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Boundary Layer Microclimate and *Angolosaurus skoogi* (Sauria: Cordylidae) Activity on a Northern Namib Dune

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Boundary layer microclimate was measured at seven locations on a representative dune in the northern Namib, using 150 mm black globe thermometers. The boundary layer microclimate offered greater temporal stability and greater spatial diversity than was evident from measurements of sand surface temperature at the same locations, and differed appreciably from the concurrent free stream microclimate, especially in having non-directional air movement with attenuated speed. Boundary layer globe temperatures, which are better indices of local heat transfer than are single microclimate parameters, correlated better than did single parameters with surface activity of *Angolosaurus skoogi* lizards resident on the dune. Site selection on the dune, and emergence/burying patterns, could be related to conditions prevailing in the boundary layer. Results confirmed a previous conclusion that thermoregulatory behaviour of *A. skoogi*, while on the dune surface, is facultative, supporting other obligatory surface activities.

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INTRODUCTION

Sand dunes are important habitats for invertebrates and small vertebrates in the Namib Desert (e.g., Koch, 1961, 1962; Seely, 1978). Animals occupy the subsurface environment of the dune for most of each 24-hour period, and some remain there permanently, but individuals may emerge at various times of day or night, and for various durations. Many dune species use the surface for feeding, drinking and social interactions (Seely, 1983), and variations of emergence with season, and with shorter-term changes in weather, suggest that microclimate is an important determinant of surface activity patterns. Microclimate-related surface activity could be directed towards satisfying primary thermoregulatory demands, or could be facultative, directed towards achieving a thermal status adequate to permit continuation of other surface activities. Thermally-induced shifts between bimodal and unimodal surface foraging activity have been recorded for a variety of dune ectotherms (e.g., Holm and Edney, 1973; Robinson and Seely, 1980; Seely, Mitchell, Roberts and McClain, 1988), although the shifts from diurnal to crepuscular or nocturnal activity noted in some deserts (e.g., Kramm and Kramm, 1972) are not prominent in the Namib. Analyses of dune microclimate and animal behaviour have shown that there is no simple relationship between any single microclimate parameter (e.g., air temperature, wind speed) and surface activity. Indeed, the way in which microclimate affects behaviour has not been elucidated for any Namib species.

Angolosaurus skoogi (Andersson) (Cordylidae) is a large (up to 120 g), long-lived, diurnal, endemic lizard, living in the northern Namib dunes (Mitchell, Seely, Roberts, Pietruszka, McClain, Griffin and Yeaton, 1987). During surface activity it appears to thermoregulate facultatively, apparently taking some advantage of variations in the microclimate across a dune which it combines with use of stereotypic postures for gaining or losing heat (Seely *et al.*, 1988). However, feeding as well as social interactions, particularly during the summer breeding season, also take place on the dune surface in locations not necessarily selected or optimal for temperature regulation. Despite several attempts (Pietruszka, 1988; Mitchell *et al.*, 1988; Seely *et al.*, 1988), we have been unable to separate out the influence of microclimate from other factors on location and timing of their surface activity.

We have attempted to exploit the relatively large day-to-day variations in microclimate that occur in winter (July) to analyse site selection (Seely *et al.*, 1988). Differential use of the top, middle and lower regions of the dune surface was manifest (Fig. 1), but no close correlation between microclimate and site selection was evident. However, on the basis of activity patterns, and concomitant microclimate data and observations in Seely *et al.* (1988), we may make the following predictions:

1) microclimate conditions on the top and crest of a dune are cooler than preferred. This prediction is based on the large proportion of crest behaviour that was thigmothermic, and the almost complete absence from the crest of juveniles, which have low thermal inertia and high surface area to mass ratio.
2) microclimate conditions on the slipface are warmer than elsewhere on the dune. This prediction is based on extensive use of the slipface by juveniles earlier in the day and by adults toward the middle of the day; in both cases, adoption of postures conducive to warming was an important part of their surface behaviour. Also supporting this prediction was use by juveniles of the avalanche base (where wind-blown detritus is concentrated) for late afternoon foraging on warm days whereas they remained on the slipface during cooler afternoons.

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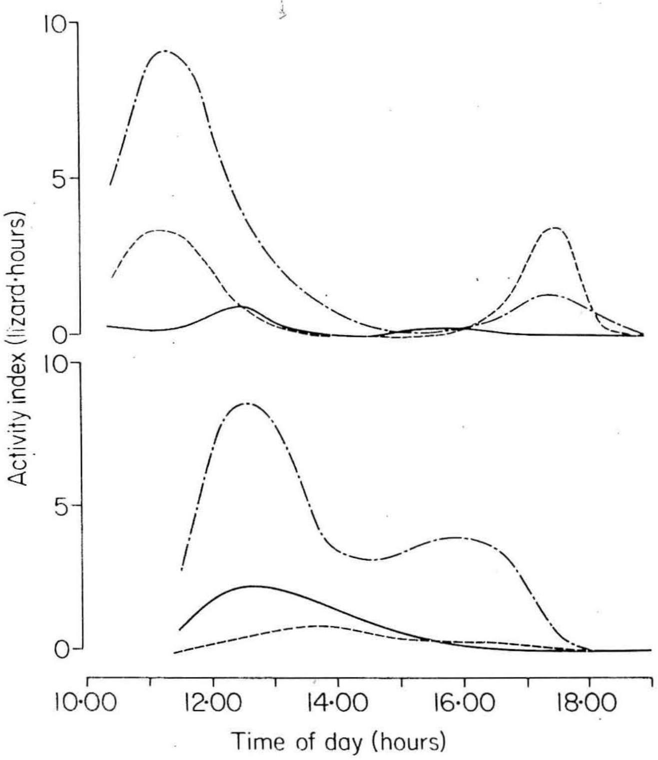

Fig. 1

Mean surface activity of *Angolosaurus skoogi* on crest (solid line), slipface (dot-dashed line) and avalanche base and adjacent plain (dashed line) on a hot July day (above), during which morning activity was concentrated on the slipface, and afternoon activity on the avalanche base and adjacent plains, and a cool July day (below), when activity was concentrated on the slipface throughout the day. The activity index was calculated as the product of the number of lizards active on the surface and the period for which they were active, based on scans at five minute intervals. Data from Seely *et al.* (1988).

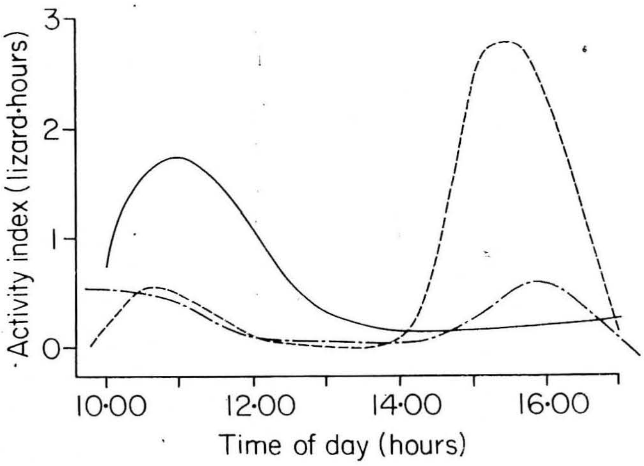

Fig. 2

Mean surface activity of *Angolosaurus skoogi* on crest (solid line), slipface (dot-dashed line) and avalanche base and adjacent plain (dashed line) during three days in February, with greatest use of top and crest during morning hours and of avalanche base and adjacent plain during the afternoon. Activity index was calculated as in Fig. 1, and averaged for three days. Data from Pietruszka (1988).

Differential use of the dune surface also was noted in summer (February), although the pattern was entirely different (Fig. 2). Working on the assumption that animals selected locations on the dune surface according to the sand surface temperatures prevailing there, Pietruszka (1988) attempted to correlate differential occupation with sand surface temperatures, but found no significant correlation for the population at large. Comparison of Pietruszka's data with those of Seely *et al.* (1988) leads to an additional prediction:

3) seasonal factors, apparently unrelated to microclimate, induce gross perturbations of surface activity patterns.

Although patterns of dune occupation differed between winter and summer, there was clear evidence for site selection on the dune surface by *A. skoogi* in both seasons. Moreover, it is highly likely that microclimate influenced site selection on a dune, even though no straightforward connection has been found. Animals on the sand surface are not usually in intimate contact with the sand, but occupy the boundary layer adjacent to the surface, so sand surface temperature itself may not be an appropriate parameter of the dune microclimate. Seely *et al.* (1988) found that, of all factors they investigated, globe temperature correlated best with surface activity of *A. skoogi*. Since globe temperature integrates the effects of air temperature, radiation, and wind speed, it is a potentially better index than any single microclimate parameter of heat transfer between lizard and environment.

Seely *et al.* (1988) measured globe temperature at just one location on the dune. We considered that a better understanding of the relation between microclimate and lizard activity might be obtained by measuring globe temperature at all the dune locations occupied by surface-active lizards. We therefore placed globes in the boundary layer at seven sites across a dune slipface and, with corresponding sand surface probes, measured boundary layer and sand surface temperatures throughout the activity period of *A. skoogi*. We also compared wind speed in the boundary layer with free stream wind measurements.

MATERIALS AND METHODS

The study area and specific dune were described in Seely *et al.* (1988). The area was located on the south bank of the usually dry Unjab River, approximately 15 km inland from the coast on the eastern side of the northern Namib dunes (20° 09′ S, 13° 14′ E). In this area, S to SW winds create barchanoid ridges up to 10 m high.

Mean monthly temperatures range between 13 °C and 19 °C, recorded mean annual rainfall is 22–25 mm per year, and winds of 4 m/s blow for up to 50 % of the time (Lancaster, 1982). Boundary layer microclimate was measured and *Angolosaurus skoogi* were observed during January 1987 on a single dune typical for the region, with a surface area approximately 2000 m^2.

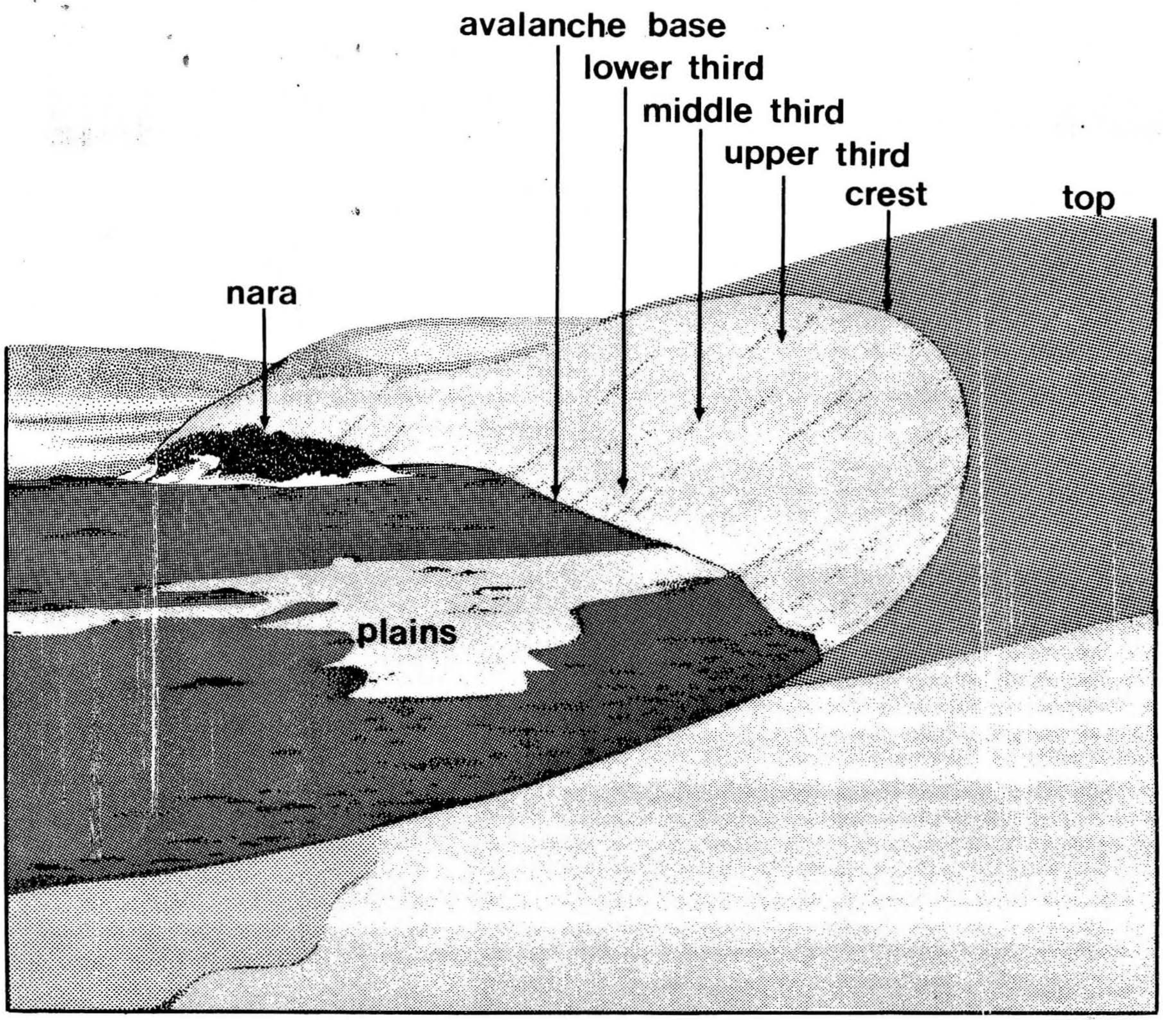

Fig. 3

Sketch of a typical slipface identifying locations used in the text. With permission, from Seely *et al.* (1988).

Microclimate parameters measured were globe temperature (Yaglou, 1968) and sand surface temperature at seven locations on the dune: dune top; dune crest; upper, middle and lower thirds of the slipface; avalanche base; and plain (Fig. 3). The globes consisted of 150 mm diameter hollow copper balls, painted matt black, with copper-constantan thermocouples inserted through a small hole into the centre. Each globe was mounted on a peg that maintained the globe in position on the dune and about 10 mm above the sand surface. To measure surface temperature, a copper-constantan thermocouple was soldered on to a 80 mm × 80 mm square of expanded copper mesh. This sand shoe, floating on the sand surface, provided a local average rather than a point measure of surface temperature and helped to maintain the thermocouple in contact with the shifting sand surface. Globe and sand surface temperatures were measured at five minute intervals throughout the day using a portable thermocouple thermometer (Bailey BAT-12) located in a hide near the study dune.

Free stream microclimate data were collected in the study area on another slipface, approximately 500 m from the observation dune, to avoid disturbance of the lizards. On the top of this dune, at 1,5 m above sand surface, hourly averages of one-minute readings were recorded by a data logger (Campbell CR-21). The variables logged were ambient temperature, ambient relative humidity, solar radiation flux, free stream wind speed, and local sand surface temperature (using a white thermistor thermometer lying on the sand surface). Wet and dry bulb temperatures were measured at hourly intervals with a sling psychrometer, and relative humidity and water vapour pressure were calculated using psychrometric charts (Barenbrug, 1974). Wind speed also was measured on the upper half and lower half of the slipface, using Lambrecht totalizing cup anemometers approximately 300 mm above the surface, and near the avalanche base using an Alnor hot-wire anemometer approximately 20 mm above the surface.

Using binoculars from a hide, we counted all *A. skoogi* active on the surface of the study dune at five minute intervals throughout the day. During each scan (e.g., Altmann, 1974), every individual was classified into one of six size groups and its location on the dune was recorded (Seely *et al.*, 1988).

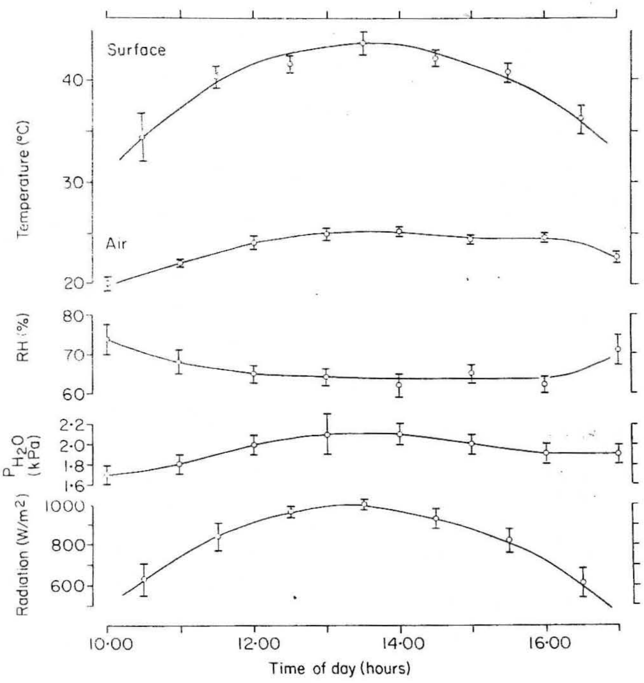

Fig. 4

Free stream microclimate of dune top (mean ± *S.E.*, *n* = 4 days): ambient air temperature (°C), ambient relative humidity (%), ambient water vapour pressure (kPa) and solar radiation flux (W/m2). Nearby sand surface temperature on dune top is also shown.

RESULTS AND DISCUSSION

During five days of intense observation the weather was similar for four days, largely clear with intermittent cloud in the morning. The fifth day was overcast throughout the morning. On all days a cool SW wind was blowing. Mean values of free stream microclimate conditions were calculated for the four similar days (Fig. 4). Although it was mid-summer, relatively cool conditions prevailed: air temperatures varied between 20 °C and 25 °C throughout the day, radiation at 13h30 was 1000 W/m2, and the water vapour pressure remained relatively constant at about 2 kPa.

On the study dune slipface, globe temperatures in the boundary layer were, as expected, much lower than sand surface temperatures and, unexpectedly, were less variable from day to day (Fig. 5). Moreover, the time course of globe and sand surface temperatures differed. For example, on the avalanche base globe temperatures peaked between 11h00 and 11h30, whereas sand surface temperatures were at a maximum at 13h30. Solar noon occurs at 13h00 in this area. These observations demonstrate that it is not possible to predict times of maximum heat stress on the lizards either from sand surface temperatures or from solar radiation measurements. Rate of heating and cooling also differed between globe and sand surface, with globe temperatures remaining relatively constant over long periods at all sites. Both sand temperature and boundary layer globe temperature increased rapidly in the morning, and, in contrast to measurements of Hamilton (1973), sand temperature fell only slightly less rapidly in the late afternoon. However, boundary layer globe temperature fell much less rapidly in the afternoon, a phenomenon that may explain why afternoon activity periods (in bimodal patterns) tend to be much longer than morning periods.

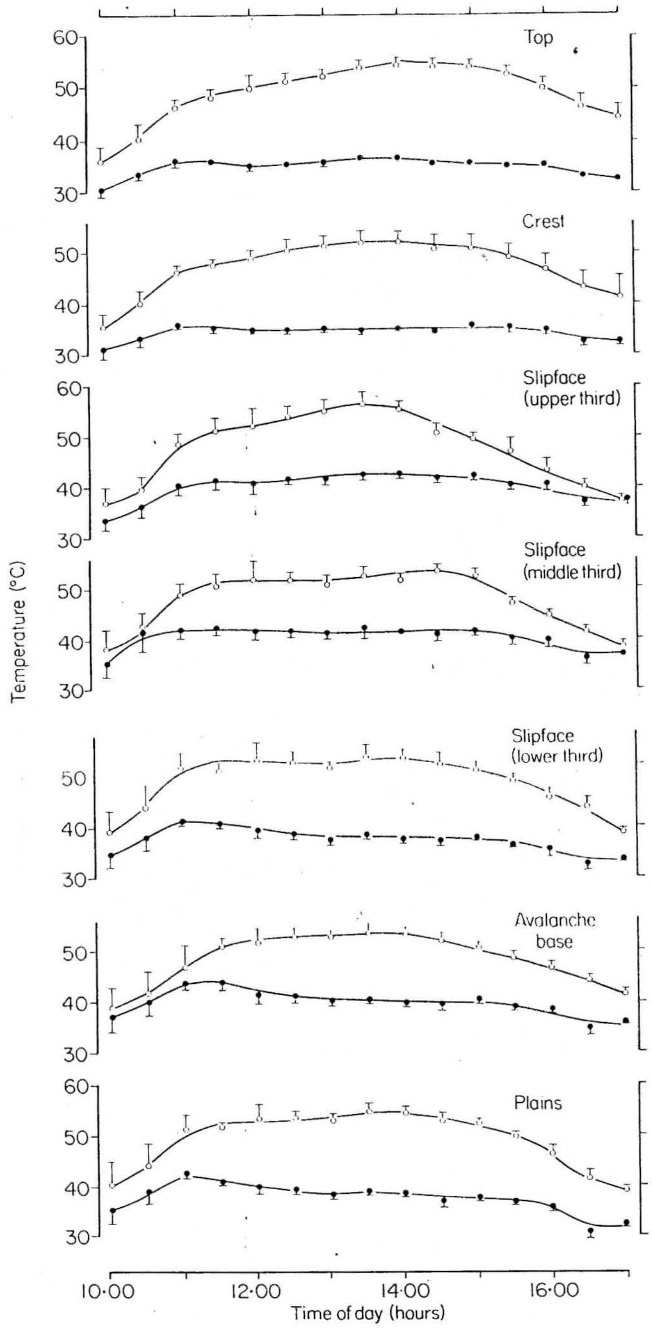

Fig. 5

Sand surface (open circles) and boundary layer globe (closed circles) temperature (mean ± *S.E.*, *n* = 4 days) for dune top, crest, upper third of slipface, middle third of slipface, lower third of slipface, avalanche base and adjacent plain.

During the day, sand surface temperatures of above 50 °C were measured frequently. Such high temperatures are not compatible with survival, if lizards active on the surface attained these temperatures. In contrast, globe temperatures in the boundary layer increased to a maximum of 43 °C at the hottest part of the day. The difference between globe and sand surface temperatures varied with position on the dune (Fig. 5). Although sand temperature varied little between dune top and base, boundary layer globe temperature remained below 36 °C on the top and crest, while exceeding 42 °C for many hours on the slipface.

As air temperature and radiation are the same across a dune, the differential effect of wind on globe and sand surface temperature, combined with differences in wind speed at different locations on the dune, must be responsible for the positional variations. Speed of the free wind stream increased until about 12h00 each day (Fig. 6). From midday onward to the end of the lizard activity period, wind speed remained at approximately 5–6 m/sec. Wind speed on the slipface remained substantially lower than free stream wind speed throughout the day. Wind totalizers on the upper and lower half of the slipface measured similar wind speeds, the time course of which differed from that of free stream wind, increasing slowly until about 12h00 and then decreasing at the end of the day. This unexpected decrease we presume to be caused by changing wind direction. Wind speed measured very close to the sand surface near the avalanche base using a hot-wire anemometer was low and consistent throughout the day (Fig. 6). No difference was noted if the wand was held perpendicular or parallel to the slope of the slipface, indicating no directionality of wind flow very close to the surface. Thus, wind speeds indicated by an anemometer in the free air stream bear no resemblance to the wind regimen experienced by lizards and other organisms living close to the slipface surface.

Although microclimate conditions were similar on four of the five days of measurement, as indicated by small standard errors in Fig. 4, differences occurred between daily values and mean conditions. Lizard activity also differed. On a day with higher than average ambient temperature (Fig. 7a), average wind speed, and average radiation (except in the early morning and late evening), boundary layer globe temperature was higher than average throughout the day. Lizard activity began early and recurred later in the day; few animals were active after 12h00 and before 15h00, even though boundary layer globe temperature on the crest remained below 38 °C. On a very gusty day with intermittent cloud leading to low radiation flux (Fig. 7b), lizards were active throughout much of the day after initially emerging. Globe temperatures varied widely between five minute readings, even on the crest, providing a continually changing thermal environment. Temperatures on the slipface and avalanche base were reduced below the mean, such that globe temperatures of 35 °C to 40 °C were available in the boundary layer throughout even the hottest part of the day. Boundary layer and microclimate conditions on the day that remained overcast for the entire morning differed considerably from mean values (Fig. 7c). Intermittent lizard activity commenced later and ceased earlier than on the ordinary or gusty day; boundary layer globe temperatures were below average during both morning and late afternoon. Globe temperatures reached their highest values of the entire study on the avalanche base and slipface for a short period after the

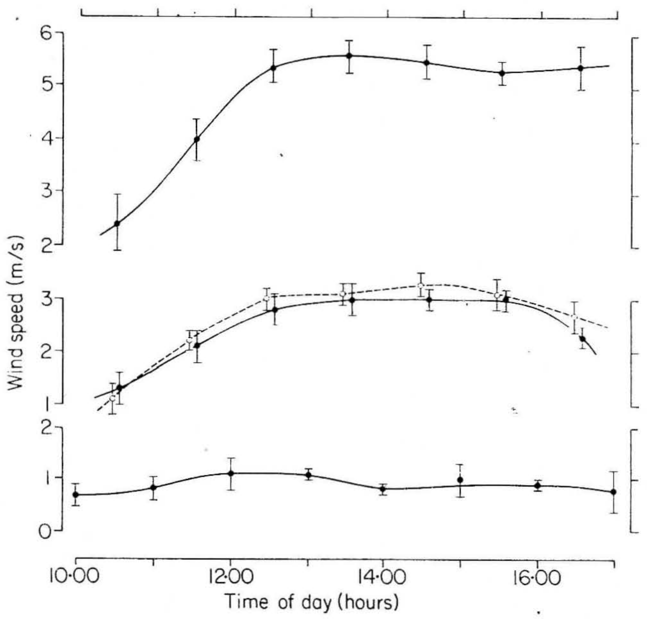

Fig. 6

Wind speed (mean ± *S.E.*, *n* = 4 days) of the free wind stream measured on dune top (above), on the slipface measured by totalizers on the upper and lower half (centre), and on the avalanche base measured by hot-wire anemometer (below).

cloud cover had disappeared, and lizards relinquished the surface.

Lizard surface activity, recorded at five minute intervals, was summarized for the four days with similar weather conditions (Fig. 8). Overall activity level was relatively low and not as polarized as during warmer conditions (compare Fig. 1 and Fig. 8). The very clear-cut variation of activity with time, previously noted particularly for juveniles, was not evident in activity of the total population (Fig. 8). Instead, the pattern was of weakly bimodal surface activity with avoidance of top and crest of the dune, where temperatures were cooler than on the slipface.

When given a choice, *A. skoogi* selects a temperature in the laboratory of 36,8 ± 0,4 °C (Mitchell *et al.*, 1988) and is most active in the field at a globe temperature range of 38 °C to 40 °C, as measured by a globe thermometer on the sand surface (Seely *et al.*, 1988). Globe temperatures in this range were available in the boundary layer during much of the lizards' activity period during our recent study (Fig. 9). Moreover, the thermal mosaic of temperatures that affect lizards, i.e., those indicated by integrated measure of the globe, was more variable than would be predicted from sand surface temperatures. The coefficient of variation *(C. V.)* of sand surface temperatures measured at one time and several locations on a dune has been used as a measure of variability of the thermal mosaic (Pietruszka, 1988). On the basis of our recent data, the *C. V.* of globe temperatures in the boundary layer was two-thirds greater than that of concurrent sand surface temperatures, indicating greater opportunities for microclimate selection than evident from sand surface temperature.

Our measurements indicate that the microclimate in the

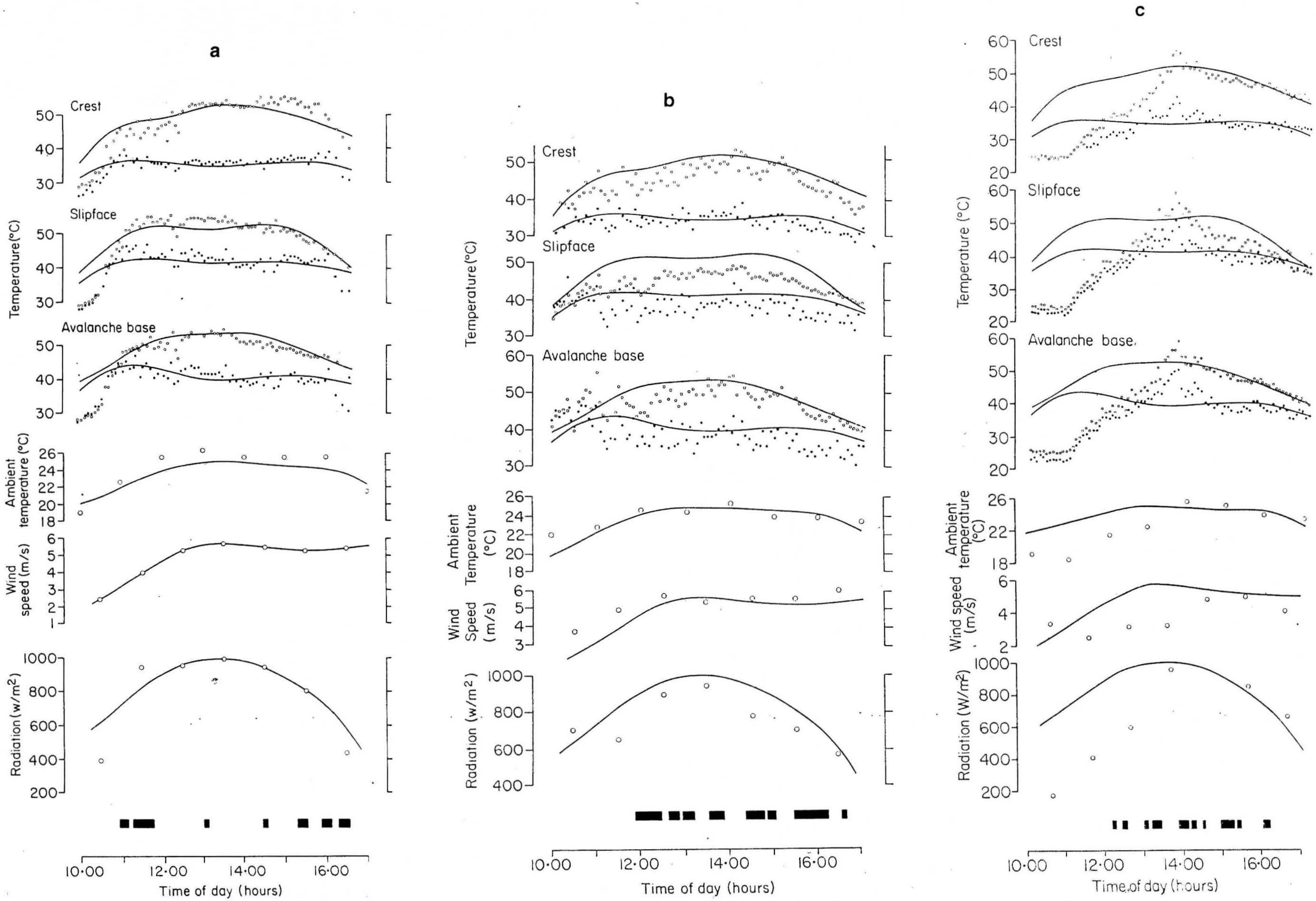

Fig. 7. Selected boundary layer (at crest, middle slipface, avalanche base) and free stream (ambient temperature (°C), wind speed (m/s) and radiation (W/m2)) microclimate measurements for an ordinary day (**7a**), a gusty day with intermittent cloud (**7b**) and a partially overcast day (**7c**) in January 1987. Dots represent individual five minute measurements of sand surface (open circles) and globe (closed circles) temperatures at three dune locations and mean hourly microclimate measurements (open circles) on the dune top. The solid line represents mean values for four days during the same period (Figs 4 & 5). At the bottom of the figures, solid bars indicate times of lizard activity.

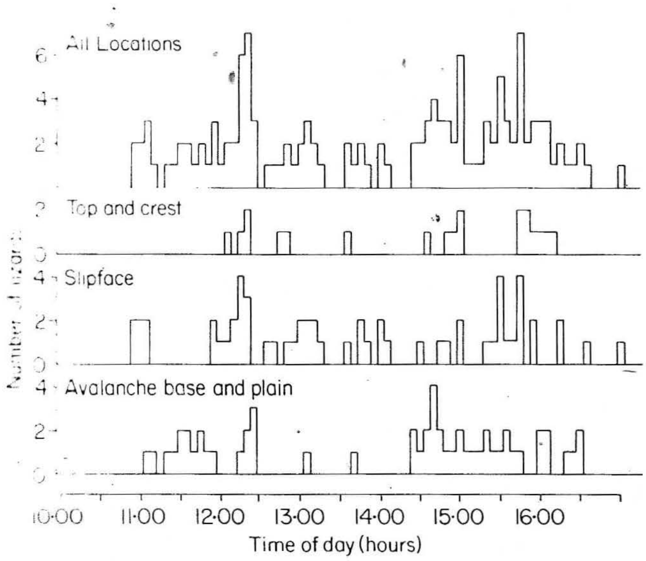

Fig. 8

Total number of lizards sighted during scans at five minute intervals over four days of observation for all locations, dune top and crest, slipface, and avalanche base and plain.

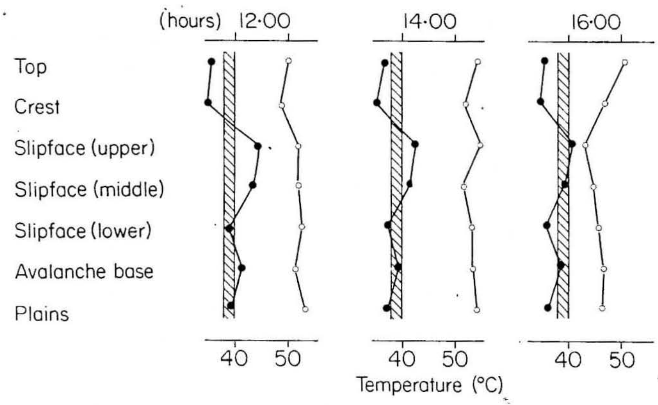

Fig. 9

Mean sand surface (open circles) and boundary layer globe (closed circles) temperatures ($n = 4$ days) for seven locations on the dune at three times of day. The hatched vertical bar indicates the range of globe temperature at which the greatest number of *Angolosaurus skoogi* are active, based on previous extensive measurements at the same site (Seely *et al.*, 1988).

thermal boundary layer with which lizards exchange heat has several characteristics not self-evident from measurements either of free stream microclimate or sand surface temperatures. The microclimate prevailing in the boundary layer is less extreme, and more stable throughout the day, than would be predicted from measurements of sand surface temperature, radiation and ambient temperature. Moreover, the thermal mosaic is richer than predicted from sand surface temperature or free stream measurements. On the slipface, wind speed is much lower than cool free stream wind speed typical of the region.

Measurements of thermal conditions in the boundary layer indeed confirmed the predictions we made concerning the nature of dune microclimate and factors affecting lizard surface activity. First, during our study, conditions on the dune top and crest were conducive to greater heat loss rates than the lizards required (see Fig. 9). We expect that a similar situation would prevail throughout most of the year. Hamilton and Coetzee (1969) suggested that *A. skoogi* preferentially select the dune top and crest because other dune locations are too hot. Their suggestion may be correct for very hot days, but we believe that, in general, the dune top and crest is unfavourably cool for *A. skoogi* thermoregulation, and their presence there must be related to other activities, in line with our third prediction. Secondly, although it is not evident from measurements of sand surface temperature, lower locations on the dune continue to offer a relatively warm, still microclimate in the late afternoons, when free stream wind speeds typically are high. Although this microclimate may not be warm enough for adults, juveniles and hatchlings, with their high surface area to mass ratio, can exploit it to prolong surface activity, particularly foraging, as we observed in winter months when there are many young lizards in the population (Seely *et al.*, 1988).

It remains for us to identify the seasonal factor unrelated to microclimate that induces occupancy of dune top and crest. We believe the factor is breeding behaviour; high regions of the dune offer the best vantage and patrolling areas. Breeding behaviour is at its peak in February, and that is when dune top and crest occupation is most prevalent (see Fig. 2). We suggest that during January 1987 the crest was mainly too cold for prolonged occupation by *A. skoogi* (Figs 8 & 9), despite the advancing breeding season. In winter, even though there are extremely hot days (hotter, for example, than the summer days we encountered in January), the dune top and crest is largely neglected, because breeding behaviour is in abeyance.

In conclusion, we have shown that analysis of the effect of microclimate on surface activity of *A. skoogi* can be improved by measuring microclimate variables that actually influence the lizards' heat transfer, by using an integrating thermometer positioned in the boundary layer. Moreover, measurements outside the boundary layer, of either free stream microclimate or sand surface temperature, can be misleading, because they represent conditions that bear no straightforward relationship to the lizards' heat transfer. We suspect that the same principles will apply to other surface-active animals.

The best instrument for measuring appropriate thermal factors will be one having heat transfer characteristics similar to the organism under investigation; it should have similar conductive, convective, radiant (and ideally evaporative) transfer coefficients. Artificial lizards have been used in this way (Bakken, Santee, and Erskine, 1985). In our study, we used the standard (Yaglou, 1968) 150 mm diameter black globe thermometer. Although our current measurements clearly are an improvement over previous procedures, they are still not ideal. The 150 mm globe is too big to be appropriate for *A. skoogi* for two reasons. The first is that the instrument should have cross-sectional area transverse to the wind direction similar to the physical dimensions of the lizard, to approximate the convective (and evaporative) transfer coefficient (see Mitchell, 1974). The second is that the thermal boundary layer is so steep close to the sand surface that much of the globe would be exposed to a microclimate closer to free stream microclimate than lizards would be. Globes of appropriate size should be used for each organism.

Finally, our study, as before (Seely *et al.*, 1988), failed to reveal surface behaviour so devoted to thermoregulation that it excluded other behaviour. On the contrary, we believe that *A. skoogi* has a band of tolerated body temperatures that allows it to continue other surface activities, and its thermoregulatory behaviour is facultative, aimed at keeping body temperature within that band but not at any selected level. The width of the band may depend on the strength of drives competing with thermoregulation; so, for example, breeding behaviour may induce acceptance of otherwise unacceptably cool locations. The potency of surface site or posture selection as a thermoregulatory behaviour is modest, particularly on a vegetationless dune, compared with the option of seeking refuge below ground (Stevenson, 1985; Seely *et al.*, 1988), and the only thermoregulatory behaviour we have seen *A. skoogi* use at the expense of other functions is sand-diving. Bradshaw (1988) denies that behaviour can represent an adaptation, in the rigorous evolutionary sense, of a desert reptile, but we believe that sand-diving is the heritable modification that allows *A. skoogi*, but not other members of its family, to occupy the Namib dunes.

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