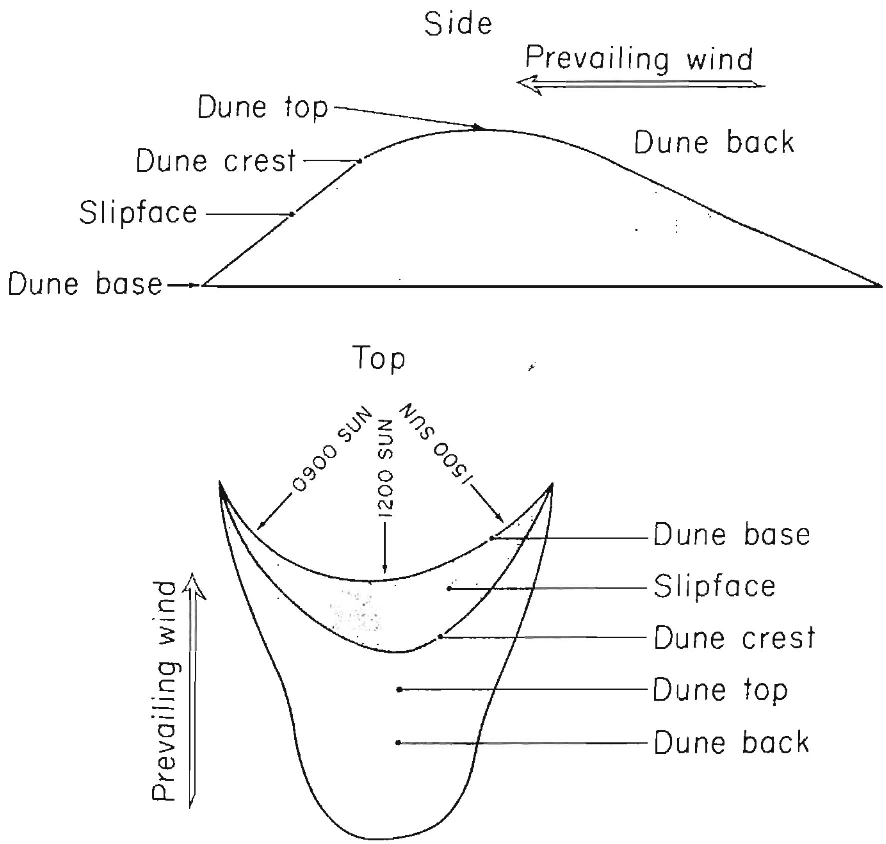


Figure 2: Terminology used to describe action of *Angolosaurus* lizards on dunes.

special feature of the environmental conditions which would favour this particular level. This leads to the conclusion that this level represents the *maximum* effectively tolerated temperature, and that this maximum or some lower value is common to all lizards living in environments where body temperatures this high can be attained. If one assumes the validity of this hypothesis, then the activity patterns of *Angolosaurus* seen on the dunes seem appropriate and finely attuned to the requirement they serve.

One obvious alternative hypothesis, that these desert animals are simply attempting to remain as cool as possible, is untenable. Many of their activities involve deliberate exposure to more extreme temperature and radiation levels than would be required for the routine execution of other activities such as feeding and socializing.

A more plausible alternative, that they are attempting to raise body temperatures as high as possible, is also not supported by the field observations of behaviour described here. Higher temperatures could clearly be generated by remaining exposed on the surface longer in the morning in the face of sand surface temperatures far above body temperature levels and radiation intensities which would contribute to further heat gain. Furthermore, most individuals have retreated to the cooler subsands by the time the heat of the day has developed.

An obvious test of many of the ideas presented here would be to provide an extensive series of deep body temperatures taken during various behavioural events.

Table 1. Deep body temperatures of *Angolosaurus skoogi*, excavated from dune slipface sands: A, after an undetermined interval of voluntary burial; B, after plunging into the slipface sands voluntarily, probably to prevent further cooling; and C, after being interrupted by us. Sample size in parenthesis.

	Body temperature	Surface temperature	Ambient temperature, 3 cm above sand
A	33.1° C (7)	39.4° C	32.8° C
B	35.1° C (4)	41.8° C	42.4° C
C	38.7° C (4)	35.7° C	36.8° C

We have provided a smattering of this sort of evidence (Table I). These data were obtained by excavating lizards from the loose sand and taking rectal temperatures with a calibrated probe of a YSI telethermometer. There are considerable problems in evaluating such determinations. Because of the extreme wariness of *Angolosaurus*, it is almost impossible to take them by surprise and, once alerted, they dive into the slipface sand and must be dug out before a body temperature can be determined. Since these sands during most of the day are relatively cool, body temperatures probably begin to drop as soon as they plunge. Unfortunately, there is no way in which to determine the extent or rate of these declines, and the data of Table 1 must be considered minimum values for the stated conditions.

Such determinations are not easily made because each involves a protracted period of observation to determine antecedent behaviour and a chase to secure the animal for probing. Only about a third of all specimens observed are subsequently captured. The ideas presented here could be precisely evaluated with radio telemetry signals providing deep body temperatures. Hopefully, these techniques, already developed, can be applied to future studies of the thermal behaviour of *Angolosaurus*.

SPATIAL ADJUSTMENTS TO THERMOREGULATION

The dune environment inhabited by *Angolosaurus*, both above and below the surface, is a thermal mosaic and during the day a rapidly changing one. Furthermore, the distances from one thermal condition to another are sharply telescoped because the slipfaces are in a wind hiatus and are generally perpendicular to solar radiation while the dune tops are exposed to full wind action and radiation intercepts this part of the dune at an oblique angle. The spatial response by adult *Angolosaurus* to these environments are described here in the order in which they generally appear during a day's activities.

Subsurface Basking

In the earliest part of the activity cycle of the morning most individuals move to a position just below the sand surface of the slipfaces. Often the head and neck are exposed, sometimes the forelegs as well. During this behaviour the body is just below the surface in the hottest layer of surface sand. Cooler temperatures are immediately available a few centimeters deeper, and these depths are quickly reached by these lizards during escape or when body temperatures become excessive. They may remain motionless in this position for considerable periods, 30 minutes or more on cool mornings. This relatively persistent behaviour undoubtedly reflects the comparatively stable thermal conditions of the subsurface sands compared with the surface. The time interval from lower to upper acceptable temperatures will in any case last longer than it would if the animal had surfaced completely.

This behaviour emphasizes conductive heat exchange and appears to be favoured when other heat exchange modes are relatively less acceptable. Thus, it is resorted to when (1) ambient temperatures are low and there is considerable wind, both of which would tend to lower body temperatures through convective heat loss, and (2) when the combination of heat exchange conditions on the surface have led to a sufficiently high body temperature which, given further surface exposure, will continue to rise to excess.

It seems likely that this behaviour also serves as a lookout for predators, such as the Chanting Goshawk, *Melierax musicus*, which we have seen attacking these lizards, often from perches at the dune crest.

Slipface Basking

Following the morning feeding session and subsequent feeding bouts, most adults climb up into the steep dune slipfaces to bask in the morning sun. Throughout the Northern Namib these slipfaces are oriented to the north or northeast and hence face the sun during much of the day throughout the year (Fig. 2). Because of the steepness of the slipface slopes (29° 07' to 31° 55' in a sample of 15 measured slipfaces, mean 30° 38') incident sunlight intercepts these faces at approximately right angles, and lizards basking on them intercept maximum solar radiation on their dorsal surface regardless of their orientation on these slopes. The situation is as if the sun were directly overhead. The males, however, vary little from a position which either faces directly up or down the slipface. Here they may remain motionless for some minutes, usually with the chin and shoulders raised. During this behaviour heat gain by conduction and radiation is emphasized. Convection here may be close to neutral and may have a cooling effect since ambient temperature levels are generally lower than body temperatures at the time of day when this behaviour takes place.

Slipface basking is particularly favoured on cool mornings when there is scattered cloud cover. This is common in the Unjab River mouth area where most of our observations were made. On such mornings, because of the sharp angle of incidence of solar radiation, the surface sand of these slipfaces warms rapidly in an otherwise cool environment. By comparison, on particularly warm cloudless mornings this behaviour may not be seen at all.

Crest Basking

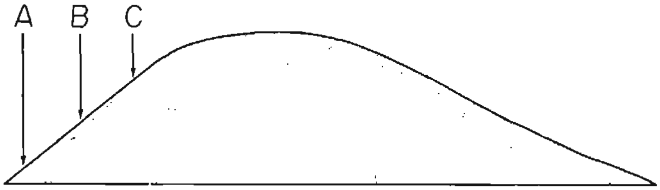
During thermoregulation *Angolosaurus* exploits fully the range of thermal conditions unique to the shifting vegetationless dunes. Of these, the dune crest environment is peculiar to dunes. The closest comparison to other South West African lizards is with several of the Namib Desert gravel plains lizards which often seek the slight elevation of small boulders to escape the extreme heat of the terrain surface. Northern Namib sand dunes differ considerably from the sharp dune crests of the main mass of Southern Namib sand dunes which generally run north-south and have pointed ridges from which sand streams during high winds. By comparison, the dunes inhabited by *Angolosaurus* on the Northern Namib have rounded crests, and slipfaces do not develop from the high point of these dunes but from the leeward side (Fig. 2). This area, between the crest and the break to the slipface, is where crest basking takes place. The crest is generally reached following first emergence from the sand, 0910 hours at one site on November 13, 1967, 0942 hours at another site 200 meters away on the same date. It is often preceded by a short interval of slipface basking. From any given site on the slipface they move rapidly upslope, usually running rather than walking until they reach the crest. The ascent may be made at a slight angle to the slope or directly. When the face sands become excessively warm, over 50° C, the run to the top may be interrupted by plunges through the sand (see below). These plunges are preceded by behavioural indications of heat stress — leg and tail lifting (see below) — which confirm that the slipface transit cannot be accomplished in one run because of the extreme heat. Sometimes instead of plunging they may only stop momentarily, raising the feet and tail, then run to the crest as fast as their heavy bodies permit. Adult females may make two or even three such stops in ascending a 20 meter slipface, but the adult males generally make the run with a single stop. Often the last run to the top is made with a final burst of speed, especially by the adult males. Then, gaining the crest, they stop to hoist up the feet and tail before moving on to more favoured parts of the dune top.

Differences between the behaviour of males and females can presumably be attributed to the considerably larger size of the males. Because of their size they must heat more slowly. Since the heat tolerance of both sexes is presumably the same (it is in other lizards), the more interrupted ascent of the females is understandable.

On the dune top the sand is harder and locomotion can be more rapid and extensive and thus safer. Here they often move laterally for considerable distances, always within a few meters of the slipface. Much time is spent in places where they reach the crest, with movements limited to postural adjustments to thermoregulation (see below).

Plunging

There is a striking change in the diurnal temperature gradient on the slipfaces from the surface to the attainable (for an *Angolosaurus*) substrate. In a distance of considerably less than half a meter, sand temperatures may drop from over 60°C to near 30° C (Fig. 3). These cool subsands are almost instantly available to a mature *Angolosaurus*,



TEMPERATURES (C°)

	Air (Im)	Surface	–5 cm	–10 cm	–15 cm	–25 cm
A	27.8	51.0	43.8	35.8	31.2	28.7
B	27.9	60.4	47.5	37.8	32.4	31.3
C	27.2	42.0	37.8	33.4	29.0	26.9

Figure 3: Thermal profile of a dune inhabited by *Angolosaurus*. Time, 1400 hours, November 8, 1967. All *Angolosaurus* are buried in and about position C.

especially those individuals which are crest basking, by diving into the loose, freshly blown slipface sand just beyond the dune crest. This behaviour is commonly associated with escape from predators and excessive heat. The soft sloping sand of the slipface is close to the packed, gently rolling dune crest sands (Fig. 1). On many occasions we noted individuals on the crest undergo a rapid increase in the rate of posture changes — leg, tail, and body lifting — just before running across the ridge of the dune and diving into the slipface sands. Diving to a depth of 15 cm or more takes only a few seconds.

The slipface sands just beyond the crest (position C, Fig. 3) are the best ventilated. Winds blowing over the dune back swirl about at the top of the slipface but further down the slope the air is quieter and the surface sand warmer. The hot surface further down these slipfaces results in an increased thermal gradient and warmer sands well below the surface, a condition which prevails throughout the day. The behaviour of *Angolosaurus* in selecting the region of the slipface just below the crest may thus represent the choice of the most moderate environment available on the slipface. Even cooler conditions prevail on the dune top and back, but these regions are packed sand and do not permit quick deep plunges. These dune top sands are often traversed by jackals and excavation by these predators would also be relatively more effective because of the sand hardness. In the deep dry sand of the slipfaces *Angolosaurus* is well protected from predators because digging movements are ineffective in excavation, and sand refills each depression as it is formed. The method we use to capture them is to thrust the forearm as deep as possible into the sand. No relevant non-human predator has this capability.

On some occasions we observed individuals which had plunged re-emerge several minutes later. More commonly plunging, when not induced by disturbance, terminated the morning or the afternoon activity session. Table I summarizes some scattered measurements of body temperatures of individual *Angolosaurus* which were detected by the disturbed surface sand and excavated during the heat of the day. These measurements, made rectally with a calibrated YSI model 402 thermister, emphasize the cooling effect of the subsand.

A few measurements of body temperatures following voluntary plunging (Table I) were taken in the afternoon and probably represent conditions when body temperatures have cooled to levels which terminate the daily supersurface activity cycle.

POSTURAL ADJUSTMENTS TO THERMOREGULATION

Within the range of possible body temperatures there is a considerable potential for behavioural thermoregulation by postural maneuvers. These manipulations modify the role of conduction by changing the amount of the animal's surface in

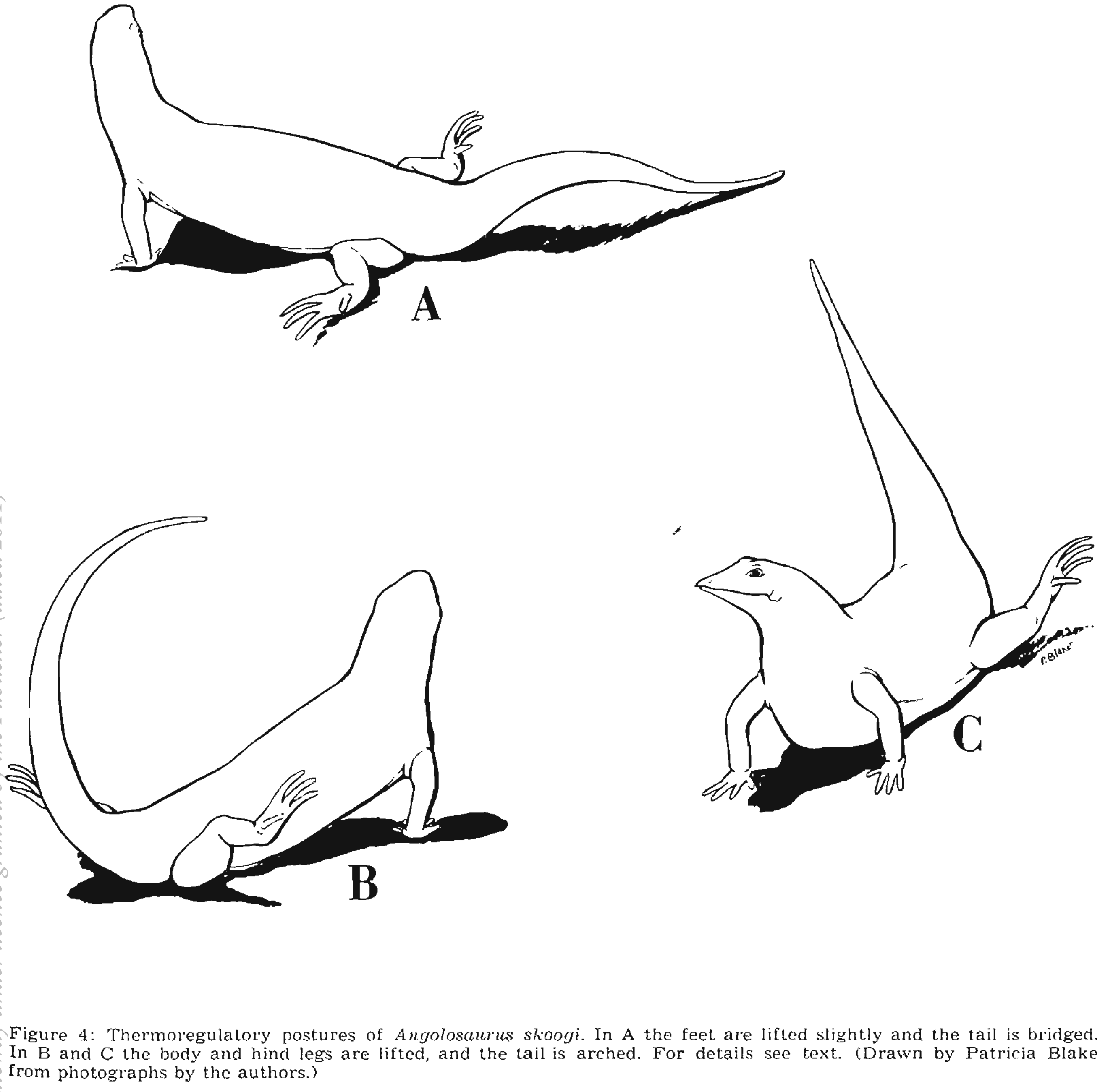


Figure 4: Thermoregulatory postures of *Angolosaurus skoogi*. In A the feet are lifted slightly and the tail is bridged. In B and C the body and hind legs are lifted, and the tail is arched. For details see text. (Drawn by Patricia Blake from photographs by the authors.)

contact with the substrate. They may also modify convection. The latter is accomplished by moving the mass of the body up or down, thereby changing the ambient temperature. This is effective because of the sharp thermal gradient *above* the surface, from surface levels to heights attainable by postural changes. Description of these postural adjustments follows.

Tail Lifting

The bulky tail may be lifted above the sand in one of two ways. Either it may be bridged, with the tip braced against the sand (Fig. 4 A) or curled into a crescent and held high above the back (Fig. 4 B and C). Both of these postures minimize the amount of tail in contact with the substrate. It also reduces convective heat gain because the higher air is cooler. The use of more than one posture presumably permits localized cooling or at least a lowered rate of heat gain while other parts are taking the brunt of the heat gain. When the posture of Figure 4 A is adopted, there is less surface contact of the body near the hind legs than there is when the positions of Figure 4 B and C are adopted.

Body Lifting

When the tail lifting postures are adopted, the forelegs are straightened, raising the forepart of the body well above the sand surface. The head is further elevated by bending the neck backwards. We have not seen *Angolosaurus* lift the forelegs like some other Namib Desert lizards, *Aporosaura anchietae*, for example. These considerably smaller lizards may proceed through a series of leg and tail lifting maneuvers in rapid sequence, literally dancing on the hot sand. The heavier bodied *Angolosaurus* are less agile in their movements. Another movement, seen in several of the desert gravel plains lizards east of Gobabeb, consists of foot waving when the leg is lifted. During our observations, we never saw *Angolosaurus* perform this activity.

Leg Lifting

This behaviour is adequately described by the illustration (Fig. 4). Whenever we saw this movement, it was associated with tail lifting. Leg lifting does not always accompany tail lifting, however, and for that reason it is considered here as a separate movement. Sometimes the smaller individuals will haul up only one hind leg, and in this case it is hoisted considerably higher than when both legs are raised.

Head Lifting

The head lifting posture is also well described by Figure 4, and its thermoregulation relevance is the same as that of the other postural changes.

OTHER THERMOREGULATORY RELATIONSHIPS

Soil Probing

On a number of occasions we witnessed individuals move obliquely downward across the dune face, poking the chisel-like snout into the hot sand. These movements generally followed crest basking and a series of postural maneuvers. Soil probing generally preceded plunging, and at the time the observations were made, we assumed that these lizards were testing the temperature of the soil before plunging. Subsequently, we have seen *Angolosaurus* searching for grass seeds on the lee slopes of the dunes in Angola and the possibility that these are feeding movements cannot be dismissed.

Shading

Because of the orientation of the dunes to the sun, there is normally no shade available on the dunes during the normal *Angolosaurus* activity period. At the east side of the crescentic slipfaces (Fig. 2) there is some shade in the morning, but the surface sands and air temperatures at this time favour heat gain behaviour rather than thermal shelter. The same applies to the late afternoon when the western end of each slipface is the first to become shaded. It is irrelevant to the thermoregulation process of *Angolosaurus* because it occurs after most of them have retreated to the slipface sands for the night. Those that are still active are already cooling rapidly and have a heat loss rather than a heat gain problem.

Not all activity is confined to the dune slopes and faces. Many of the smaller *Angolosaurus* spend most of their time in and about the Narras bushes at the dune bases where they occur, and they are thus able to take advantage of the partial shade provided by this vegetation. Where the dunes have overflown the Narras vegetation, these small *Angolosaurus* individuals may also make sorties into the open area adjacent to these plants, concentrating their foraging activities upon the fallen green blossoms. On other occasions we have seen adult *Angolosaurus* move to the cucurbit clumps during extremely hot conditions by travelling in the shade at the edge of nearby Narras patches. But the use of shade is an uncommon event for adults and, because of the perpetual presence of cool subsands, unnecessary. When maintained in captivity, *Angolosaurus* regularly take advantage of the shade cast by their container. Other dunes and gravel plains lizards may take advantage of the shelter of a vehicle or even a shovel rather than retreating in their normally shadeless environments.

Age and Size Relationships

Young animals, under 15 cm in total length, do not participate in the thermoregulatry activities on the vegetationless dunes to the same extent as adults. They remain about the Narras vegetation and, when pressed, dive into the partly shaded sands of these clumps. These afford particularly good protection because the ever-changing sands continually cover the spiny Narras stems and the spiny matrix of these buried stems is enough to discourage human and probably other predaceous intruders as well. Jackals do dig about these Narras clumps, sometimes extensively, but the excavations seem to be blocked by the buried stems and the looseness of the sand. In some places, however, there is no macroscopic vegetation in *Angolosaurus* habitat. We have seen widely scattered adult individuals on the isolated barchan dunes along the road entering the Torra Bay camp from Welwitchia and on the relatively low, absolutely vegetationless barchan dunes between this point and the Unjab River on the *inland* side of the main dune mass. It may be that these adults have wandered to these sites from distant areas. If not, then the juveniles in these regions must depend exclusively upon the thermal mosaic and plunging for thermal control.

The differences between the thermoregulatory patterns of males, females, and juveniles may be related to their different sizes. We have already indicated the greater difficulties encountered by females in ascending the slipfaces. The general absence of small juveniles on these slipfaces is probably simply an extension of the heat-gain-rate/size relationship.

The same relationship presumably explains the leg lifting and tail lifting behaviours. These relatively small diameter parts may be expected to heat more rapidly than the chunky body, reaching stress-levels first.

Another explanation is that these behaviours are an adaptation to cooling the body. According to this hypothesis the leg and tail lifting movements would be an adaptation to dissipating deep body heat. At best this is secondary response, since the leg lifting actually increases the area of body surface in contact with the substrate and thus exaggerates total body heat gain. We are thus forced to conclude that the primary adaptation is protection of the more easily overheated smaller diameter parts, the legs and tail. Any vasomotor adaptation must be a secondary adaptation to the limits imposed by this necessary response to overheating of the extremities.

DISCUSSION

The thermoregulatory behaviour of *Angolosaurus* is highly adapted to its unique environment. The general behaviour is similar to that of diurnal lizards living in vegetated regions in terms of basic requirements. For *Angolosaurus* cool subsands substitute for the shade of vegetation or burrows (Norris, 1953). By human standards these vegetationless dunes appear to be the most severe of terrestrial environments, but relative to the special conditions of the dunes, and the morphology and behaviour of *Angolosaurus*, the soft, easily penetrated slipface sands offer an easily attainable refuge from excessive heat or predation, a refuge unavailable to a large animal. The slipfaces are, in fact, considering the morphology and behaviour of these lizards, a particularly favourable environment.

The use of the vegetationless and generally resource-depauperated dunes in thermoregulation emphasizes the importance of attaining and maintaining body temperature in a context other than as a simple concession to foraging or social processes.

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