

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 move-

ments 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 (Ha-

milton, 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 tole-

rated 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

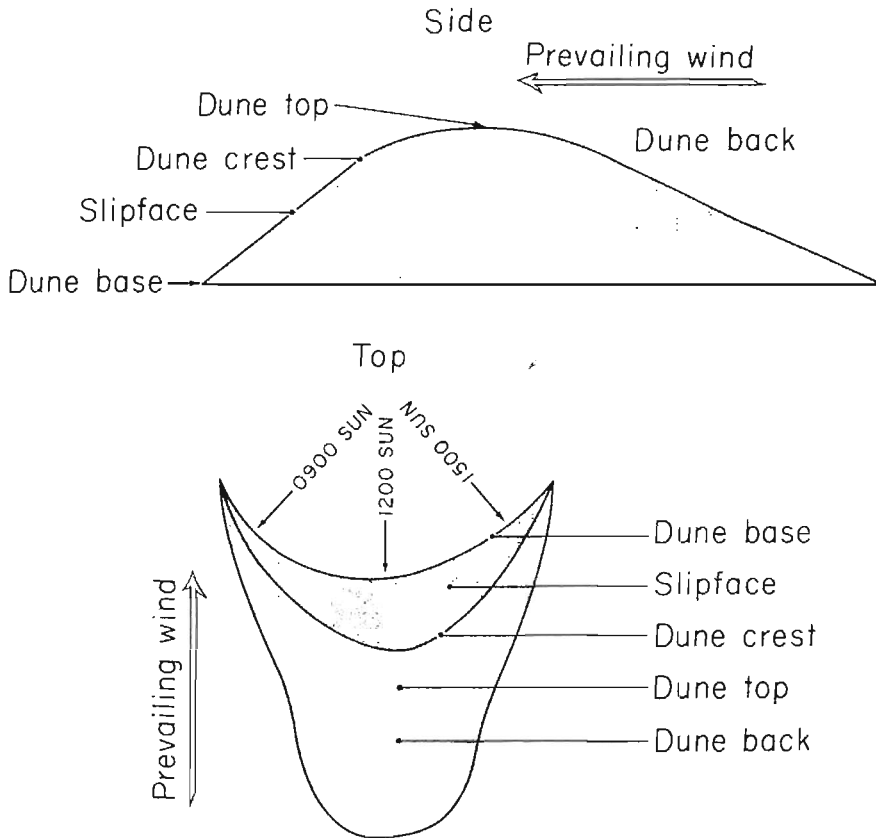


Figure 2: Terminology used to describe action of *Angolosaurus* lizards on dunes.

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