

Microclimate and activity of the lizard *Angolosaurus skoogi* on a dune slipface

M.K. Seely*¹, D. Mitchell**, C.S. Roberts* and E. McClain** 1988

*Desert Ecological Research Unit, P.O. Box 1592, Swakopmund, 9000 and **Department of Physiology, University of the Witwatersrand Medical School, Parktown, 2193

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The lizard *Angolosaurus skoogi* inhabits the surface and subsurface environments of sand dunes of the northern Namib Desert. We have related posture, locomotion, and other aspects of surface activity to the microclimate prevailing above and below the surface. Globe temperature was the best microclimatic correlate of surface activity. From our analysis, we concluded that surface thermoregulatory behaviour of *A. skoogi* is facultative, and aimed at maintaining a body temperature compatible with foraging and other obligatory surface activities.

Die akkedis *Angolosaurus skoogi* bewoon die oppervlak- en substraat-omgewing van die sandduine in die noordelike Namibwoestyn. Ons het die verband tussen die houdings, bewegings en ander aspekte van oppervlak-aktiwiteit en die mikroklimaat bo en onder die oppervlak vergelyk. Swartboltemperatuur was die beste mikroklimaatkorrelant van oppervlak-aktiwiteit. Uit ons analise lei ons af dat termoreguleringsaktiwiteit op die oppervlak by *A. skoogi* gerig is op handhawing van liggaamstemperatuur wat vir noodsaaklike oppervlakbedrywighede soos kossoek, geskik is.

¹To whom correspondence should be addressed

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Vegetationless slipfaces of sand dunes are important habitats for a variety of invertebrates and small vertebrates in the Namib Desert (Koch 1961, 1962; Robinson & Seely 1980; Seely 1978; Seely & Louw 1980). The uncompacted sand allows easy access to the subsurface environment for those animals able to bury; they 'swim' through the loose substrate without benefit of constructed burrows (Coineau, Lancaster, Prodon & Seely 1982; Seely 1984). Although thermal conditions amenable to life always are available below the sand surface (e.g. Seely & Mitchell 1987), most slipface species come to the surface for food and water, and for social interactions (e.g. Seely 1983). While on the surface, diurnal species encounter high levels of solar radiation, which may create an unacceptable thermal environment. The possibilities for behavioural temperature regulation on a slipface are limited: they include using shade under the sparse vegetation, adopting warming or cooling postures, or re-entering the thermally amenable substrate. Re-entering the substrate is the only viable alternative when radiation is very high, so a thermoregulatory crisis may terminate surface activities.

Angolosaurus skoogi (Andersson) is a large (up to 120 g), long-lived lizard occurring on sparsely vegetated slipfaces in the northern Namib Desert dunes of Angola and Namibia (Andersson 1916; Fitzsimons 1953; Steyn 1963). Predominantly herbivorous (Pietruszka, Hanrahan, Mitchell & Seely 1986), it feeds on the surface, mainly on the endemic, perennial desert cucurbit *Acanthosicyos horrida* (Welw. ex Bentham & Hooker fil.) commonly known as nara. Individual lizards do not routinely come to the surface every day; they can remain within the slipface sand for at least seven days (Mitchell, Seely, Roberts, Pietruszka, McClain, Griffin & Yeaton in press). When they do appear on the surface, their behaviour suggests that much of their

activity is directed toward regulating their body temperature, apparently at a fairly high level (Hamilton & Coetzee 1969).

Although relative to some other deserts average temperatures in the Namib Desert are equable throughout the year (Figure 1), day to day variation can be extreme (e.g. Lancaster 1982). Alternation between hot, dry conditions and cold, foggy conditions is particularly abrupt in winter, when adiabatically heated winds from the interior may be replaced within a day by cool, onshore winds from the South Atlantic, and *vice versa*. With such variations, there are no consistent thermal conditions above surface to which dune animals can adjust their activity, or to which they can become acclimatized (e.g. Hertz 1981; Spellerberg 1972). In such circumstances rapid response and opportunistic use of acceptable surface conditions, when they occur, appear to be the rule (e.g. see Bogert 1949; Huey 1982).

In this paper, we report an analysis of the relationship between dune microclimate and activity of *A. skoogi*. Activity may be dictated by thermoregulatory requirements, as occurs, for example, in the case of some birds, where gular fluttering, shade seeking, and other heat-avoidance behaviour virtually immobilizes the bird during high heat stress conditions. At the other extreme, the lizards may be so thermally tolerant that thermoregulatory behaviour is absent or receives low priority, a situation enjoyed by some large mammals, for example the oryx. Another possibility is that thermoregulatory activity is facultative, that is, thermoregulation is given just sufficient attention to maintain a body temperature compatible with other surface activities. By analysing posture, site occupation, and other aspects of surface activity for individuals of different sizes, we attempted to assess the role of thermoregulatory activity, within the constellation of surface activities undertaken by the lizards.

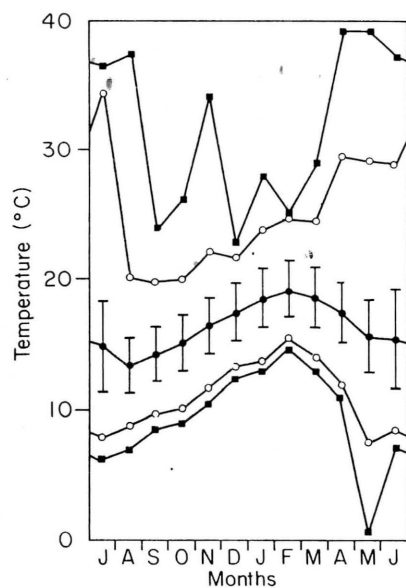


Figure 1 Six-year summary (from Monthly Weather Report, S.A. Weather Bureau) of the march of air temperature at Möwe Bay. Square symbols are the absolute maximum and minimum, open circles are the mean maximum and minimum, and filled circles are the mean temperatures. Vertical lines connect the mean daily maximum and minimum (after Schulze 1972). The diel temperature range is approximately the same as the inter-seasonal range of mean monthly temperatures.

Study area

The study area was located on the south bank of the usually dry bed of the Unjab River, approximately 15 km from the coast on the eastern (inland) side of the northern Namib dunes (20°09'S / 13°14'E). The dominant south to south-west winds create north-easterly directed slipfaces of 31–34° slope on the barchanoid dune ridges which are mainly 3–10 m high. Winds capable of moving sand (> 4 m/s) blow for up to 50% of the time (Lancaster 1982). The permanent meteorological station nearest to the study area, located on the coast about 100 km to the north at Möwe Bay, recorded rainfall of 22–25 mm per year during 1974–1977 with fog occurring on 11–25 days per month (Lancaster 1982). Mean monthly air temperatures range between 13 and 19°C (Figure 1).

We selected a single large dune, with morphology and biology typical for the region. In our study area of 2000 m², 27% of the area was active slipface of which one sixth was covered by nara, the only plant on the dune. The remaining 73% of the area was made up of steep dune slope, although it too would have been active slipface under the dominant SW wind regime. The mean distance, along the slope, from base to the top of the dune was 24 m.

Methods

Using binoculars from a hide, we counted the entire population of *A. skoogi* active on the surface of the study dune, at 5-min intervals throughout the day for six

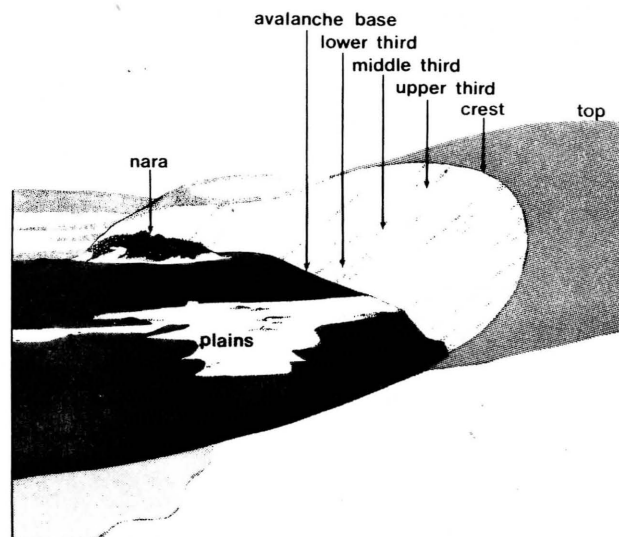


Figure 2 Sketch of a typical slipface identifying the locations used in the text. Art work by Terence Boraine, University of the Witwatersrand.

days. During each scan (e.g. Altmann 1974), every individual was classified into one of six groups: hatchling; juvenile; adult (i.e. adult female or large subadult male); male; head-only (animals lying in the superficial substrate with heads, but not bodies, exposed); unidentified lizard. Its location on the dune was recorded, following the nomenclature of Figure 2.

Focal animal observations (Altmann 1974) were conducted during the last two days of the study period. An individual animal was selected from the population active on the slipface and observed for 5 min or until it disappeared beneath the sand surface if that were sooner. We attempted to observe a similar number of individuals for 5 min from each size group, at each of the different time periods of the day. Whenever the lizard under observation moved or changed posture, its location on the dune, posture, orientation of its body, and activity were recorded and time was noted. Ten postures, assumed while the lizard was not moving, and four patterns of locomotion, which we had identified during preliminary observations, were used during focal animal observations. Orientation of the lizard was recorded in 45° compartments, as the angle between the body, viewed rostrally, and the perpendicular to the dune crest.

Microclimate data were collected at the study site on another slipface, approximately 500 m from the observation dune, as it was not possible to use the same dune without disturbing the lizards. Hourly averages of 1-min readings were recorded by a data logger (Campbell CR-21). The variables logged were ambient temperature, ambient relative humidity, solar radiation flux, wind speed, and sand surface temperature, as well as globe temperature (Yaglou 1968), and the temperatures of two 'mock' lizards (cylindrical, black plastic bodies of a size comparable to that of the average *A. skoogi* and filled with water). Wet and dry bulb temperatures were measured at hourly intervals with a

sling psychrometer, and water vapour pressure was calculated using psychrometric charts (Barenbrug 1974). Subsurface sand temperatures were measured at nine depths using an array of copper-constantan thermocouples which were mounted on a thermally inert rod and connected to a portable thermocouple thermometer (Bailey Bat-12). The relative humidity of the sand pore space was measured with a piercing humidity probe (Vaisala HMP 15 with HM 1 14 RM indicator) located 150 mm below the sand surface. Statistical analyses followed Sokal & Rohlf (1981).

Results

Population activity and microclimate

The extremes of microclimate which occurred during our six days of observations of *A. skoogi* are depicted in Figure 3. The surface activity pattern of the lizards varied as the days warmed from the 14th July to the 17th and then cooled again by the 19th (Figure 4). On cooler days the lizard population was active continuously from

approximately 11h00 to 17h00. However, on the warmer days the activity was largely restricted to the morning. The population became less active, or was entirely submerged, during the midday hours, after which there was an increase in surface activity on some days.

Lizards in the different size classes exhibited different surface activity patterns (Figure 5). On cool days (Figure 5a) the hatchlings and juveniles were active for most of the day with only a short period of inactivity in the early afternoon, the hottest time of the day. In contrast, the female and subadult male, adult male, and 'heads-only' sightings were largely confined to the hotter early afternoon hours. On a warm day the morning activity periods of all the size classes were earlier and they all overlapped (Figure 5b). As temperatures rose towards the middle of the day, the smaller lizards (juveniles and hatchlings) buried below the sand surface before the larger animals. The smaller animals, but not the larger ones, had a second activity period in the late afternoon.

There was an overall increase of 17,5% in sightings on the warm day. This increase was due largely to a 2,5-fold increase in sightings of adult females and subadult males, as well as a 2,2-fold increase in the number of 'heads only' sightings (Table 1). The smaller lizards (hatchlings and juveniles) showed a slight decrease in activity on the warm day (13% and 15% respectively). The number of sightings of adult male lizards was identical on both days.

Examination of the locations at which surface activity

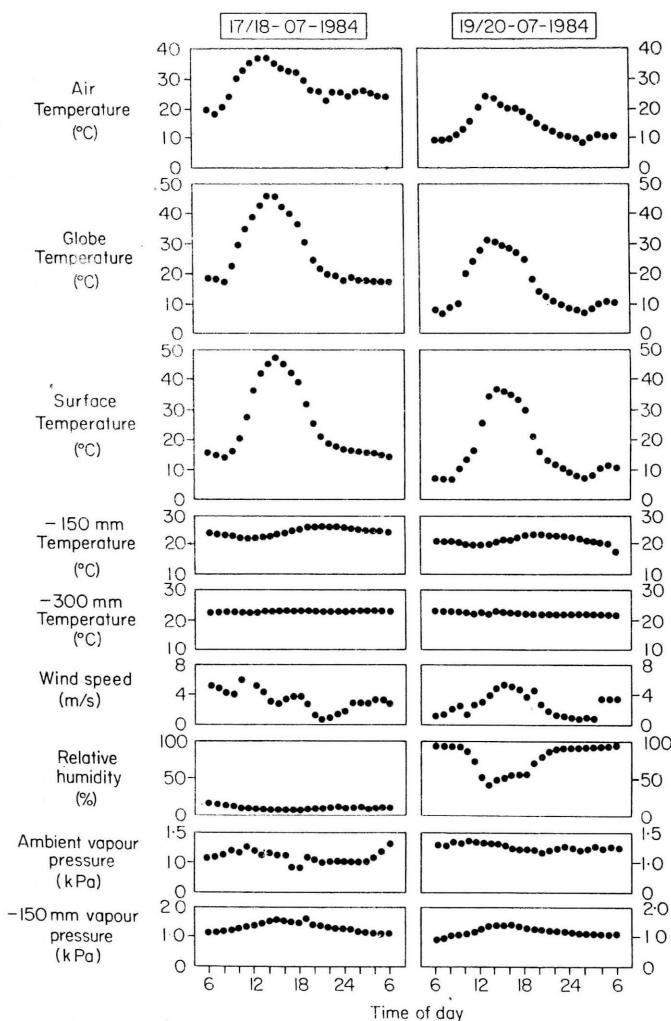


Figure 3 Temperature, wind speed, relative humidity and vapour pressure on the warmest and coolest day during our observations of lizard activity. Temperatures of subsurface environments are given at various depths below the sand surface.

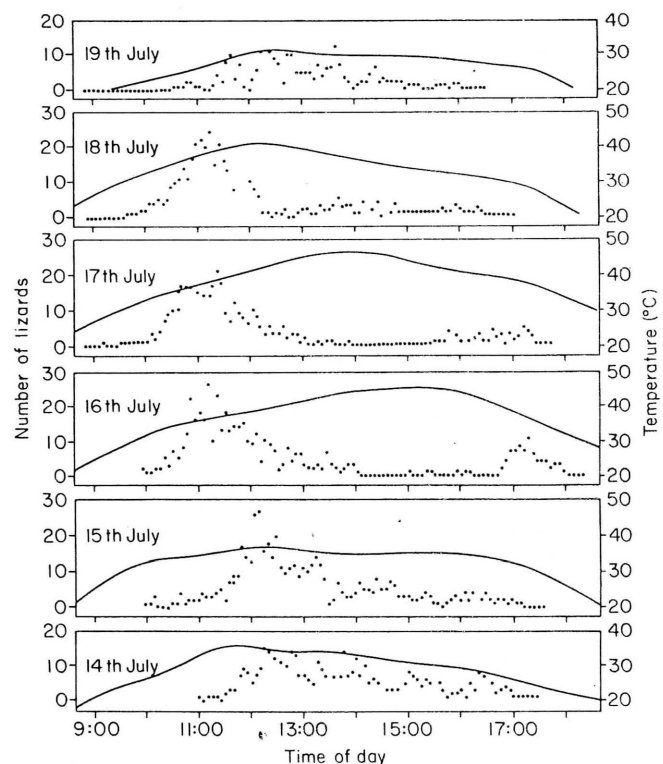


Figure 4 The total number of lizards sighted during scans at 5-min intervals over the six days of observation and corresponding mean hourly globe temperatures. Over the six consecutive days, mean globe temperatures during the lizard activity period increased from 30°C to 39°C and decreased again to 27°C.

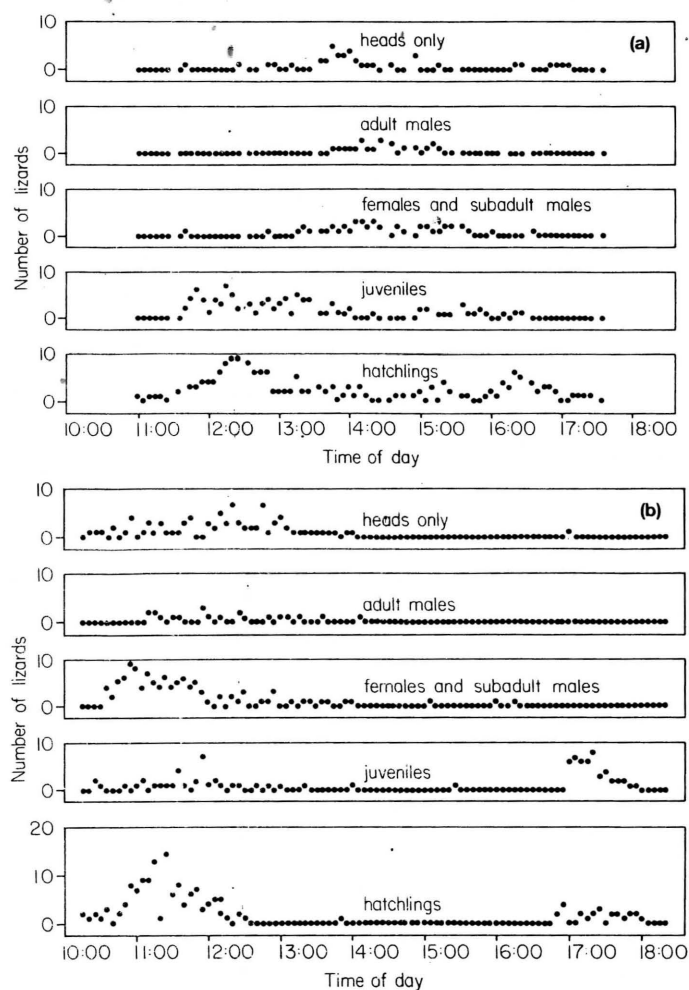


Figure 5 Number of lizards in each of five size categories sighted during scans at 5-min intervals on two days of observation (see text for details of categories). Observations for Figure 5a were taken on a cool day and for Figure 5b on a warm day (see Figure 3).

took place showed a distinct shift with temperature (Figure 6). From the upper areas of the dune (crest, and upper and middle slopes) on the cool day (Figure 6a), activity shifted to the avalanche base, plain, and nara on the warm day (Figure 6b). The activity on the lower third of the slope remained more or less constant (Table 1). The increased activity on the lower slipface and avalanche base later on the warm day reflected the use of these areas predominantly by smaller individuals (compare Figure 5b).

The numbers of lizards sighted during each 5-min scan were summed over the hour to give an index of lizard population activity per hour. Means and standard errors of these indices then were calculated over the six days, and plotted against time (Figure 7a), mean hourly globe temperatures (Figure 7b), and mean hourly wind velocities (Figure 7c) between 10h00 and 18h00. On average, over the six days, population activity reached a maximum less than 2 h after the first morning emergence, i.e. between 11h30 and 12h30 (with solar noon occurring at 13h00 at the study site), and then

Table 1 (A) Contributions (%) of the different size groups, head-only sightings and unidentified individuals to total surface sightings, and (B) distribution of sightings (%) according to location on the dune, during a cool day (14 July; 401 individual sightings) and a warm day (16 July; 471 individual sightings)

(A)

	Group					
	Hatchling	Juvenile	Adult	Male	Head-only	?
14 July cool day	43,1	24,9	11,2	5,2	10,0	5,5
16 July warm day	31,8	18,0	23,6	4,5	18,9	3,2

(B)

	Location on dune						
	Slipface				Avalanche		
	Crest	Upper	Middle	Lower	base	Plains	Nara
14 July cool day	17,5	24,7	23,2	26,2	6,5	0,7	1,2
		65,3				8,5	
16 July warm day	9,3	39,5	15,9	24,4	21,0	36,1	9,6
		14,2				5,5	

activity decreased slowly over the following 6 h. One should recall, however, that these averaged results incorporate quite different daily patterns (Figure 4).

Globe temperature, which integrates wind speed, radiation flux, and air temperature, appeared to correlate better with lizard activity (Figure 7b), than did wind speed (Figure 7c), air temperature, or sand surface temperature. Peak lizard activity coincided with globe temperatures between 36°C and 40°C (Figure 7b) and with wind velocities between 5 m/s and 6 m/s (Figure 7c). No lizard was active on the surface at globe temperatures below 24°C or above 46°C.

Again combining the six days' observations, we calculated the percentage of the hourly mean number of active smaller (hatchling and juvenile) and larger (adult female and male) lizards. As one would expect from the results shown in Figure 5, there was a tendency for smaller animals to contribute more to the population activity later in the day (Figure 8a). One explanation for this would be a preference of smaller lizards for lower temperatures; there was a trend towards smaller lizards being more active at lower temperatures and larger lizards being more active at the higher end of their temperature range (Figure 8b). Population proportions did not vary as markedly at different wind velocities, but our results suggested that a higher proportion of smaller individuals was active at lower wind speeds (Figure 8c). As Figure 7a shows, lower wind speeds occurred at both high and low globe temperatures.

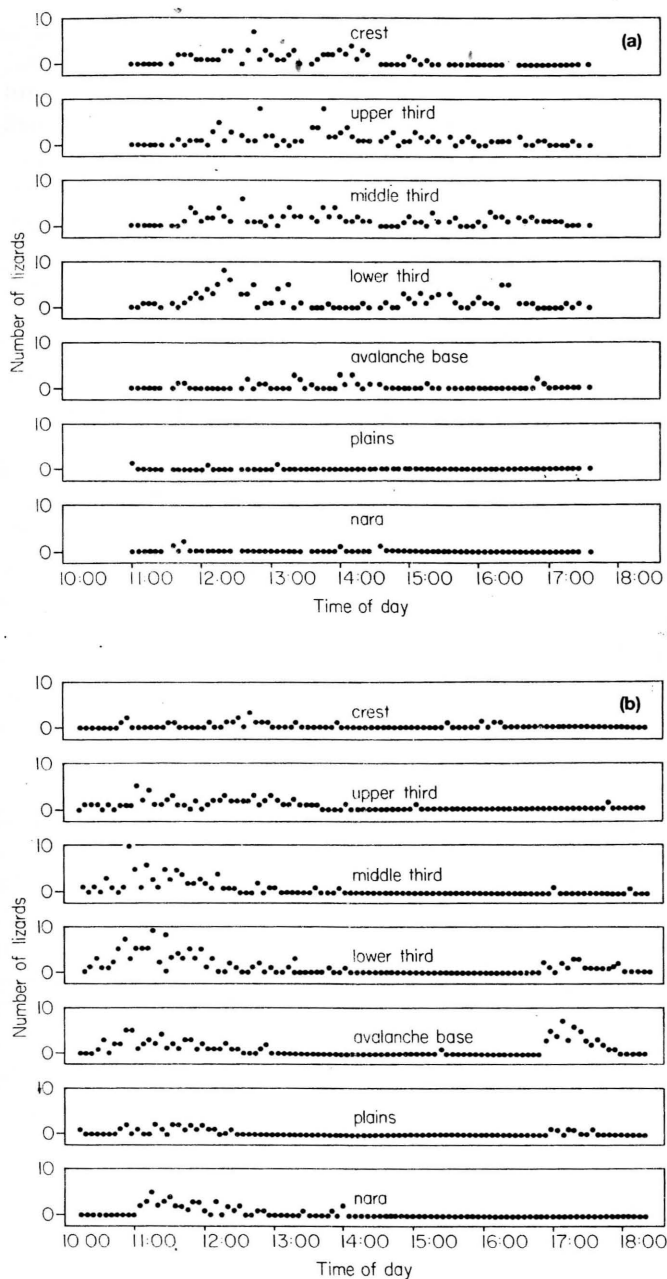


Figure 6 Number of lizards sighted at each of seven dune locations during scans at 5-min intervals on six days of observation (see Figure 2 for locations). Observations for Figure 6a were taken on a cool day and for Figure 6b on a warm day (see Figure 3).

Posture, orientation, and movement

Our observations revealed four distinct patterns of locomotion for *A. skoogi*. 'Walking' entailed moving slowly but steadily forward across the sand surface. On occasion, the lizards would interrupt their forward movement and periodically 'tap' their heads on the sand, which constituted the second mode of locomotion. This tap may have taken place when the individual was smelling items of interest on the sand surface. The third mode of locomotion involved 'rhythmic bobbing' of the head against the sand surface and was used more frequently by smaller individuals. 'Sprinting' was the

fourth mode of locomotion.

When stationary, the lizards assumed one of at least 10 different postures (Figure 9). Immediately locomotion ceased, they adopted the stereotyped postures, but after a time they appeared to 'relax', and the postures degenerated. Hamilton & Coetzee (1969) previously described the distinct nature of some postures assumed by *A. skoogi* on the slipface, and ascribed them to thermoregulatory behaviour. We recognized many more postures than they did, however, and as postural changes will affect heat transfer (Mitchell 1974), the thermoregulatory significance of the postures needs further, more specific examination.

Postures 1 and 2 (Figure 9), in which the lizards lay flat on the sand surface or raised only their heads off the sand, were very similar and often used early in the day; we considered them thigmothermic postures which the lizards used to warm themselves on the sand surface. Postures 3 and 4, alert postures in which the lizards elevated the fore part of their body only, appeared to be used when thermal stress was not too great and when the lizards were attentive to their surroundings. Posture 5 was used for urinating and defecating, often soon after the lizards had emerged from beneath the sand surface. Postures 6 and 7, in which the hind legs and tail were elevated and which we considered to have a cooling function, appeared to be the postures most closely associated with temperature regulation at the warmer end of the scale. In these postures the lizards could use convective heat loss, especially from the lower limbs, and so dissipate heat while remaining alert. Postures 8, 9 & 10, standing postures, usually were assumed in moderate thermal conditions, often between periods of locomotion and foraging on the surface of the lower parts of the dune.

Hamilton & Coetzee (1969) described four postural adjustments used by *A. skoogi*: tail lifting, body lifting, leg lifting and head lifting, and attributed them all to thermoregulatory behaviour. Although we described the 10 postures partially in terms of their effect upon the heat transfer of an individual, and some postures (e.g. 1, 2, 6 & 7) appear to be primarily thermoregulatory in function, we do not believe that temperature regulation is the only objective of postural adjustment. If postural adjustments were exclusively thermoregulatory, one would expect a good correlation between posture and microclimate. However, analysis of our results shows a lack of a close relationship between postures assumed by *A. skoogi* and locations on a dune (Figure 10) and also between postures and time of day (Figure 11a) or temperature (Figure 11b).

The observed directions of orientation of the focal animals are presented in Table 2. Lizards of all size classes spent at least half of the time on the surface parallel to the dune crest. The hourly temperatures of the two 'mock lizard' models, placed at right angles to each other on the sand surface, were averaged over the last five 24-h cycles of study (Figure 12). Between sunrise and 13h00, the main activity period of *A. skoogi* (Figure 7a), the 'mock lizard' lying parallel to the dune

crest was significantly warmer ($\chi^2 = 1732$; $df = 10$; $P < 0,005$) than the 'mock lizard' lying perpendicular to it. For the ensuing hours the temperature favoured first the perpendicular model and then again the parallel model before they became equal. The parallel orientation preferred by the live lizards therefore was more likely to favour warming than cooling.

Discussion

During the six consecutive days of observation which we conducted in July, we fortuitously experienced a great range of weather conditions. For example, mean globe temperatures during the usual activity period of *Angolosaurus skoogi* (09h00–18h00) ranged from 39°C on 16 and 17 July to 27°C on 19 July. The variety of

weather conditions within such a short period allowed us to assess the relative importance of time, temperature, and wind on the surface activity of the lizards, without the problem engendered by confounding variables such as growth, photoperiod, or any other seasonal factors.

Breeding behaviour of *A. skoogi* appears to be seasonal and concentrated in late summer (R.D. Pietruszka, pers. comm.). Thus our observations of thermoregulatory behaviour, carried out in July, were not confounded by simultaneous breeding behaviour. The timing of our observations also ensured that there was a large proportion of hatchlings in the active population on the slipface (Mitchell *et al.* in press), providing a range of sizes for comparative observations.

In contrast, Hamilton & Coetzee (1969) carried out their observations in November and it is possible that some of the behaviour they considered typical thermoregulatory behaviour may have been influenced by breeding activity. They noted a relative absence of individuals of less than 150 mm length on the slipfaces and observed that smaller individuals did not participate in thermoregulatory activities to the same extent as adults did. We know that in November there are few very small individuals in the population in general. However, we too found that small individuals did not use the more obvious thermoregulatory postures as much as adults did, which was not surprising as the smaller individuals spent a lesser proportion of time stationary on the surface than did adults (Mitchell *et al.* in press). In addition, smaller lizards tended to make more use of the cooler, and less windy portions of the diurnal activity period (Figure 8), when the cooling postures (6 & 7) would be both less necessary and less effective.

We agree with Hamilton & Coetzee (1969) that the

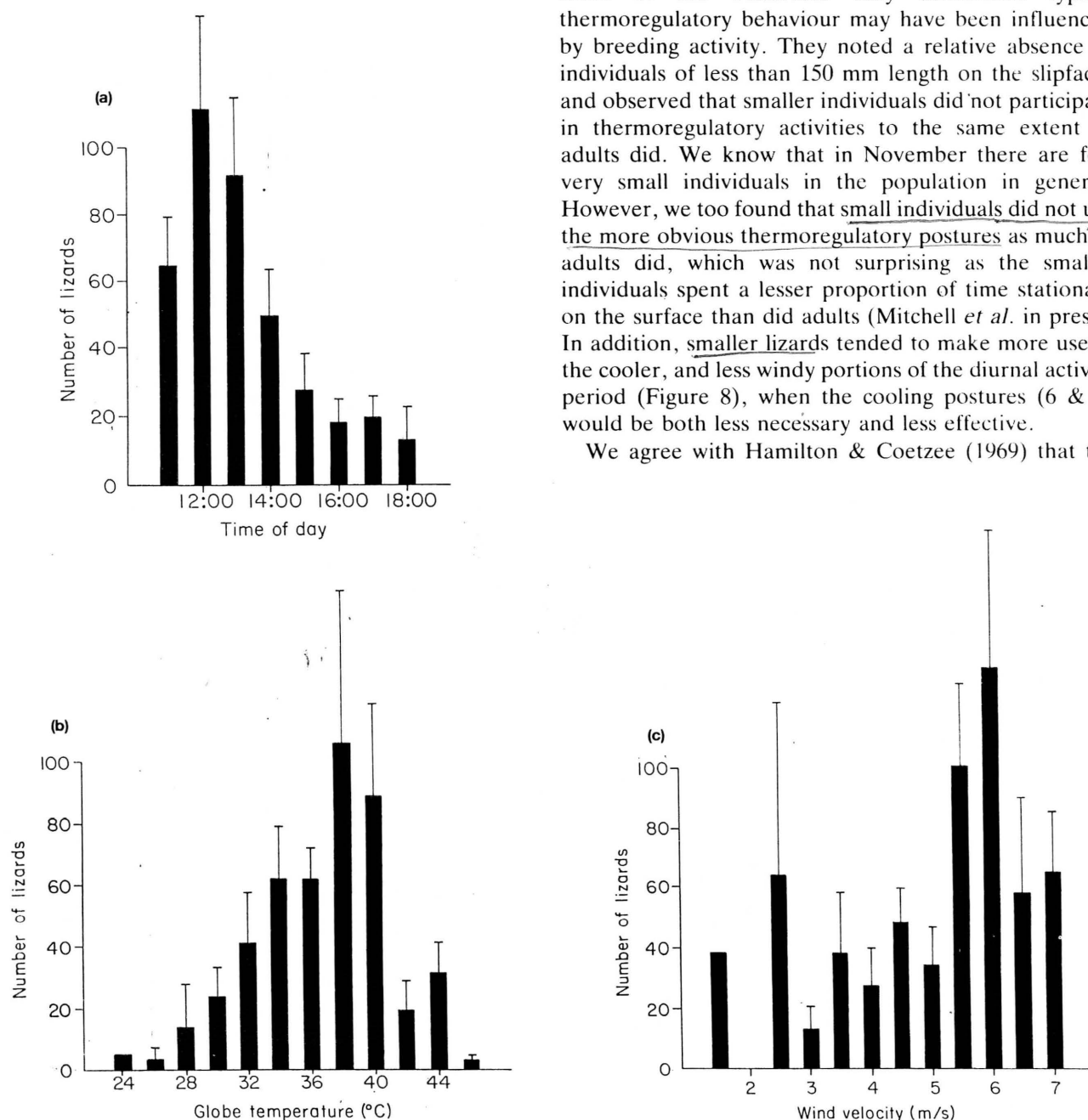


Figure 7 Mean (\pm SE) of hourly totals of all lizards sighted during each 5-min scan for the six consecutive days as a function of time of day (Figure 7a), globe temperature (Figure 7b), and wind velocity (Figure 7c).

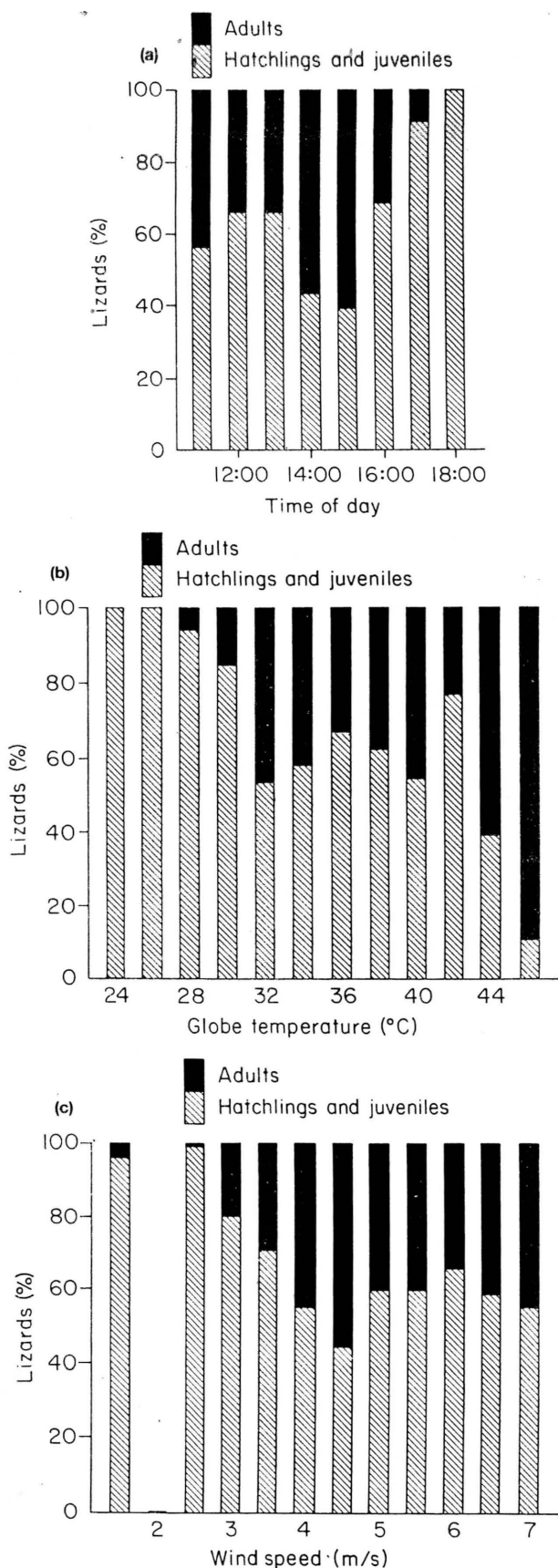


Figure 8 Percentage of smaller (hatchling and juvenile) and larger (subadult male and adult female and male) lizards, calculated from mean hourly number of lizards sighted during each 5-min scan for six days, as a function of time of day (Figure 8a), globe temperature (Figure 8b), and wind speed (Figure 8c).

peculiarities of thermoregulatory behaviour of smaller lizards can be explained, at least partially, by consideration of the relationship of body temperature to body size. The lower thermal inertia and higher surface area-to-mass ratio of the smaller animals makes them more susceptible to hyperthermia induced by solar radiation, so limiting activity in the hottest parts of the day, as well as more able to benefit from the lower radiation fluxes of the early morning and late evening. This ability to be active at lower ambient temperatures would have advantages for the smaller lizards. Not only would it extend the time available for uninterrupted foraging, but also the foraging would be less costly energetically, since metabolic rate increases rapidly with increasing ambient temperature (Mitchell *et al.* in press). We believe that smaller lizards need longer and less costly foraging, not only because they are growing, but also because of the greater proportion of wind-blown plant detritus in the diet of smaller individuals of *A. skoogi* (Pietruszka *et al.* 1986). Composed of relatively small fragment sizes, detritus requires the smaller lizards to forage longer to consume the requisite amount of food, compared with the larger individuals, who consume large portions of nara stem or other food at a single bite.

Another point addressed by Hamilton & Coetzee (1969), to which we are able to contribute only peripherally, concerns the actual body temperatures which the lizards strive to attain. Hamilton & Coetzee (1969) suggested that *A. skoogi* on the dune slipface attempts to attain and maintain body temperatures in the range of 38°C–42°C, attempts to remain on the surface as long as possible, and that the postural adjustments serve to protect the extremities from noxious temperatures but do not serve to cool the lizard's body. Mitchell *et al.* (in press) measured mean preferred body temperatures of 36.8°C ($SE \pm 0.4^\circ C$) for *A. skoogi* in the laboratory. In our study, we noted that the greatest number of lizards were active when globe temperature was in the range 36°C–38°C (Figure 7b), figures compatible with the laboratory measurements, but not reconcilable with Hamilton & Coetzee's (1969) interpretation. Other unanswered questions include the importance of temperature variation in the upper subsurface environment (0–100 mm) to *A. skoogi* in body temperature regulation and in detection of surface conditions as well as the range of body temperatures tolerated by individual lizards in the field.

We cannot agree with Hamilton & Coetzee (1969) that the thermoregulatory postures of *A. skoogi* are concerned with protecting extremities against noxious temperatures, rather than regulating whole-body temperature. In the first place, in the two thigmothermic postures, there is maximum body contact with the substrate. Secondly, in the cooling postures on the dune, the lizards never raised the front limbs (Figure 9) and there is no reason to believe that the hind limbs are more sensitive to noxious heat. If lizards were placed experimentally on to a surface heated to noxious temperatures, they indeed lifted all four limbs simultaneously, and assumed a stereotyped posture we

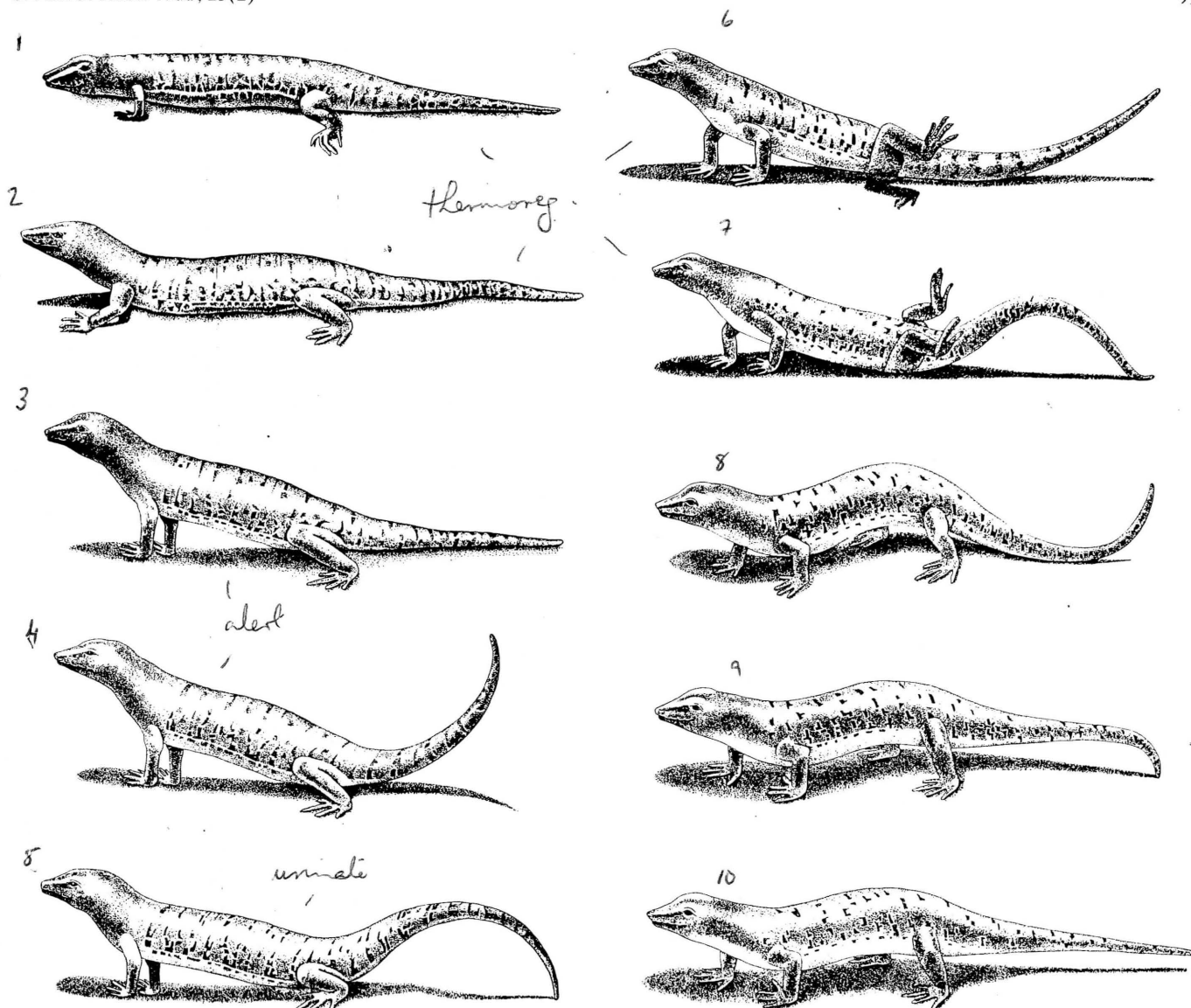


Figure 9 Stereotyped postures adopted by *Angolosaurus skoogi* when not in motion on the slipface. Postures 1 to 5 and 6 to 10 are arranged in two columns from upper left to lower right. We identified postures 1, 2, 6 & 7 as primarily thermoregulatory, 3 and 4 as alert postures, 5 as associated with defecation/urination, and 8, 9 & 10 as associated with locomotion. Art work by Valerie Myburgh, University of the Witwatersrand.

never saw on the slipface. We believe that these lizards use only their hind limbs as convective heat exchangers. Their large surface areas, and the fine diameters of the toes, provide them with high convective heat exchange coefficients, and the coefficients will be further enhanced if the lizard raises its feet into the mobile air above the surface boundary layer (Mitchell 1974). Provided air temperature is less than body temperature, raised feet constitute an effective mechanism for dissipating metabolic heat or heat derived from solar radiation. Indeed, we believe that the thermoregulatory 'dances' of other Namib lizards, for example *Aporosaurus anchietae* which lifts from one to four legs simultaneously (Louw & Holm 1972), serve the same function.

As a result of the effects of radiation and wind, the subsurface sands and the slipface surface provide a thermal mosaic of which *A. skoogi* is able to take advantage. The animals we observed appeared to modify

their surface activity pattern according to the prevailing microclimate. A prominent variation in activity pattern was the trend towards a bimodal pattern on 'warm' days and a unimodal pattern on 'cooler' days. *A. skoogi* not only altered time and duration of surface activity with varying microclimates, but also surface behaviour, for example position on the slipface, posture, and locomotion.

Our original question concerned the role thermoregulatory behaviour plays in the overall surface activity of *A. skoogi*. If thermoregulatory behaviour were trivial or absent, orientation on the dune as well as postures, patterns of locomotion and locations on the dune would be determined by non-thermal factors or be entirely random. Our observations of a population of *A. skoogi* active on a slipface during a variety of weather conditions suggest that these features of the lizard's surface activity indeed are non-random, and may be related to temperature regulation.

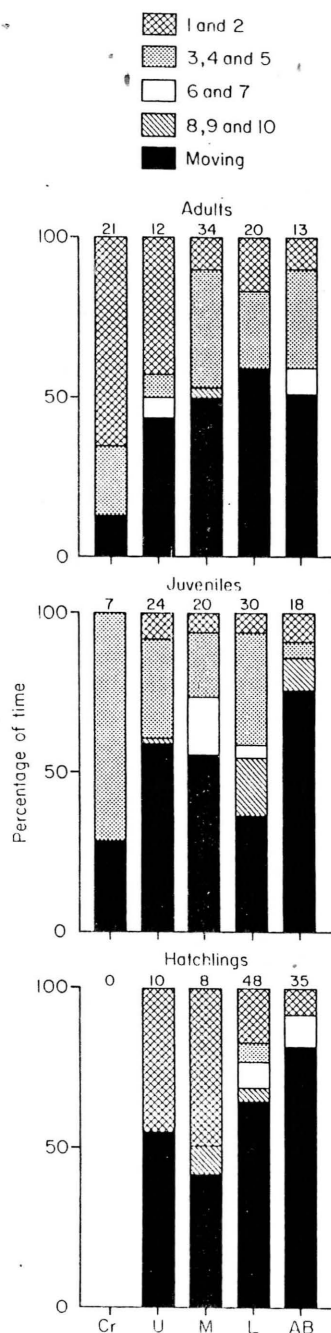


Figure 10 Percentage of time which hatchling, juvenile, and adult lizards spent in the four types of posture while at five locations on the dune (Cr — crest; U, M and L — upper, middle and lower slipface; AB — avalanche base; see Figure 2).

At the other extreme, surface activity could be exclusively thermoregulatory, or be largely dictated by thermoregulatory demands. For theoretical reasons, discussed elsewhere in the context of tenebrionid beetles (Seely & Mitchell 1987), we believe that if the lifestyle of *A. skoogi* were dictated by thermoregulatory demands, it would never emerge from the sand. The lizard does emerge, and when it does so, its surface activity is multi-functional, rather than exclusively thermoregulatory.

For example, about half of all time spent on the surface, by lizards of all sizes, is spent in locomotion, an

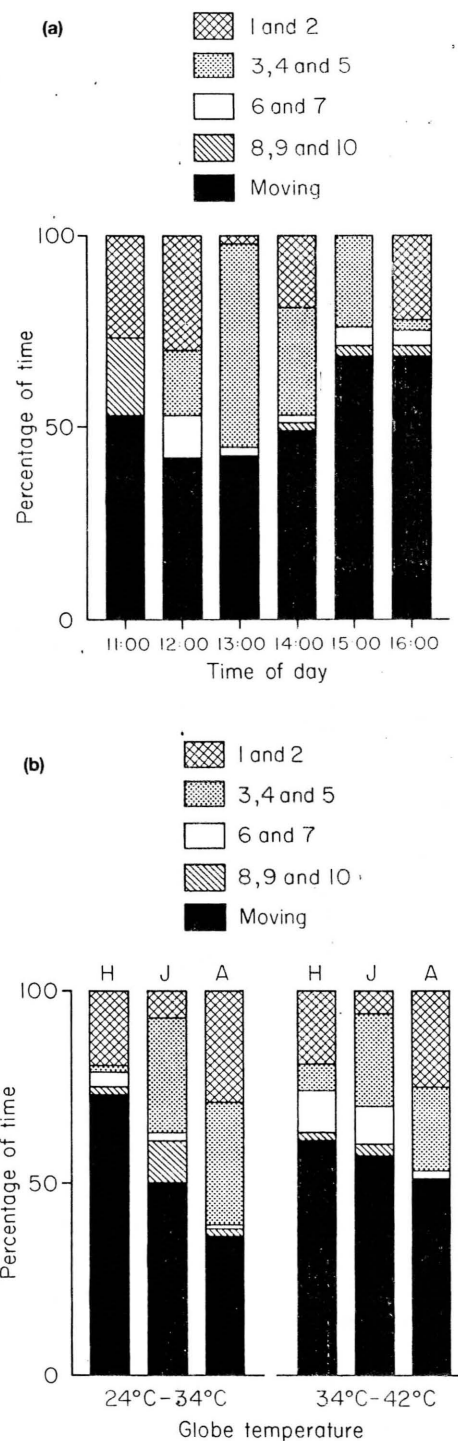


Figure 11 Percentage of time which the lizards spent in the four types of posture during different times of the day (Figure 11a) and as a function of globe temperature (Figure 11b).

activity associated with foraging or social interaction rather than thermoregulation.

On the basis of our results, we conclude that thermoregulatory behaviour is facultative in the surface activity of *A. skoogi*. The lizards, it would appear, do not emerge primarily for thermoregulatory purposes but also for other important activities. We think that emergence is primarily governed by an innate circadian rhythm. Laboratory observations also have indicated that the lizards continue to emerge, at approximately the

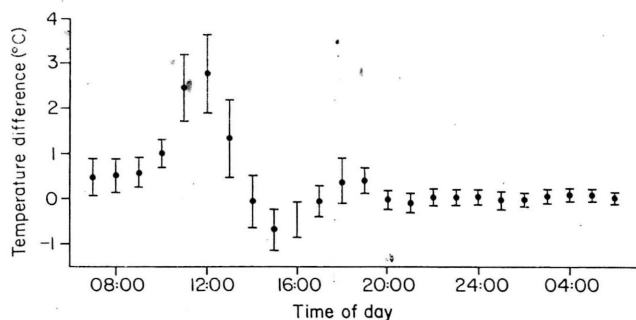


Figure 12 Difference between temperatures of the 'mock' lizards parallel to and perpendicular to the dune crest: mean (\pm SE) over five days of observation.

same time of day as they do in the field, even under constant temperature, continuous lighting conditions (Mitchell *et al.* in press). As shown by the different activity patterns which we recorded for the different size groups, this innate pattern of diurnal surface activity can be modified extensively by prevailing microclimate, of which the important parameter is globe temperature and perhaps wind. As has been the case with other slipface species (e.g. Holm & Edney 1973; Louw & Holm 1972; Robinson & Seely 1980), *A. skoogi* appears to take opportunistic advantage of suitable environmental conditions as they occur within the thermal mosaic of the subsurface and surface sand of the dune slipface. Also, it has at least four clearly thermoregulatory postures, which it employs intermittently, to increase or decrease body temperature. However, it has at least six other stereotyped postures which are not primarily thermoregulatory. By relatively minor variations in its site selection on the slipface, augmented by transient use of behavioural thermoregulation, *A. skoogi* can attain a body temperature within a range which allows continuation, for several hours each day, of the foraging activity or social interaction for which the lizards have emerged.

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References

- ALTMANN, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49: 227-267.
- ANDERSSON, L.G. 1916. Notes on the reptiles and batrachians in the Zoological Museum at Gothenburg. *Meddelanden fran Goteborgs Musei Zoologiska Afdelning* 9, 41 pp.
- BARENBRUG, A.W.T. 1974. Psychrometry and Psychrometric Charts. Chamber of Mines of South Africa, Johannesburg. 59 pp.
- BOGERT, C.M. 1949. Thermoregulation in reptiles, a factor in evolution. *Evolution* 3: 195-211.
- COINEAU, Y., LANCASTER, N., PRODON, R., & SEELY, M.K. 1982. Burrowing habits and substrate selection in ultrapsammophilous tenebrionid beetles of the Namib Desert. *Vie Milieu* 32: 125-131.
- FITZSIMONS, V.F. 1953. A new genus of gerrhosaurid from southern Angola. *Ann. Transvaal Mus.* 22: 215-217.
- HAMILTON III, W.J. & COETZEE, C.G. 1969. Thermoregulatory behaviour of the vegetarian lizard *Angolosaurus skoogi* on the vegetationless northern Namib Desert dunes. *Sci. Pap. Namib Desert Res. Sta.* No. 47, 95-103.
- HERTZ, P.E. 1981. Adaptation to altitude in two West Indian anoles (Reptilia: Iguanidae): field thermal biology and physiological ecology. *J. Zool. (London)* 195: 25-37.
- HOLM, E. & EDNEY, E.B. 1973. Daily activity of Namib Desert arthropods in relation to climate. *Ecology* 54: 45-56.
- HUEY, R.B. 1982. Temperature, physiology and the ecology of reptiles. In: *Biology of the Reptilia*, Vol. 12., (eds.) C. Gans and F.H. Pough. Academic Press, New York. pp. 25-91.
- KOCH, C. 1961. Some aspects of abundant life in the vegetationless sand of the Namib desert dunes. *J. S.W. Afr. Sci. Soc.* 15: 8-34, 77-92.
- KOCH, C. 1962. The Tenebrionidae of southern Africa. XXXI. Comprehensive notes on the tenebrionid fauna of the Namib Desert. *Ann. Transvaal Mus.* 24: 61-106.
- LANCASTER, N. 1982. Dunes on the Skeleton Coast, Namibia (South West Africa): geomorphology and grain size relationships. *Earth Surface Processes and Landforms* 7: 575-587.
- LOUW, G.N. & HOLM, E. 1972. Physiological, morphological and behavioural adaptations of the ultrapsammophilous, Namib Desert lizard *Aporosaurus anchietae* (Bocage). *Madoqua* 1: 67-85.
- MITCHELL, D. 1974. Convective heat loss from man and other animals. In: *Heat Loss from Animals and Man*, (eds.) J.L. Monteith and L.E. Mount. Butterworths, London. pp. 59-76.
- MITCHELL, D., SEELY, M.K., ROBERTS, C.S., PIETRUSZKA, R.D., McCLAIN, E., GRIFFIN, M., & YEATON, R.I. In press. On the biology of the lizard *Angolosaurus skoogi* in the Namib Desert. *Madoqua*.
- PIETRUSZKA, R.D., HANRAHAN, S.A., MITCHELL, D. & SEELY, M.K. 1986. Lizard herbivory in a sand dune environment: the diet of *Angolosaurus skoogi*. *Oecologia (Berlin)* 70: 587-591.
- ROBINSON, M.D. & SEELY, M.K. 1980. Physical and biotic environments of the southern Namib dune ecosystem. *J. Arid Environ.* 3: 183-203.
- SCHULZE, B.R. 1972. South Africa. In: *World Survey of Climatology*, Vol. 10, *Climates of Africa*, (ed.) J.F. Griffiths. Elsevier, Amsterdam. pp. 501-586.
- SEELY, M.K. 1978. The Namib Dune Desert: an unusual ecosystem. *J. Arid Environ.* 1: 117-128.
- SEELY, M.K. 1983. Effective use of the desert dune environment as illustrated by the Namib tenebrionids. In: *New Trends in Soil Biology*, (eds.) P. Lebrun, H.M. Andre, A. de Medts, C. Gregoire-Wibo, G. Wanthly. Dieu-Brichart, Louvain-la-Neuve, Belgium. pp. 357-368.

- SEELY, M.K. 1984. The Namib's place among deserts of the world. *S. Afr. J. Sci.* 8: 155-158.
- SEELY, M.K. & LOUW, G.N. 1980. First approximation of the effects of rainfall on the ecology and energetics of a Namib Desert dune ecosystem. *J. Arid Environ.* 3: 25-54.
- SEELY, M.K. & MITCHELL, D. 1987. Is the subsurface environment of the Namib Desert dunes a thermal haven for chthonic beetles? *S. Afr. J. Zool.* 22: 57-61.
- SOKAL, R.R. & ROHLF, F.J. 1981. *Biometry*. W.H. Freeman, San Francisco.
- SPELLERBERG, I.F. 1972. Thermal ecology of allopatric lizards (*Sphenomorphus*) in southeast Australia. I. The environment and lizard critical temperatures. *Oecologia* (Berlin) 9: 371-383.
- STEYN, W. 1963. *Angolocaurus skoogi* (Andersson) — a new record from South West Africa. *Cimbebasia* 6: 8-11.
- YAGLOU, C.P. 1968. Thermometry. In: *Physiology of Heat Regulation and the Science of Clothing*, (ed.) L.H. Newburgh. Hafner, New York. pp. 70-77.

Erratum

S. Afr. J. Zool. 23(2) (1988) page 96 (last paragraph second column)

Table 2 was omitted and is printed below

Table 2 Orientation assumed when lizards were inactive on a sand dune, as a percentage of all sightings

	Parallel to crest (%)	Perpendicular to crest (%)	Intermediate orientation (%)
Hatchlings	63	21	16
Juveniles	51	18	31
Females and immature males	50	37	13
Adult males	72	27	17