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WATER AND ENERGY BALANCE IN THE NAMIB SAND-DUNE LIZARD, *ANGOLOSAURUS SKOOGI*

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ABSTRACT

The field metabolic rate (FMR) and water flux of the herbivorous Namib sand-dune lizard, *Angolosaurus skoogi*, was measured during the summer non-breeding period (early January) by means of doubly labelled water. FMR was about half that expected for a lizard of this size. Water flux and laboratory measured standard metabolic rates were, however, typical of other desert lizards. It thus appeared *a priori* that this species was behaviourally reducing metabolic costs through reduced activity. This generated questions with regard to the ecological and physiological significance of low FMRs. Is the reduction forced by intolerable environmental conditions or the need to stay in positive water and energy balance ? Alternatively, is activity reduction voluntary and geared towards optimizing growth and storage, possibly in preparation for periods of physiological stress ? The research required to answer these questions forms the basis of this thesis.

There has been much discussion about the evolutionary and ecological significance of growth rates. The consensus seems to be that, under most circumstances, animals are adapted in ways that maximize growth or optimize growth in relation to realistically attainable rates of gross energy intake. Animal behaviour may be influenced by factors unrelated to growth considerations such as starvation, involuntary hypo/hyperthermia, predator evasion and social interactions. These factors may be difficult to identify and isolate, making this hypothesis difficult to test.

Previous studies on the biology of *A. skoogi* have shown that this species has a perennially available food source, a wide range of potential body temperatures at its disposal and a low predation risk. Social interaction appear to be confined to the breeding season. This species is thus a particularly suitable subject for a scope for growth optimization study.

In the laboratory, the various components of water and energy losses and gains that were relevant to a field growth optimization study were quantified. Resting and active metabolic rates were measured using constant volume respirometry. The ratio of active to resting (A/R) rates increased with temperature, ranging from (mean ± S.D.) 2.5 ± 1.5 at 15 °C to 3.8 ± 0.5 at 40 °C. Resting and active evaporative water loss (EWL) rates were measured gravimetrically. EWL A/R rates also increased with temperature, showing a similar increase to metabolic rates. When these measurements are applied to realistic field conditions (observed resting and active body temperatures), it is predicted that activity results in about an 8-fold increase in both resting metabolic and EWL rate. Specific dynamic action also had a marked effect on metabolic rate, depending on the temperature and the volume of food eaten. Increases of 50 - 105% over resting, post-absorptive metabolic rates were measured.

Energy and water intake were quantified in two separate feeding experiments. Energy intake showed a 5-fold and water intake a 4-fold increase between 23 and 37 °C. Digestive efficiency averaged 63 % for animals fed their natural diet (the cucurbit *Acanthosicyos horrida* and the grass *Stipagrostis hermannii*) and approximately 80% in animals fed on an artificial diet of carrots. The difference is attributed to the relatively high fibre content of the natural diet. Digestive efficiency was independent of temperature. The gut passage time of food was, however, strongly temperature dependent, ranging from 5.6 ± 1.7 days at 23 °C to 2.4 ± 0.3 days at 37 °C. Compared to the diets of other desert reptiles, the natural diet of *A. skoogi* has a high water content and a relatively low electrolyte load. Electrolyte excretion was accomplished by means of an efficient urate pellet concentrating system and a nasal salt gland. The concentration of sodium and potassium in urate pellets indicates that this avenue alone could deal with the daily salt load while using a small proportion (roughly 10%) of the daily water intake.

In the field, focal animal field studies were conducted on male subjects during spring (October 1989), the late summer breeding period (February 1990) and winter (July 1990). Observations concentrated on water flux rates, body temperature measurements (radio-telemetry) and activity patterns. Water flux rates showed large seasonal variability ranging from 5.4 ± 2.8 ml/kg.day in spring to 50.3 ± 15.0 ml/kg.day in late summer. The exceptionally high flux rate during the latter period is attributed to the intense breeding activity that takes place at this time of the year. Average submerged body temperatures ranged from 22.5 °C (winter) - 31.9 °C (late summer). Animals buried in the slipface to a depth where a stable body temperature could be maintained for 24 hours per day. On the surface, high body temperatures were maintained, averaging 39.9 ± 0.73 °C in spring and 39.3 ± 1.1 °C in late summer. There were striking differences in the frequency and duration of activity periods between the two seasons. In spring, animals were active on average every 2.5 ± 1.7 days. Activity occurred within a 90 minute period (12h30 - 14h00, n = 10), averaging 21 ± 20 (n = 5) minutes per day. Animals thus spent less than 1 % of their time on the surface. Taking possible unnoticed feeding into account, October (spring) animals fed, on average, every 3.7 ± 2.2 days. In contrast, February animals were active every day. Activity was observed over a much longer period (11h00 - 16h30), averaging 142 ± 44 (n = 7) minutes per day. Animals thus spent about 10 % of their time on the surface. Feeding was rarely observed (animals were often obscured by foliage) but, considering the high water flux rates in summer, it is probable that animals fed on a daily basis.

By combining laboratory studies of water and energy losses and gains and field observations of water flux rates, body temperatures and activity patterns, it is estimated that animals would run into negative water and energy balance if active for longer than 2.5 and 4 hours, respectively. Using a simple modelling procedure, it is concluded that outside the breeding season animals are behaving so as to optimize their scope for growth. This is achieved by regulating both the frequency and duration of activity. Essentially, activity is very expensive in terms of water and energy losses and is kept to a minimum. The negative effects of reduced activity are small compared to the reduction of losses. During the breeding season, however, energetic considerations take second place to gamete dispersal and animals appear to engage in breeding activities for as long as their energy and water resources will permit.

Although diet-related reduction or cessation of activity has been documented in reptiles, this appears to be the first demonstration of a voluntary reduction of activity. The conclusions drawn from this study disagree with the maxithermy hypothesis of Zimmerman and Tracy (1989) which predicts that, when food is abundant, ectotherms should maximize their body temperatures for as long as possible to optimize energy gain. In this, and several other studies, inadequate consideration has been given to the costs involved with maximizing body temperature. It is suggested that the hypothesis probably only holds true in animals which have low resting body temperatures (and subsequently poor resting digestion rates) and moderate activity body temperatures (with moderate activity costs).

A detailed theoretical analysis of the factors determining reptile body temperature is provided. This, together with an analysis of *A. skoogi*'s thermal environment (using copper models), was used to analyze thermoregulatory behaviour in the field. Although the environment can be thermally harsh, by selecting appropriate locations and adopting thermoregulatory postures, lizards can be active all year round even at the hottest times of the day. When submerged, animals appeared to behave as optitherms, striving to obtain a specific body temperature. This is attributed to optimizing energy returns (digestion rates) relative to energetic costs. When active, animals were maxitherms. Maxithermy is attributed to optimizing predator evasion outside the breeding season and, in males, territorial defence during the breeding season.

Other field observations make a useful contribution to existing data on the breeding behaviour and diet of this species. The diet is much more varied than previously reported. In (October) spring, the cucurbit *Acanthosicyos horrida* formed the major component of the diet, primarily because it was the only well hydrated plant at this time of the year. During the rainy season (February), the plant *Merremia guerichii*, which grows on small mounds of sand on the interdunal gravel plains, formed the most important plant component of the diet of breeding male animals. *Merremia* was still the most favoured food source during winter (July). Of particular interest is the apparent connection between territory size and food source exclusion. Territories are large enough to exclude some males from primary food sources (*Acanthosicyos* and *Merremia*). They then become opportunistic omnivores, feeding on *Stipagrostis* grass and arthropods.

During periods of starvation, scope for growth optimization (or more correctly, energy conservation) can still be practised by selecting low body temperatures. The thermal response of *A. skoogi* to starvation was tested in the laboratory. Animals did not behave as predicted - they selected higher body temperatures (about 30 °C) than the minimum available (about 23 °C). As no physiological benefits (including water conservation and electrolyte regulation) for this response could be isolated, this behaviour is attributed to the lack of any selective pressure in *A. skoogi*'s evolutionary history for a positive thermal response in the face of starvation (food is perennially available).

Finally, this study makes an important contribution to other aspects of *A. skoogi*'s physiology and to experimental protocol. Two unusual phenomena observed in the laboratory were

the lack of diel cycles of metabolism and the lack of a thermophilic response after feeding. Both these phenomena are attributed to the stability (thermal and photic) of *A. skoogi*'s subsurface habitat. No significant difference could be detected in the metabolic or EWL rates of animals resting above and below the sand at 30 °C. Oxygen consumption rates averaged 0.044 ± 0.004 (above) and 0.044 ± 0.005 (resting) ml O_2/g.h. ($p > 0.05$). EWL rates averaged 12.9 ± 2.5 (above) and 10.6 ± 4.7 (below) µl H_2O/g.h.mmHg ($p > 0.05$). Both temporal and thermal acclimation of resting metabolic rate (RMR) was demonstrated in the laboratory. Exact duplication of a 30 °C RMR experiment after 21 days yielded a metabolic rate 20 % lower than the original value ($p < 0.001$). Exact duplication of this experiment 9 days later with an alteration of thermal pretreatment (continuously at 30 °C instead of 23 °C with 3 hours of thermoregulation/day) resulted in a 12 % drop in RMR ($p < 0.05$). Finally, the RMRs of submerged animals took a remarkably long time to stabilize after handling (which involved weighing and, if necessary, forcing animals to bury). After burying, RMRs only stabilized after about 3 - 4 hours.

In conclusion, the major contributions of this thesis are :

- the addition of the reduced activity hypothesis to the list of adaptations to desert survival
- emphasizing the importance of considering both costs and gains in energetic studies
- laying down guidelines and protocol for subsequent studies of this nature
- new important considerations with regard to laboratory techniques, particularly the effect of handling animals prior to experimentation and laboratory acclimation..

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DECLARATION

The experimental work described in this thesis was approved by the Animal Experimentation Committee of the Faculty of Science, University of Cape Town.

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Chairman : Animal Experimentation Committee

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CHAPTER 1

GENERAL INTRODUCTION

Since the pioneering work on lizard thermoregulation by Cowles and Bogert (1944), reptiles have been the subject of intensive physiological and ecological research. Ideally suited to both laboratory and field investigations, they have been described as model species for testing ecological and evolutionary theories (Huey 1982). Initial research concentrated on field studies of temperature regulation in a great variety of reptiles, particularly desert species (see Avery 1982, for review). This was soon supplemented with an equally voluminous data base regarding water and energy metabolism from laboratory studies (see Bennett and Dawson 1976 ; Minnich 1982 ; Mautz 1982). More recently, field technological advances such as the isotopic determination of field metabolic rates and water flux have provided new insights into ecological energetics and water relations (see Nagy 1982 ; Nagy 1988 ; Nagy and Peterson 1988). The latest trend in lizard biology is the use of biophysical analysis which, by using environmental variables to predict body temperature, has been used to explain ecological variables such as time-space utilization and distributional limits (see, for example, James and Porter 1989 ; Porter 1989 ; Porter and Tracy 1983 ; Scott *et al.* 1982 ; Spotila and Standora 1985). Such studies have greatly increased our understanding of reptile behaviour.

There has been much debate about the ecological and evolutionary significance of growth rates. The general consensus seems to be that animals, under most circumstances, are adapted in ways that maximize growth or optimize growth in relation to realistically attainable rates of gross energy intake (Avery 1984). The amount of food eaten (benefits) per unit energy or time spent in attaining that food (cost) has been treated in a series of hypotheses known as optimal foraging theory (Pyke *et al.* 1977). An important assumption of the theory is that the overall fitness of an animal increases as a function of the net rate of energy intake. As such, the theory forms one of the cornerstones of modern-day evolutionary thought. Animals genetically predisposed to maximize their overall fitness are those which survive periods of stress and whose genetic traits become fixed in populations. Although cost-benefit analyses have been extensively applied to fish (Crowder and Magnuson 1983), very litle attention has been paid to this concept in reptiles. This is surprising considering (1) the enormous data base that has been collected over the past five decades, (2) the powerful analytical and technological tools such as biophysical analysis, telemetry and isotopes at our disposal, and (3) that lizards are ideally suited for testing ecological and evolutionary theories. The guidelines for cost-benefit analyses in reptiles were laid down almost two decades ago by Huey and Slatkin (1976). To date, however, only a few studies have attempted to integrate parameters of microclimate and lizard physiology and behaviour with growth (Anderson and Karasov 1981 ;

Karasov and Anderson 1984 ; Nagy, Huey and Bennett 1984 ; Merker and Nagy 1984 ; Porter 1989). The introduction to Chapter 5 describes the contribution of these studies in more detail.

Recent studies have demonstrated or predicted how individual parameters of lizard physiology and behaviour may interact among themselves or with growth. Avery (1984), for example, has demonstrated the importance of body temperature in determining growth rate in lizards. Growth increased in thermoregulating *Lacerta vivipara* to an extent that was directly proportional to the period for which high body temperatures could be maintained. The increase in growth was entirely due to increased voluntary food consumption - thermoregulation had no effect on net growth conversion efficiency. Zimmerman and Tracy (1989) have addressed the question of optimal thermoregulation in relation to gross energy intake by expanding on the foraging strategy predictions of Sibly (1981) : that when food is abundant, lizards should select high body temperatures for as long as possible to maximize the extraction of energy from food with respect to time. When food is limited, they predict that lizards should conserve energy by selecting cooler temperatures, depending on how limited the resource is. Porter (1989), incorporating data from Waldschmidt (1984), has combined laboratory experiments and a biophysical model to predict growth potential (net energy gain) of the lizard, *Scleropus undulatus*, under different environmental conditions. This is one of the few efforts in the literature on reptilian energetics to relate body temperature to net energy gain.

Among others, these three studies make it clear that correlating lizard physiology and behaviour with growth or (in evolutionary terms) fitness optimization is not beyond the scope of ecophysiologists. Growth determinants have been investigated, predictions are available for testing and protocols involving well established procedures have been documented.

In theory, the hypothesis that animals behave so as to optimize their net energy intake is easy to test. Taking food availability into account, measurements of energy gains and losses under different thermal regimes can be measured in the laboratory and used to predict optimal thermoregulatory strategies and activity patterns. Field thermoregulatory strategies and activity patterns can, in turn, be monitored and compared to predictions. In practice, however, there may be several problems associated with a study of this nature. Body temperature telemetry is at present confined to larger species. Estimates of maximum gross energy input are difficult without the cooperation of the experimental subject. Less obvious, the main obstacle in field growth rate investigations is the complexity of factors influencing lizard behaviour. Behaviour may be influenced or determined by factors totally unrelated to growth considerations. High predation pressure, competition, social interactions, involuntary hypo/hyperthermia and food shortages are all factors which can complicate and confuse a scope for growth investigation. The complexity of factors determining lizard behaviour may well be the reason for the paucity of investigations dealing with the question of scope for growth optimization.

The ideal experimental subject for a study of this nature is one which has a low predation risk, experiences little inter- or intraspecific competition for food or space, seldom interacts socially, has a wide range of environmental conditions at its disposal and has a permanent, abundant food source. The Namib-sand dune lizard, *Angolosaurus skoogi*, appears to fit most of these criteria. Due to intensive research over the last decade, much is now known about the biology of this species. The most notable contributions are those of Mitchell *et al.* (1987) on its general biology ; Pietruszka (1988) on sexual dimorphism and social structure ; Pietruszka *et al.* (1986) on diet ; Pietruszka (1987), Seely *et al.* (1988), Seely *et al.* (1990) on microclimate, thermal biology and activity patterns.

Also known as Skoog's or the sand-plated lizard, this species is a member of the saurian family Cordylidae, a reptilian group endemic to southern Africa. *A. skoogi* is only found along the narrow coastal strip of sand dunes extending from northern Namibia to southern Angola. Periods of inactivity are spent buried in the soft sand of dune slipfaces. The only other lizard species known to occupy the same habitat is the relatively smaller *Aporosaura anchietae* (maximum mass 9 g compared to *A. skoogi*'s 100+ g). *A. skoogi* is by far the most conspicuous of the two species. *A. anchietae* is, in fact, rarely seen and there are no records of any sort of competition for food or space between the two species.

The breeding season of *A. skoogi* is confined to six weeks, from mid-January to the end of February. During this period, social interactions between males are intense. For the rest of the year, lizards on a particular dune appear to constitute a socially unstructured and tolerant society. Rare interactions involving size related dominance have been observed in the vicinity of concentrated food sources (detritus accumulation at the slipface base). There is no competition for other food sources such as the large, succulent cucurbit called nara (*Acanthosicyos horrida*). *A. skoogi* is the only herbivorous species in the family Cordylidae. Diet analysis to date has revealed that the staple food is nara. This is supplemented by the grass *Stipagrostis*, and less importantly, by arthropods. Although other vegetation grows on the interdune plains and may form a small proportion of the diet, nara is the only truly perennial plant species. This is because it is independent of precipitation, obtaining its water from the underground table via a long tap root. As a result, *A. skoogi* never experiences food shortages and spends minimal energy obtaining its food. Predation intensity is also low for this species. The dominant predators appear to be the crows, *Corvus albus* and *Corvus capensis*. Visits of these predators to slipfaces are, however, rare. Other potential predators such as jackals and snakes appear to pose little threat to *A. skoogi*.

The unvegetated slipface habitat of *A. skoogi* appears superficially to be a uniform thermal environment. Several studies have, however, demonstrated that in actuality it is a broad thermal mosaic strongly influenced by sand temperature, solar radiation and wind. On the basis of location choice alone, *A. skoogi* has a wide range of body temperatures at its disposal. Temperatures below the sand surface also provide the choice of a wide range of body temperatures.

This is but some of the information that has been collected on this interesting desert reptile. Only points pertinent to the growth investigation criteria listed above have been extracted here. Clearly, *A. skoogi* is an ideal candidate for relating net energy gain parameters and behaviour to growth. This thesis is essentially such an investigation.

Chapter 2 descibes the pioneering field study which provided the stimulus to pursue a growth optimization study on *A. skoogi.* The work was done in collaboration with K. A. Nagy (team leader), M. K. Seely, D. Mitchell and J. R. B. Lighton. Of particular relevance here is the combined observations of an exceptionally low field metabolic rate (FMR) and high water loss rates when active. Low FMR's are attributed to reduced surface activity. This immediately generates questions with regard to the ecological and evolutionary significance of reduced FMR's. Is the reduction forced by intolerable environmental conditions or the need to stay in positive water and energy balance ? Alternatively, is activity reduction voluntary and geared towards optimizing growth and storage, possibly in preparation for periods of physiological stress ? The research required to answer these questions is described in the next three chapters.

Chapter 3 describes the laboratory studies necessary to determine net energy gain under various thermal and activity regimes. These include metabolic and water loss experiments on resting and active animals and feeding experiments to determine the various parameters of gross energy gain.

The following Chapter (4) deals with the complex phenomenon of the exchange of energy between an animal and its environment. It begins by providing a detailed introductory analysis of the physical parameters determining an ectotherm's body temperature. This is followed by a detailed microclimatic study of *A. skoogi*'s surface and subsurface habitat. Copper models are used as an indicator of lizard body temperature at different locations on the dune slipface. The temperatures of copper models are related to microclimatic parameters. Combined data are used to gain insight into observed thermoregulatory behaviour (particularly posturing and site selection) described in Chapter 5. Additional information on humidity conditions both above and below the slipface surface is also provided.

Chapter 5 describes the focal animal studies conducted on *A. skoogi* at three different times of the year. The main emphasis is on the physiological and ecological significance of thermoregulatory strategies and activty patterns. The questions and ideas generated in Chapter 2, the laboratory data collected in Chapter 3, the insight into thermoregulatory strategies gained from Chapter 4, and the field observations made in this section are all integrated to relate lizard physiology and behaviour to growth considerations. Other important components of this chapter include water flux, diet choice and observations on breeding behaviour.

Finally, Chapter 6 deals with a laboratory test of an expansion of the scope for growth optimization hypothesis. It stands to reason that an ectothermic scope for growth optimizer will, from an energy conservation point of view, select as low a body temperature as possible when experiencing starvation. In this species, there is a clear lack of the predicted starvation/energy conservation response. Various reasons for this are considered.

The temperature transmitters (telemeters) used during field trips (Chapter 5) were the culmination of more than 12 months of technological research during which numerous prototypes were laboriously tested. Distance range and battery life requirements precluded miniaturization of the final product beyond the size reported here. They could consequently be force-fed only to animals weighing in excess of 80g. This prevented any telemetry studies from being conducted on females (which attain a much smaller size than adult males) or juveniles. With the exception of Chapter 2, Section 5.2.4 (Chapter 5) and Chapter 6, only large adult males have been used throughout this study.

CHAPTER 2

WATER AND ENERGY BALANCE IN THE NAMIBIAN SAND DUNE LIZARD, *ANGOLOSURUS SKOOGI* : PRELIMINARY STUDY *

Abstract

Skoog's lizards (family Cordylidae) live on and in the slipfaces of shifting sand dunes in the hyperarid Namib Desert. We measured field metabolic rate (FMR) and water flux (doubly labelled water), diet (stomach content analysis), chemical composition of food items (water, energy and mineral contents), evaporative water loss in the field, and standard metabolic rate (SMR) in the laboratory. These lizards had FMRs and food requirements that are about half those of other lizards, although their SMR was not notably low. Water intake rates in the field were high due to the consumption of very succulent growing shoots of nara, a perennial shrub in the cucumber family that stays green year round on underground water obtained via a long tap root. Consumption of windblown, dry plant material (detritus, comprising about 20 % of the dry matter in the average diet) may be related to mineral nutrition. Behavioural adaptations (reduced above-ground activity, which lowers food and energy requirements, and selection of succulent plant food) rather than physiological adaptations that reduce resource requirements, appear to be most important in permitting survival of this lizard in its bleak habitat.

2.1. INTRODUCTION

Skoog's lizard, *Angolosaurus skoogi* (Andersson 1916), a member of the saurian family Cordylidae, occurs only on coastal dunes in northern Namibia and southern Angola, Africa (Steyn, 1963).

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These dunes are mobile, and harbour little vegetation, so the animal biomass in the hyperarid dune sea is relatively low. Nevertheless, Skoog's lizards occur in surprisingly dense populations in some parts of the habitat, where they far outnumber all other vertebrates (Mitchell *et al.* 1987)

How are these lizards able to make a living in such a seemingly inhospitable place ? This question has several important components, which include : what do they eat, how much food do they need and how do they get it, how much water do they need and how do they get it, how do they use their thermal environment to avoid overheating yet maintain acceptable body temperatures in this essentially shadeless habitat, how do they reproduce and where do they deposit their eggs, and how do they deal with predators ? Several of these questions have already been addressed. *A. skoogi* is primarily herbivorous, the population studied ingesting mostly the green, succulent tissues of the perennial curcubit plant called nara (*Acanthosicyos horrida*) that grows in portions of the dune sea (Pietruszka *et al.* 1986). The lizards are diurnal, and are active only when environmental conditions permit them to attain and maintain relatively high body temperatures (35 - 40 °C). They have characteristic postures thought to be thermoregulatory in function, and they dive into, and remain below the surface of the dune slipfaces when inactive (Hamilton and Coetzee 1969, Mitchell *et al.* 1987, Seely *et al.* 1988). Nara flowers and growing shoots are preferred foods, and are thought to provide the main source of water to the lizards, which do not normally have access to free water at any time of the year (Mitchell *et al.* 1987). Dry, wind-blown detritus and dry grass and other plants are also consumed, though the benefits of consuming other material when nara is available are not clear (Mitchell *et al.* 1987).

Adaptations that facilitate maintenance of water and energy balance in reptiles in desert habitats have been described for several species living in other deserts. The Namib desert may be much older than most other deserts (Crawford 1981), so one might expect the reptiles living in this desert would possess more advanced or even novel adaptations, and some are known to do so (Louw and Holm 1972). We studied water and energy metabolism of free-living *A. skoogi*, by using doubly labelled water, in order to evaluate the hypothesis that these lizards have lower water, energy and food requirements than other desert lizards. In addition, we measured aspects of diet composition to determine whether the consumption of nara might entail some penalty to the lizards, such as osmotic and ionic stress (Mitchell *et al.* 1987), and to try to understand why the lizards consume dry detritus.

2.2 MATERIALS AND METHODS

2.2.1 Study site

We studied *Angolosaurus skoogi* lizards living in a single dune slipface at the same study site used by Pietruszka *et al.* (1986), Mitchell *et al.* (1987), and Seely *et al.* (1988). This site is located on the south bank of the Unjab river bed (usually dry) in the Skeleton Coast National Park, Namibia, in southwestern Africa (20° 09' S, 13° 14' E). The cold Benguela current of the Atlantic Ocean is about 15 km to the west, and the air temperature is determined not so much by season but by whether the wind is blowing onshore or offshore. During our study, onshore winds and morning clouds moderated the minimum air temperatures (measured just above ground level at the base of a nara plant using a maximum/minimum thermometer) : mean = 16.6 ± 2.0 °C (n = 7). The clouds usually evaporated by 08h00, and daytime maximum air temperatures averaged 32.1 ± 1.6 °C (n = 7). Maximum globe temperatures would have been at least 10 °C higher (Seely *et al.* 1988). During the study period, 5 - 18 January 1988, a trace of rain fell on the last day, after all sampling had been completed. No dew or precipitating fog occurred during our study.

The sand dunes in this area are barchanoid, and move slowly to the north over the underlying gravel plain. The dominant plant in the study area is nara (*Acanthosicyos horrida*), a leafless member of the cucumber family, which has a long taproot and occurs primarily along the edges of river courses. Other plants making up less than 1 % total vegetation cover include the low growing perennials *Merremia guerichii* and *Suaeda plumosa*, which had some green tissues during our study, and the grasses *Stipagrostis hermannii* and *Bracharia psammophila*, which were visibly dry and brown.

2.2.2 Doubly labelled water (DLW)

To measure field metabolic rate (FMR) and water flux rates with doubly labelled water (Nagy 1983), we captured, sexed, weighed, and marked 20 *A. skoogi* by toe clipping and with water soluble paint. We injected them with 0.3 ml of sterile water containing 95 atom % oxygen-18 and 0.1 mCi of tritium. After waiting for at least 90 minutes for the isotopes to mix completely in the body water (Nagy and Cost 1980, Nagy 1980), we took about 50 µl of blood from an infraorbital blood sinus, and the lizards were released where captured. Beginning 10 days later (during which time the study area was not disturbed by us), we attempted to recapture marked lizards. The ten recaptured animals were weighed, their blood was sampled and they were released again. Blood samples, along with samples of the injection solution, were flamed sealed in glass microhematocrit capillary tubes, and stored on ice pending analysis in Los Angeles. Additional samples of plasma, along with urine and sap from succulent nara stems were flame-sealed in capillary tubes pending the analysis of osmotic concentrations.

2.2.3 Diet

Twenty one *A skoogi* were captured from dunes adjacent to our study dune for the analysis of diet. Stomach contents were removed using a fire-polished glass tube as an esophogeal cannula, and the lizards were released unharmed. Four of the lizards had empty stomachs. Stomach contents of the remaining 16 lizards were sorted under a dissecting microscope and dried to constant mass in an oven a 65 °C. The average diet, on a dry mass basis, was calculated using weighted means of each diet item. Fresh samples of each diet item were collected from the study area into tared, sealable containers for subsequent measurements of water, energy and mineral contents. We took care to select only items that lizards could reach, and we collected items during the time of the day the lizards might have eaten them. Samples of freshly-voided feces from recaptured lizards were collected opportunistically for chemical analyses. (These feces could have been voided prematurely due to capture stress, and may have had higher water contents as a result.)

2.2.4 Evaporative water loss

In order to estimate the amount of water these lizards lost by evaporation while buried in the sand, we measured body mass losses of marked animals buried continuously for 24-hour periods. (This procedure requires the reasonable assumption that the lizards did not defecate or urinate while submerged). Fine thread, 1m in length and having a small piece of colored plastic surveyor's tape on one end, was tied around the waists of six lizards. After being weighed, they were allowed to bury in a dune slipface, and their positions were marked with stakes. Exactly 24 h later, those that showed no evidence of having emerged since initial burial were recaptured, weighed, and released for a second 24 h measurement period.

2.2.5 Standard metabolic rate

Three *A. skoogi* living on sand dunes at the Samanab river bed 15km north of our study site were collected and returned to Los Angeles for measurements on standard metabolic rate. The lizards were housed for several months in a terrarium containing Namib sand, with an incandescent light bulb providing a photothermal gradient 10 h/d. After being held without food for two days, they were placed individually in a flow through gas exchange system kept at 30 ± 0.5 °C. Rates of

CO_2 production (STPD) during the inactive (nocturnal) phase of the diel cycle were measured using a Li-cor 6251 CO_2 analyser and a Sigma mass flow controller. We assumed a respiratory quotient of 0.71 and an energy equivalent of 27.7 kJ/l CO_2 (fat metabolism) for purposes of interconverting among units of standard metabolic rate.

2.2.6 Sample analyses

Blood samples were microdistilled to obtain pure water, which was then analysed for tritium by liquid scintillation counting, and for oxygen-18 by proton activation analysis (Nagy 1983, Wood *et al.* 1975). Body water volumes of injected animals, which are required in the calculations, were estimated as dilution spaces of injected oxygen-18 water. Rates of CO_2 production and water flux were calculated using the equations for linearly-changing body water volumes (Nagy 1980, Nagy and Costa 1980), and heat equivalents of CO_2 volumes were calculated assuming a diet of plant matter yields 21.7 J/ml CO_2 (Nagy 1983).

Plasma, urine and nara sap samples were measured for osmotic concentration using a Wescor model 5100B vapour pressure osmometer. Samples of food and faeces were weighed fresh, dried to constant mass at 65 °C, and reweighed to determine water content. The remaining dry matter was powdered in a Spex Mixer/Mill using only plastic utensils and containers to minimize metal contamination. Energy contents were determined with a Phillipson microbomb calorimeter, and metal concentrations were estimated with an Applied Research Laboratories optical emission spectrophotometer.

2.2.7 Statistics

Results are shown as means and standard deviations. Possible correlations between variables were examined by the method of least squares regression analysis (Dixon and Massey 1969). Differences between means were tested for significance ($P < 0.05$) using a two-tailed t-test, except where an F-test indicated that the variances were heterogenous. In those cases, the Mann-Whitney U-test was used. Other statistical procedures used are described below.

2.3 RESULTS

Of the ten lizards we recaptured, four were females and six were males (Table 2.1). There were no statistically significant differences in body mass or mass-specific rates of CO_2 production or water influx, so the results were pooled. Mean body mass was 57.4 g, of which an average of 73 ± 2 % (n = 10) was body water. Most lizards lost slight amounts of body mass over the 11-13 day measurement periods, and the mean rate of body mass change differed significantly from zero ($p < 0.005$, t-test). Because animals that are not maintaining constant body mass may have atypical feeding rates, FMRs and water influx rates, it is important to obtain estimates of these rates in steady-state animals before comparing field results with other species. To do this, we first corrected the DLW results in Table 2.1 for individual animal differences due to body mass by regressing log kJ/day and log ml H_2O influx/day on log g body mass, then dividing the DLW data by g mass to the appropriate exponent. Both regressions were highly significant ($F_{1,8} = 17.4$, $p < 0.005$ for FMR and $F_{1,8} = 10.9$, $p < 0.025$ for water influx, via F-tests for the significance of the regression), and yielded exponents of 1.06 for FMR and 1.48 for water influx rate. The mass-normalized results were then regressed against the rate of change of body mass. Neither of these regressions was statistically significant ($p > 0.50$ via F-tests), indicating no detectable relationship between body mass change and the physiological variables within our data set. Thus, we could use the mean values shown in Table 2.1 to represent FMR and water influx rate of *A. skoogi* lizards maintaining constant body mass in the field during January.

The 17 stomach contents examined were made up mostly of fresh, green nara (*Acanthosicyos horrida*) stem tips (shoots) and flower parts (71.6% by dry mass of total diet). Eight stomachs contained only green nara shoots and flowers. Dry nara flower petals made up 1.4% of the diet, so nara stem tips accounted for a total of 70.2% of the diet's dry mass. Dry leaves and stems of the grass *Stipagrostis hermannii* comprised 19.0% of the diet, and dry seeds (apparently also from *S. hermannii*) accounted for 1.3% of the diet. These two items were apparently consumed as windblown detritus available at the base of dune slipfaces. Faecal pellets, apparently from *A. skoogi* but possibly from *Aporosaura anchietae* lizards also living on the slipfaces accounted for 6.1% of the diet, loose sand (not in faecal pellets) made up 0.3%, and aphids comprised 0.2% of the diet. The aphids may have been ingested incidentally along with nara shoots, as many nara plants in our study area were infested with these homopteran insects.

The water content of nara shoots was high, averaging 4.04 g of water per g of dry matter, or 80 % water, whereas the grass contained less than 15 % water (Table 2.2). (The water content value in Table 2.2 for faeces was measured on freshly-voided faeces from recaptured lizards. The faeces in stomach contents most probably was ingested after it had dried to below 20 % water). Energy contents of nara and grasses are typical of other desert plants (Nagy and Shoemaker 1975),

TABLE 2.1. Field metabolic rates (FMR), body masses, and water flux rates of Skoog's lizards *Angolosaurus skoogi* in summer (January) of 1988 in the Namib Desert.

Animal		Body mass		F M R		Water influx	
No.	sex	Mean (g)	Change (%/d)	(ml CO_2/g.h)	(kJ/d)	(ml/kg.d)	(ml/d)
2	F	48.2	-0.26	0.106	2.65	10.0	0.48
4	M	90.1	-0.17	0.114	5.36	11.0	0.99
8	F	47.5	-0.59	0.073	1.82	4.1	0.19
13	M	42.0	-0.74	0.099	2.17	12.2	0.51
14	M	92.9	-0.23	0.089	4.32	18.2	1.69
16	M	43.6	-0.17	0.058	1.32	9.5	0.41
17	F	41.6	-0.16	0.095	2.06	8.3	0.35
18	M	56.6	-0.13	0.108	3.17	16.3	0.92
19	M	75.4	+0.09	0.106	4.19	17.2	1.30
20	F	36.4	-0.30	0.141	2.67	16.5	0.60
	Mean	57.4	-0.27	0.099	2.97	12.3	0.74
	S.D.	21.0	0.24	0.023	1.28	4.6	0.47

but that of faeces is relatively low, probably because the faeces contained much sand. Faeces from captive *A. skoogi*, which probably ingested less sand with their food than did free-living lizards, had higher energy contents [21 kJ/g (Pietruszka *et al.* 1986) and 20.2 kJ/g (Chapter 3)]. These faecal energy values yield an apparent assimilation value for energy of about 60%, which is probably more accurate than the 72 % value shown in Table 2.2.

The high concentrations of silicon, sodium, iron, aluminium, manganese, titanium and other substances in the faeces are also probably due to sand contamination rather than to undigested residues from the food (Table 2.2). The electrolyte contents we measured in our plant samples are similar to those measured by Mitchell *et al.* (1987), although the K : Na ratios differ somewhat between studies. We estimated the apparent assimilation coefficients for the substances listed in Table 2.2 by assuming that the diet was approximately 80 % nara and 20 % Stipagrostis, and that one gram dry matter of this diet yields 0.372 g dry faeces (Chapter 3). The negative assimilation values shown for ten of the substances in Table 2.2 are probably due to the effects of sand in the faeces, along with the fact that our dietary intake calculations do not account for sand ingestion by the lizards. The elemental concentration values determined by emission spectrometry (Table 2.2) are

TABLE 2.2. Composition of diet items and faeces, and estimated assimilation of dietary substances by *Angolosaurus skoogi*. Units shown are on a per gram dry mass basis, and means are given with standard deviation in parentheses.

Substance	*Acanthosicyos horridus* shoots (n=2)	*Stipogrostis hermannii* stem,leaves (n=2)	*A. skoogi* faeces (n=6)	Apparent assimilation[1]
Water, g	4.04 (0.0)	0.17[2]	1.70(0.9)	81
Energy, kJ	19.9 (0.9)	16.1 (0.3)	14.4 (3.9)	72
Potassium, mg	33.0 (3.4)	1.2 (0.02)	26.2 (10.5)	63
Calcium, mg	4.3 (0.2)	3.4 (0.2)	3.1 (1.0)	72
Phosphorous, mg	3.3 (0.04)	3.6 (0.5)	20.2 (2.4)[3]	-124[3]
Magnesium, mg	4.2 (0.0)	2.1 (0.04)	5.1 (1.5)	50
Sodium, mg	0.18 (0.02)	3.2 (0.3)	5.3 (3.3)[3]	-151[3]
Silicon, mg	2.1 (0.3)	5.5 (0.4)	15.2 (2.0)[3]	-103[3]
Iron, mg	0.33 (0.006)	1.1 (0.4)	4.4 (0.6)[3]	-233[3]
Aluminium, ug	104 (28)	533 (150)	3050 (1500)[3]	-503[3]
Zinc, ug	47 (13)	0 (0)	115 (45)	-14
Copper, ug	14 (0.1)	5.4 (1.2)	47 (8)[3]	-42[3]
Manganese, ug	26 (1.1)	94 (24)	719 (390)[3]	-580[3]
Boron, ug	17 (0.8)	14 (2)	26 (5)	41
Titanium, ug	18 (1.9)	82 (44)	880 (210)[3]	-963[3]
Chromium, ug	0.07 (0.09)	1.6 (0.8)	12 (3)[3]	-1100[3]
Strontium, ug	2.5 (0.03)	14 (1)	29 (4)[3]	-125[3]
Tin, ug	0.5 (0.2)	0.8 (0.1)	1.3 (0.4)	14
Lead, ug	23 (0.6)	7.3 (1.2)	34 (4.6)	36

[1] Apparent assimilation = 100 [(estimated amount of substance/g dry diet, assuming a diet of 80% *A. horridus* shoots and 20% *S. hermannii* leaves and stems) - (amount of substance per 0.372g *A. skoogi* faeces)] / (amount of substance per g dry diet) ; dry matter assimilation value of 62.8% assumed from feeding experiment in Chapter 3

[2] n = 1 only

[3] Results affected by sand in faecal samples

relatively inaccurate and variable (as indicated by the high standard deviations for many values), and are best viewed as approximations of the metal content of samples.

The six lizards used to measure evaporative water loss during submersion had an average mass of 31.1 g (range 15.4 - 46.7 g) and lost an average of 0.251 g (range 0.177 - 0.314 g) of body mass per 24 h of burial in a slipface. As might be expected, log water loss rate was correlated with log body mass ($p < 0.05$ via an F-test). The relationship is described by the equation log (g water lost/day) = 0.91 log (g body mass) - 2.0, with $r^2 = 0.66$, standard error of slope = 0.32, and S.E. of intercept = 0.48.

Osmotic pressures of plasma samples from free-living lizards averaged 357 ± 19 mOsm/l (n = 7). Fresh urine samples had concentrations of 313 ± 50 mOsm/l (n = 9), while samples of sap from nara shoots averaged 491 ± 8 mOsm/l (n = 3).

Standard metabolic rates (SMR) of three *A. skoogi* at a body temperature of 30 °C averaged 0.063 ± 0.013 ml CO_2/g.h. Their body masses averaged 28.7 ± 20.3g. This SMR value is only about 30 % of the value of 0.30 ml O_2/g.h (equivalent to 0.21 ml CO_2/g.h) reported by Mitchell *et al.* (1987) for *A. skoogi* weighing 15.6 g. We suspect that their lizards were not completely at rest and post-absorptive.

2.4 DISCUSSION

2.4.1 Comparative energetics and water fluxes

The daily energy requirement of free-living *Angolosaurus skoogi* is remarkably low in comparison to that of most other lizards studied to date. Iguanid lizards of similar size have FMRs during their activity seasons (Nagy 1982) that are much higher than the FMRs of *A. skoogi* (Figure 2.1). The FMR predicted for an iguanid lizard having a body mass of 57.4 g is 5.7 kJ/day (Nagy 1987). Thus, *A.skoogi* have a mean FMR (2.97 kJ/day, Table 2.1) that is only about half of that required by other lizards to exist for a day. This low energy requirement is clearly of adaptive value in an environment having sparse food resources.

How does *Angolosaurus* achieve such a low energy requirement ? Several other species of lizards also have FMRs about half of those expected on the basis of their body mass. These include three species in the family Xantusidae ("night lizards", Mautz and Nagy, in prep.), and a Namib desert gecko (Nagy *et al.*, in prep.). The low metabolic rates of night lizards have physiological as well as ecological and behavioural components. They have SMRs that are half those of other lizards and they are reclusive, sedentary, and select relatively low body temperatures in the field (Mautz 1979). The desert gecko (*Rhoptropus afer*) also has a low SMR (Peterson 1990) along with its low FMR, but is not particularly reclusive, sedentary or thermophobic. *A. skoogi* does not seem to share the reduced SMR of xantusiids and the gecko : our measurements of SMR are virtually the same as predicted SMR for equivalent-sized squamate reptiles (Andrews and Pough 1985). Moreover, *A. skoogi* probably maintains moderate to high body temperatures (between 25 and 40 °C) thoughout the day, whether above or below the ground, during the season in which our

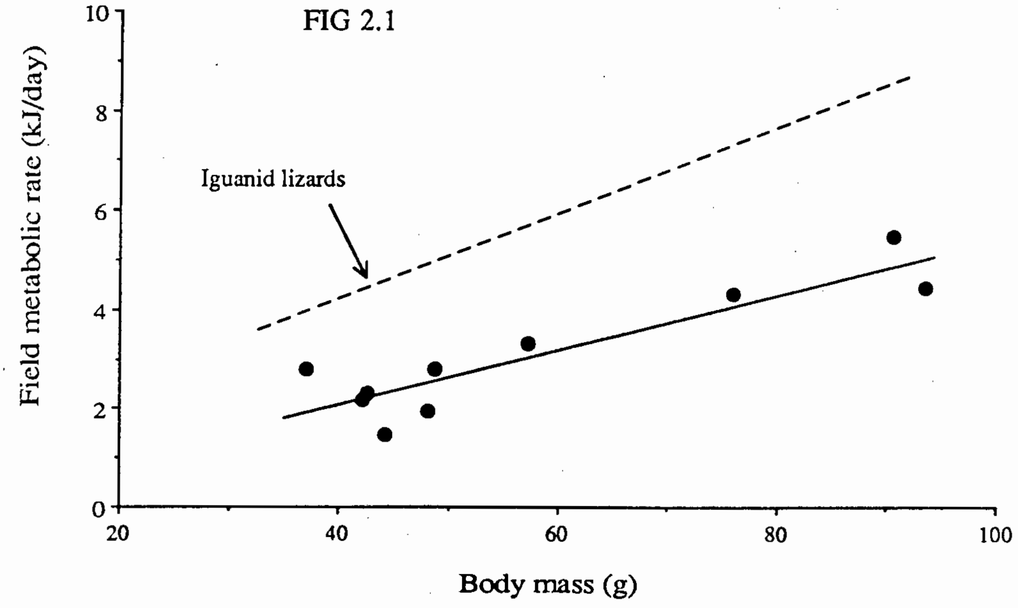


Figure 2.1. Field metabolic rates of *Angolosaurus skoogi* (filled circles and solid line) are about half of those of iguanid lizards during their activity season (represented by dashed line, from Nagy 1987)

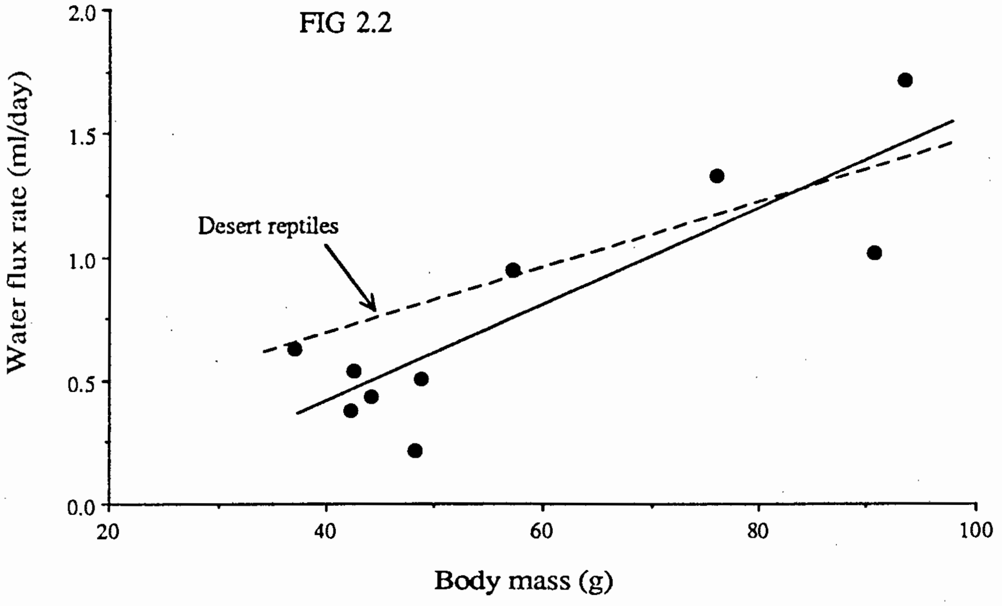


Figure 2.2. Rates of water influx in free-ranging Skoog's lizards (filled circles and solid line) are similar to those of other desert lizards (represented by dashed line, from Nagy and Peterson 1988)

measurements were made (Mitchell *et al.* 1987). Thus it appears that these lizards have low FMRs primarily because they are comparatively inactive in their natural habitats. Mark-release-resight studies (Mitchell *et al.* 1987) suggest that individual lizards are active every third day, and may remain buried for five days or longer. Focal-animal studies of time-activity budgets are needed to evaluate the question of whether individual lizards remain underground for long periods of time compared to other lizard species.

Despite their low FMRs, water influx rates in Skoog's lizards were typical of other desert lizards. Their mean rate of water influx (Table 2.1) is about 80 % of that predicted for a desert reptile of their average body mass (Nagy and Peterson 1988), and there is much overlap of measured and predicted values for individual animals (Figure 2.2). They achieved this rate of water consumption mostly by selecting a diet item that was unusually succulent. Nara shoots had a higher water content than many (though not all) plant foods consumed by another herbivorous desert lizard, *Sauromalus obesus* (Nagy 1973), and nara was more succulent than all diet items consumed by the plant-eating desert lizard, *Dipsosaurus dorsalis* (Mautz and Nagy 1987). Again, a behavioural difference seems to account for the ability of Skoog's lizards to obtain surprising amounts of water.

"Water economy index (WEI)" is the ratio of the total amount of water taken in each day to the amount of energy used that day (Nagy and Peterson 1988). The lower this ratio, the less water an animal uses per unit of "living". Desert vertebrates tend to have lower WEI values than their non-desert relatives, reflecting adaptations to their arid habitat. Desert reptiles have WEI values averaging about 0.20 ml water influx/kJ metabolized. *A. skoogi* lizards had a WEI value of 0.25, higher than most other desert lizards studied to date, and at the upper end of the theoretical range in WEI for herbivorous vertebrates. This indicates that behavioural adjustments (diet selection) rather than physiological adaptations that reduce water requirements directly, are probably more important to these lizards.

2.4.2 Feeding rate

It is possible to estimate the feeding rate of an animal from measurements of both its FMR and its water intake rate, provided that the diet and its metabolizable energy and water yield are known, and the food was the only source of exogenous water. A feeding experiment (Chapter 3) revealed a mean dry matter assimilation of 62.8 % in *A. skoogi* kept at realistic field inactivity temperatures and fed a diet similar to that we determined in this study. Using energy content measurements of food and faeces from several studies (see above), we estimated that 60 % of dietary energy, or 11.5 kJ/g dry matter, was assimilated. Assuming that about 10% of this, or 1.2 kJ/g was voided as chemical potential energy in urinary solids (as with *S. obesus*, Nagy and Shoemaker 1975), then the food provided 10.3 metabolizable kJ/g dry matter. The amount of food needed to just meet metabolic energy expenditures would be about 0.29 g dry matter/day [(2.97 kJ metabolized/day) / (10.3 metabolizable kJ/g dry food)] for a 57.4 g lizard.

A diet of 80 % nara shoots and 20 % dead *Stipagrostis* would contain 3.27 ml water/g dry matter (calculated from Table 2.2). Metabolic water produced from oxidation of the metabolizable energy in a gram of this food is about 0.4 ml/g dry matter (based on conversion factors in Nagy 1973), so total water yield of this diet is about 3.67 ml/g dry matter. Thus, with a water influx rate of about 0.74 ml/day (Table 2.1), and assuming no drinking water was available, a 57.4 g lizard would have to consume 0.20 g dry matter/day. This estimate is 70 % of that based on energy metabolism (above), and is in general agreement given the uncertainties in diet composition and the assumptions involved in this calculation.

A typical iguanid lizard of the body mass of our lizards may be expected to consume about 0.57 g (dry matter) per day (Nagy 1987), so *A. skoogi* lizards require only about 35 - 42 % of the food iguanid lizards need to maintain homeostasis. This low food requirement may be considered to be a desert adaptation, and it appears to be due to the small amount of time these lizards spend active above ground. Although such behaviour may confer advantages in terms of reduced energy requirements, it may occasion disadvantages such as reduced breeding opportunities and loss of social and territorial status. Observations of reproductive and social behaviour would be especially interesting to make in the light of this finding.

2.4.3 Water balance

The minimum rate at which a lizard must obtain water to achieve balance is determined by its minimum loss rate. The mean water efflux rate calculated from the hydrogen isotope data gathered in this study was 14.3 ± 4.2 ml/kg.day, or 0.82 ml/day for a 57.4 g individual. Evaporative water loss measurements on submerged lizards in the field indicate that a lizard this size would lose 0.40 ml/day if it stayed underground continuously.

Evaporation undoubtedly would be higher when the lizard emerged during daylight hours. We can estimate faecal water loss from food intake rate (0.20 - 0.24 g dry matter/day), dry matter digestibility (62.8 %), and faecal water content (1.70 ml/g dry faeces, Table 2.2) to be about 0.14 ml/day. This leaves 0.28 ml/day for urinary water loss and evaporation while above the ground. These lizards have been seen to void > 3ml of urine when active in the field (Pietruszka *et al.* 1986). It would take about 10 days for a 57.4 g lizard to accumulate that much urine, if the estimates in this study are correct. More time would be required if evaporative water loss above ground is much higher than that below ground. Casual observations of captive lizards suggest that they lose water rapidly when above ground, raising the possibility that reduced above-ground activity in the field may be more a consequence of high evaporative water loss than low food availability in the habitat.

Detailed laboratory measurements of water losses must be made to permit a more detailed evaluation of the field water budget of these lizards.

The observations that the feeding rate estimate based on water intake (above) was lower than that based on energy metabolism indicates that the lizards we studied did not drink free water. Indeed, no free water was available above ground during out study. We agree with Mitchell *et al.* (1987) that *A. skoogi* appear to obtain all the water they need from the nara they eat. We did not observe lizards drinking sap welling up on bitten-off stem stumps, as did Pietruszka *et al.* (1986), but this behaviour would not seem to be necessary to achieve water balance given that nara shoots themselves are 80 % water.

Skoog's lizards may also obtain all the energy they need from nara, because the organic matter in growing shoots is mostly in soluble form, rather than in relatively-indigestible fibre, as in more mature plant tissues. This fact raises the question of why these lizards seek out and consume dry, windblown detritus, which undoubtedly has a comparatively low energy yield, and may even require more water to excrete as moist faeces than it brings into the lizard (Nagy 1972). Does *S. hermannii* detritus contain some nutrient that is relatively unavailable in nara ? The osmotic concentration of nara sap is high [491 mOsm/l, similar to the value of 563 mOsm/l measured by Mitchell *et al.* (1987)], and it will be osmotically stressful to the lizards (their plasma and urine osmotic concentrations were relatively high.) This suggests that nara may provide more than enough salts to the lizards. However, analyses of elemental contents of nara and grass (Table 2.2) indicate that sodium may be a nutrient that is more abundant in detritus.

2.4.4 Desert survival

We agree with Pietruszka *et al.* (1986) and Mitchell *et al.* (1987) that *A. skoogi* lizards can survive in their hyperarid dune sea habitat primarily because they can eat nara shoots and flowers, which are all very succulent and provide all the necessary water to the lizards. The long tap roots of nara bring subterranean water, that fell as rain in the distant mountains, to the surface in the form of succulent, easily digestible plant tissues. Potential drawbacks to this food source include its bad taste (to humans at least), its high osmotic concentration, and its possible nutritional deficiency (perhaps sodium). Its consumption may be necessitated by a high water requirement by the lizards due to high evaporative water losses while abroad and active. Laboratory measurements of water and mineral budgets are needed to resolve these questions. In addition, we found that these lizards have a very low energy requirement in the field, which we view as an adaptation to their desert habitat. They achieve this primarily by behaviourally reducing activity costs, rather than by having an unusual metabolic physiology, as do some other desert lizards.

CHAPTER 3

WATER AND ENERGY BALANCE IN *A. SKOOGI* : LABORATORY STUDIES

3.1 INTRODUCTION

As far as the ecophysiology of *Angolosaurus skoogi* is concerned, the most relevant observation made in Chapter 2 is its exceptionally low field metabolic rate. Thus far, this has been attributed to reduced surface activity. This, in turn, generates questions with regard to the ecological and physiological significance of reduced field metabolic rates. Is the reduction forced by intolerable environmental conditions or the need to stay in positive water and energy balance ? Alternatively, is activity reduction voluntary and geared towards optimizing growth and storage, possibly in preparation for periods of physiological stress ? A clearer understanding of this situation and resolving these questions requires an integration of both laboratory and field studies. Field studies need to include detailed observations of animal body temperatures and time-activity budgets. Laboratory studies need to investigate the components of water and energy gains and losses under the range of thermal and humidity conditions experienced in the field. This involves the determination of water and metabolic costs of both fasted and fed animals while resting and active, and the use of feeding trials to quantify rates of water and energy intake and the efficiency of digestion. Combination of this data will give an indication of water requirements and net energy gain under a variety of activity and thermal regimes. Application of this combined data to field observations of animal behaviour should, in turn, give some indication of the reasons for and the significance of reduced field metabolic rates. Field studies of *A. skoogi* thermoregulatory strategies and activity patterns are dealt with in Chapter 5. This Chapter deals with laboratory studies of water and energy balance in captive *A. skoogi*.

3.2 METHODS AND MATERIALS

3.2.1 Metabolic rate and evaporative water loss (EWL)

Six - eight *Angolosaurus skoogi* were captured from the dunes adjacent to the Unjab River, Namibia (20° 19' S ; 13° 14' E) at the termination of field trips in October 1989, February 1990 and July 1990 (see Chapter 5). They were immediately transported to Cape Town and housed in a large wooden box in a constant temperature room. The animals were kept at the average subsurface temperature and humidity measured in the field prior to their capture [27 - 28 °C and 10 mmHg water vapour pressure (35 % relative humidity) in October, 30 - 31 °C and 16 mmHg vapour pressure (50 % relative humidity) in February, and 23 - 24 °C and 11 mmHg vapour pressure (50 % relative humidity) in July]. Details of these measurements are described in Chapter 4. In the February group, the physical limitations of the constant temperature room allowed a vapour pressure of only 14 mmHg. Based on field activity measurements (Chapter 5), animals were given access to a 300 W thermoregulatory quartz halogen lamp for 1 h/day (October group), 4 h/day (February group) and 2 h/day (July group). Initially all animals had to be force-fed, but gradually they began to feed voluntarily on grated carrots. Experiments were initiated once the animals had become familiar with their new surroundings, had regained mass to within 5 % of their field capture masses and were consistently remaining under the sand for periods long enough for adequate measurements to be made. This took 32, 38 and 47 days after capture in the October, February and July groups respectively.

Measurements of activity metabolism in any untrained animal are notoriously difficult. Repeated efforts to get this species to wear a respiratory mask or run on a variable speed treadmill were unsuccessful. Closed volume respirometry and gravimetrics were thus deemed to be most suitable for determining metabolic rate and water loss in both resting (buried) and active (surface) animals. Experiments were conducted in 20 litre plastic buckets. For resting metabolic experiments, buckets were filled with about 10 litres of desert sand collected from *A. skoogi*'s natural environment. Each bucket was fitted with a perspex peephole, a type-T thermocouple, a latex balloon pressure compensator and two three-way stopcocks. One stopcock was positioned below the sand (approximately 15 cm below the sand surface and 2 cm above the base of the sand column). The second stopcock was positioned just below the lid of the bucket. Cotton wool filters fitted just before the outlets of the former stopcock prevented sand from being drawn into the air sampling syringe.

The volume of air in each bucket was determined by the dilution of nitrogen. The oxygen content of a commercially obtained cylinder of nitogen (AFROX Ltd.) was determined using an Applied Electrochemistry S-3A oxygen analyser. 100 ml of nitrogen was then injected into the empty buckets and their volumes determined by the dilution of the gas. The buckets were then completely filled with a preweighed mass of sand. The process was repeated and the volume of air in this known volume and mass of sand determined. These data were then used to calculate the volume of sand in each experimental bucket, the volume of air in the sand and the volume of air above the sand. A knowledge of the volume of air in the sand was necessary because the oxygen concentration below the sand was consistently slightly lower than that above the sand This was due to the position of the animal in the bucket (submerged) and presumably an equilibrium lag imposed by the sand resistance. The difference in oxygen concentration was seldom more than 0.0002%. Nevertheless, the total oxygen concentration in a bucket was always calculated by multiplying the oxygen concentration above the sand by the volume of air above the sand and the oxygen concentration below the sand by the volume of air below the sand. The sum of these two products was then divided by the total volume of air in the bucket. In addition to this, the addition of oxygen due to any diffusion of outside air into the buckets during experimental runs, or the reduction of oxygen due to the presence of microbes in the sand, was determined by reducing the oxygen concentration in each bucket (without an animal) to typical experimental values and monitoring oxygen concentration changes over a 12 - 24h period. This process was repeated for each bucket at each experimental temperature. Reduction of oxygen concentration was accomplished by exhaling into the buckets before sealing them. Although oxygen concentration increased very slowly (about 0.0003 %/h at 15 °C to 0.002 %/h at 37 °C), these correction factors were applied to all experimental runs. Air was sampled from the buckets using an air tight syringe (Sanitex Eternamatic). Samples were analysed for oxygen content by drawing them through the oxygen analyser. Prior to analysis, ambient air was allowed to flow through the analyser via a three-way stopcock located in the pipe between the syringe port and the analyser. The ambient air inlet of the stopcock was then closed and the stopcock on the syringe opened, allowing the contents of the syringe to be drawn into the analyser. As soon as the syringe was empty, a three-way stopcock located in the pipe between the syringe and analyser was opened allowing ambient air to follow the syringe bolus. 5 ml plastic tubes containing soda lime and silica gel (CO_2 and water scrubbers) were inserted in the air line just before the analyser. The flow rate at which air was drawn through the analyser was predetermined by trial and error so that a very definite oxygen reduction "plateau" was obtained. A flow rate of about 20 ml/minute proved to be most suitable.

The temperature of the sand was monitored constantly by submerged thermocouples and was found to vary by no more than 0.5°C. The humidity of the air in the buckets was monitored at the beginning and end of each run by drawing air with a syringe through the sampling stopcocks and over an encapsulated humidity sensor (Hanna Instruments, Italy). The humidity of air below the sand roughly corresponded to that above the sand at all temperatures except 15 °C, when it was consistently lower below than above, even after a 48 h equilibrium period.

Activity measurements were conducted for a period of three hours between 10h00 and 15h00. The first air sample was taken 1 hour after an animal had been weighed and placed in an empty bucket. During these experiments animals displayed various degrees of activity, usually alternating between total immobility and vigorous movement. Similar activity patterns have been observed in the field and it is assumed that activity measurements obtained in the laboratory give fairly good approximations of overall metabolic costs of field animals during their activity periods. Resting water loss and metabolic rate measurements were conducted between 18h00 and 06h00. In accordance with findings that metabolic rates require a long time to stabilize after handling (Section 6.3.3., Chapter 6), the first oxygen sample was not taken until three hours after animals had been weighed and buried.

Experiments were conducted at 15, 23, 30, 35 and 40 °C. The protocol for each group was essentially the same. Animals were fed and then kept at their acclimated temperature and humidity. 48 hours later, they were weighed to the nearest 0.01 g (Mettler P360 balance), strips of blue and red litmus paper (urination indicators) plastered over their cloacas and then placed in the experimental buckets. After an animal had buried (in the case of resting experiments), a thin flexible gauze disc was placed just below the surface of the sand in each bucket. The displacement of the disc provided an indication of activity. Experiments were terminated as soon as this occurred. The buckets were then sealed and after the animal "settling" period, an initial air sample was taken and analysed. A few hours later (2 - 3 hours, activity measurements ; 6 - 12 hours, resting measurements) a final oxygen sample was taken and the animals removed from the buckets, their litmus strips inspected and then reweighed. Evaporative water loss was assumed to be equal to mass loss provided no urination had taken place. Oxygen consumption was calculated from the product of the reduction of oxygen concentration and the total volume of air in the buckets (Vleck 1987).

No thermoregulation (by means of quartz halogen lamps) was allowed during the period between experiments in the October or February groups. As specific dynamic action in ectotherms is temperature dependent, however, it was feared that the July group would not reach the same degree of post-absorption as the two groups acclimated to higher temperatures. The July group was thus forced to remain under thermoregulatory lamps for three hours a day on both days of the experimental preparation period in an attempt to compensate for this.

In addition to the standard experiments described above, several peripheral experiments were conducted to investigate specific dynamic action, acclimation with time in the laboratory, and the effect of different thermal treatments immediately prior to experimentation. The effect of temperature on specific dynamic action was investigated in the October (30 °C) and February groups (23 and 30 °C). Animals were fed a rationed amount of food on day 0. Resting metabolic rate was then measured immediately and every night thereafter until there was no significant difference between values obtained on two consecutive nights. Acclimation with time in the laboratory was investigated by duplicating the July 30 °C experiment exactly after 21 and 25 days. The effect of different thermal treatments during the 48 hour experimental preparation period was investigated by duplicating the 30 °C experiment three days later. Prior to this experiment, however, animals were kept at 30 °C and not allowed to thermoregulate instead of 23 °C with 3h/day thermoregulation.

Finally, the difference in water loss and metabolic rates above and below the sand was investigated. Above and below measurements were made immediately after each other. In order to standardize the level of activity, the above sand measurement was made late at night on selected animals once they had assumed their surface sleeping posture and were presumed to have fallen asleep. During the period allotted for this experiment, reliable readings were obtained for only three animals. These experiments were conducted at 30 °C and a water vapour pressure of 8 mmHg.

3.2.2 Feeding experiment 1

Ten adult males were captured at the termination of the field study described in Chapter 2. They were transported back to the laboratory and housed in empty plastic-lined cardboard boxes (60 X 30 X 20 cm) in a constant temperature room. Based on weather data collected during the field study, ambient temperature was held at between 25 and 30 °C during the day and 25 °C at night. 300W quartz halogen lamps enabled animals to thermoregulate at their preferred body temperature for 3 hours per day. Humidity was kept unnaturally high (24 - 32 mmHg, i.e. about 60 % relative humidity at 30 °C and 70 % relative humidity at 25 °C) for reasons discussed below.

The diet offered to animals was determined by the analysis of stomach contents in the field (Section 2.3, Chapter 2). It consisted of detritus (*Stipagrostis* spp., 20 % by volume) and nara (*Acanthosicyos horrida*, 80 % by volume). Animals refused to eat voluntarily and had to be force-fed. Efforts to maintain animals at their field capture masses were unsuccessful and they lost about 20 % of their field capture masses. For a period of ten days, the amount of food fed to each animal was adjusted by trial and error so that the lizards maintained body mass. During this time, seven of the animals became ill or refused to swallow and had to be removed from the experiment. At this stage it was suspected (incorrectly, in retrospect) that the deprivation of sand was possibly resulting in abnormally high rates of evaporative water loss. The increased food input to compensate for the resultant increased mass loss was possibly stressing the animals. It was thus decided to increase the humidity in the constant temperature room and allow two of the animals continual access to sand.

Early every second morning animals were weighed and then placed under their thermoregulatory lamps. This generally provides a strong stimulus to defecate in this species. Following this, animals were force-fed sufficient food to bring their body mass up to the value recorded on day 1. On day one of the feeding experiment, each animal was fed a small strip of plastic surveyor's tape with that day's food ration. The quantitative collection of faecal, urate pellet and urine samples was initiated on the day the tape appeared in the faeces and continued for the next 14 days. Rates of evaporative water loss were estimated from body mass loss between excretions. Rates of urine production were estimated from body mass loss during excretions once corrections for the mass of the solid excreta had been made. Urine was collected only from the animal deprived of sand. Samples of the urine were collected and stored in flame sealed haematocrit tubes. An aliquot from each urine sample was weighed, then dried to constant mass at 65 °C and reweighed to determine dry matter content. The remainder was analyzed for electrolytes using an Instrumentation Laboratory 243 flame photometer (K^+ and Na^+) and the titrimetric method of Schales and Schales (1941) for chloride. Osmolarity was determined using a Wescor 5100B Vapour Pressure Osmometer. Freshly produced solid excretions were treated in the same way as urine samples to determine water content. Dried solid excreta were pooled for each animal and homogenized. Energy content was determined using a Digital Data Systems 4100B bomb calorimeter. Approximately 100mg of each pooled sample was then added to 1 ml of distilled water, left to soak overnight, and the supernatant analyzed for electrolytes as above. Random food samples were treated in the same way.

3.2.3 Feeding experiment 2

The animals used in the feeding experiment 2 (n = 3 - 4) were those collected at the termination of the February 1990 field trip (see Chapter 5). On return to the laboratory, they were housed in a constant temperature cell at 30 °C and 14 mmHg. Grated carrots were offered *ad lib.* every day. From February to May 1990 they were used for metabolism and evaporative water loss experiments (see above). From May - August 1990, several feeding experiments using the natural diet (nara) were attempted. They were all consistently unsuccessful, with animals continuously vomiting up the food. These experiments were eventually terminated when two animals died after force-feeding. Grated carrots were thus used in all subsequent experiments. The carrots, which have a water content of about 90 %, were dehydrated to the same water content as nara (about 80 %) by blowing dry air over them, prior to being offered to the animals.

Experiments were conducted at 23, 30 and 37 °C and a humidity of 13 mmHg vapour pressure. The choice of humidity was determined from average humidity readings at the capture site during October 1989 (10 mmHg) and Feb 1990 (16 mmHg). Animals were acclimated to the relevant temperature for two weeks prior to each experiment. During the experiments, animals were housed in 20 litre buckets. The protocol for the three experiments was essentially the same. Early in the morning animals were dug out of the sand, weighed and exposed to a 300W quartz halogen lamp. Following defecation, animals were reweighed and then fed to a constant mass. A fine strip of litmus paper was then taped over each animal's cloaca and the animals allowed to bury in their sand buckets. On day 1 each animal was fed five small polystyrene balls with that day's food ration. Quantitative collection of faecal material was initiated only when balls started appearing in the faeces, and continued for about ten days. The 37 °C experiment was, however, aborted after 5 days when two animals died following force feeding. Rates of urine production and evaporative water loss were determined as above. Solid excreta (faeces and urate pellets) were also treated as above.

3.3 RESULTS

3.3.1 Metabolic rate and evaporative water loss (EWL)

Metabolic rate and EWL as a function of temperature and activity are shown for the three experimental groups in Figures 3.1 and 3.2 respectively. EWL values have not been standardised in the usual way (i.e. in terms of water vapour deficit). Instead, they are expressed in terms of µl H_2O/g.h. at 10 mmHg (October and July group) or µl H_2O/g.h. at 16 mmHg (February group). The values reflect the actual EWL rates that would occur under the humidity conditions measured in the field, making them directly applicable to field data. As expected, both resting and active metabolic and evaporative water loss rates increased with temperature. The difference between resting and active metabolic rates was significant in all cases with the exception of the February 30 °C group ($p > 0.05$, d.f. = 7, Students t-test). Differences in resting and active EWL rates were slightly less consistent (October 15 °C - $p > 0.05$, d.f. = 10 ; July 15 °C - $p > 0.05$, d.f. = 6 ; February 23 °C - $p > 0.05$, d.f. = 9). The ratio of active to resting (A/R) rates generally also increased with temperature. Combined A/R metabolic rates for the three groups ranged from 2.5 ± 1.5 (at 15 °C) to 3.8 ± 0.5 (at 40 °C). The highest recorded A/R metabolic rate was 6.45 in the July 23 °C group. Combined A/R EWL rates for the three groups ranged from 2.0 ± 0.6 (at 23 °C) to 2.6 ± 0.3 (at 40 °C). The highest recorded A/R EWL rate was 3.61 in the February 15 °C group.

Thermal acclimation is apparent in the resting metabolic rates of the three groups. Metabolic rates of the October group (acclimated to 27 - 28 °C) were consistently higher than those of the July (acclimated to 23 - 24 °C) group at all temperatures. Rates of the July group were in turn consistently higher than those of the February (acclimated to 30 - 31 °C) group. These differences are significant ($p < 0.05$) with exception of the October and July 15 °C groups and the February and July 40 °C groups. Likewise, humidity acclimation is apparent in the EWL rates of the three groups. At temperatures above 30 °C, resting EWL rates of the February group are similar to those of the other two groups (Figure 3.2a). When one considers, however, that the values of the February group are expressed at a much higher humidity than the other two groups, standardization of all the values (to, for example, 10 mmHg) would result in the February group having higher values than shown in Figure 3.2. The values of the other two groups would be unaffected. On standardization, significant differences occur at 30 °C (Feb. vs Oct - $p < 0.05$, d.f. = 9 ; Feb vs July - $p < 0.05$, d.f. = 8) and 35 °C (Feb. vs Oct. - $p < 0.05$, d.f. = 9).

A particularly interesting finding was the difference in humidity changes in air above and below the sand during metabolic and EWL rate experiments. Below sand experiments almost always resulted in a negligible change in air humidity. Conversely, above sand experiments consistently resulted in significant increases in air humidity. For example, in the October 30 °C experiment,

FIGURE 3.1a. Resting subsurface metabolic rate of male *Angolosaurus skoogi* captured during October (spring), February (summer) and July (winter). Vertical bars are the standard deviations of means. All experiments were conducted between 18h00 and 06h00. Animals were given at least 3 hour to settle after buring. Sample size ranged from 4 - 6 at all temperatures except 40 °C where most animals emerged prior to the termination of the experiment (n = 1 - 5).

FIGURE 3.1b. Active metabolic rate of male *Angolosaurus skoogi* captured during October (spring), February (summer) and July (winter). Vertical bars are the standard deviations of means. All experiments were conducted between 10h00 and 15h00. Sample size ranged from 4 - 6 at all experimental temperatures. The resting metabolic rate of February animals has also been plotted for comparative purposes.

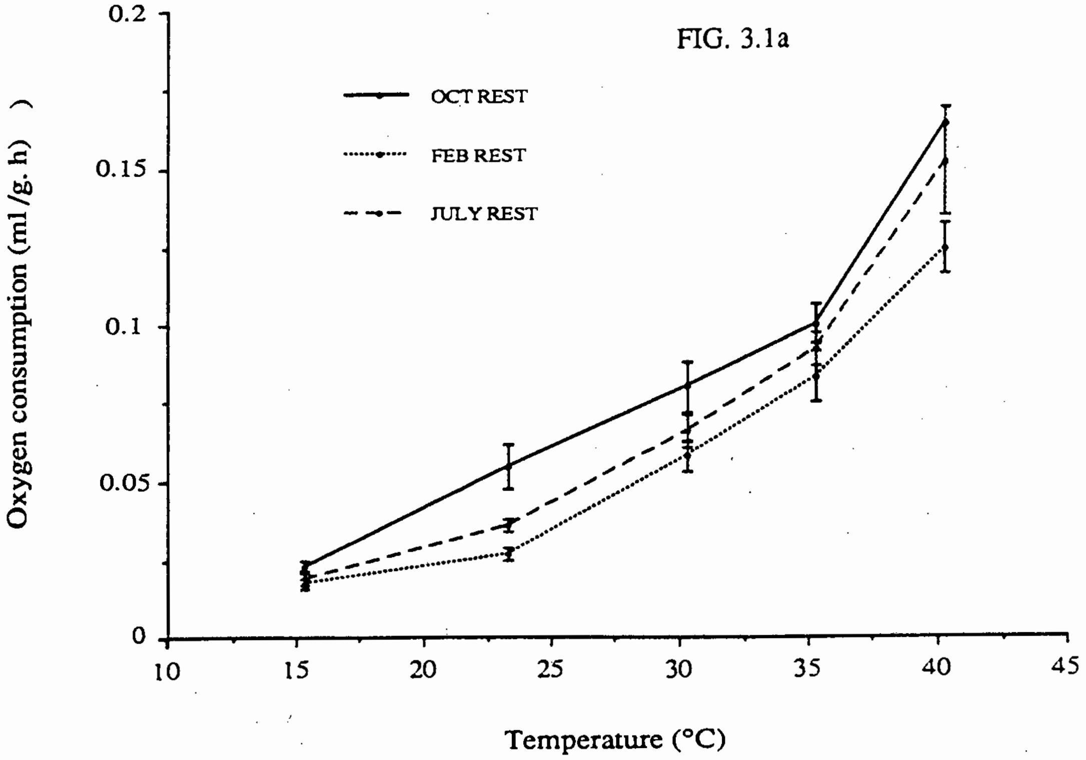


FIG. 3.1a

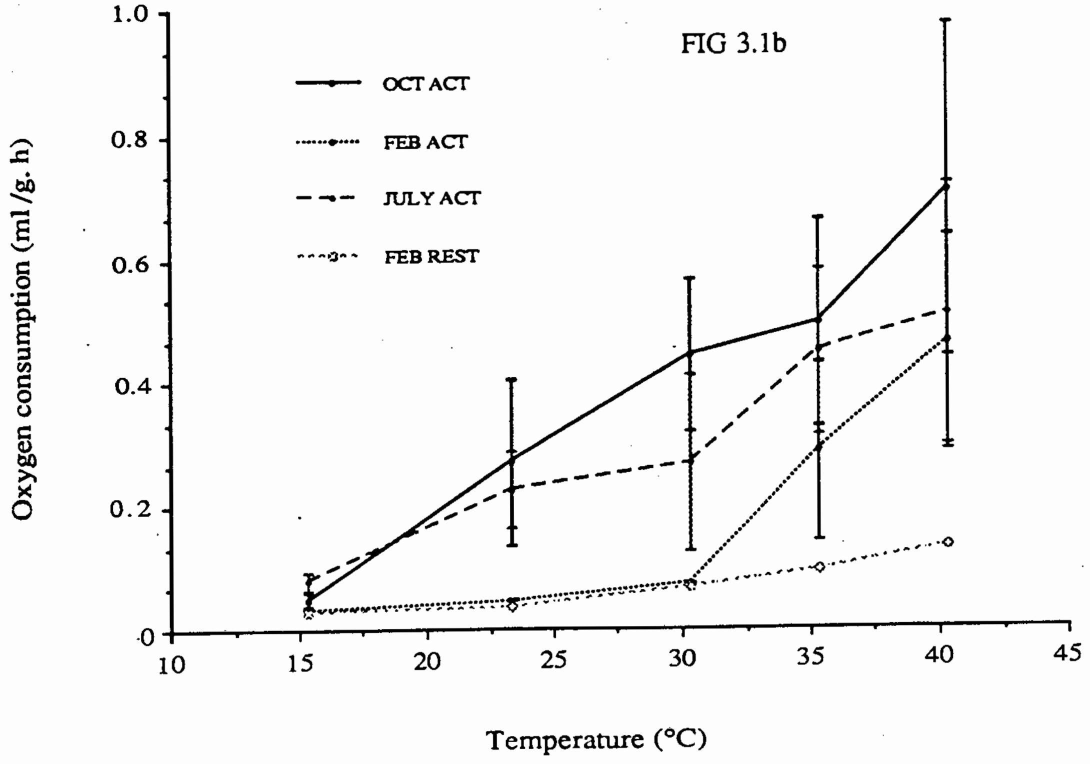


FIG 3.1b

FIGURE 3.2a. Subsurface evaporative water loss (EWL) rates of male *Angolosaurus skoogi* captured in October (spring), February (summer) and July (winter). Vertical bars are the standard deviations of means. Experiments were conducted at a water vapour pressure of about 10 mm Hg in the October and July groups, and 14 mm Hg in the February group. Where necessary, results have been corrected to rates that would occur at vapour pressures of 10 mm Hg in the October and July groups and 16 mm Hg in the February group. All experiments were conducted simultaneously with resting metabolic rate measurements between 18h00 and 06h00. Sample size ranged from 4 - 6 at all experimental temperatures except 40 °C where most animals emerged or urinated prior to the termination of the experiment (n = 1 - 2).

FIGURE 3.2b. Evaporative water loss (EWL) rates of active male *Angolosaurus skoogi* captured in October (spring), February (summer) and July (winter). Vertical bars are the standard deviations of means. Experimental parameters and correction of results as for Figure 3.2b. All experiments were conducted simultaneously with active metabolic rate measurements between 10h00 and 15h00. Sample size ranged from 4 - 6 at all experimental temperatures except 35 and 40 °C where most animals urinated prior to the termination of the experiment (n = 2 - 3). The resting EWL rate of February animals is also been plotted for comparative purposes.

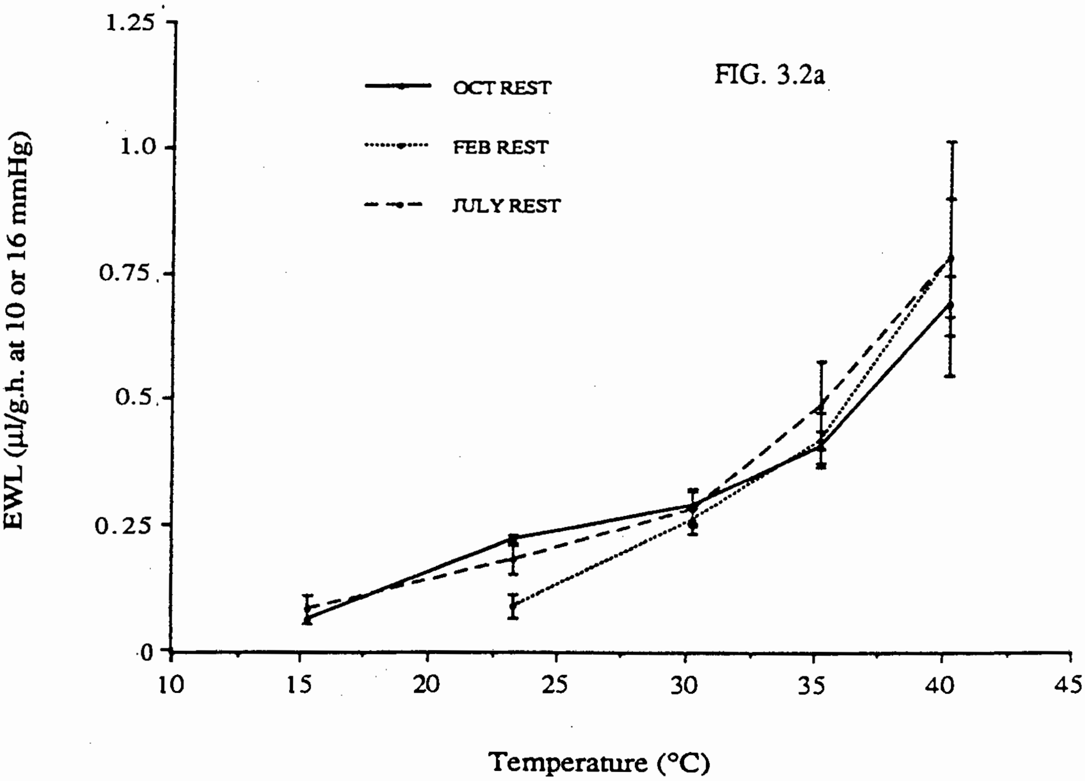


FIG. 3.2a

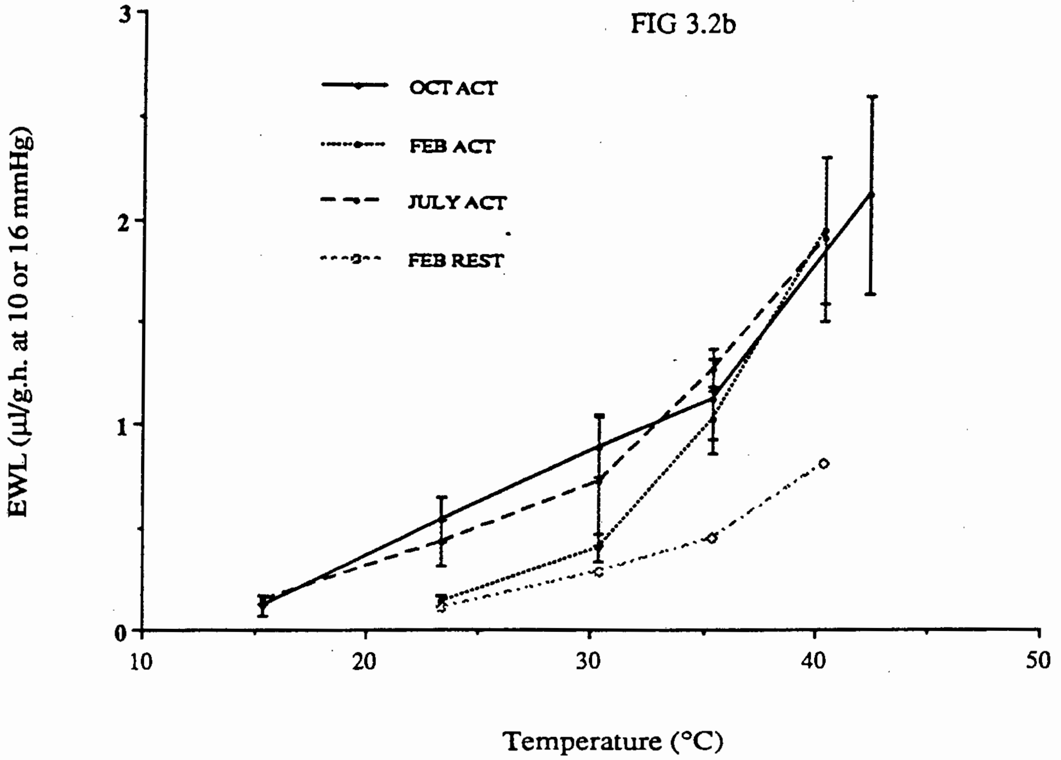


FIG 3.2b

subsurface humidity changed from 9.1 ± 0.6 mmHg to 9.8 ± 0.3 mmHg during the experiment. The difference is only slightly significant ($p < 0.05$, d.f. = 5). In the above sand experiment, humidity changed from 9.1 ± 0.3 to 14.1 ± 0.8 mmHg. This difference is highly significant ($p < 0.001$, d.f. = 5).

Specific dynamic action (SDA) had a marked effect on resting metabolic rate. In October, metabolic rate at 30 °C immediately after a 7 % body mass meal averaged 0.116 ± 0.01 ml O_2/g.h (n = 6). 24 hours later, metabolic rate averaged 0.079 ± 0.005 ml O_2/g.h. (n = 6). This decrease of 32 % is highly significant ($p < 0.001$, d.f. = 10). After another 24h, metabolic rate averaged 0.077 ml O_2/g.h. This slight decrease of 3 % is not significant ($p > 0.05$, d.f. = 10). The post-feeding increase in metabolic rate (at 0 h) over stabilized post absorptive metabolic rate (at 48 h) was thus about 50 %. A similar but more drawn out pattern was demonstrated in the July 23 °C group. Post-feeding metabolic rate averaged 0.043 ± 0.004 ml O_2/g.h. Metabolic rate remained at this value until 48h later when a 23 % decrease (0.033 ± 0.002 ml O_2/g.h.) was observed. Another 48 h later metabolic rate stabilized at 0.021 ± 0.002 ml O_2/g.h. This group thus displayed a 105% post-feeding increase in metabolic rate. The magnitude and duration of SDA depends not only on temperature but also on the volume of food consumed. In the July group, the post feeding metabolic rate of animals fed 5 % and 11 % body mass and held at 30 °C averaged 0.076 ± 0.004 and 0.095 ± 0.008 ml O_2/g.h. respectively, a significant increase of 25 % ($p < 0.001$, d.f. = 10). In the latter group, metabolic rate stabilized after 48 h at a value of 0.053 ml O_2/g.h. This group thus displayed an 80 % post-feeding increase in metabolic rate.

Exact duplication of the July 30 °C experiment after 21 and 25 days yielded metabolic rates of 0.052 ± 0.004 and 0.050 ± 0.005 ml O_2/g.h, respectively. These values are not significantly different from each other but significantly different from the original value which averaged 0.063 ± 0.005 ml O_2/g.h. ($p < 0.001$, d.f. = 10 ; $p < 0.01$, d.f. = 10).

Exact duplication of these two experiments 4 days later with an alteration of thermal pre-treatment (30 °C instead of 23 °C with 3h thermoregulation/day) yielded a metabolic rate of 0.046 ± 0.004 ml O_2/g.h. This value is significantly different from the 21 day experiment ($p < 0.05$ d.f. = 10) but not significantly different from the 25 day experiment ($p > 0.05$, d.f. = 10).

No significant difference could be detected in the metabolic or evaporative water loss rates of animals resting above and below the sand. Oxygen consumption rates averaged 0.044 ± 0.004 (above) and 0.044 ± 0.005 (below) ml O_2/g.h. ($p > 0.05$, d.f. = 3). EWL rates averaged 12.9 ± 2.5 (above) and 10.6 ± 4.7 (below) µl H_2O/g.h. mmHg ($p > 0.05$, d.f. = 2).

3.3.2 Feeding experiments

Gut passage time (GPT) in *A. skoogi* as measured by the transit time of surveyor's tape in Feeding experiment 1 (ambient temperature = 25 - 30 °C) averaged 5.3 ± 1.2 days (n = 3). Gut passage time

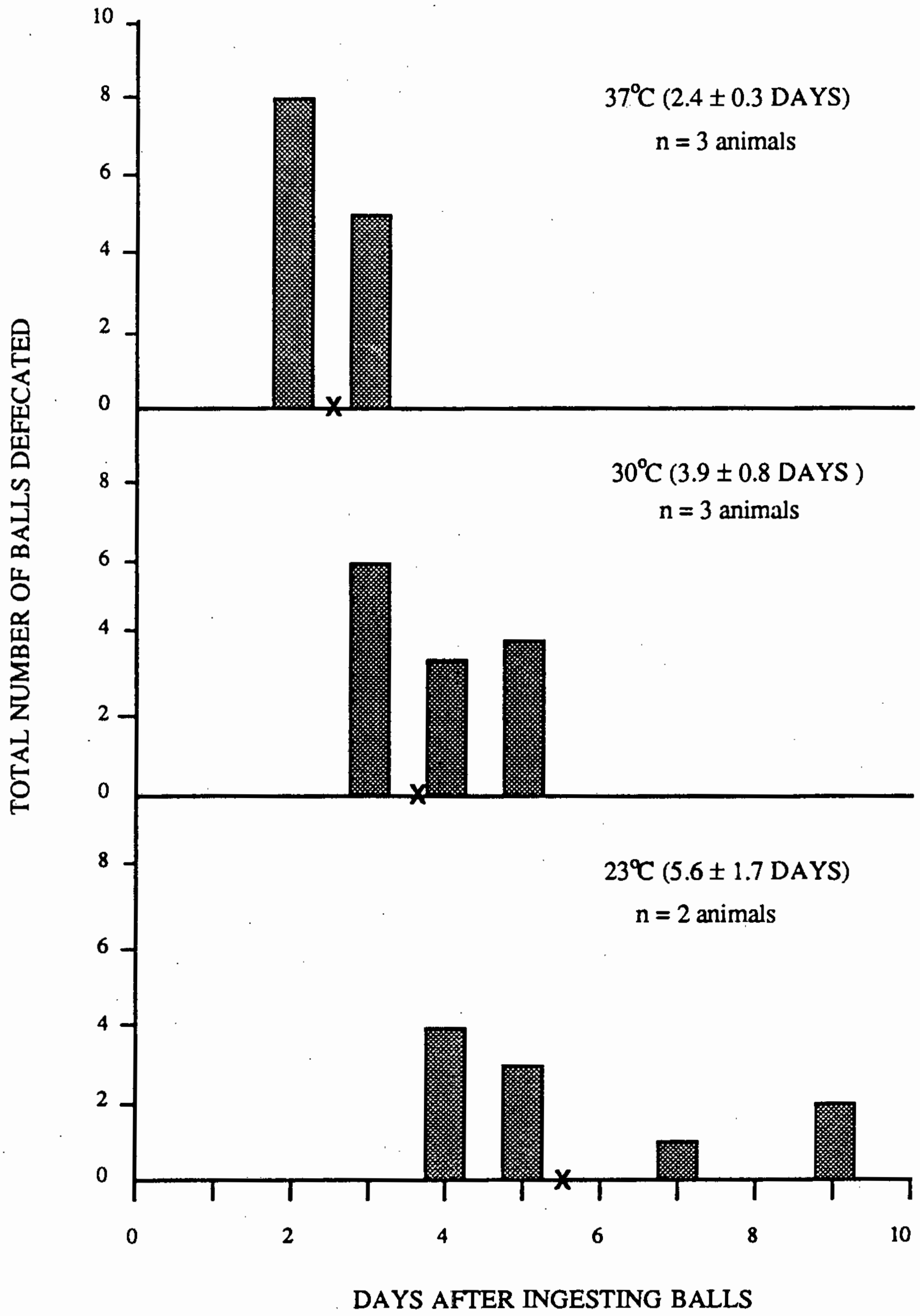


FIGURE 3.3. Gut passage time of male *Angolosaurus skoogi* as determined by the passage rate of small polystyrene balls. Each animal was fed five balls on Day 0. The crosses on the horizontal axes indicate the average gut passage time at each temperature.

as measured by the transit passage time of polystyrene balls in Feeding experiment 2 is shown in Figure 3.3. GPT clearly decreases and becomes less variable with increasing temperature. At each temperature, the average gut passage time of each individual was quantified by multiplying the number of balls defecated each day by the day of defecation. These values were then summed and divided by the total number of balls the individual had defecated during the experimental period. Individual gut passage times at each temperature were then averaged and are shown in Figure 3.3. Unpaired t-tests show no significant difference in average GPT at 23 and 30 °C ($p > 0.05$, d.f. = 3) but a significant difference between 30 and 37 °C ($p < 0.05$, d.f. = 4).

Energy, water and electrolyte balance in *A. skoogi* fed their natural diet is shown in Table 3.1. Dry matter input averaged 3.0 ± 0.3 g/kg.day. The nara/*Stipagrostis* food mix had an energy content of about 20 kJ/g dry matter, resulting in an average daily energy intake of 60.9 ± 5.6 kJ/kg animal. Of this, 38.2 kJ were absorbed through the gut, resulting in an digestive efficiency of about 63 %. Water input averaged 12.6 ± 1.2 ml/kg.day. Roughly 50 % of this was lost through evaporation, 45 % in faecal water and urine and 5 % in urate pellets. The output rates of both potassium and sodium were higher than input rates. This difference was significant in the case of sodium ($p > 0.05$, d.f. = 2). Urate pellets play the most important role in the excretion of potassium, dealing with about 78 % of the potassium load. In the case of sodium, the most important excretory pathway is urine. Only a small proportion of the ingested chloride was excreted through the cloaca. This was accomplished via the urine. Neither faeces nor urate pellets contained any trace of this electrolyte.

Energy and water balance of *A. skoogi* fed carrots is shown in Table 3.2. As expected, the components of enery and water balance showed a marked increase with increasing temperature. Energy intake showed a five-fold and water intake a four-fold increase between 23 and 37 °C. The proportion of energy lost at each temperature decreased slightly with increasing temperature. Unpaired students t-tests, however, reveal no significant differences in digestive efficiencies at the three temperatures (23 vs 30 °C, $p > 0.05$, d.f. = 5 ; 23 vs 37 °C, $p > 0.05$, d.f. = 4 ; 30 vs 37 °C, $p > 0.05$, d.f. = 4). A similar trend is apparent in the digestive efficiencies of water. Once again, however, there are no significant differences in the digestive efficiencies at the three temperatures (23 vs 30 °C, $p > 0.05$, d.f. = 5 ; 23 vs 37 °C, $p > 0.05$, d.f. = 4 ; 30 vs 37 °C, $p > 0.05$, d.f. = 4). Urine consistently accounted for about half the water loss at each temperature. EWL made up about 35 % of the water loss and excretory solids the balance of 15 %.

In comparing the two feeding experiments, two apparent inconsistencies are evident and require discussion. Firstly, the dry matter and water input of animals fed nara (Table 3.1) are similar to (in the case of water input, less than) that of animals kept at 23 °C and fed carrots (Table 3.2) even though the former group was kept at a higher temperature (25-30 °C). This is inconsistent with the observations made on the effect of temperature on food and water input. The nara group was, however, kept at an unrealistically high humidity during Feeding experiment 1 (see Methods and Materials for explanation). This, in effect, would decrease evaporative water loss and subsequent

TABLE 3.1. Energy, water and electrolyte balance in captive male *Angolosaurus skoogi* (body mass range = 53 - 73g, n=3) force-fed their natural diet. Animals were kept at 25 - 30 °C during the day and at 25 °C at night. Access to thermoregulatory lamps was allowed for 3 h / day. Standard deviations are shown in parentheses.

	INTAKE			LOSS						
	food	M.W.[1]	total	faeces	urate	urine	EWL	metabolism[2]	total	D.E.[3]
Dry matter g/kg.d	3.0 (0.3)			1.1 (0.2)	0.9 (0.1)	0.2 (0.03)		0.9 (0.3)		62.8 (5.6)
Energy kJ/kg.d	60.9 (5.6)			22.7 (4.5)	11.5 (1.4)			26.7 (4.4)		62.8 (5.5)
Water ml/kg.d	11.8 (1.1)	0.8 (0.1)	12.6 (1.2)	2.4 (1.0)	0.6 (0.1)	3.2 (0.5)	6.6 (1.3)		12.7 (1.4)	80.2 (7.2)
% water	94	6	100	19	4	25	52		100	
K^+ µmol/kg.d	1705 (157)		1705	139 (60)	1399 (149)	261 (39)			1799	91.9 (3.3)
Na^+ µmol/kg.d	121 (11)		121	25 (13)	91 (20)	131 (20)			247	79.1 (10.4)
Cl^- µmol/kg.d	261 (24)		261	0	0	22 (3)			22	100 (0)

[1] M.W. = metabolic water, assuming 0.556 ul H_2O produced per g dry carbohydrate absorbed (from Nagy 1983)

[2] Estimated by difference between intake and loss

[3] D.E. = digestive efficiency = [(dry mass ingested - dry mass of faeces) / (dry mass ingested)]

TABLE 3.2. Energy and water balance in captive *Angolosaurus skoogi* (mass range = 73-84g, n=3 at 23 °C and 37 °C and 4 at 30 °C) force-fed an artificial diet of carrots. Standard deviations are shown in parentheses.

	INTAKE			LOSS						
	food	M.W.[1]	total	faeces	urate	urine [2]	EWL	metabolism[3]	total	D.E.[4]
23°C										
Dry matter g/kg.d	2.8 (0.8)			0.4 (0.3)	0.1 (0.05)	0.4 (0.09)		1.9 (0.4)		86.3 (9.8)
Energy kJ/kg.d	44.4 (12.2)			5.9 (4.2)	1.1 (0.7)			37.4 (8.6)		86.9 (5.7)
Water ml/kg.d	13.1 (3.6)	1.3 (0.3)	14.4 (3.9)	2.4[5] (2.1)		8.3 (1.7)	4.5 (0.7)		15.2 (3.9)	84.0 (12.5)
(% water)	91	9	100	14		56	30		100	
30°C										
Dry matter g/kg.d	6.5 (1.5)			1.3 (0.3)	0.1 (0.02)	0.9 (0.2)		4.17 (1.1)		79.3 (5.1)
Energy kJ/kg.d	104.2 (3.6)			13.8 (6.4)	1.0 (0.2)			89.5 (21.7)		86.6 (6.1)
Water ml/kg.d	28.3 (6.6)	2.9 (0.8)	31.2 (7.3)	5.4[5] (4.3)		16.2 (3.9)	11.0 (1.6)		32.7 (8.3)	82.4 (11.8)
(% water)	91	9	100	17		49	34		100	
37°C										
Dry matter g/kg.d	12.9 (2.3)			2.4 (0.6)	0.5 (0.4)	1.3 (0.6)		8.8 (2.1)		80.9 (5.9)
Energy kJ/kg.d	207.3 (37.4)			40.3 (5.9)	8.8 (6.6)			158.2 (37.6)		79.9 (5.6)
Water ml/kg.d	52.1 (9.4)	6.2 (1.0)	58.3 (10.1)	13.5[5] (4.7)		24.3 (11.7)	23.5 (2.9)		61.3 (10.8)	74.1 (7.7)
(% water)	89	11	100	22		40	38		100	

[1] M.W. = metabolic water, assumed at 0.556 ul H_2O/g dry carbohydrate absorbed (from Nagy 1983)

[2] In the case of dry matter, 5% wet mass of urine assumed to be dry matter

[3] Estimated by difference between intake and loss

[4] D.E. = digestive efficiency = dry mass ingested - dry mass defecated (feces) / dry mass ingested

[5] Fecal and urate water combined

mass loss. The amount of food required to maintain body mass would consequently decrease. Secondly, the digestive efficiency of carrots is about 20 % higher than that of the nara/*Stipagrostis* mix. This has important implications for the extrapolation of laboratory data to field energy budgets. A possible reason for this difference and the suitability of applying data from Feeding experiment 2 to the field situation is discussed later.

3.4 DISCUSSION

3.4.1 Energy and water metabolism

The casual observations that water loss and metabolic rates in *Angolosaurus skoogi* increase considerably during surface activity (Chapter 2) are confirmed by the data presented in this Chapter. The activity metabolic estimates reported here are similar to other investigators' estimates of increased metabolic rate during periods of activity. Bennett and Gleeson (1979) have calculated that oxygen consumption in active *Cnemidophorus murinus* at 40 °C is four times higher than resting levels. Similarly, Bennett and Gleeson (1976) have measured a four-fold increase in metabolic rate at 35 °C in active *Sceloporus occidentalis* (increment estimated from Figure 1, Bennett and Gleeson 1976). Wilson and Lee (1974) have demonstrated a 5.5-fold increase in active over resting metabolic rate in *Egernia cunninghami* at a body temperature of 30 °C (increment obtained from equations supplied in this paper).

The two- to four-fold increase in active versus resting metabolic rates and the similar increase in evaporative water loss rates in *A. skoogi* become even more significant when one considers that body temperatures are invariably higher when animals are above the ground (see Chapter 5). Consider a subsurface lizard at rest at 30 °C. Metabolic rate would be approximately 0.065 ml O_2/g.h (Figure 3.1a) if the animal were post-absorptive and, according to the results of SDA studies, 0.106 ml O_2/g.h if it were digesting food. An active animal at 40 °C would have a metabolic rate of approximately 0.5 ml O_2/g.h (Figure 3.1b). This represents an eight-fold increase over post-absorptive resting metabolic rate and a five-fold increase over digesting resting metabolic rate. Similarly, EWL of a subsurface animal at 30 °C and 10 mmHg would be approximately 0.26 µl H_2O/g.h (Figure 3.2a). When active at 40 °C, EWL would be approximately 2.0 µl H_2O/g.h. (Figure 3.2b), an eight-fold increase. Data presented for *Sceloporus occidentalis* in Table 2 of Bennett and Nagy (1977) indicate that the increase in activity over resting metabolic estimates reported here are not unrealistic. Free-living individuals in spring, for example, incurred a daily metabolic expenditure (measured by means of doubly labelled water) of 141 kJ/g. 16kJ of this were expended during a 16 hour period of inactivity in burrows at 18.5 - 20 °C (estimated from laboratory determinations of field metabolic rate at assumed burrow temperatures). The remainder (125 kJ) represents the cost incurred during 8 hours of activity at 35 °C. The quotient of the metabolic cost when active (16kJ/h) and the metabolic cost when resting (1 kJ/h) is 16. Considering that this quotient is calculated over a temperature difference of about 16 °C, the increase in activity metabolic rate over resting metabolic rate in *A. skoogi* (5 - 8 times, calculated over a temperature difference of 10 °C) is in good correspondence with that of *S. occidentalis*. Indeed, laboratory measurements of active and resting metabolic rates in *S. occidentalis* predict only a 10 - fold difference in active metabolic rate at 40 °C and resting metabolic rate at 30 °C (Bennett and Gleeson 1976, increment estimated from Fig 1). Several other studies illustrate that the increase in active over resting metabolic rates is also influenced by factors other than temperature differences, such as breeding behaviour and foraging strategy. During their breeding season (spring), active *Scleropus virgatus* females (at 35 °C) have metabolic rates which are 46.5 times higher than resting metabolic rates at 12 °C (Merker and Nagy 1984). Activity in males at this time is only about 16 times more expensive than resting. The widely foraging lizard, *Eremias lugubris*, has activity metabolic rates (at 34 °C) which are 30.9 times higher than resting rates at 26 °C and 13.6 times higher than resting rates at 34 °C (burrow temperatures). The sympatric sit-and-wait forager *E. lineoocellata*, on the other hand, displays an activity metabolic rate which is only 6.8 times higher than resting rates at 26 °C.

Due to the period elapsed between the time of capture and experimentation, differences in the metabolic and EWL rates of the three groups probably represent laboratory acclimation rather than seasonal acclimatization. As seasonal field temperature and humidity conditions were simulated in the laboratory, however, the data can be taken to represent seasonal acclimatization to a certain degree. Most studies of laboratory acclimation in reptiles have compared metabolic rates of cold- versus warm-acclimated animals (Waldschmidt *et al.* 1987). Acclimation has always occurred to some extent. The direction of response to cold acclimation varies among groups of reptiles. Some species (e.g. *Uta mearnsi*) increased metabolic rate when acclimated to cold temperature (Murrish and Vance 1968). Other species (e.g. *Dipsosaurus dorsalis*) decreased metabolic rate when cold acclimated. In *A. skoogi*, cold-acclimated individuals (23 - 24 °C, July) display higher metabolic rates than warm-acclimated individuals (30 - 31 °C, February). It should be noted, however, that the 27 - 28 °C group (October) displays higher metabolic rates than the 23-24 °C acclimated group. No consistent pattern is thus evident. This could be a function of the small acclimation temperature increments (3 °C) between the groups. Also, there are other complicating factors such as temporal acclimation in the laboratory (see below).

Humidity acclimation also occurs in reptiles. In general, animals acclimatized to higher humidities display higher rates of EWL than those acclimatized to lower humidities (Minnich 1982). Laboratory acclimation produces the same effect. For example, Kobayashi *et al.* (1983) obtained an EWL rate of 5.63 ± 3.02 ml H_2O/g.h in lizards acclimated to a temperature of 24.5 °C and 95 %

humidity and exposed to a temperature of 30 °C and 12 % relative humidity. Under the same conditions, the same individuals displayed a rate of 2.59 ± 0.44 mlH_2O/g.h when acclimated to a temperature of 24 °C and < 30 % relative humidity. The same response occurs in *A. skoogi.*

All studies of reptiles that have investigated the metabolic rates of fed versus fasted animals have reported significantly higher resting metabolic rates in the former (Waldschmidt *et al.* 1987). This has important implications for the extrapolation of laboratory data to field studies. Values in the literature range from a 32 % increase in the lizard, *Uta stansburiana,* at a test temperature of 30 °C (Roberts, 1968), to a 200 % increase in the alligator, *Alligator mississippiensis,* at a test temperature of 25 °C (Coulson and Hernandes 1973). The volume of food consumed also affects the magnitude of specific dynamic action. S.R. Waldschmidt and S.M. Jones (unpublished observations, in Waldschmidt *et al.* 1987) found that the metabolic rate of the lizard *Scleroporus undulatus*, fed *ad lib.*, increased by 100 % over the rate of fasted animals, whereas individuals fed a restricted diet increased their metabolic rate by only 50 %. The data reported in the present study are all consistent with these observations.

Duplication of the July 30 °C experiment showed a definite acclimation in metabolic rate with time in the laboratory. This may explain the lack of a pattern in the resting metabolic rates of the three groups of animals. Similarly, the significant difference observed in resting metabolic rates when the July 30 °C experiment was duplicated with an alteration of the thermal pre-treatment could also be a contributing factor. What is clearly evident is that determination of resting metabolic rates in the laboratory is a complex procedure and the effect of the complicating factors discussed above should be thoroughly investigated in pilot experiments, particularly when the data are for field application.

The lack of any significant difference in EWL rates of animals resting above and below the sand is surprising when one considers potential factors that could reduce water loss below the sand. These include decreased convection around the skin, reinhalation of exhaled water vapour and the retention of water vapour beneath the sand with subsequent enhancement of the boundary layer around the animal. Although lizard skin has a high resistance to water movement, convection still has an appreciable effect on cutaneous water loss (Porter 1989). The supersurface measurements were, however, conducted under relatively windless conditions (20 litre buckets) making the degree of convection above and below the sand similar. Under more realistic field conditions (appreciable convection above the sand surface), cutaneous water loss would probably be substantially higher in animals resting on the surface. The negligible change in air humidity in below sand experiments makes the remaining two factors (i.e. reinhalation of exhaled water vapour and enhancement of the boundary layer below the sand) unlikely. Water lost from the respiratory tract and skin appears to be absorbed by the sand and provides no direct benefit to the submerged animal.

As far as metabolic rates are concerned, the lack of any significant difference in values obtained for animals resting above and below the sand suggests that there is no increased mechanical cost to breathing under the sand. The data obtained for submerged *A. skoogi* are consistent with observations on the burrowing sand lizards, *Uma* spp. (Pough 1969). Although attempts to measure the submerged metabolic rates of these lizards were unsuccessful, he found no reduction in breathing or heart rate not attributable to a reduction in activity in buried lizards compared to those on the surface. This is in sharp contrast to diving (water) lizards which show profound bradycardia when submerged (Bartholomew and Lasiewski 1965 ; Belkin 1963).

The most likely advantages of spending prolonged periods buried in the sand are two-fold. Firstly, animals are extremely well protected from predators when submerged. Secondly, the thermal mosaic under the sand provides animals with a wide choice of body temperatures when submerged. Of particular significance is the ability to maintain a body temperature higher than when on the surface, especially at night (Section 5.3.4, Chapter 5). Although this increases metabolic and water costs, there is the thermal benefit of improved energy processing and assimilation. There is thus the potential for improvement of net energy gains

3.4.2 Water and electrolyte balance

Compared to the food of other desert reptiles, the diet of *A. skoogi* has a relatively low electrolyte load. Table 3.3 lists the water and electrolyte concentrations of a variety of natural foods consumed by desert reptiles. As excretion of electrolytes involves the obligatory use of water, the most meaningful way of expressing concentrations is in µmol electrolyte / ml water consumed. The water content of *A. skoogi*'s nara/*Stipagrostis* mix is more than double that of most of the foods consumed by the other species. Furthermore, the major component of the diet (nara) is perennial and its water content remains constant throughout the year (Section 5.3.2, Chapter 5). This is in contrast to the diet of at least three of the species listed in Table 3.3 (*Sauromalus obesus*, *Uromastyx acanthinurus* and *Gopherus agassizii*), whose diet seasonally dehydrates to the extent that animals have to cease feeding (Grenot 1976 ; Minnich 1976, 1977 ; Nagy 1972). This behaviour appears to prevent accumulation of toxic levels of dietary potassium and retards excretory water losses.

A more important consequence of the high water content of nara is the low electrolyte load ingested by animals maintaining water balance (Table 3.2). Table 3.4 contrasts the daily electrolyte load ingested by two other desert reptiles with that of *A. skoogi*. The total electrolyte load imposed on *A. skoogi* (1987 µmol/kg.day) is only 66 % of that ingested by *Gopherus agassizii* (3018 µmol/kg.day) and 20 % of that ingested by *Sauromalus obesus* (10140 µmol/kg.day).

In the case of potassium and sodium, animals apparently excreted more electrolytes than they ingested (Table 3.1). The difference is only significant in the case of sodium ($p < 0.05$, d.f. = 2). This can probably be attributed to the inevitably small sample size and the high variability in the sodium concentration of the food mix used during the feeding experiment. Sodium concentration in the four food samples analysed varied between 23 and 54 µmol/g dry matter. This could cause

TABLE 3.3. Water and electrolyte content of the natural diets of various desert reptiles.

Reptile species	Diet description	Water ml/g dry matter	K^+ µmol/ml	Na^+ µmol/ml	Cl^- µmol/ml	References
Dipsosaurus dorsalis	summer diet	1.0	364	34	105	Minnich and Shoemaker (1970)
Uromastix acanthinurus	fall diet	1.4	320	15	80	Grenot (1976)
Gopherus agassizii	spring diet	2.1	150	62	105	Nagy and Medica (1986)
Sauromalus obesus	spring diet	1.4	426	33	198	Nagy (1972)
Angolosaurus skoogi	summer diet	3.9	144	11	22	This study

TABLE 3.4. Comparison of daily electrolyte loads of three species of desert reptiles force-fed their natural diets.

Reptile species	Daily electrolyte load μmol/kg.day K^+	 Na^+	 Cl^-	Reference
Gopherus agassizii	1431	591	996	Nagy and Medica (1986)
Sauromalus obesus	6550	510	3080	Nagy (1972)
Angolosaurus skoogi	1705	121	161	This study

large errors in estimates of sodium consumption. The potassium concentration in food showed substantially less variation than did sodium. In addition to this, the extraction of electrolytes from food samples may not have been as efficient as their extraction from faecal samples. This would also result in consumption underestimates.

In the case of potassium, urate pellets were the major avenue of excretion, taking care of 78 % of the total load. The efficiency of this system is striking when one considers that this was achieved while expending only 4 % of the total water loss. The desert iguana, *Dipsosaurus dorsalis*, shows a similar water conservation efficiency in its urate pellet excretion (about 3 % of the total water loss). This species is, however, only excretes about 40 % of the ingested potassium in the form of urate pellets (Minnich 1970). Urate pellets are also important in sodium excretion in *A. skoogi*, taking care of 37 % of the total load. Overall, the concentration of these two anions in urate pellets indicates that this avenue alone could deal with the daily salt load while using a small proportion (roughly 10%) of the daily water intake. The importance of urate electrolyte excretion becomes even more apparent when one considers that if *A. skoogi* were to excrete its dietary potassium entirely at concentrations normally found in its liquid urine (about 80 μmol/ml), it would loose urinary water at a rate equal to about 1.8 times its daily water intake.

Cloacal waste products are clearly not the means by which chloride excretion is accomplished (Table 3.1). Only about 8 % of the ingested chloride leaves the body via the urine. No trace of chloride could be detected in either the faeces or urate pellets. Nasal salt glands have been established as important organs of electrolyte excretion in a variety of lizards (Templeton 1972). At no stage during Feeding experiment 1 was the presence of a nasal salt gland evident. During pilot experiments to Feeding experiment 2, however, salt exudates were frequently observed covering the nostrils of *A. skoogi*. The exudates were generally only obvious if animals had been deprived of sand for extended periods of time. Nasal salt from five animals was pooled, dried and dissolved in distilled water. The supernatant was analysed for electrolytes using the methods described above. Ion concentrations were 5214, 8507 and 7875 µmol/g dry mass for K^+, Na^+ and Cl^- respectively. These high values establish beyond doubt the presence of a functional salt gland in *A. skoogi*. Considering the low cloacal chloride output, the nasal salt gland is probably the major organ of chloride excretion in this species. This organ plays an important role in the excretion of chloride in several species. In the field, the salt gland of *Dipsosaurus dorsalis*, for example, excretes about 93 % of the ingested chloride (Minnich 1970, 1976). The electrolyte balance equations in Table 3.1 suggest that the nasal salt gland plays a minor role in coping with most of the electrolyte load imposed by the summer diet of *A. skoogi*. This implies that this species is capable of handling far greater loads than ingested with its natural diet. Individuals are, in fact, forced to feed on other plants at other times of the year (Section 5.4.2., Chapter 5). The "reserve" excretory pathway (nasal salt gland) may play an important role in maintaining electrolyte balance in these individuals. This speculation is not without supportive evidence from other studies. Stress induced changes in the structure of the salt gland of the snake *Cerberus rhynchops*, for example, suggest that the gland secretes salt only during periods of dehydration (Dunson and Dunson 1979).

As outlined in the Introduction (Chapter 1), the major obstacle to field growth rate investigations is the complexity of factors influencing animal behaviour. One of these factors is food quality. Deterioration of food quality and cessation of feeding, for example, can only complicate such an investigation. *A. skoogi* has an abundant food source with a consistently high water content (Section 5.3.2, Chapter 5) and low electrolyte load. In this respect, this lizard is unlikely to ever experience nutritional stress and, as such, is an ideal subject for the investigation in question.

3.4.3 Energy balance

The major factors determining the rate at which a lizard acquires energy are the rate of food intake, the rate of passage of food along the gut, and the efficiency with which food is digested. Numerous studies have confirmed that the former two factors are strongly temperature dependent (reviewed in Waldschmidt et al. 1987 and Zimmerman and Tracy 1989). *Uta stansburiana*, for example, increased its consumption rate of crickets (unrestricted ration) from 40 mg/g.day at 22 °C to about 90 mg/g.day at 32 °C (Waldschmidt *et al.* 1986). In the same experiment, gut passage time decreased from 9.2 to 1.9 days over the same temperature range. The data presented here (Figure 3.3 and Table

3.2) are consistent with these observations. The slight but not significant decrease in digestive efficiency with increasing temperature (Table 3.2) is, however, less consistent with existing data. The studies measuring digestive efficiency in lizards have generally shown that this process improves with body temperature (Zimmerman and Tracy 1989). Increases in digestive efficiency are, however, slight relative to the temperature range over which they have been measured. Waldschmidt et al. (1986), for example, have found that the difference between maximum and minimum digestive efficiencies averaged only 7.5 % over a range of body temperatures from 22 - 38 °C in the lizard *Uta stansburiana* . More recently, Zimmerman and Tracy (1989) have exposed a factor that appears to be responsible for misleading data on the thermal dependency of digestive efficiency. Feeding desert iguanas (*Dipsosaurus dorsalis*) just sufficient food to balance energy requirements, they measured a negligible increase in digestive efficiency (about 2.5 %) over the temperature range 33 - 41 °C. These results contrast sharply with those of Harlow *et al.* (1976) who, using the same species, demonstrated a 17 % increase over the same temperature range. The latter investigators, however, overfed lizards at all temperatures (by as much as 330 % at the lowest temperature). It is unclear whether lizards at lower body temperatures had lower digestive efficiencies because of the lower temperature, or because of some bulk limitation of the feeding apparatus at a high level of overfeeding. Additional evidence for the thermal stability of digestive efficiency in this species has been provided by Karasov and Diamond (1985). Interspecific differences in the thermal dependence of digestive efficiency undoubtedly exist. Whatever the case, however, temperature appears to have little effect on digestive efficiency in lizards. The non-significant differences between the digestive efficiencies at the experimental temperatures shown in Table 3.2 are consistent with this final conclusion.

The digestive efficiencies of herbivorous lizards are generally much lower than those of insectivorous lizards. Coefficients typically range from 30 - 70 % in the former group and 70 - 90 % in the latter group (Iverson 1982). This is attributed to the lower quality of plant food which generally contains a high indigestible cell wall fraction (Waldschmidt *et al.* 1987). Even though several species of herbivorous reptiles are known to possess fibre fermentation systems, they are still not nearly as efficient as insectivores in digesting their food. The efficiency with which nara is digested by *A. skoogi* (62.8 %, Table 3.1) falls within the range characteristic of herbivorous reptiles. The digestive efficiencies of carrots (79.9 - 86.9 %, Table 3.2) are substantially higher. This can probably be attributed to the higher fibre content of nara (about 45 %) compared to that of carrots (about 15 % ; R. Buffenstein, personal communication). Similar diet related differences in digestive efficiencies have been reported. When fed a diet low in fibre (rabbit pellets), the average digestive efficiency for the lizard *Dipsosaurus dorsalis* was 57 % (Harlow *et al.* 1976). When fed natural plant food which had a higher fibre content, the digestive efficiency varied from 30 - 57 % (Minnich 1970). Similarly, digestive efficiency in the giant land tortoise, *Geochelone gigantea*, varied from 11 - 43 % depending on the fibre content of the diet (Hamilton and Coe 1982). For the purposes of this study, application of the carrot digestive efficiency data to field energy budgets is not suitable due to the unrealistic fibre content of the food source used. The lower digestive efficiency of nara (Table 3.1) needs to be combined with observations of the thermal independence of digestive efficiency (Table 3.2) to provide the data necessary to calculate energy gains in the field. In Chapter 5, animals will thus be considered to digest their food with about 60 % efficiency, regardless of their body temperature.

The usefulness of the data reported in this chapter is two-fold. Firstly, it has been shown that, with regard to an optimization of scope for growth study, complications arising from nutritional stress are probably non-existent. *A. skoogi* feeds on a food source with a high water content and a low elctrolyte load. As will be shown in Chapter 5, this food source is perennial and its constituents show very little seasonal variation. Secondly, physiological data required to determine energetic and hydrical costs and gains under any activity and temperature regime have been determined. The most important data include components of water loss in active and resting animals, metabolic costs (when digesting and post-absorptive) in active and resting animals, and the efficiency with which animals digest their natural diet.

CHAPTER 4

LIZARD BODY TEMPERATURE MODELLING AND THE DESERT DUNE MICROCLIMATE

4.1 INTRODUCTION

The exchange of energy between an animal and its environment is a complex phenomenon involving radiation, convection, conduction and evaporation. The animal absorbs shortwave radiation from direct sunlight coming from the sun, scattered sunlight coming from the sky and sunlight reflected from clouds and the surroundings. Longwave radiation is absorbed in the form of thermal radiation from the atmosphere and the surroundings. Of the energy absorbed, some is reradiated from the body surface. If the animal is in contact with the ground, energy will flow to or from the animal's body by conduction. Energy will also flow to or from the animal body by convection if the surface temperature of the skin is different from that of the ambient air. Energy is also lost from the animal when water evaporates from the body surface.

Microclimate conditions on a dune top, slipface and base may differ considerably (Pietruszka 1987 ; Seely *et al.* 1988 ; Seely *et al.* 1990) It follows that a resident ectotherm will, at any one moment in time, exhibit any of a wide range of body temperatures depending on its position on the dune. If some knowledge of this variation is obtained, it may provide insight into observed activity and thermoregulatory patterns. This chapter describes the use of mathematical modelling, field copper model studies and microclimate measurements to determine and analyse the range of potential body temperatures available to *Angolosaurus skoogi* in its natural environment. Additional information on humidity conditions both above and below the slipface surface is also provided.

4.2 METHOD AND MATERIALS

4.2.1 Mathematical modelling exercise

Mathematical modelling is a powerful tool enabling investigators to gain insight into complex phenomena which are difficult or impossible to determine empirically. With the aid of modelling it is possible to predict an animal's body temperature under any environmental conditions. This is done by constructing a steady-state energy balance equation incorporating all sources of energy loss and gain. The sources of heat gain are put on the one side of the equation and those of heat loss on the other. It is assumed that when body temperature is stable, heat gain equals heat loss. The equation is programmed into a computer which does successive iterative approximations until a body temperature which balances the heat loss and gain terms of the equation is obtained.

The steady-state energy balance equation for an ectotherm is as follows (adapted from Gates 1980) :

HEAT GAIN

(a)(AS)(S)	gain from direct sunlight +
(a)(As)(s)	gain from scattered sunlight +
(a)(Ar)(r)	gain from reflected sunlight +
(Eb)(Aa)(Ra)	gain from atmosphere thermal radiation
(Eb)(Ag)(5.67E-08)(Es)[(Ts + 273)^4]	gain from ground radiation +
(k/d)(Ac)(Ts - Tb)	conductive heat transfer +
Qm	metabolic heat production

EQUALS

HEAT LOSS

(Eb)(5.67E-08)(Ae)[(Tb + 273)^4]	radiation from skin +
(kc)(Tb - Ta)(Aconv)[(V/D)^0.5]	convective heat loss +
Qewl	heat lost through evaporative water loss

where :

a = skin absorptance to shortwave radiation from direct, scattered and reflected sunlight (decimal fraction)

S = intensity of direct sunlight incident on body surface (Watts/m^2)

s = intensity of scattered sunlight (Watts/m^2)

r = intensity of reflected sunlight (Watts/m^2)
AS = projected surface area exposed to direct sunlight (m^2)
As = surface area exposed to scattered sunlight (m^2)
Ar = surface area exposed to reflected sunlight (m^2)
Ag = surface area exposed ground radiation (m^2)
Aa = surface area exposed to atmospheric radiation (m^2)
Ae = surface area for the emission of longwave radiation (m^2)
Ac = ventral surface area (m^2)
Aconv = surface area exposed to convectional heat transfer (m^2)
Ra = intensity of thermal radiation from the atmosphere (Watts/m^2)
Eb = emissivity or absorptance of the skin surface to longwave radiation from the ground or atmosphere (decimal fraction)
5.67E-08 = Stefan-Boltzmann constant
Es = emissivity or absorptance of the ground surface (decimal fraction)
Ts = substrate temperature
Tb = body temperature (°C)
Ta = ambient temperature (°C)
k = thermal conductivity of the skin or air (Watts/m. °C)
d = thickness of skin or the layer of air between the ground and the ventral body surface (m^2)
V = wind speed (m/s)
D = characteristic dimension for convective heat transfer, in this case, the diameter of body (m)
kc = a constant such that (kc)[(V/D)^0.5] has the units Watts/m^2 °C.

Note that if Tb > Ts, the term conductive heat transfer becomes negative and moves to the heat loss side of the equation. Similarly, if Ta >Tb, convective heat transfer becomes negative and moves to the heat gain side of the equation. In ectotherms, heat gained through metabolic heat production and lost through evaporative water loss is, during moderate to hot ambient conditions, negligible compared to other sources of heat transfer. Furthermore the two avenues of heat exchange are of comparable magnitude (Gates 1980) and tend to cancel each other out. They were not included in the balance equation for this analysis.

The following two assumptions were made :
Eb = Es = 1.0
Tb = skin temperature

Parameters :

The body shape of a lizard can be approximated as a cylinder with characteristic dimentions h (length) and D (diameter). For this analysis, the same dimensions as the copper models (see below), 0.15 m long and 0.015 m diameter, were used.

The total surface area of the cylinder (At) was calculated using the formula $(2)(\pi)(h)(D) + (2)(\pi)(D^2)$ = 0.0156 m^2 .

Surface area exposed to direct sunlight (AS) depends on the azimuth and elevation of the sun as well as the orientation (azimunth) and elevation of the animal. The procedure for calculating AS is outlined in Gates (1980).

The intensity (I) of sunlight (S) on a surface is dependent on the angle of incidence (ø) between the surface and the sun's rays : I = (cos Ø)(S). In all cases Ø was taken to be 90° , i.e. I = S.

Scattered sunlight (s) reaches an animal from the entire hemisphere if the animal has an unobstructed view of the horizon. In this case, the surface area of the animal which is exposed to the sky is about one half of its entire surface area, i.e. (0.5)(0.0156) = 0.0078 m^2.

Direct and scattered sunlight are reflected from the ground surface. The surface area exposed to this form of radiation (Ar) is also about one half of the total surface area, 0.0078 m^2. When the ventral body surface is in contact with the ground, Ar is reduced by the amount equivalent to the contact surface area (Ac). Using proportions determined by Bartlett and Gates (1967), Ac = (15%)(At) = 0.0023 m^2 . Ar is thus = 0.0078 m^2 (animal off ground)

= 0.0055 m^2 (animal on ground).

Effective areas for the emission and absorption of thermal radiation (Ae) have been investigated by Bartlett and Gates (1967). They found the total effective emitting area for the lizard, *Sceloporus occidentalis*, to be 89 % of the total surface area. In this exercise, Ae thus equals (0.89)(0.0156 m^2) = 0.0139 m^2 . Areas for the emission or absorptance of ground (Ag) or atmospheric (Aa) radiation are taken as one half of the total effective emitting area = (0.5)(0.0139 m^2) = 0.0070 m^2 . When the ventral body surface is in contact with the ground, Ae and Ag are reduced by 85 % to 0.0118 m^2 and 0.0060 m^2, respectively.

Area exposed to convection (Aconv) depends on whether or not the animal is in contact with the ground. When off the ground, Aconv = At = 0.0156 m^2. When in contact, Aconv = At - Ac = 0.0133 m^2.

To summarise the areas -

	OFF GROUND (m^2)	ON GROUND (m^2)
At	0.0156	0.0156
As	0.0078	0.0078
Ar	0.0078	0.0055
Ac	0.0023	0.0023
Aa	0.0070	0.0070
Ag	0.0070	0.0060
Ae	0.0139	0.0118
Aconv	0.0156	0.0133

Sun and thermal radiation conditions were based on desert condition measurements made by Porter *et al.* (1973)

$S = 1000\ W/m^2$

$s = 30\ W/m^2$

$r = 322\ W/m^2$

$Ra = 388\ W/m^2$

Skin absorptance (a) was taken as 0.6. This value was based on the measurements made on the desert iguana, *Dipsosaurus dorsalis* (Porter *et al.* 1973) , and absorptance estimates described below.

The conductivity (k) of lizard skin was based on values given in Gates (1980) = 0.502 W / m.°C. The conductivity of air = 0.025 W /m.°C.

Three model postures were analysed :
horizontal, on ground
horizontal, off ground
angle, cylinder axis parallel or normal to the sun's rays

Three AS (surface area exposed to direct sunlight) values were used : AS = 0.0007 m^2 (minimum surface area exposed to direct sunlight), AS = 0.0023 m^2 (half of maximum surface area exposed) and AS = 0.0045 m^2 (maximum surface area exposed).

d = 0.001 m (skin thickness through which heat is conducted when the body is in contact with the ground)

d = 0.001 or 0.01 m (air thickness throgh which heat is conducted when the body is not in contact with the ground).

Wind speed (V) was varied between 0.1 and 10 m/s.

Two Ts and Ta regimes were investigated :
Ts = 20 °C and Ta = 20 °C. (cold)
Ts = 50 °C and Ta = 30 °C. (hot)

The convection coefficient constant (kc) was assigned a generalized value of 3.49, determined from a variety of empirical laboratory investigations (Gates 1980). In the analysis illustrated in Figure 4.12b, values ± 10 % of this value were used. This corresponds to the range in kc found by Wathen *et al.* (1971) for copper cylinders where the angle of pitch betwen the cylinder axis and wind direction was varied.

4.2.2 Copper Models

Models were constructed out of 0.015 m^2 diameter copper pipe. The ends of each cylinder were sealed with copper discs. Temperatures inside the models were measured by a fine copper/constantan thermocouple wire inserted 1.5 cm through one of the discs. Two supporting wooden rods, inserted normal to the cylinder axis, enabled the models to be orientated and elevated above the substrate surface as desired.

All models were painted with enamel paint, the colour of which was determined as follows. Two models were placed vertically in a wind tunnel and illuminated from above by a 300 W quartz halogen lamp. Windspeed was set at 2 m/s. The end of one model was covered with skin, freshly removed from the dorsal surface of a frozen *A. skoogi* specimen. The second model was painted a colour that closely resembled that of *A. skoogi* skin. Initially, the paint model obtained lower temperatures than the skin model, indicating that the absorptance of the paint was too low. Black paint was gradually added to successive coats until both models obtained similar temperatures. The end result is shown in the first part of the graph in Figure 4.1. To ensure that both models were experiencing the same conditions, the positions of the models were swopped after about 20 minutes. To gain some idea of the absorptance (a) of the model to sunlight, the model was painted white (absorptance assumed 0.0) and then black (absorptance assumed 1.0). The result is shown in the second half of Figure 4.1. The ratio of the temperature difference between the skin model - white model and the black model - skin model is about six to four. This corresponds to a paint absorptivity of 0.6.

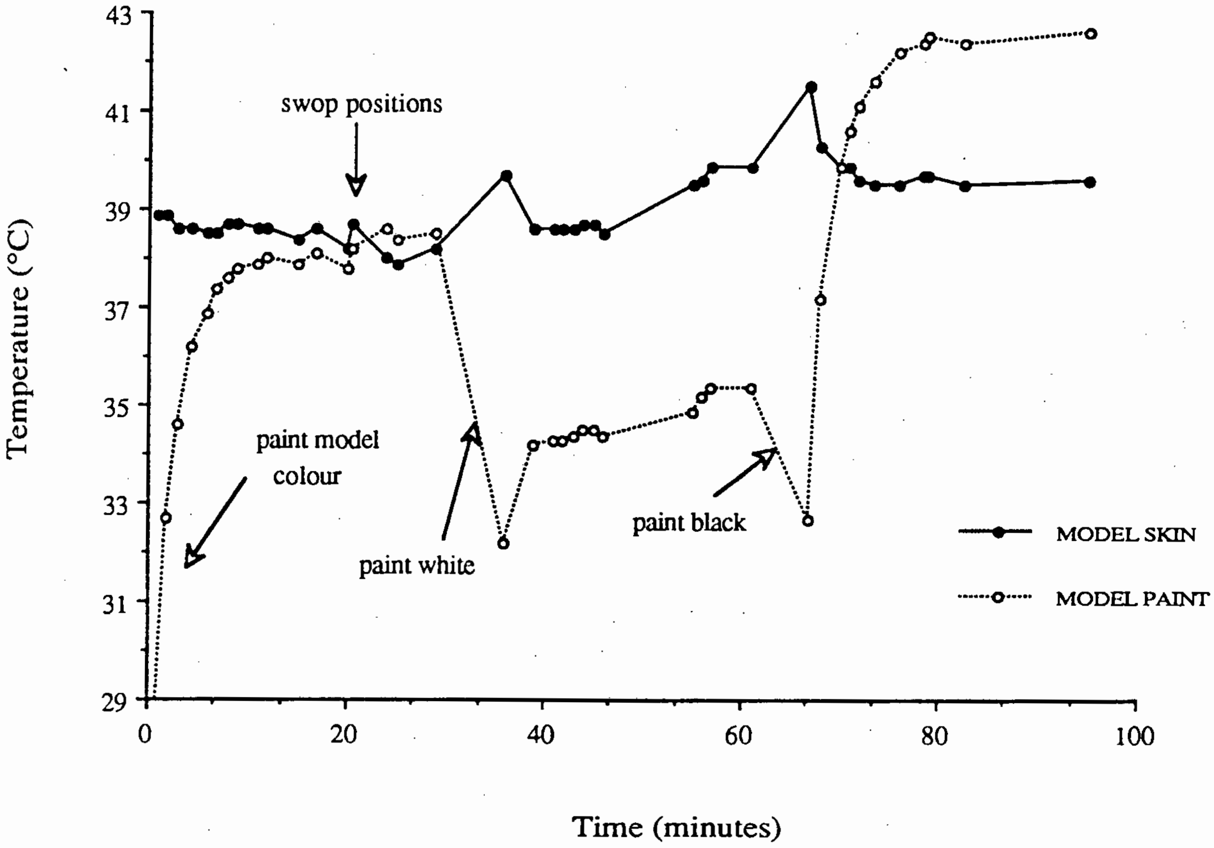


FIGURE 4.1. Core temperature of two sealed copper pipes covered with *Angolosaurus skoogi* skin (skin model) or painted various colours (paint model). Pipes were positioned vertically in a wind tunnel set at 2 m/s and heated from above by a 300W quartz halogen lamp. Black paint was gradually mixed with white paint until the two models equilibrated at similar temperatures. This is contrasted with the core temperature of the paint model coated with pure white or pure black paint.

To avoid disturbance to observation animals (Chapter 5), the copper model analysis was not conducted on the animal observation dune. A dune about 1 km away (hereafter referred to as the microclimate dune) that was similar in size and orientation to the animal observation dune, was selected for this purpose. The dune comprised two distinct slipfaces, one orientated roughly northwest/southeast (slipface A) and the other east/west (slipface B). The same dune was used in October 1989 and February 1990. In July, 1990, animal observations were being made at the microclimate dune and another dune with a single east/west slipface was used for the copper model studies.

On the slipfaces, one of three model orientations was used

1) model orientated at right angles to the slipface crest - DIP model
2) model orientated parallel to the slipface crest - STRIKE model
3) model orientated at 45 degrees to the slipface crest - ANGLE model

Models were either placed in contact with the sand (ON models) or elevated 1 cm above the surface (OFF models).

The slipfaces were divided into four measurement areas

1) The gravel plain (GP), about 1m away from the base of the slipface
2)The lower slipface (BOTTOM), about 1m up from the botom of the slipface
3) The upper slipface (TOP), about 1 m down fron the crest of the slipface.
4) The dune top (TOP TOP), a few meters from the crest of the slipface.

The microclimate dune and model locations are shown in Figures 4.2 - 4.4. In October (Figure 4.2), the main aim was to investigate the effect of orientation on model temperature. STRIKE and DIP models were placed at all sites. With the exception of two models at A BOTTOM, all models were placed in contact with the sand. In February (Figure 4.3), the main objective was to investigate the effect of conduction on model temperature. ON and OFF models were placed at all sites. All models were placed at the ANGLE orientation. In July (Figure 4..4), ON and OFF models were also placed at all sites. On this occasion, all models were placed in the STRIKE orientation.

Model temperatures were monitored for four successive days during each field trip. In February, an additional copper model study was conducted for one day (5/3/90) on the animal observation dune (Figure 4.5). This study is hereafter referred to as the one day model thermoregulation study. The main objective here was to simulate a variety of animal postures observed on the animal observation dune. These postures are described in Chapter 5. In addition to the standard model positions, two models were placed horizontally, at 90° to one another, on top of the leaves of a low lying shrub, *Merremia guerichii*. A third model was moved to point directly towards the sun at all times (SUN TRACK model). A fourth model was moved so that the axis of the cylinder was continuously at right angles to the sun's rays (SUN AWAY model).

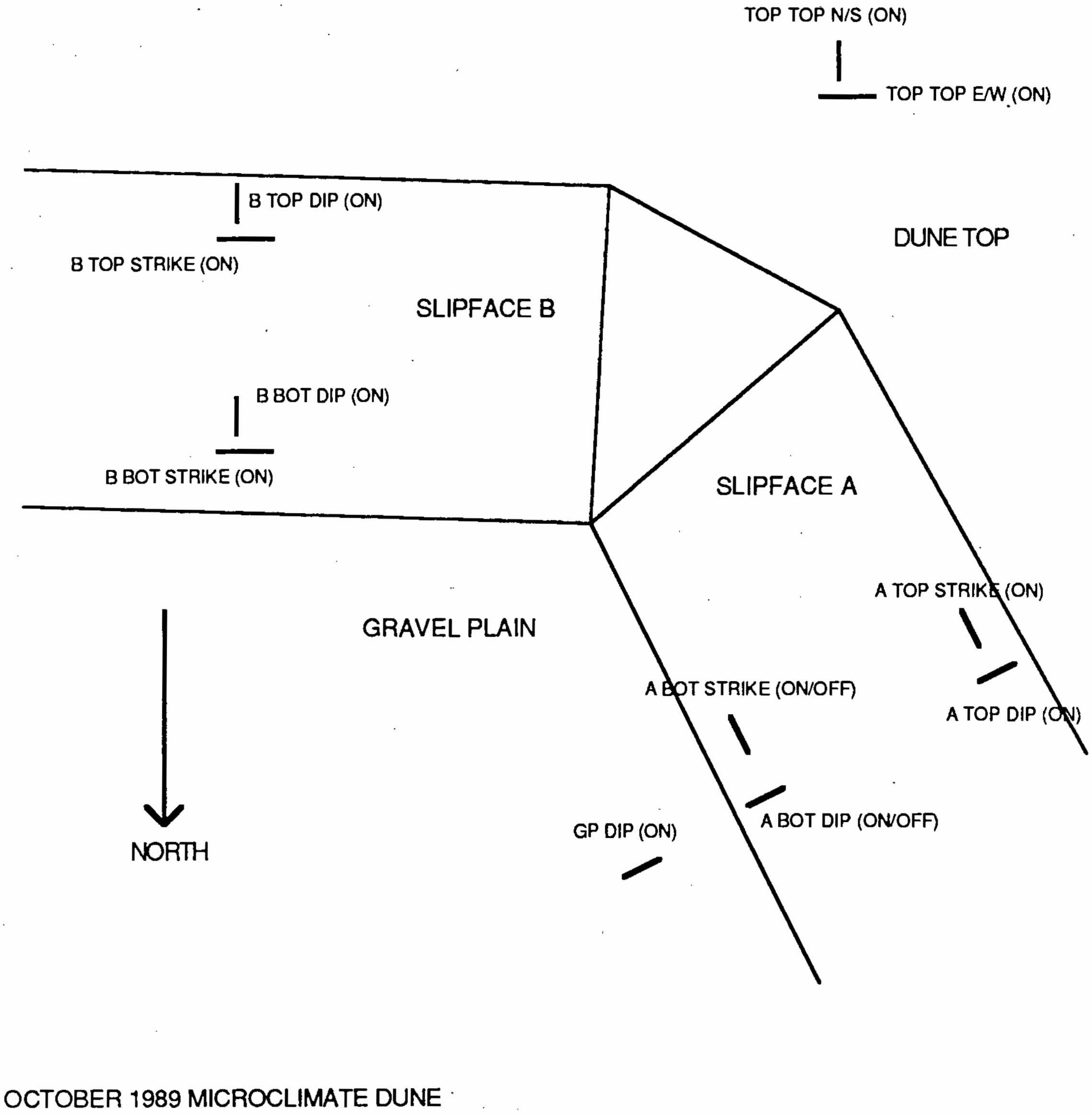


FIGURE 4.2. Schematic aerial view of the dune used for microclimate measurements in October 1989. The black bars indicate the position and orientation of copper models. The models are not drawn to scale. On (contact) models were placed at all sites. Off (elevated) models were only placed at the A bottom (BOT) site.

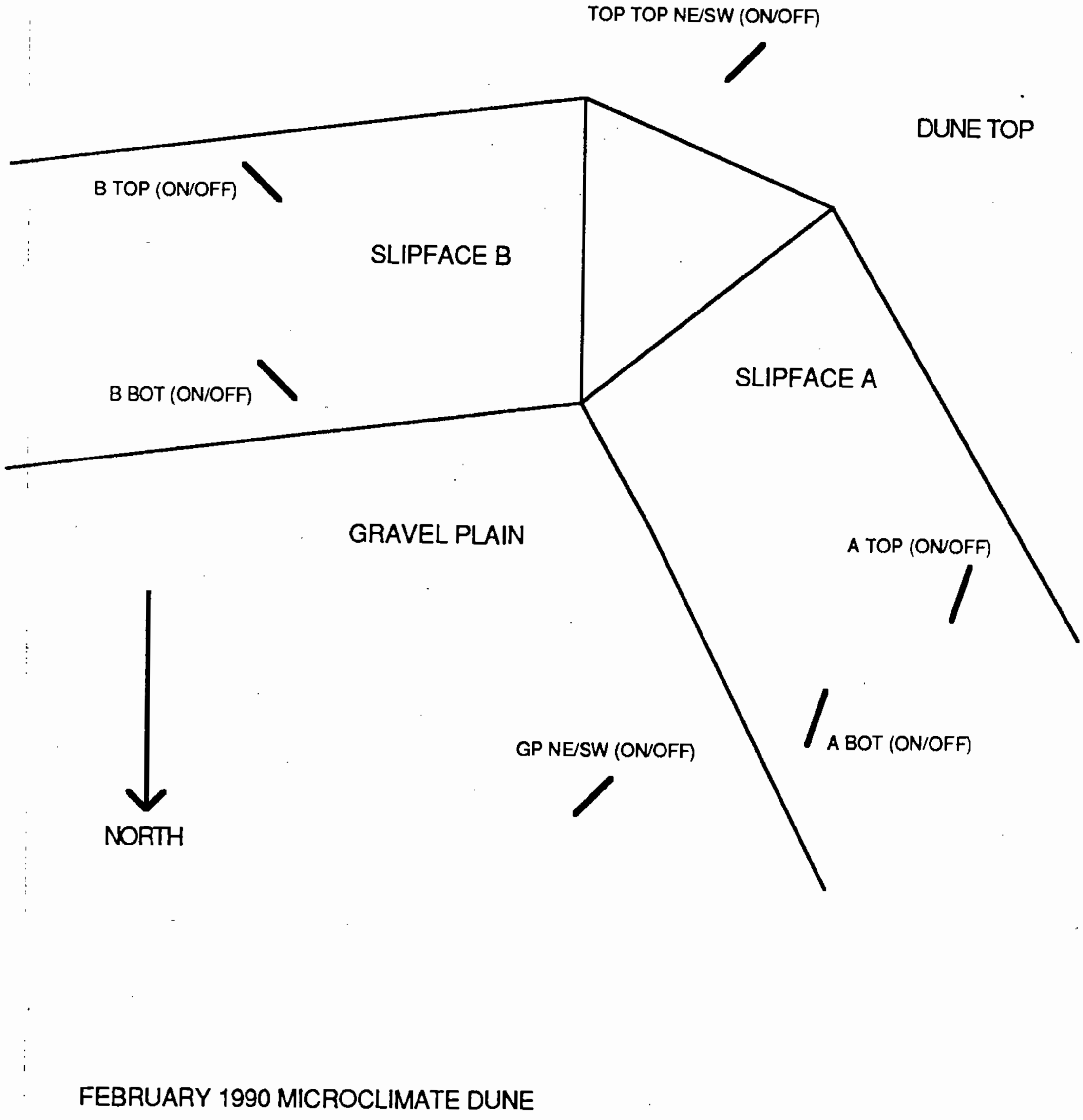


FIGURE 4.3. Schematic aerial view of the dune used for microclimate measurements in February 1990. The black bars indicate the position and orientation of copper models. The models are not drawn to scale. On (contact) and off (elevated) models were placed at all sites.

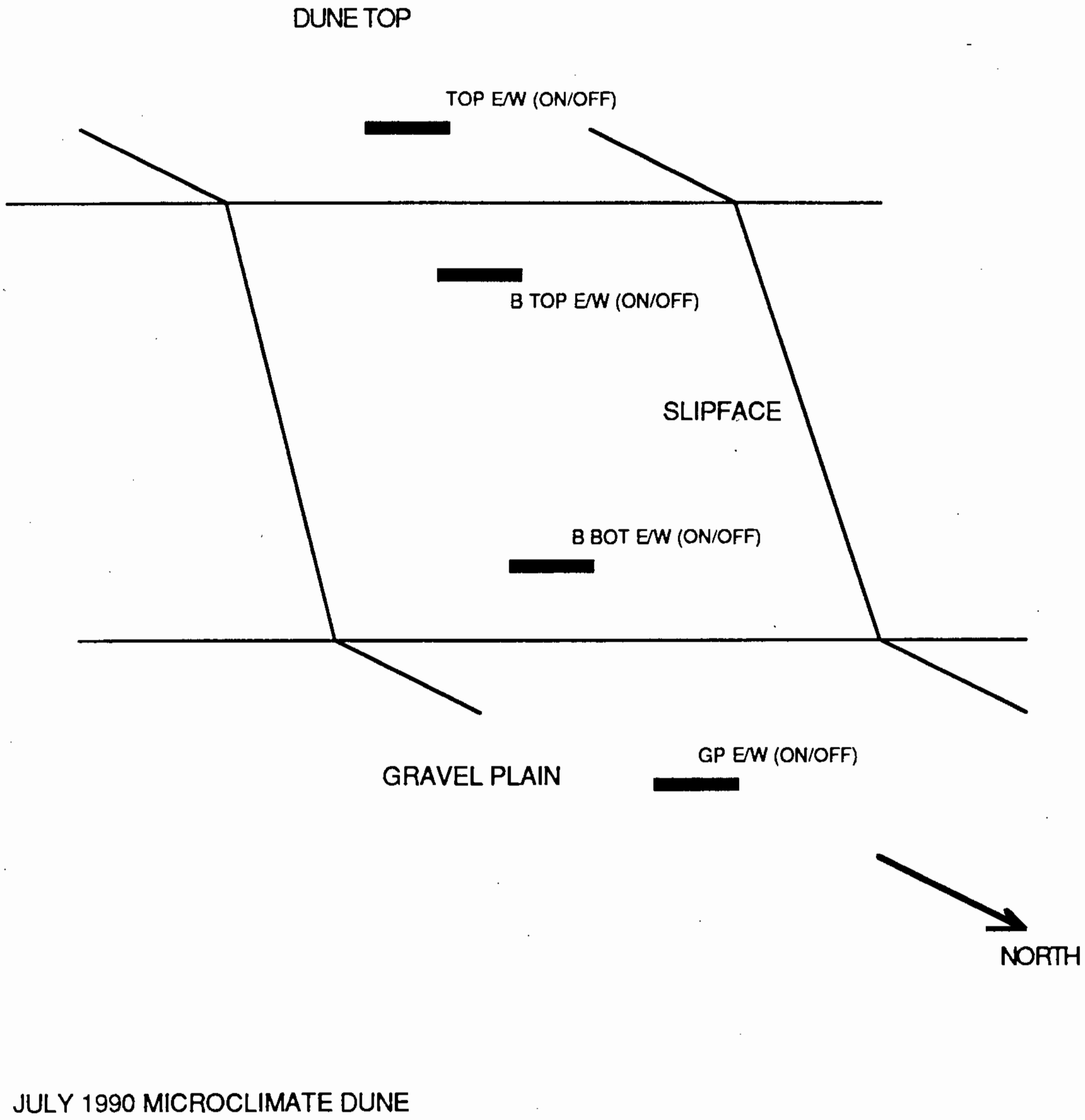
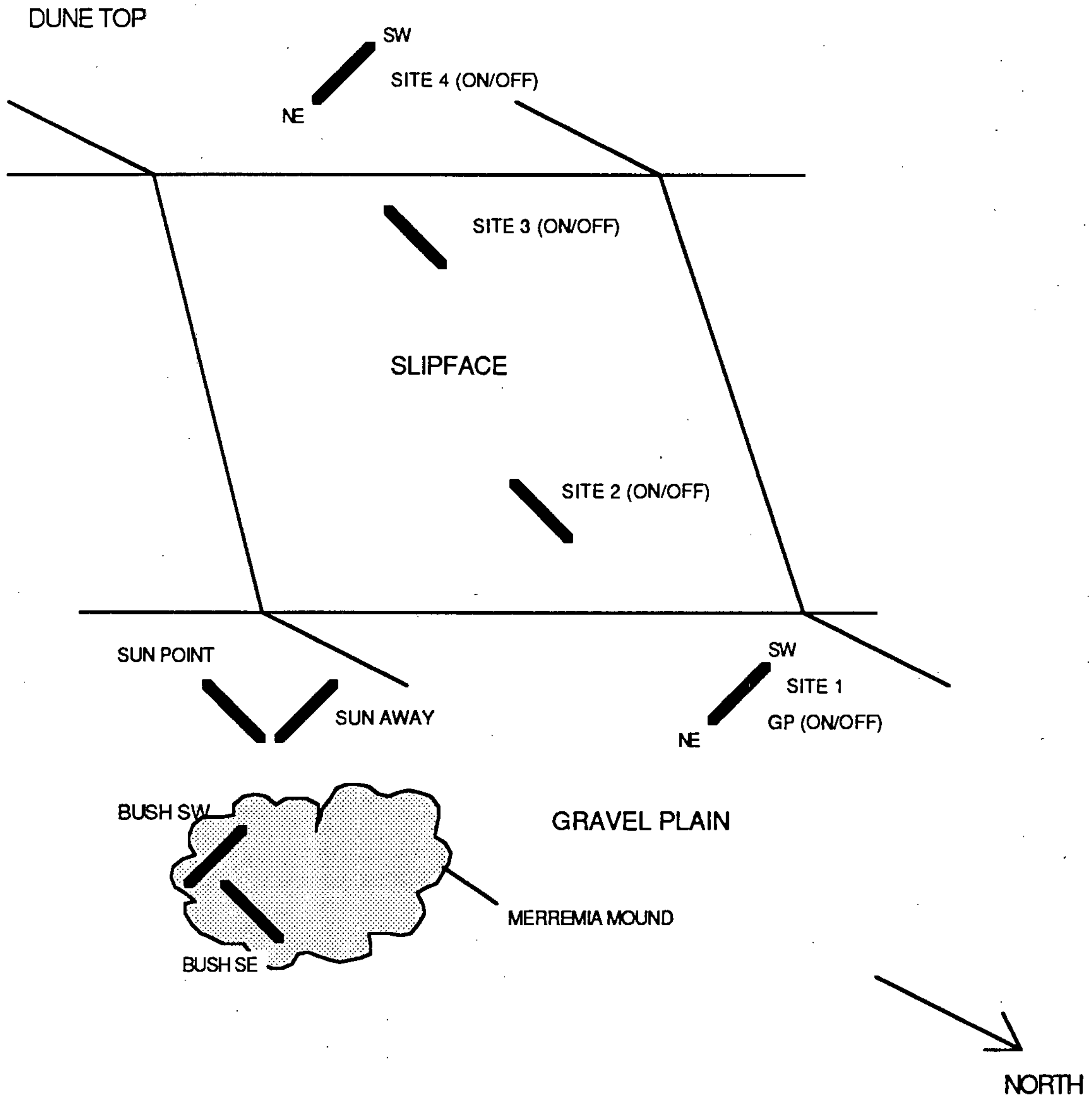


FIGURE 4.4. Schematic face-on view of the dune used microclimate measurements in July 1990. The black bars indicate the position and orientation of copper models. The models are not drawn to scale. On (contact) and off (elevated) models were placed at all sites.



FEBRUARY 1990 ANIMAL DUNE

FIGURE 4.5. Schematic face-on view of the dune used for microclimate measurements during the one day model thermoregulation experiment in February 1990. The black bars indicate the position and orientation of copper models. See text for details. The models are not drawn to scale.

Meteorological parameters measured at each site comprised wind speed 5 cm above the sand surface (hot wire anemometer in October and cup anemometer totalizers in Febuary and July), sand surface temperature (copper/constantan thermocouple, Model Bat-12, Bailey Instruments, Inc.), air temperature 1cm above the sand surface (shaded copper/constantan thermocouple), humidity and air temperature 2m above the ground (Hanna Instruments, Italy), wind direction and sun elevation and azimunth (gnomon and protractor). In addition to this, several measurements of subsurface temperatures and humidities at both the microclimate and animal observation dune were made during October 1989 and February 1990. These measurements were obtained with a specially constructed sand probe consisting of seven hollow aluminium tubes, ranging in length from 5 - 50 cm. The tubes were sealed at the bottom end and two small holes drilled just above the point of closure. One hole housed a copper/constantan thermocouple. Air was drawn through the second hole, up the tube and over an encapsulated Hanna thermohygrometer by means of a 100 ml glass syringe.

4.3 RESULTS AND DISCUSSION

4.3.1 Mathematical Modelling exercise

Results of the modelling exercise are shown in Figures 4.7a - 4.12b. All graphs express model temperature as a function of wind speed. As scales on the y-axis vary, temperature differences between curves are shown in parentheses at wind speeds of 0.5, 2.0, 5.0 and 10 m/s. Figure 4.6 explains all other text appearing on the graphs.

Wind speed

The effect of wind speed on model temperature (decrease in temperature with increasing wind speed) is clear in all graphs. As convective cooling or warming is essentially a function of the difference between the model and the surrounding air (see balance equation), the effect is more pronounced during the hotter conditions (see, for example, Figs 4.7a and 4.7b).

Orientation

The surface area of a model exposed to direct sunlight (AS) is a function of the model's orientation relative to the sun. In most of this analysis, the two extreme orientations (maximum and minimum exposed surface area, AS = 0.0045 m^2 and 0.0007 m^2, respectively) have been used. Generally, the difference between the temperatures of differently orientated models is greater at lower wind speeds where convective cooling plays a smaller role. Temperature differences are, however, at realistic field wind speeds (1 - 5 m/s), never more than about 1 °C if the model is in contact with the sand (Figs 4.7a and 4.7b), or more than about 4 °C if the models are horizontally elevated (Figs 4.8a and 4.8b) or at an angle (Figs 4.9a and 4.9b). When one considers that in realistic field situations differently orientated models will have more moderate AS's (with a smaller difference), it is clear that in the case of a cylinder, orientation has a small effect on model temperature.

Contact with substrate

The difference in the temperatures of models in contact and elevated only 1cm above the substrate is striking, particularly at higher temperatures (Figs 4.10a and 4.10b). A combination of heat conduction into contact models and convective heat loss from elevated models can result in large temperature differences. At realistic field wind speeds, temperature differences of between 2 and 8 °C can be expected.

Degree of elevation above the substrate

Figs 4.11a and 4.11b clearly show that under both hot and cold conditions, the distance elevated above substrate surface has little effect on model temperature. This can be largely attributed to the very low conductivity of air. The heat conduction term in the balance equation is of small magnitude regardless of the elevation. It should be remembered, however, that wind speed increases steadily with height above the ground (Porter *et al.* 1973). Elevation could enhance any form of convective cooling and result in more depressed temperatures. Ambient temperature, too, may decrease with increasing elevation, particularly if the sand is hot (Porter *et al.* 1973). Elevation to a layer of air slightly cooler than that just above the sand surface can result in substantial decreases in body temperature (Figure 4.12a), especially at higher windspeeds where convective cooling is more pronounced. Convection coefficient differences (which may result from different orientations to wind) produce small but noticeable differences in temperature (Figure 4.12b). Combining convection coefficient and ambient temperature differences can result in substantial model temperature differences. For example, a horizontally elevated cylinder in ambient air of 30 °C and having an hc of 3.14 W/m^2 °C would, at a wind speed of 5m/s, be 3.6 °C warmer than an angled cylinder having an hc of 3.84 W /m^2. °C and exposed to an ambient air temperature of 27 °C.

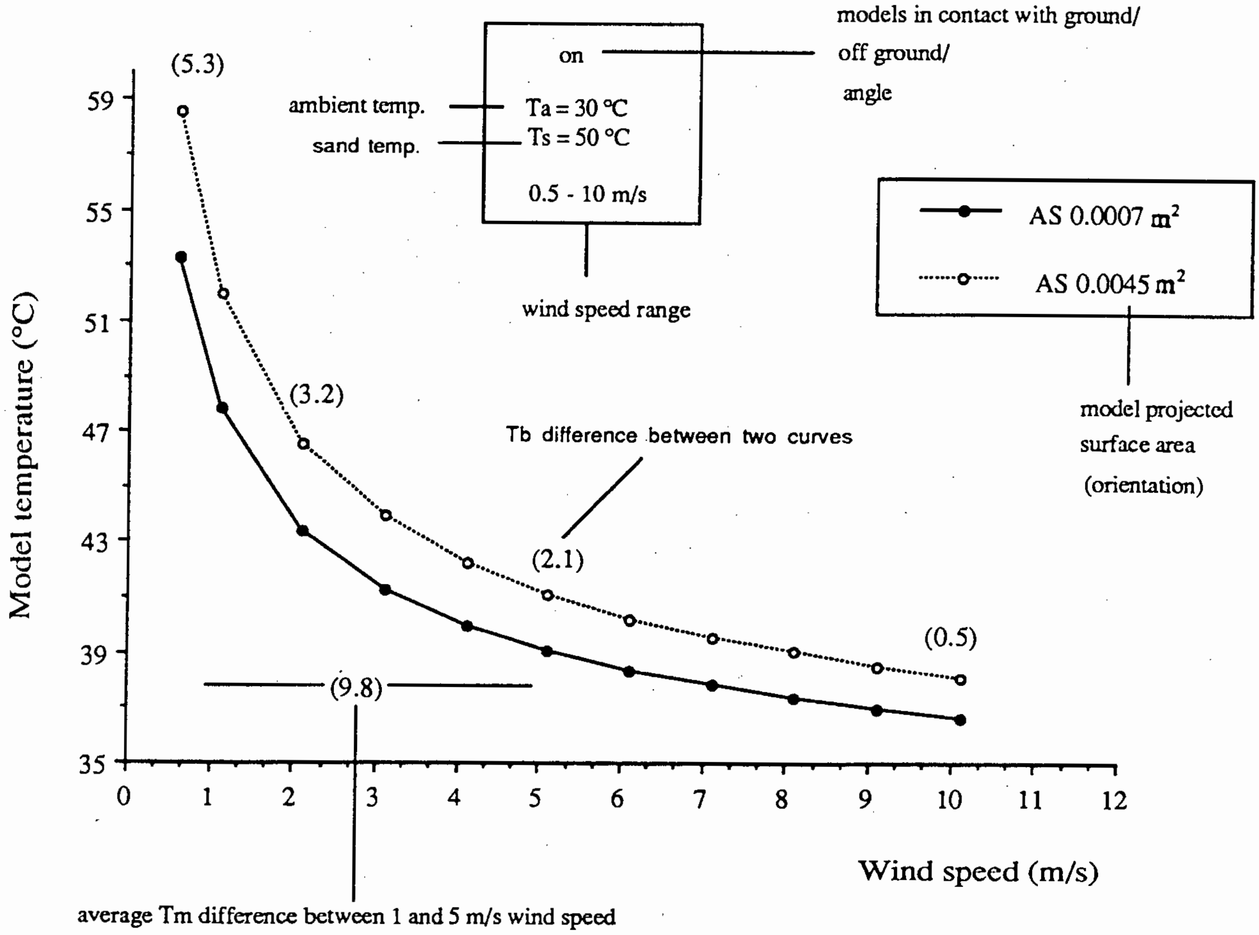


FIGURE 4.6. Explanation of the text and values appearing on Figures 4.7a - 4.12b. Model temperatures (in °C, horizontal axis) are always expressed as a function of wind speed (in m/s, vertical axis). The left hand side box indicates the parameters of each exercise (Ta - ambient temperature ; Ts - substrate temperature ; m/s - wind speed range in meters per second) of each exercise. Unless specifically stated, models are orientated horizontally, either elevated above the surface (off) or in contact with the substrate(on). Elevation distance of off models is always indicated in meters (e.g. off, 0.01 m). The right hand side box generally refers to the orientation of models relative to the position of the sun. This is expressed in terms of the surface area exposed to direct sunlight. Values in parentheses above the upper curve indicate the temperature difference between the two curves at selected wind speeds. The vertical bar below the lower curve indicates the average difference between model temperatures at 1 and 5 m/s wind speed.

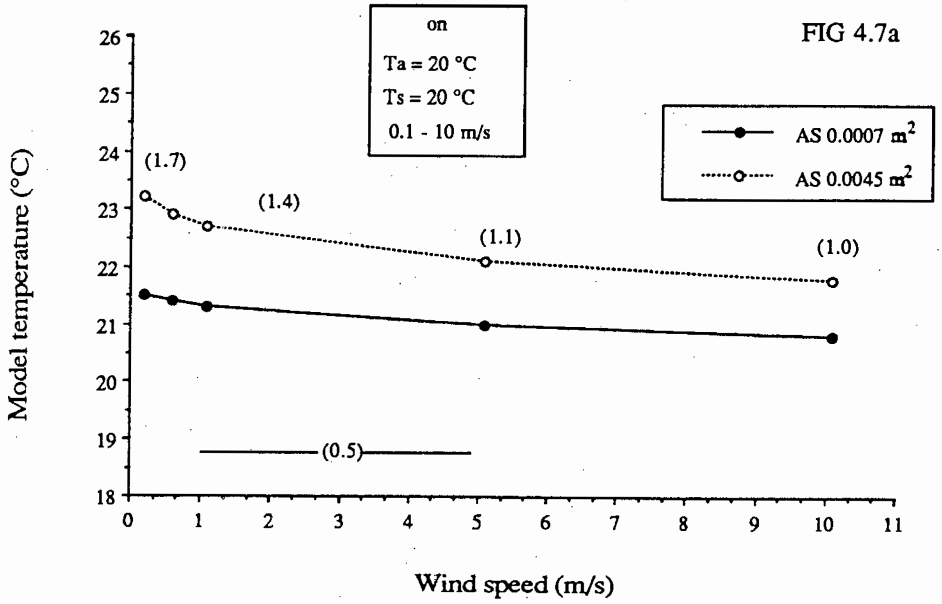


FIG 4.7a

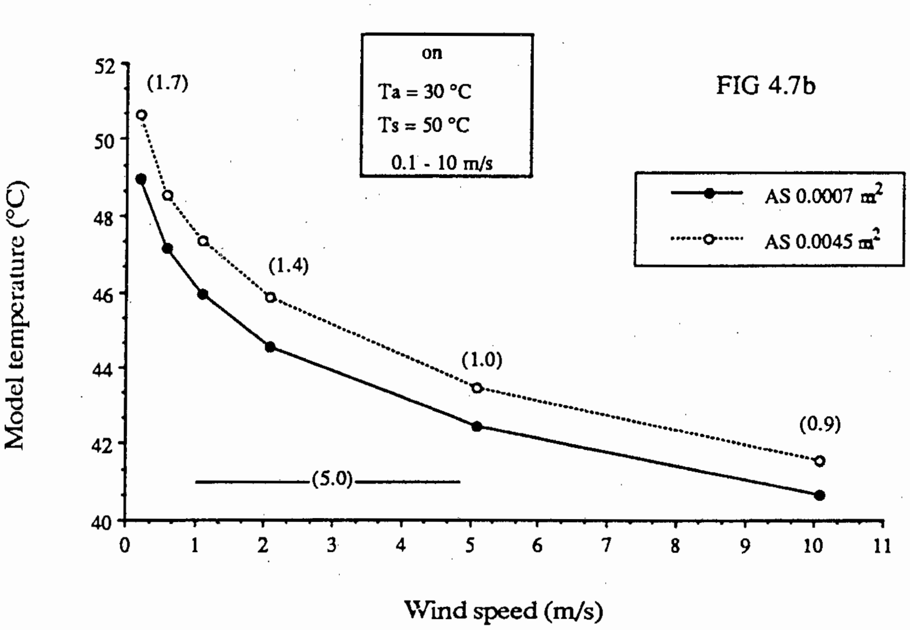
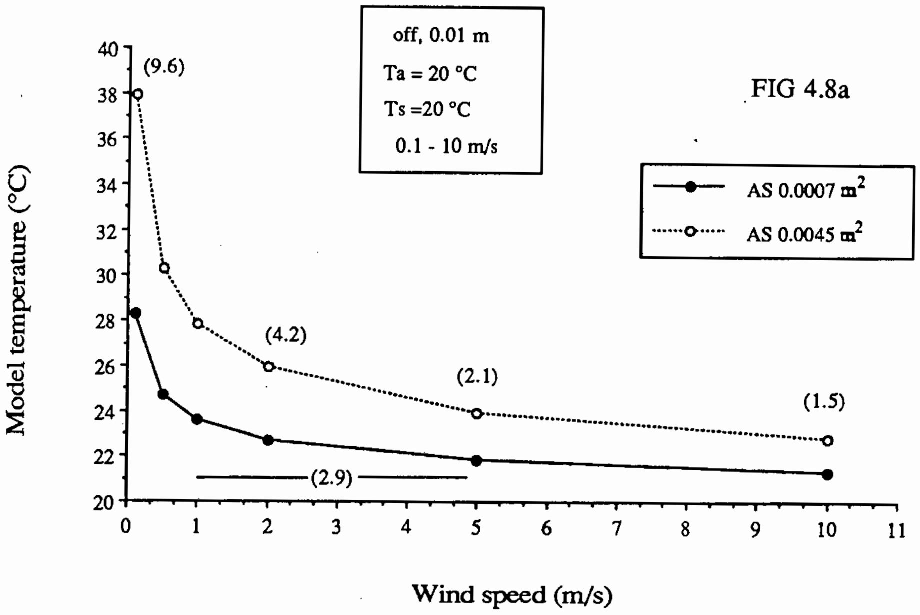


FIG 4.7b

FIGURE 4.7. The effect of wind speed (m/s) and orientation [surface area exposed to direct sunlight (AS in m^2)] on the temperature of horizontally orientated copper models in contact with the substate at (a) low and (b) high ambient and substrate temperatures. Maximum AS is presented by the the upper curve model (i.e. the model axis is orientated perpendicularly to the sun's rays). Minimum AS is presented by the lower curve model (i.e. the model axis is orientated parallel to the sun's rays).



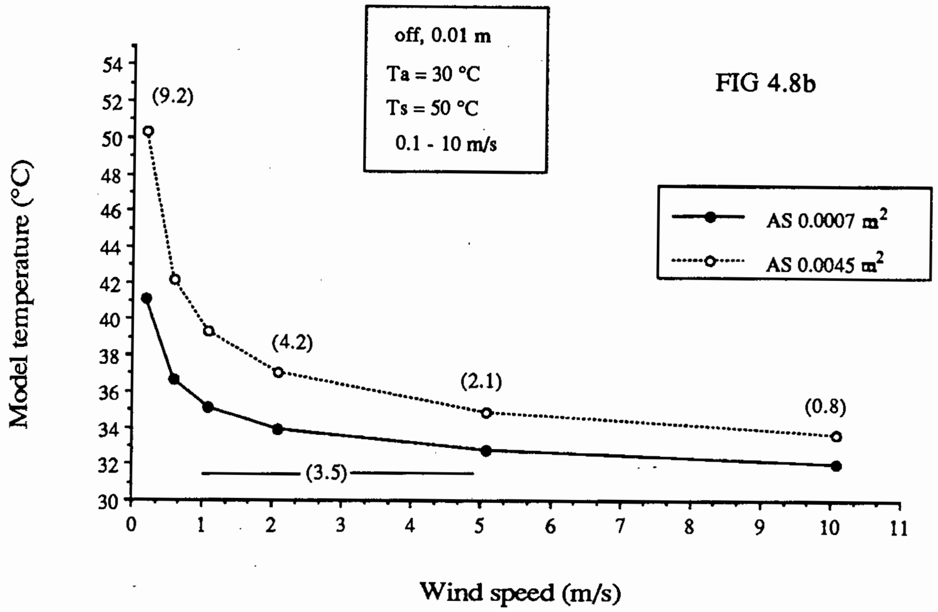


FIGURE 4.8. The effect of wind speed (m/s) and orientation [surface area exposed to direct sunlight (AS in m^2)] on the temperature of horizontally orientated copper models elevated 0.01 m above the substate at (a) low and (b) high ambient and substrate temperatures. Maximum AS is presented by the the upper curve model (i.e. the model axis is orientated perpendicularly to the sun's rays). Minimum AS is presented by the lower curve model (i.e. the model axis is orientated parallel to the sun's rays).

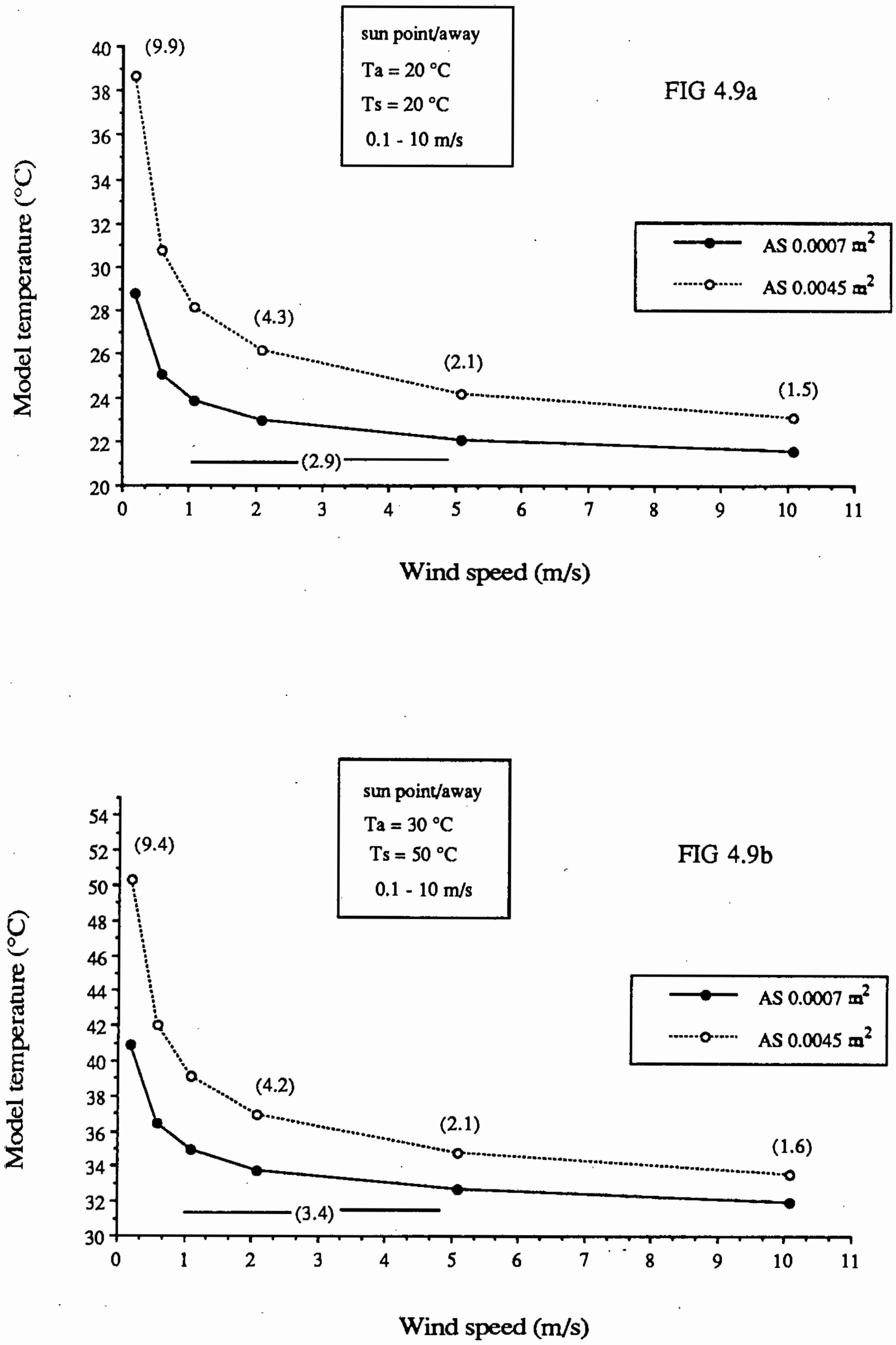


FIGURE 4.9. The effect of wind speed (m/s) and orientation [surface area exposed to direct sunlight (AS in m^2)] on the temperature of copper models resting on the substrate and angled towards or away from the sun at (a) low and (b) high ambient and substrate temperatures. The axis of the upper curve model is orientated perpendicularly to the sun's rays (sun away). The axis of the lower curve model is orientated parallel to the sun's rays (sun point). The parameters in this excercise are identical to those in Figure 4.8 except that only a small area of the model's surface is in contact with the substrate here.

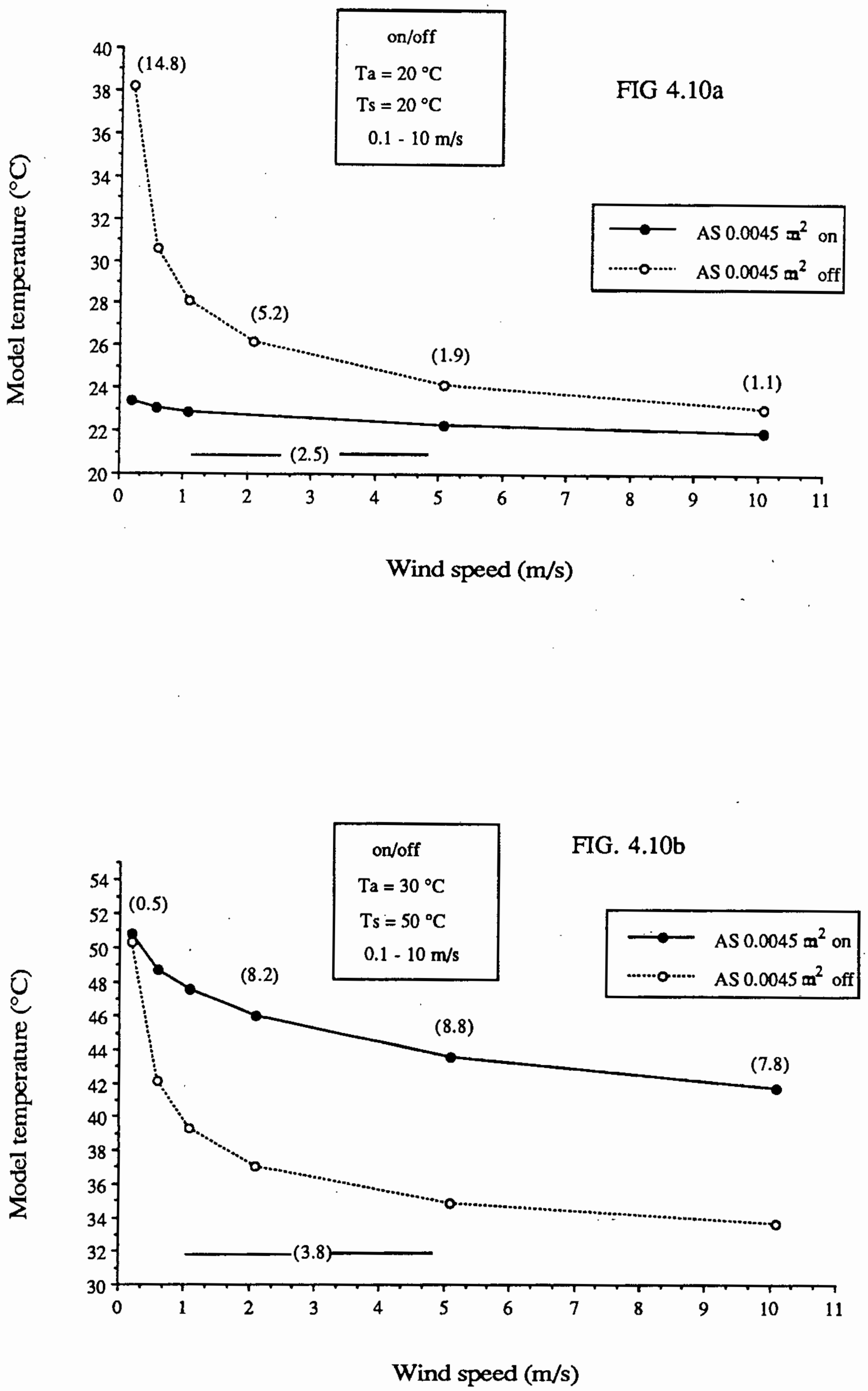


FIGURE 4.10. The effect of wind speed (m/s) and the degree of contact with the substrate on the temperature of horizontally orientated copper models at (a) low and (b) high ambient and substrate temperatures. The upper curve model is elevated 0.01 m above the substate. The lower curve model is in contact with the substrate. Both models are orientated so that their maximum surface areas (AS) are presented to the sun.

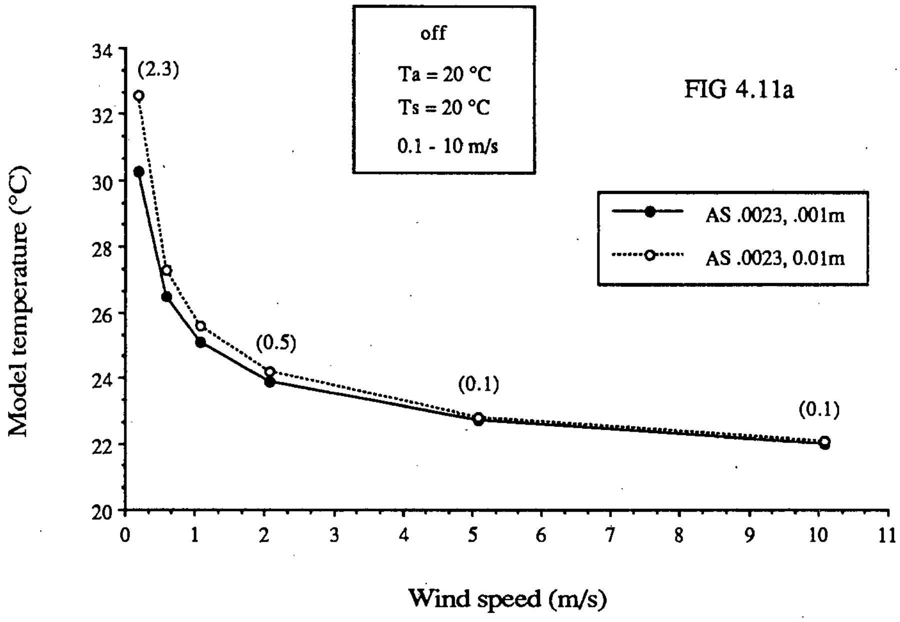


FIG 4.11a

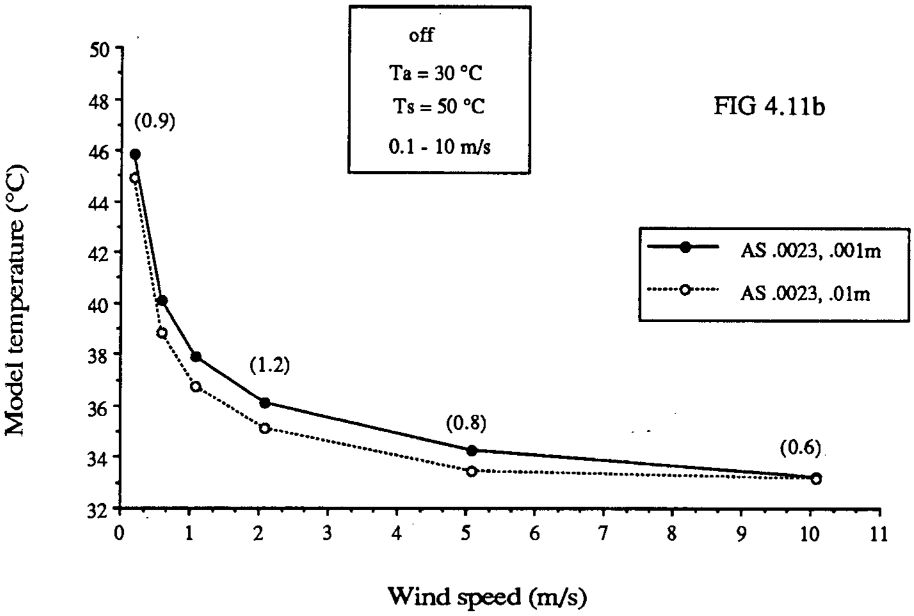


FIG 4.11b

FIGURE 4.11. The effect of wind speed (m/s) and degree of elevation above the substrate on the temperature of horizontally orientated copper models at (a) low and (b) high ambient and substrate temperatures. The upper curve model is elevated 0.01 m above the substrate. The lower curve model is elevated 0.001 m above the substrate. Both models are orientated so that half their maximum surface area (AS) are presented to the sun.

FIG 4.12a

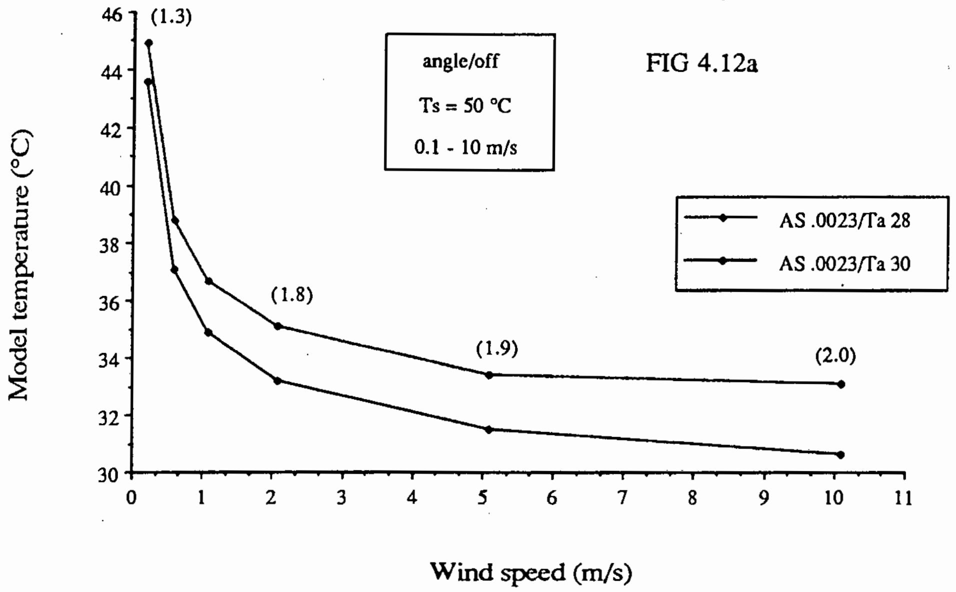


FIGURE 4.12a. The effect of wind speed (m/s) and a small difference in ambient temperature (Ta) on the temperatures of vertically angled copper models at high ambient and substrate temperatures. The upper curve model is exposed to an ambient temperature of 30 °C and the lower curve model to an ambient temperature of 28 °C. These differences in ambient temperature represent a decrease in values which may occur with increasing elevation above the substrate (Porter *et al.* 1973). Both models are elevated above the substrate and conduction of heat from the substrate to models is assumed to be negligible. Both models are elevated above the substrate and are orientated so that their maximum surface areas (AS) are presented to the sun.

FIG 4.12b

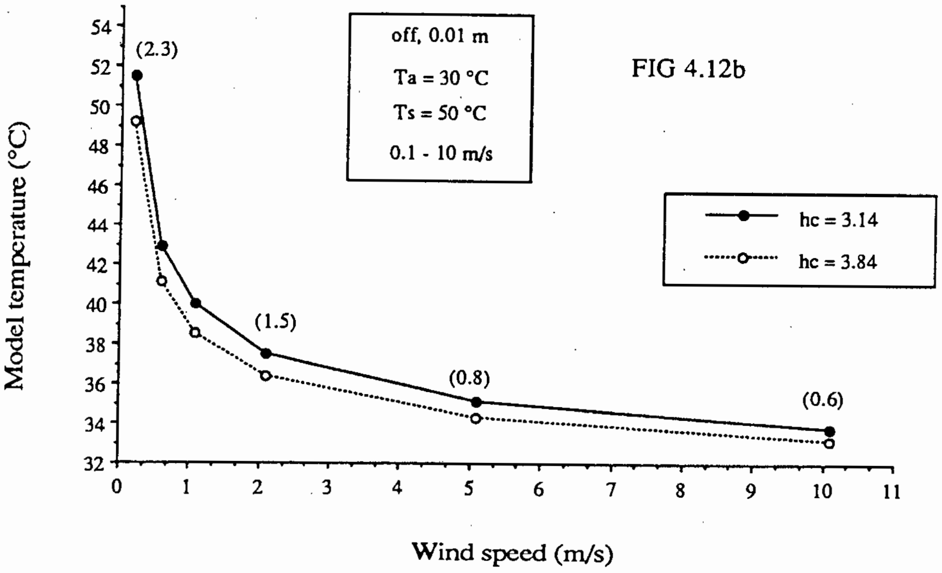


FIGURE 4.12b. The effect of wind speed (m/s) and orientation to wind (expressed in terms of the convection coefficient, hc) on the temperatures of vertically angled copper models at high ambient and substrate temperatures. The difference in hc values corresponds to the range measured by Wathen et al (1971) for copper cylinders where the angle of pitch between the cylinder axis and wind direction was varied. Both models are elevated above the substrate and are orientated so that their maximum surface areas (AS) are presented to the sun.

4.2.2 Copper Models

General weather conditions

Weather conditions in October (spring) were characterized by cold nights, cool overcast mornings and warm clear days. Fresh south-westerly winds prevailed. Ambient temperatures were moderate, ranging from about 8 - 27 °C. No rain fell during the course of the study.

Weather conditions in February (late summer) were characterized by much warmer nights and hot days. Ambient temperatures ranged from about 18 - 35 °C. Wind direction was once again predominantly south-westerly. Rain fell on average every third day.

In July (winter), conditions depended on wind direction. During the moderate south- westerly winds, cool conditions prevailed with ambient temperatures ranging from about 8 - 18 °C. During the strong easterly winds, hot temperatures prevailed with ambient temperatures ranging from about 20 - 35 °C. No rain fell during the course of the study.

February - one day model thermoregulation experiment

Temperatures of models used in the one day (5/3/90) February model thermoregulation experiment (Figure 4.5) are shown in Figure 4.13. The variation in model temperture was striking with a maximum difference of 12.4 °C between the BUSH SE and site 3 ON models at 14h00. The model temperatures have been divided into four categories. The lowest temperature category comprises the ANGLED (sun point and away) and BUSH models on the gravel plain. These are followed by all of the OFF models with the exception of the OFF model at site 3. The next category comprises the GP, 2 and 4 ON models and the 3 OFF model. Finally, in a class of its own, is the 3 ON model which is consistently about 3 - 4 °C warmer than any other model.

Figures 4.14a - 4.14c show some of the microclimate conditions experienced by the models at each site. Air temperatures (Figure 4.14a) were highest at sites 3 and 4 and noticably lower at sites 1 and 2. Ambient temperature 2m above the ground surface was notably lower than ambient temperatures measured just above the ground at the four sites. Sand temperatures (Figure 4.14b) were similar at sites 2,3 and 4. The lower temperatures observed at site 1 (gravel plain) can possibly be attributed to different sand composition (and subsequently different absorptive properties) at this site. The prevailing wind direction during February was S - SW. The effect this had on wind speeds at the four sites is shown in Figure 4.14c. Wind speed was consistently higher at the dune top (site 4). The wind appeared to overshoot the dune crest and then curl down towards the dune base. This resulted in a lee just below the crest making wind speeds at site 3 consistently lower than those at site 2. The reason for the lowest wind speeds on the gravel plain (site 1) is unapparent.

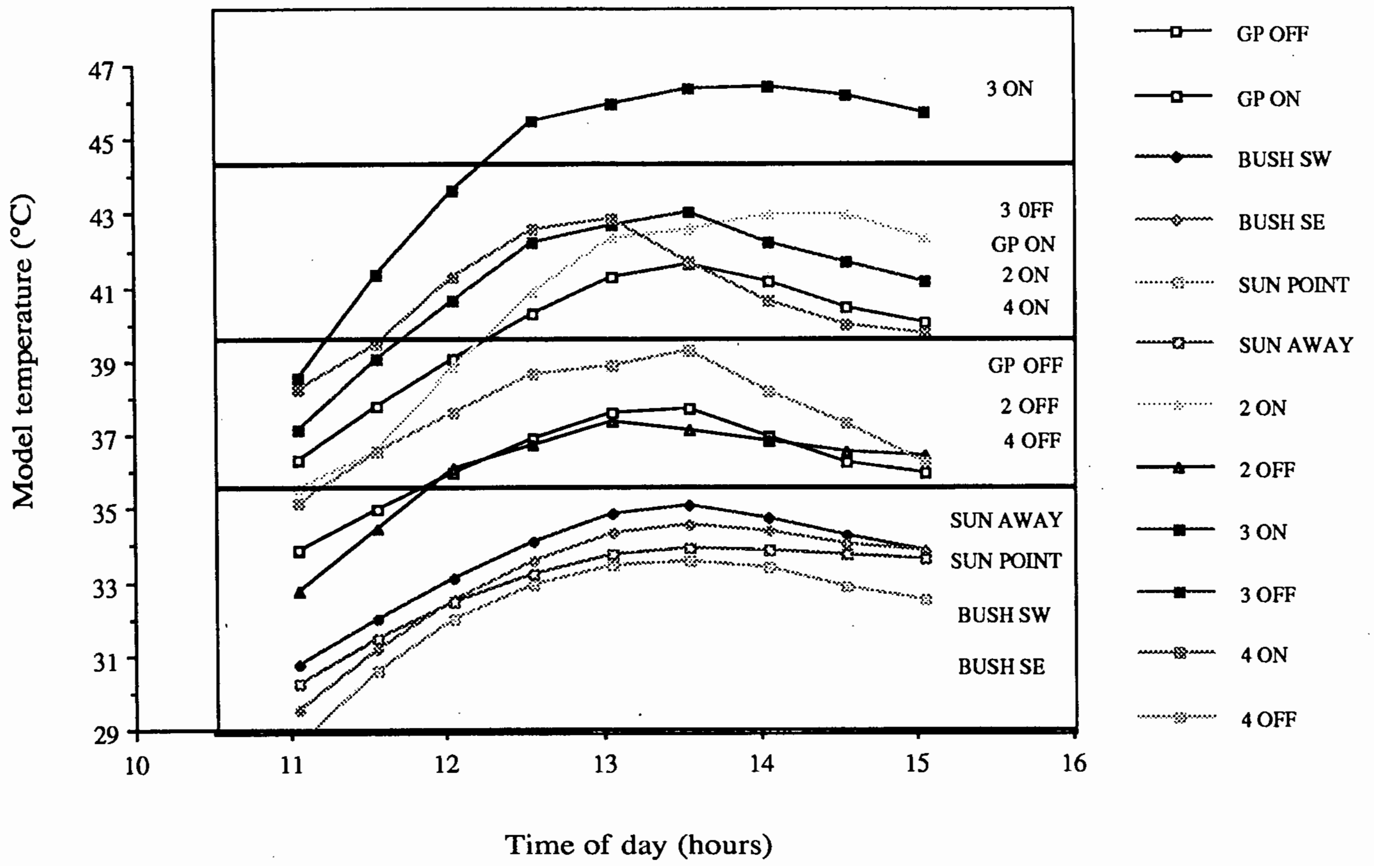


FIGURE 4.13. Temperatures of copper models placed at various locations in *Angolosaurus skoogi's* natural habitat on a typical February day (one day model thermoregulation study, 5/3/90). Model orientations and locations are shown in detail in Figure 4.5. The horizontal lines divide the temperature profiles into the four categories referred to in the text. GP = gravel plain.

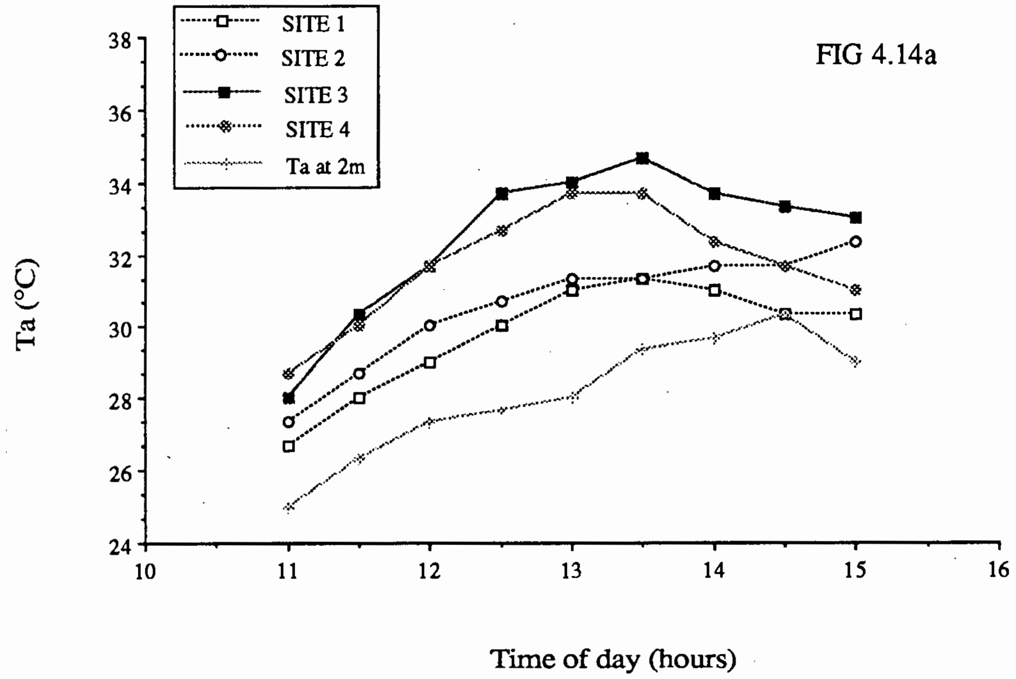


FIGURE 4.14a. Ambient temperatures (Ta) measured 1 cm above the substrate surface during the one day model thermoregulation study in February (5/3/90). The four sites are shown in Figure 4.5. The lowest curve shows ambient temperature (Ta) 2m above the gravel plain.

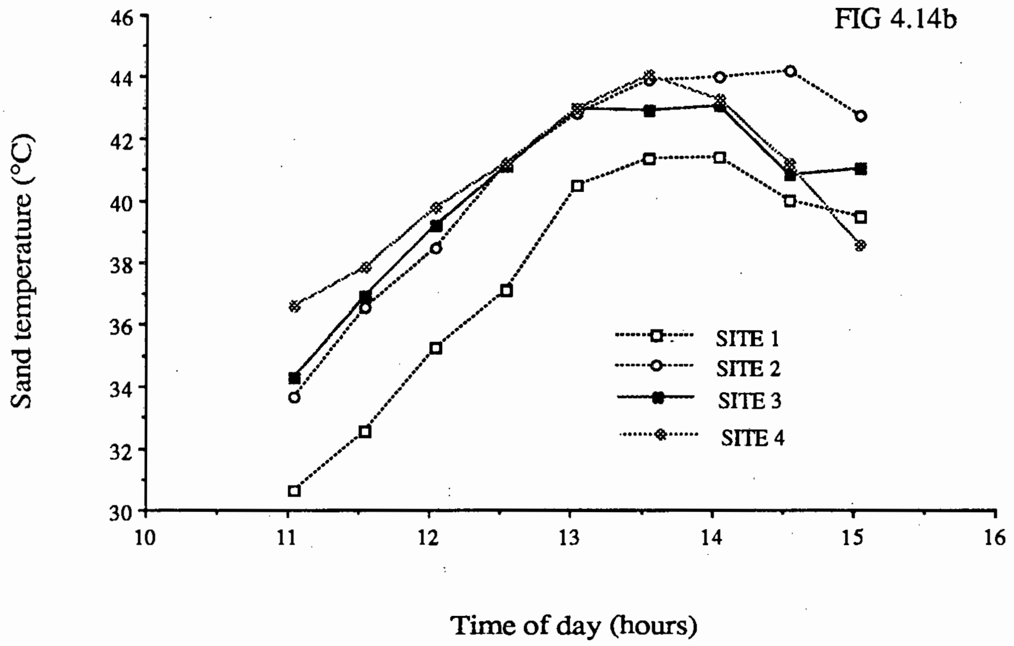


FIGURE 4.14b. Sand temperatures measured during the one day model thermoregulation study in February (5/3/90). The four sites are shown in Figure 4.5.

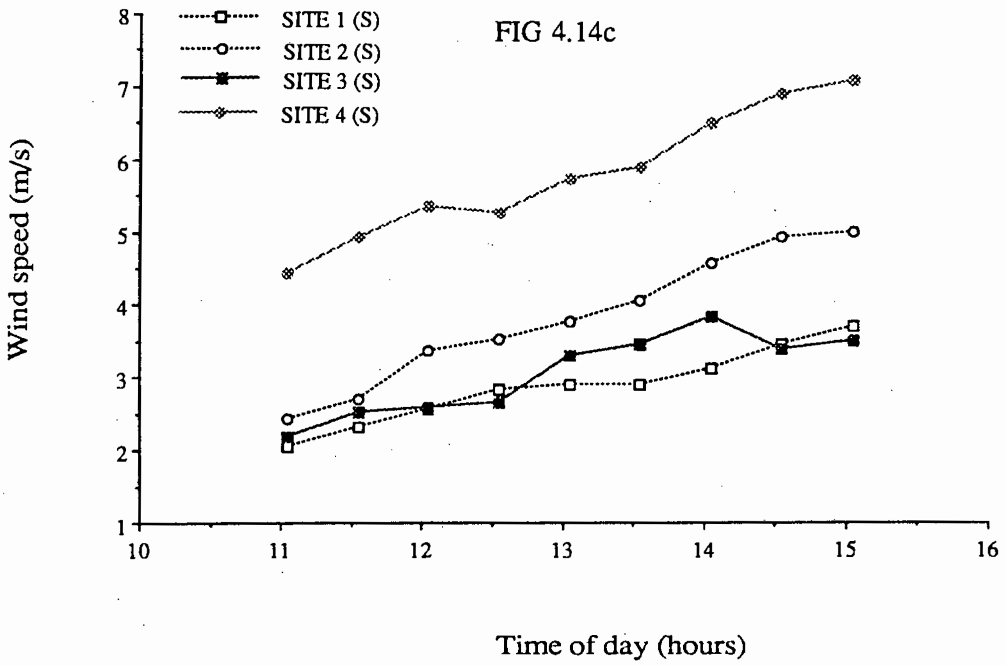


FIGURE 4.14c. Wind speeds measured 5 cm above the substrate surface during the one day model thermoregulation study in February (5/3/90). The four sites are shown in Figure 4.5.

Using the knowledge obtained from the modelling exercise, it is possible to explain some of the widely varying model temperatures observed in Figure 4.13 : The small and often negligible difference in the sun point and sun away models (0.5 - 1.5 °C) is at first surprising when one considers that the former model always had its minimum surface area exposed to the sun whereas the latter model consistently had its maximum surface area exposed. Figures 4.9a and 4.9b, however, show that under both cool and warm conditions and at wind speeds of about 3 m/s, temperature differences of no more than about 2.5 °C can be expected.

Sun point and away models were consistently about 4 °C cooler than the other OFF models. When one considers that the distance elevated above the ground makes a negligible difference to body temperature (Figures 4.11a and 4.11b), and that the angled models have a small conduction factor, this observation is surprising. Lower sand temperature and subsequently lower ground thermal radiation gain on the gravel plain could account for the difference between angled and slipface models. Differences in convection coefficients and ambient temperatures (Figures 4.12a and 4.12b) could account for differences observed in the GP OFF and the angled models.

Resting a model on foliage (BUSH models) resulted in considerably lower temperatures than elevating the model above the naked gravel plain surface (GP OFF model). This could be attributed to several factors. Firstly, foliage provides shade which will result in cooler sand temperatures below foliage than on the exposed gravel plain. Heat gain by thermal radiation from the ground would thus be reduced when resting on foliage. Provided that the leave's surface temperatures are lower than the gravel plain's surface temperature, heat gain from conduction will also be less from the foliage. Additionally, *Merremia* bushes are not particularly dense and the surface area in contact with leaves would probably be substantially less than for a model resting on a flat surface. Secondly, there is the possibility that foliage models, because of their slightly better elevation above the gravel plain surface (*Merremia* mounds are about 30 cm high), may experience slightly lower ambient temperatures and higher wind speeds. The effect of this on reducing model temperature is illustrated in Figure 4.12a.

Figure 4.15 is a more detailed look at the ON and OFF models at sites 2 and 3 only. The difference between ON and OFF models was striking, with a maximum difference of 8 °C. This is consistent with predictions made in Figs 4.10a and 4.10b. Just as striking were the differences in model temperatures between the two sites. Orientation of models to the sun's rays were identical (Figure 4.5) and sand temperatures very similar (Figure 4.14b) at the two sites. The difference can be attributed to two factors. Firstly wind speed was consistently higher at site 2 (Figure 4.14c), resulting in greater convective cooling of models at this site. Secondly, ambient temperatures were up to 3 °C cooler at site 2 (Figure 4.14a). The combination of the two factors (Figure 4.12b) could account for the observed differences.

Copper models - October and February microclimate dunes

The simplest and clearest way to project the microclimate senario that the models on the microclimate dune were exposed to in October and February is to isolate the hottest and coldest models at any particular time and analyse the reasons for the temperature extremes. Figure 4.16 shows the range of temperatures obtained by models during a typical October/November day (3/11/89). Table 4.1 isolates the models responsible for these extreme temperatures. OFF models were only situated at the A BOTTOM site and, based on our knowledge of the effect of conduction on ON models, were understandably the coldest during the major part of the day. (A better analysis of coldest models is provided in the February analysis where OFF models were placed at all sites - see below).

From 07h00 to 09h00, the B BOTTOM ON STRIKE model was the coldest. This can be attributed to several factors. Firstly, this is the time of the day when the sand is still cool and conduction of heat out of the model would help to keep an ON model cooler than any OFF model. Secondly, the intensity of sunlight on a surface is dependent on the angle between the sun's rays and the surface (Gates 1980). The larger the angle, the more thermal energy transferred to the surface.

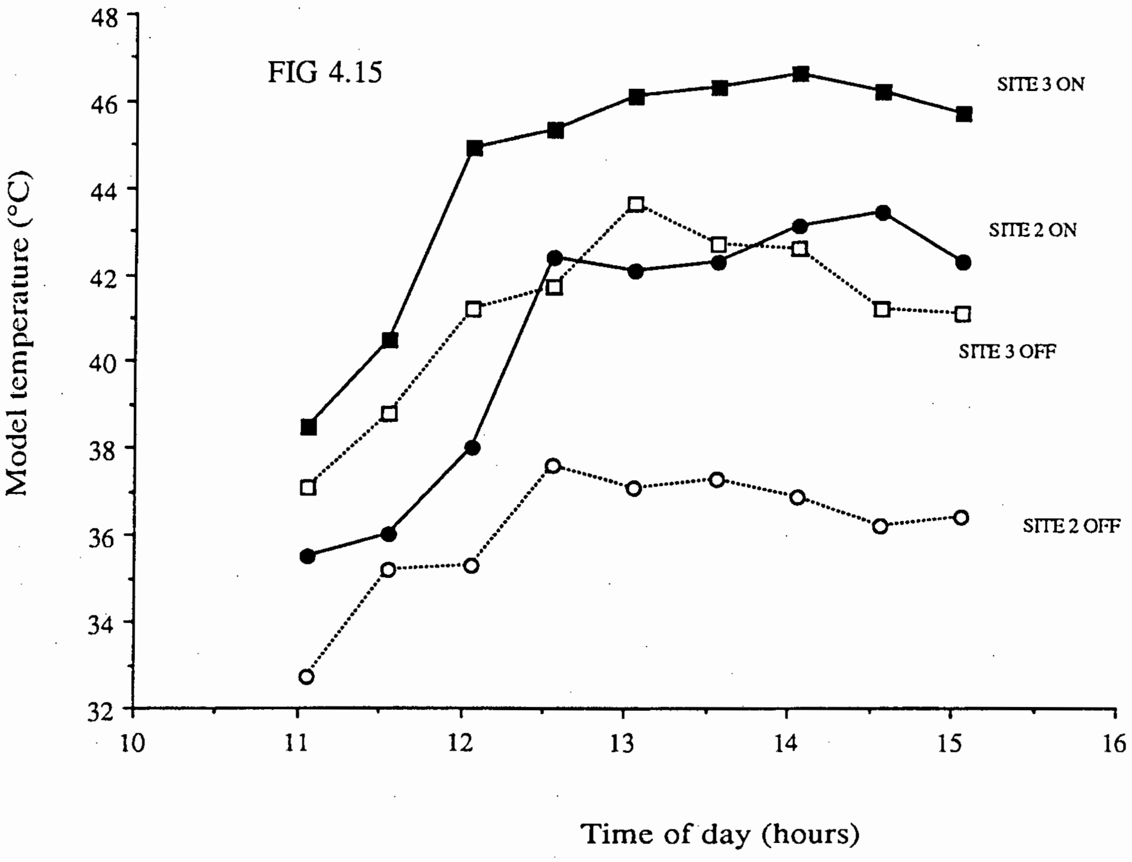


FIGURE 4.15. Temperatures of copper models in contact with (on) and elevated above (off) the slipface surface during the one day model thermoregulation study in February (5/3/90). The two site locations are shown in Figure 4.5.

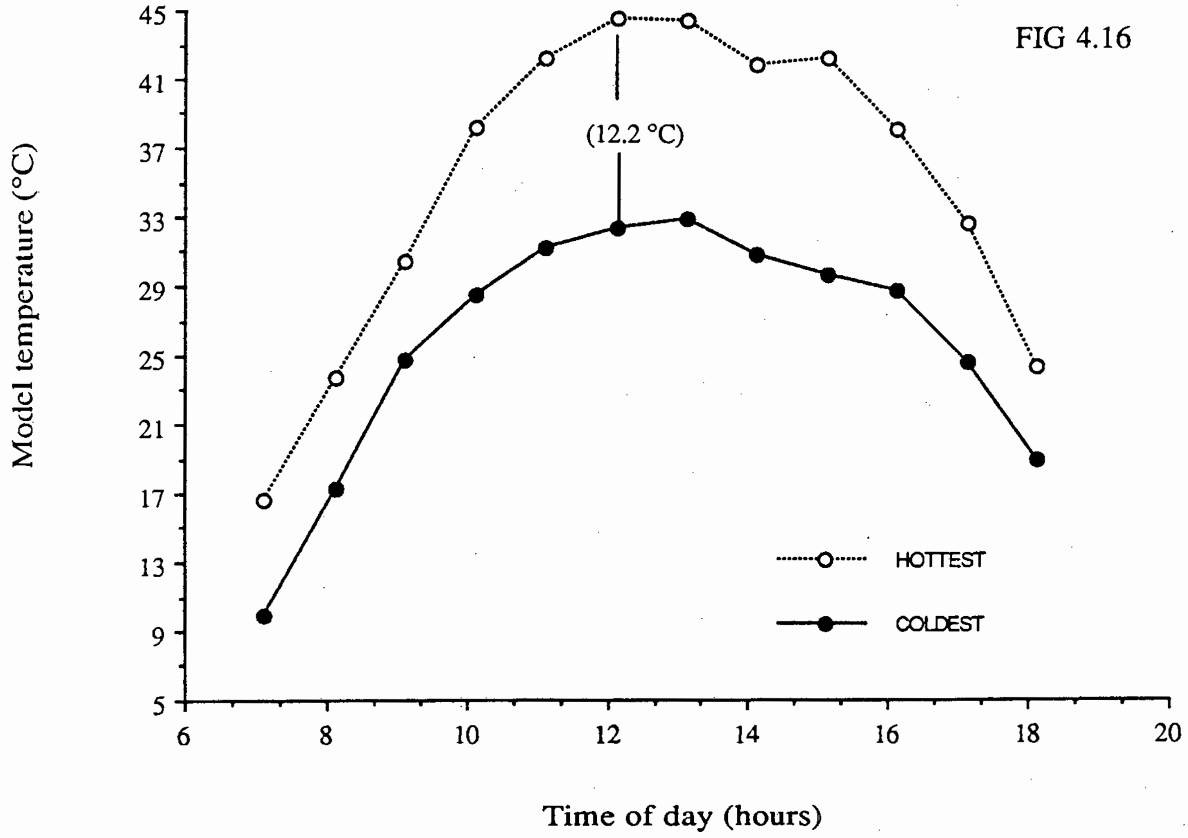


FIGURE 4.16. Temperatures of the hottest and coldest copper models placed in various locations on the microclimate dune during a typical October/November day (3/11/89). The specific locations of all models are shown in Figure 4.2. The particular models responsible for the curves are identified in Table 4.1. The time at which the maximum temperature difference (12.2 °C) occurred is indicated by the horizontal bar.

TABLE 4.1. Temperatures of the hottest and coldest copper models placed in various locations on the microclimate dune during a typical October/ November day (3/11/89). The specific localities of all models are shown in Figure 4.2. The first two letters in columns 2 and 4 refer to model location : A = slipface A, B = slipface B, TOP = dune top, t = top (slipface), b = bottom (slipface). Models in contact with the sand are referred to as **on** ; those elevated above the sand referred to as **off**. The last letter in columns 2 and 4 refers to model orientation : D = dip, S = strike, N/S = north/south orientation.

Time	Hottest model (°C)	Temperature (°C)	Coldest model	Temperature
07h00	Ab on D	16.1	Bb on S	9.4
08h00	Ab on D	23.2	Bb on S	16.7
09h00	At on D	29.9	Bb on S	24.2
10h00	At on S	37.7	Ab off S	28.0
11h00	At on D	41.6	Ab off D	30.7
12h00	At on S/Bt on D	44.0	Ab off D	31.8
13h00	Bt on D	43.9	Ab off D	32.4
14h00	TOP on N/S	41.3	Ab off D	30.3
15h00	Bt on S	41.6	Ab off D	29.1
16h00	Bt on D	37.5	Ab off D	28.2
17h00	Bt on D	32.1	Ab off D	24.1
18h00	Bt on S	23.8	Ab off S	18.4

In the morning, the sun angle was substantially better on slope A than slope B. At about 13h00, the situation reversed (Figure 4.17a). The effect on sand temperature was as predicted with sand on slope B being cooler than sand on slope A in the morning and vice versa in the afternoon (Figure 4.17b). Thirdly, that the B ON BOTTOM STRIKE model was cooler than its 90° counterpart can possibly be attributed to AS (surface area exposed to direct sunlight) differences. Figure 4.18a shows the differences between AS for DIP and STRIKE models on the B slipface. The DIP model projected a maximum AS to the sun's rays throughout the day. The STRIKE model, on the other hand, presented a poor AS for the first three hours of the day.

Once sand temperatures reach about 30 °C (10h00), the A BOTTOM OFF DIP model took

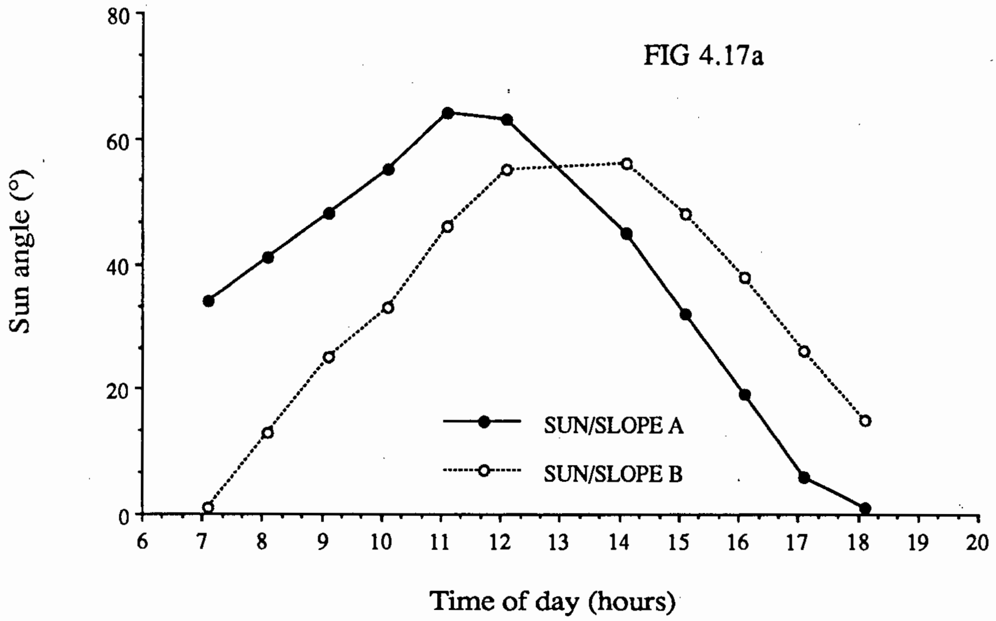


FIGURE 4.17a. Angle between the sun's rays and the two slipfaces (SLOPE A and B) of the October/November microclimate dune as a function of time (3/11/89). A schematic aerial view of the dune is shown in Figure 4.2.

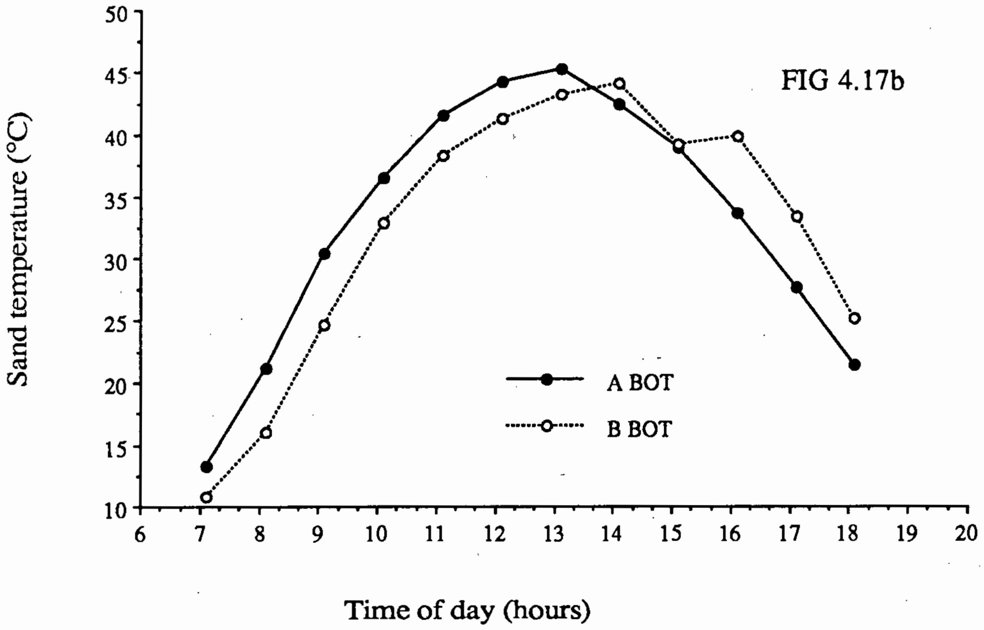


FIGURE 4.17b. Sand surface temperature (Ts) of the two lower (BOT) slipfaces of the October microclimate dune as a function of time (3/11/89). A schematic aerial view of the dune is shown in Figure 4.2.

FIG 4.18a

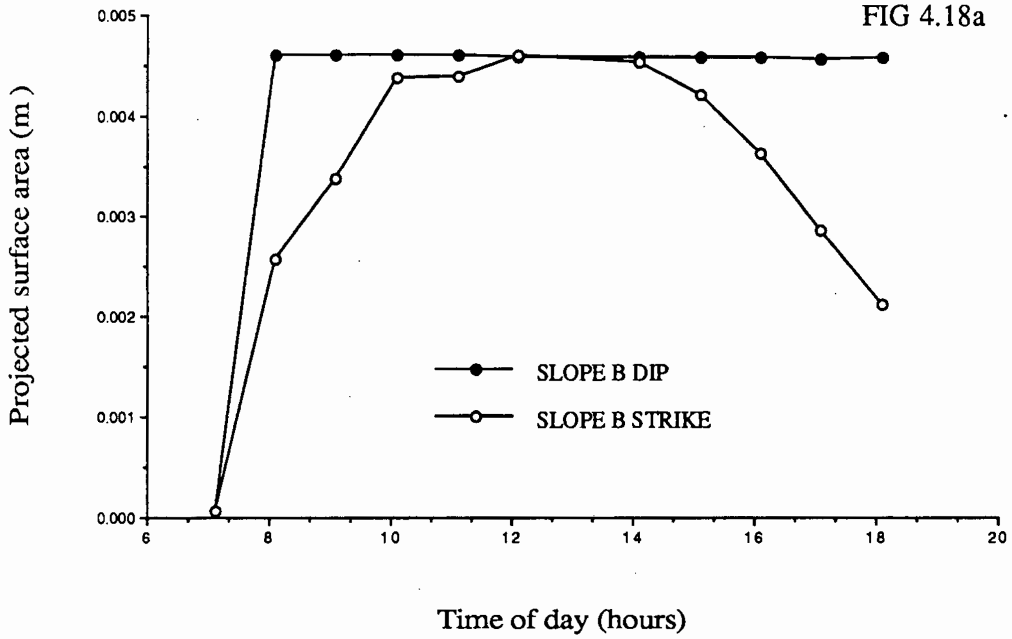


FIG 4.18b

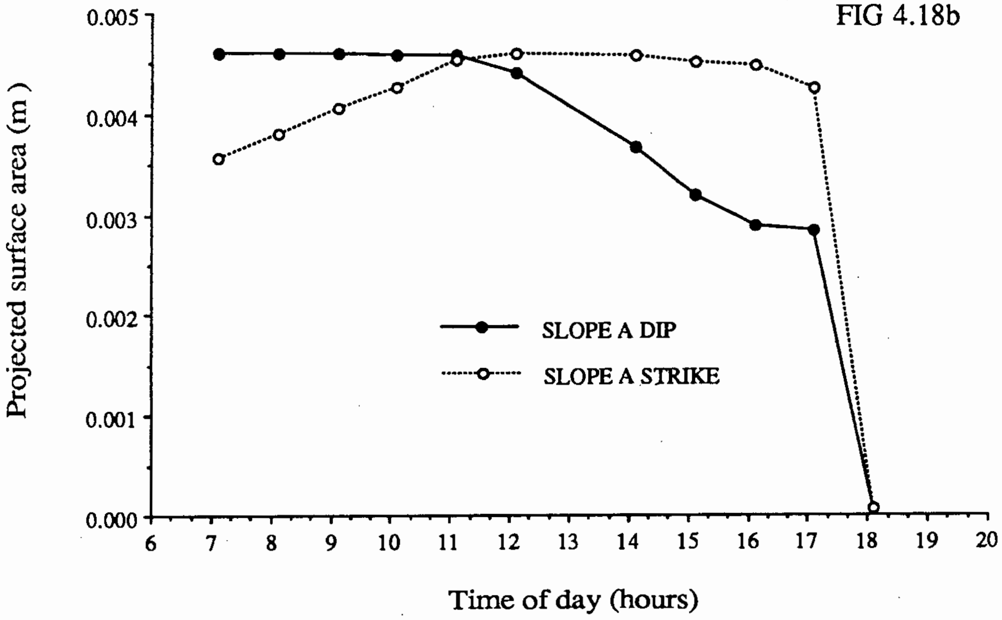


FIGURE 4.18. The projected surface area exposed to the sun's rays (AS) of DIP and STRIKE copper models on (a) slipface B and (b) slipface A of the October microclimate dune (3/11/89). A schematic aerial view of the dune is shown in Figure 4.2.

over as the coolest for the rest of the day. The low conduction factor of OFF models makes them the most appropriate candidates for the coolest category under these hotter conditions That the OFF DIP model remained cooler than the OFF STRIKE model is once again attributable to a poorer AS for the DIP model from about 11h00 onwards. This is shown in Figure 4.18b.

Temperatures obtained by A BOTTOM OFF STRIKE and DIP models, and A BOTTOM ON STRIKE and DIP models are shown in Figs 4.19a and 4.19b. The STRIKE OFF model was 1 - 5 °C hotter than the DIP OFF model after 11h00. During the same period, the STRIKE ON models were only about 1° C hotter than the DIP ON models. The reason for STRIKE models being hotter is apparent when one considers the conclusions drawn from the AS modelling analysis in Figures 4.7b and 4.8b and the AS of STRIKE and DIP models (Figure 4.18b). Up to about 11h00, the AS's of DIP models were better than that of STRIKE models. After 11h00, however, the AS's of DIP models declined rapidly whereas that of STRIKE models remained at maximum. According to Figure 4.7b, differently orientated ON models should, as observed, show at the most a 1 °C difference in temperature at wind speeds experienced by A BOTTOM models (2 - 3 m/s, Figure 4.20a). According to Figure 4.8b, the STRIKE OFF model should, as observed, be about 3 °C hotter than its 90° counterpart after 11h00.

Except for early in the morning, TOP ON models are predominantly the hottest throughout the day. The sun elevation angle on the slipfaces and its influence on sand temperature (Figures 4.17a and 4.17b) once again play an important role in determining which slipface holds the hottest models. In the morning, slipface A has hotter sand and consequently hotter models. The situation is reversed in the afternoon. Note that, unlike with the OFF models, DIP and STRIKE models feature equally well.

The influence of AS on model temperature was more important in OFF models where conduction was relatively unimportant (see Figures 4.8a and 4.8b) and almost negligable in ON models (see Figures 4.7a and 4.7b). That TOP models were consistently hotter than BOTTOM models can, as in the February one day exercise, be attributed to higher wind speeds and more convective cooling at bottom sites. Wind speeds were consistently higher at both A and B BOTTOM sites (Figures 4.20a and 4.20b). The influence this has on the temperatures of models under these conditions has already been discussed.

Figure 4.21 shows the range of temperatures obtained by models during a typical February/March day (1/3/90). Table 4.2 isolates the models responsible for these extreme temperatures. Note that the range of temperatures is substantially higher than during the October study (9 - 45 °C, October, versus 19 - 55 °C, February). Unlike October, OFF models were placed at every site. The overall coldest model category (gravel plain and dune slipface) was dominated by the GP OFF model. The AS of the GP OFF model can not account for this observation as it was equal to or higher than the AS's of the slipface models (Figure 4.22). Similarly, enhanced convective cooling was probably

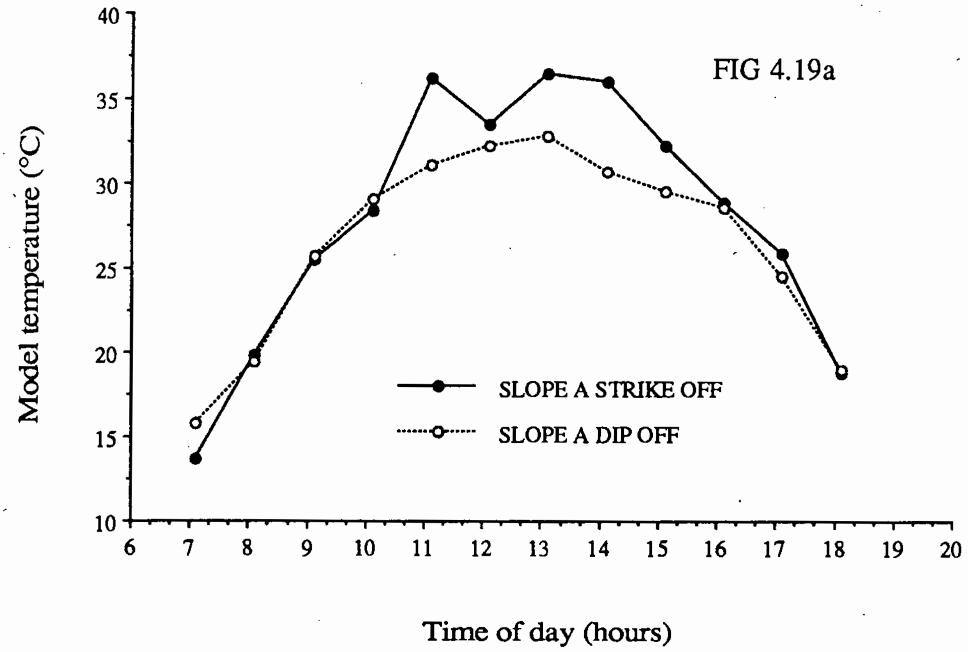


FIGURE 4.19a. Temperatures of STRIKE and DIP models on the lower slipface A of the October microclimate dune (3/11/89). Both models are elevated 1 cm above the substrate. A schematic aerial view of the dune is shown in Figure 4.2.

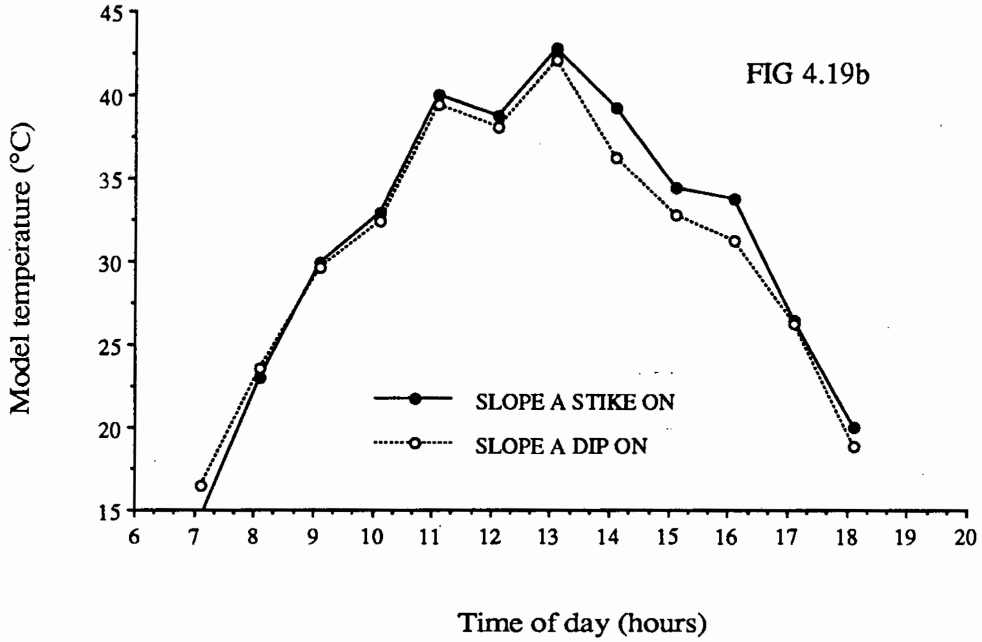
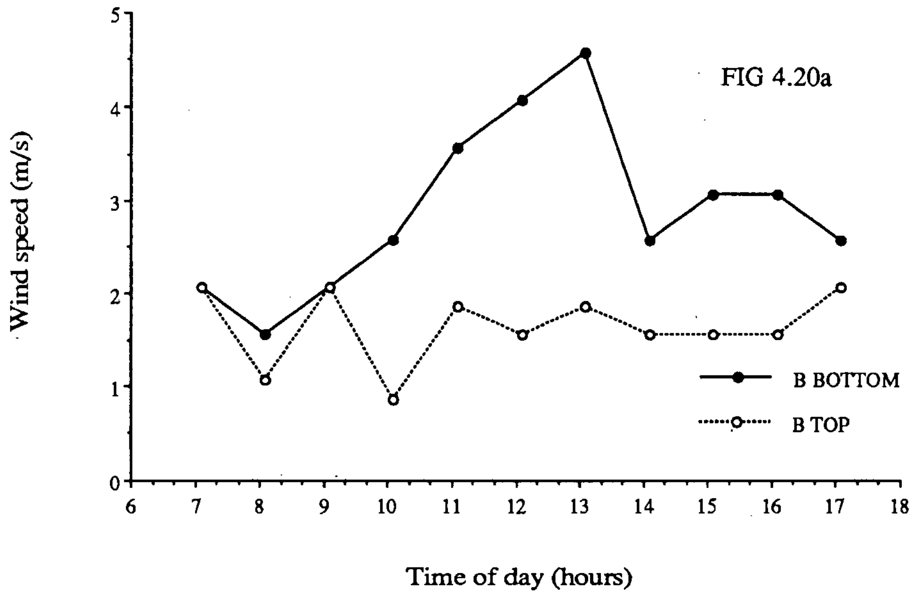


FIGURE 4.19b. Temperatures of STRIKE and DIP models on lower slipface A of the October microclimate dune (3/11/89). Both models are in contact with the substrate. A schematic aerial view of the dune is shown in Figure 4.2.



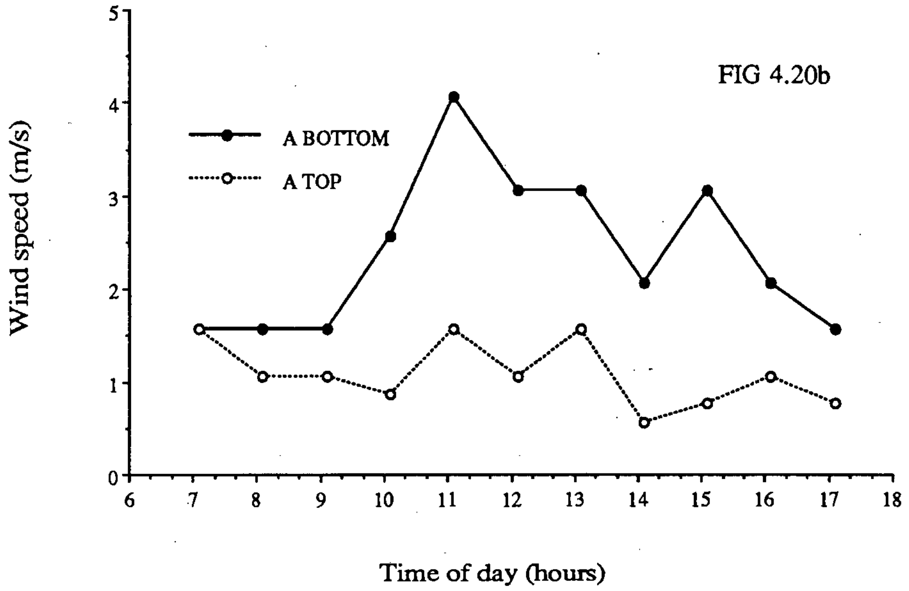


FIGURE 4.20. Wind speed measured on (a) upper (TOP) and lower (BOT) slipface A and (b) upper (TOP) and lower (BOT) slipface B of the October microclimate dune (3/11/89). A schematic aerial view of the dune is shown in Figure 4.2.

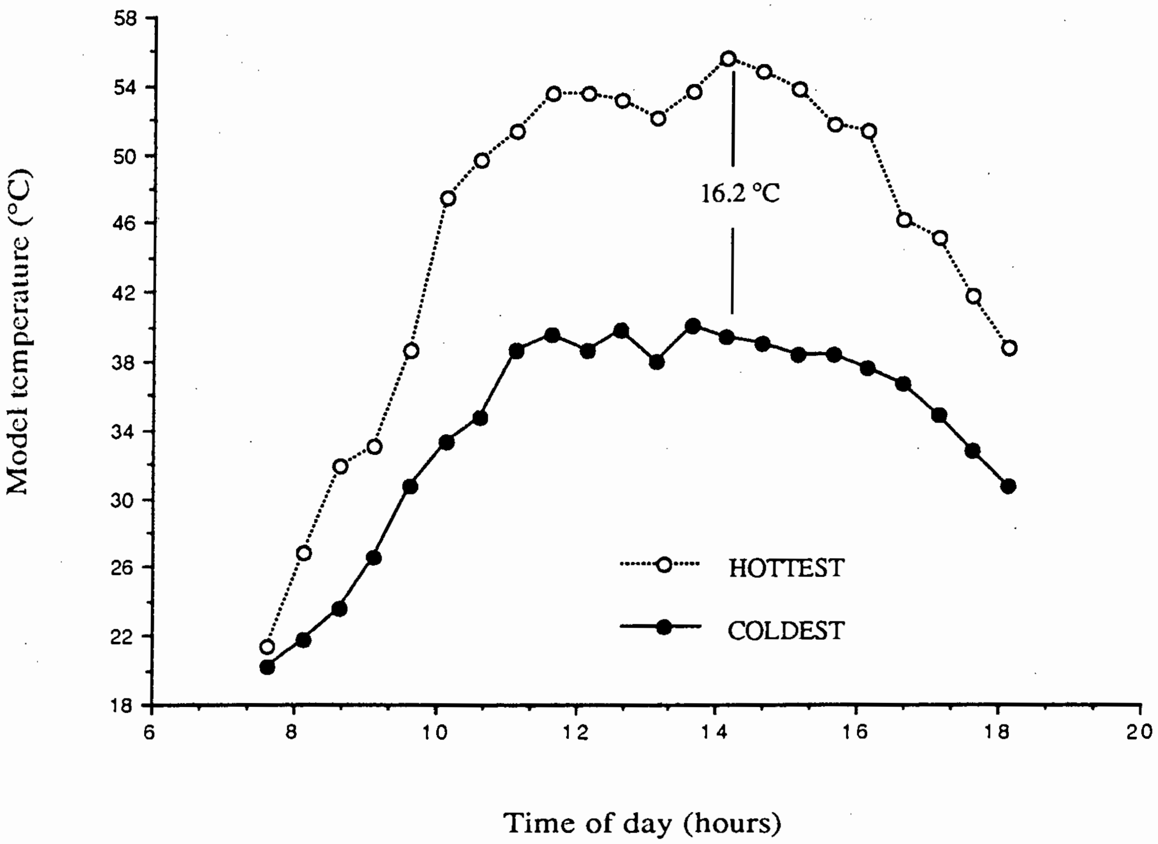


FIGURE 4.21. Temperatures of the hottest and coldest copper models placed in various locations on the microclimate dune during a typical February/March day (1/3/90). The specific locations of all models are shown in Figure 4.3. The particular models responsible for the curves are identified in Table 4.2. The time at which the maximum temperature difference (16.2 °C) occurred is indicated by the horizontal line.

TABLE 4.2. Temperatures of hottest and coldest copper models placed in various locations on the microclimate dune during a typical February/March day (1/3/90). The specific localities of all the models are shown in Figure 4.3. The first two letters in columns 2,4 and 6 refer to model location : **A** = slipface A, **B** = slipface B, **GP** = gravel plain, **t** = top (slipface), **b** = bottom (slipface). Models in contact with the sand are referred to as **on** ; those elevated above the sand referred to as **off**.

Time	Hottest model	Temperature (C)	Coldest model	Temperature (°C)	Coldest model	Temperature (°C)
	all locations		all locations		slipface only	
07h30	Bt on/Ab off	20.9	GP off	19.7	Bb off	19.8
08h00	At on	26.3	Bb on	21.2	Bb on	21.2
08h30	At on	31.4	Bb off	23.1	Bb off	23.1
09h00	At on	32.5	GP off	26.1	Ab off	26.5
09h30	At on	38.1	Bb off	30.2	Bb off	30.2
10h00	At on	46.9	Bb off	32.8	Bb off	32.8
10h30	At on	49.2	Bb off	34.2	Bb off	34.2
11h00	At on	50.9	Bb off	38.1	Bb off	38.1
11h30	At on	53.0	GP off	39.0	Bb off	39.1
12h00	At on	53.1	GP off	38.1	Bb off	40.7
12h30	At on	52.7	GP off	39.3	Bb off/Ab off	40.8
13h00	Bt on	51.7	GP off	37.5	Ab off	39.6
13h30	Bt on	53.2	GP off	39.5	Ab off	41.7
14h00	Bt on	55.1	GP off	38.9	Ab off	39.8
14h30	Bt on	54.4	GP off	38.5	Ab off	39.8
15h00	Bt on	53.3	GP off	37.9	Ab off	39.0
15h30	Bt on	51.3	GP off	37.9	Bb off	41.3
16h00	Bt on	50.9	GP off	37.1	Ab off	37.0
16h30	Bt on	45.6	Ab off	36.2	Ab off	36.2
17h00	Bt on	44.6	GP off	34.3	Ab off	34.5
17h30	Bt on	41.2	Ab off	32.3	Ab off	32.3
18h00	Bt on	38.2	Ab off	30.2	Ab off	30.2

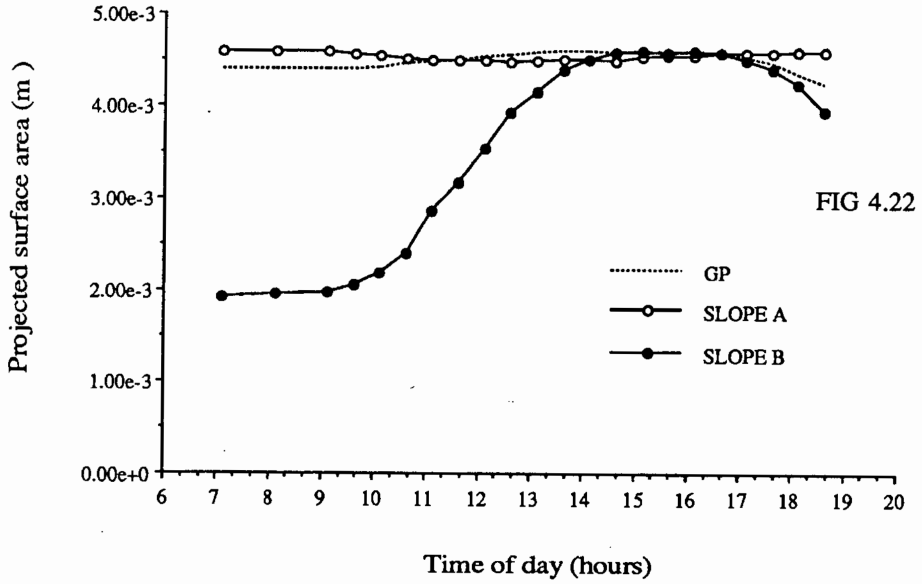


FIG 4.22

FIGURE 4.22. The surface area exposed to the sun's rays (AS) of gravel plain (GP), slipface A and slipface B copper models of the February microclimate dune (1/3/90). A schematic aerial view of the dune is shown in Figure 4.3.

not a factor as wind speed is similar at the gravel plain and both the bottom slipface sites (Figure 4.23). The reason is probably the consistently lower sand temperatures (and subsequently lower ground thermal energy gain) on the gravel plain. This is illustrated in Figure 4.24.

Considering the slipface only, the B BOTTOM OFF model was predominantly the coldest in the morning and the A BOTTOM OFF model the coldest in the afternoon, the crossover occuring at about 12h30 (Table 4.2). There are several reasons for this. Firstly, the angle of elevation and sun intensity was poorer on slope B in the morning and slope A in the afternoon (Figure 4.25a). This caused hotter sand on slope A in the morning and slope B in the afternoon (Figure 4.25b). The B BOTTOM OFF model thus received less ground thermal radiation in the morning than the A BOTTOM OFF model and vice versa in the afternoon. Furthermore, the B BOTTOM OFF model had a much lower AS than the A BOTTOM OFF model in the morning (Figure 4.22). This further reduced its radiation load in the morning. The domination of bottom models in the coldest slipface category was striking. Enhanced convective cooling was once again responsible for the exclusion of the top models. As in October, the prevailing winds were S - SW. The lee effect just below the crest was once again evident on both slipfaces. This is illustrated for face A in Figure 4.26.

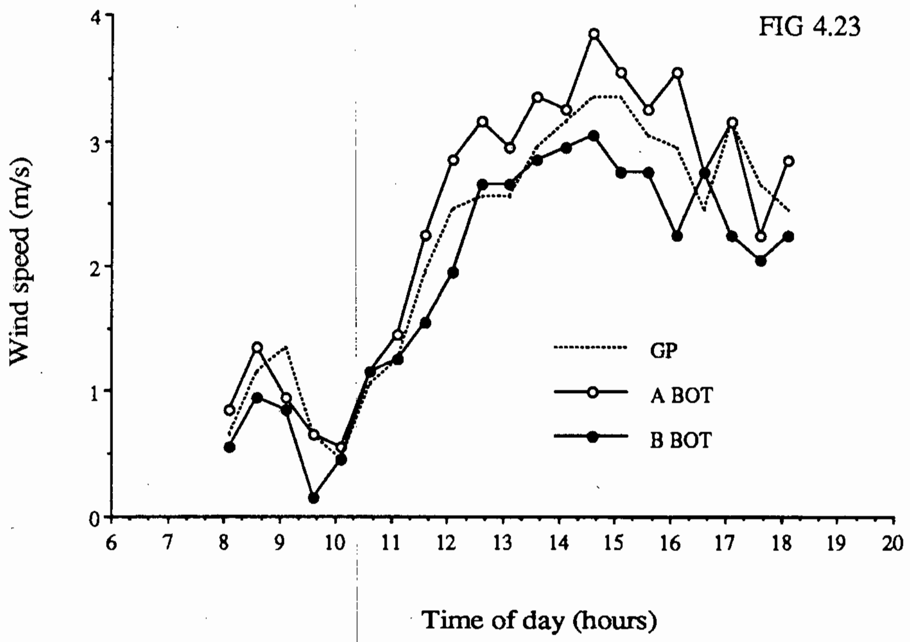


FIGURE 4.23. Wind speed measured 5 cm above the gravel plain (GP), lower (A BOT) slipace A and lower (B BOT) slipface B of the February microclimate dune (1/3/90). A schematic aerial view of the dune is shown in Figure 4.3

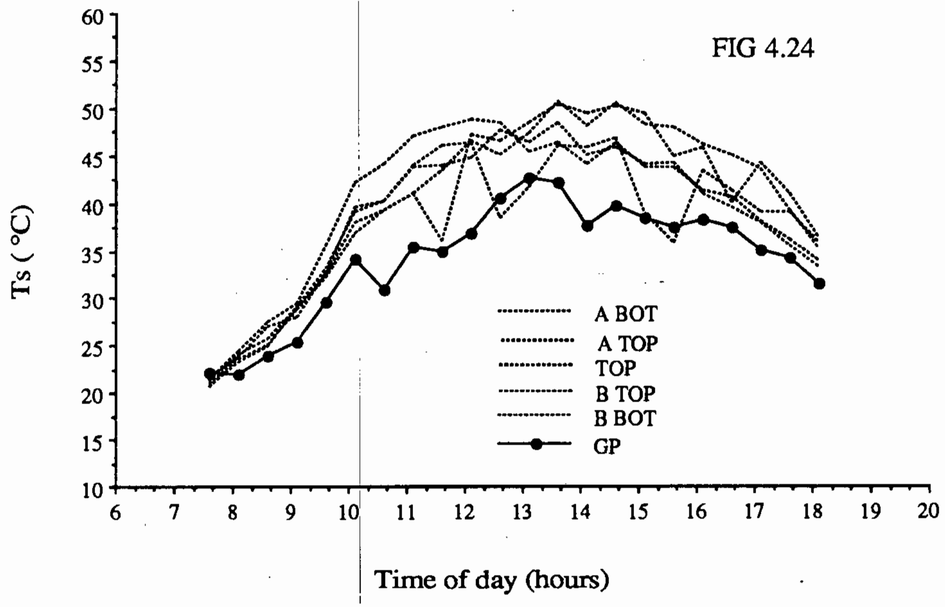


FIGURE 4.24. Sand surface temperature (Ts) measured at all the sites on the February microclimate dune (1/3/90). The location of sites is shown in Figure 4.3.

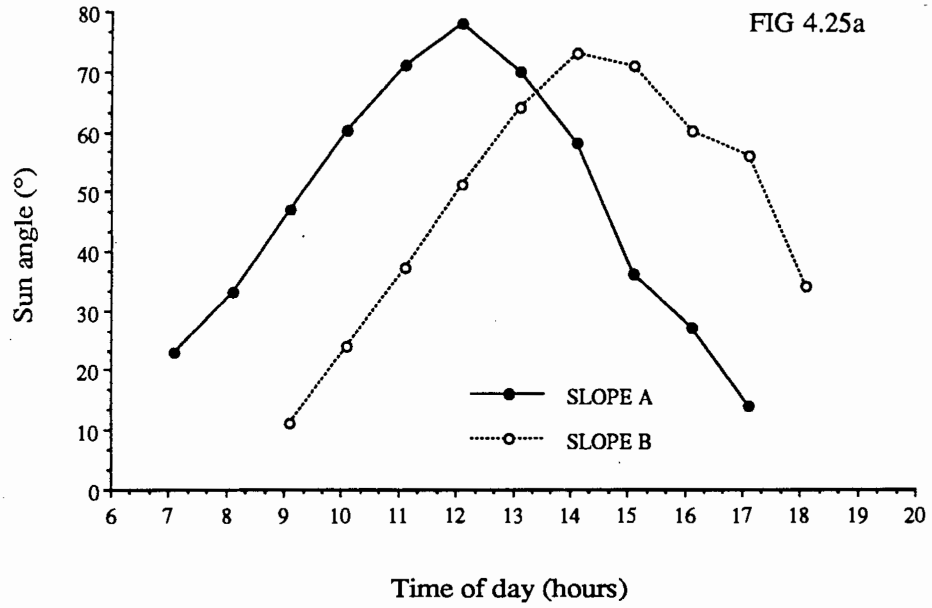


FIGURE 4.25a. Angle between the sun's rays and the two slipfaces (A and B) of the February microclimate dune as a function of time (1/3/90). A schematic aerial view of the dune is shown in Figure 4.3.

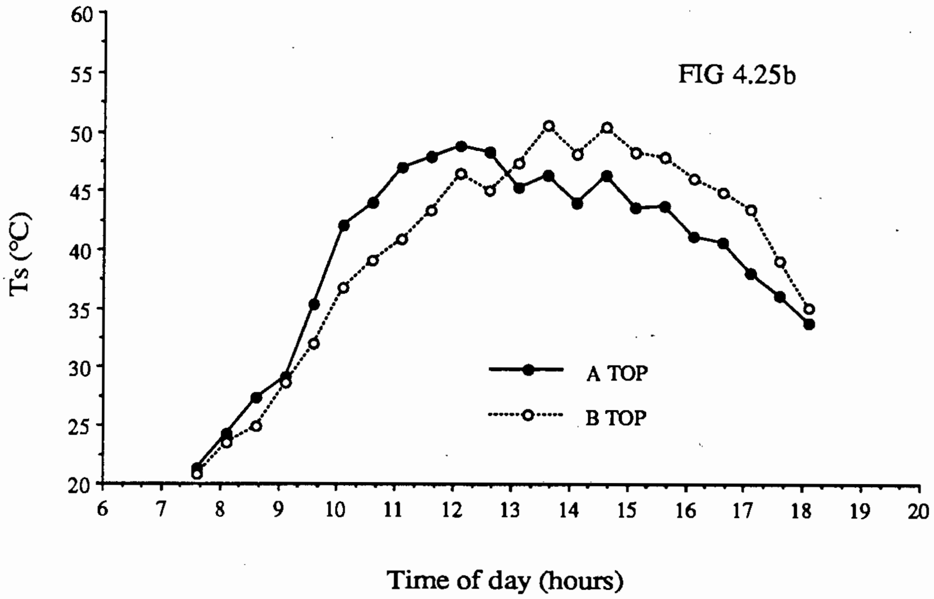
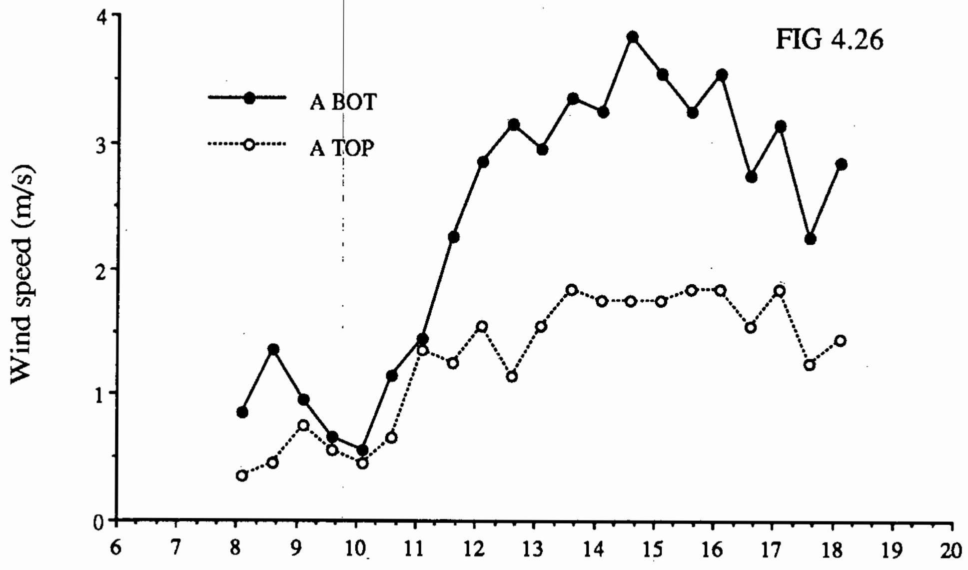


FIGURE 4.25b. Sand surface temperature (Ts) of the two upper slipfaces (A and B TOP) of the February microclimate dune as a function of time (1/3/90). A schematic aerial view of the dune is shown in Figure 4.3.



Time of day (hours)

FIGURE 4.26. Wind speed measured 5 cm above the upper (TOP) and lower (BOT) slipface A of the February microclimate dune (3/11/89). A schematic aerial view of the dune is shown in Figure 4.3.

The same factors outlined above were responsible for the domination of the A TOP ON model during the morning and the B TOP ON model during the afternoon in the hottest model category (Table 4.2). Top models were consistently hotter than bottom models due to less convective cooling (Figure 4.26). The sun intensity (Figure 4.25a) and its effect on sand temperature (Figure 4.25b) resulted in more conductive heat transfer to A models in the morning and B models in the afternoon. Finally, and least important,. the better AS for A models in the morning (Figure 4.22) provided for enhanced sun radiation transfer.

Copper models - July microclimate dune

As animal observations were being made on the microclimate dune in July, data which could have been compared with October and February conditions could not be collected during the July trip. Another slipface with a similar orientation to slipface B of the microclimate dune was selected for copper model studies. Metereological sand temperature measurements were only made on the dune top. Wind direction, wind velocity and ambient temperature varied drastically on a day to day basis. On the first few days (including 22/7/90), conditions were characterized by a moderate S - SW wind and moderate ambient temperatures. Overnight (23/7 - 24/7/90), these conditions changed to a strong E - NE wind and high ambient temperatures. The contrast is shown in Figures 4.27 and 4.28. The change in weather was so drastic that OFF models during the hot conditions were hotter than ON models during the cooler conditions (Figure 4.29). Consistent with observations in October and February, the B TOP ON model was the hottest and the GP OFF model usually the coldest during the cooler conditions when the SW wind was blowing (Figures 4.30a and 4.30b). During the hotter conditions, The B TOP ON model was the hottest and the TOP TOP OFF model the coldest. (Figure 4.31a and 4.31b). Without knowledge of the wind pattern on the slipface during this easterly wind, analysis of these observations is not possible. Excessive convective cooling on the dune top model may explain the latter observation.

East winds are fairly infrequent events occuring during winter only and lasting a few days at a time. For the major part of the year, the prevailing winds are those described in October and February (i.e S - SW).

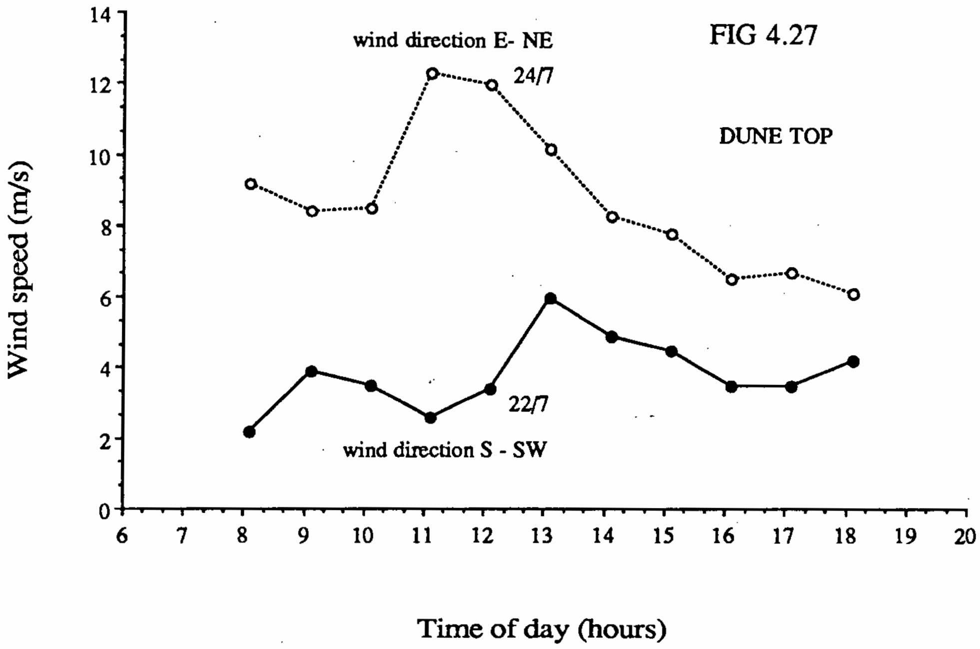


FIGURE 4.27. Wind speed measured 5 cm above the top of the July microclimate dune during normal (wind direction S - SW, 22/7/90) and east wind (wind direction E - NE, 24/7/90) conditions. A schematic face-on view of the dune is shown in Figure 4.4.

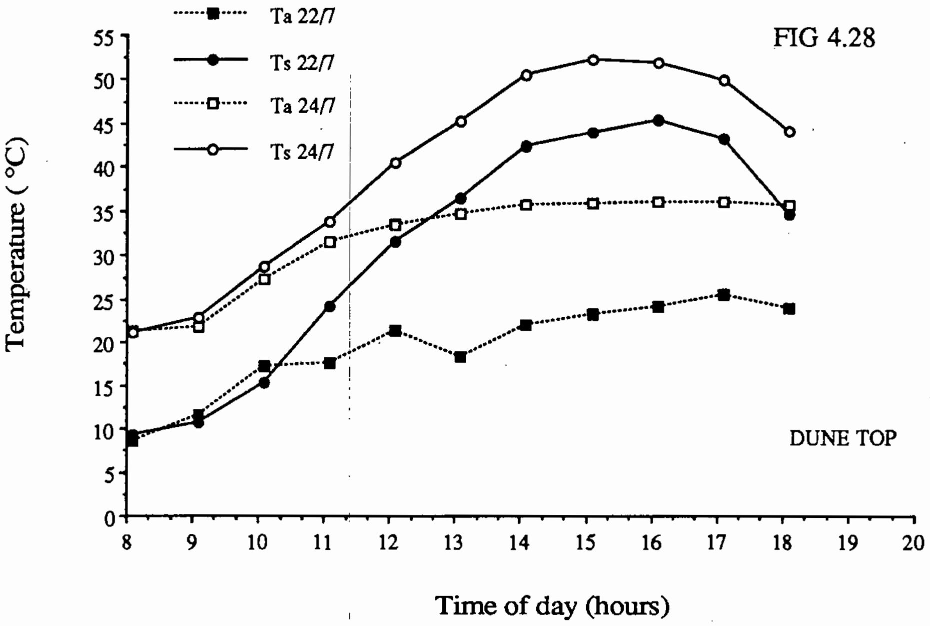


FIGURE 4.28. Ambient temperature (Ta) and sand surface temperature (Ts) measured on the top of the July microclimate dune during normal (wind direction S - SW, 22/7/90) and east wind (wind direction E - NE, 24/7/90) conditions. Ambient temperature measurements were taken 1 cm above the sand surface. A schematic face-on view of the dune is shown in Figure 4.4.

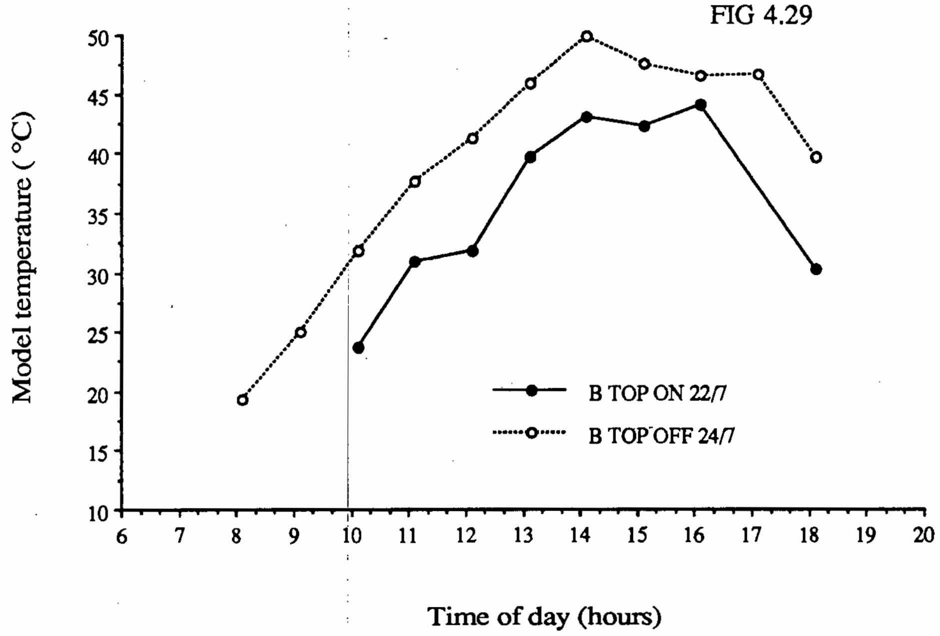
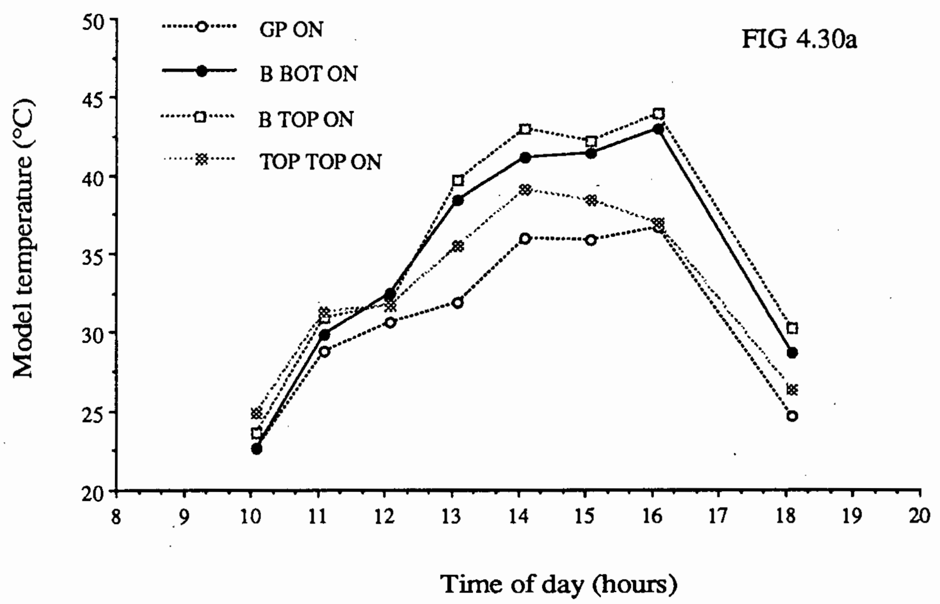


FIGURE 4.29. Temperatures of a copper model positioned on the upper (B TOP) slipface of the July microclimate dune during normal (wind direction S - SW, 22/7/90) and east wind (wind direction E - NE, 24/7/90) conditions. On th 22/7, the model was in contact with (ON) the sand surface. On the 24/7, the model was elevated above (OFF) the surface. A schematic face-on view of the dune is shown in Figure 4.4.



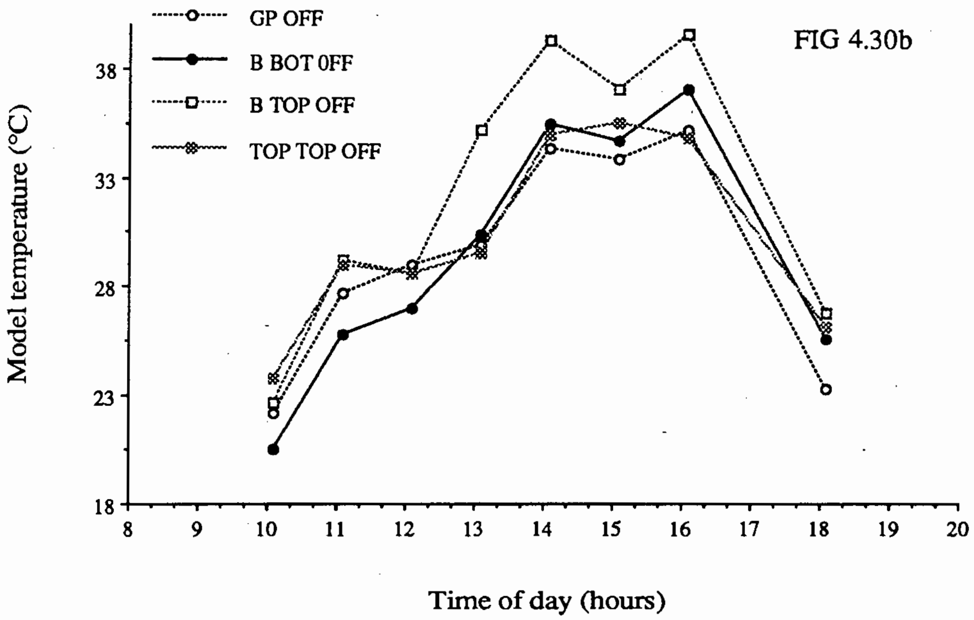


FIGURE 4.30. Temperatures of copper models, (a) in contact with (ON) the sand surface and (b) elevated 0.01 m above (OFF) the sand surface at the four measurement sites on the July microclimate dune. Measurements were made on the 22/7/90, prior to the onset of hot east wind conditions. A schematic face-on view of the dune is shown in Figure 4.4.

FIG 4.31a

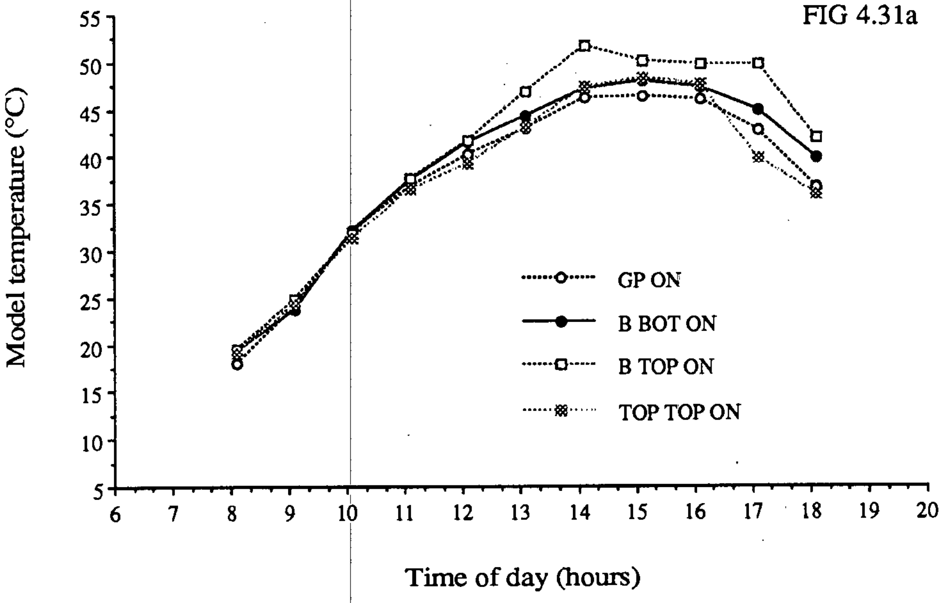


FIG 4.31b

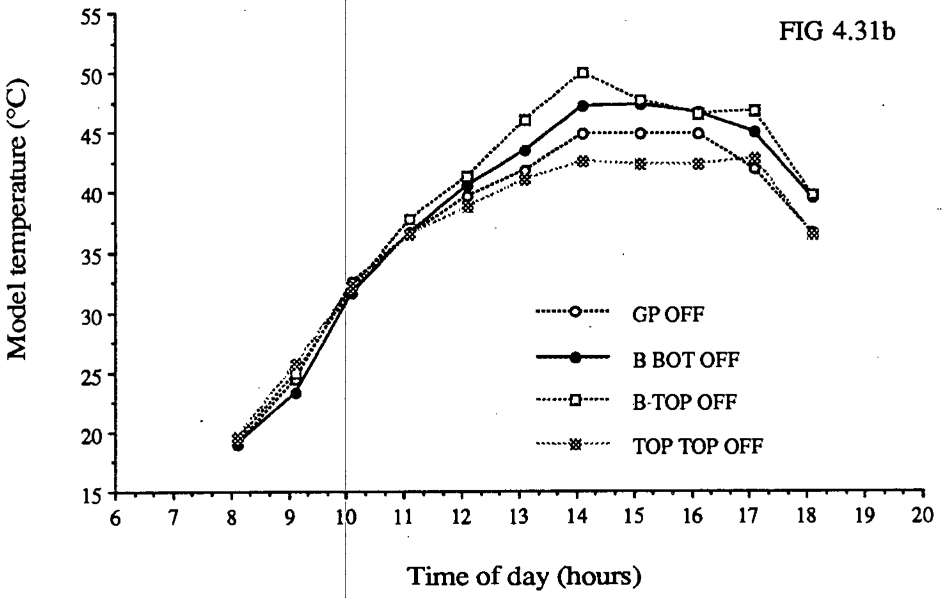


FIGURE 4.31. Temperatures of copper models, (a) in contact with (ON) the sand surface and (b) elevated above (OFF) the sand surface at the four measurement sites on the July microclimate dune. Measurements were made on the 24/7/90 during hot east wind conditions. A schematic face-on view of the dune is shown in Figure 4.4.

4.2.3 Ambient humidity, subsurface temperature and humidity.

Figure 4.32 shows ambient humidity measurements made over 4 - 8 day periods during October/November 1989, February 1990 and July 1990. Water vapour pressure was similar in October and July (about 10 mmHg) and higher during February (about 16 mmHg) when rain fell frequently . The good correlations between relative humidity and temperature reveals the obvious fact that water vapour pressure is independent of and remains the same regardless of ambient temperature.

Subsurface humidity was similar to ambient (above the surface) humidity during October. Figure 4.33a shows several subsurface humidity measurements made between 5 and 50 cm depth (closed squares) and ambient humidity measurements (open squares) made during the course of a day. Using the subsurface and ambient regression equations, at 27.5 °C (the temperature at the depth animals bury to - Table 5.8, Chapter 5), water vapour pressure is only 1.2 mmHg higher than ambient vapour pressure at the same temperature. Figure 4.33b shows an individual set of measurements taken between 0 (ambient) and 50 cm below the sand. Subsurface water vapour pressures are only slightly higher than those above the sand.

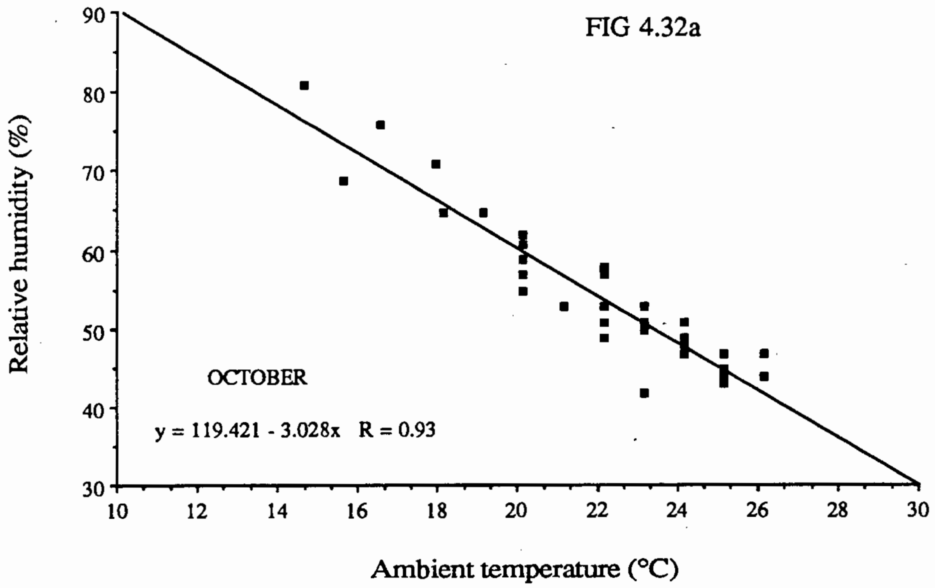


FIGURE 4.32a. Ambient relative humidity measurements made over a four day period during October/November 1989. The linear regression represents a water vapour pressure [(relative humidity) (saturated vapour pressure at corresponding temperature)] of about 10 mm Hg.

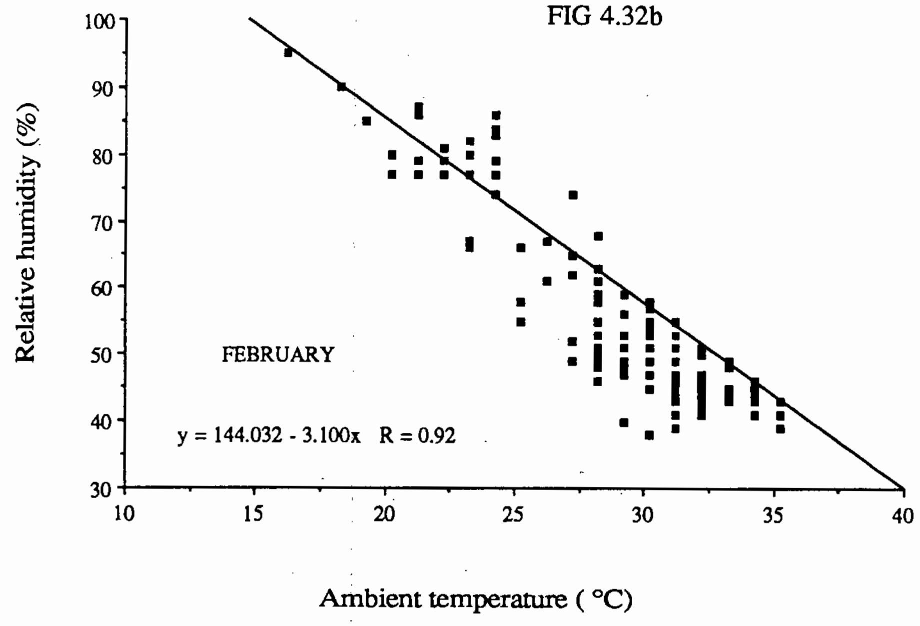


FIGURE 4.32b. Ambient relative humidity measurements made over an eight day period during February 1990. The linear regression represents a water vapour pressure [(relative humidity) (saturated vapour pressure at corresponding temperature)] of about 16 mm Hg.

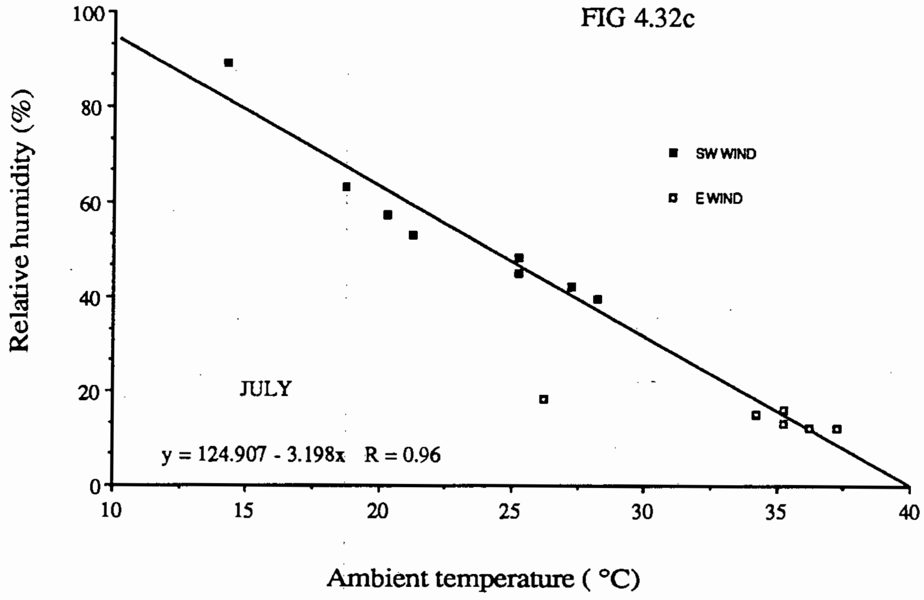


FIGURE 4.32c. Ambient relative humidity measurements made over a four day period during July 1990. The linear regression represents a water vapour pressure [(relative humidity) (saturated vapour pressure at corresponding temperature)] of about 10 mm Hg. Water vapour pressure values during east wind conditions (open squares) are similar to those during normal, south west wind conditions (closed squares).

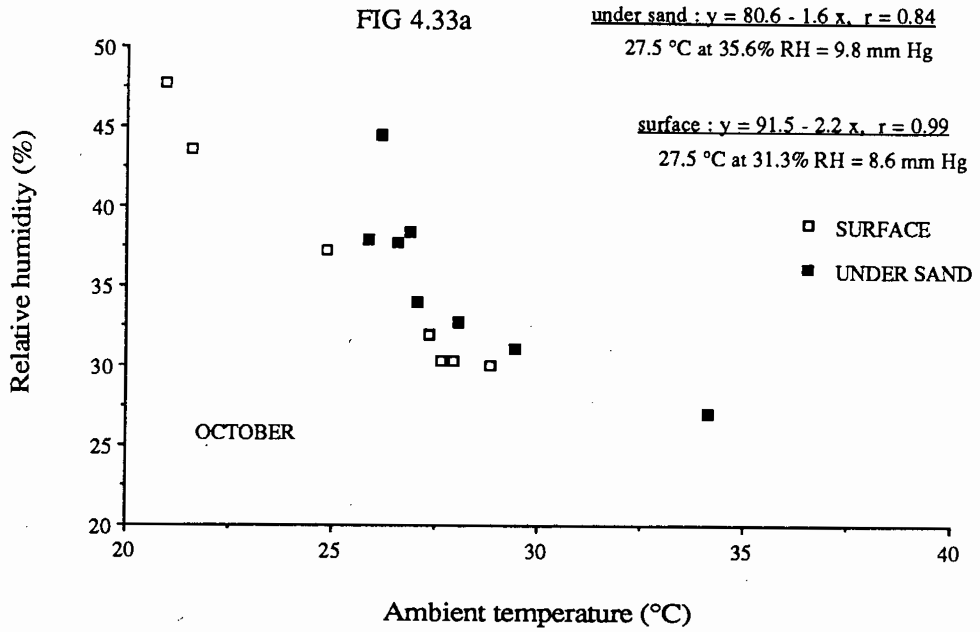


FIGURE 4.33a. Representative example of under-sand (closed squares) and ambient (open squares) relative humidity measurements taken during October 1989. The under-sand measurements were taken at depths between 5 and 50 cm below the surface of the lower slipface A of the October microclimate dune (4/11/89, 12h55). Ambient measurements were taken during the course of the same day.

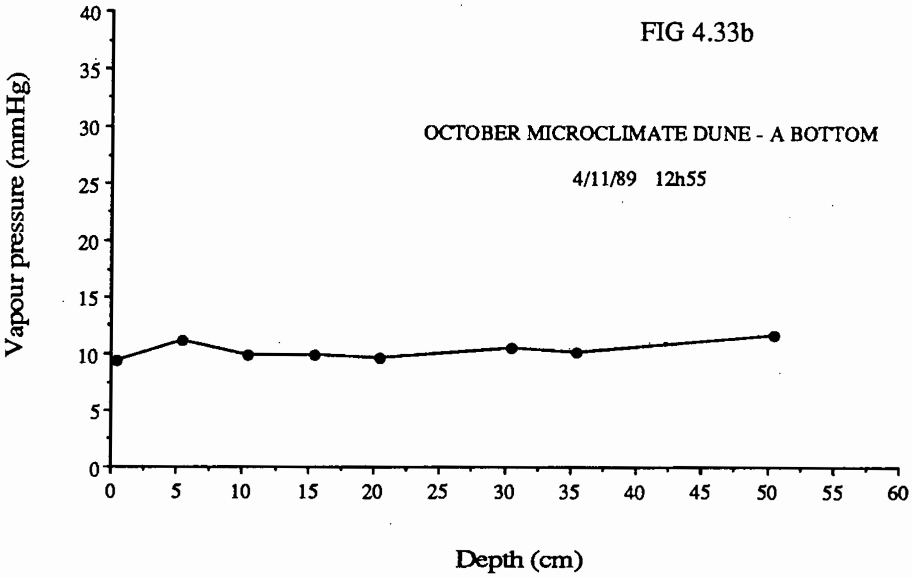


FIGURE 4.33b. Representative example of water vapour pressure as a function of depth below a slipface surface in October/ November 1989. Measurements were taken at depths between 5 and 50 cm below the surface of the lower slipface A of the October microclimate dune (4/11/89, 12h55). Ambient (above sand) humidity has been plotted at 0 cm depth.

FIG 4.34a

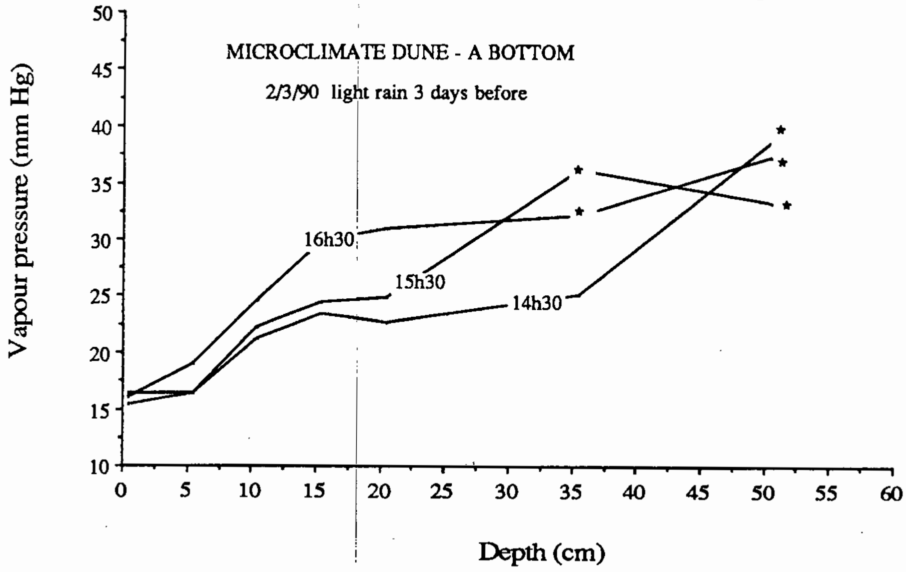


FIGURE 4.34a. Water vapour pressure as a function of depth below a slipface surface in February 1990. Measurements were taken at depths between 5 and 50 cm below the surface of the lower (BOTTOM) slipface A of the February microclimate dune (2/3/90) at 14h30, 15h30 and 16h30. Light rain had fallen three days prior to measurements being taken. Ambient (above sand) humidity has been plotted at 0 cm depth. Asterisks indicate saturated (relative humidity = 100 %) conditions.

FIG 4.34b

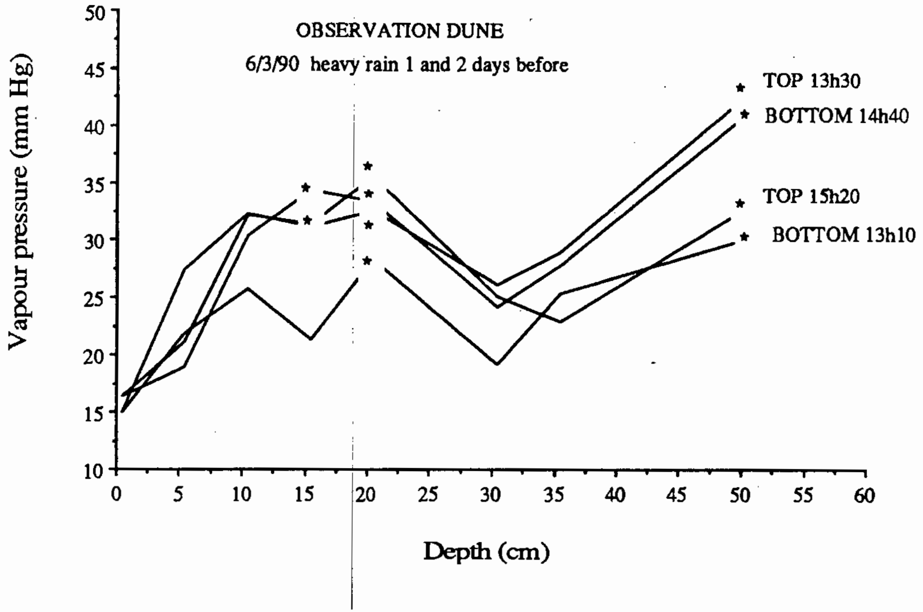


FIGURE 4.34b. Water vapour pressure as a function of depth below a slipface surface in February 1990. Measurements were taken at depths between 5 and 50 cm below the surface of the lower and upper east/west slipface of the February animal observation dune (6/3/90; upper (TOP) slipface at 13h30 and 15h20, lower (BOTTOM) slipface at 13h10 and 14h40). Heavy rain had fallen 1 and 2 days prior to measurements being taken. Ambient (above sand) humidity has been plotted at 0 cm depth. Asterisks indicate saturated (relative humidity = 100 %) conditions.

FIG 4.34c

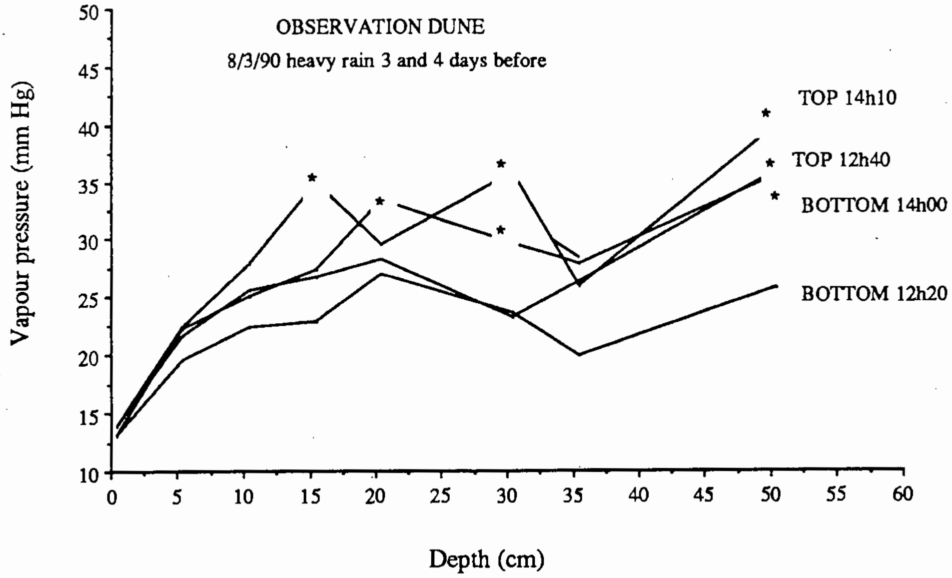


FIGURE 4.34c. Water vapour pressure as a function of depth below a slipface surface in February 1990. Measurements were taken at depths between 5 and 50 cm below the surface of the lower and upper east/west slipface of the February animal observation dune (8/3/90; upper (TOP) slipface at 12h40 and 14h10, lower (BOTTOM) slipface at 12h20 and 14h00). Heavy rain had fallen 3 and 4 days prior to measurements being taken. Ambient (above sand) humidity has been plotted at 0 cm depth. Asterisks indicate saturated (relative humidity = 100 %) conditions.

In February, the humidity depth profiles were very different. Due to rain penetration into the sand, water vapour pressures were much higher below the slipface surface. Generally water vapour pressure increased with depth. Superimposed on this increase were peaks associated with rain penetration. Figure 4.34a shows measurements made in a slipface three days after a light rain. Asterisks indicate saturated conditions, in this case occurring at lower depths only. Figure 4.34b depicts a profile 24 h after heavy rain. In addition to the lower depths being saturated, the sand between 15 and 20 cm is also now saturated. Two days later (Figure 4.34c), the rain has penetrated even further into the sand (to about 30 cm) and the 15 - 30 cm layers are beginning to dry out. Extrapolation from this point would probably show a progression towards the profile depicted in Figure 4.34a.

During the day, temperature profiles below the sand differ remarkably at different depths. The top layers start off cold and then, due to sun radiation, warm rapidly as the morning progresses (Figure 4.35). Temperatures peak at about 14h00 and then decline swiftly during the afternoon.

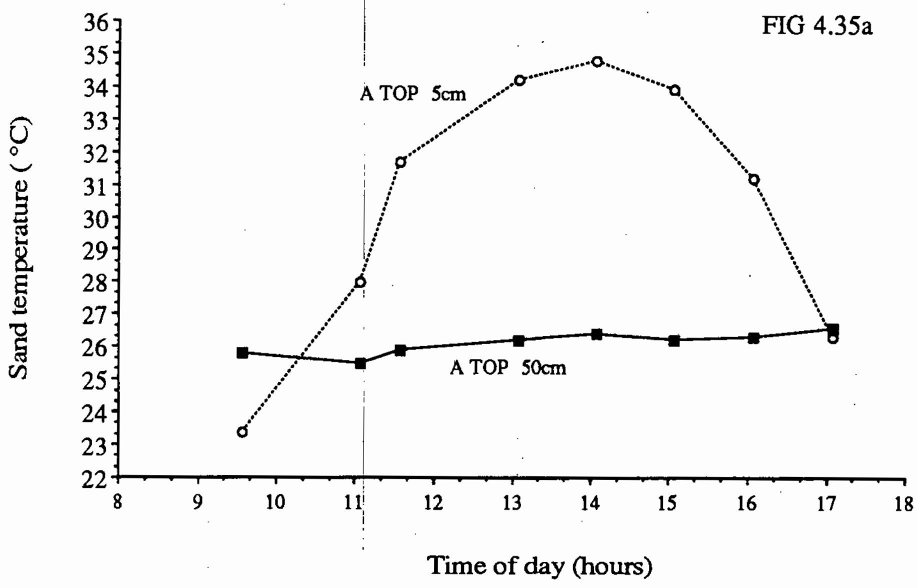


FIGURE 4.35a. Temperature of sand at 5 cm (open circles) and 50 cm (closed squares) below a slipface surface as a function of time. Measurements were taken during the day at upper (TOP) slipface A of the October microclimate dune (see Figure 4.2).

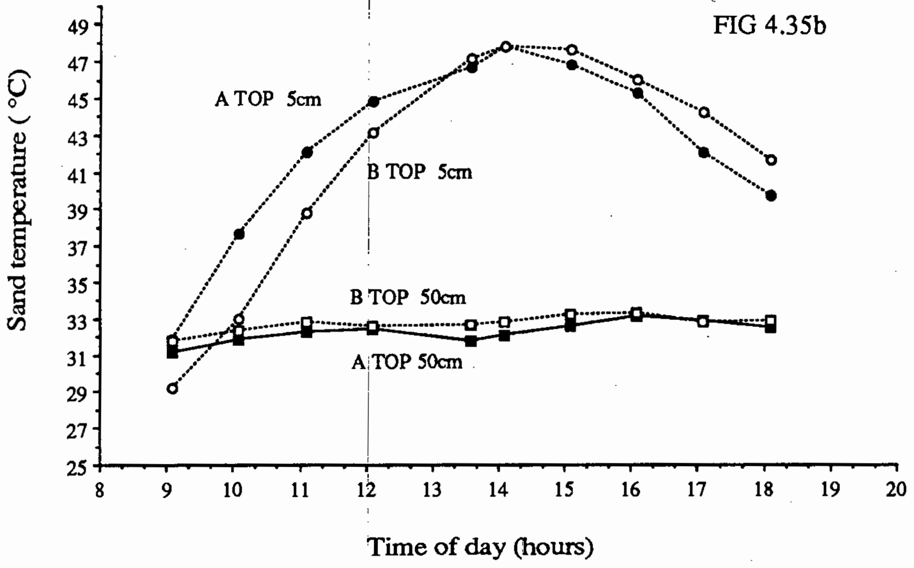


FIGURE 4.35b. Temperature of sand at 5 cm (circles) and 50 cm (squares) below two slipface (TOP) surfaces as a function of time. Measurements were taken during the day at upper (TOP) slipface A and B of the February microclimate dune (see Figure 4.3).

The lower layers show a negligible change in temperature during the entire course of the day. An identical trend was observed during October and February. Temperatures were, however, substantially higher during the latter month.

At night, the reverse trend is observed (Figure 4.36). The top layers show a steady decrease in temperature as the night progresses. As during the day, the bottom layers show a negligible change in temperature. The trend is similar for the two months with temperatures once again being much hotter during February. With the rising of the sun, the pattern repeats itself.

4.3 SUMMARY

The modelling exercise presented here clearly demonstrates the complexity of a desert lizard's thermal biology. The factors influencing body temperature are numerous and, depending on various parameters, differ in their degree of importance. One of the more interesting findings is the relatively unimportant role orientation plays in influencing the heat load a cylindrically-shaped body gains from solar radiation. Under hot conditions and when in contact with the substrate, body temperature is predicted to never vary more than about 1.5 °C, regardless of orientation (Figures 4.7a and 4.7b). The height of elevation above the substrate is also of relative unimportance due to the low conductivity of air and the subsequent relatively small magnitude of the heat conduction term in the heat balance equation (Figure 4.11a and 4.11b). This factor only becomes important when it results in enhanced convective heat exchange (Figure 4.12b) or exposure to different ambient temperatures (Figure 4.12a), both of which may occur when resting on *Merremia* mounds. In a shadeless habitat (such as a desert dune), the major ways a lizard can control its body temperature are by varying the degree of contact with the substrate (Figures 4.10a and 410b) and the degree of wind exposure (Figures 4.7a - 4.12). In the former case, this can once again be done by making use of foliage or adopting postures which reduce the surface area of the animal in contact with the substrate. In the latter case, this can be achieved by selecting different locations on the dune habitat.

The surface dune microclimate offers *Angolosaurus skoogi* an extremely diverse thermal mosaic. Assuming the results of copper model studies are representative of potential lizard body temperatures, an animal can obtain a wide range of surface body temperatures depending on the season, its body posture and its location in the dune habitat. Although certain locations are thermally lethal at certain times of the day (particularly in summer, Table 4.2), careful location selection will permit surface activity for most of the day. As outlined in the Chapter 1, a number of factors can complicate a scope for growth optimization study. These factors include involuntary

FIG 4.36a

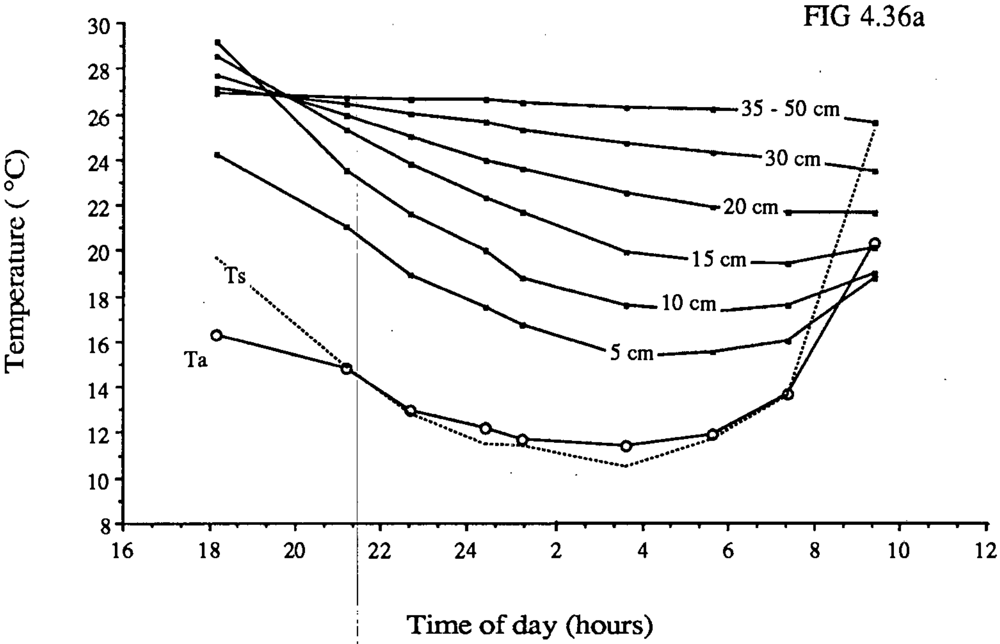


FIG 4.36b

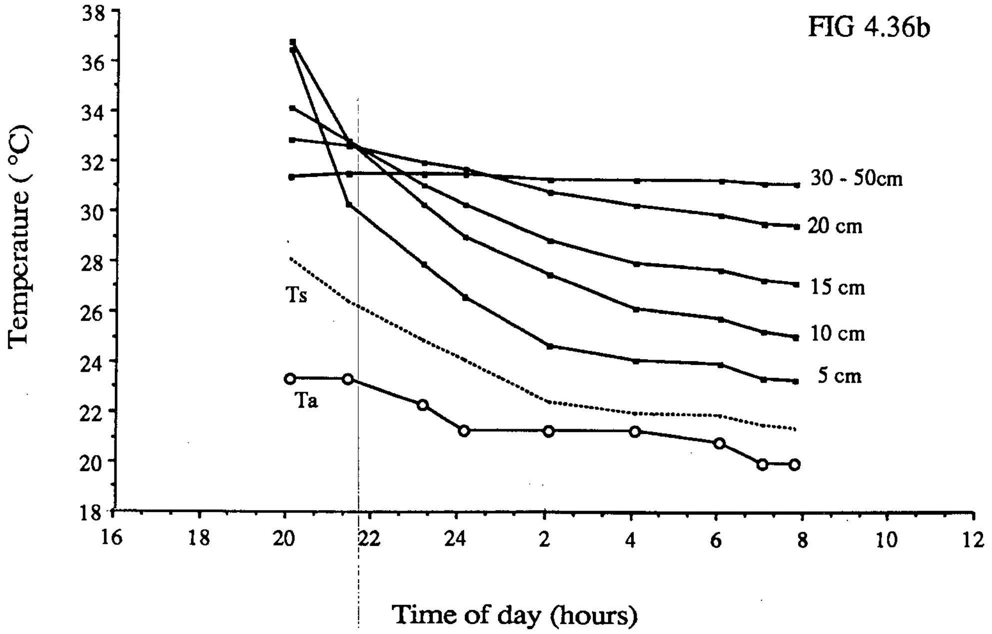


FIGURE 4.36. Ambient air (Ta), sand surface (Ts) and subsurface sand (5 - 50 cm) temperatures of a dune slipface as a function of time. Measurements were taken during the night at the upper east/west slipface of the animal observation dune in (a) October 1989 and (b) February 1990.

hypo/hyperthermia and thermally induced restriction of activity. The data presented here suggest that these factors should not apply to *A. skoogi*.

A more subtle complicating factor may be obligatory activity in order to to achieve body temperatures high enough for digestive processes to function normally. The digestive machinery of reptiles has thermal limits below which inefficient digestion occurs and other complications arise. The snake *Thamnophis elegans*, for example, regurgitates its prey when kept at 10 °C (Stevenson *et al.* 1985). Feeding experiments on *A. skoogi* kept at January field surface temperatures (day and night) had to be aborted for the same reason (B. C. Clarke, unpublished data). The thermal microclimate below the slipface surface, however, makes surface thermoregulation for efficient digestion unnecessary. Animals can maintain body temperatures in excess of 26 °C during spring (October) and 31 °C during summer (February) for 24 hours a day (Figures 4.35a,b and 4.36a,b). Vertical subsurface excursions during the day will result in body temperatures even higher than these values (Figures 4.36a and b). If scope for growth optimization involves, for example, as little activity as possible, animals can achieve this (by remaining submerged) without compromising too much on their food processing capacity.

Finally, subsurface humidity measurements indicate the potential for water conservation during periods of inactivity. During October (spring), water vapour pressure below the surface of the slipface is virtually indistinguishable from that above the surface (Figure 4.33b). This means that, in terms of water vapour deficit, animals are at no disadvantage when submerged. The physical properties of the subsurface environment do not reduce evaporative water loss from submerged animals compared to resting, exposed animals (Section 3.4.1., Chapter 3). Inactivity, however, may result in substantial water conservation (Chapter 5). In February (summer), rain penetration results in water vapour pressure below the surface of the slipface being consistently higher than that above the surface (Figure 4.34). In addition to water conservation due to inactivity, lower water vapour deficits below the surface will result in reduced evaporative water loss rates in submerged animals.

CHAPTER 5

WATER AND ENERGY BALANCE IN *ANGOLOSAURUS SKOOGI* : FIELD STUDIES

5.1 INTRODUCTION

Strategies of thermoregulation and activity patterns in reptiles have been related to several biotic and abiotic factors. Avery and McCardle (1973) and Zimmerman and Tracy (1989), for example, have (1) correlated emergence times of the lizards *Lacerta vivipara* and *Sauromalus obesus* with the earliest time of the day permitting rapid warming to preferred activity body temperatures. They attribute this to avoidance of thermally induced lethargy which would make the lizards more vulnerable to predators. This hypothesis is particularly attractive in the case of animals which have "ambush" or "surprise attack" predators. Both Pietruszka (1987) and Seely *et al.* (1988, 1990) have (2) concluded that thermoregulatory behaviour in active *Angolosaurus skoogi* is facultative, supporting other obligatory surface activities such as territorial defence and social interactions. Christian et al. (1983) attribute the maintenance of homeothermy in the iguana *Conolophus pallidus* (at a temperature below what can be achieved at certain times of the day) to optimization of the efficiency of operation of some enzyme system (3). Using biophysical analysis (predicting body temperature from meteorological parameters), a number of investigators have shown that stategies of thermoregulation and activity patterns can be (4) restricted by environmental conditions. Using multichannel telemetry and copper models, Spotila and Standora (1985) have shown that potential lethal heat gain during the day is one of the factors selecting for nocturnal nesting activity in the green turtle, *Chelonia mydas*. The montane snake, *Thamnophis elegans vagrans*, lives in a particularly harsh physical environment (Scott *et al.* 1982). In July (summer), for example, the maximum voluntary body temperature (35 °C) is exceeded for about 5 hours each clear day. Optimum (preferred) body temperatures (26 - 32 °C) can only be maintained for about 2 hours each day and lethal body temperatures would be exceeded for at least 3 hours each day. Porter and Tracy (1983) have demonstrated that in the desert iguana, *Dipsosaurus dorsalis*, environmental conditions at certain times of the year would result in lethal body temperatures (> 43 °C) between about 10h00 and 14h00. Body temperatures in excess of 38 °C are obtainable between 06h00 and 18h00. During winter, body temperatures greater than 38 °C are not attainable. In contrast, the more tropical rainbow lizard, *Agama agama*, never appears to experience a restrictive physical environment (Porter and James 1979). Temperatures in excess of 37 °C are available all year round and conditions never produce lethal body temperatures.

It has been suggested (5) that thermoregulatory and activity patterns may be geared towards optimizing digestion. The amount of energy gained relative to foraging costs has been treated in a series of hypotheses known as optimal foraging theory (review in Pyke *et al.* 1977). An important assumption of the hypothesis is that the overall fitness of an animal increases as a function of the net rate of energy intake. Applied to ectotherms, it predicts that animals will adjust their thermoregulatory and activity behaviour so as to optimize their scope for growth. Sibly (1981) predicted that when food in the environment is abundant, optimal digestion occurs when animals maximise their rate of ingestion and minimize the passage time of food along the gut. This strategy will reduce digestive efficiency, but will maximize the rate of extraction of energy from food with respect to time. Alternatively, when the availability of food is limited, animals will digest optimally by retaining food in their gut for as long as possible to enhance digestive efficiency and thereby to extract as much energy as possible from each unit of food. Zimmerman and Tracy (1989) have built on this theory to predict optimal themoregulatory behaviour in relation to digestion. When food is abundant, lizards should select warmer temperatures for as long as possible to optimize digestion. When food is limited, they predict that lizards should select cooler temperatures for longer periods, depending on how limited the resource is. In the extreme case (no food), the coolest temperatures should be selected throughout the day. Using the lizard *Sauromalus obesus*, they present data in support of their predictions. Avery (1984) has also demonstrated that growth rates in lizards (*Lacerta vivpara*) fed *ad lib.* increase with increasing body temperatures.

That thermoregulatory behaviour and activity patterns are influenced by water and energy availability and requirements can not be disputed. An extreme case is forced hibernation as food dehydrates and becomes scarcer, known to occur in at least three species of reptiles (Grenot 1976 ; Minnich 1976, 1977 ; Nagy 1972). In animals where evaporative water loss is a significant component of the water budget, increased water availability may allow warmer body temperatures to be selected and activity times to be increased (Bury and Balgooyen 1976). This, in turn, may increase foraging returns. Thermoregulatory behaviour and activity patterns may also influence water and energy requirements. Animals have to leave their refuges to eat, defecate and perform social obligtions such as territorial defence. During these activity periods, a high body temperature may be inevitable, resulting in increased water and energy costs. In extreme cases (such as rigorous territorial defence or activity during periods of poor food quality), stress in the form of reduction of fat reserves, elevated plasma electrolyte levels and body mass loss may result (Minnich 1982).

The factors outlined above probably all influence thermoregulatory behaviour to a greater or lesser degree. Optimal strategies for different factors may clash, however, and a compromise may be required (Huey 1982). For example, a lizard undergoing starvation may still have to select high body temperatures when active, in order to optimize predator evasion.

Huey and Slatkin (1976) have constructed a mathematical cost-benefit model of thermoregulation in lizards. The key to the model is the realization that thermoregulatory adjustments have associated costs (water and energy loss) which, if extensive, may make seemingly optimal thermoregulation disadvantageous. The thermoregulatory strategy which will optimize net water gain or net energy gain (scope for growth) may be very different to the one that will optimize, for example, foraging returns. Despite this excellent analysis, many important studies have neglected to include increased costs of thermoregulatory adjustments in their attempts to elucidate or explain thermoregulatory strategies and activity patterns. Zimmerman and Tracy (1989) and Christian *et al.* (1983) are two cases in point. Although, in the former study, mention is made of the need to select cool temperatures to reduce temperature-dependent metabolism and evaporative water loss during periods without food, no mention is made of the interaction between costs and benefits when lizards are supposedly selecting body temperatures as high as possible for as long as possible during periods of food abundance. In the latter study by Christian *et al.* (1983), optimization of net energy gain is not considered in attempting to explain the maintenance of a low homeothermic body temperature below that which can potentially be obtained.

There are two series of studies to date which consider the effect of animal behaviour and environmental conditions on scope for growth. Firstly, there are several studies which, by combining field measurements of metabolic rate with laboratory estimates of food gain and utilization efficiency, provide insight into the cost of activity and its potential effect on energy budgets. Merker and Nagy (1984), for example, have shown that *Scleropus virgatus* lizards active for 8 hour per day had field metabolic rates 8 times higher than if they had remained inactive in retreats all day. Thus, by varying the amount of time spent abroad, these lizards can change their cost of living by nearly an order of magnitude. Anderson and Karasov (1981) and Nagy *et al* (1984) have compared the foraging costs and benefits in sit-and-wait and widely foraging lizards . Although active for longer periods and incurring higher metabolic costs, better foraging success results in widely foraging lizards having a higher rate of net energy gain than do their sit-and-wait counterparts. Secondly, there are the studies conducted on the lizard *Scleropus undulatus*, by W.P Porter, S.M. Jones and S.R. Waldschmidt (collated in Porter 1989). Using data from various sources, they calculated energy consumption as a function of body temperature under resting, resting + digesting, and active + digesting conditions. Similarly, the maximum amount of assimilated energy as a function of body temperature was calculated from laboratory investigations of the effect of temperature on assimilation efficiency, gut passage time and the ingestion rate of food. The scope for growth was computed from the differences between energy gain and loss curves. Using biophysical analysis, the influence of climate and altitude on scope for growth has been predicted.

The Namib sand-diving lizard, *Angolosaurus skoogi*, is a herbivorous member of the family Cordylidae which occurs only on coastal sand dunes in northern Namibia and southern Angola. It has been the subject of intensive research over the past 10 years and much is known about the biology of this species. A recent study (during summer, non-breeding period) has shown that *A. skoogi* has a field metabolic rate (FMR) about half that expected for a lizard of its size (Section 2.3, Chapter 2). Despite the low FMRs, water influx rates during the study period were typical of other desert lizards. The low FMRs are not a function of low standard metabolic rates and are thus thought to be due to reduced activity and possibly carefully regulated thermoregulation when on the surface. The lizards are diurnal, spending inactive periods submerged below the sand surface. Although this species lives in a hyperarid, mobile dune sea which harbors little vegetation, food is readily available in the form of a perrenial cucurbit plant called nara (*Acanthosicyos horrida*) that draws its water from the underground water table via a long tap root.

This study is primarily an investigation into the reasons for and the significance of the low FMRs observed in this species. It is hypothesized that *A. skoogi* will, when possible, behave in such a way as to optimize its scope for growth and net water gain. A time when this may not be possible will be during the breeding season. Given the complex interaction between thermoregulatory behaviour, activity patterns, foraging gains and metabolic and water losses, the parameters that need to be considered and investigated are numerous. Laboratory studies on the components of water loss and energy metabolism are described in Chapter 3. Combining these findings with field observations of thermoregulatory strategies, activity patterns, water flux rates, animal chemistry (blood electrolytes and fat reserves), and the choice, composition and quality of food, will provide the data base needed to explain observed behaviour in the field and its ecophysiological significance.

5.2 METHODS AND MATERIALS

5.2.1 Study site

Field trips were conducted during the months of October (spring), February (late summer) and July (winter). Meteorological conditions showed large seasonal differences and are reported in detail in Chapter 4 (Section 4.3.2). The same location (Unjab river, northern Namibia - Section 2.2.1, Chapter 2) was used for all three trips. The study site comprised a large gravel plain on the bank of the Unjab River, bordered by a semicircular dune (Figure 5.1). The slipface of the dune was large, consisting of a 40 m northerly facing section of about 10 m in height and a 40 m easterly facing section of about 1 - 10 m in height. The predominant vegetation on the site was two permanent nara bushes and patches of the low-lying shrub, *Merremia guerichii*. This plant tends to grow on small mounds of sand that collects on the gravel plain. The *Merremia* mounds shown here are as

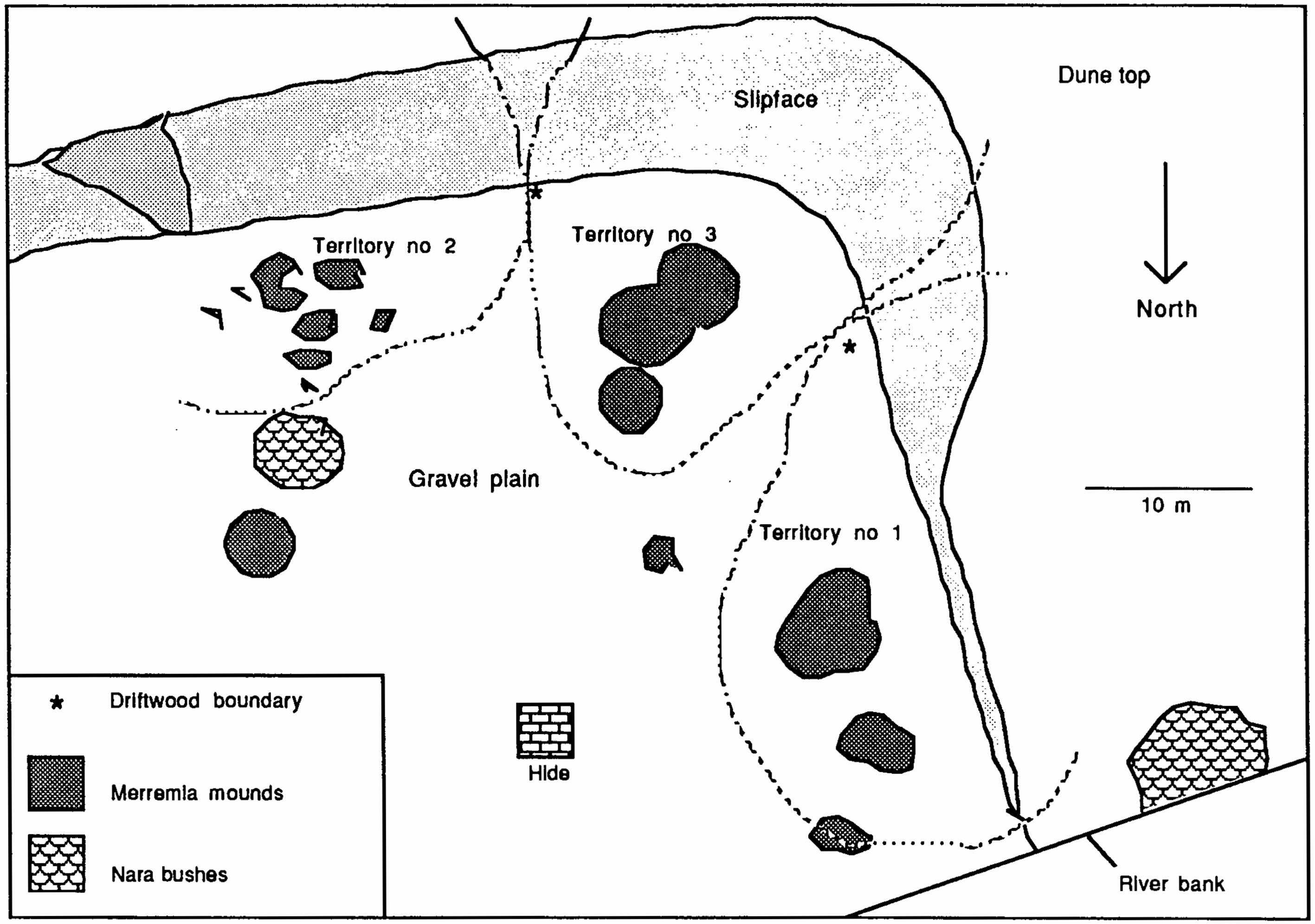


FIGURE 5.1. Scale diagram of the dune used for animal observations, telemetry and tritiated water studies on *Angolosaurus skoogi* in October 1989, February 1990 and July 1990. See text for detailed description. The dashed lines are the estimated territorial boundaries of the three telemetered male animals in February 1990. Boundaries were distinctly demarcated at the slipface base by pieces of driftwood

they occurred during the rainy season in February. During the other months, *Merremia* was much sparser than illustrated here. The observation hide was situated about 40 m from the slipface in a position where both slipfaces could be clearly observed.

5.2.2 Water flux

Water flux rates were determined using tritiated water. Five - seven male *Angolosaurus skoogi* were captured as they emerged from the sand. Due to size limitations imposed by telemeter size, only large males were used. Immediately following capture, animals were weighed and injected intraperitoneally with 0.25 ml of tritiated water of specific activity 2 mCi/ml. During the isotope equilibrium period , animals were marked with brightly coloured water soluble paint to facilitate identification and recapture. After 90 minutes, blood samples were taken from the infraorbital sinus and stored inside flame-sealed 50 μl glass capillary tubes. The animals were then released at the site of capture. After a period of five to eight days, animals were recaptured, reweighed and a second blood sample taken. All blood samples were kept on ice until analysis. In the laboratory, blood samples were microdistilled using the method of Nagy (1983). 10 μl of the distilled blood was then added to 10 ml of scintillation cocktail (Beckman Ready Safe) and the tritium concentration determined by liquid scintillation counting. Body water volumes were determined from the dilution spaces of injected tritiated water. Rates of water flux were calculated using the equations for linearly changing body water volumes (Nagy 1980).

5.2.3 Plant analysis

At the end of each field trip, potential *A. skoogi* food items were collected, stored in water-tight containers and refridgerated until analysis. The percentage water content was determined by drying samples to constant mass at 65 °C. Energy content was determined using a Digital Data Systems CP 401 bomb calorimeter. Electrolyte concentrations were determined by ashing approximately 200 mg of dried plant material at 450° C for 5 h, adding 0.67 ml concentrated nitric acid, and then making up the volume to 2 ml with distilled water. Solutions were left overnight, centrifuged and the supernatant electrolyte concentrations measured using an Instrumention Laboratory model 243 flame photometer (sodium and potassium ions) and the titrimetric method of Schales and Schales (1941) for chloride ions.

5.2.4 Sampled animals

Five - seven *A. skoogi* (both sexes, predominantly male) were captured at the end of each of the three field trips. Blood samples of 50 µl were taken from the infraorbital sinus and stored in flame-sealed glass haematocrit tubes. The animals were then weighed and killed by injecting an overdose of barbiturate. Blood samples were centrifuged in the field and the supernatant refridgerated until analysis. Due to a malfunction of field refrigeration equipment in October, blood samples decayed and were discarded. In the laboratory, plasma electrolyte levels were measured with the same equipment used for plant samples. Osmolarity was determined using a Wescor 5100B vapour pressure osmometer.

Carcasses were dissected and any food carefully squeezed out of the stomachs. Stomach volume was determined by measuring the difference in mass between empty stomachs and stomachs filled to capacity with distilled water (assuming 1g distilled water = 1ml). Stomach contents were sorted, identified and dried to constant mass at 65 °C. Subcutaneous fat reserves (abdominal fat pads) were carefully excised from each animal and also dried to constant mass at 65 °C.

5.2.5 Focal Animal Studies

Both telemetry and activity studies were conducted on free-ranging *A. skoogi* during October and February. The cassette tapes containing July activity data were stolen and so only subsurface body temperatures are reported here. The size of the telemeters restricted their use to large males only. During the equilibrium period for tritiated water studies (see above), the largest captured animals were marked with brightly coloured water-soluble paint and forced to swallow temperature transmitters (n = 4 in October, 3 in February and 4 in July). The telemeters were cylindrical in shape (16 mm long and 11 mm in diameter) and weighed approximately 1.75 g each. Range of transmission varied but was usually in excess of 40 meters. Telemeters were calibrated between 10 and 45 °C and had an accuracy of 0.1 °C. Nine of the ten telemeters were recovered and recalibrated. Drift occurred in only two cases. The maximum error resulting from the drift was 0.4 - 0.6 °C.

The degree of stress imposed by the telemeters was tested in the laboratory prior to field studies. The criterion used as a indication of stress was maintenance of body weight. Four captive animals were forced to swallow models of the telemeters. As the telemeters were still being developed at this stage, these models were not identical in shape to those finally used in the field. Instead, they were pill box shaped with a length of 16 mm, a width of 10 mm and a height of 7 mm. These dimensions give a maximal cross sectional diameter of about 12 mm which is greater than the final telemeter diameter. Food was offered on the day of telemeter ingestion and every day thereafter until the telemeters were defecated. After this, animals were starved for a few days to determine the body weight loss that would occur if the animals were not eating. Animals were weighed every evening for the entire duration of the experiment. Ambient temperature was kept at 30 °C, relative humidity at 50 % and a 300 W thermoregulatory lamp was provided for eight hours per day.

During field observation periods, the body temperatures of telemetered animals were monitored at 15 minute intervals from early in the morning until late in the evening. As soon as it was clear that an animal was intending to emerge (sudden change in signal frequency), body temperature was monitored as frequently as possible. The location and behaviour of each animal was noted from the time of emergence until burial. Daily observations were continued until telemeters were defecated (about 2 - 3 days in February) or until sufficient data had been collected (5 - 7 days in October). In February, telemeters were defecated after about 48 hours. One animal was recaptured 24 hours later and forced to reswallow its telemeter, providing an extra day's data. The entire process took less that 60 seconds. The following day (1/3/90), the animal showed no side-effects of the disturbance, going about its business as usual. The October and February field trips included an overnight monitoring period involving at least one animal. On these two occasions, simultaneous measurements of air, sand and a copper model temperatures were made. The copper model was placed in contact with the sand surface. Details of the copper model parameters and the sand depth probe are given in Chapter 4 (Section 4.2.2)

5.3 RESULTS

5.3.1 Water flux

Seasonal fluctuations in the water flux rates of *A. skoogi* are shown in Table 5.1. Animals lost mass during the recapture interval in October and July (-0.38 ± 0.2 and -0.79 ± 0.4 % body mass/day respectively) and gained mass during February (+0.44 ± 0.4 % body mass/day). Total body water (expressed as a percentage of body mass) was similar for all three months (about 72 % body mass). There were striking seasonal differences in water flux rates. Water influx was substantially higher in February than July (50.3 ± 15.0 versus 10.5 ± 2.1 ml/kg.day). July water influx was about double that of October (10.5 ± 2.1 versus 5.4 ± 2.8 ml/kg.day).

5.3.2 Plant analysis

The seasonal variation in energy, water and electrolyte content of selected potential food sources is

TABLE 5.1. Seasonal fluctuation in the water flux rates of male *Angolosaurus skoogi*. Recapture interval averaged 7 days in October, 9 days in February and 5 days in July.

Month	Animal number	Body mass		Body water	Water flux	
		mean (g)	change (%/day)	(% body mass)	ml IN / kg.day	ml OUT / kg.day
October 1989	1	82.2	-0.29	73.9	2.3	4.5
	2	83.2	-0.72	70.6	3.5	10.7
	3	79.2	-0.31	72.5	4.8	7.1
	4	94.2	-0.56	-	9.2	13.2
	5	60.5	-	70.1	-	-
	6	72.0	-	72.1	-	-
	7	70.3	-0.31	73.2	7.1	10.2
	Mean	78.5	-0.38	72.1	5.4	9.1
	S.D.	11.5	0.19	1.5	2.8	3.4
February 1990	1	83.5	0.0	-	47.1	47.1
	2	82.5	0.14	73.4	65.7	64.7
	3	83.3	0.20	74.0	46.2	44.7
	4	64.8	0.44	71.2	71.0	67.9
	5	53.5	0.84	-	33.0	29.1
	6	66.0	0.68	-	39.0	34.0
	Mean	72.3	0.44	72.9	50.3	47.9
	S.D.	12.6	0.37	1.5	15.0	15.8
July 1990	1	81.5	-	71.4	-	-
	2	99.0	-1.24	71.4	9.1	17.8
	3	87.2	-0.83	71.7	12.0	20.3
	4	75.5	-0.82	-	12.5	18.3
	5	89.5	-0.25	-	8.3	10.1
	Mean	86.5	-0.79	71.5	10.5	16.6
	S.D.	8.8	0.41	0.2	2.1	4.5

shown in Table 5.2. The most prominent potential *A. skoogi* food source during the entire year was the perenial cucurbit *Acanthosicyos horrida*. Although the other plant species shown in Table 5.2 occur all year round, they were, with the exception of *Merremia guerichii*, generally only conspicuous and healthy during the rainy season (January/February). With the exception of sodium, there was little seasonal variation in the water, electrolyte and energy content of *A. horrida*. The most variable electrolyte in the other plants was sodium, with two species, *Zygophyllum simplex* and *Sesuvium sesuvioides*, having markedly high sodium levels (1991 and 3458 µmol/g dry mass, respectively). Both water and potassium contents of potential insect food items were notably lower than those of potential plant foods. Energy contents showed large interspecific variations, ranging from 10.4 kJ/g dry mass in *Z. simplex* to about 19.5 kJ/g dry mass in *A. horrida*. Besides *A. horrida*, the most suitable food source in terms of electrolyte load and energy content was *M. guerichii*. There was little difference in the energy content of *M. guerichii* leaves and flowers (16.6 versus 17.1 kJ/g dry mass, respectively). Electrolyte concentrations in flowers were, however, notably lower than those in leaves, particularly in the case of sodium (78 µmol/g dry mass versus 239 µmol/g dry mass, respectively).

5.3.3 Sampled animals

With the exception of chloride, there was little variation in the composition of plasma in *A. skoogi* sampled in February and July (Table 5.3). There were, however, marked seasonal differences in the abdominal fat pad reserves of sampled animals. Fat reserves were highest in October (1.79 g/g empty gastro-intestinal tract mass), intermediate in July (0.98 g/g empty gastro-intestinal tract mass) and negligable in February (0.05 g/g empty gastro-intestinal tract mass).

Seasonal changes in the diet choice of *A. skoogi* are clearly evident in Table 5.4. In October, *A. horrida* flowers and leaves made up the major component of the diet. In February, *A. horrida* was virtually ignored and a more varied diet of *M. guerichii* flowers, *Stipagrostis hermanii* (grass) and arthropods were favoured. In July, there was a switch from *M. guerichii* flowers to shoots (flowers are not found at this time of the year). A notable contribution was also made by *S. hermanii* and seeds.

Stomach volumes, as determined by the mass difference of empty stomachs and stomachs filled to capacity with distilled water, averaged 11.5 ± 2.2 % empty gastro-intestinal tract mass (n = 16). That this species is able to fill its stomach to capacity in one sitting is clear from the specific dynamic action experiments discussed in Chapter 3, when after five days of starvation animals voluntarily ate 11.0 ± 0.6 % (n = 6) of their body mass.

TABLE 5.2. Seasonal variation in the energy, water and electrolyte concentrations of potential *Angolosaurus skoogi* food sources. Electrolyte and energy concentrations are expressed in terms of dry mass. Standard deviations are shown in parentheses.

Month	Plant	No. of samples	Water content (% wet mass)	Na^+ µmol/g	K^+ µmol/g	Cl^- µmol/g	Energy kJ/g
Oct. 1989	*Acanthosicyos horrida* (shoots)	5	83.1 (1.8)	186 (74)	743 (74)	363 (123)	19.1 (0.5)
Feb. 1990	*Acanthosicyos horrida* (shoots)	5	84.2 (2.1)	99 (46)	641 (71)	261 (129)	19.7 (0.5)
	Zygophyllum simplex	1	93.2	1991	676	3185	10.4
	Merremia guerichii (leaves)	1	88.5	239	1235	724	16.6
	Merremia guerichii (flowers)	1	85.2	78	1037	679	17.1
	Sesuvium sesuvoides	1	92.8	3458	463	766	12.1
	Stipagrostis hermanii	1	83.0	135	616	348	13.3
July 1990	*Acanthosicyos horrida* (shoots)	5	80.9 (0.6)	95 (39)	670 (44)	281 (70)	19.5 (0.2)
Tenebrionid beetles (from Mitchell *et al.* 1987)							
Cauricara brunnipes			66.8	-	108	-	-
Onymacris bicolor			65.2	-	60	-	-
Onymacris unguicularis			68.0	-	75	-	-

TABLE 5.3. Plasma electrolyte concentrations and fat content of *Angolosaurus skoogi* collected in October 1989, February 1990 and July 1990. S. D. = standard deviation. n = number of samples.

Month		Na^+ mmol/l	K^+ mmol/l	Cl^- mmol/l	Osmolarity mmol/l	Fat g/g EGTM [1]
October	Mean	- [2]	-	-	-	1.79
1989	S. D.	-	-	-	-	0.79
	n	-	-	-	-	7
February	Mean	192	4.3	131	362	0.05
1990	S. D.	6	1.3	5	12	0.08
	n	8	8	7	8	6
July	Mean	195	3.8	150	363	0.98
1990	S. D.	10	0.6	4	20	1.42
	n	6	6	6	6	5
Significance		0.452	0.430	0.000	0.876	

[1] EGTM = empty gastro-intestinal tract mass

[2] October samples discarded - see text

5.3.4 Focal animal studies

Telemeter stress tests

A representative example of the body mass change of an animal fed a model telemeter in the laboratory is shown in Figure 5.2. The other three animals treated in this way similarly maintained or increased in body mass during the telemeter transit time. This is in sharp contrast to the body mass loss that occurs when animals were starved. Telemeters thus appear to have no effect on the feeding behaviour of this species.

TABLE 5.4. Composition of *Angolosaurus skoogi* diet based on examination of stomach contents. Contribution = dry mass of component as percentage of total dry mass biomass in stomachs. Frequency = percentage of the number of stomachs containing this component (n = 7 in October 1989, 6 in February 1990 and 5 in July 1990).

Food component	October		February		July	
	Contribution	Frequency	Contribution	Frequency	Contribution	Frequency
Acanthosicyos leaves	31	0.43	2	0.34	0	-
Acanthosicyos flowers	60	0.57	1	0.17	4	0.20
Merremia leaves	2	0.14	1	0.50	57	0.40
Merremia flowers	0	-	34	0.34	0	-
Zygophyllum flowers	0	-	1	0.17	0	-
Sesuvium leaves	0	-	3	0.17	0	-
Stipagrostis	0	-	18	0.34	15	0.50
Arthropods	0	-	41	0.67	3	0.40
Seeds	0	-	0	-	21	0.20
Nematodes	0	-	0	-	< 1	0.20
Unidentified	7	-	0	-	0	-

Emergence times and activity patterns

The emergence times and duration of activity of telemetered animals during October and February are shown in Figure 5.3. Asterisks indicate uncertainty concerning emergence/burial times. It is quite clear that animals are emerging earlier and remaining on the surface for much longer periods in February. During this month, animals usually emerged at about 11h00 and remained on the surface for two to three hours. Very short second activity periods later in the afternoon (15h00 - 16h00) were often observed. During October, animals usually emerged at about 13h00 and never remained on the surface for more than an hour. There is no evidence of the bimodal activity pattern observed in February.

FIG 5.2

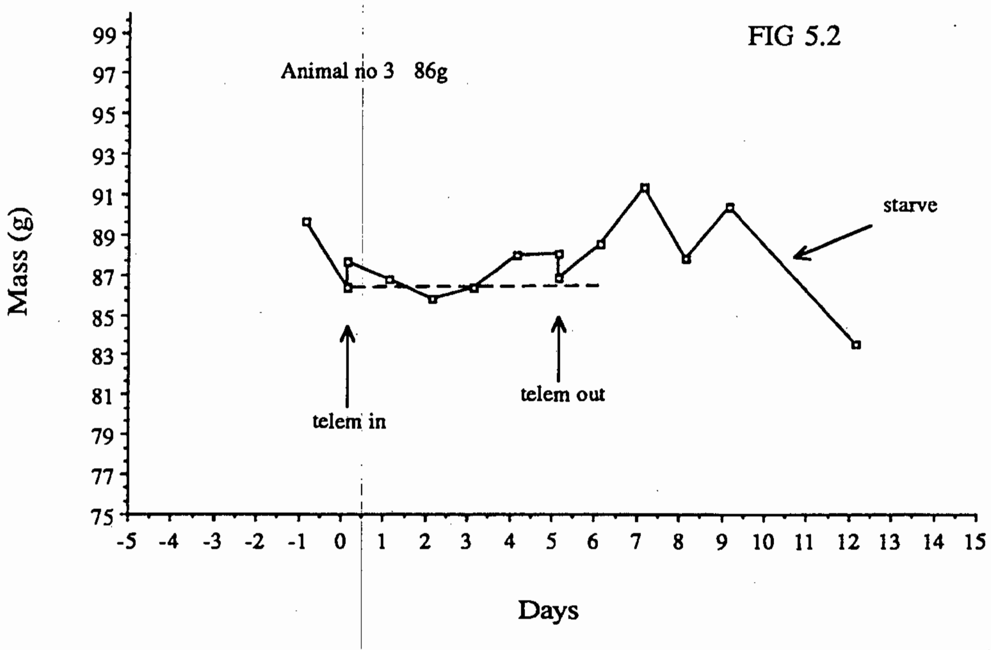


FIGURE 5.2. Representative example of a laboratory telemetry test on an adult male *Angolosaurus skoogi*. The telemeter was ingested on Day 0 and defecated on Day 5. The animal was offered freshly grated carrots *ad lib.* every day. Commencing on Day 9, the animal was starved for a period of 4 days.

Details of the frequency and duration of activity and feeding behaviour are shown in Table 5.5. In October, animals were observed for a period of 5 - 7 days. On two days, animal number 2 buried in a position which was both out of sight and out of range of the telemetry receiver. For this reason, two values appear in the "days active" column, representing "days definitely active" and "days definitely active + possibly active". Taking possible unnoticed activity into account, October animals were, on average, active every 2.5 ± 1.7 days. Activity occurred within a 90 minute period (12h30 - 14h00, n = 10). On only five occasions was the duration of activity established with certainty, averaging 21.3 ± 19.5 minutes/day. Animals thus spent on average less than 1 % of their time on the surface. It was not always possible to confirm that animals had eaten on a particular day. For this reason, the "days eat" column has also been divided into two sections - "definitely eat" and "definitely + possibly eat". Taking possible unnoticed feeding into account, October animals fed, on average, every 3.7 ± 2.2 days.

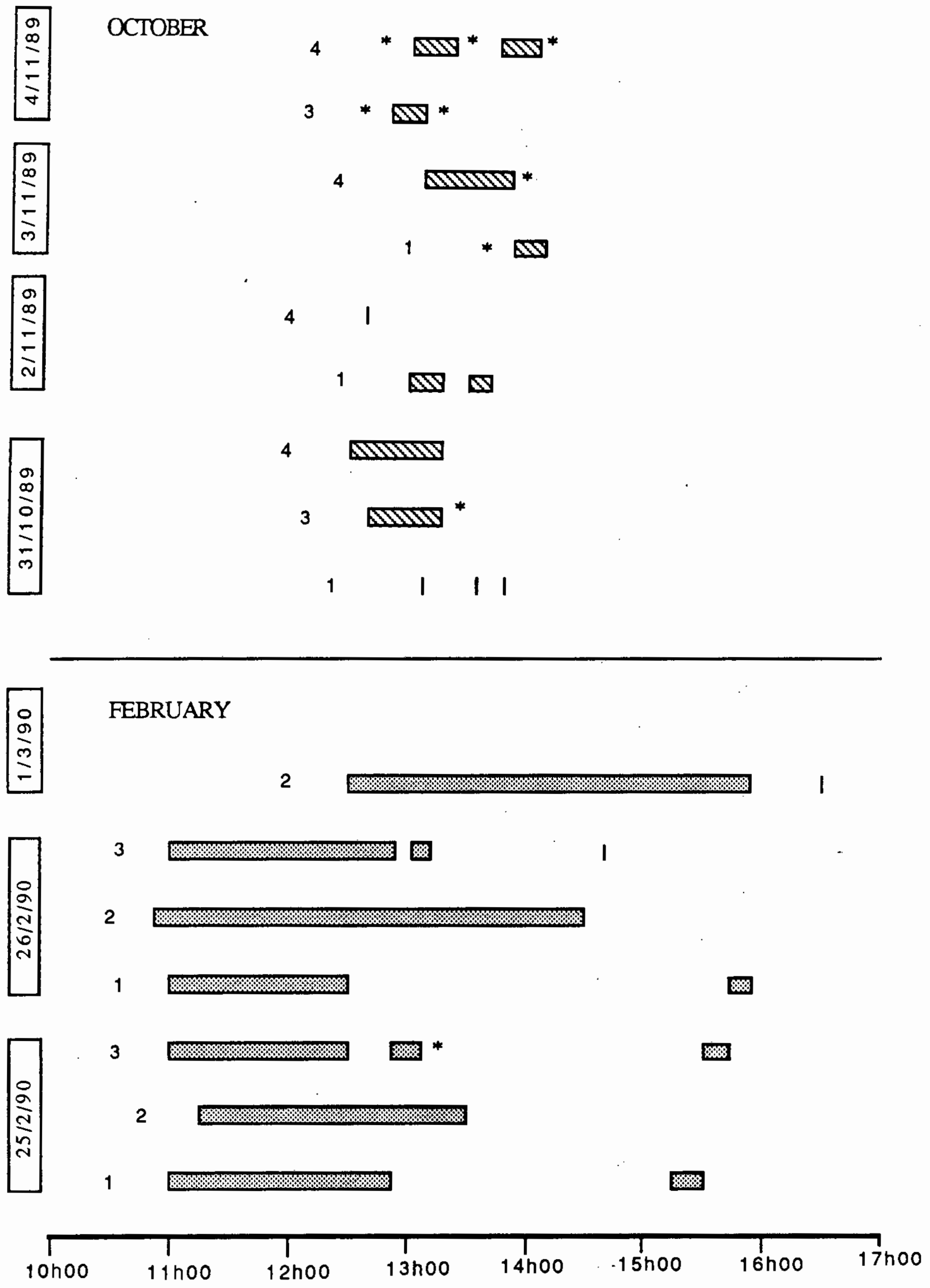


FIGURE 5.3. Emergence times and the duration of activity of telemetered male *Angolosaurus skoogi* during October 1989 and February 1990. Asterisks indicate uncertain emergence or burial times. Animal numbers are indicated on the left hand sides of the shaded bars.

TABLE 5.5. Parameters of male *Angolosaurus skoogi* activity and feeding behaviour during October 1989 and February 1990. Sample size, n / standard deviation are indicated in parentheses.

Month	#	Days observed	Days active	f activity[1]	Duration of activity	Total activity time (min)	% time active	days eat D / D + P[2]	f days eat D / D + P[2]
Oct	1	6	3	2.0	13h04-14h06 (n=3)	39+ (n=3)	0.4%+	0 / 1	- / 6
1989	2	5	1	5.0	12h26-12h44 (n=1)	18+ (n=1)	0.3%+	0 / 1	- / 5
	3	7	2 / 4[3]	3.5 / 1.8	<12h49-13h18> (n=2)	52+ (n=2)	0.5%+	2 / 5	3.5 / 1.4
	4	7	4	1.8	12h27-13h56> (n=4)	120+ (n=4)	1.2%+	1 / 3	7.0 / 2.4
	x or range			3.1 / 2.5	12h26-14h06 (n=10)	21.3	0.6%		5.2 / 3.7
	S.D.			(1.5) / (1.7)		(19.5)	(0.4)		(2.5) / (2.2)
	n			n = 4		n = 5[4]	n = 4		n = 4
Feb	1	2	2	1.0	10h59-15h43 (n=2)	207 (n=2)	7.2%	-	-
1990	2	3	3	1.0	10h53-16h23 (n=3)	538 (n=3)	12.5%	-	-
	3	2	2	1.0	10h58-15h39 (n=2)	248 (n=2)	17.3%	-	-
	x or range			1.0	10h53-16h23 (n=7)	142	9.4		
	S.D.			(0.0)		(44)	(2.7)		
	n			n = 3		n = 7	n = 3		

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[1] f = frequency

[2] D = definitely fed ; D + P = definitely + possibly fed

[3] See text for explanation

[4] Only used data for which complete activity time had been established

During February, animals were observed for a shorter period (2 - 3 days) but were, without exception, active every day. Activity was observed between 10h53 and 16h23 and averaged 142 ± 44 min/day (n = 7). The percentage time spent on the surface thus averaged 9.4 ± 2.7 %. As February animals spent much of their time on *Merremia* mounds (see below) where they were often out of sight, feeding behaviour was rarely observed and insufficient data exists to fill the last two columns in Table 5.5. Considering the high water flux rates of these animals (Table 5.1), it is probable that animals fed on a daily basis.

Location during surface activity

During October, animal activity was confined to the upper dune slipface, dune top and the most westerly nara bush shown in Figure 5.1 (Table 5.6). Out of 179 minutes of observation, 54 % of the time was spent in the Nara, 30 % on the dune top and 16 % on the dune slipface. The emergence pattern was consistent. Animals would ascend from their burial depth and lie just below the surface with only their heads exposed. This position would be maintained for about 10 - 35 minutes (x = 19 ± 12, n = 6, Table 5.6 and see Figure 5.6a below). Animals would then emerge, and slowly make their way to the dune top. On the way to the dune top, a contact posture position was often evident (see posture 1 in Seely *et al.* 1988). This involved pushing the ventral surface of the body onto the sand. This behaviour generally continued for a few minutes after which a "tail up" position was frequently observed (see posture 6 in Seely *et al.* 1988). This involved posturing the body so that minimal surface area was in contact with the ground. The forelimbs are straightened so that the head and chest were elevated above the substrate, the hindlimbs lifted off the ground and the tail curled upwards. The result was that only the ventral surface in the vicinity of the pelvic girdle was in contact with the ground. The amount of time spent stationary and moving while on the slipface and top was analysed (Table 5.6). Most of the time (about 90 %) was spent stationary.

In contrast, February animals spent very little time on the dune slipface and top and no time in the nara. Most of the time (87 %) was spent on the gravel plain and *Merremia* mounds. The emergence pattern was once again consistent. The head out position was either not adopted or, if engaged, was of very short duration (Table 5.6 and see Figure 5.6a). On emerging, animals would spend very little time on the slipface, usually running down to the gravel plain immediately. Excursions to the dune top were rare. The contact posture position was seldom observed. In contrast, the tail up position was used almost continuously when animals were on the slipface or dune top.

TABLE 5.6. Activity times and habitat location selection of male *Angolosaurus skoogi* during October 1989 and February 1990. Percentage time (%), standard deviation ( ) or sample size (n =) indicated in parentheses.

Month	#	Days active (min)	Total activity time (min)	Time location known (min)	Location time[1]					Activity state time (min) (on S/F and Top)		
					S/F	Top	Gp	Mo	Nara	active	stationary	H/O [2]
Oct.	1	3	40	35.3	17.1	18.2	-	-	-	3.7	29.3	26 (n = 1)
1989	2	1	18+	4.1	2.0	2.1	-	-	-	0.2	3.2	9 (n = 1)
	3	2	52+	49.8	2.8	3.4	-	-	43.6	0.5	2.6	7 (n = 1)
	4	4	120+	89.7	6.5	30.0	-	-	53.2	2.4	29.6	69 (n = 3)
total or x					28.4	53.7	-	-	96.8	6.8	64.7	19
(%) or (SD)					(16%)	(30%)			(54%)	(10%)	(90%)	(12)
n												(n = 6)
Feb	1	2	207	137	20	11	74	49	-			1.6 (n = 2)
1990	2	3	538	461	23	8	144	286	-			0 (n = 1)
	3	2	248	153	21	18	89	25	-			0 (n = 1)
total or x					64	37	307	360	-			0.4
(%) or (SD)					(8)	(5)	(40)	(47)				(0.8)
n												(n = 4)

[1] S/F = slipface, Top = dune top, Gp = gravel plane, Mo = *Merremia* mound

[2] H/O = head exposed, body still under sand.

Breeding behaviour

The main reason for the seasonal contrast in the parameters detailed in Tables 5.5 and 5.6 is the fact that intense breeding behaviour was in progress during February. The three telemetered February males held well-defined territories which together covered the entire slipface and most of the gravel plain in front of the dune. Figure 5.1 shows the estimated territorial boundaries, based on positions where aggressive displays by the territorial holder took place. The surface area of each territory was about 500 m^2. Territorial borders were particularly well defined at the base of the slipface and in both cases (on either side of animal number 3^S territory) were demarcated by a piece of driftwood (deposited some time in the past when the river had been in flood). Large *Merremia* mounds formed the axis of each territory. All three animals had favourite "perches" within these mounds and most of their activity time was spent on these observation posts looking out for intruding males and eligible females.

Two types of interactions were observed between territory holders and other males. Males from adjacent territories would, at least once a day, approach each other and meet at the territory border (territorial boundary confirmation, Table 5.7). A short "show of force" period of about 2 - 3 minutes would follow. Both animals would straighten up on all four legs and circle each other. Hissing was sometimes observed. In no cases was body contact made and borders were never violated. Territorial defence against intruding males was observed very infrequently (Table 5.7). On average, this form of interaction was only observed twice a day. When a foreign male encroached on a territory, however, the response of the territory holder was immediate and involved a high speed approach towards the intruder and an ensuing high speed chase until the intruder was across the border. Bodily contact was never observed, the intruder fleeing before this could occur. The most common behaviour during the activity period was courtship behaviour (Table 5.7). The three telemetered males courted females on average every 12 minutes. Courtship involved approaching a female, circling around her with a jerky motion, and bobbing the head up and down. The response of females was generally to evade the advancing male either by running away or by burying in the slipface. Copulation was never witnessed, the female pulling away as soon as the male attempted to make bodily contact.

Subsurface body temperatures

Table 5.8 shows the seasonal variation in the range and average body temperature of telemetered animals when they were under the slipface surface. These values represent measurements separated by at least an hour, and taken before activity and after 18h00 when the body temperatures of animals that had been active had stabilized.. Average body temperatures ranged from about 27 -

TABLE 5.7. Parameters of breeding behaviour in male *Angolosaurus skoogi* during a 2-3 day observation period in February 1990.

Animal	Days	Total time	Territorial defence			Territorial boundary confirmation				Courtship behaviour		
number	observed	observed (min)	Total	f[1] (/x min)	f(/day)	Total	f(/x min)	f(/day)	(# involved)	Total	f(/x min)	f(/day)
1	2	137	4	34	2.0	2	69	1.0	(3/3)	9	15	4.5
2	3	461	9	51	3.0	4	115	1.3	(3/3,3/other)	34	14	11.3
3	2	153	4	38	2.0	5	31	2.5	(1,2/1,2,2)	22	7	11.0
Total	7	751	17			11				65		
x				41	2.3		72	1.6			12	8.9
S.D.				(9)	(0.6)		(42)	(0.8)			(4)	(3.8)

[1] f = frequency

TABLE 5.8. Subsurface body temperatures (Tb) of field male *Angolosaurus skoogi* during October 1989, February 1990 and July 1990. Standard deviations are shown in parentheses. Measurements were separated by at least an hour, and taken before activity or after 18h00 when the body temperatures of animals that had been active had stabilized.

Month	Animal number	Observation period (days)	n	Average Tb (°C)	Range (°C)	Temperature Stability (time, hours / range, °C)
October 1989	1	5.5	47	27.2 (0.3)	26.5 - 27.8	53.3 / 27.0-27.1[1]
	2	5.0	33	26.8 (2.6)	20.7 - 31.0	
	3	4.2	25	26.5 (0.6)	25.7 - 28.2	
	4	6.2	35	27.7 (0.6)	26.0 - 28.3	24.2 / 27.4-27.8[1]
February 1990	1	2.5	11	33.2 (0.6)	31.8 - 33.7	
	2	4.3	30	32.2 (1.4)	30.1 - 34.3	11.2 / 31.8 - 34.0[1]
	3	2.5	11	30.2 (1.2)	28.4 - 33.0	
July 1990 (pre east wind)	1	2.2	40	21.8 (0.2)	21.4 - 22.2	34 / 21.7-22.2[1]
	2	2.2	38	23.3 (1.0)	20.9 - 24.2	33 / 23.4-23.9[1]
	3	2.5	11	30.2 (1.2)	28.4 - 33.0	34 / 22.4-22.7[1]
(east wind)	1	1.8	23	29.5 (4.3)	22.2 - 34.0	
	2	1.8	25	28.2 (0.4)	22.2 - 34.0	

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[1] included overnight monitoring

28 °C in October, 30 - 33 °C in February and 22 - 23 °C in July. During the hot east wind conditions in July, animals clearly took advantage of warm conditions that persisted in the upper layers of sand and had average body temperatures of between 27 and 30 °C. This is shown in Figure 5.4. The spikes on each trace in Figure 5.4a are due to activity. The east winds had no effect on sand temperatures at lower depths (Figure 5.4b), so animals were clearly only burying to shallower layers which were being influenced by the hot conditions. With one exception (October animal no. 2 which spent some time in shallow sand) body temperatures generally showed a range of less than about 3 °C. The temperature stability (as good as 0.1 °C over a period of 53 h) indicate that animals bury to a depth where only small temperature fluctuations occur.

Overnight measurements of air, copper model, sand and lizard body temperatures in October and February are shown in Figures 5.5a and 5.5b, respectively. It is clear that by burying animals are able to maintain body temperatures 10-15 °C higher than they would if they remained on the sand surface. Body temperatures during both months show very little variation throughout the night, as do sand temperatures below about 30 - 35 cm. Thus animals must overnight at a depth exceeding 30 cm. In both months, body temperatures are consistently about 2 °C higher than the temperature recorded at the lower depths. There could be several explanations for this. Firstly, it was not possible to put the sand probe in the same vicinity as the lizard as its exact position was unknown and there was a danger of disturbing or even injuring the animal. Spatial heterogeneity in temperature at certain depths may thus account for the discrepency observed. Secondly, animals could be burying to a depth in excess of 50 cm where sand temperatures may be warmer. This, however, is unlikely as there is a negligible change in sand temperature between 30 and 50 cm. Finally, lizard body temperature may be elevated above sand temperature due to some physiological process such as digestion.

Rates of heating (before and after emergence) and cooling (after burial) are shown for October and February in Figures 5.6 and 5.7 respectively. Time 0 equals emergence/burial time. Head basking in October clearly serves to bring body temperature up from about 27 to 31 - 34 °C (Figure 5.6a). The heating rate during head basking averaged 0.31 ± 0.06 °C/min (n = 4). After emergence, heating rates more than doubled, averaging 0.88 °C/min (n = 3). This enabled animals to reach their preferred surface body temperature in less than 10 minutes. In February, when head basking was observed only once, a heating rate of about 0.45 °C/minute was observed (Figure 5.6b). Following emergence, heating rates averaged 0.82 ± 0.16 °C/min (n = 3). It is interesting to note that the range of emergence temperature (31 - 34 °C) is the same for both months. In February, head basking is not required to reach the lower limit of the range. There is a marked contrast between the cooling rates (following burial) in October and February (Figures 5.7a and 5.7b). In October, animals appear to remain in the warmer upper layers of sand after burying. The result is that body temperatures only dropped to and stabilized at normal subsurface values after about four hours. In February, on the other hand, animals appear to burrow down to the cooler lower depths

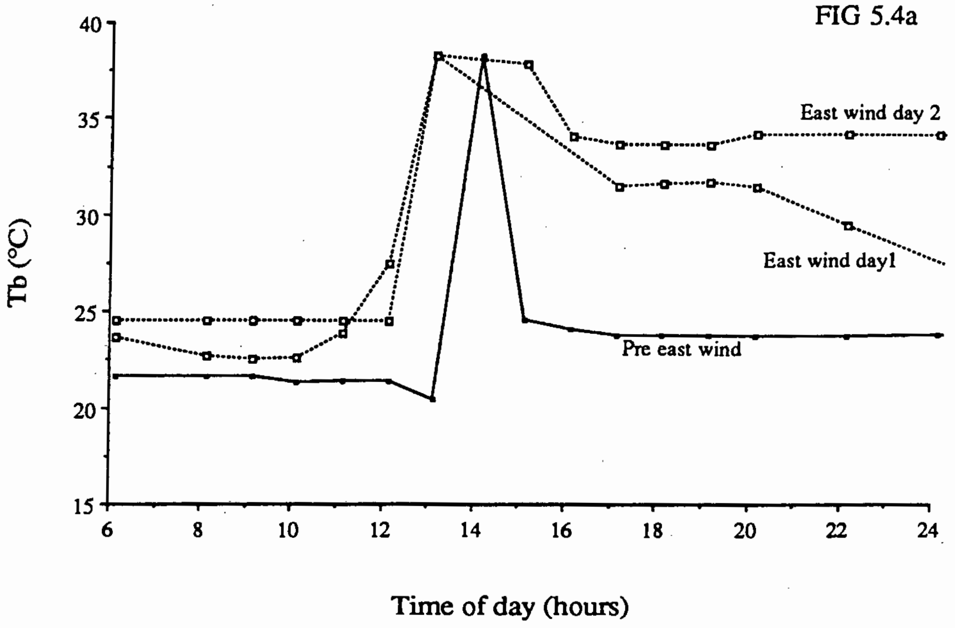


FIGURE 5.4a. Subsurface body temperature (Tb) of an individual male *Angolosaurus skoogi* as a function of time. The lower curve (closed squares) shows the body temperature over a 24 hour period during normal (pre east wind) conditions in July 1990. The upper two curves show the body temperature over a 24 hour period during hot (east wind) conditions. The spikes on each curve represent brief (< 1 hour) periods of activity.

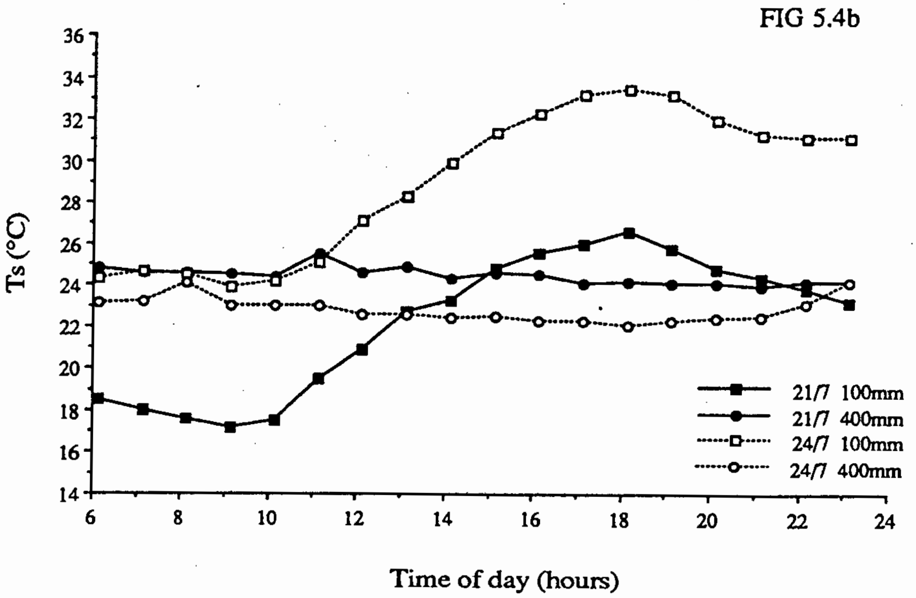


FIGURE 5.4b. Sand temperature (Ts) measured at depths of 100 and 400 mm below the upper slipface surface of the July microclimate dune. The two solid lines show temperatures during normal conditions in July 1990 (21/7/90). The two dashed lines show temperatures taken at precisely the same location 3 days later (24/7/90) during hot east wind conditions.

FIG 5.5a

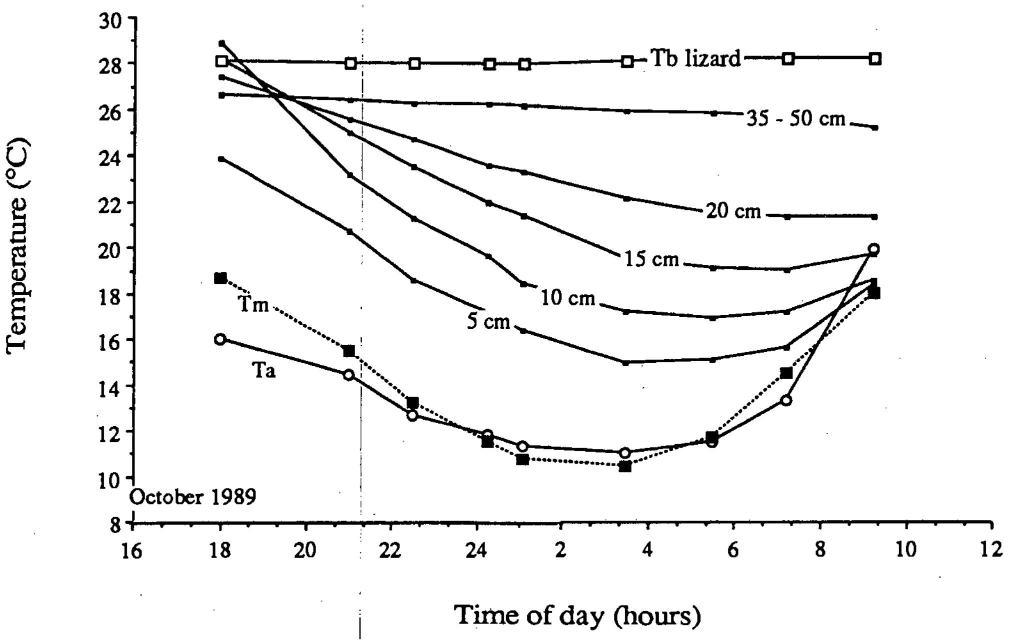


FIG 5.5b

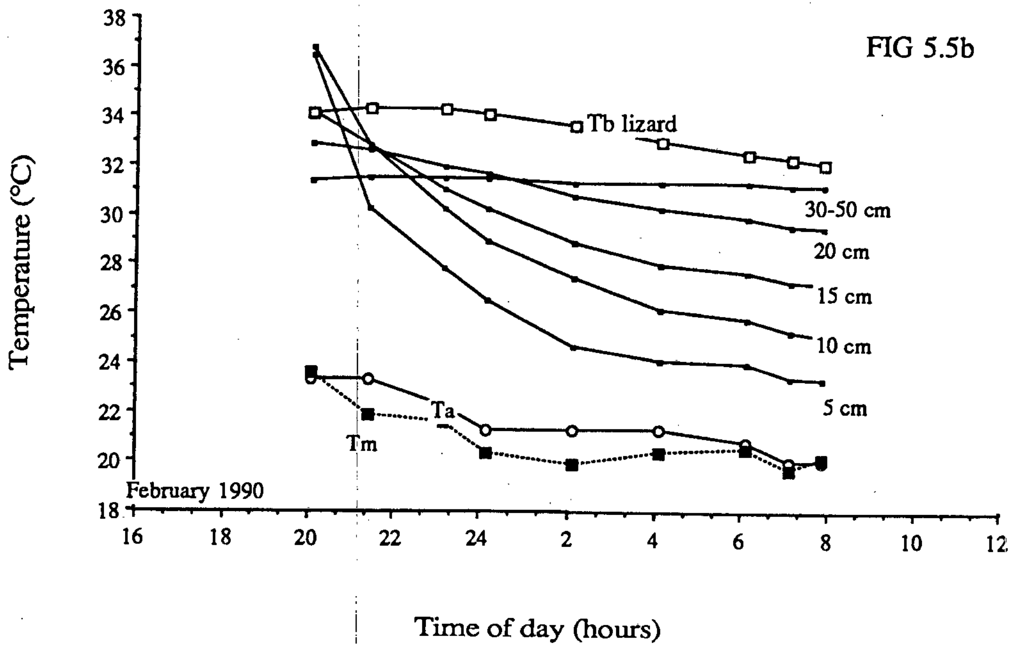


FIGURE 5.5. Ambient air (Ta), copper model (Tm), submerged lizard body (Tb) and subsurface sand (5 - 50 cm depth) temperatures of a dune slipface as a function of time. Measurements were taken during the night at the upper east/west slipface of the animal observation dune on (a) the 31/10 - 1/11 (October) 1989 and (b) the 1/3 - 2/3 (February) 1990. The sand depth probe was inserted into the slipface about 1 m from the submerged lizard.

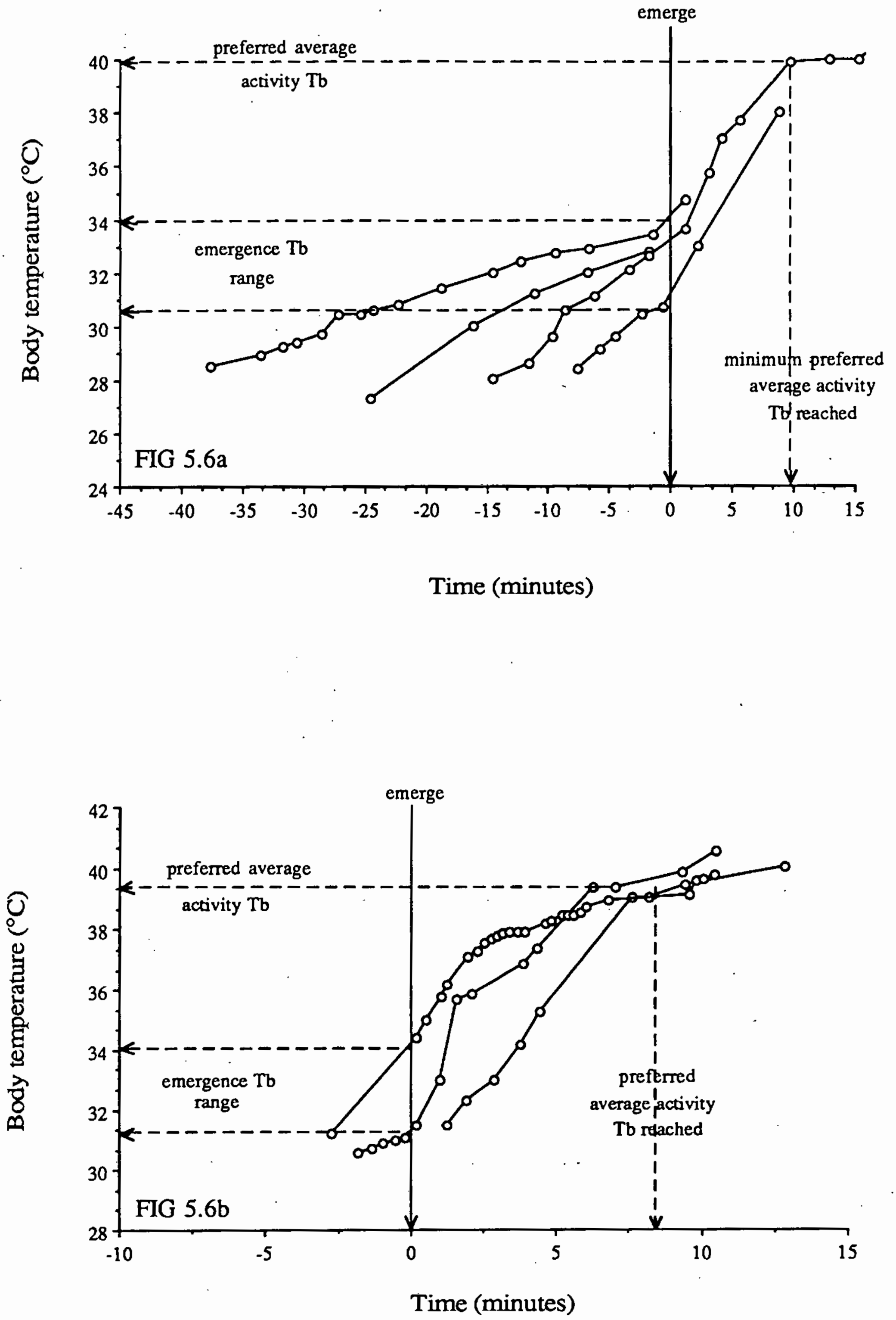


FIGURE 5.6. Heating rates of male *Angolosaurus skoogi* just prior to and following emergence from the sand in (a) October 1989 and (b) February 1990. Time 0 = emergence time. The curves before emergence are for individuals engaged in head basking (head out of sand, rest of body submerged) behaviour. Tb = body temperature.

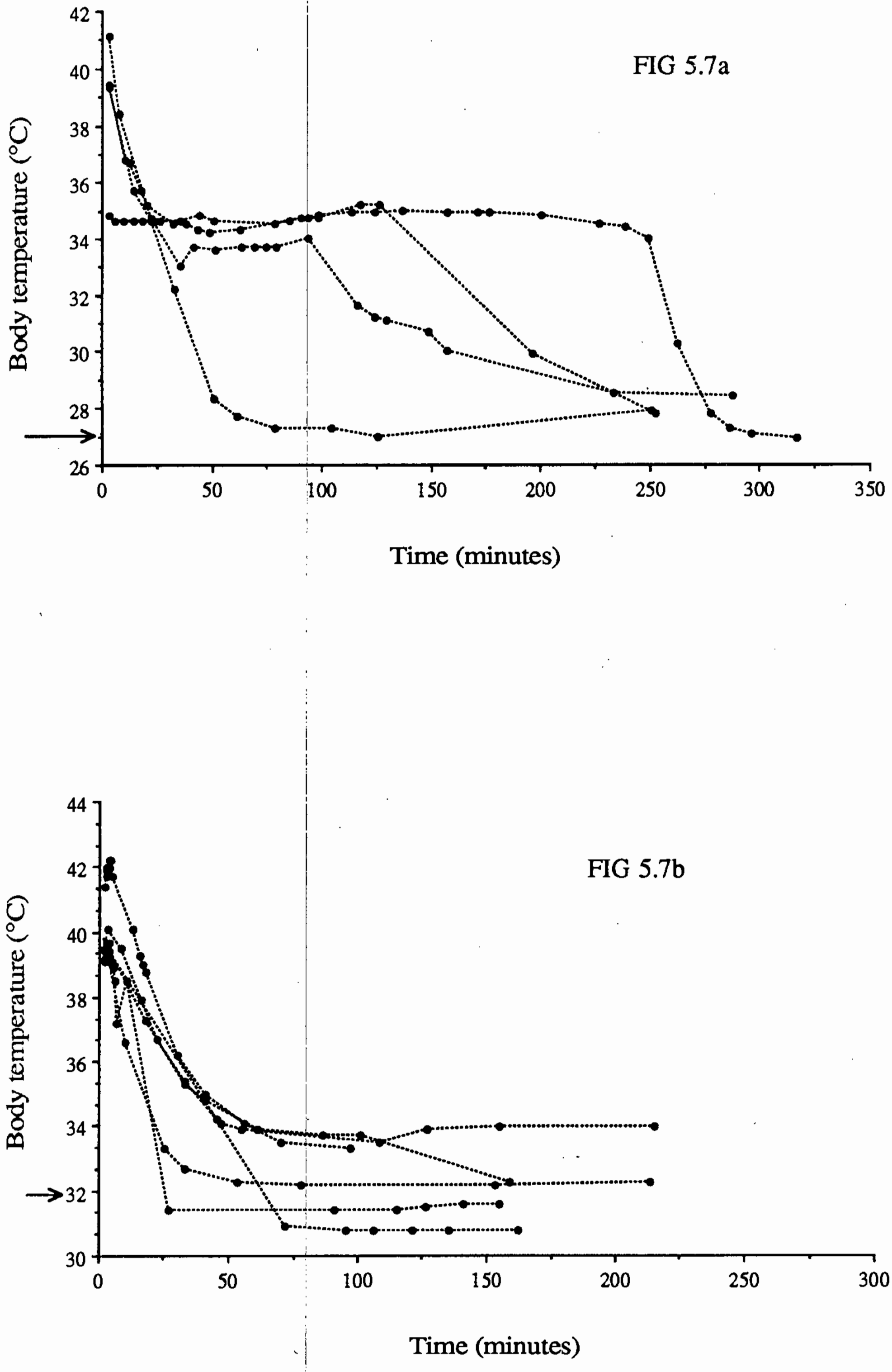


FIGURE 5.7. Cooling rates of male *Angolosaurus skoogi* after burying in slipface sand in (a) October 1989 and (b) February 1990. Time 0 = burial time. The arrows on the vertical axes indicates the average value at which body temperatures eventually stabilized (see Table 5.8).

soon after burying. The result is that body temperatures stabilized at normal subsurface values after about an hour.

Surface body temperatures

The combined observations of body temperatures of surface active animals are shown in Figures 5.8a (October) and 5.8b (February). Time 0 equals emergence time. Body temperatures recorded while animals were warming up to their surface active temperatures have been discarded. In October, surface body temperatures ranged from about 39 to 41 °C.. In February, body temperatures showed a greater range of about 37 to 43 °C.

No patterns in thermoregulatory behaviour were evident in October. In February, however, thermoregulation stategies were clear. Figure 5.9a shows a typical body temperature - time trace recorded for an individual animal in February. There appears to be no effort to maintain a precise constant body temperature. Instead, alternating periods of heating and cooling fluctuate around an average body temperature of about 39 °C. This themoregulatory pattern is known as shuttling (Avery 1979). An examination of the animal's behaviour and location during this trace reveals the cause of the fluctuating body temperature. Figure 5.9b superimposes behaviour and location on the body temperature during the last 50 minutes of the activity period shown in Figure 5.9a. Clearly, whenever the animal is inactive on a *Merremia* mound, a steady drop in body temperature results. When on the mound, one of two postures was adopted. "Perching" involved orientating the body at an angle of about 45 - 60 degrees to the ground by holding onto a dead branch or piece of driftwood with the front limbs. Alternatively, animals would climb into the *Merremia* plant. This resulted in elevation of the body above the substrate and partial to almost complete shading of the body by the leaves. The sight of potential mates or territorial intruders caused the animal to move onto the gravel plain (or in some cases the slipface). This resulted in a rapid increase in body temperature. The rate at which body temperature increased when on the gravel plain indicates that thermally dangerous body temperatures (assumed to be about 43 °C +, see Bradshaw 1988) would eventually be inevitable. The animal had to return to its mound to prevent this from happening.

Besides "perching" and shading by foliage, two other methods of cooling were observed. Firstly, animals would frequently climb onto small boulders scattered on the gravel plain. By selecting the part of the boulder which was shaded from the sun and at the same time lifting the body off the hot substrate, a decreases in body temperature could be achieved. This is illustrated in the first part of Figure 5.10a. Secondly, animals would sometimes bury in the slipface for brief periods during which they would presumably move to a depth where cooling could be achieved. This is illustrated in Figure 5.10b. Although, in this case, the animal was not seen entering the slipface, the body temperatures recorded during its out of sight (OOS) period all came from the

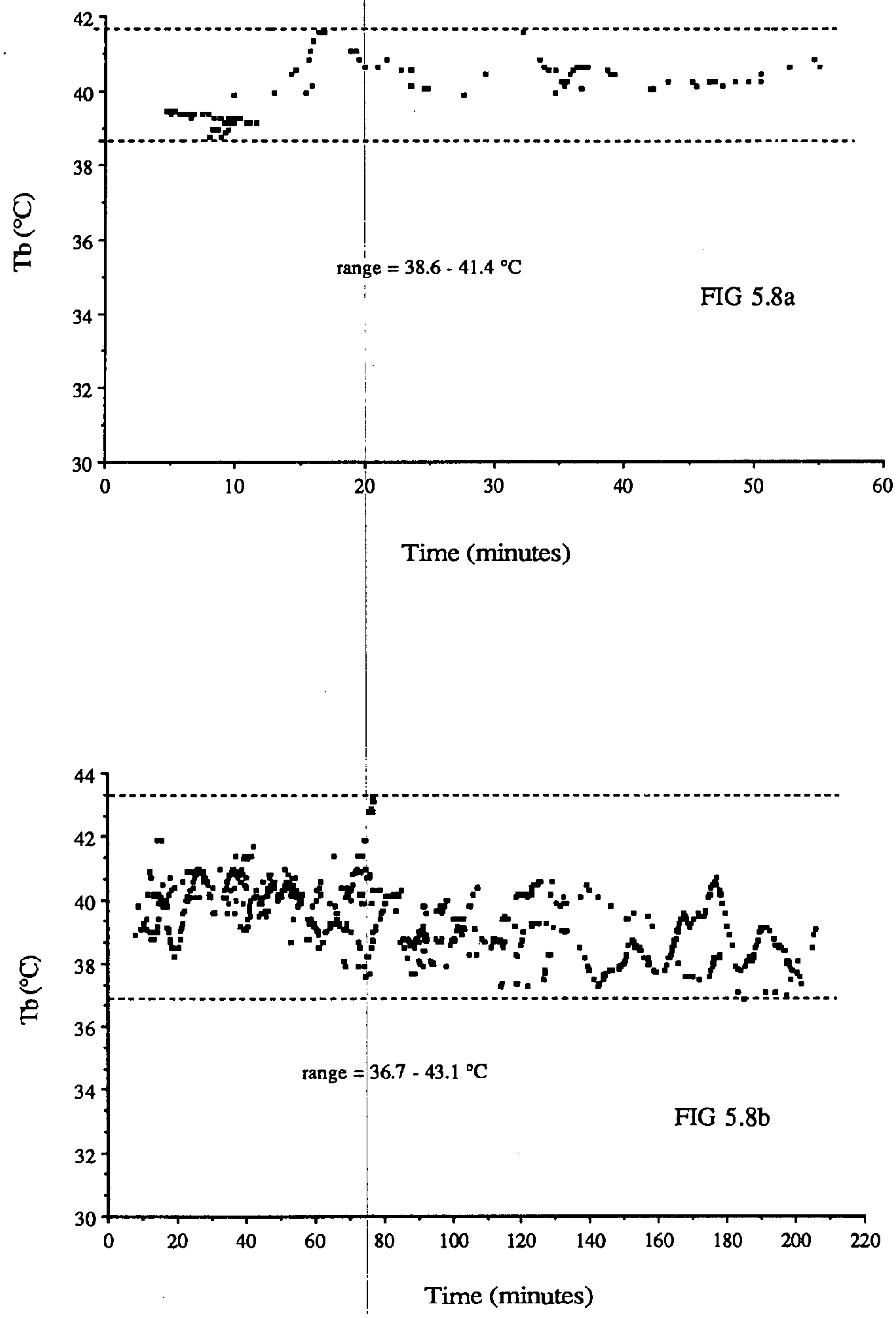


FIGURE 5.8. Combined measurements of activity body temperatures (Tb) of the four/three telemetered male *Angolosaurus skoogi* over a period of (a) 7 days in October 1989 and (b) 3 days in February. Time 0 = emergence time. Body temperatures recorded while animals were warming up to their surface active temperatures have been discarded. The upper and lower horizontal lines demarcate the range of body temperatures recorded.

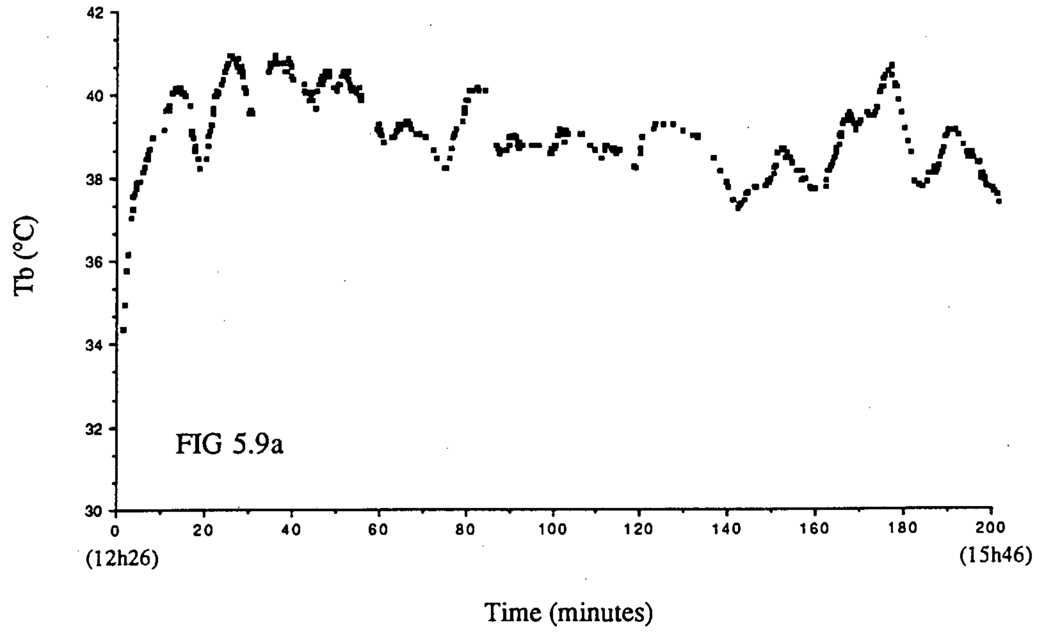


FIGURE 5.9a. Body temperature (Tb) of an individual active male *Angolosaurus skoogi* in February 1990 (animal no. 2, 1/3/90). Time 0 (12h26) = emergence time. Time 200 (15h46) = burial time.

location the animal eventually emerged from. The gravel plain was not the only place rapid heating took place. This is demonstrated in the last part of Figure 5.10a where an animal spent about 6 minutes on the dune top. During this time, the body temperature increased by 3.3 °C to a dangerous level of over 43 °C. At this point the animal moved onto and buried in the slipface.

Representative examples of simultaneous measurements of copper model temperatures (see Section 4.3.2, Chapter 4) and surface lizard body temperatures are shown in Figures 5.11 (October) and 5.12 (February). In all cases, animals were active at the hottest time of the day and body temperatures fell within the range of temperatures predicted by the copper models. Considering that in October OFF models (models not in contact with the substrate) were only placed at one site (see Chapter 4) and therefore predicted minima could be even lower, and assuming that model temperatures were representative of potential lizard body temperatures, October animals were thermoregulating at body temperatures well above the predicted minima. According to the predictions of models, higher body tempertures could have been obtained but these would have been in excess of 40 °C and possibly thermally dangerous to animals. In February, body temperatures

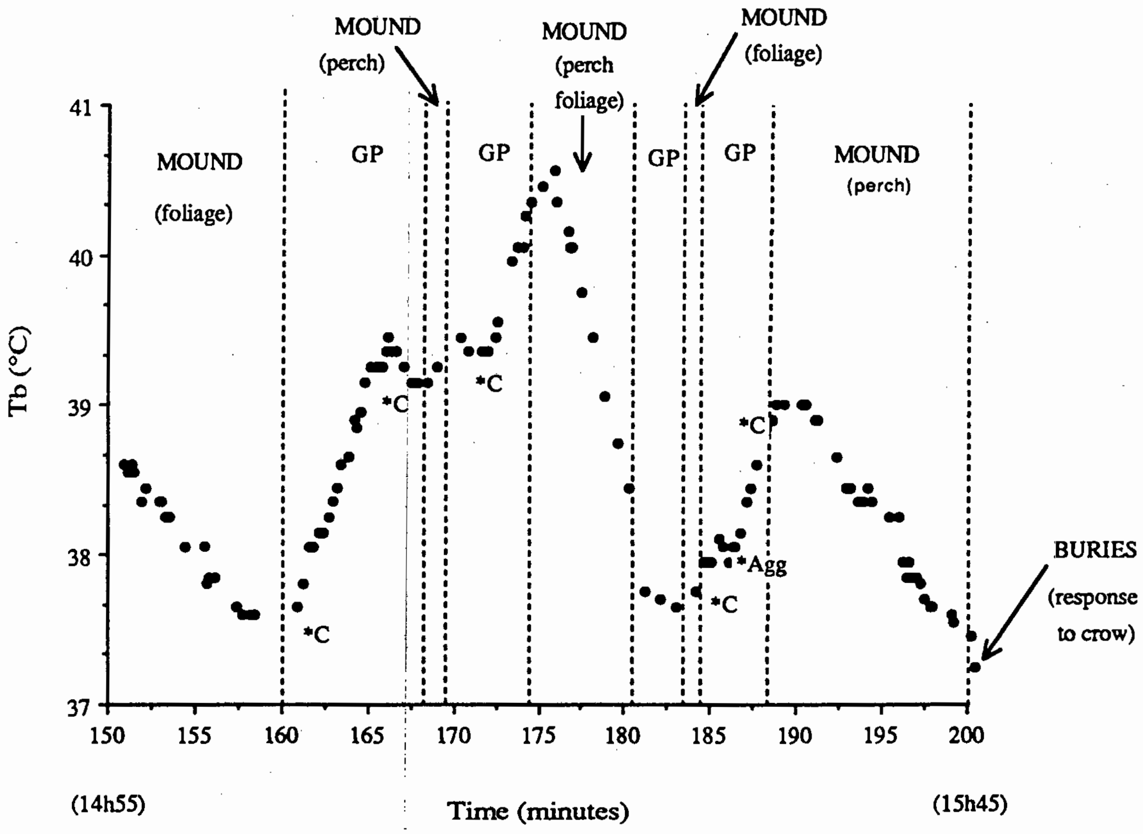


FIGURE 5.9b. Detailed analysis of a section (150 - 200 minutes) of the body temperature (Tb) trace shown in Figure 5.9a. The vertical bars indicate location changes : MOUND (foliage) = resting in or on *Merremia* leaves ; MOUND (perch) = in immediate vicinity of a *Merremia* mound, orientating the body at 45-60^{0} to the ground by holding onto a dead branch or piece of driftwood with the front limbs ; GP = moving around on the gravel plain. Asterisks indicate times when breeding behaviour was observed : C = courting ; Agg = aggressive response to a territorial intrusion by another male.

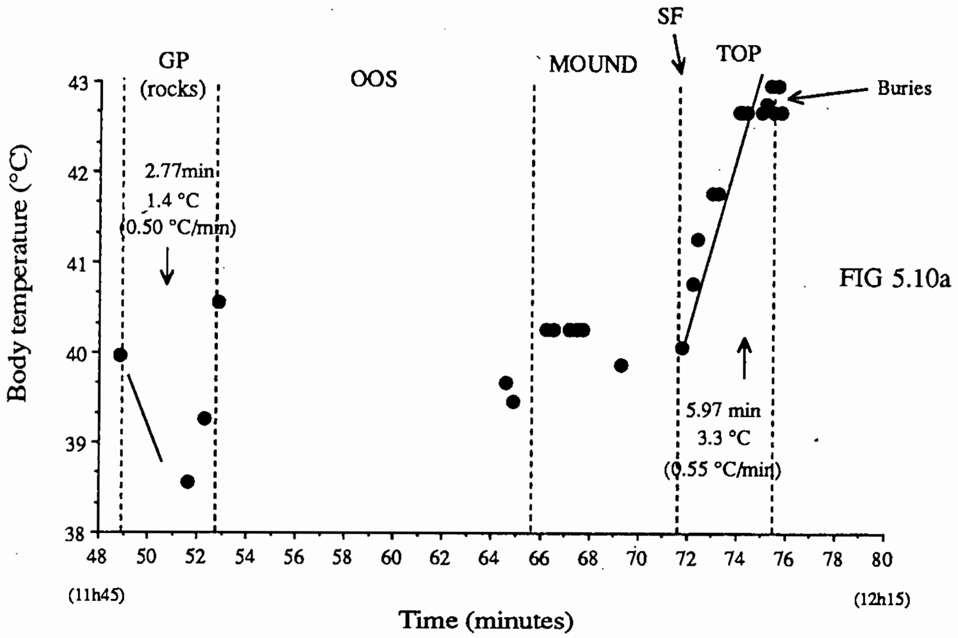


FIGURE 5.10a. Body temperature (Tb) of a male *Angolosaurus skoogi* during part of its activity period in February 1990 (animal no. 1, 26/2/90). The vertical bars indicate location changes : GP (rocks) = animal climbing onto small boulders scattered on the gravel plain ; MOUND = *Merremia* mound ; SF = moving up the dune slipface ; TOP = stationary on the dune top ; OOS = animal out of sight, telemetry signal lost. Rapid cooling took place during the rock climbing behaviour. Rapid heating occurred when the animal was stationary on the dune top.

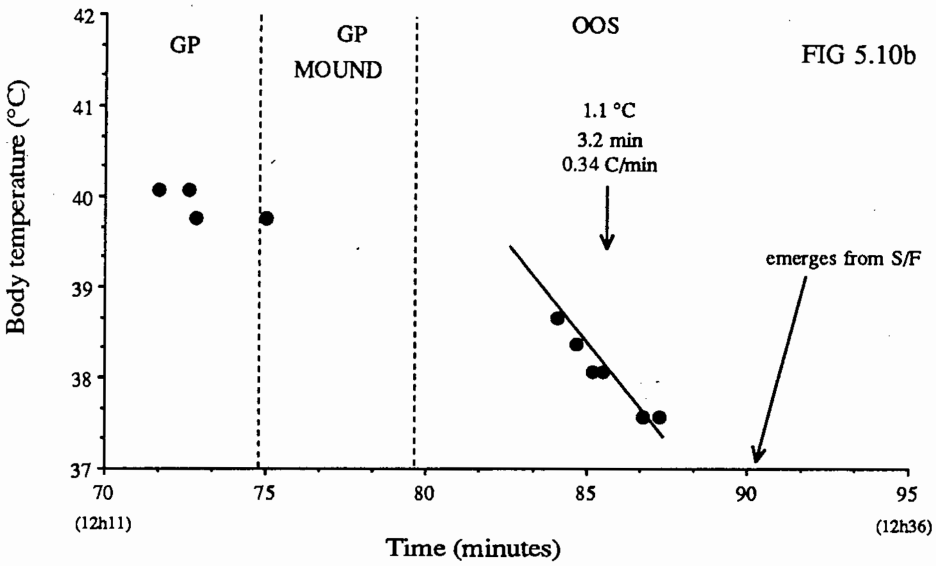


FIGURE 5.10b. Body temperature (Tb) of a male *Angolosaurus skoogi* during part of its activity period in February 1990 (animal no. 1, 25/2/90). The vertical bars indicate location changes : GP = moving around on gravel plain ; MOUND = resting on or in *Merremia* leaves ; OOS = animal out of sight, telemetry signal still audible ; SF = slipface. The animal disappeared from sight at about T = 80 minutes and was next seen emerging from the slipface at T = 90 minutes. A body temperature drop of 0.34 °C was recorded during this period.

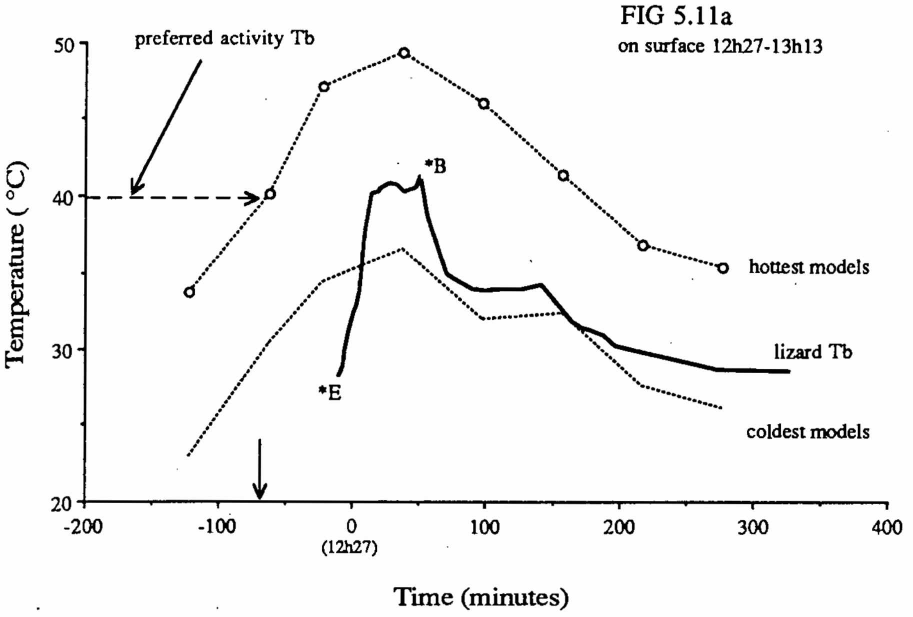
were very close to the minima predicted by the copper models. Body temperatures were also not far off from thermally dangerous values, suggesting that slightly hotter conditions could preclude surface activity at this time of the year. This may be true on the slipface and bare gravel plain but, according to the results of the copper model thermoregulatory experiment conducted on the telemetry dune (Section 4.3.2, Chapter 4), not the case on *Merremia* mounds where animals adopted "perching" postures and made use of foliage to keep cool. By making use of these locations and postures, it is predicted that animals could maintain body temperatures below 35 °C (Figure 4.13, Chapter 4). It thus appears that in both October and February, animals were maintaining body temperatures that were high relative to minima predicted by copper models and not far off what is known to be lethal to reptiles. They can thus be considered to be behaving as maxitherms during periods of surface activity.

Assuming once again that model temperatures are representative of potential lizard body temperatures, it is clear that, in both October and February, animals could emerge and obtain their preferred surface body temperature between one and three hours before they actually commence activity (Figures 5.11 and 5.12). Similarly, animals could remain on the surface and maintain preferred body temperature much longer than they actually do. If the time that animals could spend on the surface at their preferred body temperature is defined as potential activity time, actual activity time expressed as a percentage of potential activity time was only about 15 % in October and 50 % in February. Clearly, animals were not, especially in October, acting as maxitherms with respect to selected activity time.

5.4 DISCUSSION

5.4.1 Water flux rates

Water flux rates in reptiles can be extremely variable. This is usually due to changes in food quality and cessation of feeding and/or activity. Nagy (1972), for example, observed a 73-fold change in the water flux rate of the chuckwalla, *Sauromalus obesus*, between spring and its winter hibernation period. The water flux rate of *Angolosaurus skoogi* is no exception to this type of variability (Table 5.1). In February, average water influx rate shows a 10-fold increase over that in October and a 5-fold increase over that in July. The February water influx value (50.3 ml/kg.day) is three times higher than the predicted value for a desert reptile of this size (15.6 ml/kg.day - Nagy and Peterson 1988). As food quality during the different months remains similar (Table 5.2), this variability can only be attributed to increased subsurface body temperatures (Table 5.8) and activity (Table 5.5) in February, resulting in higher feeding rates to compensate for increased water losses and maintain



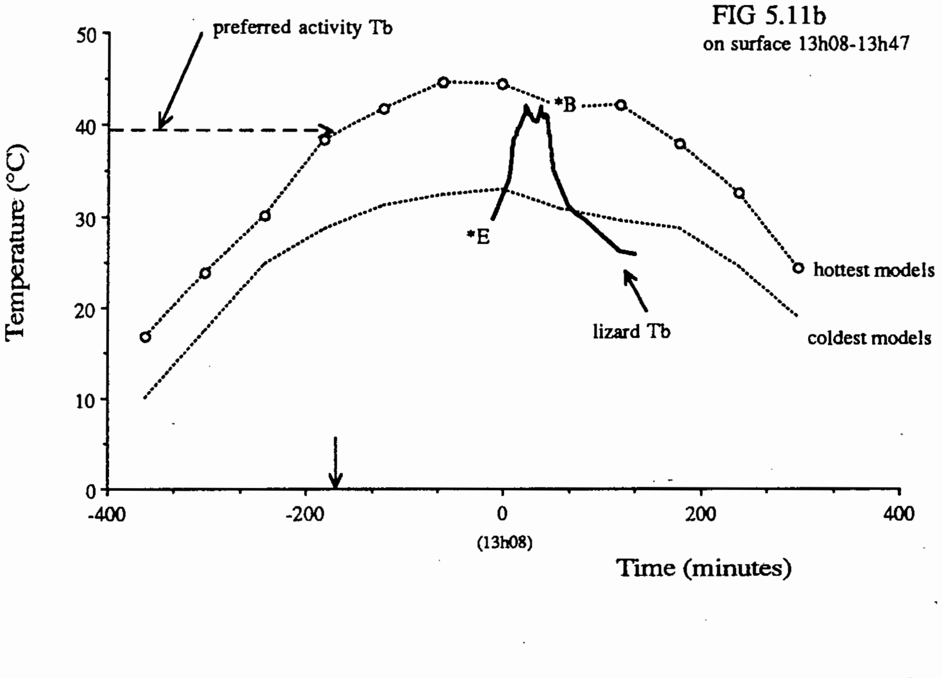
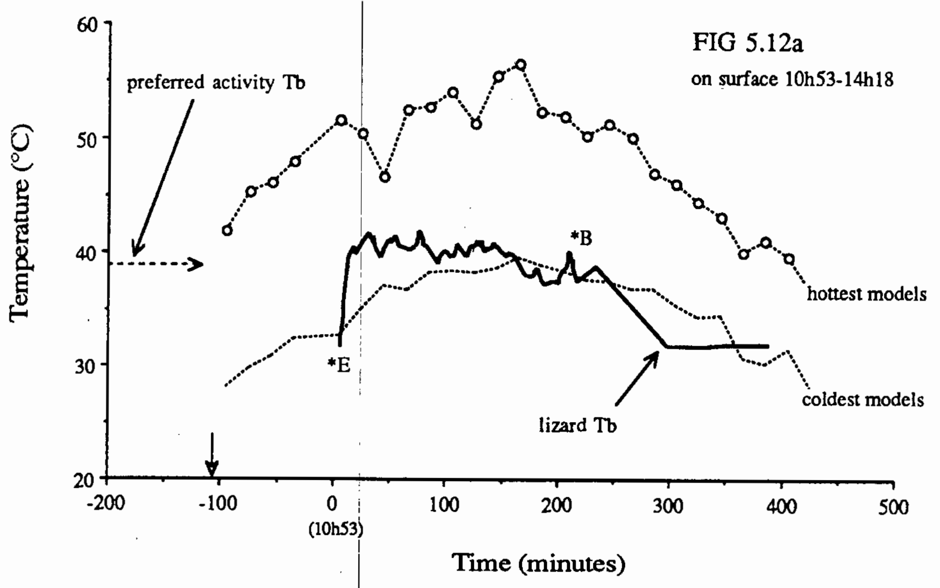


FIGURE 5.11. Representative examples of simultaneous measurements of copper model temperatures (hottest, **open circles** and coldest, **unmarked dashed line**) and active lizard body temperatures (Tb) in October 1989 : [(a) = animal number 4 on 31/10/89, (b) = animal number 4 on 3/11/89 ; **thick unmarked line**]. Time 0 = emergence time. The actual time of emergence is indicated in parentheses. The horizontal arrow indicates preferred activity body temperatures. The vertical arrow indicates the time at which preferred activity body temperatures could be achieved. *E = emergence ; *B = burial.



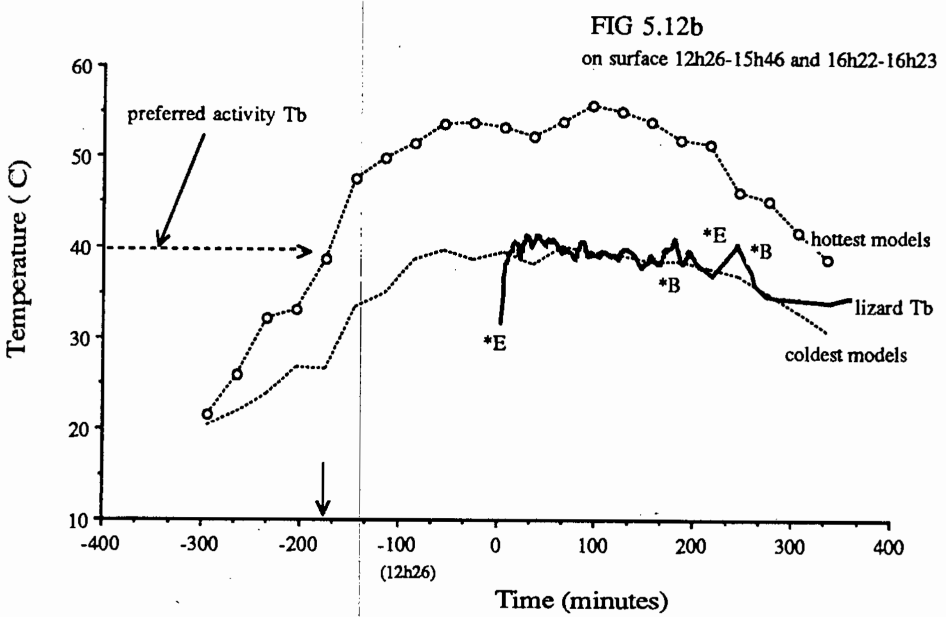


FIGURE 5.12. Representative examples of simultaneous measurements of copper model temperatures (hottest, **open circles** and coldest, **unmarked dashed line**) and active lizard body temperatures (Tb) in February 1990 : [(a) = animal number 2 on 26/2/90, (b) = animal number 2 on 1/3/90 ; **thick unmarked lines**]. Time 0 = emergence time. The actual time of emergence is indicated in parentheses. The dashed horizontal arrow indicates preferred activity body temperatures. The vertical arrow indicates the time at which preferred activity body temperatures could be achieved. *E = emergence ; *B = burial.

water balance. Subsurface body temperatures are about 5 °C higher in February. Assuming a Q_{10} of about 2, this would only result in about a 50 % increase in water loss rates. When one considers, however, that activity in this species involves a 10 °C increase in body temperature and an obligatory increase in both cutaneous and respiratory water loss, water losses incurred during February should be substantially higher than those in October.

To get a rough idea of the effect of activity on water loss rates, total water loss (ml/kg.day) in the February and October telemetered animals was regressed against their average observed daily activity time. A Q_{10} of 2 was applied to the water loss rates of October animals to standardise values to the higher subsurface body temperatures of February animals. This resulted in the linear equation $y = -0.539 + 0.053x$ ($r = 0.98$) where y = average daily activity time in hours and x = total water loss in ml/kg.day. The equation predicts that inactive animals ($y = 0$) would have total water loss rates (x) of 10.2 ml/kg.day. This compares favourably with the temperature standardized water loss rates of the virtually inactive October animals (averaging about 13.4 ml/kg.day). According to the equation, each hour on the surface would result in a water loss of 18.9 ml/kg. This is almost double that predicted for inactive animals over a 24 hour period. Clearly, surface activity is hydrically very expensive. The difference between inactive and active water loss rates may be even greater when one considers that, at certain times of the year, rain penetration into the slipface results in higher water vapour pressures (lower water vapour deficits) below than above the surface (Figure 4.34, Chapter 4).

In Chapter 3, evaporative water loss rates recorded for active animals at 40 °C and a water vapour pressure of 16 mmHg (the average surface water vapour pressure in the field during February) equalled about 2 ml/kg.h (Figure 3.2b, Chapter 3). Applied to field observations, this would result in a total evaporative water loss of about 5 ml/kg during the observed (Table 5.5) average 2.4 hour activity period (Table 5.5). Considering the large difference between the predicted total water loss for inactive animals (10.2 ml/kg.day) and the actual total water loss rates observed in February animals (47.9 ml/kg.day, Table 5.1), this estimate seems very low. This suggests that laboratory measurements of evaporative water loss from active animals are underestimates. This could be due to unrepresentative intensity of activity in metabolism buckets and may be partially attributed to a factor that could not be simulated in the metabolism buckets - convection. Ocular water loss can account for a significant fraction of a lizards total evaporative water loss under hot, dry conditions. Waldschmidt and Porter (1987) have demonstrated that, unlike cutaneous water loss, ocular water loss is significantly related to wind speed in the lizard, *Uta stansburiana*. The total lack of convection in metabolism buckets may make laboratory conditions unrealistic with regard to evaporative water loss when compared to field conditions.

5.4.2 Physiological stress

Assuming that *A. skoogi* are most active during the hottest time of the year (February, breeding season), one might expect them to experience some form of physiological stress during this period. Other than a severe reduction in fat reserves (Table 5.3), this is not apparent. Male animals are maintaining water balance and total body water content in February (Table 5.1). Furthermore, when compared to July sampled animals, there is no sign of plasma hypernatremia (Table 5.3), a common occurrence when reptiles are dehydrated (Minnich 1982). This lack of stress can be attributed to two factors. Firstly, in male animals at least, activity is restricted so that the amount of water ingested each day is sufficient to compensate for that which has been lost (particularly through evaporation). This point will be discussed in more detail later (Section 5.4.4.). Secondly, the breeding season of *A. skoogi* coincides with the rainy season and the potential food sources available during this period are well hydrated (Table 5.2). Subsequently, the problem of increasing electrolyte loads as food dehydrates (demonstrated in desert species such as *Sauromalus obesus* - Nagy, 1972 and *Gopherus agassizii* - Minnich, 1977) does not apply to this species. The plant items selected in February and July generally have higher electrolyte concentrations than *A. horrida* (Table 5.2). In February, the consumption of food items other than nara may be enforced on males by territorial exclusion (see below). It has, however, been demonstrated in Chapter 2 that *A. skoogi* is more than capable of handling the electrolyte loads in the food source nara (*Acanthosicyos horrida*), primarily through its ability to concentrate salts efficiently in urate pellets. The fact that animals voluntary choose *M. guerichii* leaves in preference to nara in July indicates that *A. skoogi* is capable of tolerating electrolyte loads higher than those in nara. The nasal salt gland, which plays a minor role in excreting nara electrolytes (Section 3.4.2, Chapter 3), may play a more important role in and possibly even enable the consumption of *M. guerichii.*

The seasonal variation in abdominal pad fat content (Table 5.3) is consistent with observations on the degree of activity in males. Animals spend the months preceeding the breeding season largely inactive, channelling a good proportion of their ingested energy into growth and building up fat reserves. By July the reserves represent about 1 % of the body mass and by October have almost doubled in mass. During the breeding season, intense activity leads to energetic stress and the rapid depletion of fat reserves.

5.4.3 Diet choice

The almost exclusive selection of *A. horrida* in October can be attributed to the simple fact that this is the only well hydrated plant at this time of the year. Although most other species (especially *Merremia guerichii*) persist throughout the year, they are generally in poor condition in October and would probably impose unnecessary pressure on *A. skoogi*'s osmoregulatory abilities. The complete switch in diet during February (to *M. guerichii*, *Stipagrostis* and arthropods, Table 5.4) can be attributed, in males at least, to the territorial behaviour of this species. Territories are established around both *M. guerichii* bushes (this study) and nara bushes (Pietruszka *et al.* 1987). As territory holders appear to never leave their territory, their choice of food must be determined by the plant species around which their territory is based. If this is so, both nara and *Merremia* should form a fairly high contribution to selected food items. That this does not occur in he case of nara can probably be attributed to the small number of animals sampled. The sheer size of territories (in this study, three spread out over an entire slipface) coupled with the reported densities of this species (Mitchell *et al.* 1987) probably precludes some males from holding territories. This would enforce feeding on food items which occur outside territories. This is suggested by the high contribution of *Stipagrostis* grass (which grows in vast fields on gravel plains) and arthropods. The marked preference of *M. guerichii* flowers over leaves (Table 5.4) is interesting considering that flowers are a more suitable food in terms of both electrolyte load and energy content (Table 5.2). By choosing flowers, *A. skoogi* not only enhances its energy ingestion, but also reduces the electrolyte load imposed by the diet (particularly in the case of sodium).

Although well hydrated, there are two species, *Zygophyllum simplex* and *Sesuvium sesuvoides*, which are avoided in February. It is well known that the ionic composition of foods may influence the choice of dietary items. For example, the desert iguana, *Dipsosaurus dorsalis*, does not feed at all on the salt bush, *Atriplex canescens*, apparently because of its high Na^+ and Cl^- content (Minnich and Shoemaker 1970). *Uromastyx acanthinurus* also avoids plants high in Na^+ (Grenot 1976). *Z. simplex* and *S. sesuvoides* may be a case in point as both have relatively high Na^+ concentrations (Table 5.2). The small and potentially unrepresentative sample size here does not, however, exclude the possibility that animals excluded from territories (and the prime food sources, nara and *M. guerichii*) may even be forced to feed on these high electrolyte foods. The nasal salt gland which, based on electrolyte excreion observations in Chapter 3, appears to play a "reserve" role in Na^+ and K^+ excretion, may play an important role in the electrolyte balance of such individuals.

As no breeding behaviour was observed in *A. skoogi* in July, the choice of *M. guerichii* leaves and *Stipagrostis* over nara is somewhat enigmatic. Due to the absence of rain, these former species are probably relatively dehydrated during this month and as such would present a poorer quality food source than the homeostatic nara. Despite their (assumed) lower water content, higher electrolyte load (in the case of *M. guerichii*) and lower energy content (Table 5.4), simple factors such as lower fibre content and higher digestibility may make them a better choice than nara.

These observations on diet selection contrast considerably with those of Pietruszka *et al* (1986), who by analysing scats collected in December, July and February, considered nara and *Stipagrostis* to comprise the major proportion of *A. skoogi*'s diet. Acknowledging the fact that the sample sizes in the present study are very small and thus may not be representative of the entire population, it is possible that a high contribution of *M. guerichii* in February and July went undetected in the scat analysis. Both *M. guerichii* flowers and leaves appear to be digested quickly and in the present study were difficult to identify, even in the stomach. Nara and *Stipagrostis*, on the other hand, appear to have hard cellulose walls which retain their shape and are easy to identify, even in scats.

5.4.4 Breeding behaviour

This study also supplements the data already collected on the breeding behaviour of *A. skoogi* (Pietruszka *et al.*, 1988). During the latter study, male *A. skoogi* established territories around the perimeter of any nara patch in the proximity of a dune slipface. Space is limited around the nara and only a few males (in one case, 4 out of 24) were able to establish territories. No mention is made of the establishment of territories around *Merremia* mounds. It is possible that *M. guerichii* was absent from the study site or that the territories associated with *M. guerichii* were disturbed (by observer proximity) or went unnoticed. The nature and frequency of interactions between nara territory holders and intruders were similar to those reported here.

5.4.5 Thermoregulation and activity patterns

There is little doubt that without special thermoregulatory behaviour, surface activity in February would be thermally dangerous (Figures 5.9b, 5.10a, 5.12a and 5.12b). Locations chosen (foliage and rocks), postures adopted ("perching" and "tail up") shuttling behaviour (to and from *Merremia* mounds) and temporary burial all contribute to avoiding lethal body temperatures and allowing surface activity at the hottest time of the day (Figure 5.12). The "tail up" posture greatly reduces the ventral surface area of the body in contact with the substrate. The reduction of the heat load being conducted into the body can be substantial, depending on other environmental conditions (Figures 4.10a and 4.10b, Chapter 4). Cooling on *Merremia* mounds is consistent with observations made during the one day copper model thermoregulation experiment in February (Section 4.3.2, Chapter 4). Copper models which were rested on *Merremia* foliage were consistently cooler than models positioned on or just above the naked gravel plain surface (Figure 4.13). As discussed in Chapter 4, this can be attributed to several factors. Firstly, foliage provides shade which will result in cooler sand temperatures below foliage than on the exposed gravel plain. Heat gain by thermal radiation from the ground will thus be reduced when resting on foliage. Provided that the surface temperatures of leaves are lower than the gravel plain surface temperature, heat gain from conduction will also be less from the foliage. Additionally, *Merremia* bushes are not particularly dense and the surface area of a model in contact with leaves will probably be substantially less than that of a model resting on a flat surface. Secondly, there is the possibility that foliage models, because of their slightly better elevation above the gravel plain surface (*Merremia* mounds are about 30 cm high), may experience slightly lower ambient temperatures and higher wind speeds. The effect of this on reducing model temperature is illustrated in Figure 4.12a. Cooling while "perching" on *Merremia* mounds is also consistent with observations made on the copper models. Models orientated with their axis parallel or perpendicular to the sun's rays were consistently cooler than all the other models elevated above the gravel plain (Figure 4.13). Differences in convection coefficients and possibly, once again, differences in wind speeds and ambient temperatures, could account for the temperature differences observed in the angled and horizontally elevated gravel plain models.

In the laboratory, *A. skoogi* has a preferred subsurface temperature of about 30° C (Section 6.3.3, Chapter 6). Three field observations suggest that submerged animals are actively trying to achieve body temperatures close to this value. Firstly, animals bury to the depth where the average sand temperature is highest. In both October and February, this happens to be below about 30 cm where no temperature fluctuations occur. Although layers closer to the surface are warmer during the day (Figures 4.35a and 4.35b, Chapter 4), they are cooler at night (Figures 5.5a and 5.5b). On average, the lower depths are generally the warmest. In October, for example, average sand temperature at 5 cm depth is about 23 °C. The temperature at 30 - 50 cm remains at about 27 °C for 24 hours a day. Secondly, an analysis of cooling curves in October and February (Figures 5.6b and 5.7b) shows that, in October, animals do not immediately descend to their overnight layers after burying. Instead they remain in the warmer upper layers (28 - 34 °C) for up to 4 hours, maintaining much higher body temperatures than they would at lower depths (about 27 °C). In February, animals descend to lower depths (about 30 °C) soon after burying. Finally, animals clearly took advantage of the east wind conditions in July, remaining in upper layers which stayed warmer (25 - 33 °C) than lower layers (23 - 25 °C) right through the night (Figure 5.4a and 5.4b). These observations all suggest that, when under the sand surface, animals behave as maxitherms. The maxithermy hypothesis (Hamilton 1971, 1973 , 1975) provides an adequate explanation for this behaviour, postulating that higher body temperatures allow for higher metabolic rates that presumably result in faster nutrient processing and growth rates. It must be kept in mind, however, that increased metabolic costs offset energy gain that there may be a body temperature at which the difference between metabolic costs and nutrient processing (energy gain) will be optimal. This temperature will probably be when the physical parameters of the digestive system simply prevent processing of additional food per unit time. This is hinted at by the results of laboratory studies dealing with food consumption and metabolism in several species of lizards. At a temperature of about 34 °C, food consumption rate in the lizard, *Scleropus undulatus* plateaus and remains constant (Porter 1989). The result is that scope for growth, which increases with increasing temperature, is optimal at about 34 °C. Metabolic costs continue to increase above this temperature, resulting in a decrease in scope for growth. Stevenson et al. (1985) have similarly demonstrated a plateau, followed by a slight decrease in the digestion rate of the snake (*Thamnophis* *elegans*) above 30 °C. In contrast, the Q_{10} value for oxygen consumption between 25 and 35 °C was 5.0. Scope for growth thus decreases above about 30 °C. Avery (1984) has demonstrated that growth rates in lizard, *Lacerta vivipara*, kept at cool temperatures (3 - 15 °C) increased in proportion to the period thermoregulation (at about 33 °C) was allowed. This was due to increased voluntary food consumption. Although animals kept continuously at 33 °C had the highest food consumption, however, their growth rates were substantially lower than expected. Once again, high metabolic costs offset the advantages of maintaining high body temperatures to optimize energy gain. Similar trends have also been reported for other ectotherms such as fish. In most fish species growth increases with temperature, as long as ration is not limiting, to an optimum beyond which it decreases (Beitinger and Fitzpatrick 1979). The unimodal relationship between temperature and growth derives from a combination of reduced voluntary food consumption and logarithmic increases in maintenance metabolism.

Bearing in mind that maxithermy may not necessarily optimize net energy gains, it is hypothesized that submerged animals in the present study are trying to achieve some optimal temperature rather than maximize body temperatures If the latter stategy were the case, submerged animals would occupy the warmer shallow layers of sand during the day. The observation that February animals quickly descend to cooler depths soon after burying is also strong support for the optimality over the maxithermy hypothesis.

In October, active animals are clearly maintaining body temperatures higher than the minima predicted by copper models (Figures 5.11a and b). Although similar body temperatures are maintained by active February animals, values during this month are similar to the minima predicted (Figures 5.12a and b). Taking cooling postures and the thermal refuge provided by *Merremia* mounds into account, however, values are much higher than the minima obtainable (Figure 4.13). Surface body temperatures (Figures 5.8a and b) are frequently in excess of 40 °C. In general, lizards start becoming thermally stressed at a body temperature of about 43 °C (panting threshold temperature - review in Bradshaw, 1988). Clearly, then, animals are maximizing their body temperatures when on the surface. In October, this appears to be intentional with the hottest region of the dune (upper slipface - Table 4.1, Chapter 4) being used to rapidly attain the preferred surface body temperature, after which the more moderate conditions of the dune top are used to maintain that temperature. In February, the reproductive obligations of territorial males appear to be largely responsible for the high observed body temperatures. Although much time is spent in the cooler confines of *Merremia* mounds, courtship and territorial defence on the hot gravel plain consistently elevate body temperatures (Figure 5.9b). Unlike October, when conditions are fairly moderate, the slipface and top are thermally dangerous (Figure 4.13, Chapter 4 and demonstrated in Figure 5.10a) and thus avoided (Table 5.6).

Several studies have investigated the effect of microclimate on activity patterns. Pietruszka (1987) related the dune location of *A. skoogi* to sand surface temperature and concluded that animals did not follow a maxithermal strategy of thermoregulation but rather used the sand dune habitat mainly for other reasons such as foraging, social interactions and predator surveillance. However, as shown in Chapter 4, there are several factors other than sand surface temperature, particularly the degree of contact with the substrate and wind speed, that determine lizard body temperature. Sand surface temperature can thus be a poor indicator of lizard body temperature. The results of the present study show directly that, when on the surface, male *A. skoogi* are, by definition, maxitherms. With the data at hand, it is not always clear whether this is intentional or incidental. In February, maxithemy appears to be largely incidental, the byproduct of territorial duties on the hot gravel plain.The same may be true for October animals with the frequent occupation of the hotter upper regions of the slipface being for no other reason than surveillance for avian predators (see below).

Using integrated thermometers (black bulbs) positioned at various dune locations, two other studies also consider surface activity in this species to be incidental, supporting other obligatory surface activities (Seely *et al.* 1988, 1990). The data in the present study are not strictly comparable with that in the latter two studies as observations were made at different times of the year and were made on populations (all occupants of a particular dune) as opposed to focal animals. There is, however, one conclusion in Seely *et al.* (1990) that deserves comment in the light of the findings of this study. They conclude that the dune top and crest (boundary between the dune top and slipface) are unfavourably cool for lizard thermoregulation throughout the year and any presence there (most prevalent in February) must be related to other factors. The seasonal factor proposed is breeding behaviour, the high regions of the dune offering the best vantage and patrolling areas. The results of the present study disagree with these conclusions on two accounts. Firstly, the dune top and (in this case) upper slipface is not unfavourably cool for lizard thermoregulation in either October or February. In fact, these locations can be considered thermally dangerous in February (Figure 4.13). Secondly, breeding males spent very little time at the locations in question. Being in the centre of the territory (in this case, on the *Merremia* mounds), appears to be the optimal location for successful courting and territorial defence.

As outlined in the introduction to this chapter, thermoregulatory behaviour and activity patterns may be related to several factors including predator avoidance, social interactions, territorial defence, limiting environmental conditions and optimizing foraging returns. These factors may apply individually or in combinations. In the light of observations in this and the abovementioned studies on *A. skoogi*, it remains to identify the factors applicable in this species. In October, environmental conditions are not as limiting as activity patterns suggest. Preferred surface body temperatures can be obtained for between 4 and 6 hours per day (Figures 5.11a and b) as opposed to the average activity time of about 20 minutes displayed by October animals. Considering that higher temperatures can be achieved when on the surface than when below the surface, this reduced activity also rules out the optimization of foraging returns (by maximizing body temperatures) when food is abundant, as proposed by Zimmerman and Tracy (1989). There were no signs of any social interactions or territorial defence. Both the selection of high regions of the dune (Table 5.6) and the display of prolonged head basking behaviour (Table 5.6 and Figure 5.6a), however, suggest that behaviour on the surface is geared towards predator evasion. One of the main predators of this species is the crow, *Corvus corvus* (Mitchell *et al.* 1987). Casual field observations suggest that its main hunting strategy takes the form of ambush attacks. This involves approaching a dune from the rear and swooping over the crest. Lizard locomotor efficiency is strongly dependent on body temperature (reviewed in van Damme *et al.*, 1991). By emerging only when a high body temperature has been achieved (31 - 34 °C, Figure 5.6a) and by occupying the best predator "spotting" point, animals appear to be behaving so as to minimise the chance of being caught by this avian predator.

In February, the predominant factor related to thermoregulatory strategies and activity patterns appears to be territorial defence. The size of territories (approximately 500 m^2, Figure 5.1) and the frequency of territorial defence and territorial boundary confirmations (Table 5.7) suggests that territories are in high demand and need to be defended conscientiously. Thermoregulatory strategies seem to be largely incidental, geared towards avoiding lethal temperatures while going about obligatory courtship and territorial duties. Once again, activity times are shorter than predicted by the optimization of foraging returns hypothesis proposed by Zimmerman and Tracy (1989). Animals could attain preferred surface body temperatures for a period of at least 6 hours (Figures 5.12a and 5.12b) as opposed to the observed average activity time of 2.5 hours (Table 5.5).

Thus, even though animals are maxitherms when on the surface, they do not strive towards maxithermy with regard to activity time. Combining accumulated knowledge on water and energy gains and losses, it is possible to provide an explanation for the observed reduced activity times in both October and February animals. According to measurements of stomach volumes, a hypothetical 1kg animal would have a stomach capacity of (11.5 %)(1000 g) = 115 ml. Assuming that 1g of food = 1ml food (reasonable considering a high proportion of food is water) and that this animal would only be able to fill its stomach once a day, maximum daily food intake would be 115g. Assuming an 83 % water content (nara, Table 5.2), this intake would comprise 95.4 ml of water and 19.6 g dry matter. According to the activity time/total water loss equation ($y = -0.539 + 0.053x$, where y = activity time in hours and x = total water loss in ml/kg.day, page 135), an animal would loose 95 ml of water if active for 4.5 hours. A small proportion of this (about 10 %, see Tables 3.1 and 3.2) would be replaced by metabolic water. The balance would have to be ingested. Due to high surface water loss rates and the physical limitation of stomach size, therefore, the animal would not be able to remain in water balance if active for longer than about 5 hours per day. It should be borne in mind that this calculation gives the animal the best deal by assuming a stomach evacuation time of 24h. If this is an underestimate (stomach evacuation time is longer), surface activity time will be limited even further (see below).

Similar calculations can be done for the effect of activity time on energy balance. Firstly, however, estimates of surface-active metabolic rates must be obtained. If we assume that about 10% of water gain in Table 5.1 is from metabolic water (see Table 3.1 and 3.2, Chapter 3), the amount of water ingested by, for example, February animal #1 (Table 5.1) would be 47.1 - 4.71 = 42.4 ml/kg.day. Assuming a water content of 83 % (nara, Table 5.2), this would translate into a dry matter input of 8.7 g of dry matter. Taking a food energy content of about 20 kJ/g (nara, Table 5.2) and an digestive efficiency of 63 % (Table 3.1, Chapter 3), this particular animal would absorb 109.5 kJ/kg.day. Assuming that about 30 % of this is voided as chemical potential energy in urate solids (Table 3.1, Chapter 3), 76.6 kJ/kg.day would remain in the animal's body. The animal was maintaining constant body mass (Table 5.1), so all this energy is assumed to be channelled into metabolism (i.e. the animal has a field metabolic rate of 76.6 kJ/kg.day). Based on laboratory measurements of subsurface metabolic rates (Section 3.3.1, Chapter 3), this animal (with a full stomach of food) would consume about 0.106 ml O_2/g.h. while below the sand. This, assuming carbohydrate digestion, would translate to a metabolic rate of about 2.1 kJ/kg.h (Nagy 1983). *A. skoogi* displays no diel cycles in resting metabolic rate (see Section 6.3.3, Chapter 6), so this value can be applied throughout the submergence period. This animal was, on average, at rest below the sand for 21.93 h/day. Energy consumption while below the sand would thus amount to (2.1 kJ/kg.h)(21.93 h/day) = 46.5 kJ/kg.day. Subtracting this value from the estimate of total energy consumption (76.6 kJ/kg.day) gives a energy consumption when on the surface of 30.1 kJ/kg over a period of 2.07 hours, or 14.7 kJ/kg.h. The procedure was repeated for the other two February animals, yielding an average surface energy consumption of 17.4 ± 3.2 kJ/kg.h (n = 3). This estimate represents an 8.3-fold increase (17.4 / 2.1) in activity metabolic rate (at 40 °C) over resting metabolic rate (at 30 °C). This is substantially higher than the 5-fold increase estimated from laboratory studies of resting and activity metabolism at the abovementioned temperatures (Section 3.4.1, Chapter 3). This suggests that, as concluded with laboratory water loss studies, the intensity of activity in metabolism buckets appears to be lower than that displayed in the field. Compared to other species, the cost of activity relative to resting in *A. skoogi* is low. This can be attributed primarily to the relatively small difference in active and resting body temperatures (40 °C versus 30 °C). During their breeding season, active *Scleropus virgatus* females (at 34 °C), for example, have metabolic rates which are 46.5-times higher than their resting metabolic rates at 12 °C (Merker and Nagy 1984).

With this estimate of surface energy consumption, it is now possible to estimate how long an animal can remain on the surface without running into negative energy balance. Assuming, once again, a maximum daily food input of 19.6 g dry matter, an energy content of 20 kJ/g, a digestive efficiency of 63% and a 30 % loss of assimilated energy in urate solids and urine, maximum energy gain per day would be 173 kJ/kg.day. Total daily energy consumption is now calculated by multiplying the number of hours active by 17.4 kJ/kg.h and adding this to the product of hours at rest and 2.1 kJ/kg.h. At approximately 8 h activity, energy consumption exceeds the maximum energy gain value of 173 kJ/kg.day. Once again, it must be remembered that the animal is given the best deal with regard to energy gain by assuming stomach evacuation time to be 24 h. If this is an underestimate, surface activity time will be limited even futher (see below).

At this stage it is necessary to obtain a better estimate of the rate at which food moves out of the stomach (stomach evacuation time). The ideal way to do this is to quantify the volume of food ingested by laboratory animals after a known period of starvation. This can easily be done by determining the volume : mass relationship of the food and weighing animals before and after feeding. Provided animals always "top up" their stomachs during each feeding session, this will give an indication of the empty volume created in (= the amount of food evacuated from) the stomach. Pilot experiments of his nature were conducted on *A. skoogi*. The wide range of food consumption data collected, however, indicated that the premise regarding consistent stomach "top ups" was not valid. A second method of determining stomach evacuation time was also attempted. Food was marked with Barium, a radio-opaque substance, and fed to animals. The passage of food out of the stomach was then monitored by means of X-ray photography. Trials were, however, unsuccessful, primarily due to the superimposition of barium-coated food in various components of the gastro-intestinal tract. It was impossible to distinguish between marked food in the stomach and small intestine, even in lateral view photographs.

A rough estimate of stomach evacuation time can be obtained from field tritiated water data. The average water input (total water in - metabolic water) of the three February animals was 47.7 ml/kg.day (Table 5.1). Assuming once again a food water content of 83 % and that 1 ml = 1 g food, this translates into a volume input of about 57.5 ml/kg.day. This is about 50 % of total stomach capacity (115ml). Animals spent an average time of 2.4 hours on the surface at about 40 °C and an average time of 21.7 hours under the sand surface at about 32 °C. Average body temperature over the full 24 h period is calculated to be about 32.5 °C. For an animal to maintain body mass, whatever leaves the gastro-intestinal tract (whether absorbed through the wall or lost through the cloaca) must be replaced via the stomach. A very simplified view of the gastrointestinal tract is that of a rigid tube completely filled with water. If this is the case, the amount of water lost from the tract should be equal to the amount of empty space created in the stomach. The amount of food ingested to fill this empty space and bring the body back to constant mass should thus give an indication of the rate at which the stomach empties. The February observation animals were all maintaining body mass during the water flux measurement period. Their daily volume input can thus be taken to represent the vacuum created in the stomach each day. At about 32.5 °C, this is about 50 % of the stomach capacity. For the purposes of the activity time limit calculations done above, it seems fairly safe to assume that February animals had stomach evacuation times of about 48 hours. This reduces the maximum activity time estimates by 50 %. To maintain water balance, therefore, maximum permissible surface time would be about 2.5 hours. In the case of energy, surface time would be restricted to a maximum of about 4 hours. The reason February activity patterns in this species (which has an abundant food source) do not agree with the predictions of Zimmerman and Tracy's (1989) optimization of foraging returns hypothesis (to maximize body temperature for as long as possible) could thus be attributed to the avoidance of negative water and energy balance. Foraging returns do increase with an increase in body temperature maximization. Attaining maximization (through surface activity) may, however, involve such high water and energetic costs, that it becomes disadvantageous. As February animals were obliged to remain on the surface for extended periods (territorial defence), it is not impossible that water and energy balances were adversely affected. The negligible amount of subcutaneous fat in February animals supports this speculation.

In contrast, October animals appeared to have no social obligations. Their activity patterns are thus more likely to reflect more careful attention to water and energy balance. According to the estimate of the duration of activity that will result in negative water balance (about 2.5 hours), October animals have no problem with maintaining water balance. The best way to demonstrate consideration towards energy balance (and storage) is to model energy balance for a hypothetical 1 kg animal under realistic field temperatures and a variety of activity regimes, as follows:

Resting (subsurface) metabolic rate at a body temperature of 30 °C is assumed to be 2.1 kJ/kg.day for animals which have eaten in the last 24 hours. Accorrding to specific dynamic action measurements (Section 3.3.1, Chapter 3), resting metabolic rate should drop to 1.8, 1.3, 1.2 and 0.9 kJ/kg.day after 24, 48, 72 and 96 hours respectively. Metabolic rate when active at 40 °C on the surface is taken as 17.4 kJ/kg.day. A full stomach of food is assumed to yield a total energy gain of 173 kJ. Stomach evacuation time is assumed to be 48 hours at 30 °C and , assuming a Q_{10} of 2, 24 hours at 40 °C. In effect this means that animals are capable of gaining a maximum of 3.6. kJ/kg.h at 30 °C and 7.2 kJ/kg.h at 40 °C. Net energy gains were calculated as follows : if an animal is, for example, active for one hour every day and eats its fill every day, its energy consumption will equal (2.1 kJ/kg.h.)(23 hours) during rest + (17.4 kJ/kg.h.)(1 hour) during activity = 65.7 kJ/kg.day. Its energy gain will equal (3.6 kJ/kg.h)(23 hours) during rest + (7.2 kJ/kg.h.)(1 hour) during activity = 90.0 kJ/kg. day. Net energy balance will equal 90.0 - 65.7 = 24.3 kJ/kg.day. The proportion of active to resting metabolic costs (17.4 : 2.1 kJ/kg.h) is much higher than the proportion of energy gain at the two different temperature regimes (7.2 : 3.6 kJ/kg.h). The result is that as activity time increases, net energy gain decreases. If, for example, an animal is active for two hours, net energy gain will equal 12.6 kJ/kg.day. Between 3 and 4 hours activity, the animal will enter negative energy balance. To optimize net energy gain, therefore, activity periods should be as short as possible. Field observations of activity periods (x = 21.3 ± 19.5 minutes, n = 5, Table 5.5) suggest that this is what October animals are doing. The availability of a microclimate that allows for rapid warming to preferred above-sand body temperature and an abundant food source makes short activity times possible.

This demonstration that growth rates increase with thermoregulation time in the lizard *Lacerta vivpara* (Avery 1984) may appear to contradict this reduced activity hypothesis. The thermoregulation experiments on *Lacerta vivipara* were, however, conducted at much lower temperatures than those experienced by *A. skoogi* in the field (3 - 15 °C and thermoregulation at 33 °C versus 27 - 32 °C and thermoregulation at 40 °C). Within limits, scope for growth does increase with increasing body temperature (Beitenger and Fitzpatrick 1979 ; Porter 1989 ; Stevenson *et al.*

1985, see above). At higher body temperatures, the amount of energy gained relative to metabolic costs may start decreasing, resulting in a decline of scope for growth. This indeed occurred in the *Lacerta* experimental group held continuously at 33 °C.

Net energy gain is not only influenced by activity time but also by the frequency of activity. Using the same procedure and parameter values as above, net energy gains were calculated for animals active for 0.5 hours every day and active for the same period every second, third and fourth day. Complete filling or topping up of the stomach was assumed to occur during each activity period. The results are shown in Figure 5.13a. Animals that are active and feed every day show a steady increase in net energy gain with time. Those that feed every second day show drops in net energy gain on inactive days but an overall higher scope for growth than the former group. The reason for this is that the every 2 days group gain just as much energy as the group active every day (stomach evacuation time is 48 hours), but have lower overall metabolic rates on inactive days. Animals which show a lower frequency of activity (every third or fourth day) spend periods with empty stomachs (no energy gain) while still incurring metabolic costs. The result is substantially lower net energy gains than in the latter two groups. Clearly, the optimal frequency of eating and activity corresponds with stomach evacuation time. Acknowledging the uncertainties regarding estimates of stomach evacuation time in this species, the field observations of activity and eating frequency (every 2.5 and 3.7 days respectively, Table 5.5) suggest that animals may be behaving in such a way as to optimize their scope for growth. The high subcutaneous fat concentrations measured in sampled October animals shows that they are, indeed, in a state of healthy, positive energy balance.

Considering that several herbivorous lizards are known to digest fibre in hindgut fermentation systems (see Zimmerman and Tracy 1989), it may be argued that an empty stomach may not necessarily mean a period of no or reduced energy gain. The stomach does, however, play an important role in digestion, even in herbivorous lizards. Troyer (1984), for example, has demonstrated that, in a known fibre fermenter *Iguana iguana*, over 60 % of at least two important dietary components (crude protein and cellulose) are digested and assimilated in the stomach. Furthermore, when one considers that gut passage time in *A. skoogi* is about 4 days at 30 °C and 2 days at 40 °C (Figure 3.3, Chapter 3), a feeding frequency of less than about 3 days may well mean periods of reduced nutrient assimilation.

Figure 5.13b depicts the same scenario as Figure 5.13a, except that activity time has been extended to 2 hours. The pattern is much the same, except that all net energy gain values are lower and the difference between net energy gain in the every day and every second day groups is greater. This is, as explained above, due to the cost of activity per unit time being disproportionate to the improvement of stomach evacuation time (and subsequent energy gain) with increasing temperature. Note that net energy gain in the every 4 days group is actually decreasing with time.

Energetic considerations with regard to the duration of activity periods and the frequency of activity should not be confused with thermoregulatory stategies during activity periods. As

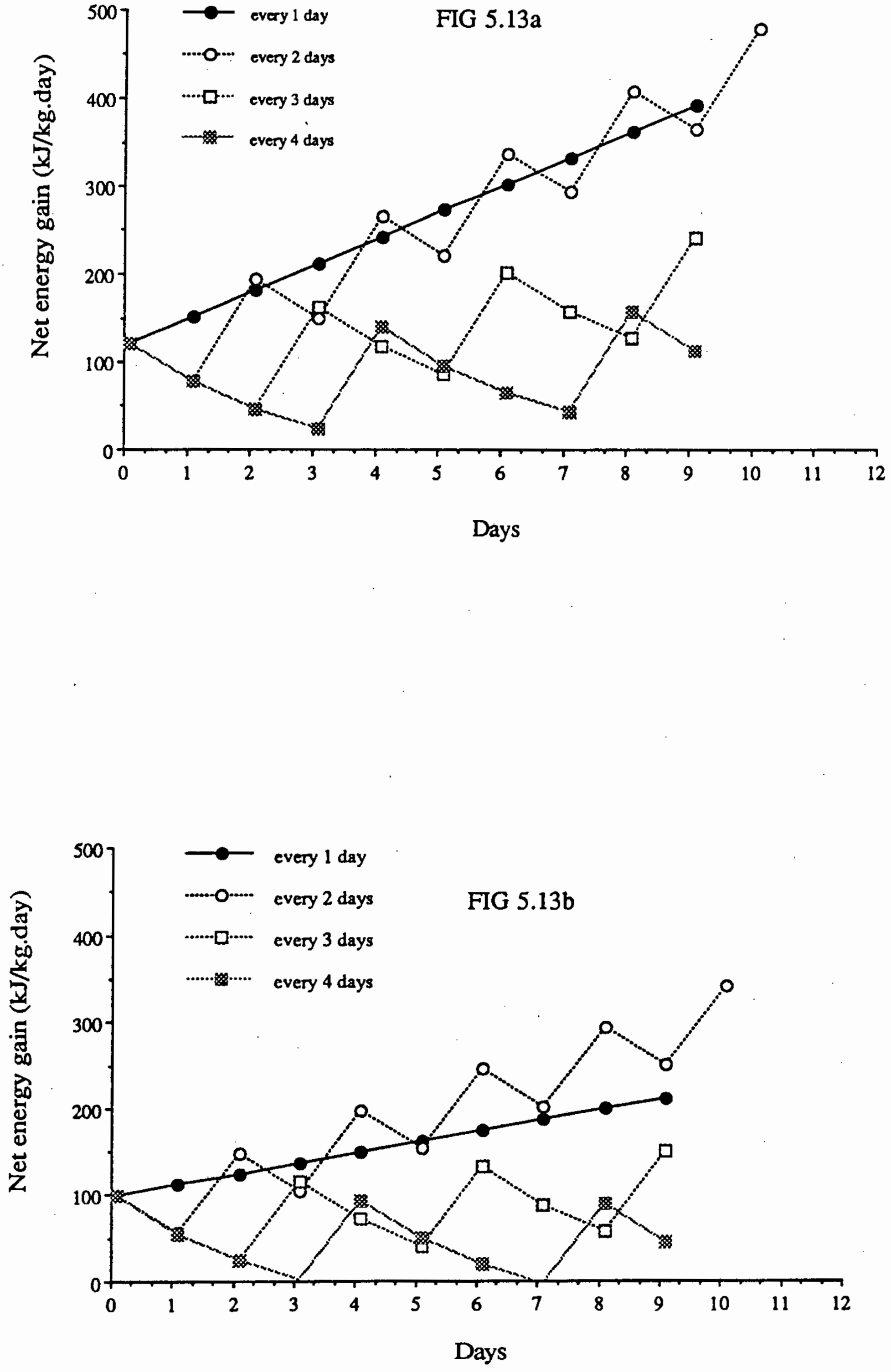


FIGURE 5.13. Predicted net energy gain in *Angolosaurus skoogi* as a function of the frequency of activity (every 1-4 days) and duration of activity : (a) = 0.5 hours ; (b) = 2.0 hours. See text for modelling procedure and parameter values.

discussed earlier, it is hypothesized that the maxithermal behaviour observed in active animals may be largely incidental, geared towards predator evasion in October and territorial obligations in February. That the thermal biology of ectotherms is a complex function of a number of factors is confirmed by this study.

In conclusion, it has been demonstrated that any attempt to explain activity patterns and thermoregulatory strategies in ectotherms needs to include more than has previously been considered. In particular, body temperatures when animals are inactive and the costs involved when animals are active need to be quantified and applied to the improvement of water and energy gains. In *A. skoogi* at least, maximizing body temperature for as long as possible does not necessarily result in the optimization of scope for growth.

It should be emphasized that the size of the telemeters used in this study restricted their use to large male subjects. The conclusions drawn from this study are therefore based on the thermal physiology and behaviour of large males only. Growth rates, activity periods, activity locations and diet differ among different size classes in this species (Mitchell *et al.* 1987, Seely *et al.* 1988,1990). Optimal thermoregulatory and behavioural stategies for growth may be considerably different for the smaller size classes, particularly juveniles which have relatively high growth rates and feed predominantly on detritus.

It should also be noted that the conclusions drawn here are based on observations made at one study site over a very short period of time. Potential ecological variations should be acknowledged and considered. *Merremia* mounds, for example, are only common along the flood plain of the Unjab River. They are not found at other dunes only hundreds of meters distant where *A. skoogi* is also common. The present study only analyses one of several habitat variations of importance to this species. Similarly, variability in day to day weather conditions render short field measurements indicative rather than representative. The conclusions in this study should be treated accordingly.

CHAPTER 6

THE THERMAL RESPONSE OF *ANGOLOSAURUS SKOOGI* TO STARVATION

6.1 INTRODUCTION

The economical utilization of energy is important to the ecology and survival of any species. As energy costs in ectotherms are temperature dependent, thermoregulatory behaviour can play a major role in the overall energetics of an individual, especially in relation to a fluctuating food supply. It stands to reason that from an energy conservation point of view, an ectotherm will select as low a body temperature as possible when experiencing starvation. On the other hand, when food is abundant, elevated body temperatures may provide all kinds of physiological benefits, including improvement of the rate of digestion (see Zimmerman and Tracy 1989 for review) and growth (Avery 1984 ; Licht *et al.* 1971). In situations where resources vary in quantity and availability through time, reduced energy intake may offset the benefits of maintaining a preferred body temperature, particular if this is accompanied by high metabolic costs.

It appears to be a general rule that patterns of thermoregulatory behaviour are influenced by nutrition in most groups of ectotherms. The most common response in reptiles, for example, is a thermophilic response following feeding (see Waldschmidt *et al.* 1987 for review). Thermophily after feeding also occurs in fish (Javaid and Anderson 1967 ; Brett 1971). In certain species of fish, ration (the amount of food available) is known to influence temperature selection. Bluegill sunfish, for example, fed low rations lost mass and steadily reduced their preferred temperature over a six day period (Stuntz and Magnuson 1976). A particularly interesting study is that of Lillywhite *et al.* (1973) who demonstrated the preferred body temperature of the toad, *Bufo boreas*, to be 26 - 27 °C when fed but 15 - 20 °C when fasted. Both energy and water conservation are implicated as being the reason for this remarkable behavioural adaptation.

Maintaining a low body temperature when faced with food shortages may involve disadvantages which outweigh the benefit of conserving energy. These may include factors such as thermally induced lethargy (which can reduce the efficiency of predator evasion) and reduced efficiency in physiological processes such as electrolyte regulation (Gilles-Baillien 1974). There is also the possibility that the conservation of water may be a more important consideration than energy conservation. Both metabolic water production and evaporative water loss increase with temperature. Net water loss may not be optimal at temperatures which are best for energy conservation.

It has been conclusively established that the Namib sand-diving lizard, *Angolosaurus skoogi*, never experiences starvation (Section 5.3.2, Chapter 5). The main reason for this is that it always has access to a perennial shrub of the cucumber family, *Acanthosicyos horrida*. The shrub remains in the same succulent condition throughout the year on underground water obtained via a long tap root. During the rainy season, a variety of other seasonal plants are available. An abundant and constant food supply is thus available all year round. This is confirmed by analysis of stomach contents of animals collected at different times of the year (Section 5.3.3, Chapter 5). Stomachs were, with few exceptions, full of plant material.

There appear to be no studies to date investigating how ectotherms which always have access to abundant food supplies respond to food shortages. The aim of this study is to investigate the thermal response of such an animal, *Angolosaurus skoogi*, to starvation. In the event of the lack of the thermophobic energy conservation response demonstrated in other ration restriction studies, other possible physiological advantages of selecting high body temperatures will be investigated.

6.2 METHODS AND MATERIALS

6.2.1 Starvation experiment 1

Eight *Angolosaurus skoogi* (both sexes, mass range 30 - 82g) were used in the initial starvation experiment. The animals had been collected from dunes adjacent to the Unjab River, Namibia (20°19' S, 13° 14' E) eighteen months earlier and housed in a large hardboard box (200 X 120 cm) at 25 °C and 50 ± 10 % relative humidity. Approximately one third of the box was filled with sand to a depth of 15 - 20 cm (Figure 6.1). The remainder of the box base was covered with a thin layer of sand. A 500 W quartz halogen lamp, placed above the sand column, enabled the animals to thermoregulate when above the sand surface (to temperatures in excess of 45 °C) and to select subsurface temperatures of 45°C - 29 °C (vertical, directly below the light) or 45 °C - ambient temperature (horizontal, from directly below the light to the point furthest away from the light). During the experiment, ambient temperature was set at 24 °C and a water vapour pressure of between 9 and 13 mmHg (40 - 60 % relative humidity).

Animals were fed *ad lib.* on a diet of carrots and lettuce for two weeks prior to the experiment. They were then weighed to the nearest 0.01g (Mettler P360 balance). A 29 day period of starvation (food and water) was then enforced. During this period, animals were dug up out of the sand every 2 - 3 days and their body temperatures measured to the nearest 0.01 °C by inserting a Type T thermocouple (Model Bat-12, Bailey Instruments, Inc.) 2 - 3 cm into the cloaca. Animals

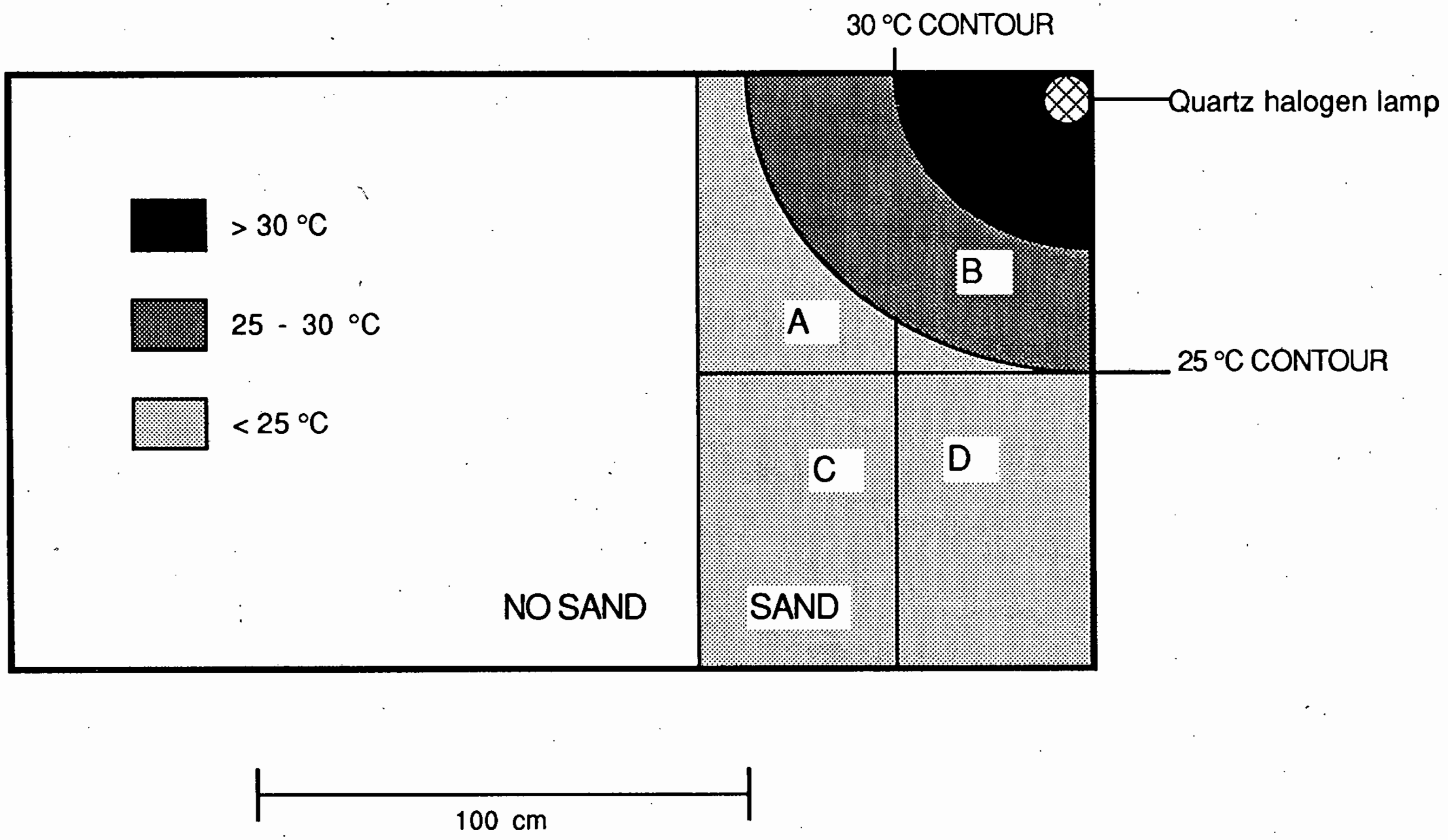


FIGURE 6.1. Schematic diagram (aerial view) of the box used to determine the thermal response of *Angolosaurus skoogi* to starvation. One-third of the box was filled with sand to a depth of 15-20 cm. This area was divided into four equal, imaginary sectors (A - D). A 500W quartz halogen lamp, suspended above the sand layer, produced both a vertical and horizontal thermal gradient in the sand column. See text for details. The horizontal gradient was divided into three sectors (> 30 °C, 25 - 30 °C, and < 25 °C), separated by two curved temperature contours.

which were already on the surface or which had been on the surface less than half an hour prior to sampling consistently had body temperatures higher than those of the other submerged animals. Data from the former animals were thus treated separately to data from the latter group.

During the experiment, the quartz halogen lamp was kept in the same position as it had been during the period prior to the experiment. During periods of food abundance, animals were consistently observed to bury in or close to the patch of sand illuminated by the light. The same behavior was observed during the starvation experiment. To test that animals were not habitually burying in this area, the light was moved to the opposite corner of the box two days prior to one of the body temperature sampling periods (21 days starved) Animals were also forced to bury in the cooler part of the sand two days prior to two of the body temperature sampling periods (25 and 27 days starved).

After twenty nine days, animals were reweighed to determine mass loss during the starvation period. On day 30, animals were fed and their body temperatures monitored over the next 48 hours.

6.2.2 Starvation experiment 2

Nine *A. skoogi* were used in the second starvation experiment (six animals from the previous experiment + three new animals, collected approximately 12 months earlier). The masses of these animals ranged from 45 - 90 g. Ambient temperature was set at 21 °C and water vapour pressure was maintained at between 8 and 10 mmHg (45 - 50 % relative humidity at 21 °C). This resulted in thermal gradients of 40 °C - 30 °C (vertical) and 40 °C - 21 °C (horizontal). Two sand temperature contours (30 °C and 25 °C) were determined by dragging a thermocouple (inserted 3.5 cm into the sand) along the entire area of the sand surface (Figure 6.1). The area within the 30 °C contour (i.e. enclosing sand where temperatures in excess of 30 °C were available) was approximately 1350 cm^2 (14 % of the total surface area). The area between the 25 °C and 30 °C contour (i.e. enclosing sand where temperatures of at least 25 °C but no more than 30 °C were available) was approximately 2600 cm^2 (28 % of the total surface area available). Finally, the are outside the 25 °C contour (i.e. enclosing sand where a maximum temperature of 25 °C was available) was approximately 5450 cm^2 (58 % of the total surface area available). Total surface area was approximately 9400 cm^2 (120 X 78 cm). The surface area of the sand mass was also divided by two imaginary lines into four equal sectors of 2400 cm^2 (60 X 40 cm) each (Figure 6.1).

The experiment was conducted approximately four months after the first starvation experiment. Animals were starved for 23 days and then forced to bury in sector D of the starvation box (Figure 6.1). After 48 hours, animals were dug up, their positions noted, and their body temperatures measured as in starvation experiment 1.

6.2.3 Water gain/loss experiment

Water conservation may be a more important consideration than energy conservation during periods of reduced food availability. In a starving animal, the only avenue of water input is metabolic water production. Once the bladder is empty, the only avenue of water loss is through evaporation from the body surface and respiratory tract. Net water loss (evaporative water loss - metabolic water produced) may be optimal at body temperatures which are not best for energy conservation. To investigate this possibility, these two components of water balance were quantified over the range of body temperatures starving animals were potentially able to obtain.

Closed volume respirometry and gravimetrics were used to determine metabolic and evaporative water loss rates in starved, submerged *A. skoogi*. Experiments were conducted in 20 litre plastic buckets filled with 10 litres of desert sand from *A. skoogi* 's natural environment. Details of the equipment used are provided in Chapter 3 (Section 3.2.1). Six *A. skoogi* were used in the experiment. The subjects were chosen from the eight animals used in the second stavation experiment.

After weighing animals to the nearest 0.01 g, strips of blue and red litmus paper (urination indicators) were plastered over their cloacas and they were forced to bury in the experimental buckets. To avoid plaster lesions, care was taken not to stick the plaster onto the sensitive ventral surfaces of the legs. After the animal had buried, a thin flexible gauze disc was placed just below the surface of the sand. Displacement of the disc provided an indication of activity. The buckets were then sealed and 50 ml air samples taken from below and above the sand and analysed for oxygen content. The sampling process was repeated just before the experiment was terminated or just after animals emerged from the sand. On rare occasions animals emerged unnoticed. Data were discarded unless it was certain that an animal had spent less than 5 % of the total measured time on the surface. After the last air sample had been taken, the buckets were opened, the animal's cloacal litmus strips inspected, and the animals reweighed. Evaporative water loss was assumed to be equal to mass loss provided no urination had taken place. Oxygen consumption was calculated from the product of the reduction of oxygen concentration and the total volume of air in the buckets. Oxygen consumption rates were converted to metabolic water production rates by assuming fat metabolism and applying the conversion factors provided in Nagy (1983) : RQ = 0.71, 0.754 ml CO_2 = 1 µl metabolic water. The length of experimental runs was largely determined by animal behaviour. Generally, however, the values reported here are for sampling periods ranging from 4 - 12 hours.

Experiments were conducted at 15, 23, 30 and 37 °C. The temperature of the sand was constantly monitored by means of submerged thermocouples and was found to never vary by more than 0.5 °C. Animals had been starved for at least seven days prior to the initiation of the 15 °C experiment. A minimum of 24 h separated measurements at each experimental temperature. Animals were maintained at the relevant experimental temperature and humidity for 24 h prior to experimental run. Ambient water vapour pressure was maintained at between 10 and 12 mmHg at each experimental temperature. The choice of humidity was determined by the humidity used during the first starvation experiment (50 % relative humidity at 24 °C). The humidity of the air in the sand was monitored at the beginning and end of each run by drawing air with a syringe through the bottom stopcock and over an encapsuled humidity sensor (Hanna Instruments, Italy). The humidity of air below the sand corresponded to that above the sand at all temperatures except 15 °C (relative humidity above surface = 10 - 12 mmHg and below surface = 6 - 8.5 mmHg, after a 24 h equilibrium period).

A number of peripheral experiments (investigating phenomena unrelated to the main objective of this study) were conducted before, during and after the water balance experiments. These comprised studies on specific dynamic action (the effect of digestion on metabolic rate), the duration of disturbance to resting metabolic rate after handling an animal, and comparison of day and night resting metabolic rates. Specific dynamic action experiments were initiated immediately after the animals were last fed. To test the effect of post-starvation feeding on metabolic rate, animals were also fed at the end of the water balance experiment (after 39 days of starvation) and their oxygen consumption determined at 30 °C just prior to and immediately after feeding. The duration of handling disturbance on resting metabolic rates was determined by sampling air from buckets immediately after an animal had buried and then at irregular intervals until oxygen consumption rates had stabilized. This took 3 - 4 hours (see below). Any metabolic data collected within four hours of burial were thus discarded when comparing day and night metabolic rates.

6.2.4 Plasma electrolytes

Besides water conservation, there may be other temperature-dependent processes that are more important than energy conservation considerations during periods of reduced food availability. Precise regulation of certain electrolyte concentrations in the body, for example, is obligatory and may take priority over conserving energy resources. Electrolyte regulation may be optimal at body temperatures which are not best for energy conservation. To investigate this possibility, the effect of temperature on the ability of starving *A. skoogi* to regulate plasma electrolytes was determined. Animals were first kept at 30 - 37 °C for 5 days (following 10 days of starvation) and then at 21 - 23 °C for 7 days (following 15 days of starvation). 50 µl blood samples were taken from the infraorbital sinus of each animal following each exposure period. Samples were centrifuged the same day and the plasma analyzed for sodium and potassium (Instrumentation Laboratory 243 flame photometer), chloride (titrimetric method of Schales and Schales, 1941) and osmolarity (Wescor 5100B Vapour Pressure Osmometer).

6.3 RESULTS

6.3.1 Starvation experiment 1

Body mass loss during the 29 day starvation experiment averaged 20.8 ± 3.4 % initial body mass (n = 8). In general, animals seldom emerged prior to body temperature readings. Data for preferred body temperature above the sand during the starvation period were obtained for days 2 (37.2 °C), 4 (36.2 °C), 21 (36.6 and 35.9 °C) and 25 (36.5 °C) ; x = 36.5 ± 0.5, n = 5. After feeding (day 29) data were only obtained for day 31 (36.1 and 37.2 °C : x = 36.7 ± 0.8, n = 2). There was no significant difference between the measured surface body temperatures before and after feeding (paired t-test, $p > 0.05$, d.f. = 5). The body temperatures of the remaining submerged animals consistently averaged in the region of 30 °C for the entire duration of the experiment (Figure 6.2). Daily average temperatures ranged from 29.2 - 31.6 °C. Average body temperatures on the two consecutive days following feeding were also not significantly different from that measured on the day prior to feeding (unpaired t-test, $p > 0.05$, d.f. = 14 and $p > 0.05$, d.f. = 12). No marked thermoregulatory response to either starvation or feeding after starvation was thus observed. Animals also consistently selected sand warmed by the thermoregulatory light. In only 7 out of 111 (6.3%) measurements were body temperatures below 25 °C observed. Four days after moving the thermoregulatory light (day 21), five out of six submerged animals had buried in the new vicinity of the light and had body temperatures in excess of 29.8 °C. The remaining animal measured 24.1 °C (= ambient temperature). 48 h after forced burial in ambient temperature sand (days 25 and 27), four out of six and five out of seven animals had selected body temperatures in excess of 28.9 and 29.6 °C, respectively. The remaining two animals had not moved from their burial positions in both cases.

6.3.2 Starvation experiment 2

Nine animals were forced to bury in sector D of the starvation box (Figure 6.1). Two days later, body temperatures of the nine submerged animals averaged 28.1 ± 4.3 °C. Two out of nine animals were found in sector D (burial sector) with body temperatures of 21.2 and 21.3 °C (= ambient temperature) and had thus made no attempt to move or had emerged and reburied in cold sand. The remaining seven animals had all moved inside the 25 °C contour (< 28 % area available) with body temperatures averaging 30.1 ± 1.9 °C. Of these seven animals, six had moved inside the 30 °C contour (< 14 % area available).

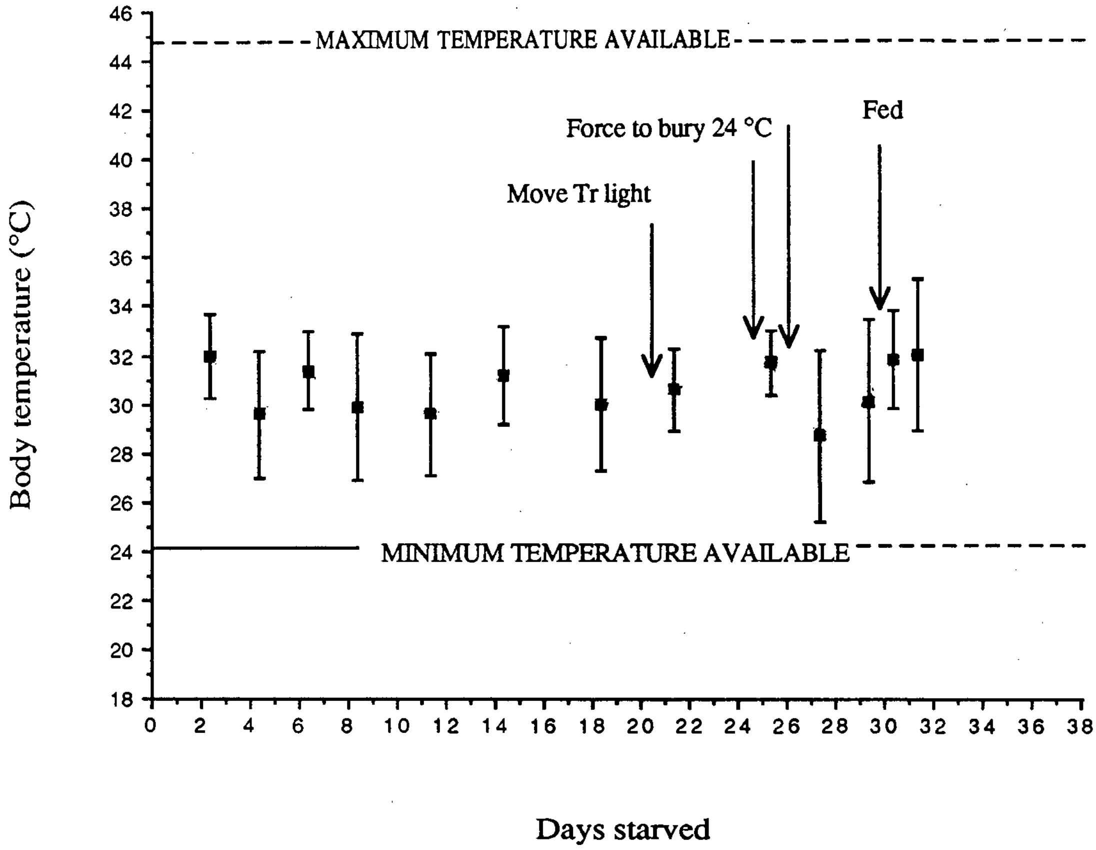


FIGURE 6.2. Preferred subsurface body temperatures of *Angolosaurus skoogi* (n = 8) as a function of starvation time. Vertical bars are standard deviations of the means. The thermal gradient available to the animals is bordered by the two horizontal bars. Animals received their last meal on Day 0. On day 21, the quartz halogen lamp was moved to the lower right hand side of the starvation box (see Figure 6.1), completely reversing the horizontal thermal gradient in the sand column. On days 25 and 27, animals were forced to bury in the coldest sector of the sand column (< 25 °C, see Figure 6.1). Animals were fed on day 30.

6.3.3 Water gain/loss experiment

Specific dynamic action caused an almost two-fold increase in metabolic rate of well-fed versus starved animals (Table 6.1). Although metabolic rates on day 0 (day fed) were not significantly different to those on day 1 ($p > 0.05$, d.f. = 5) or day 2 ($p > 0.05$, d.f. = 4) there was a clear decrease in metabolic rate over this period. Day-time metabolic rate on day 11 is almost identical to that on day 2, indicating that at 30 °C specific dynamic action last for about 48 hours in *Angolosaurus skoogi*. Feeding after a 38 day starvation period caused a highly significant three-fold increase in metabolic rate (Table 6.1) from 0.044 ± 0.006 ml O_2/g.h. to 0.150 ± 0.028 ml O_2/g.h. ($p < 0.001$, d.f. = 8).

Other peripheral experiments initiated on the day animals were last fed revealed two important phenomena. Firstly, it was clearly evident that metabolic rates required a long time to stabilize after animals had been handled. Figure 6.3 is a representative example of a consistent observation. Measurements taken at 1.65 and 4.75 h were notably higher than later measurements. After 4.75 h, metabolic rate stabilized and remained fairly constant for the rest of the afternoon and throughout the night. Accordingly, any data obtained during the first 3 - 4 hours after handling were discarded from determinations comparing metabolic rates during the day and at night. Secondly, no significant difference between day and night metabolic rate could be detected (Table 6.1).

The effect of temperature on evaporative water loss (EWL) and metabolic water production (MWP) is shown in Figure 6.4. Although both EWL and MWP showed a steady increase with temperature, the increases were disproportionate resulting in a steady increase in net water loss with temperature. At no point did MWP come close to offsetting EWL.

6.3.4 Plasma electrolytes

Plasma electrolyte levels in starved *A. skoogi* maintained at 30 - 37 °C and 20 - 23 °C are shown in Table 6.2. Although osmolarities in the two situations are identical (326 ± 7 mmol/l), the proportions of electrolytes differed slightly. Sodium and chloride levels were slightly but significantly different. There was no significant difference in potassium levels. With the exception of sodium, the mean electrolyte concentration values reported here fall within the range of concentrations measured in freshly captured field animals (Section 5.3.3, Chapter 5). The sodium concentration means (172 and 161 mmol/l, Table 6.2) are slightly lower than the range measured in field animals (181 - 208 mmol/l).

TABLE 6.1. Resting metabolic rate (VO_2) of submerged *Angolosaurus skoogi* as a function of time of day and starvation period. Standard deviations are shown in parentheses. Significance values (p) are for comparison between day and night metabolic measurements. All experiments were conducted at 30 °C and measurements were only begun 3 - 4 hours after animals had buried. Animals were fed on day 0 and refed on day 39.

Days after feeding	n	Day VO_2 ml O_2 / g.h	Measurement period	Night VO_2 ml O_2 / g.h	Measurement period	Significance
0	3	0.083 (0.024)	14h30 - 18h00	0.073 (0.018)	24h00 - 06h00	p = 0.136
1	4	0.059 (0.012)	14h00 - 18h00	0.059 (0.010)	24h00 - 06h00	p = 0.830
2	3	0.047 (0.006)	14h15 - 18h30	0.045 (0.009)	18h30 - 06h00	p = 0.208
3	2			0.048 (0.008)	19h00 - 06h00	
11	6	0.045 (0.007)	06h00 - 14h00	0.040 (0.005)	24h00 - 06h00	p = 0.050
33	3			0.053 (0.007)	23h00 - 06h30	
38	4			0.044 (0.006)	22h30 - 06h00	
39	6	animals fed		0.150 (0.028)	22h30 - 06h00	

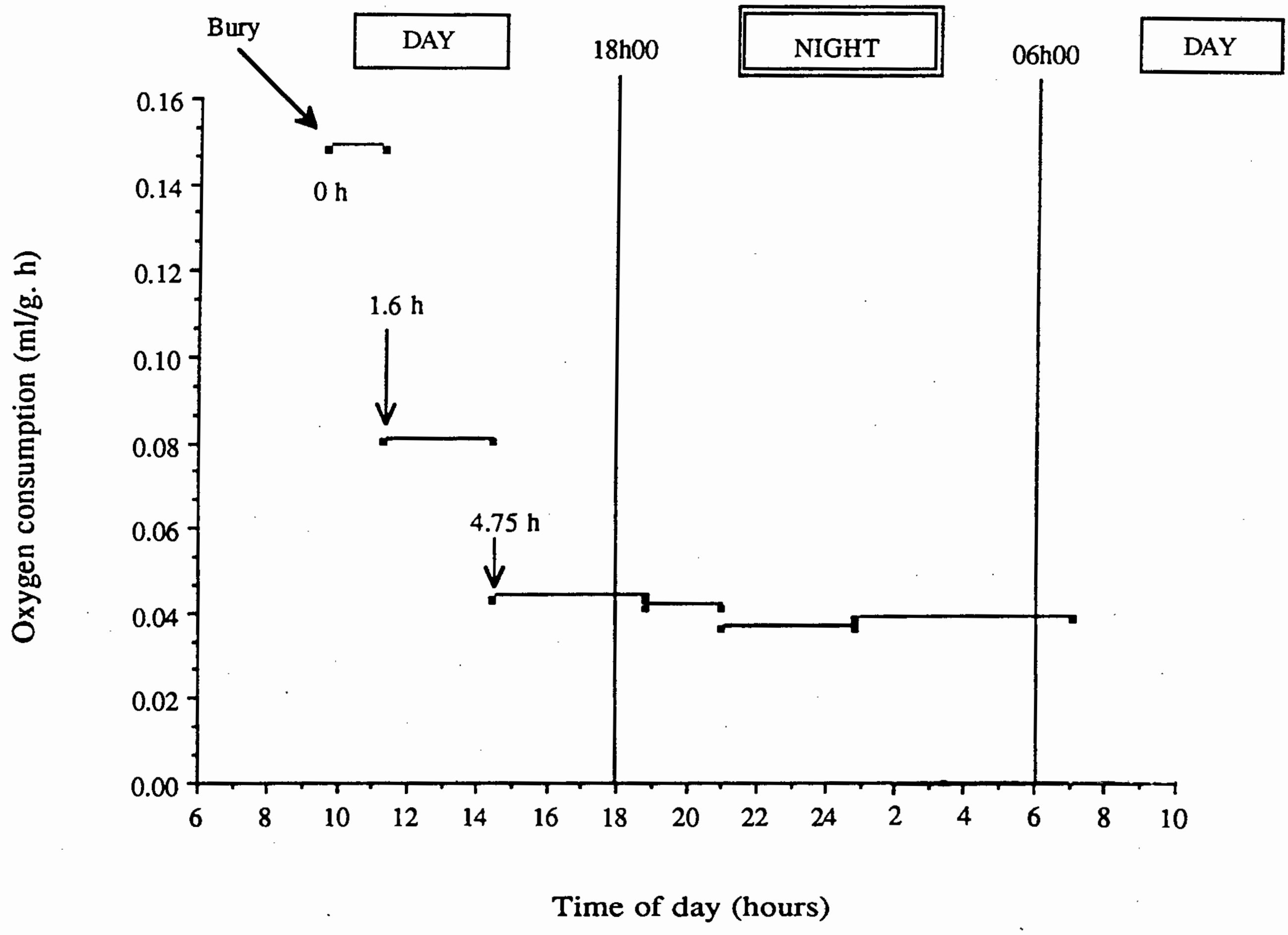


FIGURE 6.3. Representative example of the gradual decrease with time in the resting metabolic rate of a submerged *Angolosaurus skoogi* lizard. The animal was handled (weighed) and forced to bury at 09h00.

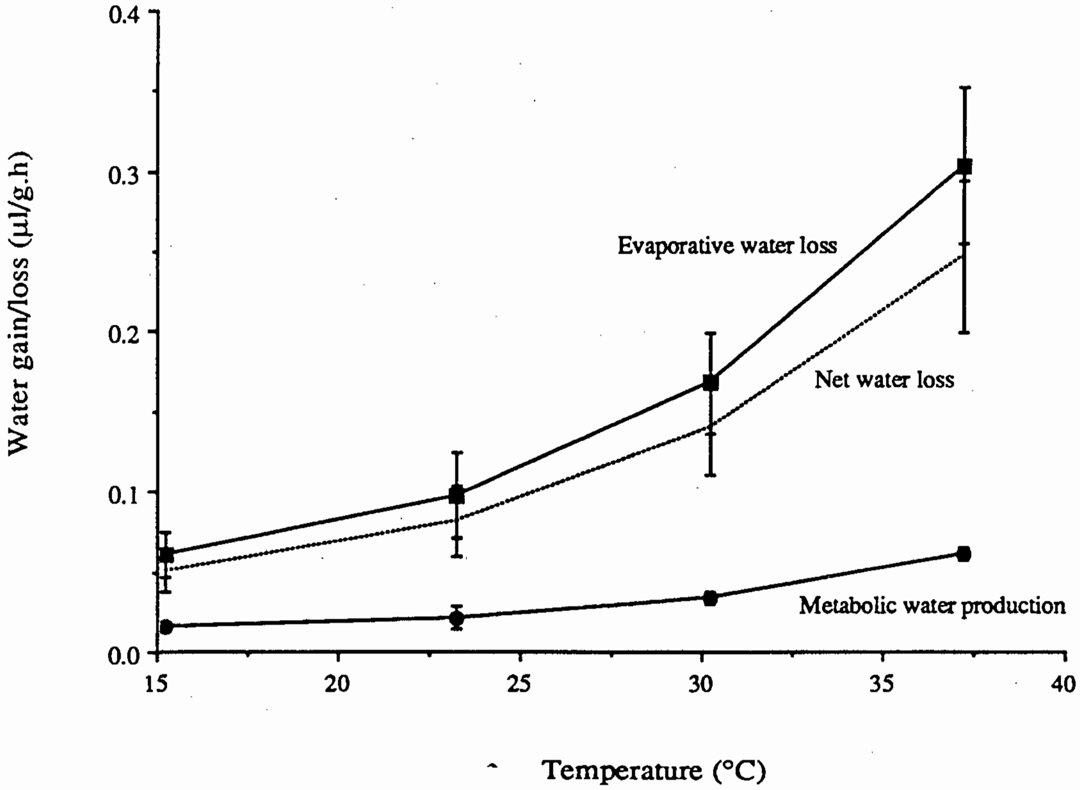


FIGURE 6.4. Rates of metabolic water production, evaporative water loss and net water loss as a function of body temperature in starved, resting *Angolosaurus skoogi* (n = 6). Metabolic water production was calculated from oxygen consumption rates, assuming a respiratory quotient of 0.71 for fat metabolism and the conversion of 0.754 ml CO_2 = 1 µl metabolic water (Nagy 1983). Evaporative water loss was determined gravimetrically. Net water loss was calculated from the difference between metabolic water production and evaporative water loss.

TABLE 6.2. Plasma electrolyte concentration of starved *Angolosaurus skoogi* (n = 8) kept at diiferent ambient temperatures. Standard deviations are shown in parentheses.

Experimental temperature (°C)	Na^+ mmol/l	K^+ mmol/l	Cl^- mmol/l	Osmolarity mmol/l
30 - 37	172 (4)	5.4 (0.9)	143 (4)	326 (7)
20 - 23	161 (6)	5.0 (0.3)	148 (4)	326 (7)
paired t-test	0.003 d.f. = 7	0.301 d.f. = 7	0.041 d.f. = 7	0.942 d.f. = 7

6.4 DISCUSSION

6.4.1 Thermal response to feeding and diel metabolism cycles

Although common, the phenomenon of post-feeding thermophily is not universal in reptiles. The crocodile *Caiman crocodilus*, for example, displays a constant range of preferred body temperatures before and up to six days after feeding (Diefenbach 1975). Although also common, diel cycles of metabolism are not displayed by all reptiles. Of the 25 odd reptile species in which 24 hour measurements of resting metabolic rate have been made, at least 6 species show no diel cycles (Waldschmidt *et al.* 1987). *A. skoogi* is thus not unique with regard to its apparent lack of a thermal response after feeding (Figure 6.2) and patterns of resting metabolism (Table 6.1).

The thermally benign environment submerged animals experience in the field may have something to do with the lack of a thermophilic response after feeding. Submerged *A.skoogi* are able to maintain body temperatures between 23 and 32 °C for 24 hours a day throughout the year (Table 5.8., Chapter 5). Considering that normal digestion can take place at these temperatures (Section 3.3.2, Chapter 3), there may have been no selective pressure in this animal's evolutionary history to develop the adaptation of seeking out warmer temperatures after feeding. Admittedly, thermophily is generally attributed to enhancing digestive rates (Waldschmidt *et al.* 1987) and thus improving an animal's energy gain. On the other hand, however, elevated body temperatures involve increased metabolic costs which may outweigh the benefits of enhanced digestion. In terms of net energy gain, it may be more beneficial to an animal to digest its food at more moderate temperatures if these are available. Another physical property of *A. skoogi*'s sand habitat may also have something to do with the absence of any diel cycles in the resting metabolic rate of this species. While submerged (20 - 24 hours per day, depending on season, Chapter 5), animals experience constant darkness. Deprivation of light has been demonstrated to destroy diel cycles in certain reptile species. Cragg (1978), for example demonstrated diel cycles in the metabolic rates of three species of *Lacerta* lizards under natural photoperiods. When exposed to constant darkness, however, two of the three species (*L. viridis* and *L. vivipara*) lost their diel cycles.

Following handling, the resting metabolic rate of *A. skoogi* took a remarkably long time to stabilize. Figure 6.2 shows that oxygen consumption measurements initiated less than about three hours after burial would result in large overestimates of resting metabolic rate. The exercise thus demonstrates the importance of quantifying the duration of handling stress prior to the initiation of any resting metabolism study. Failure to do this may make the data useless with regard to interspecific comparisons and its application to field studies, particularly time-energy budgets.

6.4.2 Thermal response to starvation

Preferred body temperatures of *A. skoogi* above the sand during starvation (36.5 ± 0.5 °C, n = 5) and after feeding (36.7 ± 0.8 °C, n = 2) correspond well with those observed by Mitchell *et al.* (1987) in fed, captive lizards offered a thermal gradient (36.8 ± 0.4 °C, n = 7). This, together with the consistent average body temperature maintained by submerged *A. skoogi* during the entire first starvation experiment, and the insistence of animals on repositioning themselves when the thermoregulatory light was moved or they were forced to bury in cold sand, clearly demonstrates that this species totally lacks a thermophobic energy conservation response while experiencing starvation.

Having established this, the pertinent question is whether this is due to a priority consideration of other temperature-dependent physiological processes or due to a lack of selective pressure in *A skoogi*'s evolutionary history for a positive conservation of energy response in the face of starvation. When considering evaporative water loss (EWL) in animals, investigators often fail to realize and assess the possible importance that metabolic water production (MWP) can play in offsetting water lost through evaporation. It is well known that in certain mammals, MWP can meet a substantial proportion of water requirements. In the kangaroo rat, for example, 90 % of water requirements can be met through MWP (Schmidt-Nielsen 1964). In this particular case, the high proportion of MWP coupled with physiological, morphological and behavioural adaptations result in more metabolic water being produced than evaporative water being lost from the animal. Reptiles also have adaptations for reducing water loss and are in fact considerably more efficient in conserving water than are endotherms of comparative size (Chew and Damman 1961). The metabolic rate of reptiles is, however, orders of magnitude lower than that of their endothermic counterparts (Nagy 1973). Thus, even though rates of water loss are low, MWP seldom seems to play an important role in the water balance of reptiles. A number of field and laboratory studies illustrate this (Dawson and Templeton 1963, Dmiel and Zilber 1971, Minnich 1976, Minnich 1977, Nagy 1972 and Templeton 1960). Thus it is accepted as a general rule that reptiles are incapable of producing metabolic water at a rate exceeding their EWL or that MWP plays an important role in the water balance of reptiles (Minnich 1979). It is evident from the literature, however, that this aspect of water balance has not been rigorously investigated and a generalization from limited studies may be premature. Only two studies to date have investigated the relationship between EWL and MWP. Dawson and Templeton (1963) have shown that between 32 and 40 °C temperature had no influence on the relationship between MWP and EWL in the lizard *Crotophytus collaris*. At temperatures above 40 °C, however, EWL increased disproportionately to MWP due to the initiation of evaporative cooling mechanisms. B.C. Clarke (unpublished data) has investigated the relationship between EWL and MWP at extreme temperatures and humidities in the giant girdled lizard, *Cordylus giganteus*. Experiments were conducted at 10 and 30 °C and relative humidities of 20 and 80 %. With two exceptions, MWP was incapable of providing significant compensation for water lost through evaporation. The two exceptional cases occurred at 10 °C and 80 % relative humidity where two individuals displayed MWP/EWL ratios of 0.5 and 0.9. The results of the present study are consistent with the above generalizations and findings. Although both EWL and MWP show a steady increase with temperature (Figure 6.4), the increases are disproportionate, resulting in a steady increase in net water loss with temperature. From a water conservation point of view, therefore, selection of the lowest body temperature possible would result in optimality. Failure to do this in this species means that water conservation can not explain the thermoregulatory behaviour of this species during starvation.

Osmotic and ionic regulation likewise does not provide a plausible explanation for the lack of a thermophobic energy conservation response. During dehydration, cold can aggravate osmotic and ionic regulatory functions in reptiles because it slows down or inhibits ionic transport processes, alters membrane permeability to water and ions and reduces glomerular filtration in kidneys (Gilles-Baillien 1974). Plasma sodium and chloride levels showed slight but significant changes when starved lizards were kept at different temperatures (20 - 23 °C versus 30 - 37 °C). The drop in both electrolyte levels at colder temperatures is consistent with observations of plasma changes in many hibernating and hypothermic reptiles (Minnich 1970, Haggag et al. 1965, Zail-Ul-Abedin et al 1969). All values reported here, however, fall well within the tolerable ranges reported for a wide variety of reptiles (Minnich 1982) and correspond well with the osmotic concentrations measured in freshly captured field animals (Table 5.3., Chapter 5). That starving *A. skoogi* select higher body temperatures than available to avoid complications with osmotic and ionic regulation does not appear to be a likely explanation for this observed thermoregulatory behaviour.

Not excluding the possibility that there are other physiological advantages to maintaining high body temperatures while starving, the most plausible explanation for this response at this stage is an eco-evolutionary one. *A. skoogi* never experiences starvation (Section 5.3.3, Chapter 5). There thus appears to have been no selective pressure in this species' evolutionary history for adaptations towards an optimal energy or water conservation response in the face of starvation. If starvation was periodically enforced, animals genetically predisposed to select lower body temperatures (the subsurface thermal profile would allow this - see Chapter 5) and subsequently conserve water and energy would outsurvive other individuals and and the trait would have become fixed in the population. This, in turn, would manifest itself in laboratory investigations of the thermal response to starvation.

An interesting follow up study, in the light of this explanation, would be a similar investigation on a related lizard which periodically experiences starvation.

CHAPTER 7

CONCLUSION

Deserts are typically characterized by low productivity, little water and harsh environmental conditions. The animals that live in them have evolved a number of adaptations to meet physiological requirements, reduce water loss and avoid thermal stress. In reptiles, adaptations include a virtually waterproof integument, nasal salt glands, the concentration of electrolytes in urate pellets and behavioural adjustments such as the cessation of activity when food quality deteriorates. Although they generally spend less energy than carnivorous species in obtaining food, herbivorous reptiles have additional problems such as low digestability of food and high electrolyte loads. It is easy to overlook the fact that once basic problems have been overcome there are still evolutionary considerations with regard to maximizing fitness in the face of both inter- and intraspecific competition. According to evolutionary theory animals should, where possible, behave in such a way as to optimize their scope for growth. Due to the complexity of animal behaviour, this prediction is not easy to test. Behaviour is often influenced by factors unrelated to energetic considerations. These factors, such as social interactions and predator evasion, may be difficult to identify and isolate, confusing investigations of scope for growth optimization. It is probably for this reason that this type of study is scarce in ecophysiological literature.

The first major contribution of this thesis is that reduced activity and its positive effect on net energy gain can now be added to the list of adaptations to desert survival and herbivory. Extreme thermal conditions and concomitant high energy costs may make the choice of activity strategies of vital importance to an ectotherm. Although reduction of activity as food quality deteriorates occurs in reptiles (Grenot 1976 ; Minnich 1976, 1977 ; Nagy 1972), this is the first demonstration of a voluntary reduction when food is still abundant. That this adaptation is necessary in this species can be attributed to three factors. Firstly, *A. skoogi* is a maxitherm when active. Whether this is intentional or incidental, it makes surface activity very expensive in terms of both water and energy loss. Secondly, *A. skoogi* feeds on a diet which has a high water content (about 85 % wet mass). It is not immediately obvious that food consisting of, for example, 70 % water contains 50 % more dry matter than a food with a 85 % water content. Compared to carnivorous lizards (which have a prey water content of about 70 %), herbivorous lizards are generally at an immediate energetic disadvantage. This, together with the lower digestability of plant material, makes the conservation and storage of energy an important consideration for herbivores. Finally, in male *A. skoogi*, the cost of territorial defence may also be an important factor with regard to reduced activity. If energetically expensive, maximization of scope for growth and fat storage outside the breeding season may be essential to survival during the breeding season. Failure to do this may result in severe negative energy balance and decreased reproductive performance.

There has been much discussion about the evolutionary and ecological significance of growth rates. The consensus seems to be that, under most circumstances, animals are adapted in ways which maximize growth, or which optimize growth in relation to realistically attainable rates of gross energy intake (Avery 1984). This forms the cornerstone of modern-day evolutionary theory. Ecological physiologists have recently recognized the need to relate physiology and behaviour to the concept of Darwinian fitness (Feder *et al.* 1988). This study makes an important contribution to that need. Although many assumptions have been used (particularly in estimating the cost of activity and stomach evacuation rate), the methodology and protocol used here should be useful to subsequent studies of this nature. Of particular importance is the awareness that animal behaviour may be influenced by factors unrelated to growth considerations. High predation pressure, competition, social interactions, involuntary hypo/hyperthermia and food shortages are all factors that can complicate and confuse a scope for growth optimization study and need to be carefully considered when choosing an experimental subject. Better methods such as doubly labelled water need to be employed to estimate the cost of activity. Estimates of gross energy intake as a function of body temperature also need to be improved. Ideally, the experimental subject should be one that voluntarily eats its fill (i.e. "tops up" its stomach) whenever offered food. This can easily be verified provided that sufficient specimens are available. Pilot laboratory experiments have established that *A. skoogi* does not always do this, presumably due to laboratory stress.

The third major contribution of this thesis is the demonstration of the importance of considering both losses and gains in ecophysiological studies dealing with water and energy balance. The data presented here have shown that optimizing digestion through behavioural thermoregulation may not necessarily result in optimization of growth rates. By considering energy losses, this study has revealed two additional factors that need to be incorporated into the optimal digestion hypothesis of Zimmerman and Tracy (1989). These factors are the cost of activity and body temperatures during non-thermoregulatory periods. If the cost of activity is high, the improvement of food and water processing rates may be disproportionate to losses and extended activity will become detrimental to water and energy balance. If non-thermoregulatory periods are spent at low temperatures, on the other hand, maximizing the thermoregulatory period may indeed optimize growth rates. This has been clearly demonstrated in the laboratory by Avery (1984). The data presented in Zimmerman and Tracy (1989) are a case in point. During most of the activity season, chuckwallas (*Sauromalus obesus*) overnight at body temperatures less than 15 °C. Animals generally thermoregulate for as long as preferred surface body temperature (about 35 °C) can be maintained. Provided that food is abundant (which is the case) and the cost of activity is not too high, this behaviour would, according to the results of Avery (1984), result in growth rate optimization. In contrast, *A. skoogi* overnights at body temperatures about double that of *S. obesus* for most of the year. Surface body temperatures are also about 5 °C higher and the cost of activity is very high. Subsequently, the strategy for growth rate optimization in *A. skoogi* is the opposite to that of *S. obesus.*

Finally, this study has brought to light important new considerations with regard to laboratory studies of resting metabolic rate. Firstly, there is the hitherto ignored phenomenon of temporal and thermal laboratory acclimation. Experiments reported in Chapter 3 show that resting metabolic rate may acclimate (decrease) with time and be influenced by exposure temperatures prior to experimentation. The former factor has also been demonstrated in endotherms (mole-rats - see Appendix 2). These findings have important implications with regard to the application of laboratory data to field situations. It is imperative that laboratory determinations of metabolic rates be conducted as soon as possible after animals have been captured. Just as important, laboratory animals should be exposed to the same thermal regime they experience in the field. These findings also have important implications with regard to making interspecific comparisons of resting metabolic rates. Unless there has been standardization with regard to the interval experiments are conducted after capture and the thermal exposure prior to experimentation, comparisons should be treated with caution.

Secondly, in *A. skoogi* at least, resting metabolic rates take a long time to stabilize after animals have been handled. This, once again, has important implications with regard to interspecific comparisons and the application of laboratory data to field situations. It is imperative that pilot studies on the duration of handling stress be conducted prior to the collection of resting metabolic rate data. Failure to do this may result in overestimates of metabolic costs during periods of inactivity.

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APPENDICES

Other reseach conducted while registered for the PhD degree

APPENDIX 1	Water flux in free-living lions (*Panthera leo*) in the Etosha National Park, Namibia. B.C. Clarke and H.H. Berry (in press, Journal of Mammology)
APPENDIX 2	A comparison of metabolic acclimation in two species of social mole-rats (Bathyergidae) in southern Africa. N.C. Bennett, B.C. Clarke and J.U.M. Jarvis (in press, Journal of Arid Environments)

APPENDIX 1

WATER FLUX IN FREE - LIVING LIONS (*PANTHERA LEO*) IN THE ETOSHA NATIONAL PARK, NAMIBIA

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ABSTRACT.-- Water flux rates of eight free-living lions, *Panthera leo* , were measured using tritiated water. Water influx rate averaged 49.5 ± 7.5 ml $kg^{-1}day^{-1}$. This is only slightly higher than predicted water influx value in captive animals under standard conditions, but over twice as high as predicted water influx in free-living eutherian carnivores. Factors influencing water flux rates and estimates of food consumption from independent studies were used to determine dependence on drinking water, a constant supply of which is maintained artificially in the study area. Drinking comprised approximately 40 % of the total water influx.

A1.1 INTRODUCTION

Most literature on water flux in free-living mammals pertain to herbivores (Nagy and Peterson, 1988). Carnivorous mammals play an important role in certain ecosystems and can have a large influence on prey population dynamics. It is of vital importance that game management procedures are based on sound ecological and physiological principles. In hot weather, drinking contributes significantly to water influx in free-living lions, *Panthera leo* (Green, Anderson and Whatley, 1984). A knowledge of the effect that water shortages or excesses have on the population dynamics of this species and the subsequent effect on population dynamics of its prey therefore is of particular relevance to game management programmes.

The Etosha National Park in Namibia, a reserve of 22,270 km^2, forms one of the last refuges for the rapidly declining population of lions in southern Africa. Etosha's lion population undergoes irregular fluctuations resulting in too few or too many lions in relation to prey animals. The reasons for the underpopulation periods are obscure but are related to periods of unexplained cub mortality. The reasons for the overpopulation periods are better understood. Three main causes have been isolated (Berry 1981, Berry 1982). Etosha National Park is totally fenced, precluding seasonal immigration and emigration of ungulates. Mortalities (particularly in lion cubs) during long journeys when adult lions were obliged to move with the migratory herds of prey now no longer occur. Also, during the rainy season, the numerous gravel pits made for road building in the reserve form ideal breeding environments for anthrax, *Bacillus anthracis*, a bacterial disease that causes mass mortalities in herbivores in the reserve. This not only causes a decline in prey populations, but also provides an overabundance of food for the lions which are opportunistic scavengers and immune to the disease. Finally, and most relevant to this study, numerous boreholes have been drilled inside the reserve to provide a permanent source of drinking water for animals. These boreholes stabilize the environment, providing both water and places of ambush for hunting lions throughout the year.

For the past 7 years, lions have formed the subject of an intensive research programme in the Etosha National Park (Melton *et al.*, 1987 ; van Wyk and Berry,1986). Selected results of this programme suggest that lions are unable to meet their water requirements through their diet alone, and therefore are dependent on drinking water. For example, shifts in territorial boundaries inevitably occur when waterholes, that usually form the center of territories, dry up. Programes for the control of the lion population in Etosha National Park requires some knowledge of the influence of artificial water points on their population dynamics. Ultimately this will require knowledge water requirements of lions in the reserve. This study was undertaken as part of the current research programe in order to quantify water requirements of lions and to assess their dependence on drinking water. An additional motivation for the study was to contribute to the much needed picture of water flux in free-living carnivorous mammals.

A1.2 METHODS AND MATERIALS

The study was conducted during September and October 1987 in the Etosha National Park, Namibia (19° 15' S ; 15° 55' E). Surface water was available throughout the study in the form of artificially maintained boreholes and natural springs.

Lions were immobilized by means of a Palmer CO_2 gas Cap-chur rifle fired from the window of a vehicle. The darts contained 600 - 1000 mg ketamine hydrochloride and 300 - 500 ml xylazine hydrochloride, depending on the estimated body mass of the animal. Booster doses were administered as required to immobilize the animal as long as was necessary. Tolazoline hydrochloride was used as an antagonist to the immobilization drugs. Immobilization required approximately 15 minutes. after which the rest of the pride was driven away and the captive animal transported to the shade. All immobilizations took place during the day.

After taking an initial blood sample to determine background radioactivity counts, the immobilized animals were injected with 3 - 5 ml of tritiated water (7.4 X 10^7 Bq s^1/ml) via the jugular vein. Animals were weighed, permanently marked and fitted with radio-transmitter collars. One hour before the estimated isotope equilibrium time (3 - 6 h, depending on the feeding status of the animal), a second blood sample of about 3ml was taken from the jugular vein. A final blood sample was taken one hour later. The second and final samples were taken to check that the equilibration of the isotope in the body water of the animal was complete. Blood samples were centrifuged in the field and the plasma fractions transferred to Eppendorf plastic vials. They were kept on ice in the field until they could be frozen and stored. When animals urinated, samples of urine were then collected and stored in plastic vials for later analysis. The quantity of urine collected in this way ranged from a few drops to several decilitres. In the latter case, subsamples were taken randomly throughout the duration of the flow. The samples were thus not standard with regard to collection time and volume.

Positions and movements of lions were monitored regularly to obtain distances moved and the frequency of eating and drinking. Eating frequency was estimated by noting changes in the degree of distension of a particular lion's stomach between sightings. Animals were recaptured between 13 and 21 days in the same manner as the original captures, after which another duplicate blood sample was obtained, the collar removed and the animal reweighed. A total of eight lions were injected and recaptured during the course of the study.

Radioactivity of all samples was determined by adding a 200 µl aliquot of plasma and 200 µl of hydrogen peroxide to 10 ml of Packard Instagel scintillation cocktail and counting in a Packard Tri-Carb 460C liquid scintillation counter. The volume of plasma added was corrected for dry- matter content by drying selected plasma samples to constant mass and subtracting the calculated dry matter content from the mass of plasma added to the scintillation cocktail. Samples were counted until < 2 % counting error was obtained. A counting error of this magnitude results in negligible errors in the calculation of water flux rate. Standards were prepared by diluting the original injection solution 1: 20 000 in double distilled water and counting 200 µl. Duplicate standards never differed by > 2.5 %. Counts were not corrected for quenching as the quench factor (determined by the samples channels ratio method) was constant for all samples, including standards.

Changes in tritium concentration were used to determine rates of water influx and efflux assuming linear changes in pool sizes (Lifson and McClintock, 1966; Nagy, 1975). The initial pool sizes were determined by the dilution of tritium during the 3 - 6 h before release, and final pool sizes were estimated as a product of final mass and the initial mass - specific pool sizes.

The concentrations of sodium, potassium, urea and the total osmolarity of urine samples were determined by use of an Instrumentation Laboratory model 234 flame photometer (Na^+ and

K^+), a Boehringer urea test kit (Fawcett and Scott, 1960) and a Wescor Incorporation 5100B vapor pressure osmometer (osmolarity).

Regression lines were calculated by the least squares method. The F-statistic was used to evaluate the significance of regressions. Climatic data during the study period were obtained from the meteorological station at the Okaukuejo base camp in the park.

A1.3 RESULTS

Weather conditions during the study period were characterized by cool moderately humid mornings, hot dry afternoons, and warm dry evenings (Table 1). Body mass, total body water and water flux values are shown in Table 2. Four of the lions showed fairly large changes in body mass during the study period (+1.1, +0.5, +0.4 and -0.4 %/day). This reflects the erratic feeding patterns of individuals rather than linear mass changes related to growth or starvation. Mass specific total body water ranged from 58.9 to 71.0 % (x = 65.1 ± 4.0 %). Water influx averaged 49.5 ± 7.5 ml kg^{-1} day^{-1} and was also variable, ranging from 40.0 ml $kg^{-1}day^{-1}$ to 60.5 ml $kg^{-1}day^{-1}$. This once again reflects differences in feeding and drinking patterns among individuals.

Observational success, distances moved, and eating and drinking frequencies are summarized in Table 2. In an attempt to isolate factors influencing water flux, these values were regressed individually against water influx (independent variable). The allometric transformation of water flux (Macfarlane and Howard, 1972) was applied to influx data to eliminate the influence of body size. None of these regressions were significant ($r^2 = 0.009$ -distance moved ; 0.254 -eating frequency ; 0.391 -drinking frequency ; d.f = 4, $P > 0.05$). Drinking and eating frequencies were subsequently averaged and regressed against water influx rate. This regression was significant ($r^2 = 0.755$; d.f = 4 ; $P < 0.05$).

The concentrations of sodium, potassium, and urea in urine samples were highly variable, again most likely related to the feeding status of the animal. Sequential electrolyte concentrations in samples from an individual also were variable. Sodium concentration averaged 104 ± 62 mmol/l with individual samples ranging from 36 to 275 mmol/l. Potassium concentrations were generally lower, averaging 63 ± 39 mmol/l and ranging from 8 to 152 mmo/l. Urea concentrations were markedly dependent on how recently an animal had fed and what quantity of food it had consumed. Concentrations averaged 1,190 ± 498 mmol/l, ranging from 506 mmol/l in an animal that had had a light meal > 24 h before sampling, to 2,159 mmol/l in an animal that had gorged itself within 12 h of sampling. Compared with other animals, lion kidneys are able to produce urine of a moderately high concentration (Schmidt-Nielsen,1964). The maximum osmolarity we recorded

TABLE 1. Climatic data measured at the Okaukeujo weather station during the study period (September - October 1987).

Time (h)	Average temperature (°C ± S.D)	Range (°C)	Average relative humidity (% ± S.D.)	Range (%)	Average temperature (°C)	
					max.	min.
08h00	15.8 ± 3.3	8.8 ± 22.0	43.7 ± 22.3	6 - 98		
14h00	30.3 ± 2.2	26.0 ± 33.4	18.5 ± 13.2	2 - 48	32.6 ± 1.8	12.7 ± 3.9
20h00	25.4 ± 2.4	20.9 ± 30.5	17.0 ± 13.2	2 - 52		

here (2,388 mmol/l) is about two thirds of the maximum urine concentration recorded in domestic cats.

A1.4 DISCUSSION

Water flux in animals is not a simple function of body size and can be extremely variable (Nagy and Peterson, 1988). Changes in the water content of food, degree of activity, increased need for evaporative water loss during periods of heat stress and increased thermogenisis during cold periods all contribute to the complexity of water flux rates in any species. The present study was conducted during the hot, dry spring-summer transitional period. Due to heat stress, water flux rates reported herein (49.5 ± 7.5 ml kg^{-1}day^{-1} , Table 2) probably fall within the higher range of values characterisic of this species. Green *et al.* (1984), however, report statistically similar flux values (53.9 ± 12.5 ml kg^{-1}day^{-1}) for another population of lions during a colder winter-spring transitional period (d.f = 11, $P > 0.05$). This similarity may reflect elevated water flux rates due to an increased need for thermogenisis in winter and an adundance of drinking water (rivers) in the study

TABLE 2. Distances moved, eating and drinking frequencies (F) and parameters of water flux in free-living lions.

Lion no.	Sex	Sighting success[1]	Distance moved (km/day)	F. eating (/day)	F. drinking (/day)	Initial mass (kg)	Mass change (%/day)	Body Water (%)[2]	Water flux (ml/kg.day)		Water influx	
									in	out	(ml/kg$^{0.82}$.day)	(ml/l.day)
1	F	8/14	7.0	0.5	0.4	129	+1.1	58.9	60.5	54.7	145.1	102.6
2	F	10/14	4.7	0.1	0.4	123	+0.5	64.7	37.8	34.3	89.3	58.0
3	F	8/17	3.5	0.3	0.3	129	+0.4	67.2	48.8	46.2	117.1	72.7
4	M	9/14	1.8	0.8	0.1	192	-0.2	67.4	49.7	50.7	128.0	73.3
5	F	3/13	4.3	0.3	0.3	172	-0.1	67.4	51.7	52.6	130.6	76.7
6	F	10/16	5.1	0.3	0.2	111	0.0	71.0	40.0	40.0	93.3	56.3
7	F	0/21	-	-	-	80	-0.4	62.6	55.9	58.7	123.0	89.3
8	M	0/21	-	-	-	125	+0.2	61.3	51.2	52.4	122.4	86.3
x			4.4	0.4	0.3	133	+0.2	65.1	49.5	48.7	118.6	77.0
S.D.			1.7	0.2	0.1	35	0.5	4.0	7.5	8.1	18.8	15.6

[1] number of days sighted / recapture interval

[2] mass specific total body water

area. The former factor may also apply to the lions in this study. Variabilty in body mass changes and isotope flux rates (Table 2) are also prevalent in this study and are probably the result of sporadic feeding patterns of individuals. This influence, emphasized by Green *et al.* (1984), would be substantially reduced by extending recapture intervals.

Comparison of water flux values reported here to those of other carnivorous mammals presents problems. The reasons for the variability of flux rates makes standardization difficult. Also, there is a notable paucity of data. Nicol (1978) has shown that water flux in captive eutherians and marsupials is significantly related to body mass ($kg^{0.82}$) when ambient temperatures are moderate and drinking water is freely availble. The mean water influx rate of animals under these standard conditions is approximately 102 ml $kg^{0.82}day^{-1}$ ($n = 41, r^2 = 0.966$). Although habitats and diets of experimental animals differed considerably and only 7 animals weighed >10kg, the highly significant correlation suggests that the above equation can be used to approximate water flux for any mammal under standard conditions. When the allometric transformation of flux rates is applied to the data of this study, rates of water influx approximate 119 ml $kg^{0.82}day^{-1}$ (Table 2). The mean rates of free-living lions thus are only about 17 % higher than the estimate for captive animals under ideal conditions. Nagy and Peterson (1988), on the other hand, have derived an equation relating water flux to mass in a variety of free-living carnivorous eutherians. According to this equation, predicted water flux for a 133 kg animal = 22.1 ml $kg^{-1}day^{-1}$. The observed flux rate, 49.5 ml $kg^{-1}day^{-1}$, is more than twice the predicted estimate. Although the correlation for this equation is also highly significant ($r^2 = 0.906, P < 0.001$) there is a dire paucity of data for larger mammals. Besides three species of seals (which were nursing, lactating or fasting), data only exists for three species > 1 kg. The validity of the equation for larger animals is thus debatable. Comparison of our data to these two data sets thus gives contradicting results and should be treated with caution. Clearly, the contradiction will only be resolved in time as more data are accumulated. Valid reasons for both relatively high and low flux rates further complicate the issue. The hot, dry conditions experienced during the study (Table 1) could more than adequately account for elevated flux rates. On the other hand, physiological and behavioural factors could account for substantial water conservation and reduced flux rates. Lion kidneys have at least a moderate urine concentrating ability. Lions are predominantly nocturnal, moving at night and in the early, cool mornings. Days are spent resting in the shade of trees. This habit reduces net evaporative water loss from the respiratory tract during periods of activity. Also, feeding patterns of lions are characterized by periodic engorgements alternating with periods of low activity with no feeding for as long as a week. These long periods of inactivity probably represent a substantial saving of water compared with other animals that have more regular foraging patterns.

Attempts to isolate the predominant factor influencing water flux rates were unsuccessful. Distance moved is unlikely to influence water efflux greatly (and subsequent compensatory water influx) as lions are nocturnal and evaporative water loss rates during night activity probably are low. Consequently, distances moved should have little effect on the total water budget. The lack of a correlation between eating frequency and water flux rates or drinking frequency and water flux rates, coupled with the significant correlation between combined eating and drinking frequency and water flux rates, suggests that these two avenues of water gain make complimentary contributions to water influx.

As lions were never observed on a kill and observations on of various activities were erratic, food consumption or energy requirements could not be determined. However, Lamprey (1964) estimated the mean energy expenditure of lions in Tanganyika to be 270 kJ $kg^{-1}day^{-1}$ whereas Green *et al.* (1984) measured a mean digestible energy intake of 295 kJ $kg^{-1}.day^{-1}$ in lions in Natal, South Africa. Assuming a mean energy prey content of 7.1 $kJ.g^{-1}$ (Gorecki, 1975) and a digestive efficiency of 90 % (Green and Eberhard, 1979 ; Wagner, 1970), these energy values equal to a food intake of 42.3 and 46.1 $g.kg.^{-1}day^{-1}$ respectively. Assuming a water content of prey of about 65%, this would result in a water input from prey of approximately 29 ml $kg^{-1}day^{-1}$. If one assumes that the lions in the present study have a water intake from prey of this value, it is possible to get a rough idea of what percentage of daily water intake is met by eating and drinking. Average water influx was approximately 49 ml kg^{-1} day^{-1}. Water imput from prey would thus comprise approximately 60% and drinking 40% of the total water influx. In lions in Natal, South Africa, Green et al. (1984) found a similar situation during the summer months where drinking contributed approximately 50 % to the total water influx.

These estimates suggest that, in hot conditions, lions are unable to meet their water requirements through their prey alone. This immediately raises pertinent questions with regard to the maintenance of artificial water supplies in the reserve. We show that a large proportion of water requirements are met through drinking and thus suggest that lions would struggle to survive without access to artificial water supplies. As the reserve is totally fenced, migration to other water sources is prevented. Conversely there are reports of lions going without drinking water for extended periods (Eloff, 1973 ; Owens and Owens, 1984 ; Smithers, 1983). A well documented case is that of lions in the central Kalahari, Botswana, which met all their water requirements through their diet alone for > 9 months (Owens and Owens, 1984) . The dependence of lions on drinking water thus is debatable. They are capable of surviving without drinking water, but when it is available, appear to make good use of it. In the case of the Kalahari lions, however, the lack of drinking water had a marked influence on behavior and the social cohesion of prides (Owens and Owens, 1984). Such behavioral deviations may be impractical in certain areas, making resident lions more reliant on drinking water than their Kalahari counterparts.

With the information at hand, no definite conclusions can be drawn with regard to the effect of the artificial water supplies on the population dynamics of lions. A better knowledge of energy requirements is needed to obtain a more accurate estimate of the utilization of drinking water when it is available. Studies like that of Green *et al.* (1984) and Gales (1989) have shown that good estimates of prey consumption can be obtained for predators by monitoring radioactive sodium flux. Although this use of radioactive sodium in certain species has been criticized recently (Wilkinson and Skinner, 1988), it still appears to be the best method for estimating prey consumption in animals for which continuous, direct observations are difficult.

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APPENDIX 2

A COMPARISON OF METABOLIC ACCLIMATION IN TWO SPECIES OF SOCIAL MOLE-RATS (BATHYERGIDAE) IN SOUTHERN AFRICA

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Abstract

The social Common mole-rat *Cryptomys hottentotus hottentotus* has a mean (± SD) resting metabolic rate (RMR) when newly captured of 1.38 ml O_2 / g.h (n = 12), within a thermoneutral zone (TNZ) of 27 - 30 °C. Three months after maintenance in the laboratory at 25 °C, the RMR of the same animals showed a concomitant drop in value of 43 % at 28 °C (TNZ) to a mean of 0.92 ± 0.11 ml O_2 / g.h, indicating that laboratory acclimation had occurred. The body temperature of the mole-rat is low (34 ± 0.78 °C) and remains stable at ambient temperatures (Ta) from 10 to 27 °C. The conductance is high (0.14 ± 0.018 ml O_2 /g.h.°C, n = 24) at the lower limit of thermoneutrality. The mean resting metabolic rate at 15 °C (the lowest Ta tested) was 2.84 ± 0.24 ml O_2 / g.h, which is twice that of the RMR in the TNZ.

The highly social Damaraland mole-rat *Cryptomys damarensis* has a mean (± SD) RMR when freshly captured of 0.66 ± 0.07 ml O_2 /g.h (n = 12) within a TNZ of 28 - 31 °C. Two months after maintenance in the laboratory at 25 °C, the RMR of the same animals was unchanged (0.69 ± 0.06 ml O_2 /g.h, n = 12) at TNZ indicating that laboratory acclimation had not occurred. Body temperatures of this species averaged 35.1 ± 0.56 °C and remained stable over Ta from 18 - 28 °C. The conductance in C. damarensis is low (0.065 ± 0.014 ml O_2 /g.h.°C, n = 24) at the lower limit of themoneutrality. The mean metabolic rate at 18 °C was 1.07 ± 0.30 ml O_2 /g.h, which is 40 % above the RMR.

The nest (where mole-rats rest for up to 80 % of the day) is the focal point of the burrow system. The characteristics and temporal changes in nest microclimate (influenced by depth) may be an important factor affecting acclimation and seasonal acclimatization in the mole-rats. Selection for *C. h. hottentotus* to acclimate within its TNZ may relate to seasonal fluctuations of the microclimate in a shallow nest - exhibited by seasonal acclimatization in RMR, whereas the absence of acclimation observed in *C. damarensis* may relate to a more constant microclimate in its deep nest.

A2.1 INTRODUCTION

The common mole-rat (*Cryptomus hottentotus hottentotus*) and the Damaraland mole-rat (*Cryptomus damarensis*) are social subterranean rodents living in colonies composed of as many as 25 individuals (Bennett 1988, 1989, 1990a ; Jarvis and Bennett 1990). Reproduction is restricted to 1 - 3 of the largest males and to the largest female in the colony (Bennett 1989 ; Bennett and Jarvis 1988 ; Bennett and Jarvis 1991 ; Rosenthal 1989).

The burrows of *C. h. hottentotus* tend to be constructed in more compact soils than those of *C. damarensis* (Jarvis and Bennett 1990). The burrow systems consist of numerous long subsurface foraging runs 10 - 25 mm deep and a deeper central area more protected from predators and temperature extremes, containing a nest and bolt hole (Davies and Jarvis 1986 ; Jarvis and Bennett, unpublished data). Both species feed on corms, bulbs and tubers (Davies and Jarvis 1986 ; Bennett 1988) harvested from foraging runs as the mole-rats burrow. Subterranean rodents spend their lives underground, rarely venturing above the surface (Nevo 1979).

The existing literature on metabolism and respiratory physiology in subterranean rodents suggests that representatives occupying this ecotype generally exhibit low resting metabolic rates (McNab 1979 ; Lovegrove 1986 a,b, 1987). A low RMR is apparently an adaptation to hypoxia and hypercapnia (Arieli 1979 ; Arieli *et al.* 1984). It has also been suggested that low RMR's may represent an energy-saving adaptation to alleviate the vast energetic costs of burrowing (Jarvis 1988 ; Vleck 1979, 1981 ; Lovegrove 1987).

The nests of these two species differ greatly in depth. The nest of *C. hottentotus* is shallow (± 4 cm) and exhibits seasonal thermal fluctuations. By comparison, nests of *C. damarensis* are deeper (1.6 - 2.3 m) and more insulated from daily and seasonal thermal change (Bennett *et al.* 1988). We therefore predicted that the RMR of *C. h. hottentotus* should exhibit greater plasticity in acclimation than the RMR of the latter. This paper compares and contrasts the RMR's of freshly captured *Cryptomys* of both species occurring in arid habitats and investigates the change of the RMR in the TNZ with time in activity.

A2.2 METHODS AND MATERIALS

A2.2.1 Study animals

Six *Cryptomys hottentotus hottentotus* (3 males and 3 females) were collected at Steinkopf (29° 15' S ; 17° 44' E) near Springbok, northern Cape, South Africa. Body mass (m) of the individuals ranged from 67 - 104 g. Six *Cryptomys damarensis* (2 males and 4 females) were collected at Dordabis (22° 58' S ; 17° 41' E) in the Rheoboth district, Namibia. Body mass of these individuals ranged from 130 - 192 g. The mole-rats were housed in glass terreria in a constant temperature room at 26 °C. Wood-shavings and paper towelling were provided as nesting material. The mole-rats were fed a variety of vegetables and Pronutro cereal daily.

A2.2.2 Experimental Procedure

Resting metabolic rate was measured by means of flow-through respirometry. Air flow rate was measured using a bubble flowmeter constructed from a modified burette and filled with soap water. The respirometer comprised a transparent cylindrical plastic chamber (volume 600 ml) fitted with 6 mm inlet and outlet ports. Ambient temperature inside the chamber was kept constant by placing it in a small (0.11 m^3) temperature controlled cabinet. Air was drawn through the respirometer and into the oxygen analyser (Applied Electrochemistry model 3-A) at a flow rate of 300 - 360 ml/minute. Soda lime and silica gel scrubbers were fitted in the pipe between the chamber and analyser to remove carbon dioxide and water from excurrent air. Control readings were obtained by a parallel flow-through system incorporating an empty chamber.

The method of Bartholomew et al (1985) and Lighton (1985) was used to measure oxygen consumption. All data was recorded on a BBC microcomputer. Oxygen consumption, expressed as a mass-specific rate, was calculated according to Depocas and Hart (1957) as :

$$VO_2 = (F_1\,O_2 - F_2\,O_2)\,V_2 \;/\; (1 - F_2\,O_2)\,m$$

where VO_2 = oxygen consumption rate in ml O_2 / g.h, $F_1\,O_2$ = the oxygen fraction of the inlet air (control), $F_2\,O_2$ = the oxygen fraction of the excurrent air and V_2 = flow rate in ml air/h. Values were corrected to STP conditions.

The progress of each run was visually monitored on the computer monitor and markers were placed on each trace to record behavioural observations made during the run. Each run was programmed to last for 180 minutes, with data points being collected every 17 seconds. The initial

60 minutes of each run was used to allow the animal to settle and consequently this section of the trace was not analysed.

Only portions of traces of approximately 20 minutes which corresponded to the lowest stable oxygen consumption when animals were completely at rest were analysed. At lower temperatures, however, portions of traces of approximately 10 minutes were used because animals were reluctant to rest for longer periods of time.

The relationship between oxygen consumption and ambient temperatures below the thermoneutral zone (Tl) was analysed by the method of least squares regression (Zar 1984). Thermal conductance below Tl was calculated for individual measurements of oxygen consumption using the formula Cm = VO_2 / (Ta - Tb) where Cm is thermal conductance in ml O_2 /g.h.°C, VO_2 is oxygen consumption in ml O_2 / g.h, Ta is ambient temperature in °C and Tb is body temperature in °C.

Oxygen consumption was measured in both species within three weeks of capture and repeated on the same animals two and a half to three months later. In *C. h. hottentotus*, initial measurements were conducted at seven ambient temperatures ranging from 15 - 33 °C, and at 28 °C three months later. In *C. damarensis*, initial measurements were conducted at a seven ambient temperatures ranging from 18 - 34 °C and at 27, 30 and 34 °C two and a half months later. Experiments were run between 08h00 and 18h00 to avoid the effect of endogenous rhythms of metabolism. Animals were deprived of food for three hours prior to measurements of metabolic rate to ensure post-absorbtive states and avoid the influence of specific dynamic action.

To investigate the relationship between ambient and body temperature, animals were placed in the constant temperature cabinet at selected ambient temperatures. The temperature inside the cabinet was monitored by means of a copper-constantan thermocouple. After three hours, animals were removed from the cabinet and their rectal temperatures measured using the same thermocouple.

A2.3 RESULTS

A2.3.1 *Cryptomys h. hottentotus*

The body temperature of *C. h. hottentotus* remained stable at ambient temperatures between 18 - 27 °C with a mean value of 34.4 ± 0.78 °C. Above 30 °C, body temperatures increased to 35.4 ± 0.77 °C, n = 12 (Figure 1a). The mean resting metabolic rate of recently captured (three weeks in captivity) animals was 1.38 ± 0.29 ml O_2 / g.h (n = 12) within a thermoneutral zone of 27 - 30 °C (Figure 2a). Below the lower limit of thermoneutrality, the increase in metabolic rate is given by

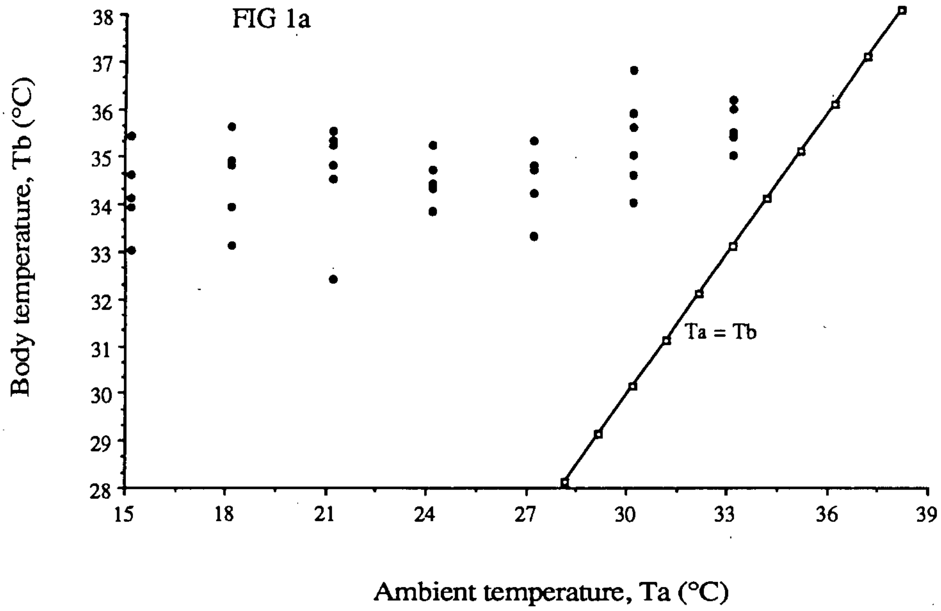

FIGURE 1a. Body temperature (Tb) of six common mole-rats (*Cryptomys hottentotus hottentotus*) as a function of ambient temperature (Ta). The line with open squares indicates the temperature relationship Tb = Ta.

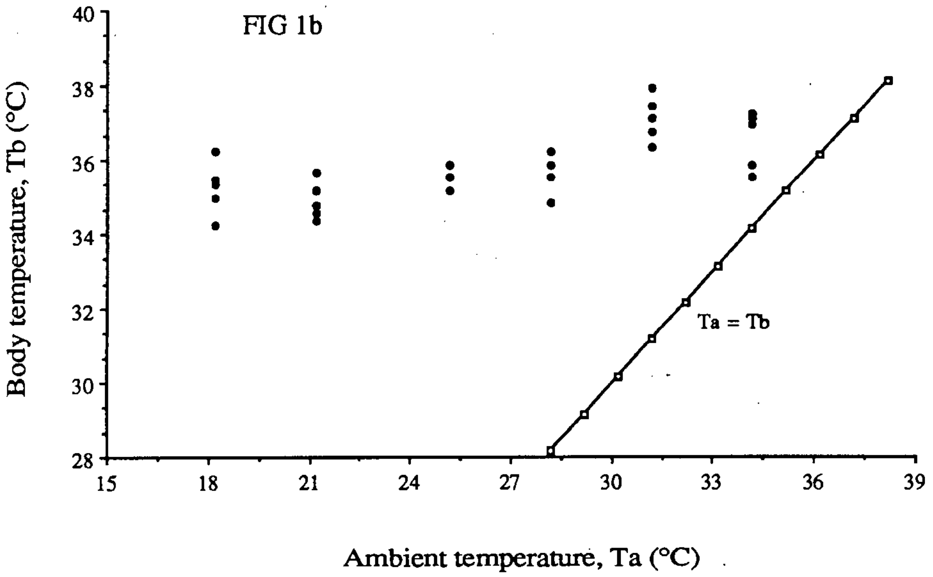

FIGURE 1b. Body temperature (Tb) of six Damaraland mole-rats (*Cryptomys damarensis*) as a function of ambient temperature (Ta). The line with open squares indicates the temperature relationship Tb = Ta.

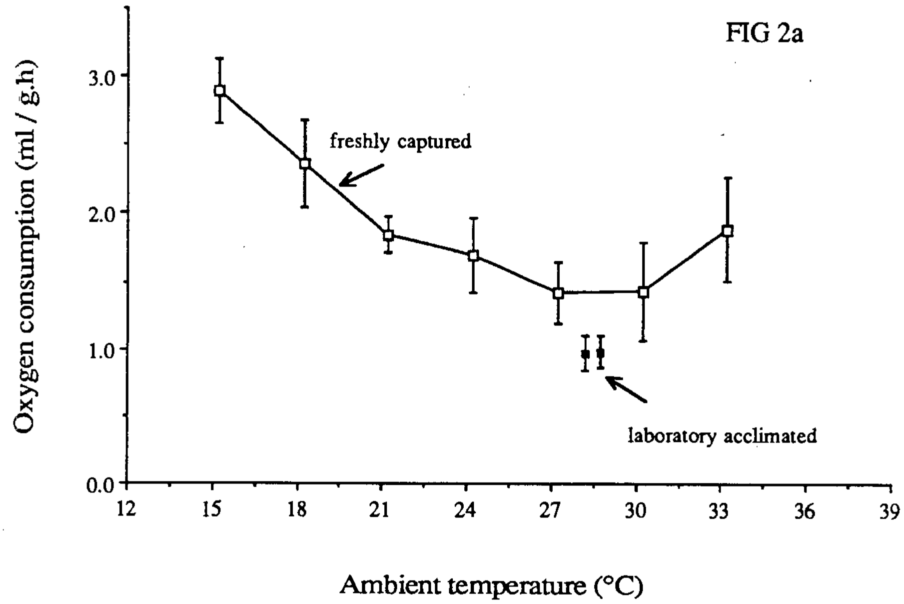

FIGURE 2a. Mean (± S.D.) oxygen consumption of six recently captured common mole-rats (*Cryptomys hottentotus hottentotus*) as a function of temperature (open squares). Small closed squares indicate values measured in the thermoneutral zone after three months of captivity.

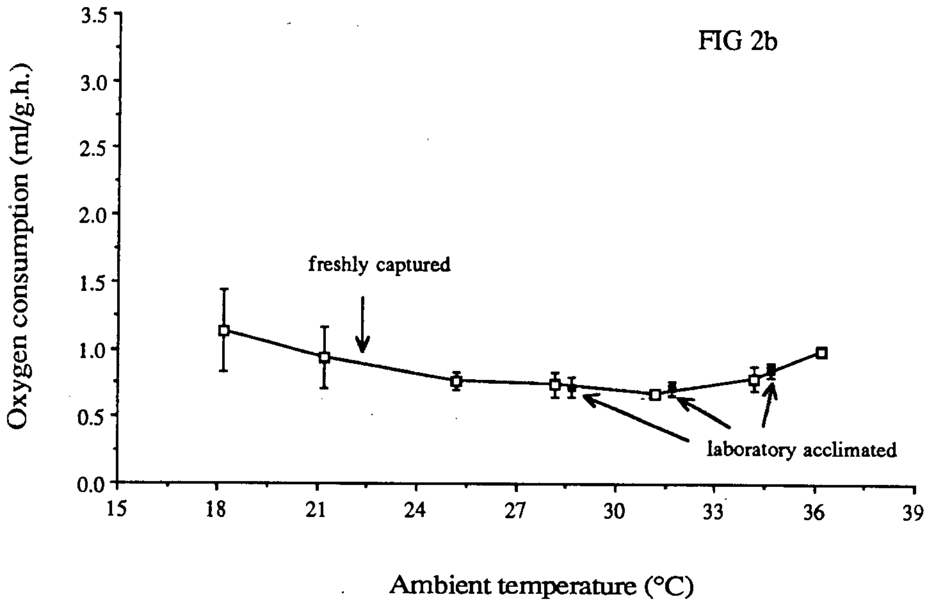

FIGURE 2b. Mean (± S.D.) oxygen consumption of six recently captured Damaraland mole-rats (*Cryptomys damarensis*) as a function of temperature (open squares). Small closed squares indicate values measured in the thermoneutral zone after two and a half months of captivity.

the equation $VO_2 = 4.811 - 0.137$ Ta ($n = 24$, $r = 0.875$, $P < 0.0001$). The conductance was high, averaging 0.14 ± 0.018 ml O_2 /g.h.°C ($n = 24$) at the lower limit of thermoneutrality. The conductance of this species at a mean body mass of 77 g after calorific conversion to STDP and assuming an RQ of 0.8 was 59 mWatts.

The mean resting metabolic rate at 15 °C, the lowest ambient temperature used, was 2.84 ± 0.24 ml O_2 /g.h, which is twice that of the resting metabolic rate in the thermoneutral zone. The mean resting metabolic rate of the same animals after being maintained at 26 °C for three months showed a decrease of 43 % at 28 °C (thermoneutral zone) to a mean of 0.92 ± 0.11 ml O_2 /g.h (Figure 2b), indicating metabolic acclimation to laboratory conditions.

A2.3.2 *Cryptomys damarensis*

The body temperature of *C. damarensis* remained stable at ambient temperatures between 18 - 28 °C with a mean value of 35.1 ± 0.56 °C. Above 31 °C, body temperature increased to 36.6 ± 0.69 °C (Figure 1b). The mean resting metabolic rate of newly captured (two weeks in captivity) *C. damarensis* was 0.66 ± 0.07 ml O_2 /g.h ($n = 12$) within a thermoneutral zone of 28 - 31 °C (Figure 2b). Below the lower limit of thermoneutrality, the increase in metabolic rate is given by the equation $VO_2 = 1.946 - 0.05$ Ta ($n = 17$, $r = 0.56$, $P < 0.05$). The mean metabolic rate at 18 °C was 1.09 ± 0.30 ml O_2 /g.h, which is 40 % above the resting metabolic rate in the thermoneutral zone.

The conductance was lower, averaging 0.065 ± 0.014 ml O_2 /g.h.°C ($n = 24$) at the lower limit of thermoneutrality. Converting to the thermal units of conductance at STDP and assuming a RQ of 0.8, the conductance in this species at a mean body mass of 125 g was 35 mWatts.

The resting metabolic rate of the same animals maintained in captivity at 26 °C for two and a half months averaged 0.69 ± 0.06 ml O_2 /g.h within the thermoneutral zone (Figure 2b). This is indistinguishable from metabolic rates measured soon after capture, indicating that acclimation to laboratory conditions had not occurred.

A2.4 DISCUSSION

Subterranean rodents spend their lives underground in sealed burrows and rarely, if ever, come to the surface (Nevo 1979). These animals show cosiderable specializations. Morphological and physiological adaptations of mole-rats permit efficient excavation, foraging and locomotion in their underground habitat (Eloff 1958 ; Jarvis and Bennett 1990, 1991 ; Lovegrove 1987).

Foraging burrows are shallow (ca 10 - 25 cm depth), and temperatures recorded in these burrows represent the extremes to which the mole-rats are exposed to in the field. In the localities in which study animals were captured, the mean seasonal change in foraging burrow temperatures for *C. h. hottentotus* and *C. damarensis* at a depth of 13 - 14 cm are 16.2 and 14.9 °C, respectively (Bennett *et al.* 1988). The annual amplitude in temperature fluctuation is greatest at the soil surface, diminishing with increasing depth. Mean annual soil temperatures vary minimally at depths exceeding 0.6 m (Bennett et al. 1988). The mole-rats spend between 70 - 80 % of the 24 h day resting or sleeping within a well defined nest (Bennett 1990a), and temperatures experienced in this locality will greatly influence their daily energy expenditure (D.E.E.). The nest of *C. h. hottentotus* is shallow (± 30 - 35 cm, J.U.M. Jarvis, unpublished data) in comparison to the depths of the nests of *C. damarensis* (1.6 - 2.3 m, N.C. Bennett and J.U.M. Jarvis, unpublished data). The shallower nests of *C. h. hottentotus* probably experience a seasonal change in core temperature, while in *C. damarensis* nests probably have a stable core temperature. The relative stability of the nest temperature in *C. damarensis* may explain why this species is an aseasonal breeder while the reproductive activity of *C. h. hottentotus* is restricted to a single breeding attempt (Bennett 1988, 1989, 1990a,b ; Bennett et al. 1988). If temperature is the cue for breeding in *C. h. hottentotus*, then change in nest temperature must constitute an integral component of this regulation.

Physiologically, subterranean rodents show traits such as low body temperatures, low resting metabolic rates and high conductances (McNab 1979). Both of the study animals exhibited physiological adaptations characteristic of subterranean bathygerids except that *C. h. hottentotus* had a higher conductance and resting metabolic rate than most bathygerids (Lovegrove 1986a, 1987 and see Table 1). Conductance in *C. h. hottentotus* is more similar to that of geomyids and spalacids and is consistent with the hypothesis that a low body temperature and high conductance reduces the potential for overheating in burrows where evaporative cooling and convection play minor roles in the thermoregulation of these animals (McNab 1966, 1979).

In contrast to previous reports on the resting metabolic rates of bathyergids (Lovegrove 1986a,b ; 1987), *C. h. hottentotus* has a markedly higher resting metabolic rate, similar to those recorded for spalacids, geomyids and the solitary bathyergid, *Heliophobius argenteocinereus* (Bradley et al. 1974 ; Bradley and Yousef 1975 ; McNab 1979 ; Nevo and Shkolnik 1974 ; Pearson 1947 - Table 1). The resting metabolic rate in *C. h. hottentotus* may be an allometric consequence of the body size of this small species (Bennett 1989).

Our work has shown that *C. h. hottentotus* maintained in captivity for three months had a mean resting metabolic rate 43 % lower than that measured three weeks after capture. Three possible expanations for this are proposed : 1) Capture stress followed by gradual settling down in the laboratory, 2) resting metabolic rate may have decreased in the captivity as a result of reduced foraging costs, and 3) the depth of the nesting chamber in naturally occurring colonies could account

TABLE 1. Mean body mass, resting metabolic rate (RMR) and social status of 15 species of subterranean rodents.

Species	Family	Mean body mass (g)	RMR ml O_2/g.h	Social status	Habitat (degree of rainfall)	Reference
Thomomys talpoides	Geomyidae	105	1.22	Solitary	Mesic	Bradley *et al.* 1974 Gettinger 1975 Kenagy and Vleck 1982
Thomomys umbrinus	Geomyidae	95.3	0.85	Solitary	Mesic	Bradley et al. 1974
Geomys pinetis	Geomyidae	185	0.83	Solitary	Mesic	McNab 1979 Ross 1980
Geomys bursarius	Geomyidae	197	0.70	Solitary	Mesic	Bradley and Yousef 1975
Spalax ehrenbergi (2n = 52)	Spalacidae	116	0.95	Solitary	Mesic	Nevo and Sholnik 1974
Spalax ehrenbergi (2n = 58)	Spalacidae	120.5	0.86	Solitary	Mesic/semi-arid	Nevo and Shkolnik 1974
Spalax ehrenbergi (2n = 60)	Spalacidae	121	0.62	Solitary	Semi-arid	Nevo and Shkolnic 1974
Spalax leucodon	Spalacidae	151	0.84	Solitary	Mesic	McNab 1973 Gorecki and Christov 1969 Bradley *et al.* 1974
Heliophobius argento-cinereus	Bathyergidae	88	0.85	Solitary	Mesic	McNab 1979
Bathyergus suillus	Bathyergidae	620	0.49	Solitary	Mesic	Lovegrove 1986
Georychus capensis	Bathyergidae	181	0.59	Solitary	Mesic	Lovegrove 1987
Bathyergus janetta	Bathyergidae	406	0.53	Solitary	Semi-arid/arid	Lovegrove 1987
Cryptomys h. hottentotus (N. Cape)	Bathyergidae	75	0.9 - 1.38	Social	Semi-arid	Bennett, Clarke and Jarvis (this study)
Cryptomys h. hottentotus (Transvaal)	Bathyergidae	95	0.68	Social	Mesic	Haim and Farrell 1986
Cryptomys damarensis	Bathyergidae	125	0.57 - 0.66	Social	Semi-arid/arid	Lovegrove 1986 Bennett, Clarke and Jarvis (this study)
Heterocephalus glaber	Bathyergidae	39.5	0.64	Social	Semi-arid	McNab 1979 Withers and Jarvis 1980

for the observed acclimation. This last explanation is probably the most feasible since both species experienced equal post capture stress levels. Similarly, the decrease in foraging costs should not differ between species.

Mole-rats within or utilizing deep nests (experiencing no fluctuations in nest core temperature) thus have negligable selective pressures acting upon them to acclimate. In contrast, *C. h. hottentotus* experiencing seasonal fluctuations in nest core temperature, probably respond to these changes in temperature by changing the resting metabolic rate.

The higher resting metabolic rate of the common mole-rat contrasts greatly with the trend found for other bathyergids. Nevertheless, the relationship between ambient and body temperature and the thermal conductance below the lower limit of thermoneutrality fits the standard subterranean trend.

These data fail to support Lovegrove's (1986a) hypothesis that all social subterranean bathyergids display resting metabolic rates lower than solitary bathyergids. Similarly, comparisons based on microhabitat (mesic and arid) can not be made because the micro-environment of the burrow system of all mole rats experience similar temperature regimes and humidity levels. Furthermore, generalizations drawn amongst the Bathyergidae are complicated by the vast diversity in social structure. This ranges from the strictly solitary individuals such as *Bathyergus suillus* and *Bathyergus janetta* through to the eusocial *Heterocephalus glaber.*

This comparative study demonstrates how the resting metabolic rate of two mole-rat species respond to laboratory acclimation. Within a thermoneutral zone of 27 - 30 °C, the resting metabolic rate of *C. h. hottentotus* shows a marked change whereas that of *C. damarensis* shows no response. Future comparative work amongst populations of species should ensure that there is uniformity in the time animals have been incaptivity. In such studies, resting metabolic rates of both recently captured and acclimated individuals should be reported.

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