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.

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.
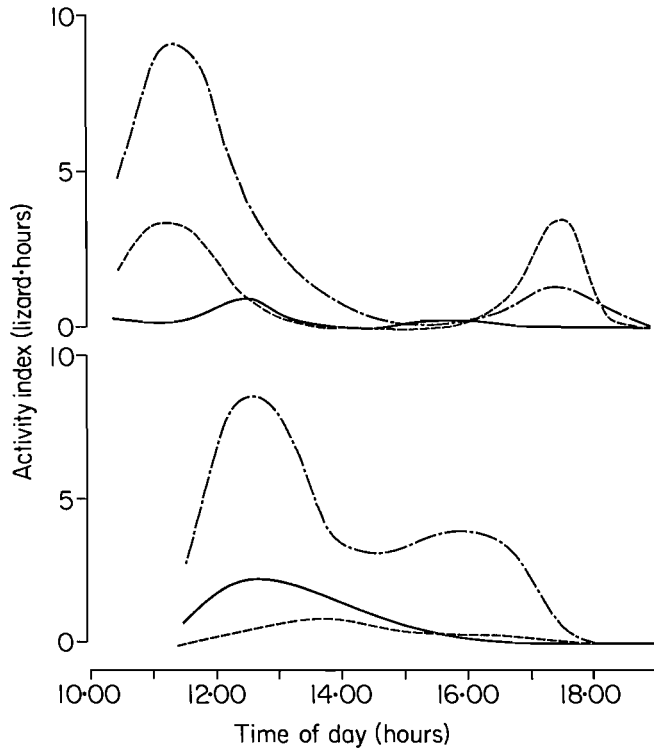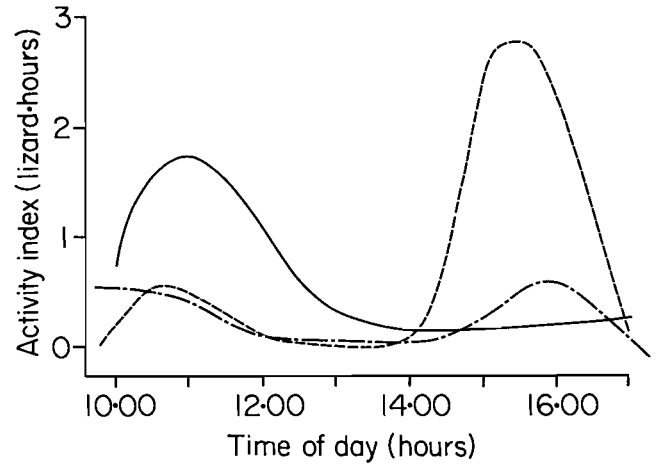
Fig. 1

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 m².
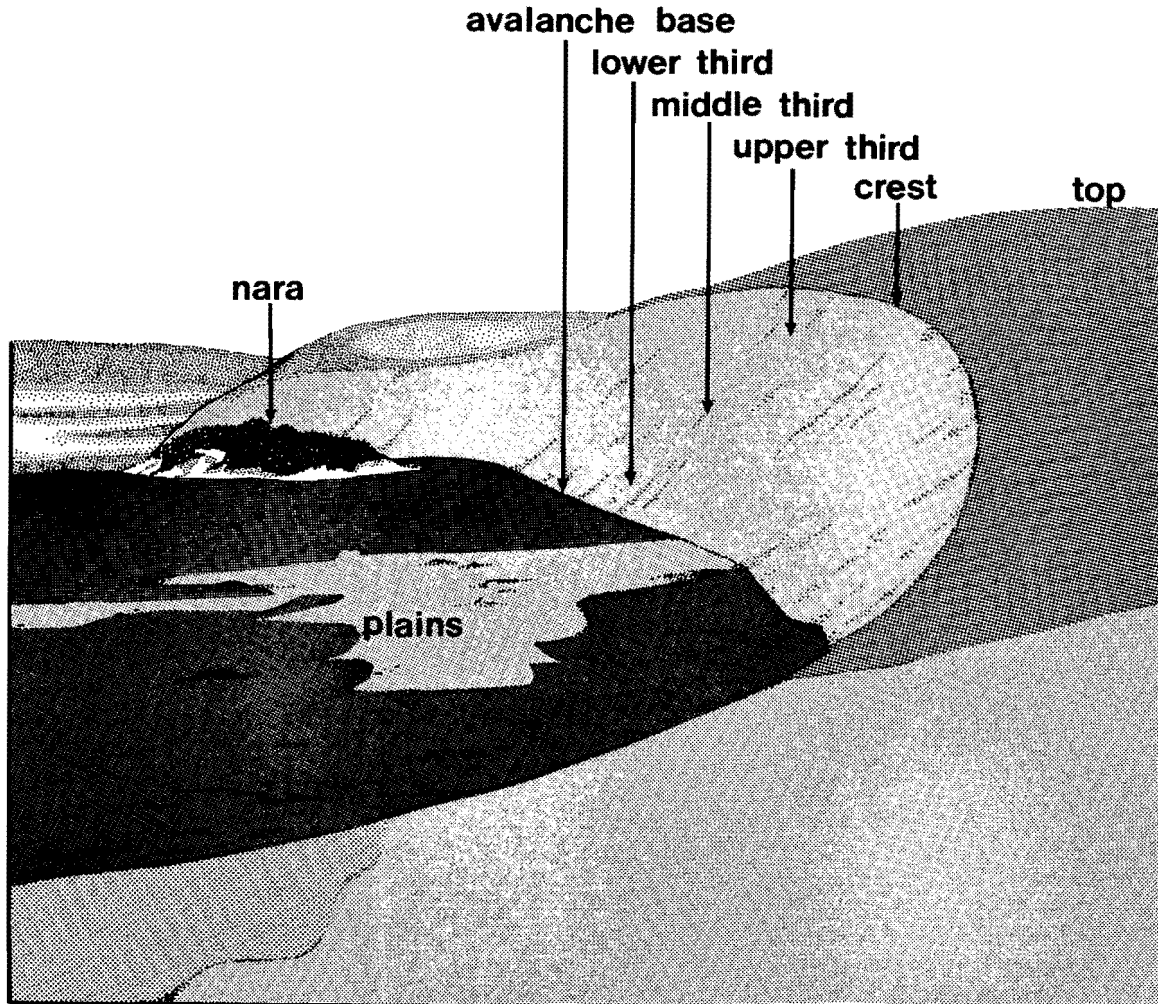
Fig. 3
Sketch of a typical slipface identifying locations used in the text. With permission, from Seely *et al.* (1988).

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 obser-

vation 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).
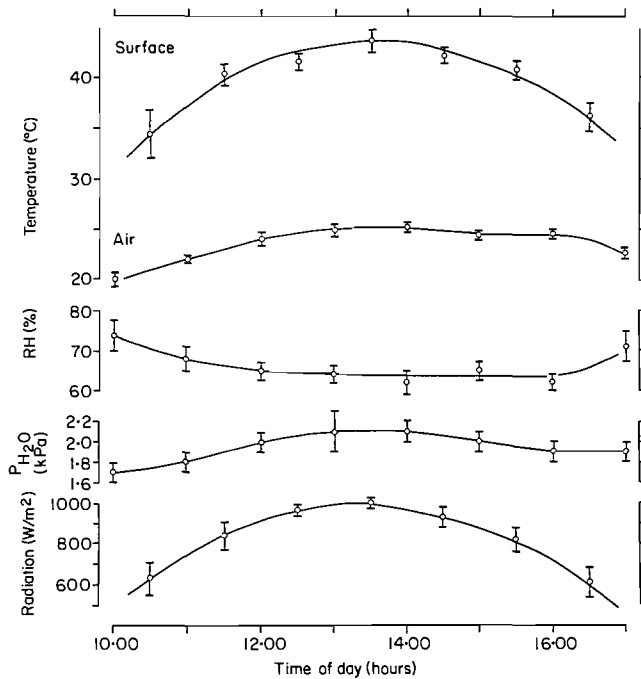
Fig. 4

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
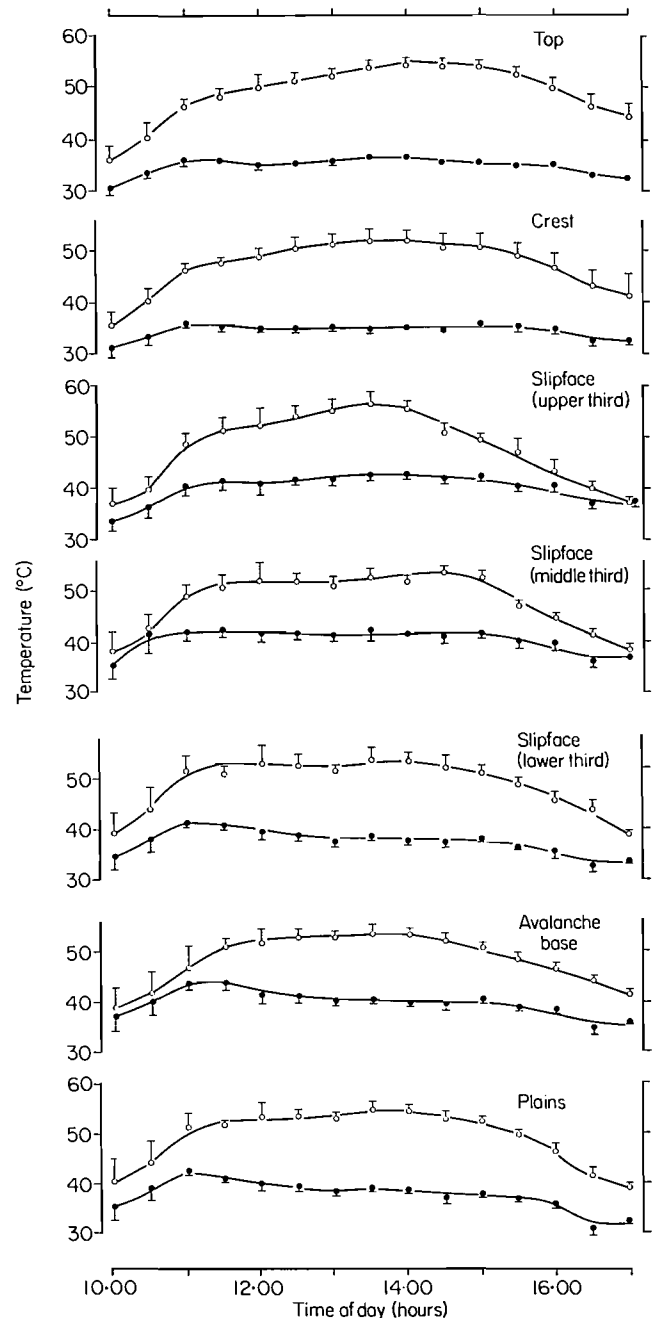
Fig. 5

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.

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.

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
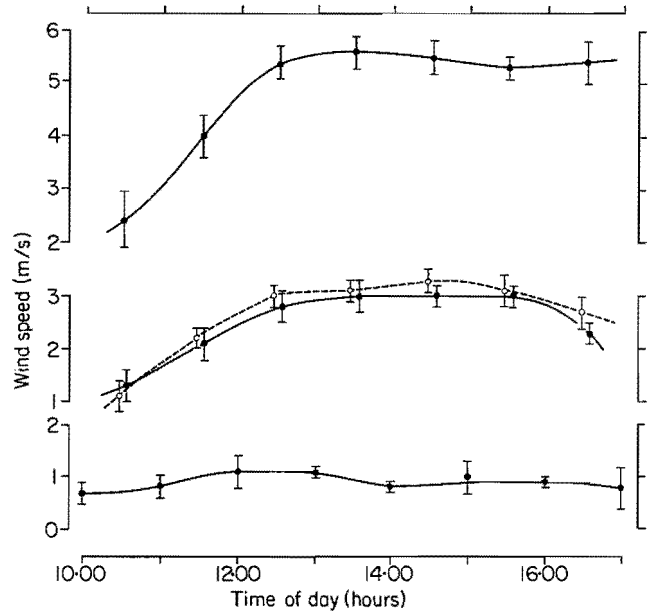

Fig. 6

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
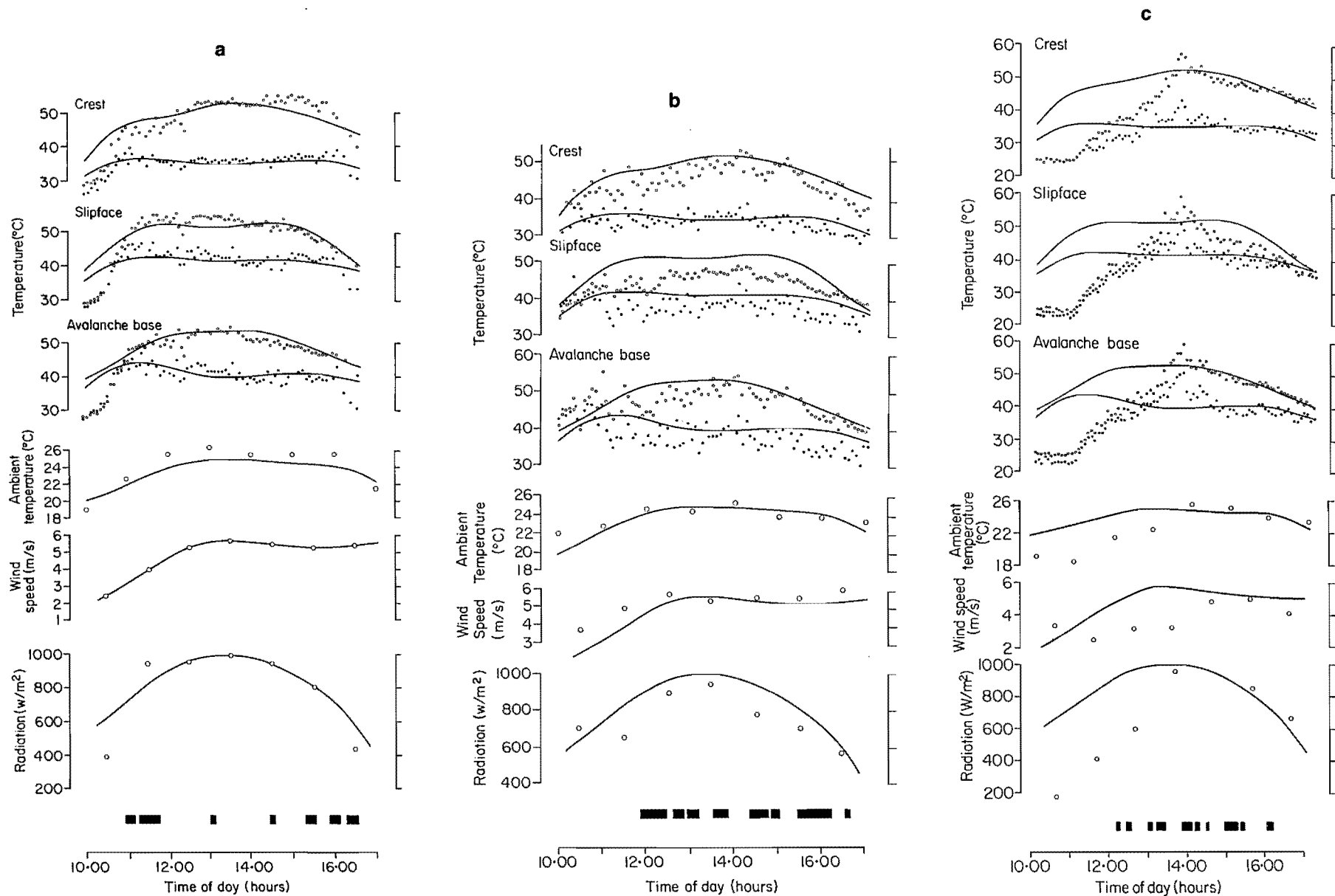
Fig. 7. Selected boundary layer (at crest, middle slipface, avalanche base) and free stream (ambient temperature (°C), wind speed (m/s) and radiation (W/m2)) microclimate measurements for an ordinary day (**7a**), a gusty day with intermittent cloud (**7b**) and a partially overcast day (**7c**) in January 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.
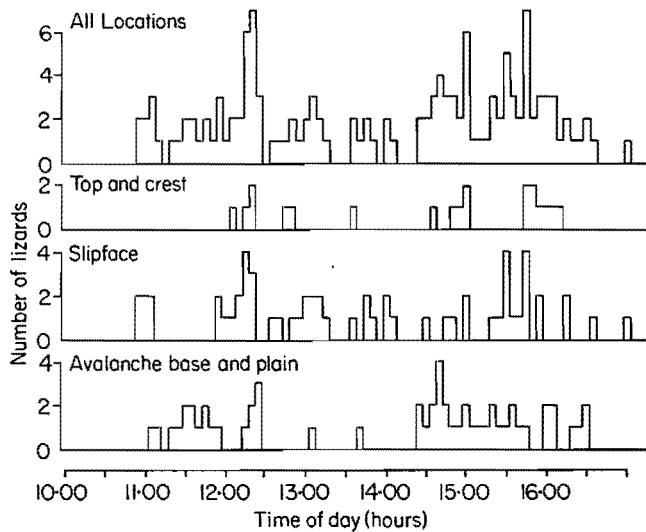
Fig. 8

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).

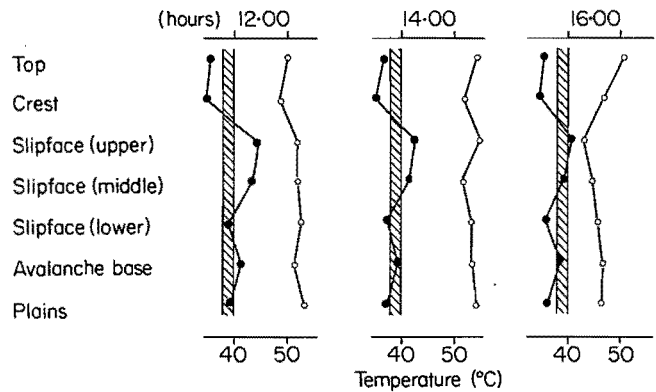It remains for us to identify the seasonal factor unrelated to

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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Comments on the Reproductive Biology of the Namib Desert Dune Lizard, *Aporosaura anchietae*, During Two Years of Very Different Rainfall

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Aporosaura anchietae maintained continuous reproduction over a 24-month period during which rainfall, prey diversity and prey abundance changed greatly. Lizards responded rapidly to improved environmental conditions by accumulating large quantities of fat. Females utilized the fat body to produce various clutches of one or two large eggs over a prolonged period. The annual egg production declined by approximately 50 % when rainfall decreased from 125 mm to 12 mm. The average clutch was 1,52 and 1,19 eggs in the wet and dry years, respectively. Territorial males used stored energy to offset caloric imbalances caused by restricted foraging. The advantages of small female body size and a large hatchling are discussed in relation to the Namib dune habitat. Environmental conditions favouring aseasonal reproduction in extreme deserts are described, and aspects of the reproductive behaviour and polygynous breeding system are related to the dune ecology.

INTRODUCTION

Much of our knowledge about the reproductive biology of desert lizards is derived from studies of species living in temperate habitats and having well-defined seasonal cycles (Ballinger, 1983; Dunham, Miles and Reznick, 1988). With few exceptions (Hoddenbach and Turner, 1968; Vinegar, 1975; Ballinger, 1977; Vitt, Van Loben Sels and Omart, 1978; Dunham, 1980; Van Loben Sels and Vitt, 1984), reproductive cycles have been analysed for a single season. Thus, limited information exists on how changing levels of rainfall and productivity affect lizard reproduction.

Outside tropical latitudes aseasonal reproduction in lizards is uncommon, and in desert species it is rare. To my knowledge, besides *Aporosaura anchietae*, only two small lacertids (*Acanthodactylus pardalis* and *Eremias olivieri*) in the north-western Sahara Desert are reported to have continuous spermiogenesis (Saint Girons, 1984).

Previous research on the reproductive biology of *A. anchietae* has shown that males and females undergo gametogenesis throughout the year, but fat bodies have distinct seasonal cycles. The proportion of reproductive females varies monthly, and the average clutch size, 1,3 eggs, is one of the lowest known for non-gekkonid lizards (Dunham *et al.*, 1988). Lizards mature in 4 to 7 months, and females can produce a maximum of 4 clutches per year (Goldberg and Robinson, 1979).

Eighty-two months before the initiation of this research (March 1969 to January 1976) the study site (Gobabeb) did not receive one month with effective rainfall (i.e., 20 mm, Lancaster, Lancaster and Seely, 1984). In January 1976 and continuing to March, 123,6 mm of rain fell at Gobabeb (Table 1). In 1977 rainfall was 12,9 mm.

The purpose of this paper is to analyse how changing levels of rainfall and prey abundance affected the amount of energy stored and the number of eggs produced; to determine how different fat reserves are utilized for reproduction and maintenance; to describe the reproductive behaviour of *A. anchietae;* and to briefly consider under what environmental conditions aseasonal reproduction is possible in extreme deserts.

MATERIALS AND METHODS

The results reported here are derived from analyses of collections of lizards taken in the sand dunes near Gobabeb from January 1976 to December 1977. Sample sizes and collection periods are indicated in the relevant tables.

The histological techniques used to determine the reproductive and fat body cycles of males and females are described in Goldberg and Robinson (1979). Total fat was quantified by the Soxhlet total fat extraction procedure. The ash-free dry weight was determined by incinerating carcasses in a muffle furnace at 550 °C. Behavioural and demographic data are from a long-term study of a marked population near the Namib Research Institute, Gobabeb. The monthly rainfall (1975–1979) was provided by the Desert Ecological Research Unit of Namibia, Gobabeb.

RESULTS

Lipid cycles and reproduction

Lipids were stored in a single, visceral, abdominal body and in paired, lateral, subcutaneous fat bodies. Monthly changes in the total fresh weight of the two fat depots are summarized in Table 2 and illustrated for females in Fig. I. Fat body weights increased rapidly following the unusually heavy rains during the first months of 1976. No sample was taken in February 1976, but it is assumed that fat accumulated, eggs developed,

Fig. I
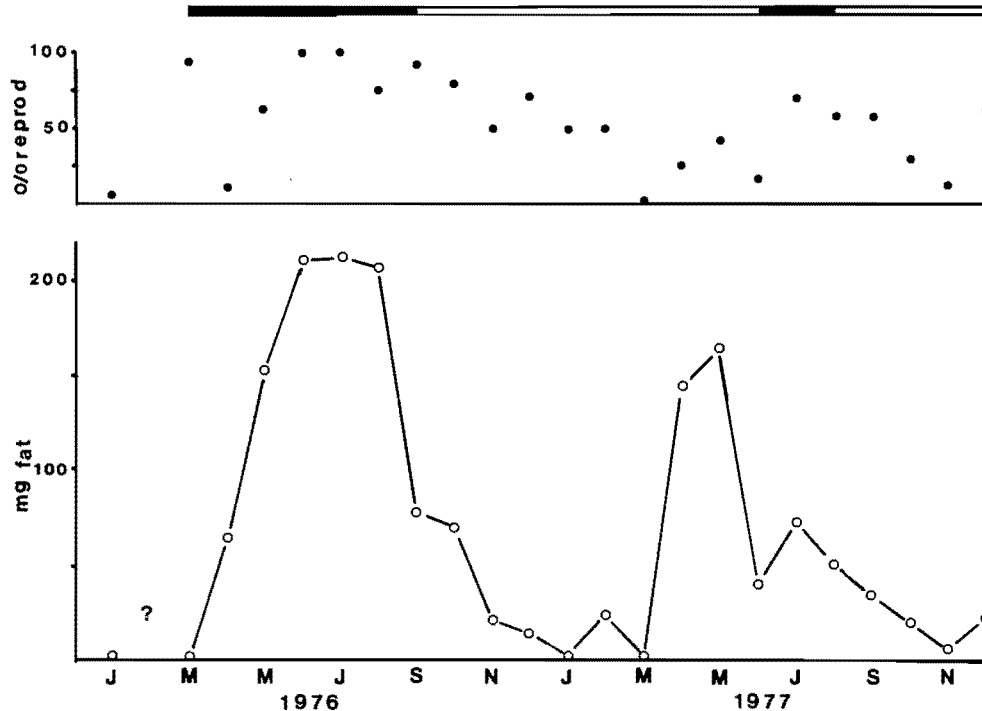
Fresh weight (mg) of female fat body and percent of the females with oviducal eggs. Solid and clear bars indicate periods when two- and one-egg clutches were produced, respectively.

and lipids were depleted, as occurred from January to March 1977. Beginning in March 1976 the fat bodies grew continuously, reaching maximum mass after approximately 120 days. By July males had stored an average of 109,1 mg fat/gm lean body weight (3,89 mg/day), and females 67,2 mg/gm lean body weight (1,80 mg/day). Depletion of the fat bodies required about 180 days. Males used 2,54 mg fat/day and females 1,17 mg/day.

From January to April 1977 the desert received 12,8 mm of precipitation (Table 1), and the lizards responded opportunistically to the January rainfall by accumulating fat and reproducing. As in the previous year, fat body mass began to increase rapidly in March. However, maximum mass was attained by males in 30 days and was 55 % less than the year

before; females reached peak fat body weights after 60 days, and the mass was 23 % less. Females had larger fat bodies than males (47 mg fat and 36 mg fat per gram lean body weight), a reversal of the previous year's trend. Fat body lipids were depleted by November.

Females were sampled in January, April, June and September of 1977 to determine how the reproductive cycle was related to storage and utilization of lipids contained in the fat bodies and the carcass tissues (Table 3). Tissue lipids accumulated rapidly from January to April, but then more slowly through the winter. The fat body mass increased gradually from January to April, then quickly rose to the maximum level in June. Most of the fat body had been used by September. In general, there was an inverse relationship between the

Table 1

Monthly rainfall (mm) at Gobabeb, Namibia, during the period 1975–1978. Data for the 10-year mean are from Seely and Stuart (1976).

	J	F	M	A	M	J	J	A	S	O	N	D
1975	0,9	0,0	0,9	0,0	1,0	0,0	2,1	0,0	0,0	0,0	1,8	0,0
1976	84,0	6,5	33,1	0,0	0,0	0,0	0,0	0,0	0,0	1,5	0,0	0,0
1977	0,1	4,3	0,0	8,5	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
1978	1,0	49,3	41,3	17,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
10-year mean	2,2	1,8	5,7	1,2	1,2	0,2	0,4	1,8	1,4	0,7	0,7	0,6

Table 2

Fresh weight (mg) of the fat bodies and proportion of reproductive male and female *Aporosaura anchietae* (Goldberg and Robinson, 1979). Eggs refers to the number of females in the sample with one or two oviducal eggs.

	Males			Females				
	n	mg fat	% sperm	n	mg fat	% reprd.	eggs one	two
1976								
Jan.	9	0,0	100	14	0,0	8	0	0
Mar.	12	2,4	100	13	2,6	92	3	2
Apr.	11	103,8	100	18	65,7	11	0	1
May	11	281,4	100	8	154,1	63	0	0
June	12	268,5	100	8	213,2	100	0	7
July	10	466,9	100	7	215,7	100	0	2
Aug.	12	200,9	100	9	208,6	78	2	3
Sept.	12	154,7	100	10	78,9	90	3	3
Oct.	9	155,0	100	12	72,0	83	7	0
Nov.	13	152,9	100	13	23,8	50	4	0
Dec.	10	34,0	100	9	16,1	70	5	0
1977								
Jan.	9	9,5	100	15	4,6	50	2	0
Feb.	10	48,0	90	13	25,2	46	4	0
Mar.	9	34,7	67	16	4,3	0	0	0
April	9	211,1	78	8	145,7	25	0	0
May	14	115,6	86	5	164,6	40	0	0
June	10	87,0	100	7	41,2	14	1	0
July	14	53,1	100	10	74,6	70	2	4
Aug.	11	93,5	100	5	52,4	60	1	1
Sept.	9	51,3	100	9	36,9	60	4	0
Oct.	12	26,8	100	12	21,0	31	3	0
Nov.	10	11,9	100	12	7,5	15	1	0
Dec.	12	21,4	100	14	23,0	67	4	0

Table 3

Distribution of lipids in the tissues and fat bodies of female *Aporosaura anchietae* in 1977. Lipid mass in mg dry weight and body mass is ash-free dry weight (AFDW). Values are mean and standard deviation (below).

	n	Tissue	Fat body	Total fat	Body mass	Fat/ AFDW
January	10	45,6	41,6	87,2	436,8	0,182
		27,8	64,9	81,1	67,9	0,152
April	16	98,5	63,2	161,7	584,9	0,262
		46,8	48,5	95,7	97,1	0,122
June	17	115,6	138,0	253,6	625,1	0,385
		38,0	105,9	127,8	130,1	0,136
September	17	120,6	43,2	163,8	588,7	0,280
		35,3	16,0	47,6	61,8	0,086

Table 4

Frequency distribution of the number of females in various standard length classes (and approximate age) in relation to the number of oviducal eggs.

Length (mm)	38–39	40–41	42–43	44–45	46–47	> 47	n
Approximate age (months)	4–6	6–12	12–18	18–36	> 36	> 36	
Two eggs	0	6	21	4	2	0	33
One egg	5	6	18	12	1	1	43

proportion of reproductive females in a sample and the fat body mass (Fig. 1, Tables 2 & 3).

This suggests that energy stored in the fat bodies is primarily allocated to vitellogenesis. Apparently, females mainly use tissue lipids for maintenance during the hottest season (September to January), a time when reproduction is less and many lizards suffer from negative energy and water balance (Robinson, *in press*).

In 1976 females produced two-egg clutches over a period of seven months, during which time the fat body mass was increasing, remained constant and then declined (Fig. 1, Table 2). For the next five months females in the samples contained one egg. In March 1977 fat bodies were very small and no reproductive females were collected. During April and May the fat body mass was at peak levels, but no female in the small samples was ovigerous, probably due to chance. It seems likely that two-egg clutches were produced during that period. Generally, females developed two eggs synchronously when lipid reserves were greatest; otherwise, single-egg clutches were most common. In the wet year 42 % of the females had double-egg clutches, but only 20 % developed two oviducal eggs in the dry year (Table 2). The number of eggs that would have been laid by the females sampled decreased 47 % as a result of the ten-fold decrease in precipitation. The loss in fecundity resulted from less stored energy

and a shorter period when two eggs were matured. The average clutch size was 1,52 in 1976 and 1,19 in 1977.

Recapture data of marked females were insufficient to clearly establish how rainfall, energy and seasonality affected the frequency of egg laying. Two females produced four clutches in twelve-month periods following the January 1976 rains. One female had three clutches from May 1976 to April 1977. Six females laid two clutches in 1977. None of these females was captured every month; therefore, oviposition was probably more frequent.

A sample of 76 females that contained oviducal eggs and were collected at various seasons of 1976 and 1977 was analysed in relation to their standard length and clutch size (Table 4). Seventy-five percent of the females bearing two eggs were 42–45 mm, or about 1–2 years old (M.D.R. unpublished data). Most females with a single egg also belonged to this age (size) group. No recently matured female (< 40 mm, 4–6 months old) had two oviducal eggs. Thus, recently matured females are less fecund.

Reproductive behaviour

Male *A. anchietae* maintain territories that persist from several months to more than two years. Juvenile lizards and mature females reside in a male's territory for variable periods. The breeding system is polygynous and territorial males were

observed mating with up to four different females. Recapture records show that two types of females live in a territory: resident females remain for periods of up to 23 months, whereas transient individuals are present from several days to three or four weeks.

During spring and summer, territorial males spend a considerable amount of the activity period (73 % to 92 %) observing their area from various vantage points on the dune slipface. In addition to repelling intruding males from neighbouring areas, males concern themselves with vigilating females. After emerging from the sand, a female is approached by the territorial male. As he nears, the female faces and halts the male by touching rostra (Fig. 2). This is usually followed by tongue flicking. At this point a 'receptive' female turns 180 degrees and with her tail arched over the back presents the cloaca. As the male advances she jumps ahead preventing his contact. This routine may be repeated from few to many times before the male attempts copulation by rushing the female and securing himself in the coital position by biting the nape of the female and entwining their tails. Sometimes the female avoids the male by running ahead and burying herself in the sand, only to be excavated by him. This behaviour may be repeated several times until the female escapes or is mated by the male. Nineteen of the 41 'receptive' females observed, escaped from the male. Two of these females copulated with the same male one and three days later.

When in the face-off posture (Fig. 2) a female may also reject the male, which she accomplishes by aggressively biting the male's shoulder and pushing him in front of her. Males normally return to face the female and must be rejected several times before leaving.

Fourteen females that were observed repelling or accepting a male were captured and autopsied to determine their reproductive status. Six females that had repelled males had yolked follicles or oviducal eggs greater than 4 mm diameter. The eight females that appeared receptive all contained small follicles (< 2 mm) without yolk.

DISCUSSION

The exceptional rains that fell over the central Namib Desert from January to March 1976 had profound effects on the flora and fauna. Seely and Louw (1980) estimated that plant detritus and animal biomass in the dune ecosystem increased seven- and six-fold, respectively. On the dune slipface, the primary habitat of *A. anchietae,* detritus biomass was 104 times greater in the wet year, and animal biomass increased 71 times (Seely and Louw, 1980).

Pronounced changes also occurred in the diet of *A. anchietae.* In 1976 the diet was more diverse and prey were more abundant. Qualitative estimates of the arthropod populations indicated that the elevated prey densities persisted throughout most of the wet year (Robinson, 1987). The rainfall-induced increases that occurred in the temporal availability and productivity of the prey were reflected in the energy storage and reproductive patterns of the lizards.

During the wet year male and female lizards accumulated lipids over a four-month period. In the dry year fat storage was limited to one (males) or two (females) months. The difference in the maximum mass of the fat body between the two years

Fig. 2

Male (left) *Aporosaura anchietae* testing the receptivity of a female. From this position the female will accept or repel attempts by the male to copulate.

was greatest in males. During periods of fat accumulation females were simultaneously diverting lipids to egg production. Had the lipids contained in the eggs been accounted for, the amount of energy stored by each sex would not have been so disparate.

In 1976 approximately 40 % of the females sampled contained two eggs, but the following year only 20 % developed eggs synchronously (Table 2). Thus, the ten-fold decrease in rainfall and the concomitant decline of prey reduced the egg crop by almost 50 % and the average clutch size by 22 %. Vitt *et al.* (1978) noted that the proportion of reproductive females and the timing and frequency of reproduction in the Sonoran Desert iguanid, *Urosaurus graciosus,* changed during two years of different rainfall. Clutch size and frequency of a Chihuahuan Desert lizard, *Urosaurus ornatus,* increased in response to greater rainfall and prey abundance (Ballinger, 1977).

In both years females were reproductive except when the fat body was almost completely depleted. Concurrent reproduction and lipid accumulation are possible because excess food is available, and only one or two eggs are developed. Licht (1974) was able to increase the fat body weight of *Anolis cristellatus* during reproduction by supplemental feeding. In contrast, temperate desert lizards that lay larger clutches abstain from reproduction until a large energy reserve is obtained (Derickson, 1976; Ballinger, 1983).

Aporosaura anchietae responds quickly to improved environmental conditions. After the January 1977 rains, females garnered sufficient energy to oviposit, depleting the fat body by March. Although no sample was taken in February 1976, a similar pattern was evident (Fig. I). *Aporosaura's* opportunistic reproduction is probably facilitated by the small female mass ($\overline{X}$ = 3,0 g). I have suggested that in extreme deserts where productivity is normally low, small body size could be advantageous because maintenance costs are low, enabling

females to rapidly sequester energy for small clutches (Robinson, *in press*).

When food and water are present, the tropical iguanid lizard *Anolis* produces a single egg every seven to 14 days (Andrews and Rand, 1974). The minimal time between oviposition is not known for *Aporosaura,* but several factors indicate that it is longer, perhaps around 30 days. First, the egg and hatchling size (length or mass) of *Aporosaura* is about 45 % greater than that of an *Anolis* species of similar adult size (Andrews and Rand, 1974). Second, synchronous egg development probably lenghtens the time between clutches.

The exceptionally large hatchling is one of the distinctive features of *Aporosaura* reproductive biology. Eighty-four hatchlings averaged 0,62 g (range 0,56–0,77) and their standard length was 25–27 mm, or approximately 20 % of the female's mass and 60 % of her length. A large hatchling would have several advantages. A greater mass reduces the surface to volume ratio, and consequently dehydration is slower. Most hatchlings are born when environmental temperatures are highest (January to March). Large neonates would also have a wider potential prey spectrum. Finally, larger propagules reduce the time needed to reach maturity (Sibly and Calow, 1986).

Seasonal changes in mass of the female fat body and tissue lipids suggest that each depot is used primarily for reproduction and maintenance, respectively. The abrupt decline in the fat body weight coincides with a greater proportion of reproductive females in the population and with a greater frequency of egg development (Table 2). Female *Anolis* asynchronously mature two eggs when their fat body is largest; single eggs are produced as energy reserves become depleted (Licht and Gorman, 1970; Sexton, Ortleb, Hathaway, Ballinger and Licht, 1971).

Tissue lipids began to decline in September after most of the fat body had been used, and reproduction had decreased. Energy from tissue lipids is probably used mainly for metabolism during the hottest months when many lizards are in negative energy and water balance (Robinson, *in press).*

Autumnal fat storage appears to result from lower metabolic costs due to decreased environmental temperatures and from increased prey availability. Some arthropod prey (e.g., Thysanura and Coleoptera) are most abundant in pitfall traps from April to August (Holm and Scholtz, 1980). Other species (carabid, tenebrionid and curculionid beetles) become abundant following rains of 20 mm or more (Holm, 1970; Robinson and Seely, 1980).

The territorial behaviour and polygynous breeding system of *A. anchietae* are related to the ecological characteristics of the sand dune habitat. Detritus, seeds and arthropods are not randomly distributed on the dune slope (Robinson and Seely, 1980). Seeds concentrate along the base of the slipface and arthropods are attracted to the patches of detritus. Lizards preferentially forage at these sites. Thus, the uneven distribution of food and the attraction of females to these areas permits males to monopolize mates and to defend a portion of the slipface against subordinate males. The asynchronous nature of the females' ovulatory cycles further enhances the probability that one male can defend and breed with several females. Under these circumstances the potential is great for territoriality and polygyny based on the male's ability to defend renewable resources essential to the female (Emlen and Oring, 1977). By maintaining frequent contact with the resident females, a territorial male constantly receives behavioural stimuli relating the females' reproductive status, thereby increasing the probability that he will be present when they are receptive.

What ecological conditions favour aseasonal reproduction in desert environments? Several recent reviews of the physical factors regulating lizard reproductive cycles have concluded that spermiogenesis, and to a lesser degree androgenesis, are inhibited by low temperatures (Duvall, Guillette and Jones, 1982; Saint Girons, 1984). The importance of the fat body for ovarian follicle development was demonstrated by Hahn and Tinkle (1965), and fat body cycles are regulated by seasonal patterns of food availability (Derickson, 1976).

Freezing temperatures are uncommon in the subtropical Namib Desert. Winter maximum air temperatures frequently exceed 20 °C to 25 °C (Lancaster *et al.,* 1984), and sand surface temperatures are even warmer (Robinson and Seely, 1980). Therefore, many dune arthropods are active throughout the year, although their relative abundances do vary seasonally (Holm and Scholtz, 1980).

Seeds, an important food of *A. anchietae,* are continuously present, as is detritus, the basic energy resource of the heterotrophic slipface community (Robinson and Seely, 1980; Louw and Seely, 1982). Consequently, environmental temperatures are conducive to aseasonal reproduction, and food resources are normally sufficient throughout the year.

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Aspects of Drinking by Baboons *(Papio ursinus)* in a Desert Environment

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A troop of chacma baboons *(Papio ursinus)* living in the Kuiseb River canyon, Namib Desert, depends on restricted water sources when residual pools dry up after annual flooding. Intervals between drinking may last up to 11 days. At these sources only one baboon at a time drinks, which accentuates aspects of social status and ranking. An unexpected finding was that low-ranking females enjoy longer drinking times than high-ranking females.

INTRODUCTION

The importance to baboons of ready access to drinking water is emphasized in studies which have shown that most baboons, including the semi-desert dwelling hamadryas baboon, *Papio hamadryas,* drink free water daily (Kummer, 1968) or sometimes once every two days (Altmann and Altmann, 1970). Shifts in the position of water supplies have resulted in baboon troops adjusting their movement patterns so that they always have access to water within their daily ranges (Stoltz and Saayman, 1970; Hamilton, Buskirk and Buskirk, 1976). Hall (1962) provided the first evidence that baboons may not be absolutely reliant on free drinking water: on the Cape Peninsula the baboons he studied drank water irregularly and obtained moisture from dew and moist plant material. His study, however, was carried out in a high rainfall area and was based on observations made on one day per week for a year.

Hamilton (1986) reported that a troop of chacma baboons *(Papio ursinus)* in the Namib Desert foraged some distance away from free water for periods of up to five days. In December 1986 the same troop did not drink water for a period of 11 days (Brain, 1988). Their drinking behaviour appeared to be related not only to food and water distribution at differing times of the year, but also to social interactions during the acquisition of food and water.

This paper describes the circumstances surrounding the occurrence of less than daily drinking in the troop of baboons studied by Hamilton (1986) and Brain (1988) and their behaviour at small water sources where only one baboon at a time can drink.

STUDY AREA

The troop under consideration occupied a 30 km stretch within the seasonally dry Kuiseb River canyon approximately 150 km SE of Walvis Bay (22° 59' S, 14° 31' E for Walvis Bay). The Kuiseb incises a deep, narrow gorge as it passes through the central Namib Desert, forming a linear oasis and a northern boundary to the dunes of the main Namib sand sea (Seely, Buskirk, Hamilton and Dixon, 1981). An alluvial flood plain within the canyon supports a riparian forest dominated by *Acacia albida* and *Acacia erioloba* trees.

Included in the home range of the baboons are 10 irregularly spaced *Ficus sycamorus* trees and numerous large (15 m²) clumps of *Salvadora persica* covering much of the area between the acacias. The baboons are restricted to this linear oasis and depend on it for food, water, shelter and sleeping cliffs.

Although dry for most of the year, the Kuiseb usually floods each year between December and March following rains in its catchment area. Water flow at Gobabeb (24° 34' S, 15° 03' E), 20–50 km downstream from the baboon troop has lasted from 0–101 days per year (Seely *et al.,* 1981). Following flooding, as the sandy river bed dries up, residual open pools form and then disappear. Water then is available in excavations in the sand made by gemsbok, *Oryx gazella,* or mountain zebra, *Equus zebra,* and often re-excavated and deepened by the baboons (Hamilton, 1985; Hamilton, Buskirk and Buskirk, 1978). A separate source of water for the baboons during the dry months is a small seep (20 cm × 30 cm) in a crack against a vertical cliff located 40 km upstream from Gobabeb. The observations reported were in those months (June to February) when the only water available to the baboons was from excavations and the seep.

Food, especially *Acacia* pods, *Euclea pseudebenus* fruits and *Salvadora persica* berries, is abundant at different periods throughout the year in those downstream areas that are the first to lose their surface water following flooding (Hamilton and Tilson, 1982) and less abundant near the persistent water holes. During the months preceding a flood, the distance between preferred foraging sites with abundant food and the nearest free water is at least 8 km (Brain, 1988).

The climate of the study area is moderate for a desert, with little seasonal temperature variation. At Gobabeb, the nearest first order weather station, the mean daily relative humidity from June to end February is 52 % and the mean daily

maximum and minimum temperatures are 35,8 °C and 6,9 °C. Mean annual rainfall is 27,2 mm (Lancaster, Lancaster and Seely, 1984), but there was no rain during my observation period.

THE TROOP

The troop currently occupies a canyon range stretching from a point 27 km upstream from Gobabeb to approximatly 20 km further upstream.

On 16 December 1988 the troop originally described as the 'lower troop' (Hamilton et al., 1976) consisted of 15 individuals: five adult males, a shadow male (Hamilton and Tilson, 1982), seven adult females and two two-year-old juveniles. This is about half the number of individuals present in 1979 (Hamilton, 1985). Each baboon can be identified visually. The two infants born in late November 1986 appear to be the only ones to have survived since 1981, as the age of the next youngest baboon in the troop is estimated to be 8–9 years (Brain, 1990). All seven infants born between December 1986 and December 1988 died. Female ranking was determined by observing 892 female-female interactions, noting the ability of one female to directly supplant another at either a food source, water, sleeping/resting site or grooming partner.

RESULTS AND DISCUSSION

Resource availability and movements.

In January 1973, the 'lower troop' was observed to make three excursions from its only remaining water source to eat ripe *Ficus sycamorus* fruits (80 % moisture content) 5,1 km further downstream (Hamilton, 1986). Two of these excursions lasted for four days each, and one for five days. On the return journey the adult and sub-adult males arrived at the water more than two hours ahead of females and juveniles (Hamilton, 1986). No data regarding drinking order at the water was recorded.

During an uninterrupted observation period of six weeks in December 1986/January 1987, the troop spent a maximum of 11 days at foraging sites without drinking. During that period the baboons mainly ate *Salvadora persica* berries (69 % moisture content) and ripe figs (Brain, 1988). The feeding sites were at least 8 km downstream from the seep, the only water source used when the troop did drink.

The average daily distance travelled by the baboons during the six weeks was 3,0 km (± 1,6 SD) with a maximum of 9 km being covered in one day on the journey from the foraging sites to the water seep (Brain, 1990). The baboons spent an average of 6,5 (± 0,9 SD) daylight hours per day resting and sleeping in the shade of trees (Brain, 1990).

In December 1987, following a food shortage at sites used in 1986/1987, the troop moved further upstream. A 7,6 km range, stretching from the seep to an excavation further upstream, was then occupied; drinking occurred regularly at both the seep and excavation. An average daily distance of 5,1 km (± 2,5 SD) was travelled during this period with a maximum daily distance of 16 km (Brain, 1990).

Events at the water

I observed 11 drinking sessions, five at the seep and six at
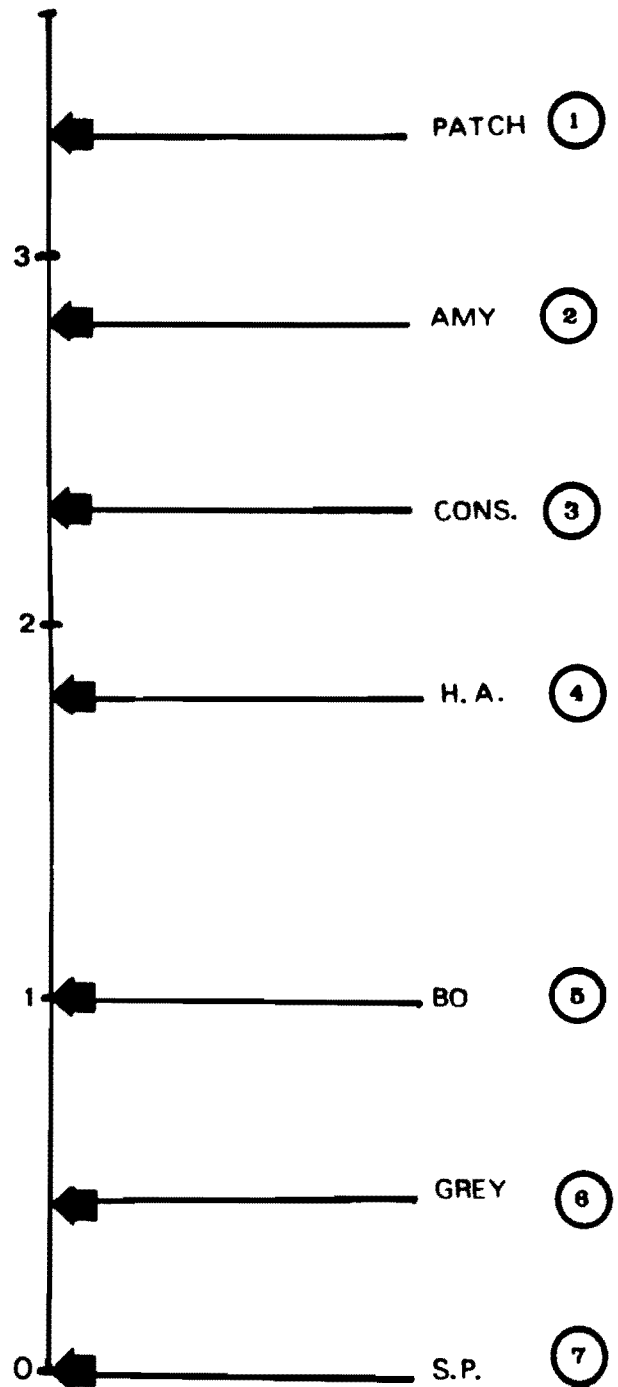

Fig. 1

Interval scale derived from Thurstone's (1959) case scaling model for order of female baboon drinking as recorded for 11 drinking sessions. Rank of individual females circled.

a more upstream excavation. Only one baboon at a time drank, resulting in drinking being an unusually tense activity and allowing me to assess social status with respect to drinking. Drinking usually occurred between 10h00 and 11h00 (Brain, 1990). On seven of 11 approaches to water, when approxi-

Fig. 2

'Xhabbo' (adult male) about to supplant 'Amy' (adult female on left) at the excavated seep, while 'S.P.' (female on right) looks on. 'Smudge' in the background is one of the only two juveniles that have survived during the last 6–8 years.

mately 1 km away, the lowest-ranking females ran in front of the troop and reached water first. However, zebra trampling at the excavation necessitated re-excavation each time, so that the low-ranking baboons could not drink before the rest of the troop arrived and supplanted them. They could, however, on two occasions drink before the others for short periods at the cliff seep (Brain, 1990). An adult male always drank first when the troop arrived at water but there appeared to be no further consistent drinking order for male troop members. This inconsistency contrasts with the females who, on each occasion, after the entire troop arrived at the water, followed almost exactly the same drinking order. Female drinking order for 11 drinking sessions is shown in Fig. 1 where data has been constructed into a unidimensional interval scale as described by Thurstone (1959). On nine occasions the highest ranking females' first drink was terminated by one of two adult males, a new immigrant or the shadow male.

Of 82 observed male-female supplantings at water, 96 % were directed against one of the three top-ranking females, the females losing access to water every time (Fig. 2). A 26 % incidence of female-female supplanting occurred amongst the three top-ranking females. When the supplanting male had left the water or simply chased the female away, there appeared to be confusion amongst the high-rankers as to who should drink next: the female who had been chased off or the one who was next in line. The resulting interaction invariably involved the supplanted female and the next highest-ranking female. If the higher ranked female still wanted to drink, she did so, which

was the case on 52 % of such occasions (n = 28). The four lower-ranking females drank after the three top-ranking females. There was a 9,5 % incidence of female-female supplanting amongst this group and a 4 % incidence of male-female supplantings.

On nine of 11 occasions, low-ranking females remained at water when the rest of the troop had moved off. They then drank in a peaceful and unhurried manner leaving the water up to 2 km behind the rest of the troop. Probably due to fewer disruptions and supplantings amongst the low-ranking female baboons, they had fewer drinks (1,3 ± 0,4 SD) per drinking sessions than the high-ranking female baboons (2,5 ± 0,8 SD). The four low-ranking female baboons had longer mean drinking times than the three high-ranking females (Fig. 3).

CONCLUSIONS

During prolonged periods when no drinking occurred, the baboons maintained their water balance by selecting food with a high moisture content (Brain, 1988). Probably because berries and fruits in *Salvadora persica* clumps and on individual *Ficus sycamorous* trees are widely dispersed, there was no rank-related behaviour associated with eating these main food items. There was also no noticeable difference in the time spent eating by individual baboons. This behaviour contrasts markedly with what took place at the water sources. A very strict female drinking order and a high incidence of male-female supplantings, predominantly involving high-ranking

females, resulted in the paradoxical situation of low-ranking females enjoying longer drinking times than high-ranking females. The adult male responsible for most supplantings of high-ranking females was either a shadow male of uncertain troop status or a new immigrant. A further finding was that for high-ranking females, multiple drinks appeared to be required at each drinking session.

The environmental and social pressures on this troop of baboons, and particularly on females, may contribute to the extremely poor infant survival rate (two infants in approximately eight years). Findings reported here suggest that the low-ranking female baboons make better use of the limited available water than high-ranking females. This could prove significant in the future as the only surviving juveniles in the last 9 years have been born to low-ranking females. I am currently investigating this hypothesis.

ACKNOWLEDGEMENTS

Fig. 3

Mean drinking times for seven adult female baboons as recorded during 11 drinking sessions.

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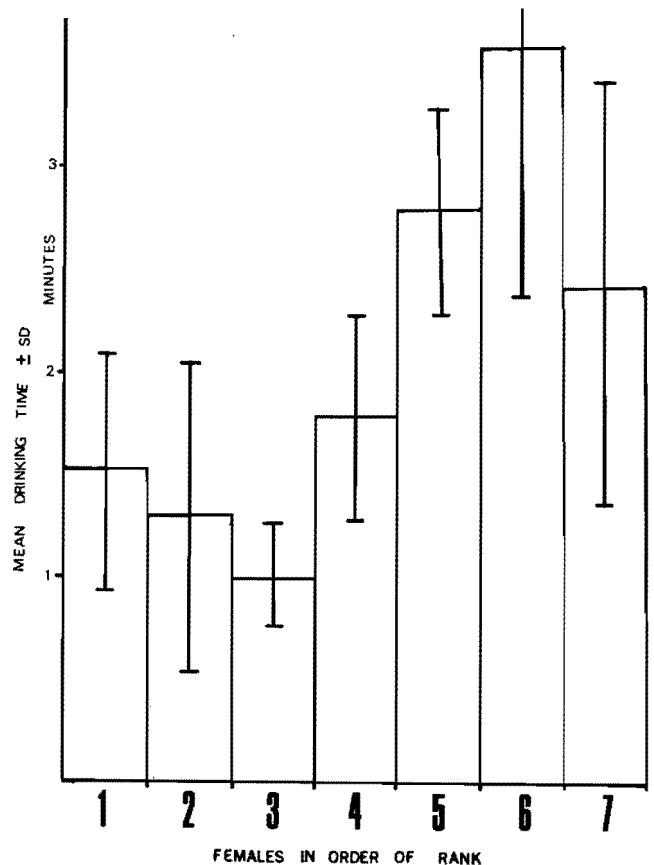THURSTONE, L. L., 1959. *The measurement of values.* University of Chicago Press, Chicago.

Water Relations of the Namib Tenebrionid Beetles

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Physiological research on water balance in the Namib tenebrionid beetles is reviewed. Most of the work described has been published in the last 10 years and concerns a single genus, *Onymacris*. Drinking of fog water is probably the main avenue of water gain in the adult insects, while the larvae depend on active uptake of atmospheric water. Metabolic water may be significant under certain conditions, and *Onymacris* species are efficient osmoregulators when water-stressed. Adaptations to minimize water loss via the cuticular, respiratory and excretory routes are well developed, although the function of the diuretic hormone in this genus is not clear. None of these adaptations is unique: it is rather the combination of them that contributes to the success of the flightless tenebrionids in the desert environment.

INTRODUCTION

Much of the research carried out on the tenebrionid beetles of the Namib Desert has focussed, naturally, on their thermal and water relationships. This review summarizes physiological research on the water relations of these beetles, most of it published in the last 10 years. Although work in this field has tended to be environmentally oriented, some more specialized studies have used the desert tenebrionids to examine fundamental biological principles. The emphasis is almost exclusively on a single genus, *Onymacris*, of the tribe Adesmiini (Penrith, 1984). The 14 species are all psammophilous and form a conspicuous element of the dune fauna. They are flightless, long-legged, fast-moving diurnal beetles that have a long lifespan and may be locally very abundant.

For all desert arthropods, the problems of living in a hot, dry environment are exacerbated by small size and relatively large surface areas, which lead to rapid exchanges of heat and water with the surroundings. In addition, the water activity of insect haemolymph (about 300 mOsm) is equivalent to 99,5 % r.h., with the result that the net gradient for water movement is invariably outwards, except in saturated atmospheres (Edney, 1977). This applies to all terrestrial insects, not just desert forms. Water is exchanged with the environment through various avenues, in both liquid and vapour states (Fig. 1). Continuous loss of water through the body surface and the respiratory and excretory systems must be balanced by water intake from food and drinking, by metabolic water and by uptake from the atmosphere.

The water content of Namib tenebrionids is lower than the average of about 70 % for arthropods in general (Edney, 1977). This is not a consequence of living in a desert, but is due to the relatively heavy integument and sometimes extensive fat reserves. Water content of the insects remains constant as long as water intake is sufficient to balance water expenditure: if not, dehydration is inevitable and osmoregulatory mechanisms are necessary until body water can be replenished.

WATER GAIN THROUGH DRINKING, FOOD AND METABOLISM

As described elsewhere in this volume, the aridity of the Namib Desert is tempered by the fairly frequent occurrence of advective fog. The importance of fog in the water economy of various animals inhabiting the Namib dunes was first described by Louw (1972).

Two unusual behavioural responses, involving the direct collection of fog, appear to be unique to the Namib Desert: fog basking in *Onymacris unguicularis* (Hamilton and Seely, 1976), and trench building in species of the genus *Lepidochora* (Seely and Hamilton, 1976). Most Namib beetles, however, rely simply on drinking fog water that has condensed on vegetation, detritus or stones (Seely, 1979). Such water has a surprisingly low osmotic concentration (14–38 mOsm; Louw, 1972). The amount imbibed may be substantial; for example, up to 34 % of pre-fog weight in *O. unguicularis* (Hamilton and Seely, 1976). The subelytral cavity of these flightless tenebrionids permits body expansion after imbibition of large quantities of water at irregular intervals (Slobodchikoff and Wisman, 1981). When *O. plana* are dehydrated slowly under laboratory conditions, and then provided with free water, they will drink approximately 100 mg in a few minutes, restoring their body weight to its original value (Nicolson, 1980). The physiological control of drinking behaviour is complex and not necessarily the same in different insect species: so far, it has been examined only in acridids and flies. In *Locusta migratoria* a decrease in abdominal volume leads to a positive response to water, while a rapid drop in haemolymph osmotic concentration stops the drinking response (Bernays, 1977). Desert tenebrionids might be good material for this type of research.

The only quantitative estimate of the importance of drinking to Namib tenebrionids is that of Cooper (1982), who found that in active *O. unguicularis*, drinking represented 50 % of water input.

The rich beetle fauna in the Namib dunes depends not only

on water in the form of advective fog, but also on food in the form of wind-blown plant detritus. Detritus is not a good source of pre-formed water for the beetles because, unlike those observed by Broza (1979) in Israel, they do not appear to take advantage of the hygroscopic absorption of water by detritus. Feeding occurs only during the diurnal surface activity period (Seely, 1979). For example, *Lepidochora* feed on detritus with a water content of about 2 %. Instead of constructing sand trenches during fogs, they could be consuming detritus with a water content of 60 % (Seely and Hamilton, 1976). There is apparently no quantitative information on the water intake of Namib tenebrionids during feeding. In contrast to herbivorous insects in other deserts and carnivorous arachnids, these essentially detritivorous beetles acquire little pre-formed water in their food, hence the relative importance of drinking in their overall water balance.

Metabolic or oxidation water may be an especially important component of water gain when no free water is available and the water content of the food is low, as in arthropods living in stored grain (Edney, 1977). It is also important during flight, but this is not applicable to the majority of desert insects. More detail is available for the mealworm *Tenebrio* than for its desert relatives. During 12 days of dehydration *O. plana* metabolized sufficient lipid to maintain a constant water content (Nicolson, 1980). In this species and in *O. unguicularis*, water produced by metabolism may account for a third to a half of that lost by transpiration (Nicolson, 1980; Cooper, 1982). Two recent measurements of metabolic rate in *Onymacris* (Bartholomew, Lighton and Louw, 1985; Louw, Nicolson and Seely, 1986) permit calculation of the extremes of metabolic water production in these beetles: these extend from $4{,}12$ mg g^{-1} h^{-1} during fast running in *O. plana* down to $0{,}02$ mg g^{-1} h^{-1} in resting *O. unguicularis*, a 200-fold range. Cooper (1982) calculated metabolic water production in free-ranging *O. unguicularis* to be $8{,}4$ mg g^{-1} day^{-1} or $0{,}35$ mg g^{-1} h^{-1}, a value intermediate between these extremes.

An impression of the potential importance of metabolic water may be gained from dissecting larvae or adults of *Onymacris*. Both life stages are able to accumulate remarkable reserves of fat. The relationship between lipid reserves, water balance and reproduction certainly merits further study in the Namib beetles.

UPTAKE OF WATER VAPOUR

Another source of water for insects is the atmosphere. It is important to distinguish between passive and active absorption of water vapour. Passive vapour influx occurs in all insects in direct proportion to ambient humidity (Wharton, 1985). The net loss of water through the body surface is the difference between efflux and a sometimes substantial influx. The latter component of an insect's water balance has been much neglected, and no measurements exist for the Namib tenebrionids.

More is known about active absorption of water vapour, which occurs via specialized processes and is restricted to certain wingless arthropods (Edney, 1977). For desert forms, the adaptive significance of this ability is obvious, and the Namib tenebrionids have been the subject of quite extensive research in this area. Larvae of *Onymacris plana* and

O. marginipennis gain weight when exposed to relative humidities above 83 % (Coutchie and Crowe, 1979a). Active water vapour uptake has been closely studied in the familiar mealworm *Tenebrio*, but *Onymacris* larvae have the experimental advantage of much larger size and have been a useful model for investigation of the mechanism of absorption (Coutchie and Crowe, 1979a; Machin, 1981; Coutchie and Machin, 1984). Uptake rates of *Onymacris* are over double those of *Tenebrio* in larvae of the same size at identical humidities.

Tenebrionid larvae possess a cryptonephric complex, in which the distal portions of the six Malpighian tubules form a sheath around the rectum. This complicated, concentrically arranged structure apparently evolved as a powerful mechanism for withdrawing water from the rectal contents (Ramsay, 1964), but is also used for the uptake of water vapour from unsaturated air. Space does not permit description of the process here: Wharton (1985) gives a concise summary. Whether water is being resorbed from faecal material or from air, the mechanism is solute-dependent, with a unidirectional gradient causing water movement from rectal lumen to tubule lumen. The driving force is the osmotic pressure generated by the Malpighian tubules, a biologically extraordinary 9 Osmol for *Onymacris* (Machin, 1981). This runs down to haemolymph levels (about $0{,}6$ Osmol) at the time of moulting, so that the complex undergoes cycles of transport activity. The epithelial cells possess remarkable abilities in terms of volume regulation (Machin, 1981).

OSMOREGULATION

As Machin (1981) has observed, in larvae of tenebrionid beetles all the problems of water regulation come together: they can survive prolonged dehydration as well as rapid water vapour intake without exchanging solutes with their environments. (This also applies to the adults, except that water intake is in the form of fog moisture.) For the Namib tenebrionids, osmoregulation is unfortunately the only other aspect of water balance that has been examined in the larval stages. As a result of the thorough study of Coutchie and Crowe (1979b), *O. marginipennis* is probably the only insect surviving a wide range of water contents in which all major osmotically active solutes have been analysed (Machin, 1981). In these larvae, all the components of the haemolymph (roughly equal proportions of sodium, chloride, trehalose and amino acids) were found to participate in osmoregulation.

Adult *Onymacris* are also excellent osmoregulators. Twelve days of dehydration resulted in a 60 % decline in haemolymph volume in *O. plana*, although the tissue water remained unchanged and the haemolymph osmolarity rose by only 14 % (Nicolson, 1980). Regulation was equally good during rapid rehydration. From work on other Namib tenebrionids (Cooper, 1982; Hattingh, Ganhao and Naidu, 1984; Naidu and Hattingh, 1986), it seems that efficient osmoregulation is characteristic of at least the desert representatives of the family.

Even in the desiccation-resistant *Periplaneta*, in which ion regulation has been best studied, tissue water declines along with haemolymph water during dehydration (Hyatt and Marshall, 1985). *Onymacris* is thus an unusually good example of an insect's haemolymph acting as a water reservoir for its tissues, and the mechanism, as in cockroaches, appears to
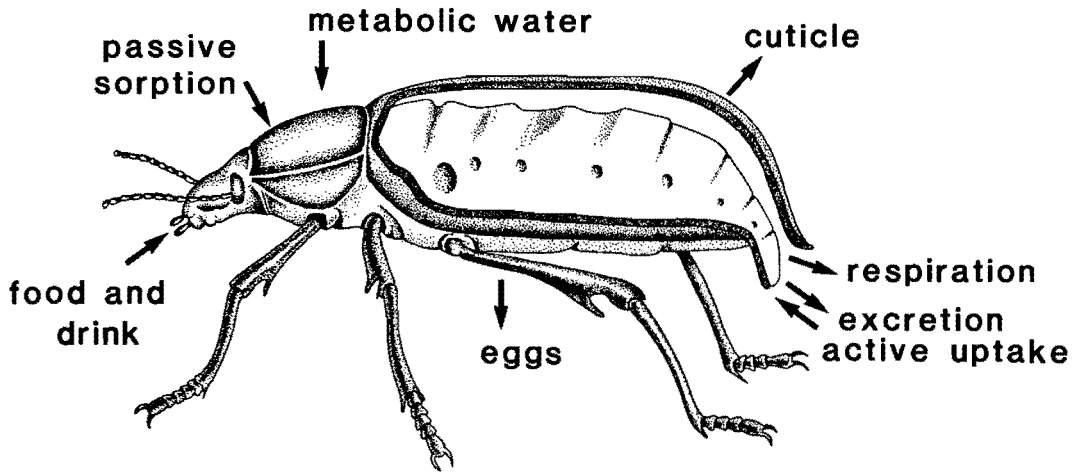
Fig. 1

Avenues of water gain and loss in a tenebrionid beetle. Beetle silhouette, showing the subelytral cavity, after Ahearn (1970)

involve reversible sequestration of ions in the fat body (Nicolson, 1980). Desert tenebrionids would be appropriate material for detailed study of the redistributions of solutes and water between different compartments of the body during water stress.

CUTICULAR WATER LOSS

Low rates of evaporative water loss are characteristic of desert arthropods (Cloudsley-Thompson, 1975). The first such study of the Namib tenebrionids was that of Edney (1971), who took advantage of the variety of species by comparing rates of water loss in beetles of different sizes. He found that their evaporative water loss was very low, that it was inversely proportional to body size, and that differences between the species correlated well with their behaviour and ecology.

Evaporative water loss in arthropods has traditionally been measured gravimetrically, on the assumption that weight loss represents water loss. However, during slow dehydration the loss of dry matter may be considerable in relation to water loss (e.g., Nicolson, 1980). Also, gravimetric methods measure only net flux and lead to difficulties in separating the cuticular and respiratory components of transpiration. We therefore developed an alternative technique using tritiated water and ventilated capsules, and applied it to *O. plana* (Nicolson, Louw and Edney, 1984). Water loss through the elytra, expressed in terms of surface area and vapour pressure difference, was $0.75 \ \mu g \ cm^{-2} \ h^{-1} \ mm \ Hg^{-1}$. This is almost the lowest cuticular permeability ever reported for an insect, and is comparable to that of desert scorpions (Edney, 1977), which usually have the advantage of larger size.

Cuticular water loss of the Namib tenebrionids has also been examined from another perspective, emphasizing the surface waxes. The arthropod cuticle has been the subject of extensive research, and its impermeability is known to be due to lipids associated with the outer epicuticular layer. Hadley (1981) has

reviewed the waterproofing function of surface lipids in both plants and arthropods. Various studies on desert tenebrionid beetles have attempted to relate the quantity and chemistry of the epicuticular lipids to cuticular permeability: an example from the Namib Desert is the work of Hadley and Louw (1980) on *O. plana* and *Lepidochora discoidalis*. Lockey has examined the chemistry of the epicuticular lipids from another point of view, attempting to demonstrate taxonomic differences in tenebrionids from the Namib and elsewhere (e.g., Lockey, 1982). If such differences exist, the Namib is obviously a good place to look for them.

In addition to the normal epicuticular waxes, some insects extrude additional wax in a powdery or filamentous form, thus giving rise to 'wax blooms'. This ability is exceptionally well developed in the Namib tenebrionids (McClain, Seely, Hadley and Gray, 1985), including some species of *Onymacris* (Penrith, 1984), and is described in detail by McClain elsewhere in this volume. The significance for the water balance of these insects is that the wax blooms develop at low humidities and presumably increase the resistance to water vapour diffusion from the cuticle (Hadley, 1979).

RESPIRATORY WATER LOSS

A special feature of flightless tenebrionids of arid environments is the subelytral cavity, an air-filled space between the fused elytra and the abdomen (Fig. 1). Instead of opening directly to the exterior, the abdominal spiracles open into the subelytral cavity, and expired air leaves through a single aperture above the anus (Ahearn, 1970). Functions suggested for the subelytral cavity include reduction of respiratory water loss, thermal buffering, and providing space for water storage (Cloudsley-Thompson, 1975; Slobodchikoff and Wismann, 1981). Of course there is no reason why these possible functions should be mutually exclusive. Although experimental evidence is not yet available, the anatomy of the respiratory

system suggests that the humid microenvironment surrounding most of the spiracles may serve to minimize respiratory water loss.

The technical difficulties encountered in sealing an insect's spiracles, in order to separate the cuticular and respiratory components of transpiration, have been discussed by Edney (1977). Desert tenebrionids provide an opportunity to avoid this problem; we have used the ventilated capsule technique (Nicolson et al., 1984) to measure subelytral water loss in O. plana. In immobilized beetles, cuticular and subelytral water losses were both extremely low at about 0,1 mg g^{-1} h^{-1}. This is the only measurement of respiratory water loss in a Namib beetle. Unfortunately it includes water lost from the cuticular lining of the subelytral cavity, and excludes any water which may leave the remaining spiracles.

In addition to the protection for the spiracles afforded by the subelytral cavity, discontinuous respiration may further reduce respiratory water loss in tenebrionid beetles. With the development of sophisticated respirometry techniques, it has become apparent that discontinuous respiration is widespread among insects. Bartholomew et al. (1985) found oxygen consumption to be strongly cyclical in three Namib tenebrionids. The pattern persisted when the elytra were perforated, i.e., it depended on ventilatory movements and spiracular opening rather than on periodic opening of the subelytral cavity. The same authors found that intermittent respiration was still apparent when the beetles were running on a treadmill at 35 °C. One of the species, O. plana, runs very rapidly in the field and its respiratory water loss could then be potentially serious.

Because many of the adult tenebrionids spend a considerable part of each day submerged beneath the sand, we examined patterns of gas exchange in O. unguicularis under such conditions (Louw et al., 1986). We found an extremely low metabolic rate, and very long intervals (up to 60 min) between cyclical peaks of CO_2 release and O_2 uptake. Periodic CO_2 release as a mechanism for reducing respiratory water loss has been thoroughly investigated in two groups of insects: diapause pupae of large Lepidoptera (see Edney, 1977) and quiescent cockroaches (reviewed by Kestler, 1984). Kestler discusses physical principles in some detail, and has demonstrated the unexpected finding that ventilation is favourable for water retention, especially in small insects and at low metabolic rates. He stresses the importance of studying gas exchange and the associated water loss in undisturbed insects in their natural environment. By waiting until the insect closes its spiracles, it is even possible to separate cuticular and respiratory water losses under these conditions (Kestler, 1984). It is obvious that desert tenebrionid beetles are excellent material for further research in this still largely unexplored field, but accurate measurement of respiratory water loss during activity and at high body temperatures seems technically impossible at present.

EXCRETORY WATER LOSS

Water conservation would be expected to dominate the excretory physiology of the Namib tenebrionids. It was therefore surprising to find that the Malpighian tubules of O. plana were dramatically stimulated by a diuretic hormone (Nicolson and Hanrahan, 1986). Secretion rates of isolated tubules some-

times reached 100 nl min^{-1}, which is comparable to those of the tubules of bloodsucking insects during rapid elimination of a water load. Obviously this rate of fluid loss would dehydrate a beetle in a few hours. The only conceivable occasion on which O. plana might require a diuretic hormone is after drinking too much fog water. The hormone is not particularly unstable, although inactivation mechanisms are probably present for finer control: Nicolson and Hanrahan (1986) found that the hormone was destroyed by prolonged contact with the beetle's haemolymph.

Dangerously high water losses may not necessarily follow release of a diuretic hormone. Insect Malpighian tubules open into the gut and modification of the primary excretory fluid takes place in the hindgut, usually involving morphologically complex structures – the cryptonephric complex in the case of many beetles. Recycling processes are fundamental to the insect excretory system. Possibly, reabsorptive mechanisms in the cryptonephric complex of Onymacris are able to recover all the water produced during 'diuresis'. Also, since potassium concentrations are very high in the tubule fluid (Nicolson and Hanrahan, 1986), the cryptonephric complex may function in retention of this ion. Until further information is available, the excretory system of O. plana seems to be equipped with two conflicting adaptations: a potent diuretic hormone and a cryptonephric complex.

This research on the Malpighian tubules of O. plana (Nicolson and Hanrahan, 1986) was initiated because of the complete lack of physiological studies on beetle Malpighian tubules. However, because of their large size and pronounced secretory and electrical responses to stimulation, we have found them to be ideal experimental material for a detailed electrophysiological study of the mechanism and control of fluid secretion (Nicolson and Isaacson, 1987; Isaacson, Nicolson and Fisher, 1989). The Malpighian tubules of O. plana have also been the subject of a complementary ultrastructural study (Hanrahan and Nicolson, 1987), and have recently been used to demonstrate that the technique commonly used to measure transtubular potentials in insect epithelia is not valid (Isaacson and Nicolson, 1989). These studies, however, are too specialized for description in this review.

The functioning of the cryptonephric complex was briefly mentioned in the section above on water vapour uptake. From work on Tenebrio and its desert relatives, it has been assumed that this structure is an adaptation for producing dry faeces, and that it is secondarily used for atmospheric water uptake in larvae only. There have been no measurements of their faecal water loss, but in adult Onymacris faecal water loss is apparently only a small proportion (11–14 %) of total water loss (Nicolson, 1980; Cooper, 1982).

CONCLUSION

In her recent review of the environmental physiology of insects and its relationship to microclimate, Willmer (1982) has said that 'some of the most elegant and comprehensive studies .... have concerned the lives of beetles, particularly the desert tenebrionids and their strategies for maintaining a favourable hygrothermal state'. This remark is borne out by the research I have described. There are, however, deficiencies which need to be remedied by future investigations.

First, it is much easier to work on isolated aspects of an insect's physiology in the laboratory, than to attempt to integrate all the avenues of water exchange between a free-living organism and its environment (Edney, 1977). Labelled water has now made it possible to study water and energy turnover in free-living animals. So far the only application of this methodology to Namib beetles has been the study of Cooper (1982) on *O. unguicularis*. The field situation is complex and also constantly changing: for example, a more detailed study on seasonal water budgets in American tenebrionids (Cooper, 1985) demonstrated that, although the largest component of water loss was always evaporative, food, drink or passive vapour sorption could be the main avenue of water gain. More thorough studies along these lines would be very welcome for the Namib beetles.

Second, there are several aspects of the water exchange of desert beetles about which we know nothing at all. One is egg production, which probably represents a considerable water loss to the female. The egg itself must be very vulnerable to water stress, and in fact we have no information about the water relations of the eggs and pupae of these holometabolous insects, and only patchy information on their relatively inconspicuous larvae. As far as acquiring water is concerned, passive sorption of water vapour may be a significant avenue of water gain, because submerged beetles are surrounded by a boundary layer of still air and probably increased humidity, thus increasing rates of passive influx.

The concentration of research on a single genus, *Onymacris*, has led to a fundamental understanding of the physiological adaptations that are central to its water economy. On the gain side, the important features are rapid drinking of fog water, the use of metabolic water, and the uptake of water vapour. Tolerance of water stress involves efficient osmoregulation in which the haemolymph serves as a water store. Losses are minimized by a low cuticular permeability supplemented by waxy blooms, by the combined effects of the subelytral cavity, intermittent respiration and a low metabolic rate, and by the cryptonephric complex. It is apparent that these adaptations are concerned more with conserving than with acquiring water. Moreover, none of these adaptations is unique; it is rather the total assemblage and their efficiency which matter to this insect. The obvious discrepancy is the possession of a diuretic hormone, and of course fast running and a preference for high body temperatures are not conducive to water conservation. Flightlessness is of great significance here: overheating and desiccation are potentially serious disadvantages of flight in desert insects (Heinrich, 1975). Avoidance of the same problems by retreating to the sub-surface thermal refuge in the middle of the day also contributes to the conspicuous success of the Namib tenebrionids.

ACKNOWLEDGEMENTS

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Fever in Namib and Other Ectotherms

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We examine the role of fever in the context of the evolutionary implications of host-pathogen interactions. Some ectotherms elevate their body temperatures behaviourally, following administration of pathogenic bacteria or other potential pyrogens. In a few species, the elevated temperature has been demonstrated to have positive survival value for the host. Representatives of all classes of vertebrate ectotherm have been reported to develop fever, as have representatives of the Arthropoda and Annelida, but not the Mollusca. We do not think that fever is ubiquitous amongst vertebrate ectotherms, however; we have not been able to obtain fever in seven African reptile species we have tested.

Studies of reactions of Namib ectotherms to potential pyrogens are important for several reasons. One is that some Namib species have selected body temperatures in the mammalian range, higher than most ectothermic species. Another is that the Namib Desert provides a suitable environment for studying endemic ectotherms in their natural habitat. The tenebrionid beetle *Onymacris plana* selected warmer than normal substrate temperatures, in a thermal gradient chamber, following administration of large doses of the endotoxin of gram-negative bacteria. However, the endemic lizard species *Aporosaura anchietae* and *Angolosaurus skoogi* showed no thermoregulatory responses to potential pyrogens. Future studies on the survival value of fever should include analysis of non-thermal as well as the traditional thermal components, which may have evolved separately. Also, studies are required of naturally-infected animals in their natural habitats.

FEVER AND EVOLUTION

Fever is a complex biological response of a host animal subjected to pathological insults, including infection, inflammation, tissue necrosis, antibody-antigen reactions and malignancy (Hellon, Townsend, Laburn and Mitchell, 1990). In addition to the characteristic rise in body temperature, the febrile response, at least in mammals, has several characteristic biochemical features: release of acute-phase proteins (e.g., C-reactive protein and fibrinogen), activation of lymphocytes and macrophages, and changes in serum metallic ion concentrations (decrease of iron and zinc, increase of copper) (Dinarello, Cannon and Wolff, 1988). Fever is also associated with gross behavioural changes, for example somnolence in several mammals, and both somnolence and malaise in humans (Feldberg, 1975).

Fever is a metabolically costly phenomenon; for each degree Celsius rise in body temperature, energy requirements increase by 10 % or more (Kluger, 1986). Fever also suppresses appetite, so compensatory increases in food intake usually do not occur, and febrile animals enter negative nitrogen balance and tend to lose mass.

The biochemical and physiological features of the host response that occurs during fever are largely independent of the cause of the fever. For example, the same pattern of events occurs whether the host is responding to gram-negative infection, viral infection, protozoal infection, crush injury or incompatible blood transfusion. The similarity of features arises primarily because most, if not all, of the host defence reactions

have a common biochemical mediator, namely endogenous pyrogen (EP). EP is a hormone-like polypeptide, or family of polypeptides, released by macrophages, and other cells of the host, in response to any one of a variety of pathological stimuli. Four EPs have been identified, namely interleukin 1 (IL 1) and interleukin 6 (IL 6), tumour necrosis factor and interferon (Hellon *et al.*, 1990); they have little or no amino acid homology, but remarkably similar biochemical action (Dinarello *et al.*, 1988).

From the neo-Darwinian point of view, it would be anomalous for a biological phenomenon to exist, which is metabolically costly and which has similar biochemical and physiological features irrespective of the stimulus and host species, unless the phenomenon has survival value for the host. Indeed, such philosophical arguments in favour of a survival value for fever have been expressed for at least 2000 years (Kluger, 1981). However, it has proved surprisingly difficult either to show quantitatively that fever indeed favours the host's survival, or to identify components of the febrile response beneficial to the host (Ewald, 1980). Only recently has it become clear that the release of EP contributes to the host's survival in infection, and in other conditions like malignancy (Dinarello, Conti and Mier, 1986; Duff, 1986). What is still not established satisfactorily is whether pyrexia, the high body temperature characteristic of fever, *per se* has any survival value for the host (Banet, 1983; Kluger, 1986; Blatteis, 1986; Banet, 1986; Hellon *et al.*, 1990).

Pyrexia in endotherms is very different from other forms of hyperthermia (Stitt, 1979; Mitchell and Laburn, 1985). In

pyrexia, the thermoregulatory system is neither malfunctioning nor overwhelmed. On the contrary, a well coordinated set of thermoregulatory effectors, the nature of which depends on ambient temperature, is brought into play to elevate the temperature to the febrile level, at which it is actively regulated. The thermoregulatory system behaves as if its set-point has been reset at an elevated level. Consequently, attempts to restore 'normal' temperature by physical cooling of the host are counteracted by additional heat generation and conservation (Mitchell and Laburn, 1985).

As one might expect intuitively, many of the biochemical components of the febrile response appear to be more effective in host defence at elevated host temperature (Roberts, 1979; Kluger, 1986). For example, the combination of high temperature and low serum iron concentration which occurs in fever is inimical to some species of bacteria (Kluger and Rothenburg, 1979). Elevation of body temperature to typically febrile levels, along with other forms of stress, induces production of heat shock proteins, which protect cells against subsequent stress (Barbe, Tytell, Gower and Welch, 1988). In *Drosophila*, haematocytes are immune-competent at 29 °C but not 21 °C (Nappi and Carton, 1985). Nevertheless, there is no consistent relationship between body temperature and host mortality in febrile disease. Indeed, some reports suggest that the high body temperature actually compromises the host. Some of these reports are based on epidemiological studies; for example, a group of untreated patients with pneumococcal pneumonia showed increased mortality with increasing body temperature (Bennett and Nicastri, 1960). Others derive from experimental elevation of the body temperature to febrile levels, by cooling the hypothalamus and thereby initiating heat conservation; this procedure reduced survival in rats following *Salmonella* infection (Banet, 1979).

Both epidemiological and experimental investigations of the possible survival value of pyrexia in humans and other endotherms tend to be confounded by the relatively narrow range of body temperatures within which endotherms thermoregulate, even when febrile. Pyrexial mammals and birds seldom reach body temperatures more than 2,5 °C above normal deep body temperature (Hellon *et al.*, 1990). This obstacle was overcome when Vaughn, Bernheim and Kluger (1974) (through an act of lateral thinking) successfully induced fever in an ectotherm[1], the desert iguana *Dipsosaurus dorsalis*.

Vaughn and her colleagues injected killed *Aeromonas hydrophila* (now called *Aeromonas sobria*, according to Muchlinsky, Stoutenburgh and Hogan, 1989), a gram-negative bacterium pathogenic in lizards, as well as in other animals, into desert iguanas kept in a photothermal gradient chamber. Following *A. hydrophila* injection, the lizards selected warmer parts of the chamber than they did following injection of the same volume of saline. Their body temperatures consequently rose. The peak elevation, about 2 °C, was very similar to that usually exhibited by febrile endotherms.

With hindsight, it does not seem anomalous that an animal could become pyrexial through primarily, or solely, behavioural mechanisms; behavioural mechanisms supplement autonomic mechanisms in fever in endotherms (Cabanac, 1972).
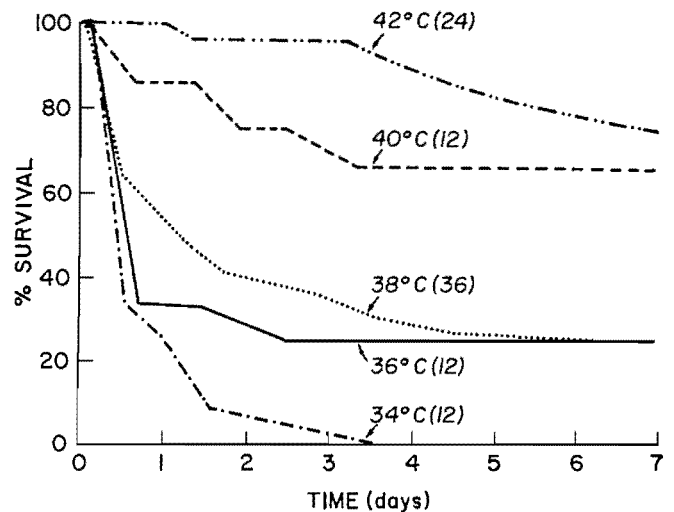

Fig. 1.

Survival of five groups of desert iguana *Dipsosaurus dorsalis*, maintained at temperatures between 34 °C and 42 °C following intracardiac injection of the live bacterium *Aeromonas hydrophila*. Numbers in parentheses are initial numbers of lizards in each group. From Kluger, Ringler and Anver (1975), by copyright permission of the American Association for the Advancement of Science.

For example, selection of warmer clothing is a common thermoregulatory behaviour in humans developing fever, initiated by the conscious sensation of feeling cold. Moreover, the biochemical mechanisms involved in the neural control of behavioural thermoregulation in ectotherms seem to be similar to those involved in endothermic thermoregulation (Bligh, Louw and Young, 1976). Before Vaughn's experiments, however, endothermy implicitly was considered a prerequisite for pyrexia.

The paper by Vaughn and her colleagues (1974) actually was not the first to report elevation in the body temperature of an ectotherm following infection. More than a decade earlier, Sauerlander and Kohler (1961) had published a brief paper describing experiments in which the cockroach *Periplaneta americana* was inoculated with bacteria; body temperature was elevated by up to 12,6 °C, and remained elevated for days. However, the cockroaches were kept in a constant temperature environment (20 °C) throughout, so the response reported would require the insects to have manifested a degree of endothermy they are not known to possess. No subsequent studies have confirmed the phenomenon, and the paper tends to be disregarded by fever experts.

If ectotherms are maintained in an isothermal environment, they necessarily adopt the temperature of the environment, except for very brief periods of hyperthermia due to muscle contraction, a fact exploited to assess the advantages of pyrexia in lizards (Kluger, Ringler and Anver, 1975). Five groups of *D. dorsalis* were infected with live *A. hydrophila*, and each group was maintained for a week at a fixed temperature between 34 °C and 42 °C. The consequences for survival are

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[1]The term 'ectotherm' describes an animal that relies mainly on environmental sources of thermal energy for thermoregulation; such animals usually have a high coefficient of variation of body temperature, that is, they are also poikilothermic.

shown in Fig. 1; the higher the ambient temperature (and therefore the body temperature), the greater the proportion of animals which survived the infection. In separate experiments, infected lizards were provided with a thermal mosaic in a photothermal gradient chamber, and were given the antipyretic drug salicylate. They no longer sought out warmer environments and their survival was reduced (Bernheim and Kluger, 1976b).

Reduced survival in ectotherms prevented from attaining behavioural pyrexia apparently is not confined to lizards. Covert and Reynolds (1977) subsequently showed that mortality in the goldfish *Carassius auratus*, infected with live *A. hydrophila*, also increased as body temperature was reduced from 32,7 °C to 25,5 °C. More recently, Boorstein and Ewald (1987) have shown that inoculation of the grasshopper *Melanoplus sanguinipes* with the pathogenic protozoan *Nosema acridophagus* resulted in the grasshoppers selecting a body temperature of about 40 °C, rather than their normal 34 °C. In a subsequent experiment, maintaining a group of infected grasshoppers at a temperature of 34 °C, rather than 40 °C, not only reduced survival rate (Fig. 2), but also impaired growth.

In the seven years that followed the first reliable report (Vaughn *et al.*, 1974) of fever in an ectotherm, sixteen other species of ectotherm were investigated (Kluger, 1986; Firth, Ralph and Boardman, 1980). Species studied included two other lizard species, five amphibian species, three fish species, and six species of arthropod; all exhibited pyrexia. Since fever was already known to occur in all mammals and birds that had been tested, a view began to prevail, explicitly or implicitly, that all animal species that had evolved with or since the arthropods could develop fever. If fever indeed was ubiquitous, that alone would be a powerful argument in favour of it having survival value (Kluger, 1979a, b). Moreover, if the pyrexia of fever can be shown to be advantageous to the host in the case of some species, it is tempting to extrapolate its survival value to all other species.

In 1981, we reported the consequences of injecting killed *A. hydrophila* on body temperature in the armadillo lizard *Cordylus cataphractus* (Laburn, Mitchell, Kenedi and Louw, 1981). It was the first report of a species failing to develop pyrexia in response to a pyrogen, and therefore suggested that fever was not ubiquitous. We have subsequently discovered a number of other species in which pyrexia does not occur. We report our data on other lizard species here, review the state of knowledge concerning fever in ectotherms, and also point out the particular contribution to the field of study of Namib Desert species. Some of our new data have been reported briefly to the International Congress of Physiological Sciences (Mitchell, Laburn and Matter, 1989).

FEVER IN INVERTEBRATES

Fever has been reported to develop in several species of arthropod, and more recently in an annelid. Within the arthropods, it was amongst the crustaceans that behavioural fever was first detected (Table 1). The freshwater crayfish *Cambarus bartoni*, given injections of killed *A. hydrophila*, selected warmer water, such that its selected body temperature rose almost 2 °C above the normal 22 °C (Casterlin and
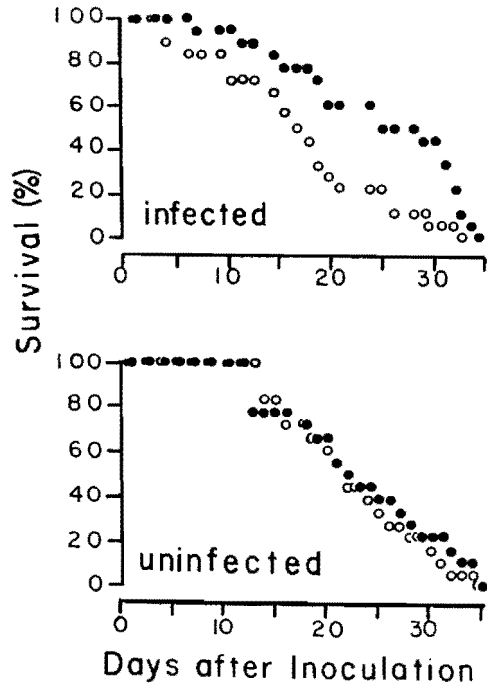

Fig. 2

Survival of the grasshopper *Melanoplus sanguinipes*, maintained at 34 °C (open circles) and 40 °C (closed circles), following ingestion of the live microsporidian protozoan *Nosema acridophagus* (top panel) or not infected (bottom panel). Maintaining the animals at 34 °C reduced survival rates significantly below the natural life expectancy curve. From Boorstein and Ewald (1987), by copyright permission of the University of Chicago Press.

Reynolds, 1977b). The pyrexial action of endogenous pyrogens, which are known to be released in invertebrates (Beck, Vasta, Marchalonis and Habicht, 1989) as in other animals during fever, is mediated in the nervous system of endotherms by eicosanoids, one of which is prostaglandin E (PGE) (Stitt, 1986; Mitchell, Laburn, Cooper, Hellon, Cranston and Townsend, 1986; Cooper, 1987; Hellon *et al.*, 1990). Injection of PGE into the central nervous system of vertebrates rapidly produces a potent pyrexia (Milton, 1982). Prostaglandins are released during inflammatory reactions in invertebrates too (Brady, 1983), but whether they mediate fever in ectotherms had not been tested. Systemic injection of PGE in *C. bartoni* evoked a behavioural fever (Casterlin and Reynolds, 1978); it also did so in two marine decapods, *Penaeus duorarum* and *Homarus americanus* (Casterlin and Reynolds, 1979). The aspirin-like drugs produce antipyresis by inhibiting eicosanoid synthesis (Dascombe, 1985), and dissolving one of these drugs, paracetamol (= acetominophen), in the water surrounding *C. bartoni* abolished the pyrexial response to *A. hydrophila* injection (Casterlin and Reynolds, 1980).

No specific survival value has been demonstrated for the pyrexia exhibited by crustaceans. However, as noted above, pyrexia does appear to benefit one of the insects, the grasshopper *Melanoplus sanguinipes*, during protozoal infection (Boorstein and Ewald, 1987). This grasshopper was not the

Table 1
Ectothermic species reported to develop fever when given pyrogens.

Species		Pyrogen	Reference
Invertebrates			
Nephelopsis obscura	(leech)	Endotoxin,PGE	Cabanac, 1989
Limulus polyphemus	(horseshoe crab)	PGE	Casterlin and Reynolds, 1979
Buthus occitanus	(scorpion)	PGE	Cabanac and Le Guelte, 1980
Androctonus australis	(scorpion)	PGE	Cabanac and Le Guelte, 1980
Gromphadorhina portentosa	(Madagascar cockroach)	Endotoxin, bacteria	Bronstein and Conner, 1984
Gryllus bimaculatus	(cricket)	Rickettsia	Louis *et al.*, 1986
Melanoplus sanguinipes	(migratory grasshopper)	Protozoa	Boorstein and Ewald, 1987
Onymacris plana	(tenebrionid beetle)	Endotoxin	McClain *et al.*, 1988
Cambarus bartoni	(freshwater crayfish)	Bacteria	Casterlin and Reynolds, 1977*b*
		PGE	Casterlin and Reynolds, 1978
Homarus americanus	(American lobster)	PGE	Casterlin and Reynolds, 1979
Penaeus duorarum	(pink shrimp)	PGE	Casterlin and Reynolds, 1979
Fish			
Micropterus salmoides	(largemouth bass)	Bacteria	Reynolds *et al.*, 1976
Lepomis macrochirus	(bluegill sunfish)	Bacteria	Reynolds *et al.*, 1976
Carassius auratus	(goldfish)	Bacteria, endotoxin	Reynolds *et al.*, 1978*b*
Amphibians			
Hyla cinerea	(green tree frog, adult)	Bacteria	Kluger, 1977
Rana pipiens	(leopard frog, tadpole)	Bacteria	Casterlin and Reynolds, 1977*a*
Rana catesbeiana	(bullfrog, tadpole)	Bacteria	Casterlin and Reynolds, 1977*a*
Rana esculenta	(edible frog, adult)	Bacteria, PGE, EP	Myhre *et al.*, 1977
Necturus maculosus	(mudpuppy)	PGE	Hutchinson and Erskine, 1981
Reptiles			
Dipsosaurus dorsalis	(desert iguana)	Bacteria	Vaughn *et al.*, 1974
		EP	Bernheim and Kluger, 1977
Iguana iguana	(green iguana)	Bacteria	Kluger, 1978
Crotaphytus collaris	(collared lizard)	Bacteria	Firth *et al.*, 1980
Saurimalus obesus	(chuckwalla)	Bacteria	Muchlinski *et al.*, 1989
Terrapene carolina	(eastern box turtle)	Bacteria	Monagas and Gatten, 1983
Chrysemys picta	(painted turtle)	Bacteria	Monagas and Gatten, 1983
Alligator mississippiensis	(American alligator)	Bacteria	Lang, 1986

first insect in which behavioural fever was observed; it had been reported previously in the Madagascar cockroach *Gromphadorhina portentosa* (Bronstein and Conner, 1984) and the cricket *Gryllus bimaculatus* (Louis, Jourdan and Cabanac, 1986). The cockroaches selected higher body temperatures when given injections of killed *E. coli*, another gram-negative bacterium, and of endotoxin, the lipopolysaccharide component of the cell wall that is considered to be the pyrogenic moeity of all gram-negative bacteria (Kenedi, Laburn, Mitchell and Ross, 1982). The crickets were infected with *Rickettsiella grylli*, thereby extending the range of pathogenic organisms tested to the rickettsials. The hosts not only selected higher body temperatures, but also survived better in thermal mosaics than they did at a fixed temperature equal to that of the uninfected animals (Louis *et al.*, 1986). Post-mortem examination of infected crickets showed exacerbation of the infectious process at lower body temperatures. The significance of Boorstein and Ewald's investigation of grasshoppers is that it was the first, and so far the only, report of a host benefiting from pyrexia when infected via a natural route, as the pathogenic protozoa were applied to the grasshoppers' food.

Until recently, the insect species in which fever has been reported were all members of the Orthoptera. The first demonstration of pyrexia in a non-orthopteran insect relied on a Namib Desert species, the tenebrionid beetle *Onymacris plana* (McClain, Magnuson and Warner, 1988). Namib tenebrionids are unusual amongst insects in that their selected body temperatures are high, falling in the mammalian range (Seely, Roberts and Mitchell, 1988). McClain and her colleagues placed adult *O. plana* in a photothermal gradient chamber. Injection of purified endotoxin into the haemocoel of the beetles resulted in their selecting a warmer position in the chamber (see Fig. 3); this behavioural pyrexia had an onset latency of less than an hour, and lasted about twelve hours.

The chelicerate arthropods are phylogenetically much older than the (mandibulate) insects, and demonstration of fever in chelicerates would suggest an ancient evolutionary origin of the phenomenon. Persistence of fever from an ancient origin to modern times again would be supportive of survival value. Such was the significance attached by Cabanac and Le Guelte (1980) to their discovery that PGE in doses between 1 and 5 mg/kg evoked behavioural pyrexia in the two scorpion species, *Buthus occitanus* and *Androctonus australis*. Both higher
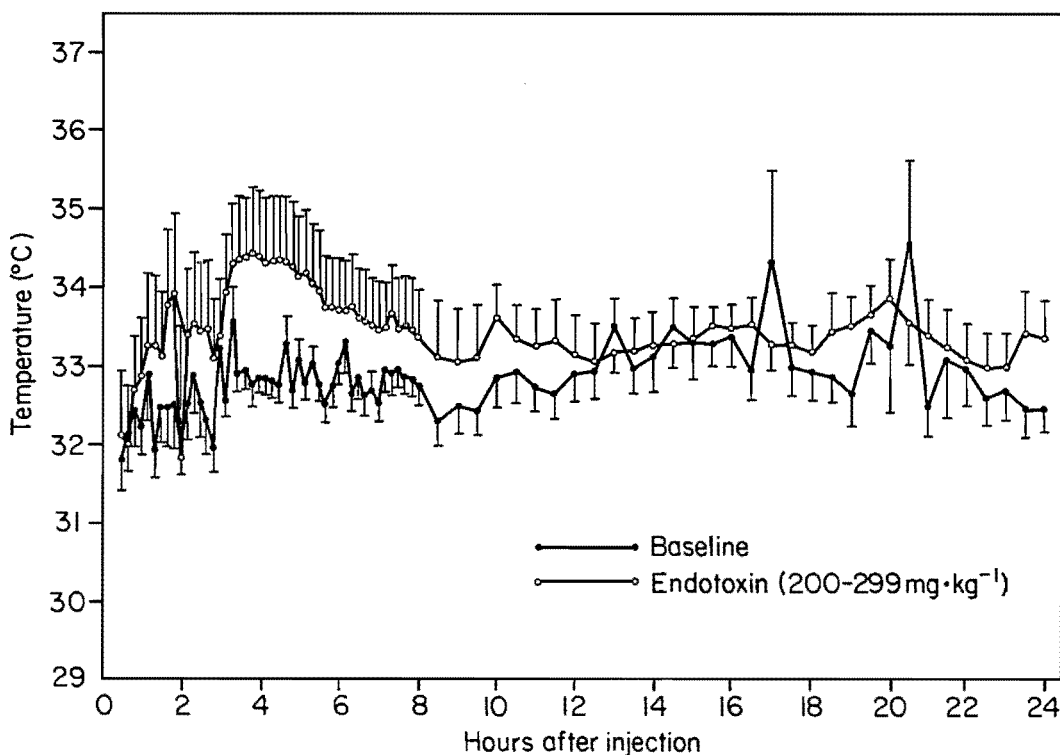
Fig. 3

Substrate temperatures selected by the Namib tenebrionid beetle *Onymacris plana*, maintained in a photothermal gradient chamber, with no intervention (closed circles) and following injection of purified endotoxin (open circles). Beetle thoracic temperatures were about 4 °C higher than substrate temperatures. From McClain, Magnuson and Warner (1988), by copyright permission of Pergamon Press.

and lower doses were without effect. The temperatures of the scorpions reached 40 °C, and the behavioural pyrexia in some individual scorpions lasted more than twenty hours. Another ancient chelicerate arthropod reported to develop behavioural fever is the horseshoe crab, *Limulus polyphemus* (Casterlin and Reynolds, 1979), which is more closely related to scorpions than to true crabs. Identification of fever in the chelicerates bestows on the phenomenon a potential evolutionary age of 300 million years (Cabanac and Le Guelte, 1980).

Three non-arthropod invertebrates have been tested for responsiveness to pyrogens, two snail species and a leech. The snails are the freshwater snail *Limnaea auricularia* (Cabanac and Rossetti, 1987) and the Japanese freshwater snail *Semisulcospira libertina* (Rossetti and Nagasaka, 1988). Challenged with either PGE or endotoxin, they failed to develop pyrexia (Table 2), a result the authors interpreted to mean that fever evolved after the molluscs diverged from the main evolutionary line, and before divergence of the arthropods. The study should be repeated with terrestrial snails, the habitats of which contain much richer thermal mosaics than those of aquatic snails.

The Annelida share a common divergence with the arthropods, and Cabanac (1989) recently has examined the responses of one of them, the leech *Nephelopsis obscura*, to endotoxin and prostaglandin injection. This leech did not take up a preferred position in an aquatic thermal gradient, but

traversed both warmer and colder areas. The proportion of time spent in warmer areas increased following injection of bacterial endotoxin (0,25 mg/kg) and PGE (4 mg/kg). The preference for warmer water was abolished by paracetamol, dissolved in the water, in animals given 10 mg/kg of endotoxin; whether paracetamol had any effect on the thermal behaviour of control animals was not investigated.

FEVER IN FISH

Work that predated the studies of Vaughn and her colleagues (1974) by twenty years had established that fish survived viral infections better at warmer water temperatures than at cooler temperatures (Watson, Guenther and Rucker, 1954; Amend, 1970). However, the earlier workers had not investigated whether infection altered thermoregulatory behaviour in fish. Fish usually are exposed to less variation in ambient temperature than are terrestrial animals, and hence have less opportunity to develop behavioural pyrexia. Experimental investigation of fever in fish has relied on an aquatic shuttlebox for determining thermal preferences. The fish are able to swim between two chambers held at different temperatures, but cannot remain in any chamber, because their presence in the chamber is used to trigger heating or cooling of the surrounding water (Neill, Magnuson and Chipman, 1972). Behavioural fever was first reported in fish by Reynolds, Casterlin and

Table 2
Ectothermic species reported not to develop fever when given pyrogens.

Species		Pyrogen	Reference
Invertebrates			
Limnaea auricularia	(freshwater snail)	Endotoxin, PGE, EP	Cabanac and Rossetti, 1987
Semisulcospira libertina	(Japanese freshwater snail)	Endotoxin, PGE	Rossetti and Nagasaka, 1988
Fish			
Lepomis gibbosus	(pumpkinseed sunfish)	Endotoxin, PGE	Marx et al., 1984
Reptiles			
Cordylus cataphractus	(armadillo lizard)	Bacteria, EP	Laburn et al., 1981
Sceloporus occidentalis	(western fence lizard)	Protozoa	Schall and Sarni, 1987
Pachydactylus bibronii	(Bibron's gecko)	Bacteria, EP	present paper
Aporosaura anchietae	(shovel-snouted lizard)	Bacteria	present paper
Angolosaurus skoogi	(desert plated lizard)	Bacteria, endotoxin	present paper
Geochelone pardalis	(leopard tortoise)	Bacteria, endotoxin	Zurovsky et al., 1987c
Psammophis phillipsii	(olive grass snake)	Bacteria, endotoxin	Zurovsky et al., 1987a
Lamprophis fuliginosus	(brown house snake)	Endotoxin	Zurovsky et al., 1987a

Covert (1976), who found that killed *A. hydrophila,* injected into the bluegill sunfish *Lepomis macrochirus* and largemouth bass *Micropterus salmoides,* caused a 1 °C to 3 °C increase in selected body temperature. Reynolds and his colleagues subsequently showed that *L. macrochirus* displayed behavioural pyrexia not only in response to the gram-negative bacterium *A. hydrophila* but also to the killed gram-positive bacterium *Staphylococcus aureus* (Reynolds, Casterlin and Covert, 1978). As mentioned previously, elevated body temperature, and reduced mortality also occurred in *Carassius auratus* infected with live *A. hydrophila* (Covert and Reynolds, 1977).

Another sunfish, the pumpkinseed sunfish *Lepomis gibbosus,* was investigated by Marx, Hilbig, and Rahmann (1984). In this species, endotoxin, injected intracranially, had no significant effect on selected body temperature. Intracranial injection of PGE produced a phenomenon that appeared to be pyrexia, but Marx and his colleagues demonstrated that the phenomenon actually was an artifact, caused by sedation of the fish and consequent passive heating. Their results raise the disturbing question of whether other pyrexias apparent after PGE injection (Table 1) might be confounded by the consequences of sedation, in those studies in which the apparatus used to test behavioural thermoregulation did not require the test animals to move in order to achieve and maintain a constant body temperature.

FEVER IN AMPHIBIANS

Aquatic shuttleboxes, used to investigate the action of pyrogens in fish, can be used equally well to study tadpoles. Intraperitoneal injection of killed *A. hydrophila* in tadpoles of the bullfrog *Rana catesbeiana* and the leopard frog *Rana pipiens* resulted in an increase of selected body temperature of almost 3 °C (Casterlin and Reynolds, 1977a). In adults of the green tree frog *Hyla cinerea,* an unusually good thermoregulator for an amphibian, injection of killed *A. hydrophila* resulted in selection of warmer positions in a damp thermal gradient chamber, such that body temperature increased

about 2 °C, with an onset latency of 2–4 hours (Kluger, 1977). Adults of the edible frog *Rana esculenta* were tested in a similar gradient by Myhre, Cabanac and Myhre (1977). They found that two strains of mycobacterium, *Mycobacterium xenopi* and *M. ranae,* injected intraperitoneally, increased selected body temperature by about 6 °C, while a third strain, *M. aquae II,* had no effect. Myhre and colleagues explained this strain difference by pointing out that the first two strains were pathogenic in the frogs while the third was not; this argument seems spurious, however, since all the bacteria were killed before injection. In the same frogs, cross-transfusion of plasma from donor frogs, previously given *M. ranae* injections, induced pyrexia in recipients. Intracranial injection of PGE caused a marked hyperthermia, and death in two out of five animals.

Body temperature elevation in amphibians given PGE is not confined to frogs. It occurs too in a salamander, the mudpuppy *Necturus maculosus* (Hutchison and Erskine, 1981); intracranial injection of PGE resulted in a 5 °C rise in selected body temperature, to about 17 °C, sustained for at least 24 hours.

No specific survival value of fever has been demonstrated in amphibians.

FEVER IN REPTILES

It was in a reptile that ectothermic fever first was discovered and it is in reptiles that ectothermic fever has been investigated most thoroughly.

In the desert iguana *Dipsosaurus dorsalis,* killed and live gram-negative organisms cause a behavioural pyrexia with onset latency of 3–4 hours and duration of days (see Fig. 4) (Vaughn et al., 1974; Kluger et al., 1975). The behavioural fever can be abolished by antipyretic drugs (Bernheim and Kluger, 1976b). As noted previously, administration of the antipyretic drug compromised survival in infected lizards, as did confinement to afebrile body temperatures (Fig. 1).

Fever in *D. dorsalis* is not specific to one pathogenic organism. Intracardiac injection of two other bacteria, *Pasteurella*
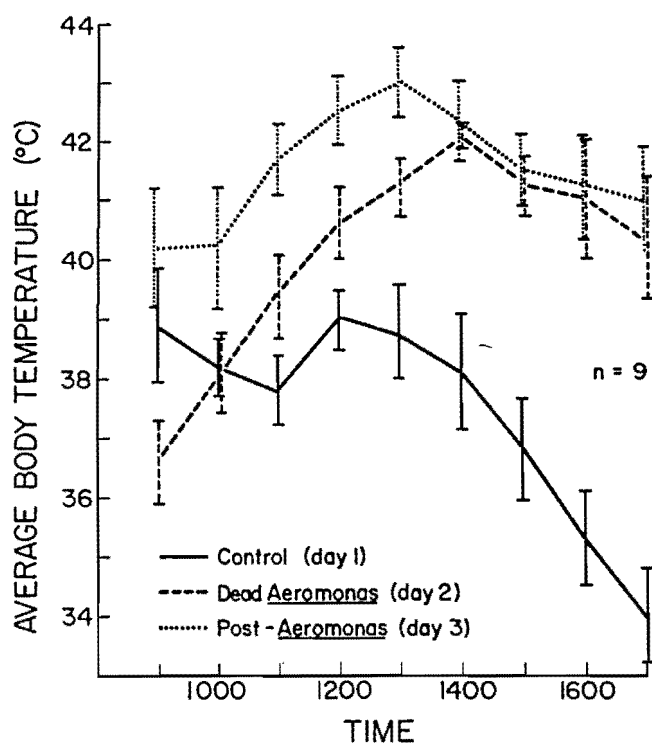
Fig. 4

Body temperatures of the desert iguana *Dipsosaurus dorsalis* in a photothermal gradient chamber, on a control day (Day 1), and on two days following intracardiac injection of the dead bacterium *Aeromonas hydrophila* at 09h00 on Day 2. From Bernheim and Kluger (1976a), by copyright permission of the American Physiological Society.

haemolytica (Kluger, 1978) and *Citrobacter diversus* (Kluger, 1979a), also resulted in elevation of selected body temperatures. The biochemical foundation of fever in *D. dorsalis* appears similar to that which prevails in mammals: peritoneal macrophages from the lizard synthesize EP *in vitro* (Bernheim and Kluger, 1977), and the lizards developed pyrexia both in response to this lizard EP and to rabbit EP. Components of fever other than pyrexia are displayed by *D. dorsalis* too: plasma concentrations of iron and zinc show the characteristic changes after injection of *A. hydrophila* (Hacker, Rothenburg and Kluger, 1981). The combination of elevated temperature and reduced iron concentration depressed the proliferation of *A. hydrophila in vitro* (Grieger and Kluger, 1978). Also, injecting iron into lizards along with live *A. hydrophila* compromised survival of the lizards (Grieger and Kluger, 1978). In infected lizards kept at their febrile temperature of 41 °C, granulocytes accumulated more rapidly at infection sites, and there was more rapid containment of the bacteraemia (Bernheim, Bodel, Askenase and Atkins, 1978). Serum antibody levels, and granulocyte chemotactic and phagocytic functions, were not improved, however.

Pyrexia following injection of killed *A. hydrophila* has been observed in three other lizard species, all members of the iguanid family. The second iguanid demonstrated to develop fever was the green iguana *Iguana iguana*, which exhibited behavioural pyrexia (Kluger 1978); there was no endothermic component (e.g., shivering, vasoconstriction) to its response (Malvin and Kluger, 1979). The third was the collared lizard *Crotaphytus collaris* (Firth *et al.*, 1980). More recently (Muchlinski, Stoutenburgh and Hogan, 1989), a fourth iguanid, the chuckwalla *Sauromalus obesus,* has been shown to elevate its selected body temperature at least 2 °C above its normal 36–40 °C, following *A. hydrophila* injection, not just in laboratory conditions but also in its natural habitat in the field. *S. obesus* fever was particularly evident on the second day after injection.

Pyrexia following pyrogen injections is not ubiquitous in lizards, however. We measured the body temperatures of the armadillo lizard *Cordylus cataphractus*, following intracardiac injections of the same dose of killed *A. hydrophila* that produced pyrexia in *D. dorsalis* (Laburn *et al.*, 1981). *C. cataphractus* is a cordylid lizard, with approximately the same body mass as *D. dorsalis;* it inhabits arid regions of southern Africa and is known for its sunbasking behaviour. It showed no change in selected body temperature after *A. hydrophila* injection, nor after injection of rabbit EP (Laburn *et al.*, 1981).

One possible explanation for the failure of *A. hydrophila* injection to cause fever in *C. cataphractus* is that the dose used was too high in this species (even though its mass was similar to that of *D. dorsalis*), and the lizard entered the equivalent of endotoxic shock. To check this possibility, we exposed *C. cataphractus* in the same photothermal gradient chamber, and injected 1/10 and 1/100 of the original dose: the selected body temperature following these lower doses of killed bacteria was the same as that which followed saline injection (Fig. 5).

Having demonstrated that at least one species of African lizard did not become pyrexic following pyrogen injection, we set out to investigate other species. *Pachydactylus bibronii* is a nocturnal gecko (mass approximately 14 g) which has widespread distribution throughout southern Africa. We constructed a thermal gradient chamber for the lizards by placing a glass flask containing water at one end of a terrarium, and controlling the temperature of the water at about 55 °C, too hot for the lizards to remain close to it permanently, using a thermostatically regulated immersion heater. We then conducted all measurements at night, in the dark. We measured the colonic temperature of the lizards using indwelling 36 gauge copper-constantan thermocouples, the outputs of which were connected to a data logger. Figure 6 shows the nocturnal body temperatures of lizards permanently resident in the terrarium. The average body temperature of the group of lizards, given saline, varied by only 1 °C over the night; the lizards were excellent thermoregulators. Interestingly, the selected body temperature was about 32 °C, very similar to that of *C. cataphractus,* and very much higher than the lizards ever could attain for most of the night in their natural habitats. Intracardiac injection of killed *A. hydrophila* had no effect on body temperature. In subsequent experiments, we injected 0,5 ml of a solution containing rabbit endogenous pyrogen, made according to the technique of Borsook, Laburn and Mitchell (1978) and tested for pyrogenicity in rabbits; it too had no effect on selected body temperature in *P. bibronii.*

The selected body temperatures of both *C. cataphractus* and *P. bibronii* were much lower than those exhibited by *D. dorsalis.* Iguanid lizards, as a family, generally select high body temperatures (Avery, 1979) close to the mammalian range.
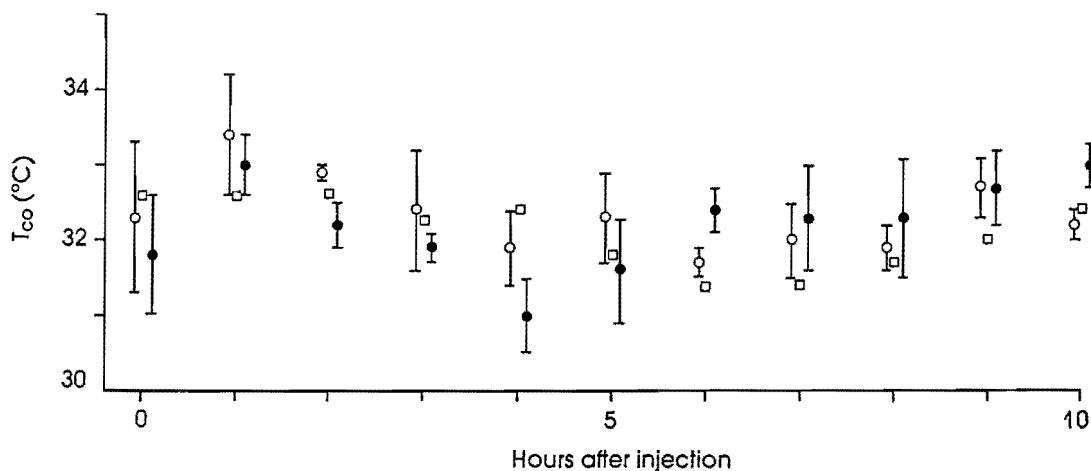
Fig. 5

Body temperatures (measured as colonic temperature, T_{co}) of armadillo lizards *Cordylus cataphractus* (mean $\pm$ *SE*, $n = 4$, mean mass = 60 g) in a photothermal gradient chamber. The direction of the thermal gradient in the chamber was reversed every 30 minutes, so that the animals had to thermoregulate actively, by changing position, to maintain a constant body temperature. At time zero, corresponding to 09h00, intracardiac injections were given, in random order, of 0,2 ml sterile saline (open circles), 4×10^7 killed organisms of *Aeromonas hydrophila* in 0,2 ml saline (squares) and 4×10^8 killed organisms in 0,2 ml saline (closed circles). Body temperatures did not differ significantly following the three treatments. These and all our other experiments were approved by the Animal Ethics Committee of the University of the Witwatersrand.

We considered it possible that fever occurred only in those species of lizards with a mammal-like body temperature. Such lizards had been reported from the Namib Desert (Hamilton and Coetzee, 1969), so we attempted to produce fever in two Namib species.

Aporosaura anchietae is a small (2–5 g) lacertid lizard, which inhabits sand dunes throughout the Namib (Louw and Holm, 1972). It is diurnally active, and present on the sand surface even when sand surface temperatures exceed 35 °C. As for most Namib dune species, the most obvious thermoregulatory behaviour available to *A. anchietae* is burying and emerging from the sand substrate. We captured *A. anchietae*
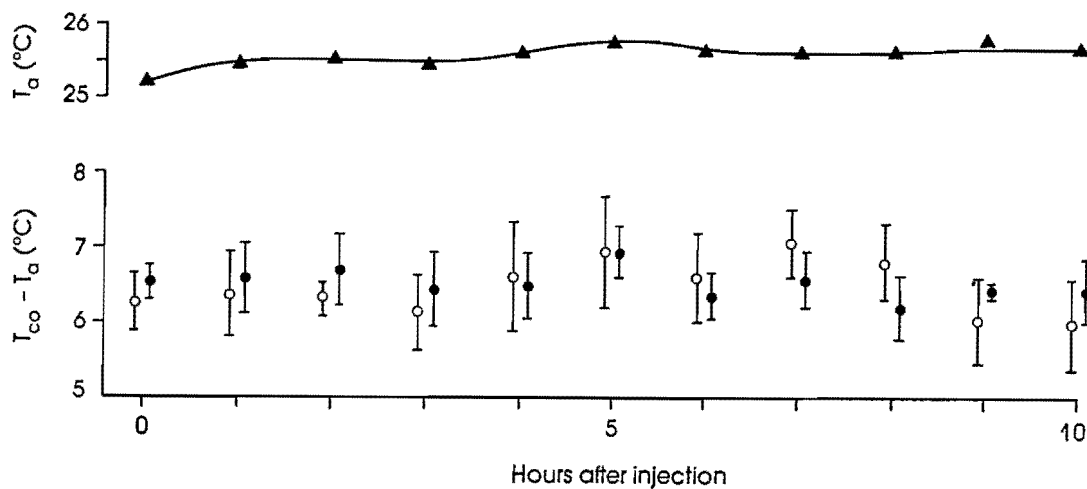
Fig. 6

Ambient temperature (T_a, triangles) and body temperature (measured as the difference between colonic temperature, T_{co}, and ambient temperature) of Bibron's gecko *Pachydactylus bibronii* (mean $\pm$ *SE*, $n = 6$, mean mass = 14 g), following intracardiac injection, in random order, of 0,2 ml sterile saline (open circles) or 0,2 ml saline containing 4×10^9 killed *Aeromonas hydrophila* (closed circles) at time zero, corresponding to 19h30. The measurements were carried out in the dark; a thermal gradient was obtained by including a glass flask of water thermostatically controlled at 55 °C in one corner of the terrarium. The lizards were permanently resident in the terrarium. Body temperatures did not differ following the two treatments.
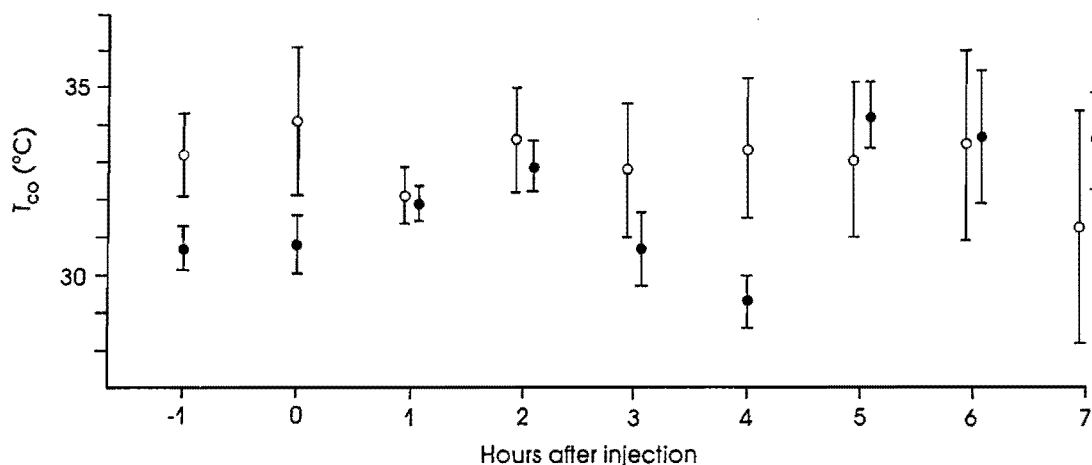
Fig. 7

Body temperature (measured as colonic temperature, T_{co}) of the shovel-snouted lizard *Aporosaura anchietae* (mean ± *SE*, *n* = 5, mean mass = 3 g), in a photothermal gradient chamber, given intracardiac injections, in random order, of 0,1 ml sterile saline (open circles) and 0,1 ml of saline containing 4 × 10^9 killed *Aeromonas hydrophila*. Body temperatures did not differ significantly between the two treatments.

on slipfaces in the central Namib dune sea near Gobabeb (23° 34′ S, 15° 03′ E) and placed them in a photothermal gradient chamber with a dune sand substrate and a tungsten lamp heat source. We measured colonic temperature using fine (36 gauge) copper-constantan thermocouples. Even this fine wire, when permanently attached, prevented the lizards from burying freely in the sand, so we did not use indwelling thermocouples but caught the lizards approximately every hour, and measured their colonic temperatures as rapidly as possible using a roving probe. Figure 7 shows that *A. anchietae* lizards showed considerable variability in body temperature, probably primarily because of their low thermal inertia, but that intracardiac injection of killed *A. hydrophila* had no effect on their selected body temperature. Moreover, all the lizards given killed *A. hydrophila* died within 12 hours of the injection, and none of those given intracardiac saline did; death following injection of killed bacteria in lizards has not been reported in other investigations of reptilian fever.

In our study, *A. anchietae* selected body temperatures closer to that of *C. cataphractus* and *P. bibronii* than to the mammal-like temperature of *D. dorsalis*. We therefore extended our investigation to another Namib dune lizard, *Angolosaurus skoogi*, a larger (up to 120 g) lizard, which is endemic to the northern Namib dune sea (Mitchell, Seely, Roberts, Pietruszka, McClain, Griffin and Yeaton, 1987). Like *C. cataphractus*, it is a cordylid lizard, and is capable of sophisticated thermoregulatory behaviour (Seely, Mitchell, Roberts and McClain, 1988; Seely, Mitchell and Goelst, 1990). We captured subadult *A. skoogi* on Skeleton Coast dunes near the Unjab River (20° 09′ S, 13° 14′ E) and placed them in an enclosure on a dune slipface, such that they were exposed to natural variations in microclimate, and were able to bury in the sand. We measured their colonic temperature with indwelling 36 gauge copper-constantan thermocouples.

The thermocouples did impair movement somewhat, but the lizards nevertheless were able to bury and emerge, and to seek out different areas of the enclosure. At solar noon, we gave the lizards intraperitoneal injections either of saline or of a cocktail of pyrogens, containing both endotoxin and killed *Staphylococcus aureus*, and Fig. 8 shows the results. The lizards emerged from the sand at a time typical of their afternoon surface activity period, and attained a temperature near 36 °C, very similar to that of *D. dorsalis*. Unlike *D. dorsalis*, however, their selected body temperatures were unaffected by the injection of the pyrogen. We have therefore failed, so far, to find an African lizard which becomes pyrexic, though we have investigated four species in three families.

Indeed, we have failed to find any African reptile that becomes pyrexic. Apart from the four iguanid lizard species, three other reptile species have been reported to select higher body temperatures following injection of *A. hydrophila*. Two of these are turtles, *Terrapene carolina* and *Chrysemys picta* (Monagas and Gatten, 1983). The leopard tortoise *Geochelone pardalis*, widespread throughout southern Africa, selected a deep body temperature of 33 °C in a photothermal gradient chamber. This body temperature was not affected by killed *S. aureus*, killed *Salmonella minnesota*, nor by endotoxin (Zurovsky, Mitchell and Laburn, 1987). We also investigated two African snakes in the photothermal gradient chamber. The same spectrum of pyrogens failed to elicit a change in selected body temperature in the olive grass snake *Psammophis phillipsii*, which is diurnally active and a sunbasker, and endotoxin did not affect selected body temperature in the crepuscular to nocturnal brown house snake, *Lamprophis fuliginosus* (Zurovsky, Brain, Laburn and Mitchell, 1987).

The third non-iguanid reptile reported to develop fever following *A. hydrophila* injection is the American crocodilian *Alligator mississippiensis* (Lang, 1986). Young animals given
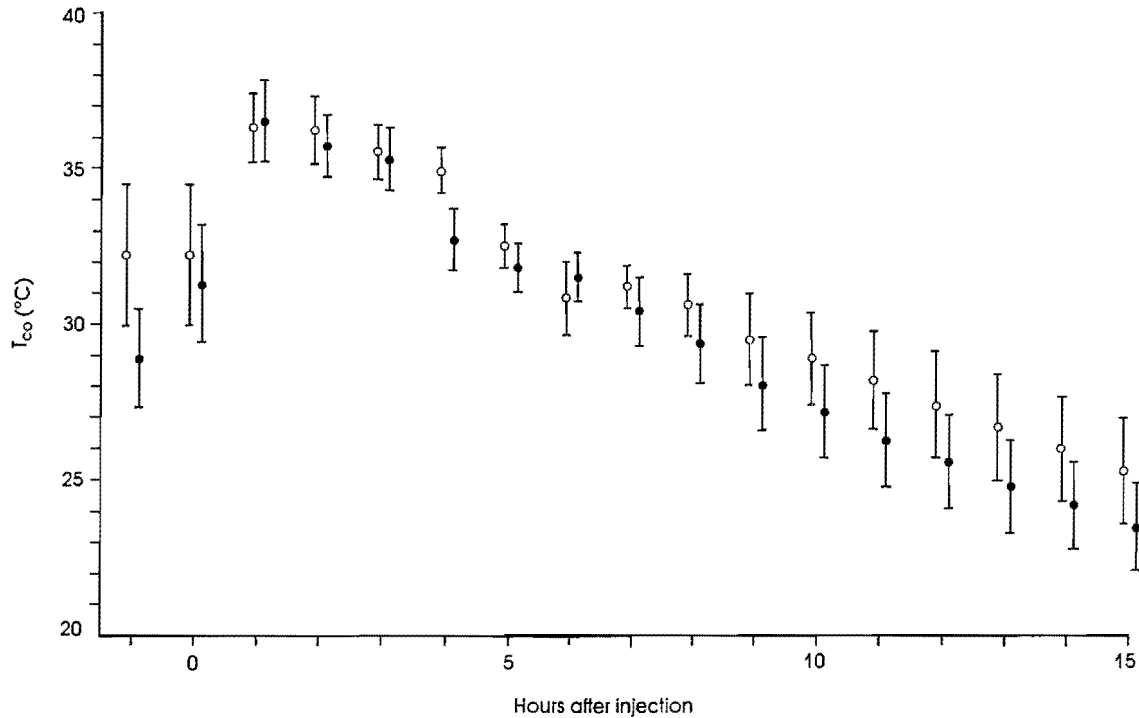
Fig. 8

Body temperatures (measured as colonic temperature, T_{co}) of the desert plated lizard *Angolosaurus skoogi* (mean ± SE, n = 6, mean mass = 60 g), following intraperitoneal injection, in random order, of 0,5 ml sterile saline (open circles) or 0,5 ml saline containing 4×10^9 killed gram-positive bacteria *Staphylococcus aureus*, and 10 µg/kg endotoxin (ex *Salmonella typhosa*, Difco) at time zero, corresponding to solar noon. Lizards were confined to an enclosure on a dune slipface, and exposed to the natural microclimate. All lizards had buried in the sand substrate within 6 hours of time zero. There were no significant differences in body temperature between the two treatments. The body temperatures of the lizards, in both cases, followed the pattern typical of animals that emerged on to the hot surface for a short period and then buried in the cooler sand for the rest of the day.

an unspecified dose of live bacteria selected warmer parts of a thermal gradient such that their body temperatures were elevated for 1–2 days, returning to normal after 3–4 days. It is difficult to know by how much the selected body temperature (normally 28–30 °C) was elevated, because the statistical analysis in Lang's paper appears to be invalid; he used 10 animals but reports a sample size between 30 and 120 in his analysis. In a previous experiment (Glassman and Bennett, 1978), the same species of alligator had been exposed to increasing doses of live *A. hydrophila* in their habitat water, while the water was was kept at constant temperatures between 20 °C and 35 °C. Host defence to the bacterial infection, as reflected in total leucocyte and neutrophilic macrophage concentrations, was optimum at a water temperature of 30 °C, close to the selected body temperatures of the animals when not infected. At a water temperature of 35 °C, all infected animals died whereas healthy animals survived: the pyrexia therefore did not appear to be beneficial.

In all the studies in which fever has been demonstrated in reptiles, the pyrogen has been injected into the host animal. Like other taxa, however, reptiles have naturally occurring infections of potentially pyrogenic microorganisms, and lizards are frequently hosts of *Plasmodium* protozoa (Schall, Bennett and Putnam, 1982). *Plasmodium falciparum* is a cause of malaria in humans, and malaria is characterized by recurring

fever of very high amplitude. Another species, *Plasmodium mexicanum*, is very prevalent in northern California in an iguanid lizard, the western fence lizard *Sceloporus occidentalis*. It is very intriguing that infected *S. occidentalis* spend more time in the shade than do non-infected animals, and have a selected body temperature in both field and laboratory conditions which is not significantly different to that of healthy animals (Schall and Sarni, 1987). It is possible that *P. mexicanum* is not a pyrogenic organism; alternatively, fever is not ubiquitous even amongst iguanid lizards.

Of the fifteen species of reptile that have been investigated, therefore, pyrexia following pyrogen injections has been reported in seven: four species of lizard, all iguanids, two species of turtle, and one crocodilian.

FEVER AND SURVIVAL

We have attempted to assemble all the available data on fever in ectotherms. In evaluating whether the data supports the concept that fever has survival value, or, in other words, contributes to the biological fitness of a host, we need to address a number of questions. To what extent do the reported hyperthermias represent true pyrexias, and to what extent are they aberrations of thermoregulation? How well do the laboratory interventions mimic the natural events that might lead to

fever in the host? How do apparent benefits of the fever weigh up against costs? To what extent can one extrapolate from one host to another, and particularly, extrapolate from ectotherms to endotherms? How widely distributed is fever phylogenetically? We have already mentioned that the hyperthermia which follows PGE injection in invertebrates may sometimes be an artifact of sedation. High doses of PGE sedated scorpions (Cabanac and Le Guelte, 1980), and either sedated or killed snails (Cabanac and Rossetti, 1987). Systemic injection of PGE cannot be used to produce pyrexia in vertebrates, because the dose required would be toxic. To produce an elevation of body temperature in invertebrates by systemic injection of PGE required a very high dose, 4 mg/kg in scorpions and leeches, for example (Cabanac and Le Guelte, 1980; Cabanac, 1989). Injection of PGE into the central nervous system in nanogram doses per kilogram body mass, causes hyperthermia in endotherms.

Regardless of which pyrogen is involved, if an elevation in body temperature represents fever, rather than any other form of hyperthermia, then that elevation must have particular attributes. Specifically, the elevated body temperature in endotherms is defended in the face of environmental heat and cold stress. No-one appears to have devised an experiment to test quantitatively whether thermoregulation remains fully competent during the elevations of temperature that have been observed in ectotherms, following injections of pyrogens. Another attribute is that the temperature should be reduced by antipyretic drugs, an attribute which has been confirmed only for the leech *N. obscura* (Cabanac, 1989), the crayfish *C. bartoni* (Casterlin and Reynolds, 1980), the desert iguana *D. dorsalis* (Bernheim and Kluger, 1976b) and the bluegill sunfish *L. macrochirus* (Reynolds, 1977). Another requirement of pyrexia in ectotherms, if it reflects true fever, is that it should be accompanied by some, or all, of the other features of fever, such as release of acute-phase proteins, and changes in metallic ion concentration, as has been demonstrated in *D. dorsalis* (Hacker *et al.*, 1981), but not yet investigated in other ectothermic vertebrates. Whether or not the pyrexia contributes to survival, some of these other features indeed do so (Duff, 1986). Prostaglandins do not elicit the acute-phase response (Hellon *et al.*, 1990), so animals in which PGE has been injected, apart from the problems arising from dose, do not have the same repertoire of responses as those given the pyrogen of a pathogenic organism. Those species in which the only pyrogen that has been used is PGE need to be reinvestigated with other pyrogens. Indeed, apart from the peculiar problems associated with PGE, we believe that more than one pyrogen should be used whenever a species is tested for the existence of fever.

Almost all investigations of reactions of ectotherms to pyrogens have been carried out in artificial environments in laboratories. If the reactions are to be used to evaluate the survival value of fever, then the experimental conditions should simulate the natural environment as far as possible. For example, in the study of Cabanac and Le Guelte (1980) on scorpions in which the experimental chamber was 'uniformly and permanently illuminated', it would have been an improvement to conduct the study in the dark since both species of scorpion used are active only nocturnally in their natural habitat; the results would not necessarily be different, of course. In the

study of McClain *et al.* (1988) on tenebrionid beetles, the beetles were prevented from using their most potent anti-hyperthermic behaviour, namely burying in the sand substrate. Similarly, the steep thermal gradients used to study aquatic animals in the laboratory are seldom, if ever, available to the animals in their natural habitats.

Even if one establishes that fever occurs in an ectotherm in a natural environment, it contributes positively to the fitness of the host only if its benefits outweigh its costs (Boorstein and Ewald, 1987). Low mortality in the presence of fever following a pathological event, and high mortality in its absence following the same event, would be a cogent argument for a positive survival value, but such an outcome has not yet been demonstrated for any species in a natural environment. In our opinion, the closest approximation is the study on the grasshopper *M. sanguinipes* by Boorstein and Ewald (1987). The lizards with naturally acquired malaria did not develop fever (Schall and Sarni, 1987). At the organ and cellular level, there are many mechanisms which one predicts would favour host survival better in febrile than in afebrile conditions (see Kluger, 1986; Dinarello *et al.*, 1986; Roberts, 1979), but whether they are specific and successful survival mechanisms requires direct proof in a living organism. It is noteworthy, for example, that the combination of high body temperature and low serum iron concentration, which presents a hostile environment to some species of gram-negative bacteria and therefore ought to benefit a host (Kluger and Rothenburg, 1979), does not occur in baboons given gram-negative pyrogens (Zurovsky, Laburn, Mitchell and MacPhail, 1987), and does occur in humans in a hyperthermic situation other than fever, where it has no obvious survival value, namely exercise (Taylor, Rogers, Goodman, Baynes, Bothwell, Bezwoda, Kramer and Hattingh, 1987).

There are undoubtedly costs associated with fever too. The energy cost of pyrexia *per se* is particularly high in ectotherms (Muchlinski, 1985). In addition, several biochemical and physiological events occur in fever in both ectotherms and endotherms which appear to compromise the host and therefore should be considered as costs; they include inactivity, lack of appetite, loss of mass, nervous system malfunction and dehydration (Roberts, 1979; Blatteis, 1986; Boorstein and Ewald, 1987). In some laboratory studies using endotherms, pyrexia has been shown actually to increase mortality (Banet, 1986). Indeed, Banet (1983) believes that the stimulation of the immune system by pyrogens benefits the host, but the concurrent pyrexia is counteradaptive; fever without pyrexia, which may well occur in many ectotherms, would be more advantageous to the host than fever with pyrexia. Such a view would be consistent with the observations of Glassman and Bennett (1978) that elevation of the body temperature of alligators to 35 °C during an infection increased mortality; their defence mechanisms are optimally active at their afebrile selected temperature of 30 °C.

If assessments of the cost : benefit ratios in a sample of species are to be used to derive general principles, then one must consider whether interspecific extrapolations are valid. In particular, extrapolations from ectotherms to endotherms are precarious. Because the temperatures of ectotherms can vary over a relatively large range, there is a concomitant large variation in the rate of biochemical processes, and depression

of such processes at febrile temperatures in infected ecto-
therms may well limit the host's ability to mount defences
through a non-specific Q10 effect (Muchlinski, 1985); in endo-
therms, however, the difference between febrile and afebrile
temperatures is much less. (Indeed, the studies showing im-
proved survival of infected ectotherms at high body tempera-
tures should be repeated with pathogenic organisms that do
not cause marked elevations in body temperature.) Also, en-
dotherms generally appear to be more sensitive to exogenous
pyrogens than are ectotherms, though there is a wide variation
in sensitivity amongst endotherms and amongst ectotherms.
The same absolute dose of killed *A. hydrophila* that will induce
a 2 °C rise in body temperature in the lizard *D. dorsalis* of mass
25–60 g (Bernheim and Kluger, 1976*a*) will do the same in 3 kg
rabbits (Laburn *et al.*, 1981), which are particularly sensitive to
endotoxin; mass-specific sensitivity therefore differs by two
orders of magnitude. The dose of endotoxin required to elevate
selected temperature in *O. plana* beetles (McClain *et al.*, 1988)
was more than a million times the pyrogenic dose of the same
endotoxin in rabbits (Warner, Mitchell, Savage and McClain,
1985).

Notwithstanding differences in sensitivity to pyrogens, the
mere existence of fever in phylogenetically disparate species
is a persuasive argument in favour of it benefiting the host. The
argument was most cogent when all species tested, including
all ectotherms, appeared to respond to pyrogens. We now
know that fever is not ubiquitous amongst ectotherms; of the
37 species investigated so far, 11 have shown no response to
pyrogens (Tables 1 and 2). Of the 26 showing a response, 6

have been tested only with PGE. We know now that there are
endothermic species, and particularly primates, highly resis-
tant to pyrogens (Zurovsky *et al.*, 1987*b*). Also, there are
circumstances in which the responses to pyrogens are sup-
pressed in normally sensitive endotherms. One is parturition,
where fever may be suppressed in both mother and neonate
(Cooper 1987; Hellon *et al.*, 1990). Another is malnutrition
(Hoffman-Goetz and Kluger, 1979; Hoffman-Goetz,
McFarlane, Bistrian and Blackburn, 1981), a circumstance in
which compromised resistance to infection can be fatal.

So fever is neither a ubiquitous nor a consistent response to
pyrogens, and the question of why it occurs, when it does
occur, remains unanswered. Further studies of Namib and
other ectotherms may help solve the problem. For example, it
may be coincidence, or it may be phylogenetically important,
that four out of five iguanid lizard species tested so far have
responded to pyrogens, but no lizards from other families have
done so, even when the species have evolved in very similar
desert habitats. Also, very few ectotherms have been tested
for non-thermal responses to pyrogens. It is possible that the
thermal and non-thermal components of fever have evolved
separately; in *Dipsosaurus dorsalis* the fall in serum iron
concentration which follows administration of bacteria is inde-
pendent of changes in body temperature (Grieger and Kluger,
1978). If the non-thermal components have more survival
value than the thermal component, the non-thermal compo-
nents may well be present even in the absence of pyrexia, and
pyrexia, when it occurs, may be incidental.

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Morphology of Wax Blooms on Selected Namib Desert Beetles (Coleoptera: Tenebrionidae)

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A number of tenebrionid beetles in the Namib Desert have a wax bloom covering either all or part of the integument. We examined the wax bloom of twelve species of Namib tenebrionids belonging to two tribes, the Adesmiini and Zophosini.

In all species the bloom is secreted as thin filaments of approximately 0,1 μm in diameter from simple pores that are often at the tips of tubercles. The pores are either widespread over the integument and regularly spaced, or localized in patches or in ridges. They can be either raised off the surface (tubercles) or open directly onto it. The secretions are in the form of streamers, whorls, tufts, mats, clumps or bundles in species-specific patterns. The resulting meshwork of loosely interwoven filaments is raised off the surface of the cuticle. Transmission electron microscopy of single filaments suggests that there may be an inner core and an outer sheath. How the morphology of the wax bloom relates to the survival of these beetles is discussed.

INTRODUCTION

Tenebrionid beetles are a major component of the fauna of the Namib Desert in Namibia (Seely, 1978). A number of the diurnal beetles in the tribes Adesmiini and Zophosini have an extracuticular secretion covering either a part or all of the cuticle. There appears to be a larger proportion of wax-producing species in this desert than in other deserts of the world. The presence of the wax bloom on these beetles is correlated with a steep climatic gradient in the Namib. The greatest number of species with the secretion are found in the inland areas of the coastal desert where temperatures are high and humidities low (McClain, Seely, Hadley and Gray, 1985). The wax bloom affords protection for these diurnal beetles exposed to deleterious high radiant energy, and desiccating conditions. The elucidation of the wax bloom morphology could give clues as to how this is brought about. Certainly in plants the morphology of the wax bloom is related to environmental conditions: wax rods, tubes, filaments, and ribbons are formed at low temperatures and plate waxes at high temperatures (Baker, 1974). The wax blooms of insects appear to have discrete morphologies similar to wax blooms found on the surface of various plant species (Hadley, 1981). Aside from playing a role in reducing water loss across the cuticular surface of insects, wax blooms afford protection from predators, microorganisms, ultra-violet light, and mechanical abrasion by the substrate, increased reflectance of solar radiation and also serve in chemical communication (Hadley, 1984).

Early work by Holdgate and Seal (1956) on the pupae of the tenebrionid beetle *Tenebrio molitor,* showed it to be covered with a fine filamentous material. A white crystalline powder appears on the surface of the cuticle of the larva of the silkworm *Samia cynthia* (Bowers and Thompson, 1965). The balsam woolly aphid, *Adelges piceae,* has a ribbon-like wax secretion on certain regions of the integument (Retnakaran, Ennis, Jobin and Granett, 1979). Specialized discs, depressions, cylinders, papillae, and spicules are involved in wax production of twenty species of coccinellid larvae (Pope, 1979). These appear to be similar to the crater-like secretory rims demonstrated by Locke (1960, 1974) for the lepidopteran larva of *Calpodes ethlius,* which also produces a wax bloom. Wax encrustations, crystals and filaments were found on the surface of the grasshopper *Trimerotropis pallidepennis,* when exposed to 50 °C and the buprestid beetle *Hippomelas planicosta,* which inhabits hot creosote flats, has a distinct yellow wax bloom (Hadley, 1982). *Cryptoglossa verrucosa,* a Sonoran Desert tenebrionid, has distinct colour phases associated with presence or absence of its wax bloom. At low humidities it appears whitish-blue due to the wax bloom but at high humidities it is black due to the absence of the bloom (Hadley, 1979). *Onymacris plana,* a large shiny black tenebrionid beetle from the Namib Desert, develops a bluish-white wax bloom in the warmer, less humid areas of the desert, but is black and remains without the wax bloom in the cooler, foggy coastal areas (McClain, Hanrahan, and Gerneke, 1986). Hadley (1982) subjected this beetle to low humidities in the laboratory and found that the bloom appears as circular patches with a central nucleus.

In tenebrionids that live in arid areas, the epicuticular wax is very thick and often there are specialized glands secreting wax in a powdery or filamentous form (Crowson, 1981). Scanning electron microscopy of *Cryptoglossa verrucosa* from the Sonoran Desert revealed tubercles distributed over the surface of the beetle out of which the wax material was secreted (Hadley, 1979). At high temperatures and low humidities numerous slender (0,14 μm diameter) filaments radiated from the

tip of the tubercles, creating a basket-like mesh which covered the entire beetle (Hadley, 1979).

The present study was undertaken in order to describe the morphology of the various coloured wax blooms that occur on Namib Desert tenebrionid beetles. Furthermore, we were interested in correlating morphology with function. What role does this extracuticular secretion play in the survival of these highly successful beetles of the Namib Desert?

MATERIALS AND METHODS

Selected tenebrionids of the tribes Adesmiini and Zophosini were collected from various habitats throughout the central and northern Namib Desert. Beetles were killed with ethyl acetate vapour and care taken to preserve the field-collected material. The elytra were removed and specimens placed into small vials containing silica gel. This was done to ensure desiccating conditions necessary for maintaining the integrity of the wax bloom material. The elytra were then mounted on Cambridge 100 stubs with conductive silver paint. Routine sputter-coating often distorted the wax bloom of the various species under consideration. Specimens were therefore first viewed uncoated in a Cambridge S180 scanning electron microscope. The same specimen was then sputter-coated under predetermined low heating conditions (Gerneke and McClain, 1981) and viewed again.

The operating parameters on the SEM were selected to give the required resolution at the lowest possible probe current, in order to reduce the electron dose and thus decrease charging. Minimal exposure to the beam before recording enabled successful micrographs to be obtained for almost all specimens. The SEM was operated at 4–6 kv and probe currents of between 1 to 2×10^{-12} A. Micrographs were recorded at 30 second frame time and 800 lines/frame. The selection of the area to be recorded, and focussing, were carried out at scan times of 1 to 4 seconds because TV scan rates increased the charging problem. The wax bloom of the different species was found to react differently to the electron beam: some species did not charge as much as others.

' The dimensions and characteristics of individual filaments were determined by transmission electron microscopy, using a JEOL 200CX. Each sample was brushed onto a 200 mesh Copper grid covered with a carbon coated formvar film, and viewed unstained in bright field mode at 200 kv. A magnification calibration was carried out at the same operating conditions at which the micrographs were recorded. All measurements were done directly on the TEM negatives using a diffraction ruler graded in 0,1 mm intervals.

RESULTS

Twelve species of the tribes Adesmiini and Zophosini were examined. Table 1 summarizes the major morphological features and Figs 1–34 illustrate the detailed morphology. Colour appears to be independent of the wax bloom morphology, although both reflective and chromatic properties of the wax bloom on the various coloured species varies (manuscript in preparation). In both the Adesmiini and Zophosini the wax is secreted as filaments from the tips of pores or tubercles, forming the architectural arrangement which is species-specific. The diameters of the filaments measured were approximately 0,1 µm. No differences were found between males and females in the microstructure responsible for wax bloom production.

In beetles of both tribes, wax filaments are continuously secreted from the tips of rounded tubercles (Fig. 28). They appear as spaghetti-like strands of various lengths (Fig. 29), and are collectively raised off the surface. As these filaments break, they remain on the cuticle surface (Figs 26, 28 & 30) as short rods which stick together (Fig. 30). TEM of individual filaments shows bands with rings (Figs 31 & 32). The lengths between the rings might indicate periods of secretion. All species examined with TEM showed the individual filaments to be composed of an outer sheath with an inner core (Figs 33 & 34).

Tribe Adesmiini

Stenocara phalangium has the white wax bloom on discrete areas of the cuticle (Fig. 1). These include the underside of the body, lateral portions of the elytra, pronotum, head and posterior portion of the abdomen (McClain, Praetorius, Hanrahan and Seely, 1984). The wax bloom is secreted from raised tubercles and forms tufts that cover localized areas of the integument (Fig. 2). Each tubercle secretes the filaments in a volcano-like pattern (Fig. 25). From the raised tip of the tubercle the filaments cascade to form a circular pattern with neighbouring filaments to create a dense mat of discrete filaments. This mat is raised off the surface of the cuticle (Fig. 2).

Onymacris laeviceps has tubercles located on the terminal portion of the abdomen in rows between ridges (Fig. 3). The wax bloom is localized on the abdomen and underside of the body but can cover the elytra and pronotum when the beetle is subjected to high temperatures and low humidities, as found in the inland portion of the desert. The filaments form tufts anastomosing with the filaments from other pores (Figs 3 & 4).

Onymacris plana has pores spaced approximately 70 µm apart and evenly distributed over the body. The wax is extruded from each pore as a single filament. The filament ultimately forms a whorl around the pore (Figs 5 & 6). Adjacent similarly formed whorls overlap. This pattern creates the meshwork that gives the otherwise black (Fig. 7) beetle a bluish appearance. The pores are found on all *O. plana* individuals but the bloom is found only on those individuals inhabiting the warm inland portion of the desert.

Onymacris rugatipennis albotessellata has patches of tubercles in depressions on the elytra (Fig. 8). The patches are 1,5 mm apart. Tubercles are also found scattered over the entire integument approximately 15 µm apart. These are raised off the surface and the secreted filaments form a patchy white mat (Fig. 9). Initially clumps that stick together are formed at the origin of the filaments, while further from the tip loosely jointed filaments radiate outward to join with others in the vicinity. Occasionally more than one wax-secreting pore is found in a tubercle (Fig. 26).

Physosterna cribipes has a thick epicuticle and upon high magnification the surface of the dorsal elytra appears smooth except for abrasion marks (Fig. 10). The wax bloom appears only after long periods of desiccation in the laboratory, or is sometimes found on individuals living in the hot inland portion
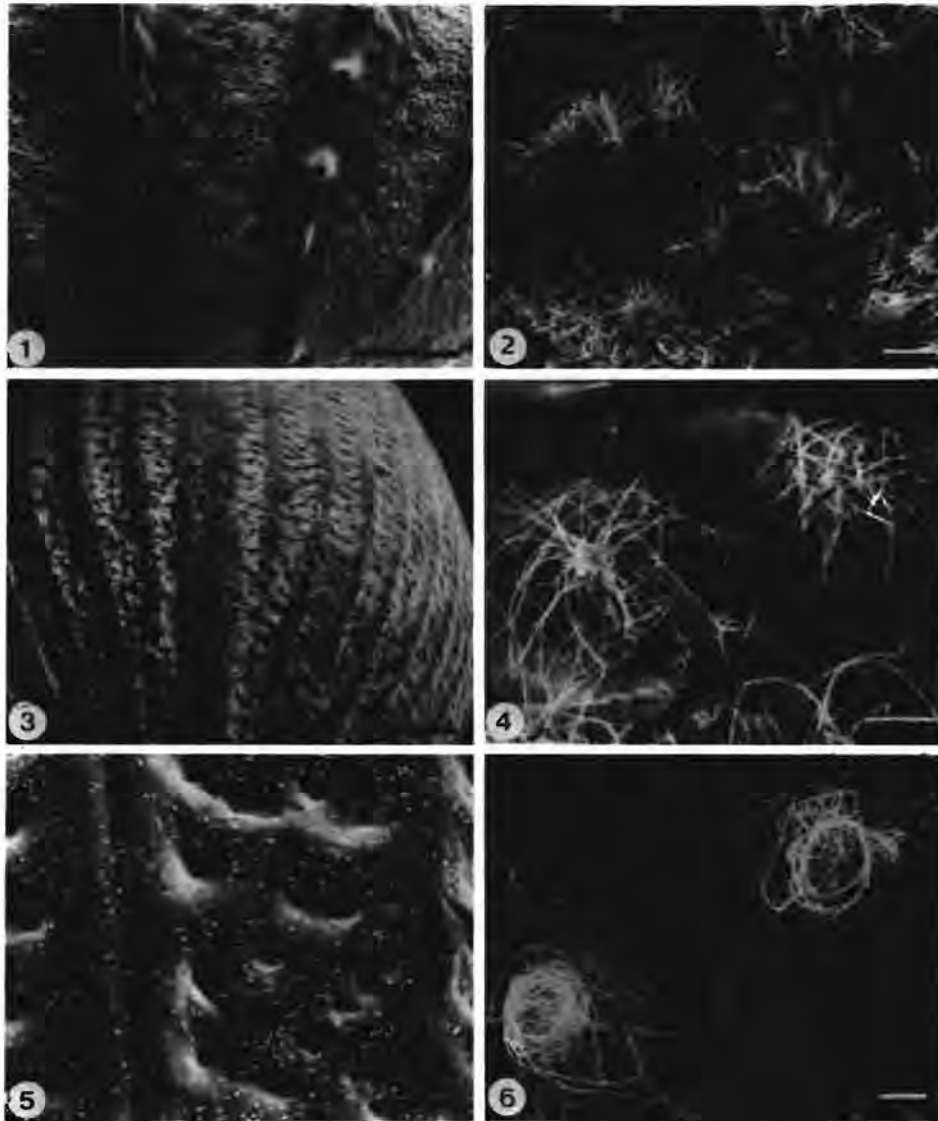
Figs 1–6

1. *Stenocara phalangium* (Bar = 0,5 mm): ridges of elytra with tubercles scattered in between.
2. *Stenocara phalangium* (Bar = 10 µm): tufts of filaments.
3. *Onymacris laeviceps* elytra (Bar = 1 mm): ridges with tufts of filaments on tubercles between them.
4. *Onymacris laeviceps* (Bar = 10 µm): anastomosing tufts of filaments.
5. *Onymacris plana* (Bar = 0,5 mm): dorsal elytra, showing small whorls.
6. *Onymacris plana* (Bar = 10 µm): wax bloom whorls from two tubercles.

of the desert. The beetles having the wax bloom are bluish-white in appearance. The pores open directly onto the surface of the cuticle. A flat mat similar to that of *Zophosis (Cerosis) hereroensis* (Fig. 17) is formed when wax bloom is fully developed.

Tribe Zophosini

In the Zophosini there are also species-specific wax bloom patterns. In the subgenus *Cardiosis* either a partial wax bloom or a few streamers of wax bloom filaments are found around the rim of the elytra. There are also a variety of colours of wax blooms found in this tribe, but the morphology is the same regardless of colour.

Zophosis carpi has a white wax bloom secreted by a few tubercles arranged in rows at the posterior end of the elytra (Fig. 11). The filaments are long, few in number, and do not anastomose to form a mat. They often adhere to setae arising from the elytra surface and frequently collect sand grains (Fig. 12).

Zophosis fairmairei has a distinct yellow wax bloom pattern,
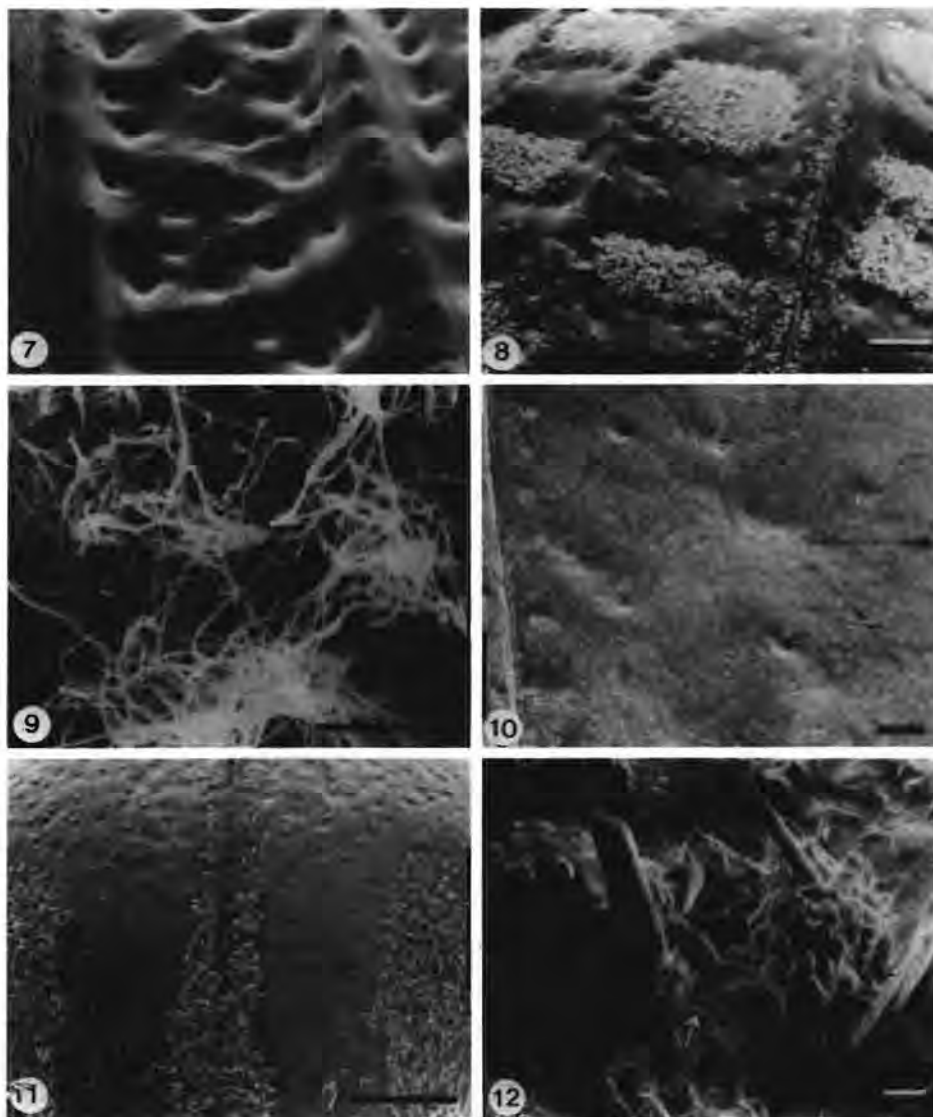
Figs 7–12

7. *Onymacris plana* (Bar = 0,5 mm): dorsal surface without wax bloom.

8. *Onymacris rugatipennis albotessellata* (Bar = 0,5 mm): depressions containing tubercles with patches of wax bloom.

9. *Onymacris rugatipennis albotessellata* (Bar = 10 μm): clumps of anastomosing filaments.

10. *Physosterna cribripes* (Bar = 100 μm): dorsal surface having no wax bloom.

11. *Zophosis carpi* (Bar = 0,5 mm): posterior region showing area of wax bloom secretion.

12. *Zophosis carpi* (Bar = 10 μm): wax bloom streamers with adhering sand grains.

which is sculptured on the dorsal portion of the beetle (Fig. 13). No wax bloom is found on the ventral surface. Tubercles, where present, are closely associated with setae (Fig. 14). Tubercles are raised and spaced approximately 20 μm apart. The filaments form a loose weave between the setae and, when the bloom is fully developed, completely cover the spines, which themselves have wax-secreting pores (Fig. 27). Much twisting of the filaments appears to occur as they leave the pore. Clumps of closely packed filaments fan out to anas-

tomose with the neighbouring filaments as in other species.

Zophosis hamiltonuli has a white wax bloom concentrated around the rim of the elytra. There are many setae covering this area and much of the dorsal surface. The wax bloom appears as long loose filaments in between the spines, resulting in a loose weave (Figs 15 & 16).

Zophosis (Cerosis) hereroensis has a continuous flat mat of wax bloom, which consists of closely woven filaments (Figs 17 & 18). The wax bloom covers the entire integument and gives
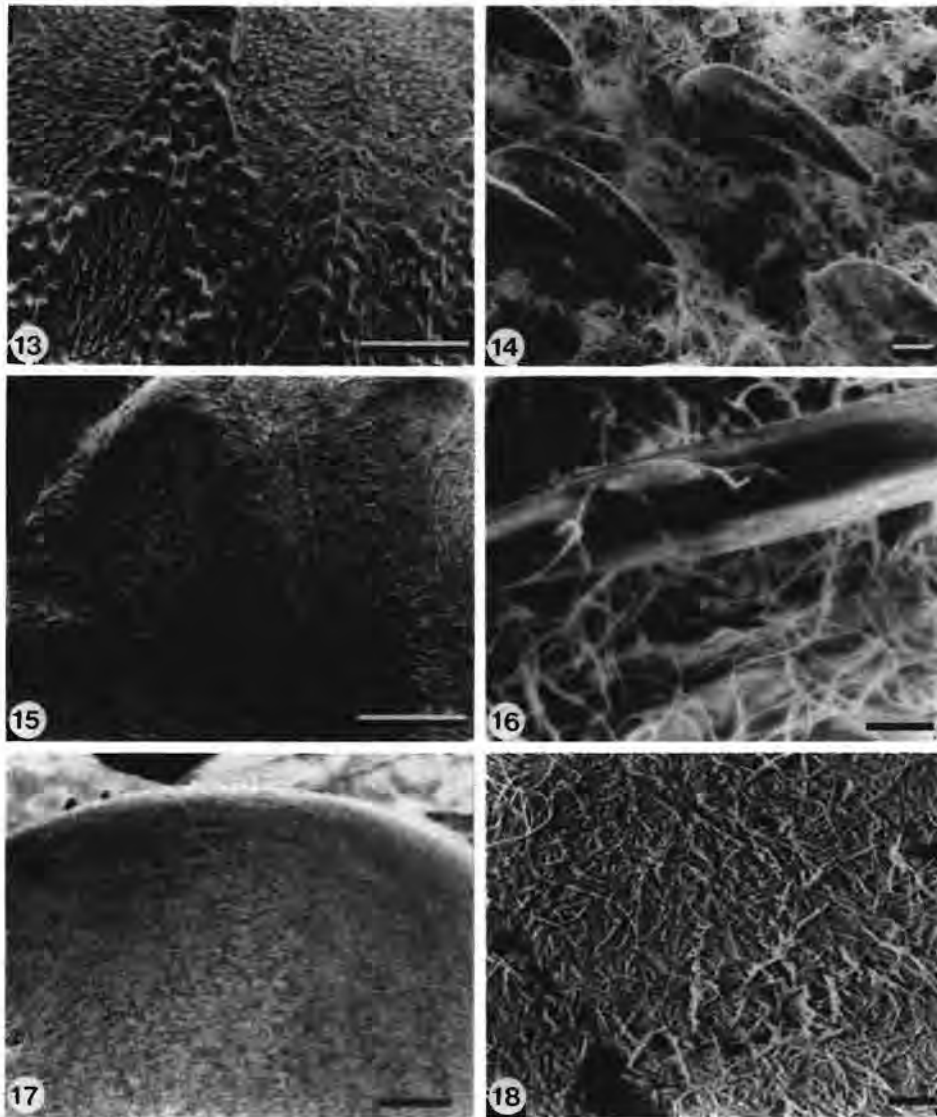
Figs 13–18

13. *Zophosis fairmairei* (Bar = 0,5 mm): elytra showing areas of setae.

14. *Zophosis fairmairei* (Bar = 10 µm): filaments and adjacent spines.

15. *Zophosis hamiltonuli* (Bar = 0,5 mm): posterior surface showing wax bloom secreting area.

16. *Zophosis hamiltonuli* (Bar = 5 µm): loose weave of wax filaments surrounding a seta.

17. *Zophosis (Cerosis) hereroensis* (Bar = 0,5 mm): flat mat of wax filaments covering entire surface.

18. *Zophosis hereroensis* (Bar = 10 µm): closely woven filaments forming a flat mat.

the species a bluish appearance. No setae are present and the pores open directly onto the surface. The filaments therefore form a flat mat close to the cuticle surface.

Zophosis mniszechi is completely covered with the wax bloom. However, the colour (pink) appears only on the dorsal surface, the ventral surface and the legs being white. The raised tubercles are located approximately 15 µm apart on the elytra between short, sparse setae. The tubercles secrete the wax filaments to form bundles, resulting in a wool-like mat (Figs 19 & 20).

Zophosis dorsata (Figs 21 & 22) has a pinkish to white wax bloom similar to that found for *Z. mniszechi*. The wool-like mat is compressed. The pores appear as bumps on the cuticle surface. As in *Z. mniszechi*, there are bundles formed by the filaments. The wax bloom covers the entire beetle, but the colour is only on the dorsal surface.

Zophosis testudinaria also has a wax bloom similar to *Z. mniszechi*, except the dorsal wax bloom is more pinkish and a fluffy clump of filaments is formed over each pore (Figs 23 & 24).
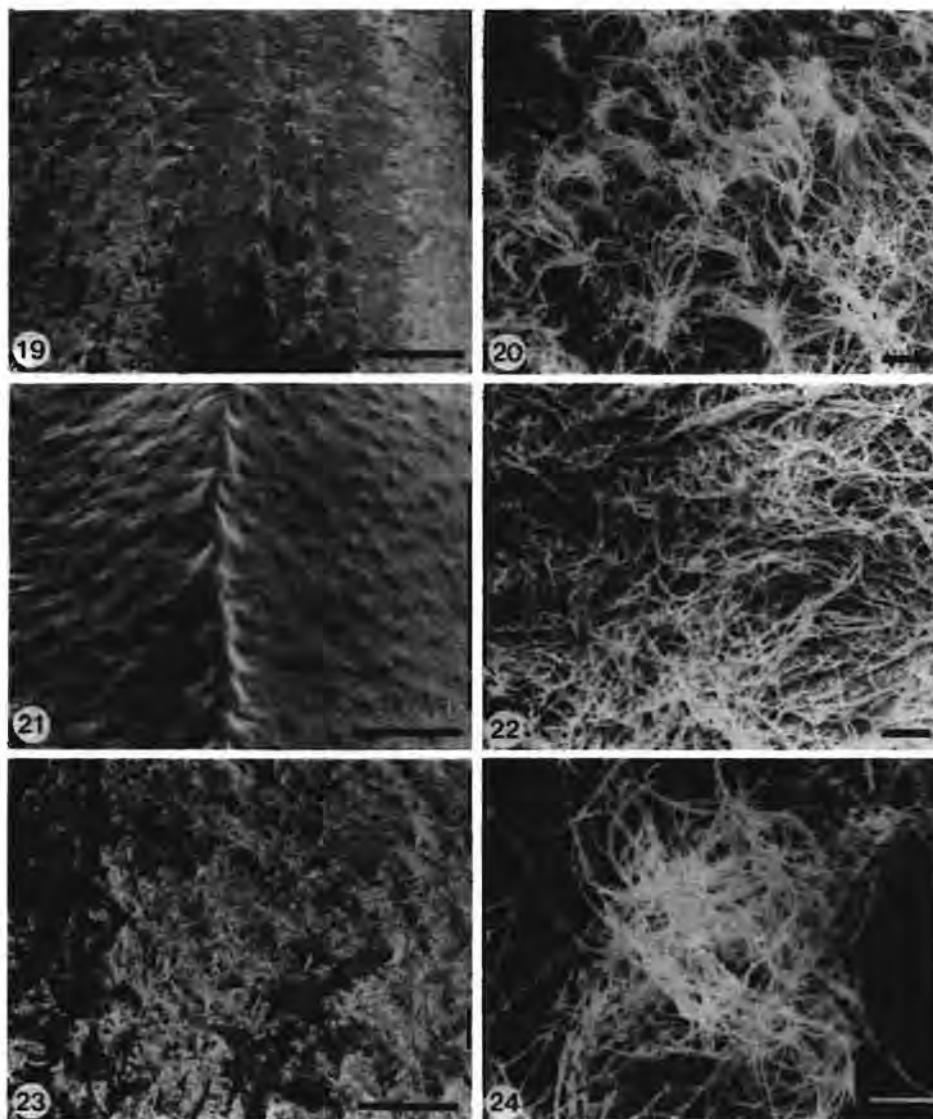
Figs 19–24

19. *Zophosis mniszechi* (Bar = 0,5 mm): surface setae and wax bloom filaments.

20. *Zophosis mniszechi* (Bar = 10 µm): wool-like mat with underlying tubercles.

21. *Zophosis dorsata* (Bar = 0,5 mm): surface showing raised tubercles.

22. *Zophosis dorsata* (Bar = 10 µm): flat compact mat of filaments.

23. *Zophosis testudinaria* (Bar = 0,5 mm): surface with wax blooms.

24. *Zophosis testudinaria* (Bar = 10 µm): clump of filaments.

DISCUSSION

The tenebrionid beetles we investigated secrete a wax bloom as single filaments via pores that open onto the surface of the cuticle. They can be level with the surface or raised off it. The pores are either uniformly widespread (*O. plana, Z. hereroensis, Z. mniszechi, Z. dorsata, Z. testudinaria*) or localized in discrete areas on the surface (*S. phalangium, O. laeviceps, O. rugatipennis albotessellata, Z. carpi. Z. hamiltonuli, Z. fairmairei*). No specialized areas of the cuticle for wax mould-

ing, as seen in the wax-producing structures of the coccinellid larva, were found. Many filaments may emerge and radiate from a single pore (Fig. 25), spreading until they merge with the output of other pores. In these Namib Desert species the pores lead to underlying dermal glands and their associated cells (Hanrahan *et al.*, 1984). The dermal glands of *Tenebrio molitor*, another coleopteran species, are similar to those of these Adesmiini and Zophosini (Hanrahan *et al.*, 1984). In only one subspecies, *Onymacris rugatipennis albotessellata*, was there more than one opening for wax secretion on any tubercle
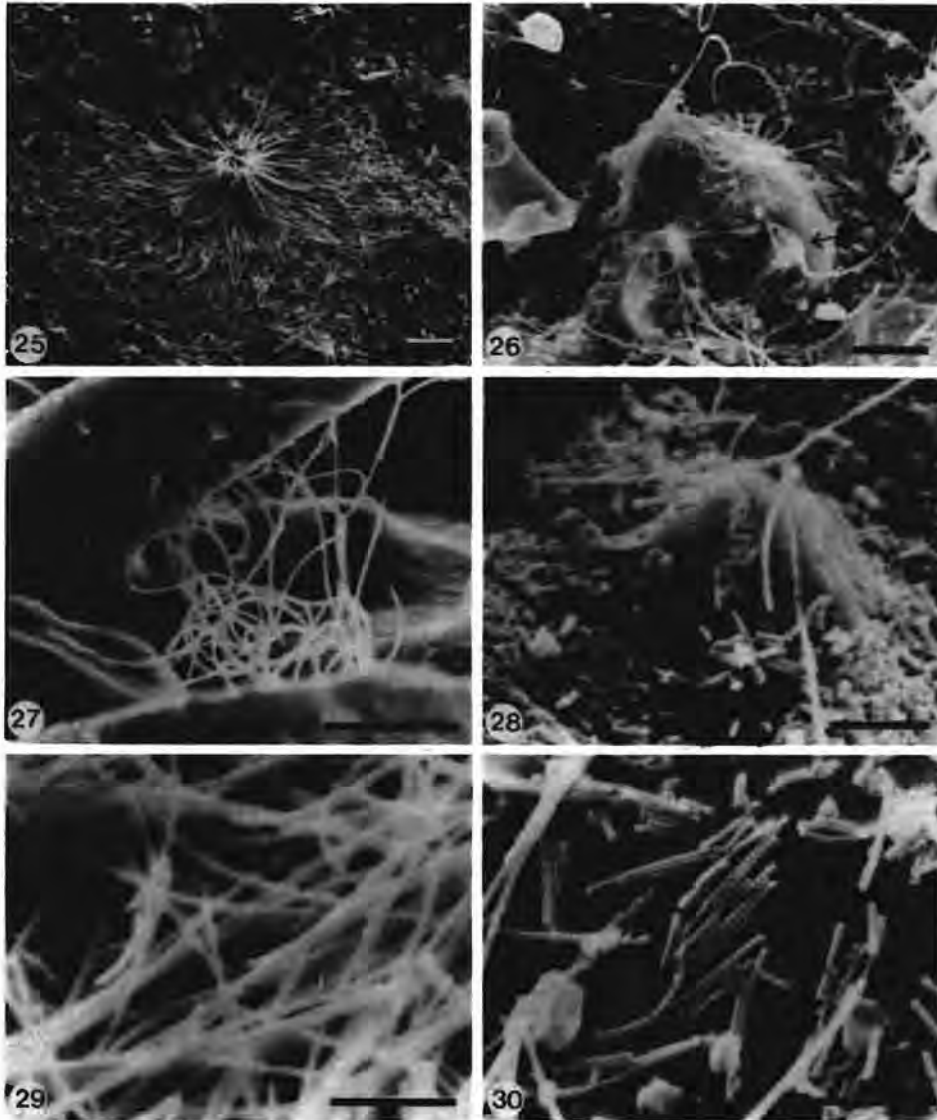
Figs 25–30

25. *Stenocara phalangium* (Bar = 10 μm): volcano-like eruption of wax filaments from one tubercle.

26. *Onymacris rugatipennis albotessellata* (Bar = 10 μm): tubercle with two wax-secreting pores.

27. *Zophosis fairmairei* (Bar = 10 μm): setae showing wax bloom secretion.

28. *Zophosis mniszechi* (Bar = 3 μm): tubercle pore with wax bloom filament being secreted. Characteristic of all species examined.

29. *Zophosis mniszechi* (Bar = 3 μm): typical wax bloom filaments seen for all species examined. They appear dense and are raised off the surface (0,1 μm in diameter).

30. *Onymacris rugatipennis albotessellata* (Bar = 3 μm): filaments adhering to cuticle surface and each other, characteristic of all species examined.

(Fig. 26). A similar arrangement of tubercles on the cuticle produces filaments in *Cryptoglossa verrucosa*, a Sonoran Desert tenebrionid (Hadley, 1979).

It appears then that the arid-adapted tenebrionids from both the Sonoran and Namib Deserts have similar microstructures for producing the wax bloom, namely dermal gland pores opening onto the surface. Dermal glands that produce wax bloom have been reported for other insects, for example for the mealy bugs (Homoptera). These are complex, having trilocular and quinquelocular-shaped pores (Cox and Pearce, 1983).

Aside from the tubercles, the setae on some Zophosini species also secrete wax filaments in a spaghetti-like form (Fig. 27). Under high temperature and low humidity (conditions
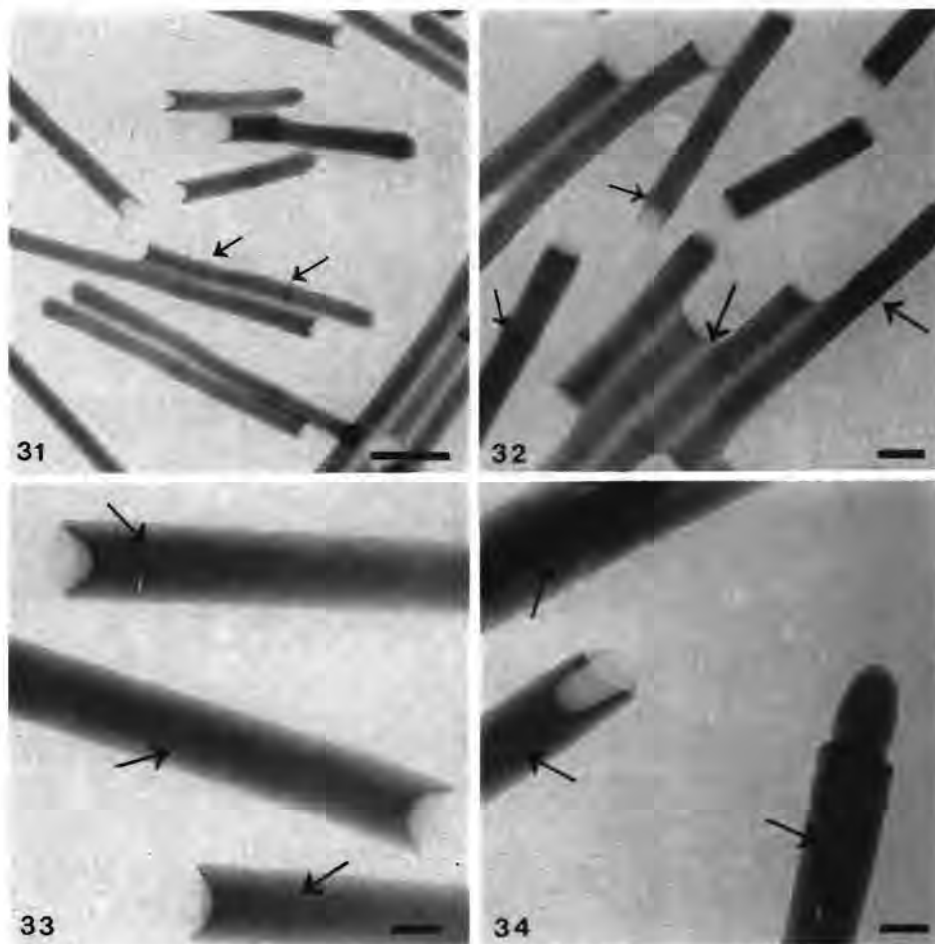
Figs 31–34

31. *Onymacris rugatipennis albotessellata* (Bar = 500 nm): TEM of wax filaments. Similar in all species examined.

32. *Onymacris plana* (Bar = 100 nm): TEM of wax filaments. Notice banding in some of the individual filaments.

33. *Zophosis mniszechi* (Bar = 100 nm): possible outer sheath and inner core structure of wax filaments.

34. *Onymacris rugatipennis albotessellata* (Bar = 100 nm): possible outer sheath and inner core of wax filaments.

which result in maximal wax bloom development), the spines are often covered with the wax bloom which gives the appearance of Spanish moss. Hairs and setae in mealy bugs (Homoptera) have also been found to secrete wax filaments (Cox and Pearce, 1983).

The wax bloom of these Namib Desert tenebrionids appears to be secreted continuously and is renewed in the field in as little as 8 hours. Measurements done with *Calpodes ethlius* indicated that the wax filaments were secreted at a rate of up to 5 μm/hr (Locke, 1960). The rings seen around the filaments of *O. plana* (Fig. 32) could also be an indication of a temporal pattern in secretion (the length between two rings for individual filaments was found to be $\overline{X} = 0,31$ μm, $S.D. = 0,095$, $n = 10$). When radioactive amino acids were injected into *Z. testudinaria* in studies of the protein component of the wax bloom, they appeared after only 8 hours in both the surface bloom and in

the underlying dermal gland reservoir and were incorporated into proteins shortly thereafter (Hanrahan, McClain and Warner, 1987). The process of wax secretion in these desert beetles is obviously a dynamic one.

Any of these species, when placed in high humidity or low temperature conditions, looses the wax bloom, exposing the otherwise black or brown cuticle surface.

Onymacris plana possesses individual whorls of wax bloom (Fig. 6) that resemble a tangled ball of knitting wool. Hadley (1982) has also examined this species and found that at higher magnification a central nucleus is apparent which gives rise to filaments that branch repeatedly, forming a structure that resembles an echinoderm basket star. The difference seen between our *O. plana* and those of Hadley probably reflect differences in sample preparation for the SEM.

The colours of the wax bloom in Namib species (Table 1)

Table 1
Characteristics of wax blooms on Namib Desert beetles.

Genus species	Colour	Pore distribution	Bloom morphology
Tribe Adesmiini			
Stenocara phalangium	white	localized	volcano-like, forms tufts
Onymacris laeviceps	blue	widespread	tuft
Onymacris plana	blue	widespread	whorls which interconnect
Onymacris rugatipennis albotessellata	white	widespread	clumps, raised, patchy mat
Physosterna cribipes	white	widespread	flat mat, appears when desert conditions are extreme
Tribe Zophosini			
Zophosis carpi	white	localized	long streamers
Zophosis fairmairei	yellow	localized	loose weave from pores and spines
Zophosis hamiltonuli	white	localized	discrete, filaments
Zophosis hereroensis	blue	widespread	continuous, flat mat
Zophosis mniszechi	pink	widespread	bundle, wool-like mat
Zophosis dorsata	white	widespread	bundles, compressed, wool-like mat
Zophosis testudinaria	pink	widespread	fluffy clump

could not be explained by the microstructure. The pigmented dorsal areas and white ventral surface were produced from similar-sized pores; obviously, the pore dictates the diameter of the filament and in all the species the pores were similar in diameter. Interestingly, reflective properties were found to vary with each species, although all wax bloom colours were of low saturation and had a flat reflectance curve throughout the visible spectrum (McClain et al., in preparation).

The wax-producing structures of sclerotized cuticle in other insects act as moulds to produce structurally different forms of wax and have been used extensively to aid in identification and classification (Pope, 1983, 1985). Only dorsal elytra of these Namib species were examined and, except for the species-specific pattern of the wax bloom, the location and distribution of the pores are too similar to be used for identification purposes. However, the only characteristic that visibly separates Onymacris rugatipennis albotessellata from a closely related subspecies O. rugatipennis rugatipennis, is the presence of the wax bloom (Penrith, 1975).

The structural arrangements of single filaments, their inorganic fingerprints and chemical composition are now being studied.

ACKNOWLEDGEMENTS

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Physiological Studies on the Namib Fauna: A Brief Critique

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The general status of physiology is examined in a modern zoological context to provide a background for critically reviewing physiological studies on the Namib fauna. The review highlights several excellent studies but concludes that many physiological studies on the Namib fauna have been too fragmentary. The necessity for sound natural history research and ecophysiological studies in the future is emphasized. The excellent research opportunities that exist in plant physiology, nitrogen cycling and the testing of various physiological hypotheses are also reviewed under the general title of recommended future research.

THE STATUS OF PHYSIOLOGY

While not wishing to encumber the start of this paper with a pointless semantic argument, it may nevertheless be useful to first reflect on what we mean by some very familiar terms such as physiology, environmental physiology, comparative physiology and physiological ecology, also known as ecophysiology. The zoology student in the period between the Great Wars still received a classic training in systematics and comparative anatomy. The study of the functions of animal organs, tissues and cells (physiology) was very much in its infancy and mostly confined to medical schools. This situation changed markedly after World War II, when the few pre-war schools of comparative physiology began to thrive and extend their influences across North America and Europe. Comparative physiology became the fashionable discipline within zoology and attracted imaginative and gifted students who were also well versed in another burgeoning sister discipline, namely biochemistry.

Comparative physiology at this time was meant to complement comparative anatomy and provide the golden thread to explain evolution in terms of chemistry and physics. Now, some forty years later, this discipline is being criticized. It is maintained, for example, that comparative physiology has merely assembled an encyclopaedia of facts and has contributed minimally to the important principles of zoology, particularly those involved in evolutionary theory. It is also true that the number of students now attracted to post-graduate study in this field is declining, whereas those attracted to ecology, behavioural ecology, conservation biology, evolutionary biology and biotechnology are increasing rapidly. Is this modern criticism of comparative physiology justified? Yes, in many instances it is valid: many of us are guilty of concentrating on snippets of biological understanding with insufficient academic or practical relevance. On the other hand, many examples can be gleaned from the comparative physiology literature which are of great fundamental significance and which have contributed to the grand intellectual sweep of evolutionary theory, a criterion which appears to have become a *sine qua non* in so many modern zoological circles (Feder, Bennet, Burggren and Huey, 1987). One need only mention the work on the evolution of endothermy or on comparative mechanisms of osmoregulation and obligatory nitrogen excretion, so ably described in *From Fish to Philosopher* by Homer Smith. More recently, the discovery of molecular clocks, the explanation of the molecular evolution of brain hormones, and many other examples can be used to soften these criticisms of comparative physiology. It has also been argued that the advent of environmental physiology has made comparative physiology more relevant and meaningful to zoology. This is, however, seldom the case as environmental physiology, strictly speaking, merely explains the effect of environmental influences on the physiological responses of an organism. In contrast, ecophysiology explores the physiological interaction between an organism (species) and its environment, with the specific goal of using this information to explain the distribution and abundance of the particular species, thereby moving much closer towards ecology and evolutionary biology. Using this background let us now critically examine some of the physiological studies carried out on the Namib fauna during the past two decades. How can they be classified and how do they rate against these criteria? No attempt will be made to review all the literature.

NAMIB STUDIES

Probably the first serious physiological study carried out on the Namib fauna was by Eric Edney (1971), who clearly showed that various species of Namib Tenebrionidae were highly tolerant to desiccation. This study provided a pattern for the rather biased approach of subsequent physiological studies. The investigator, faced with a quintessential desert of endless sand dunes, barren gravel plains, overwhelming sunshine and almost no rain, firmly believed that all Namib animals were physiologically magically different to other animals and set out to prove it. In this way, another early study examined the physiological and behavioural ecology of the sand-diving lizard *Aporosaura anchietae* (Louw and Holm, 1972); we were able to show that this species was partially herbivorous, that it engaged in a thermoregulatory dance upon the dune slipface to extend its surface activity and, most significant of all, that it stored large amounts of fog water in its digestive tract. The study was biased towards the concept of desert animals being

entirely different, and misconstrued the colon as the water-storing organ. In fact, a delicate abdominal bladder serves this function. Nevertheless, it explained the restricted distribution of this species to aeolian sand and its occurrence in the fog belt of the Namib Desert, thereby qualifying as ecophysiology. In fact, most of the physiological studies on the Namib fauna have qualified as ecophysiology or at least environmental physiology. Nevertheless, certain Namib species have also proved to be ideal subjects for pure electrophysiological research on the membranes of Malpighian tubules (e.g., Nicolson and Isaacson, 1987), but only ecologically orientated studies will be considered here.

The Namib tenebrionid beetles have been the subjects of most of the physiological studies carried out on the Namib fauna and they have provided a wealth of useful knowledge, particularly with regard to respiration, water balance and the chemistry of the cuticle. It is also noteworthy that, without any preconceived research plan, the various studies on these beetles fit spontaneously into a surprisingly logical sequence: we have gained a good understanding of their nutrition (Hanrahan and Seely, this volume), osmoregulation (Coutchie and Crowe, 1979b; Nicolson, 1980), water collection (Seely and Hamilton, 1976; Hamilton and Seely, 1976; Coutchie and Crowe, 1979a), reproduction (De Villiers, 1985), respiration (Bartholomew, Lighton and Louw, 1985; Louw, Nicolson and Seely, 1986), temperature regulation (Seely, Roberts and Mitchell, 1988) and waterproofing of the cuticle (McClain, Seely, Hadley and Gray, 1985). Some of these studies could be criticized as being too fragmentary by the 'high priests' of ecological and evolutionary theory, but taking them as a whole we can now piece together the ecophysiology of several tenebrionid species, thereby contributing to a more complete picture of the ecology of the Namib. Moreover, several of the papers, for example the brilliant field observations by Hamilton and Seely (1976) on fog basking and the elegant studies by Coutchie and Crowe (1979a) on the uptake of water vapour by *Onymacris* larvae, are outstanding in their own right. The logical way in which these papers fit together also warrants comment. For example, Nicolson's (1980) simple but well executed laboratory experiments on osmoregulation in *Onymacris plana* showed clearly that this species loses water, albeit slowly, at high vapour pressure deficits while osmoregulating efficiently. A suite of adaptations is therefore present in these animals to minimize water loss, such as waxy blooms, sunken spiracles, intermittent respiration and low metabolic rates. Because these are not sufficient to maintain a positive balance, water collection is consequently maximized by some form of fog imbibition. The larvae that do not normally appear on the surface and are not able to use fog water directly, have the remarkable ability to absorb water vapour from unsaturated air via the rectum (Coutchie and Crowe, 1979a).

The purist may object to my inclusion of Seely and Hamilton's (1976) and Hamilton and Seely's (1976) observations on trench building and fog basking by tenebrionid beetles, because they are behavioural and not physiological phenomena. A response to this criticism is required because, in my opinion, too many authors dwell too heavily on the relative importance of behavioural versus physiological adaptations in the desert and other extreme environments. In higher verte-brates we used to make a convenient distinction between behaviour and physiology by referring to the brain centres involved. If the higher cortical centres were involved, the response of the animal was described as behavioural, whereas a lower centre response was designated as physio-logical. If we now consider the relative simplicity of the cerebral ganglia of insects, this approach cannot be used, yet the osmoregulatory behaviour in insects and reptiles is frequently classed as physiological whereas courtship responses are considered behavioural. While I shall concede that a distinc-tion can be made between extreme differences, particularly among higher vertebrates, the arguments and debates on the relative importance of these phenomena are largely semantic and not very productive. Both physiology and behaviour ulti-mately become the physics and chemistry of cells.

While the tenebrionid studies combine to make a unifying theme, physiological studies on other species have been more sporadic. Marsh (1986) and Curtis (1985) have shown the importance of social insects in the general ecology of the Namib and how well they are adapted physiologically to sur-vival in the desert environment. Marsh's (1985) demonstration of how the heat-running ant *Ocymyrmex barbiger* uses its high surface area to volume ratio to off-load heat while resting in a thermal refuge is an excellent example of how careful field studies can sometimes provide critical information for unravel-ling the life history of a species (see also Marsh in this volume).

Studies on small mammals have followed the usual pattern by demonstrating the extremely high urine concentrating ability of their kidneys (Louw, 1972; Withers, Louw and Henschel, 1980). The latter study showed that water was so efficiently used by some of these small Namib mammals that the ratio of their daily energy expenditure to their daily water turnover rate actually approached the theoretical stoichiometric minimum values, calculated from the complete oxidation of protein, fats and carbohydrates. These studies have been complemented by Buffenstein, Campbell and Jarvis (1985) who showed that cricetid rodents excrete large amounts of allantoin as a nitro-genous end-product in the urine. While these small mammal studies have undoubtedly contributed to our knowledge, they were mostly short-term studies. What needs to be done in the future is to tackle a long-term field study, backed up by excel-lent laboratory facilities, to unravel the whole life history of a species through a study of its physiological ecology. Alterna-tively, a very thorough laboratory study in a carefully controlled environment of a complete water balance in the mould of Schmidt-Nielsen's (1964) much quoted study on the kangaroo rat should be rewarding.

Physiological research on large animals in the Namib has been conspicuous by its virtual absence. The logistics for carrying out this research have been very difficult to arrange and these factors, combined with the wealth of opportunities for studying smaller animals, have brought about this situation. Nevertheless, the behavioural studies on baboons by Hamilton (1986) contain a great deal of useful information on their nutrition and water use in the Kuiseb River bed during severe drought conditions, and make fascinating reading. Also, studies by Louw, Belonje and Coetzee (1969) on the ostrich, although performed outside the Namib, have ex-plained how these animals reduce water loss by efficient kidney function and very refined use of feather erection and

body orientation to maximize convective and radiant cooling. A second study on the ostrich by Withers, Siegfried and Louw (1981) provided convincing evidence that, under conditions of rest while not engaged in thermal panting, ostriches exhaled air that was not saturated with water vapour, thereby effecting very significant water savings. A similar phenomenon has been described in the camel by Shkolnik, Schroter and Schmidt-Nielsen (1980) and it remains to be seen how widespread this phenomenon is in large birds and ungulates. The springbok and the gemsbok are the most common large ungulates of the Namib Desert, yet we know very little about their ecophysiology. In the case of the gemsbok we still rely on Taylor's (1969) early studies in Kenya which suggested that the animals exhibit an extreme form of adaptive hyperthermia when dehydrated. These conclusions require verification in the field. In the case of the springbok, apart from the studies of Skinner, Dott, van Aarde, Davies and Conroy, (1987), the only desert-orientated study is that of Hofmeyer and Louw (1987). The latter study raises some intriguing questions about how the springbok can survive the temperature extremes of the desert with its relatively small body mass and very thin pelage, but it does not answer the crucial question of how the animals can survive without access to drinking water. In general then, these few studies have mostly been incomplete. They have, however, shown that interesting questions exist and that ecophysiological studies on these large species, as well as on some of our 'indigenous' sheep and goat breeds, in the mould of Shkolnik's research should prove very rewarding.

This brief review has revealed that many of the physiological studies have been worthwhile and that they have mostly been biased towards the genre of ecophysiology. In view of the unique environmental influences operating in the Namib, this trend should be encouraged. They have also been useful in supporting other studies and providing a more complete picture of this very well-studied area of our planet. Most of the physiological studies have set out to test hypotheses even if the hypotheses were simple, thereby avoiding being branded as 'only' a series of descriptive studies. The latter criticism should not be taken too seriously as there are still opportunities for well-planned descriptive studies in the Namib. Every effort should, however, still be made in the ecophysiological sphere, not only to ask clear-cut questions and test hypotheses, but to test *important* hypotheses which are relevant either academically or in a practical goal-directed fashion. I shall enlarge on this latter suggestion when discussing future research. Before then, I wish to examine the question 'Are desert animals really special?' more closely.

ARE DESERT ANIMALS SPECIAL?

This question was first posed by Cloudsley-Thompson as early as 1964. Since then it has had several proponents and in 1987 a whole conference was devoted to the theme 'What's special about desert ecology?' In his summing up of the conference, Dr Larry Slobodkin suggested 'that although the same basic physiological machinery is used by organisms that live in deserts, it is usually modified to cope with either the rich but episodic resources, or the more continuously available low quality resources that characterize desert ecosystems. In this context it would be interesting to know more about speciation

in and around deserts, in particular to discover whether they act as sources of, or sieves for, evolutionary novelties' (Dobson and Crawley, 1987). Seely (1989) contributed an important paper to the same conference, using the ecophysiological studies on Namib tenebrionids to construct several interesting hypotheses. She also concluded that the physiological adaptations of desert invertebrates are not qualitatively different from those of 'some species from other environments' and that 'behavioural adaptations are an important adjunct to physiological ones'. I have already dealt with the difficulties encountered in attempting to make a distinction between physiological and behavioural phenomena and wish now to examine this alleged similarity of the 'basic physiological machinery used by organisms that live in deserts'. I do so because young physiologists, reading these papers superficially, may be discouraged from engaging in the rewarding field of desert ecophysiological research.

To argue that all organisms, both temperate and xerophylic, are physiologically similar is obviously true. For example, we accept that all insects have six legs, breathe via tracheae, extrude hydrocarbons on the surface of the cuticle, employ the tricarboxylic acid cycle and cytochrome system for respiration. But are we justified in exaggerating small physiological differences, such as a low metabolic rate or a few extra layers of long-chain hydrocarbons on the cuticle of a desert insect, as being profoundly different to the universal norm? Nevertheless, it is misleading to deny the very real differences between an animal which produces urine with a maximum concentration of 600 mOsm and one which is able to concentrate its urine to 7000 mOsm. This is not merely a quantitative difference: it requires a different 'kind' of kidney. Similarly, the spectacular ability of *Onymacris* to absorb water vapour from unsaturated air in its gut using a Malpighian tubule fluid with an osmolality of 9 Osm is indeed 'special' (Machin, 1981).

The argument against special attributes of desert animals could include the close physiological similarities among various tiger beetle species collected from-a wide variety of habitats by Hadley and Schultz (1988), or the similarity in the high thermal tolerance of desert and temperate ant lion larvae established by Marsh (1987). To my mind, however, further debate on this issue is of limited value as the argument must eventually revolve around the strict philosophical definition of the word 'difference' and for this reason eventually becomes merely semantic. Nevertheless, the debate has been useful in cautioning physiologists against approaching the design and interpretation of their experiments with too strong a bias by expecting profound physiological differences in desert animals. It has also provided the evolutionists with interesting examples for speculating whether physiological mechanisms are sufficiently 'plastic' so that they do not place strict constraints on the distribution of animals, or whether distribution and abundance are perhaps more likely to be closely constrained by other ecological factors, such as competition and predation.

FUTURE RESEARCH

The Desert Ecological Research Unit of Namibia owes its success to various factors, not least among these being the fact that individual senior scientists have had complete free-

dom to pursue their own specialized interests. Far be it from me therefore to be prescriptive about future research in any way. I merely wish to share some thoughts on the basis of my long association with the research station. The following topics could to my mind offer some productive avenues of enquiry:

Physiology of desert plants

Recent personal experience, while studying the Nara plant, has convinced me that exceptional opportunities exist for physiological studies on Namib Desert plants. It is a neglected field and we have many endemic species growing under unusual environmental conditions that will provide ideal study material. These studies could follow the successful approach used by Park Nobel and his colleagues at the University of California, Los Angeles, by first concentrating on heat and water balances (e.g., Smith and Nobel, 1986) and then moving to the unravelling of the mechanism of fog or water vapour imbibition, which appears to be essential for the survival of many Namib plants. Hormonal control of dormancy and recovery after rain in desert perennials should provide excellent opportunities for basic studies in plant physiology.

Protein and nitrogen cycling

Much has been written about the reliable source of food energy (detritus) and free water (fog) in the dune ecosystem and how these factors sustain the remarkable variety of endemic animals (Louw and Seely, 1982). In contrast, we know almost nothing about how and where the plants obtain their nitrogen and the animals their protein. This is a difficult field, requiring a long-term fundamental study, but I feel confident it will yield important results leading to new concepts in nitrogen cycling because of the relatively simple ecosystem involved.

Physiological ecology or natural history

Many of the plants and animals in the Namib, as well as the communities they form, are so isolated that very little is known about them. There is therefore still a great need for natural history research in the Namib, particularly long-term research to eventually provide reliable data for the ecologists to either build their predictive models or explain the palaeoecological history of the region. With a little effort, these natural history studies can be designed to test specific hypotheses and, if necessary, be provided with suitable laboratory back-up to elevate them to the status of ecophysiological studies. In fact, many consider ecophysiology as merely a modern form of natural history. I anticipate that studies of this nature will continue to be an important part of the general research pattern on the Namib fauna. Recent successful studies of this nature include investigations on the ecophysiology and behaviour of the desert lizard *Angolosaurus skoogi* (e.g., Pietruszka, Hanrahan, Mitchell and Seely, 1986; Mitchell, Seely, Roberts, Pietruszka, McClain, Griffin and Yeaton, 1987).

This type of study should, if possible, incorporate the latest technology, such as radio tracking, advanced radio-telemetry and the use of doubly-labelled water, to measure water turnover rates and field metabolic rates. In this way studies of truly excellent quality, similar to that of Nagy and Medica (1986) on desert tortoises, can be achieved. The opportunities for studying large animals, pointed out previously, should also be seriously considered in this context.

Meeting the criticisms of comparative physiology

The criticisms of comparative physiology outlined at the beginning of this paper are to my mind generally valid. Comparative physiologists, whether they be evironmental, eco- or general physiologists, must respond to these criticisms by carefully planning their investigations towards the testing of important hypotheses. I am not suggesting that we have to tackle profound hypotheses, such as the evolution of osmoregulation or endothermy, with every investigation we launch. Nevertheless, the scientific relevance and significance of the hypothesis should be carefully evaluated. For example, dozens of studies have examined the water relations of Namib animals but not one of these has attempted to construct a complete water balance which would allow the testing of several hypotheses. Also of crucial importance to the survival of certain desert animals that never drink free water is the balance between metabolic water produced and the concurrent loss of respiratory water vapour which accompanies the production of metabolic water, yet there are only a handful of studies worldwide that have measured metabolic rate and respiratory water loss simultaneously. This balance is a phenomenon which lends itself to the construction and testing of hypotheses; it has wide applicability and provides excellent opportunities for marrying physics and physiology. A similar study is suggested by the significant findings of Seely and Mitchell (1987) that water vapour pressures are generally higher on the dune surface at night than in the sand below the surface. Consequently they concluded that animals seeking refuge beneath the dune sand at night were doing so for reasons other than the seeking out of high water vapour pressures. This is probably true but Clarke (1988) has recently found that the desert lizard *Angolosaurus skoogi* lost water more rapidly when prevented from burying beneath the sand than when it was allowed to submerge, even when temperatures and humidities were similar below and above the sand surface. It is possible then that in the field, boundary air layers remain intact beneath the sand, whereas above the surface, in spite of higher water vapour pressures, air movement could disrupt boundary layers and lead to more rapid evaporative water loss. Clearly a series of physical thresholds must be involved and their measurement will provide physiologists with some challenging hypothesis-testing. Many other examples could be cited, but only at the risk of appearing prescriptive. The Namib offers excellent opportunities for ecophysiological research and is itself a splendid natural laboratory. These advantages can, however, be exploited optimally only by well-planned, disciplined research, preferably of a long-term and fundamental nature. In this way we can avoid merely proving that animals can survive in their natural habitats, and rather concentrate on asking more profound questions, preferably of an evolutionary nature

Ecological Research Unit of Namibia, I would also like to use the opportunity to express my sincere thanks to the Director, Dr Mary Seely, for her generous help, guidance and cooperation over the past 15 years.

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