THE THERMAL IMPLICATIONS AND ECOLOGICAL CONSEQUENCES OF COLORATION IN SELECTED SPECIES : TENEBRIONID BEETLES (*Onymacris bicolor* AND *Onymacris unguicularis*), CAPE GANNETS (*Morus capensis*) AND CAPE CORMORANTS (*Phalacrocorax capensis*)

by

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To my parents, Anton and Audrey Lombard, for letting me grow up in the desert, and to my "old" Professor, Gideon Louw, for revealing to me how lucky I was.

DECLARATION

The research reported in this thesis is original work, completed by me between 1985 and 1988 at the University of Cape Town. Chapter two, however, is the result of the combined efforts of three authors: Dr. J.S. Turner, myself and Prof. G.N. Louw. Dr. Turner, should however, receive the major credit for this chapter. The remaining data collection, analyses and interpretations are my own, and any assistance I received is fully acknowledged.

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ABSTRACT

The thermal significance of coloration was investigated in two species of Namib Desert tenebrionid beetles and two species of marine birds. Body temperatures and heat fluxes of a black beetle (*Onymacris unguicularis*) and a beetle with white elytra (*Onymacris bicolor*) were compared in a wind tunnel in the laboratory. The effects of visible radiation, infrared radiation, conduction, convection, beetle colour and substratum colour on body temperature were analysed. Results showed that body colour has no overall effect on body temperature. Black elytra are warmed more by visible radiation, but colour is not relevant to heat loss by convection, or to heat flux between a beetle and a heated sand substratum, whether by emitted radiation or reflected visible radiation. *O. bicolor* absorbs more heat by conduction and free convection from a heated substratum, but differences in shape between the two species may explain this effect. Combining the various modes of heat exchange to simulate natural conditions reveals that the extra heat absorbed by black elytra is readily dissipated by convection, and owing to the increased heating of white beetles from the substratum, heat fluxes between the two beetles balance. Body temperatures of dead and live beetles of both species were also measured in the field. Experiments were conducted on a hot sand substratum in the beetles' natural environment, under both visible (sunny) and infrared (shaded) conditions. Results supported the laboratory experiments, and showed that when temperature differences do occur between black and white beetles, these differences are generally less than 3.5 °C. These differences are small when compared with the ranges of body temperatures experienced by active beetles in the field (± 10 °C). In addition, these temperature differences occur only at low wind speeds (< 2 m s^{-1}). Activity studies in the field showed that beetles choose to be active in high wind speeds, possibly because of the nature of their food source, which is wind-blown detritus. It is concluded that coloration does not have adaptive value in terms of the thermal biology of Namib Desert tenebrionid beetles.

Physical properties of the plumages of white Cape gannets (*Morus capensis*) and black Cape cormorants (*Phalacrocorax capensis*) were measured. Black plumages asborb more visible radiation than white plumages in still conditions. However, laboratory experiments with excised plumages showed that at wind speeds of 2 m s^{-1}, cormorant plumages and skins were only 2-3 °C warmer than those of gannets. These differences disappeared at wind speeds of 4 m s^{-1}. A biophysical heat transfer model predicted that in still, warm, sunny conditions, cormorants may gain up to 185 % of their field metabolic rates, whereas gannets would gain only 42 %. Field observations confirmed that nesting cormorants experience greater heat stress than gannets, even though cormorant nests occur in areas of lower micrometeorological temperatures. Cormorants begin to dissipate heat by evaporative water loss (*i.e.* pant) at lower environmental temperatures than gannets. The thermal consequence of coloration in these two species are that cormorants may have a lower cost of endothermy at temperatures below the thermoneutral zone, but may experience more heat stress during warm conditions; cormorants select cooler and windier nesting sites than gannets; and increased surface temperatures of black cormorant plumages may aid evaporative water loss from wet plumages, facilitating wing-drying. However, ptiloerection and wind may interact in the natural environment, negating the differential heating effects of coloration. It is concluded that the thermal implications of colour are negligible in both species, considering the temperate nature of their environment. Colour in both species is best explained by feeding ecology: white coloration is conspicuous to conspecifics and cryptic to prey in plunge divers (gannets), whereas black colour is cryptic to both conspecifics and prey in solitary swimmers (cormorants).

CONTENTS

GENERAL INTRODUCTION

During the past six decades, numerous hypotheses have attempted to explain the adaptive significance of animal coloration. These hypotheses have considered both the visual and non-visual functions of coloration, in the context of either single or multiple selective pressures. The visual functions of colour (*e.g.* crypsis, mimicry, aposematic coloration) are well defined and have been adequately researched (*e.g.* Cloudsley-Thompson 1979, Burtt 1979a, 1981, 1986, Burtt & Gatz 1982, Turner *et al.* 1984, Guilford 1986, Leimar *et al.* 1986), but controversies surround many of the proposed non-visual functions of coloration. These controversies arise from a dispute concerning the primary function of dark coloration in various animals. Considering that dark coloration is imparted to chitinous or cuticular structures mainly by the pigment melanin, the non-visual functions of dark coloration are most often related to the mechanical strength and high radiative absorbance of this pigment.

The possible non-visual functions of dark coloration suggested to date include (1) protection against ultraviolet (UV) radiation (Loomis 1967, Porter 1967, Branda & Eaton 1978, Burtt 1979b, Hamilton 1979, Tim & Kermott 1982), mechanical strength (Averill 1923, Pryor 1948, Hamilton 1973, Burtt 1979b, 1986, Barrowclough & Sibley 1980), (3) chemical defence (Burtt 1981), (4) reduced permeability to water (Kalmus 1941, Needham 1974), (5) facilitation of evaporation to enhance drying in aquatic birds (Siegfried *et al.* 1975, Burtt 1981, Hennemann 1982), and (6) thermoregulation.

As regards thermoregulation, the most frequent non-visual function proposed for animal coloration is that animals are coloured black (or white) in order to enhance their adaptiveness to their thermal environment. A thermal role for black and white coloration seems probable if one considers the physical properties of radiation absorption by different colours in the visible range of the solar spectrum, and if one accepts the general hypothesis that black animals absorb more solar radiation than white animals. However, this hypothesis has recently been questioned on theoretical grounds and subjected to rigorous experimental analysis. Various studies have shown that the thermal significance of animal coloration is greatly compounded by the interacting effects of behavioural thermoregulation, micrometeorological variables, coat structure and non-radiative processes of heat transfer across exoskeletons or coats (Kovarik 1964, Hutchinson & Brown 1969, Hadley 1970, Edney 1971b, Hamilton 1973, Cena & Monteith 1975a, Cloudsley-Thompson 1979, Lustick *et al.* 1980, Lustick 1983, Burtt 1986, Walsberg *et al.* 1978, Walsberg 1988a, 1988b, 1988c).

The hypothesis that black and white coloration has been selected for its thermal implications is thus questionable, and this thesis tests the hypothesis in two groups of animals which are dominated by species which are either black or white; (1) Namib Desert tenebrionid beetles, and (2) marine birds. Namib Desert beetles are ideal experimental animals owing to the dominance of black coloration in most species, and the presence of white elytra in some of the coastal species. This is particularly true for the diurnal genus *Onymacris* (Penrith 1975), thus the two animals investigated in this study were chosen from this genus: *Onymacris unguicularis* (black) and *Onymacris bicolor* (white elytra). With respect to marine birds, the black Cape cormorant (*Phalacrocorax capensis*) and the white Cape gannet (*Morus capensis*) are sympatric along the coasts of South Africa and Namibia, have similar feeding ecologies, and nest adjacent to one another on several offshore islands during the breeding season. This presents an ideal opportunity to compare the thermal implications of coloration to their energy budgets, considering that breeding birds of both species are confined to their nests, and experience similar environmental conditions at any particular time.

Owing to differences in the physical properties which govern heat flow across uninsulated insect exoskeletons, as opposed to endotherm skins (which are generally insulated with either fur or feathers), this thesis examines the thermal implications of coloration in ectotherms and endotherms separately. Section I, which deals with ectotherms, is structured as follows: previous research regarding the thermal consequences of black and white coloration in ectotherms is reviewed in Chapter 1. Chapter 2 investigates the effects of visible and infrared radiation, convection, and substratum and beetle colour on heating and cooling in beetles. Chapter 3 presents the results of similar experiments undertaken in the field, and reports on the reflectances in the visible range of the beetle elytra and differently coloured sand substrata. The ecological consequences of beetle coloration are examined in Chapter 4, which concentrates on the diurnal activity patterns of both species in their natural habitat, their body temperatures, and the micrometeorological conditions to which they are exposed.

Section II deals with endotherms and is structured in the following way: Chapter 5 reviews the literature concerning the thermal implications of coloration in endotherms. Chapter 6 examines the reflectance of solar radiation in excised gannet and cormorant plumages, and the effect of convection on temperature gradients in irradiated bird plumages. A model is developed for predicting heat flow across a plumage. Finally, Chapter 7 discusses thermoregulatory behaviour of breeding birds, as well as concurrent body temperatures and micro-meteorological conditions. The behavioural factors investigated include panting set points, changes in posture and orientation, and nest attendance spells.

The review chapters (1 and 5) outline further details concerning the Namib and offshore island study sites, and also outline the specific questions addressed by this thesis, and the experimental procedures used to answer these questions.

SECTION I

THE ROLE OF BLACK AND WHITE COLORATION IN NAMIB DESERT TENEBRIONID BEETLES (*Onymacris unguicularis* and *Onymacris bicolor*)

CHAPTER ONE

COLOUR AND THERMOREGULATION IN ECTOTHERMS

The adaptive significance of coloration in ectotherms has been a popular subject of research ever since Buxton (1924) pointed out that those desert animals which are not buff coloured to match the soil, are generally black. Confirmation of Buxton's findings was provided by Omer-Cooper (1948) who also noted that many black desert species are not only diurnal but also restless and conspicuous, as opposed to the quiet habits of the cryptically coloured animals. Cryptic coloration in deserts ought to be well developed owing to the lack of cover, but many diurnal desert beetles are totally black (Louw & Seely 1982). In addition to this, the proportion of black species (especially arthropods and birds) increases in deserts (Hamilton 1973, Hadley 1979a, Burtt 1981). These findings seem to present a paradox if one assumes that black coloration enhances heat gain in desert ectotherms, and the excess heat cannot be dissipated by evaporative water loss in an arid environment.

Meinertzhagen (1954) referred to this paradox as the "black beetle puzzle", and since then beetles have proven popular experimental animals in attempts to quantify the thermal role of coloration in desert animals. Several hypotheses have been invoked to explain the seeming paradox. Buxton (1924) suggested that coloration in desert beetles is an evolutionary legacy, no longer adaptive but maintained because it is not disadvantageous. No reason was offered as to the original value of black coloration. Meinertzhagen (1954) and Kalmus (1941) argued that black coloration has the offsetting advantage of reducing water loss and is maintained despite the thermal disadvantages. However, Hamilton (1973) proposed that black is advantageous in enhancing heat gain and allows beetles to maintain their preferred temperatures for longer periods of activity. Both Hamilton (1973) and Cloudsley-Thompson (1979) reviewed the above hypotheses, but Cloudsley-Thompson concluded that the "functions of the black pigments of desert animals are ecological rather than physiological", and that black desert beetles are hard and distasteful, so that their coloration serves an aposematic function. This supports Omer-Cooper's (1948) observation of the restless and conspicuous nature of black diurnal desert beetles.

However, the predominance of black desert species presents a paradox only if black is thermally disadvantageous. An examination of the biophysical aspects of colour and heat exchange for animals with uninsulated surfaces (*e.g.* insect exoskeletons) reveals that coloration affects only one avenue of heat transfer: the absorption of visible solar radiation (Fig. 1).

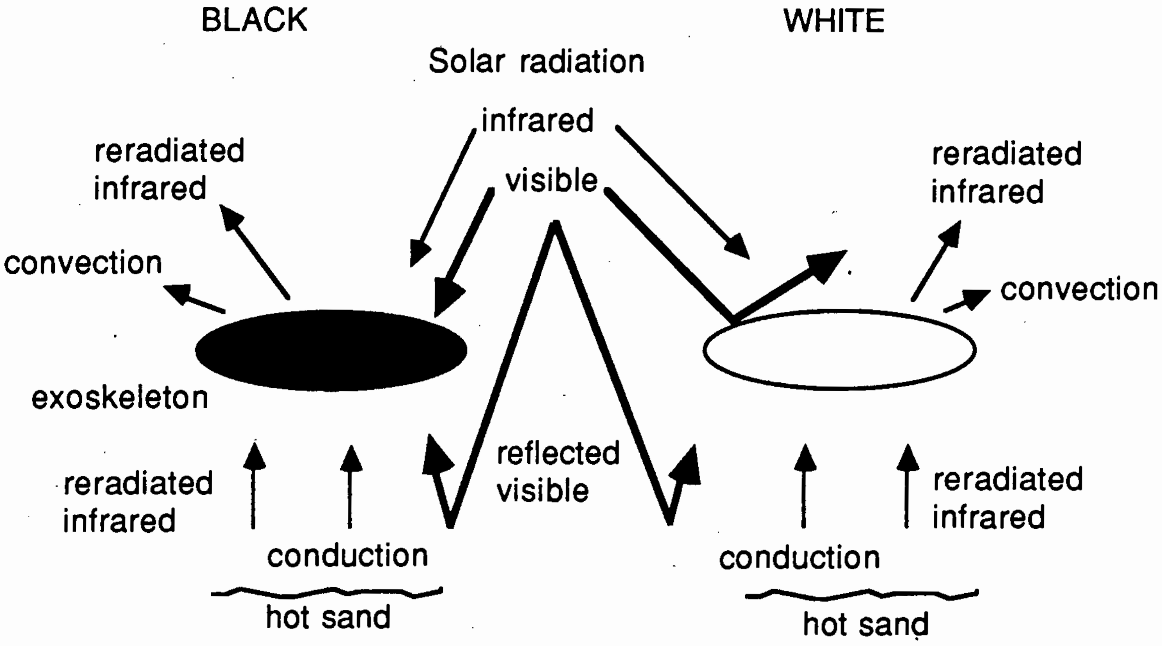


Fig. 1. The modes of heat transfer affecting black and white insect exoskeletons.

Coloration does not affect the other modes of heat transfer (conduction and convection). Infrared absorption is also independent of colour, since all animal surfaces are thought to have absorbances close to unity in the infrared region (Porter & Gates 1969), although some beetles, frogs and lizards reflect near infrared radiation (Hutchison & Larimer 1960, Norris 1967, Henwood 1975b, Schwalm & Starrett 1977). Thus, coloration affects only the absorption of solar radiation, and if one considers that approximately half of solar energy lies outside the visible range (Gates 1962), the role of colour in the thermal budgets of ectotherms becomes questionable.

During the past three decades, the tenebrionid (and recently tiger) beetles have become the favoured experimental animals used to test the thermal significance of coloration in ectotherms.

However, the tendency of researchers to conduct experiments under controlled conditions, which often lack an important component of the animal's natural environment, have led to conclusions regarding coloration which are generally conflicting, and unable to be extrapolated to field conditions. Table 1 lists the results of four studies concerning the differential heating in black and white tenebrionid beetles. In the experiments conducted by Bolwig (1957), an infrared source (heater) was used instead of a visible source of radiation, thus his results can not be used to predict the effects of visible radiation on beetle body temperatures. In Edney's (1971b) experiments, beetles were tethered, and the lower body temperatures of white beetles were obtained only during conditions when no wind prevailed. Thus, these results can not be used to predict the effects of behavioural thermoregulation and convective heat loss on beetle body temperatures in the field. The experiments of Hadley (1970) and Hamilton (1973, 1975) reveal that if animals are free to thermoregulate behaviourally, and if wind and natural sunlight are present, the differences between the temperatures of black and white beetles diminish. Despite conflicting results, the general conclusions of these four authors are that the interacting effects of behavioural thermoregulation (such as orientation, postural adjustments, microhabitat selection, the timing of activity), the angle of incidence of radiation, and wind speed may render beetle coloration less important to beetle body temperatures than previously assumed. However, various behavioural studies have shown that pale coloured Namib Desert tenebrionids are able to extend their activity patterns over the hotter parts of the day, and the authors suggest that this is possible owing to the reflection of solar radiation, and the subsequent maintenance of sub-lethal body temperatures (Hamilton 1973, 1975, Henwood 1975a, Wharton 1980). The thermal role of colour in tenebrionid beetles thus remains unsettled, and rigorous experiments which examine the body temperatures of black and white beetles in the field are required, as is an analysis of the contribution of the different modes of heat transfer (visible radiation, infrared radiation, convection, conduction) to the thermal budgets of these beetles.

The equivocal results quoted in Table 1 are paralleled in the literature concerning coloration and temperature in the Orthoptera. Comparative experiments are facilitated in this order of insects by the prevalence of species which are dimorphic with respect to colour. Many authors have found that dark animals reach higher body temperatures than pale animals: a difference of 4.5 °C was

Table 1. Summary of research investigating comparative body temperatures of black and white tenebrionid beetles.

Species	Colour	Body temperature	Radiation source	Conclusion	Author
Onymacris bicolor	black with white elytra	1-2 °C less (under 38 °C)	infrared heater	No visible source used.	Bolwig 1957
O. multistriata	black	1-2°C less (over 38 °C)			
Eleodes armata	elytra painted white	c. 1 °C less absorb reflected radiation and may override differential heating of elytra.	sunlight	Black ventral surfaces	Hadley 1970
E. armata	black				
Onymacris brincki	black with white elytra	Abdominal temps. 3-4 °C lower.	sunlight	Behaviour may override effects of colour, which may be aposematic.	Edney 1971b
O. rugatipennis	black				
Onymacris brincki	white elytra	Temps. only lower if no wind. Temps. similar if elytra painted black or both beetles in shade	sunlight	Colour and behaviour determine body temps.	Hamilton 1973, 1975
O. unguicularis	black				

found between dark and desert coloured morphs of the grasshopper *Calyptamus coelesyriensis*, when in the sun (Buxton 1924). Key & Day (1954) also concluded that colour is important to temperatures of the grasshopper *Kosciuscola tristis*, which changes from black in cool conditions to blue in warm conditions. Body temperatures of grasshoppers *Brachystola magna* painted black were significantly higher than those of animals painted white (Joern 1981), but Joern concluded that microhabitat selection and orientation are more important than coloration in determining the temperatures of these insects, although colour could extend the activity of dark morphs during the morning. Other authors have shown that dark and pale morphs reach similar temperatures: Pepper & Hastings (1952) found no significant differences in temperature between black and buff morphs of the grasshopper *Melanoplus differentialis* when exposed to sunlight, and Stower & Griffiths (1966) found no significant differences in the equilibrium temperatures of light-green and dark-red morphs of the desert locust, *Schistocerca gregaria*. However, Hamilton (1975) warned that colour morphs may differ in other morphological characters which may also determine equilibrium temperatures, *e.g.* the colour morphs of *S. gregaria* differ in both external and internal morphology.

Further proposed evidence for the thermal role of coloration in ectotherms is provided by research on colour morphs in numerous other insect orders. Various authors have demonstrated a negative correlation between the abundance of melanic morphs of certain spittlebugs, ladybirds, moth larvae and butterflies, and increasing levels of sunshine or temperatures, in both seasonal or geographic gradients (Watt 1969, Thompson 1984, Brakefield & Willmer 1985, Berry & Willmer 1986, Fields & McNeil 1988). Considering that most of these authors also demonstrated lower body temperatures for pale morphs, it is possible that coloration and temperature interact in such a way that they influence the distribution of colour morphs along both geographic and seasonal gradients.

A thermal role has also been postulated for wax blooms and metallic elytra, which occur in many beetle species. McClain *et al.* (1985) and Hadley (1979b) suggested that desert tenebrionids with wax blooms may be able to reduce their body temperatures and extend their activity periods, owing to the reflective nature of the blooms. However, neither study provided complete experimental evidence for this suggestion, and the primary function of the blooms was shown to be a reduction of transcuticular water loss. Schultz & Hadley (1987b) showed that metallic coloration in tiger beetles does not reduce solar heat gain, but that white elytra result in an average depression of 2.2 °C in body temperatures when compared to beetles with metallic red elytra.

The thermal consequence of coloration has been well researched in only one other group of ectotherms, the lizards. Unlike many insects, whose structural colours can seldom be manipulated physiologically (except, for example, by wax secretions), many lizards exhibit metachrosis (colour changes brought about physiologically, *e.g.* by the expansion of melanophores). Many authors have found that lizards (especially desert lizards) become lighter at high ambient temperatures, thereby decreasing the absorption of solar radiation (Atsatt 1939, Cole 1943, Norris 1967, Porter 1967, Pearson 1977, Rice & Bradshaw 1980). Cole (1943) also found that dark lizards overheat more easily than light lizards and an increased reflectance is found in the skins of lizards which tolerate higher temperatures.

Although most of the researchers quoted above have found that dark ectotherms reach higher equilibrium temperatures than light ectotherms when irradiated, most have concluded that either behavioural or micrometeorological factors override the differential heating effects afforded by coloration. Digby (1955) noted that the temperature differences due to colour in insects would be of minor importance, because in many light coloured insects, the thorax is dark. He calculated that wind speed, radiation and size were the main factors controlling temperature elevations in a wide range of insects. Willmer & Unwin (1981) proposed that mass and linear dimension were more important than colour in determining heat gain in insects.

In summary, factors (excluding colour) which may determine temperature elevations in tenebrionid and tiger beetles include, angle of insolation (Edney 1971b), size (Hadley 1979a), orientation and posture (Edney 1971b, Henwood 1975a, Dreisig 1980, 1984), activity patterns (Hamilton 1971, Hadley 1979a, Kenagy & Stevenson 1982, Whicker & Tracy 1987) and microhabitat selection (Edney 1971b, Hamilton 1971, Holm & Edney 1973, Henwood 1975a, Schultz & Hadley 1987a, Whicker & Tracy 1987). These observations are supported by the heat transfer model developed by Stevenson (1985), which predicts that seasonal and daily activity patterns, as well as micohabitat selection, are the most important factors controlling ectotherm body temperatures. Factors controlling insect thermoregulation are further reviewed by May (1979, 1985), Reynolds (1979), Casey (1981) and Heinrich (1981).

It is important to note that most of the differences in ectotherm equilibrium temperatures which are due to colour, are well under 5 °C, and that these differences are small compared to the variability of temperatures experienced, tolerated or even selected by animals under natural conditions. Deal (1941) tested the temperature preferences of 23 species of insects from six orders, and found that most species showed a wide range of temperature preference, as opposed to a specific temperature. It is likely that optimal temperatures do exist for ectotherms (Hamilton 1973, 1975, Heinrich 1977, May 1979), but controversy exists as to whether ectotherms exhibit temperature preferences in ranges close to optimal physiological temperatures, or ranges to which they are naturally exposed. To return to the predominance of black tenebrionids in deserts, Hamilton (1973) invoked the "maxithermy" hypothesis to explain the high temperatures sustained by Namib tenebrionids. He proposes that black coloration allows beetles to attain high body temperatures, which lead to increased rates of many biological processes (the Q_{10} effect), and that beetles attempt to attain the maximal possible body temperatures in order to maximise activity rates. According to Heinrich (1977), Hamilton overemphasizes the Q_{10} effect and ignores the fact that animals exposed to high tissue temperatures are forced to have high temperature set points. This mitigates against an advantageous role of black coloration. Heinrich also argues that biochemical adaptation equips these animals to operate at the upper temperatures encountered in the field. Heinrich's propositions are supported by Seely *et al.* (1988), who suggest that high body temperatures of Namib Desert tenebrionid beetles are related to the aseasonality of the environment and the burrowing abilities of the beetles which provide them with an immediate thermal refuge under the sand. In addition, tenebrionids of the arid but cooler steppes of eastern Washington exhibit body temperatures 10-15 °C lower than many other desert tenebrionids (Kenagy & Stevenson 1982). The authors proposed that these lower preferred temperatures are ecologically selected for, and enable the beetles to extend their diurnal activity rhythms during cool conditions.

Finally, a cost-benefit analysis of behavioural thermoregulation in lizards showed that physiologically optimal temperatures may not always be equal to ecologically optimal temperatures (Huey & Slatkin 1976). Thus, if preferred temperatures in ectotherms are determined by the temperature ranges to which they are naturally exposed, and if these ranges far exceed the temperature differences afforded by colour, coloration in ectotherms may have little or no thermal significance.

If dark and light coloration has not been selected for its thermal value, which other forces could be responsible? Widespread interest in the cryptic value of coloration was initiated by Cott (1957). Strong evidence for crypsis is provided by Hinton & Jarman (1972), who showed that the Hercules beetle *Dynastes hercules* remains cryptic by appearing black at night and yellow during the day. Colour change is brought about by changes in the level of hydration of a spongy layer beneath the transparent epicuticle. In addition, Joern (1981) stated that colour dimorphism in *Brachystola magna* is usually for crypsis. He concluded that body coloration is strongly influenced by predation, then thermoregulation, then communication. Wharton (1980) found that in six species of diurnal Namib tenebrionids beetles, black species are subject to greater predation, and he concluded that activity patterns in black and pale beetles may be determined by the combined effects of predation, interspecific competition and thermal constraints. These findings are supported by Cloudsley-Thompson (1979), who proposed that in Namib tenebrionids, black beetles and beetles with white elytra are aposematic, because of their hard and distasteful nature. He adds that beetles on lava flows are black for crypsis or as a result of evolutionary legacy. However, Buxton (1924) and Omer-Cooper (1948) both claimed that cryptic coloration has no adaptive value in deserts, owing to the absence of predators. Omer-Cooper proposes that white desert colours reflect heat and black protects against harmful radiation.

Thus, either predation pressure or thermoregulation are usually offered as the adaptive reasons for dark and light coloration in ectotherms. However, the other non-visual consequences of black coloration outlined in the general introduction should not be forgotten when attempting to explain the predominance of black coloration in desert species. Furthermore, more than one selective force may be responsible for a particular colour or pattern.

Although many authors claim that coloration may be the result of adaptive compromise, Hutchinson & Larimer (1960) found that in 26 lizards of 16 species, the effects of concealing and thermoregulatory coloration were synergistic. However, if conflicting selective forces are responsible for a particular coloration, the most critical factor is selected for (Hoppe 1979), and behavioural mechanisms can often override any negative effects of coloration (Heinrich 1972, Hoppe 1979, Joern 1981).

The results reviewed above illustrate these important points:

1. The "black desert beetle paradox" reveals more about the assumptions of previous researchers, than the physics of heat transfer in ectotherms.
2. Colour alone may have little thermal effect in the overall heat budget of an ectotherm.
3. Data regarding the thermal significance of colour are equivocal, and behavioural and environmental factors often override the effect of colour on ectotherm body temperatures.
4. The differential heating effects of dark versus light coloration are small (usually under 5 °C) and preferred temperatures often cover a very wide range. The small differential heating effects resulting from coloration may thus be unimportant to thermal budgets. This is especially true if preferred temperatures are ecologically rather than physiologically determined.
5. Thermoregulation is only one of a suite of selective factors which may select for coloration. Thus, only an integrated approach, which deals with individual species, and which encompasses all the visual and non-visual consequences of coloration, will enable us to analyse the adaptive significance of ectotherm coloration.

In this thesis, an attempt is made to analyse the thermal implications of black and white coloration to two species of Namib Desert tenebrionid beetles. As previously mentioned, prior research in this field has yielded equivocal results, and experimental designs have generally neglected to consider all of the factors which may influence beetle temperature. In this study, both laboratory and field experiments investigated the interacting effects of beetle colour, sand colour, visible radiation, infrared radiation, convection and conduction on beetle body temperatures. In addition, field activity patterns of beetles are monitored with the concurrent meteorology, and these data allow us to evaluate the thermal significance of beetle colour in natural conditions.

The two Namib beetles chosen for this study are ideal experimental animals: *Onymacris bicolor* is black with white elytra, whereas *O. unguicularis* is totally black (Plate 1). Both species have similar sizes and shapes, and both display diurnal activity rhythms. They inhabit the slipfaces of dunes and burrow into the sand when not active. During the day they emerge to feed on the wind-blown detritus which collects on the slipfaces. According to Penrith (1975) and pers. obs., the distribution of *O. bicolor* is limited to the pale, northern, coastal dunes along the Skeleton Coast of the Namib Desert (15°50' S to 20°28' S) (Fig. 2). The range of *O. unguicularis* (17°16' S to 27°23' S) overlaps with that of *O. bicolor* in this area , but *O. unguicularis* is also found further south, and further inland, in the darker dunes of the Namib Desert, where conditions are much hotter than in the north (Fig. 2). The hypothesis of this study is that the white elytra of *O. bicolor* provide a thermal advantage by reflecting visible solar radiation, thereby allowing beetles to extend their activities over the hotter parts of the day, when *O. unguicularis* is forced to retreat under the sand to avoid lethal body temperatures. This hypothesis was tested by asking the following questions:

1. Does coloration result in differential heating effects when the thermal environment is dominated either by visible radiation, infrared radiation, convection, or conduction from a hot sand substratum?
2. If so, do micrometeorological conditions or behavioural mechanisms override these effects?
3. Are activity patterns determined primarily by the need to maintain preferred body temperatures?
4. If not, which physical or ecological parameters determine activity patterns, and which other selective forces are responsible for black and white coloration in these beetles?

As outlined in the general introduction, these questions are dealt with in the following manner:

Questions 1&2: Heating and cooling rates and equilibrium temperatures of beetles under visible and infrared conditions are measured, both in the laboratory (Chapter 2) and in the field (Chapter 3). The effects of convection and sand colour on heating and cooling rates are also determined.

Question 3 & 4: Activity patterns and body temperatures of both species are monitored in the field, with the concurrent micrometeorological conditions (Chapter 4). The thermal consequences of coloration in both species are discussed.

Plate 1. The two Namib Desert tenebrionids chosen for this study, *Onymacris bicolor* (left) and *Onymacris unguicularis*.

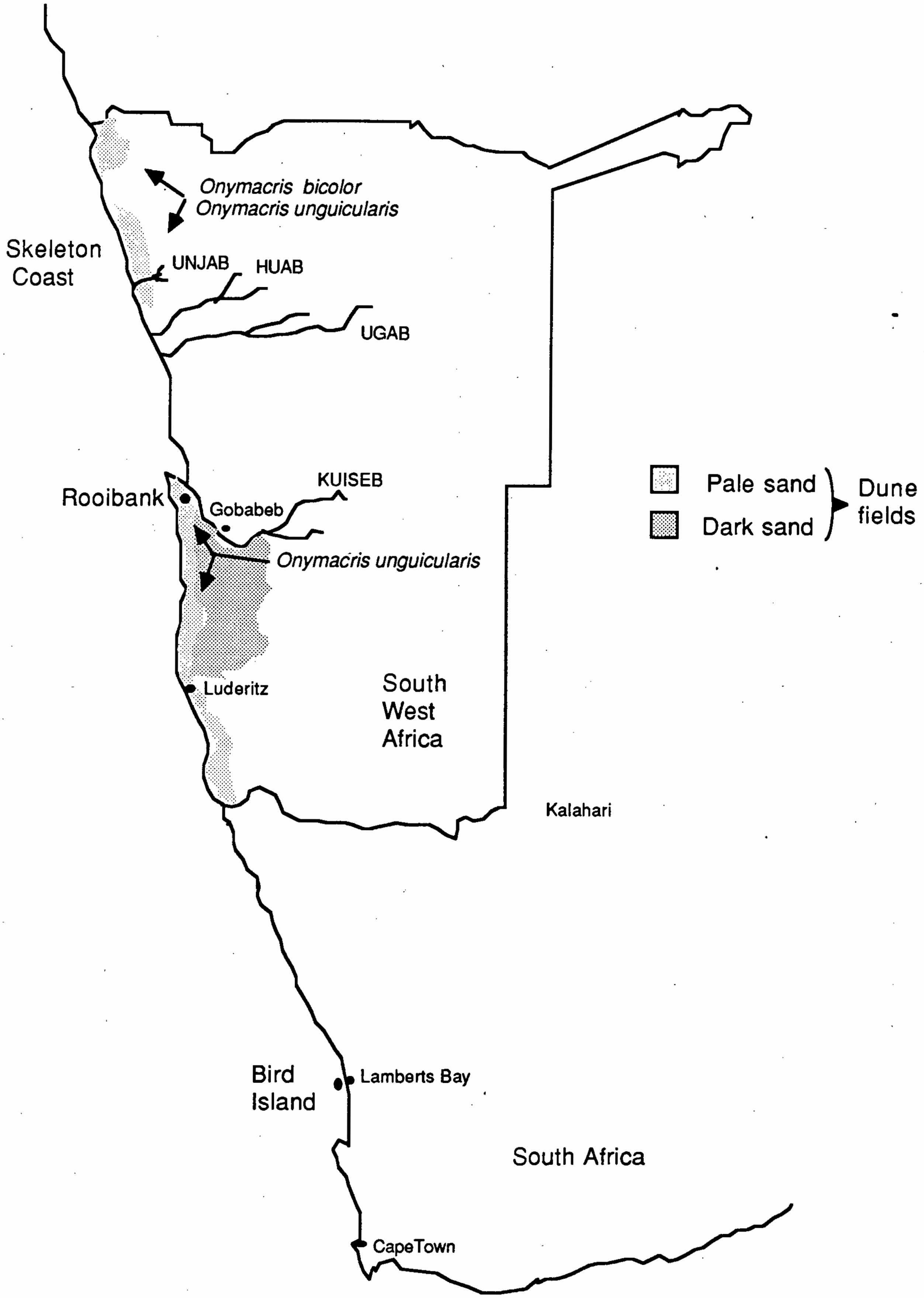


Fig. 2. Map of the west coast of Southern Africa, indicating the distribution of *Onymacris bicolor* and *O. unguicularis* in the Namib Desert. Bird Island is shown off the Cape Coast further south.

CHAPTER TWO

COMPARATIVE BEETLE TEMPERATURES: LABORATORY EXPERIMENTS

INTRODUCTION

As discussed in the previous chapter, prior research regarding the thermal significance of black and white coloration in Namib Desert tenebrionid beetles was lacking in the following respect: the contribution of visible radiation to the overall thermal budget of beetles was not investigated, *i.e.* the contributions of infrared radiation, heat conducted from the hot sand and heat lost by convection were not examined. It should also be noted that in *O. bicolor*, only the elytra are white, and the thorax and ventral abdomen are black. If the white elytra do reach lower temperatures than the rest of the body (by reflecting visible radiation), it is possible that these lower temperatures do not translate into an overall reduced body temperature for white beetles.

In this chapter, we have attempted to consider the influence of the abovementioned factors on the overall thermal budgets of black and white beetles. In four sets of experiments, we compare three body temperatures (elytral, thoracic, abdominal) of the two Namib tenebrionids, *O. bicolor* and *O. unguicularis*, as they respond to various thermal challenges in the laboratory. We attempt to identify specifically which aspects of the beetles' thermal environments, convective, radiative and conductive, are affected by beetle colour, and how this might affect the body temperatures of the beetles in natural conditions.

PROCEDURE

O. unguicularis and *O. bicolor* were collected at Rooibank and the Skeleton Coast in South West Africa respectively (Fig. 2). Beetles were returned to Cape Town and kept in terraria on a diet of lettuce and free water until used. Beetle masses averaged about 600 mg (Table 2). The two species were statistically indistinguishable in total body mass, in the distribution of mass among the body parts, and in the content of water in the body (Table 2).

Table 2. Characteristics of the beetles used in this study. Numbers are mean ± 1 standard deviation. Sample numbers appear in parentheses.

Wet mass (g)	*Onymacris bicolor*	*Onymacris unguicularis*
Body	0.656± 0.101 (15)	0.596±0.136 (15)
Thorax	0.144± 0.039 (5)	0.147± 0.027 (5)
Elytra	0.039± 0.006 (5)	0.034± 0.011 (5)
Abdomen	0.475± 0.107 (5)	0.460± 0.158 (5)
Dry mass (g)		
Body	0.278± 0.058 (5)	0.312±0.058 (5)
Thorax	0.067± 0.018 (5)	0.077± 0.013 (5)
Elytra	0.031± 0.005 (5)	0.032± 0.009 (5)
Abdomen	0.180± 0.036 (5)	0.204± 0.041 (5)

Temperature transients were measured in a small, open-flow wind tunnel (Fig. 3), that could generate wind speeds from 0-8 m s^{-1} through a test section of 18 cm X 18 cm. A 300 W quartz halogen lamp (Sylvania L2270) was mounted 50 cm above the floor of the test section. A circular hole, 15 cm in diameter, was cut in the floor of the test section, which enabled us to to place different substrata (described later) beneath the beetles. The container for the substrata, a 15 cm petri dish, had a thermocouple mounted just beneath the surface of the substratum. Air temperature was measured with a thermocouple mounted halfway up the side wall of the test section, and shielded from radiation by aluminium foil.

Prior to a series of measurements, a beetle was killed by freezing, weighed, and attached posteriorly to a small (1 mm diameter) wooden stick, which held the beetle in position in the windtunnel. Three 36 Ga thermocouples (Type T) were implanted in the beetle: one in the prothorax (henceforth referred to as thorax), one in the abdomen between legs two and three, and

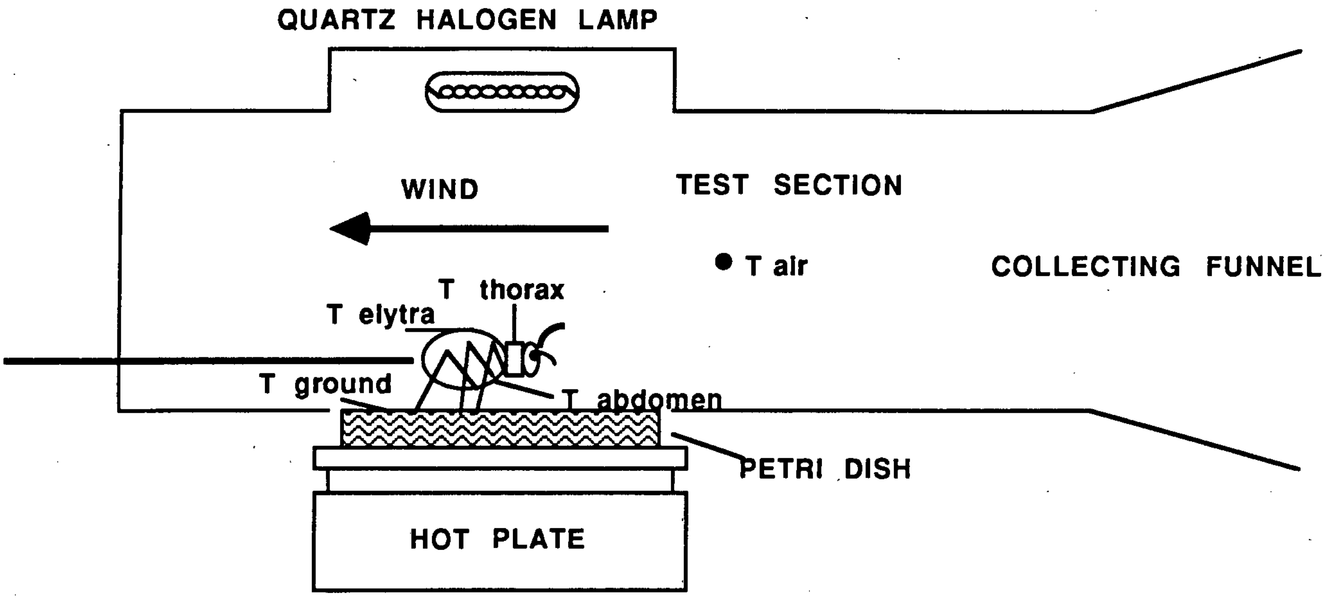


Fig. 3. Schematic diagram of wind tunnel and experimental apparatus. See text for explanation.

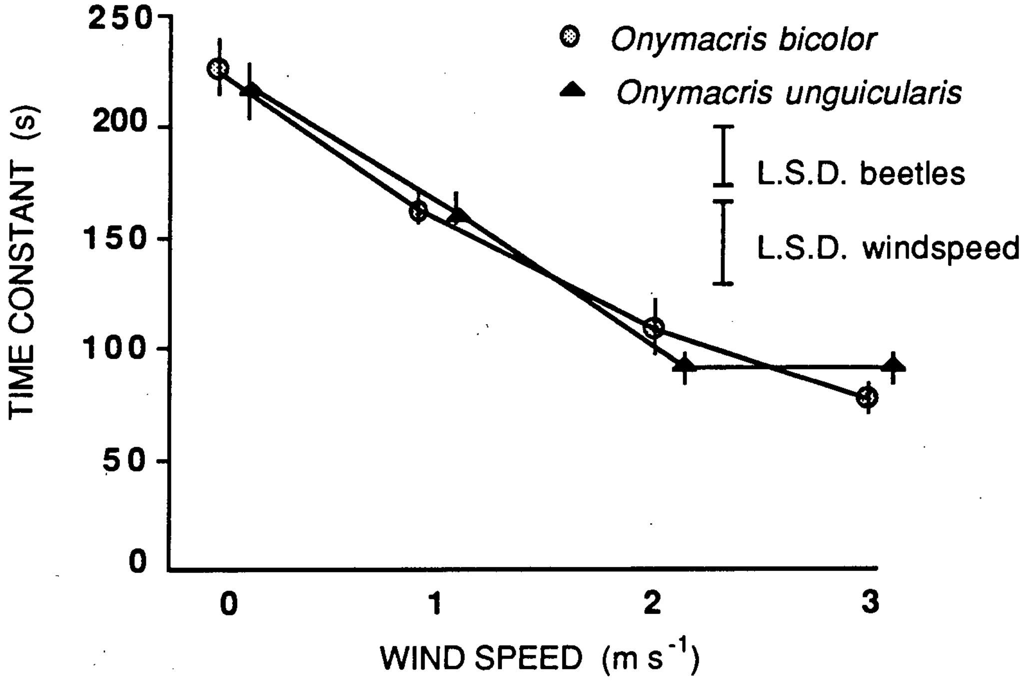


Fig. 4. Time constants (s) for cooling of abdominal temperature of two Namib tenebrionids as a function of wind speed. Points represent means, vertical bars represent ± the standard error of the mean. L.S.D. is the least significant difference, calculated by Tukey's test at $p = 0.05$.

one in the subelytral space, positioned so the junction touched the inside surface of the elytra (Fig. 3). Thermocouples were secured by small dabs of cyanoacrylate adhesive.

During the experiment, the three beetle temperatures, and the air and substratum temperatures were recorded by a microcomputer-based data acquisition system. For each condition tested, the equilibrium temperature (T_∞) and the time constant (t) were calculated from the temperature transient, using the method described by Bakken (1976b). Where possible, the equilibrium temperature was also estimated directly.

Heat loss was examined under four conditions: **(1)** convection heat loss alone, **(2)** direct and reflected visible radiation, in combination with convection, **(3)** conduction through the air and emitted infrared radiation from heated ground, in combination with convection, **(4)** over natural sands, with heat inputs from both visible and infrared sources.

EXPERIMENT (1): CONVECTION HEAT LOSS

RATIONALE

Convection heat loss is an important part of energy balance, particularly for small animals (Porter & Gates 1969, Spotila 1979, Turner 1985). However, small animals that live close to the ground may be insensitive to environmental wind, owing to the formation of boundary layers next to the ground (Hamilton 1973, Campbell 1977, Cloudsley-Thompson 1978). Therefore, it is important to see (a) if the heat loss of beetles close to the surface is affected by changes in wind speed, and if so, by how much, and (b) if the two beetle species differ in their susceptibility to convection heat loss.

PROCEDURE

Five *O. bicolor* and four *O. unguicularis* were used for this experiment. The beetles were prepared as described above. Beetles were positioned in the wind tunnel so the abdomen was 2-3 mm above the floor of the test section. This approximated the posture of living beetles. The wind speed was adjusted to 0, 1, 2 and 3 m s^{-1}, and the beetles were warmed by the lamp. When the abdominal temperature had equilibrated, or had warmed to 40-50 °C, the lamp was switched off and the beetle was allowed to cool. During cooling, the abdominal temperature was recorded for 5 min., and the time constant calculated, as described above.

RESULTS

At wind speeds of 0-2 m s^{-1}, wind significantly affected the time constant for cooling (Fig. 4, Table 3). There was no significant difference between the time constant for cooling at 2 and 3 m s^{-1} (Fig. 4). Time constants did not differ significantly between the two species, either as a main effect or as an interactive factor with wind speed (Fig. 4, Table 3).

Table 3. Analysis of variance for abdominal time constants during cooling.

Factor	F	p>F	r^2
Main Effects			
Species	0.42	0.524	0.001
Wind speed	89.62	**<0.001**	0.895
Interactions			
Species X Wind speed	1.00	0.409	0.010

DISCUSSION

The time constant for cooling is the product of the beetle's thermal resistance to heat exchange (R; K W^{-1}) and its thermal capacitance (C; J K^{-1}). There is no reason to suspect that the beetles' capacitances differ, because the contents of water and non-volatile components of the two species are identical (Table 2). Thus, the time constant is a useful comparative measure of the beetles' resistances to convection heat loss. There is no indication that the resistance to convection heat loss differs between the two species.

Wind speed does significantly affect the beetles' resistances to convection heat loss (Fig. 4, Table 3). It appears, therefore, that boundary layer effects are not sufficient to obviate the effects of wind speed on beetles' heat losses. Thus, wind is an important factor in the thermal biology of these beetles, a factor largely neglected in previous studies (Bolwig 1957, Edney 1971b, Hamilton 1973, Cloudsley-Thompson 1978).

EXPERIMENT (2): DIRECT AND REFLECTED VISIBLE RADIATION

RATIONALE

Radiation transmitted from the sun has a temperature of about 6000 K (Campbell 1977). According to Wien's Displacement Law (Campbell 1977), the wavelength in sunlight that transmits the maximum amount of energy (the peak spectral emittance) is about 500 nm. Thus, sunlight transmits a considerable amount of energy in the visible and short-wave infrared wavelengths (c. 50 %, Gates 1962). For convenience, we shall refer to this thermal radiation as visible, to distinguish it from radiant energy transmitted at longer infrared wavelengths (considered below).

A beetle exposed to sunlight absorbs radiation emitted directly from the sun. Sunlight also illuminates the soil the beetle is standing on, and depending upon the soil, some of this light will be absorbed, warming the soil, and some will be reflected back onto the beetle, adding to its radiative heat load. In this experiment, we estimate how colour affects the absorption of visible radiant energy, both in the direct and reflected components. Infrared radiation emitted by the soil is considered in experiment 3.

PROCEDURE

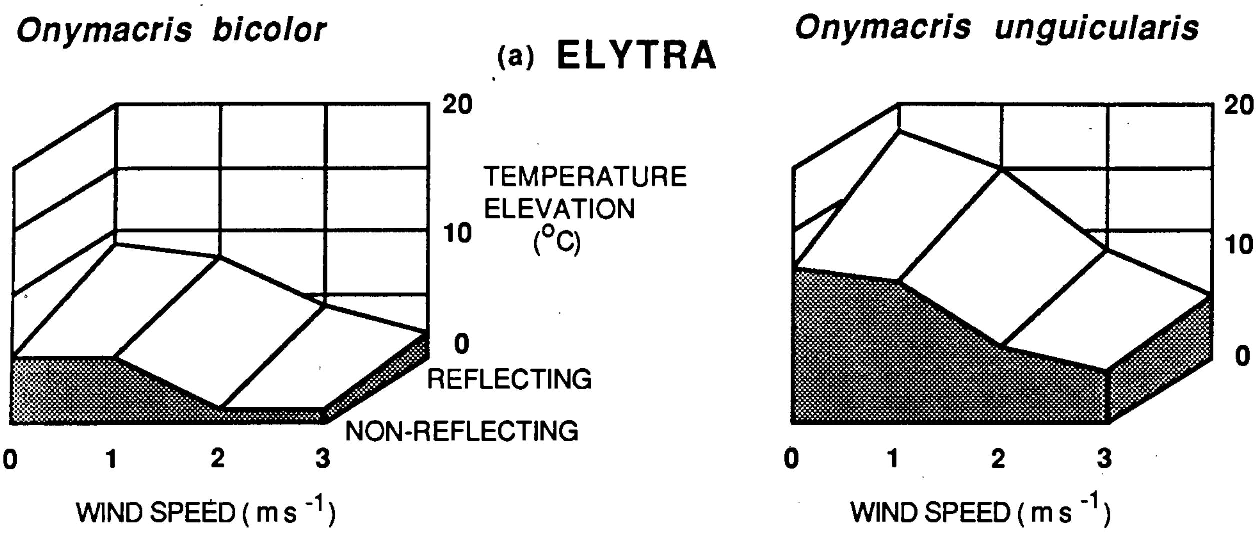
Five *O. bicolor* and four *O. unguicularis* were used for this experiment. The beetles were prepared as described above. Direct irradiance was provided by the 300 W quartz halogen lamp (Fig. 3). This lamp has a colour temperature of about 3300 K, with a peak spectral emittance at a wavelength of about 900 nm, thus the light provided is "redder" than natural sunlight. Nevertheless, the lamp provided a broad-spectrum irradiance (400-700 nm), similar to that found in the natural habitat of the beetles. We did not test the effect of various azimuths of the light source as it was always directly overhead.

To measure the effect of direct illumination alone, the floor of the test section beneath the beetle was removed and replaced with coarse (2 mm) mesh. Minimal radiation was therefore reflected back onto the beetle. Preliminary tests showed that removal of the floor did not affect the convection environment around the beetle. To estimate the maximum contribution of the reflected component, the floor of the wind tunnel was replaced with highly reflective aluminium foil. The foil was stretched over a 15 cm petri dish filled with agar gel, which acted as a high-capacitance thermal buffer to keep the foil substratum cool. The beetles were positioned directly under the lamp and about 2-3 mm above the surface. The wind speed was adjusted to 0, 1, 2 and 3 m s^{-1}. The lamp was switched on, and the temperature recorded for a period of up to 5 min. To preclude heat damage to the beetle, its temperature was never allowed to go higher than 45 °C. Equilibrium temperatures were estimated as described above.

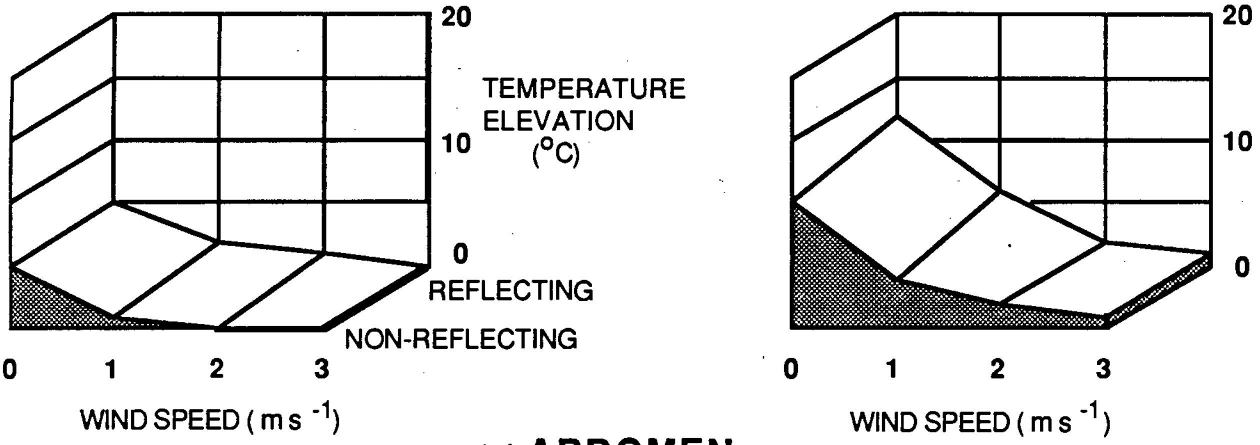
RESULTS

The results of this experiment are presented in Fig. 5 and Table 4. Illuminating the beetles with light from a quartz halogen lamp warmed them, signifying that these beetles will absorb significant amounts of visible radiation. The elytra were warmed the most in *O. unguicularis*, the abdomen was warmest in *O. bicolor*, and the thorax was always warmed the least in both species (Table 4). The beetles were warmed the most in still air, and as wind speed increased, the elevation of temperature experienced by the beetles was reduced (Fig. 5, Table 4). The black beetle

(a) **ELYTRA**



(b) **THORAX**



(c) **ABDOMEN**

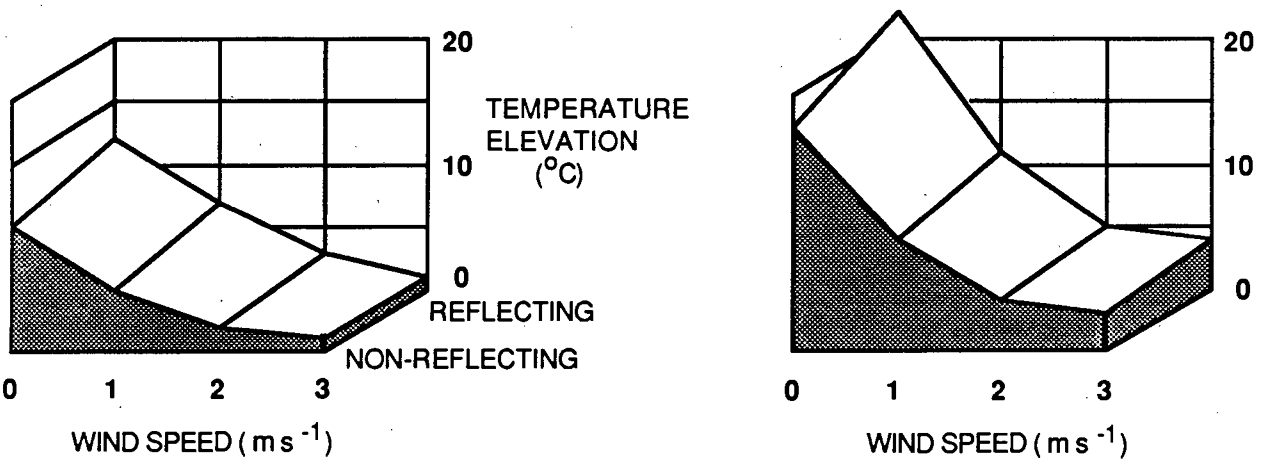


Fig. 5. Equilibrium temperatures of two Namib tenebrionids exposed to direct and reflected radiation from a quartz halogen lamp. Temperature elevation is the difference between body temperature and air temperature. Four wind speeds (0,1,2 and 3 m s^{-1}) and two substrata (reflecting and non-reflecting) are the independent variables. (a) Elytral temperature, (b) Thoracic temperature and (c) Abdominal temperature.

Table 4. Analysis of variance for elevation of (a) elytral, (b) thoracic, and (c) abdominal temperature above air temperatures during visible irradiation. Main effect means and the least significant difference (L.S.D.) are presented below.

		(a)			(b)			(c)	
Factor	F	p>F	r^2	F	p>F	r^2	F	p>F	r^2
Main Effects									
Species	79.93	**<0.001**	0.289	39.58	**<0.001**	0.154	44.17	**<0.001**	0.127
Wind Speed	37.33	**<0.001**	0.405	46.15	**<0.001**	0.538	71.88	**<0.001**	0.621
Substratum	16.51	**<0.001**	0.060	5.40	**0.023**	0.021	9.55	**0.003**	0.028
Interactions									
Species X Wind Speed	2.45	0.073	0.027	4.99	**0.004**	0.058	6.24	**0.001**	0.054
Species X Substratum	0.99	0.324	0.004	0.87	0.354	0.003	0.17	0.679	<0.001
Substratum X Wind Speed	1.13	0.346	0.012	0.49	0.693	0.006	0.83	0.482	0.007
Species X Wind Speed X Substratum	0.07	0.974	0.001	0.21	0.890	0.002	0.09	0.966	0.001

	(a) Main Effect Means	L.S.D.	(b) Main Effect Means	L.S.D.	(c) Main Effect Means	L.S.D.
Species						
O. bicolor	4.53	1.23	1.92	0.95	4.98	1.33
O. unguicularis	10.03		4.90		9.38	
Wind Speed						
0	10.83	1.73	7.76	1.33	14.61	1.86
1	9.42		3.30		7.46	
2	4.53		1.14		3.36	
3	3.11		0.80		2.31	
Substratum						
Reflecting	8.21	1.23	3.80	0.95	7.95	1.32
Non-reflecting	5.73		2.01		5.92	

(*O. unguicularis*) was warmed, on average, about twice as much as the predominantly white beetle (*O. bicolor*). Beetles exposed to both direct and reflected radiation were significantly warmer than beetles exposed to direct radiation alone (Table 4). The thorax was warmed the most by reflected radiation, as the proportional increase over the reflecting surface was higher for the thorax than for either the abdomen or the elytra.

DISCUSSION

The natural colour variation of Namib tenebrionid beetles has a definite consequence for the absorption of visible radiant energy. White beetles are warmed less than black beetles when exposed to light from a quartz halogen lamp. Undoubtedly, this is because white elytra reflect more radiant energy in these wavelengths than do black elytra. This is evident from the analyses of variance. Variation of elytral colour accounted for nearly 30 % of the total variation of elytral temperature, more than twice that for the thorax or the abdomen (Table 4). The reflected component is likewise significant. Adding a reflected component to the direct radiation raised the beetle temperature elevations by from 35 % (abdomen) to nearly 90 % (thorax, Fig. 5, Table 4). There was no significant species by substratum interaction, signifying both beetles were affected equally by the addition of a reflected component.

Important as radiation was, however, it is clear that variation of wind speed is by far the most important component of variation in beetle temperature. Variation of wind speed accounted for 41-62 % of the total variance in temperature (Table 4). Judging from Fig. 5, a considerable part of this variation occurs in the low wind speeds, 0-2 m s^{-1}. It appears, therefore, that even very slow winds can have a significant effect on how these beetles cope with a radiative heat load.

EXPERIMENT (3): SUBSTRATUM TEMPERATURE AND INFRARED RADIATION

RATIONALE

In experiment 2, surface temperatures were kept low, so that the effect of visible radiation could be evaluated independent of heating of the substratum beneath the beetle. In the natural environment, the ground is warmed by the sun, and the beetle will incur an additional heat load from the ground. Heat from the ground may be imparted to the beetle in two ways: first, it may be conducted through the air space between the ground and the beetle. Second, heat may be transmitted by infrared radiation, because heated ground radiates energy at a peak spectral emittance of roughly 8000 nm, well outside the visible range. We assumed that heat is not imparted by direct conduction between the beetle and the ground, as the contact area between the beetle and the ground is very small.

PROCEDURE

Five individuals of each species were used for these experiments. Beetles were prepared as previously described. Wind speeds tested included 0, 1, 2 and 3 m s^{-1}. The petri dish that comprised the floor of the test section was filled with sand, and then covered with aluminium foil which was in contact with the sand. The sand and foil were warmed to 45-55 °C by a hotplate placed underneath the petri dish. Two types of foil covering were used: in one set of measurements, the foil was left shiny. The emissivity of polished aluminium foil is about 0.08 (Thomas 1980). Therefore, minimal radiation was emitted from the hot, shiny foil, and the beetle was warmed mostly by conduction through the air. In a second series of measurements, the foil was coated with carbon black, which has an emissivity close to unity (Thomas 1980). The blackened foil emits considerably more infrared radiation, and the beetle was warmed by both conduction through the air and absorbed infrared radiation. Any difference in the beetles' temperatures between the shiny foil and the blackened foil would be due to absorption of infrared radiation. The data were analysed by analysis of covariance, with ground temperature being the covariate.

RESULTS

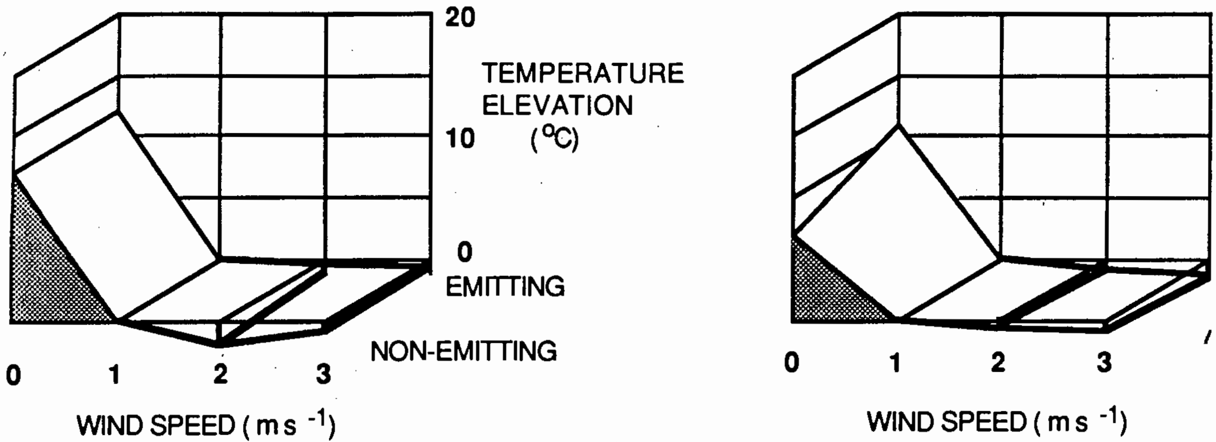
Beetles are warmed when they are placed over a warm surface, but only if the wind speed is very low (Fig. 6, Table 5). At wind speeds of 1 m s^{-1} or greater, beetle temperature is statistically indistinguishable from air temperature (Table 5). Temperatures of beetles over an emitting substratum were slightly, but significantly higher than over a non-emitting substratum. From Fig. 6, it appears that the difference is entirely attributable to *O. unguicularis* at low wind speeds. The temperature of *O. unguicularis* was affected by surface infrared radiation, while the temperature of *O. bicolor* was not. In contrast, *O. bicolor* was warmed significantly more than *O. unguicularis* (Table 5). Ground temperature was a significant factor in determining the temperature of the thorax and abdomen, but not of the elytra.

DISCUSSION

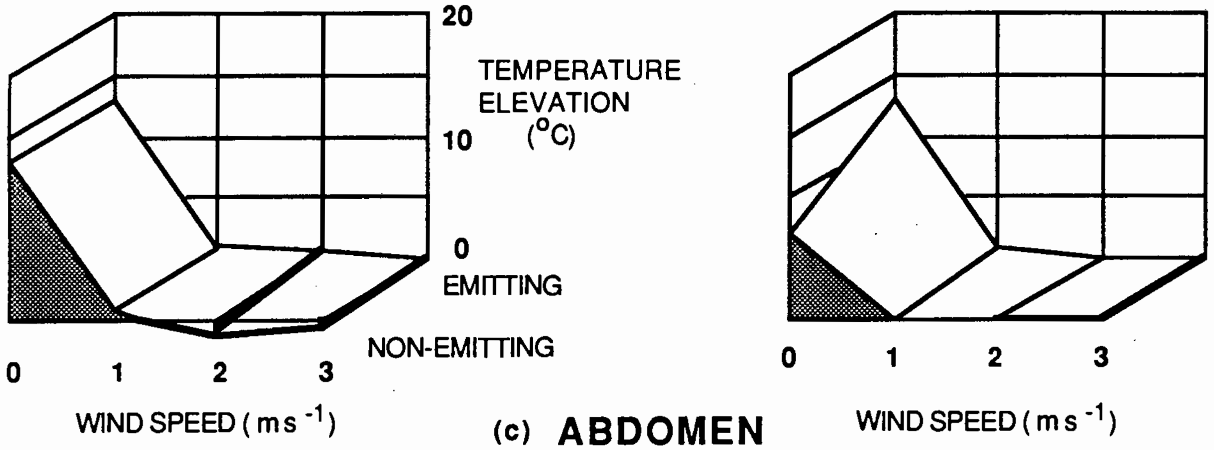
Ground temperature is clearly a factor in a beetle's thermal energy balance. However, wind speed is far more important, as it accounted for 80-87 % of the total variation of beetle temperature (Table 5). Almost all of this variation is accounted for by wind speeds between 0 and 1 m s^{-1} (Fig. 6). At wind speeds of 1 m s^{-1} or greater, beetle temperature was not distinguishable from air temperature (Table 5). If a beetle is to be warmed by hot ground at all, the air must be either still, or hot. Heating due to being in a thermal boundary is not important for these beetles. It thus appears that infrared radiation from heated ground is a relatively unimportant factor in the thermal biology of these beetles. While the addition of an infrared component to the beetles' heat loads raised their temperatures significantly, the increase was slight. This result is contrary to the assertions of some researchers (Bolwig 1957, Edney 1971b, Hamilton 1973, Cloudsley-Thompson 1978), but supports the measurements of Parry (1951) and Digby (1955), who showed that infrared radiation contributes little to the temperature of a variety of arthropods.

The predominantly white *O. bicolor* were not at all affected by infrared radiation from the substratum (Fig. 6), as the temperatures of these beetles did not change with different substratum

Onymacris bicolor **(a) ELYTRA** *Onymacris unguicularis*



(b) THORAX



(c) ABDOMEN

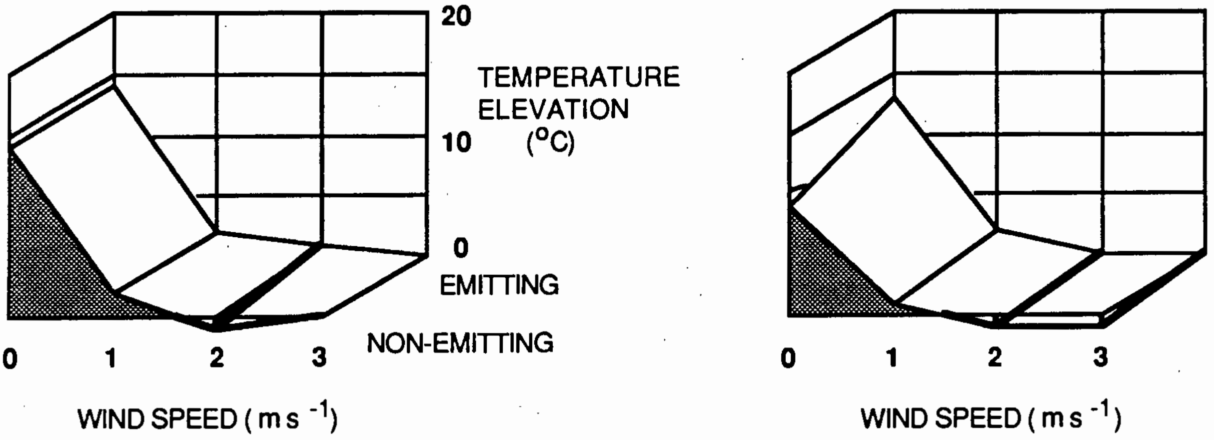


Fig. 6. Equilibrium temperatures of two Namib tenebrionids exposed to a heated substrate. Temperature elevations are as defined in Fig. 5. Points are the least-squares means, corrected for variation of ground temperature by analysis of covariance. Four wind speeds (0,1,2 and 3 m s^{-1}) and two substrata (emitting and non-emitting) are the independent variables. (a) Elytral temperature, (b) Thoracic temperature and (c) Abdominal temperature.

Table 5. Analysis of covariance for elevation of (a) elytral, (b) thoracic, and (c) abdominal temperature above air temperatures during infrared radiation. Main effect means and standard errors (S.E.M.) are presented below.

		(a)			(b)			(c)	
Factor	F	p>F	r^2	F	p>F	r^2	F	p>F	r^2
Main Effects									
Ground Temp.	3.01	0.088	0.004	5.28	**0.025**	0.008	4.84	**0.032**	0.011
Species	5.18	**0.026**	0.007	4.12	**0.046**	0.006	4.37	**0.041**	0.010
Wind Speed	220.11	**<0.001**	0.869	181.72	**<0.001**	0.828	118.22	**<0.001**	0.803
Substratum	4.53	**0.037**	0.006	6.86	**0.023**	0.010	4.51	**0.038**	0.010
Interactions									
Species X Wind Speed	4.32	**0.008**	0.017	2.85	**0.044**	0.013	1.83	0.151	0.012
Species X Substratum	0.85	0.359	0.001	1.86	0.178	0.003	0.69	0.409	0.002
Substratum X Wind Speed	1.72	0.171	0.007	2.35	0.080	0.011	0.46	0.709	0.003
Species X Wind Speed X Substratum	1.62	0.195	0.006	5.42	**0.022**	0.025	0.84	0.479	0.006

	(a) Main Effect Means	S.E.M.	(b) Main Effect Means	S.E.M.	(c) Main Effect Means	S.E.M.
Species						
O. bicolor	2.66	0.27	3.32	0.30	4.04	0.38
O. unguicularis	1.88	0.27	2.55	0.30	3.00	0.38
Wind Speed						
0	10.66	0.38	11.40	0.42	12.23	0.54
1	0.22	0.38	0.88	0.42	1.81	0.54
2	-0.91	0.38	-0.36	0.42	0.01	0.54
3	-0.88	0.38	-0.17	0.42	0.05	0.54
Substratum						
Emitting	2.67	0.27	3.48	0.30	4.09	0.38
Non-emitting	1.87	0.27	2.39	0.30	2.96	0.38

emissivities. In contrast, the totally black *O. unguicularis* was affected by infrared radiation. Temperature of this species was higher over an emitting hot surface, when wind speed was low (Fig. 6). Nevertheless, the temperatures attained by *O. bicolor* were, on average, warmer than the temperatures attained by *O. unguicularis* (Table 5). This difference cannot be explained by the beetles' infrared absorptivity. If *O. bicolor* was warmer because its infrared absorptivity was greater, one would expect to see a difference between temperatures over the emitting and non-emitting surfaces. This is not evident from the data (Fig. 6). Likewise, it is difficult to ascribe the differences to convection heat exchange, because no apparent difference between the species was evident for convection heat loss (Fig. 4, Table 3). It is also difficult to ascribe the difference to differences in treatment between the white and black beetles, as both species were usually tested on the same day, and great care was taken to match placement of the beetles and to ensure uniformity of conditions. The most likely explanation is that conduction of heat through the air, and by free convection from a heated surface, is more effective for *O. bicolor* than it is for *O. unguicularis.* A mechanism for this is unknown, but the different shapes of the beetles may be a factor. *O. bicolor* in cross-section is more rectangular than the more rounded *O. unguicularis.* This may present a larger surface for absorption of heat from the ground in *O. bicolor*. Although this possibility is not investigated in the present study, some simple experiments using appropriately shaped models, or exoskeletons of the beetles themselves, should be designed in a future study in order to determine the effects of shape on beetle temperatures.

EXPERIMENT (4): TEMPERATURE AND TEMPERATURE DYNAMICS OVER SAND SUBSTRATA

RATIONALE

The rationale of the previous experiments was to isolate and estimate the importance of the various components of the thermal energy regime a beetle is likely to experience: convection, direct and reflected visible radiation, conduction through air and free convection from a warmed surface, and emitted infrared radiation from a warmed surface. A beetle in a natural situation is likely to face all components at once, and all to varying degrees. Therefore, it is useful to measure the beetles' thermal behaviour in a relatively natural situation.

Equilibrium temperatures are not the only important factor to a beetle. Beetles have thermal capacity. Thus, they may be able to endure very high environmental temperatures without deleterious effects, provided the exposure lasts for a short time. It is useful to know the length of this short period. The "natural situation" used here consists of a beetle placed over a warmed sand substratum, and simultaneously exposed to radiation from a quartz halogen lamp, and wind.

PROCEDURE

Four individuals of each species were used for these experiments. Beetles were prepared as described above. Wind speeds tested were 0, 1, 2 and 3 m s^{-1}. Two types of sand were used: (1) A white sand from a beach along the Cape Peninsula in Cape Town, and (2), a darker brown sand from Gobabeb in South West Africa (Fig. 2). (Beach sand was used owing to difficulties in obtaining pale sand from the Skeleton Coast, which is the natural home of *O. bicolor*). The sand in the petri dish was arranged so that the surface was coplanar with the floor of the wind tunnel. The sand was heated from above by the lamp. The beetle was carefully positioned over the sand surface, and its temperature change was measured as described previously.

RESULTS

As in experiment 2, the elytra of *O. unguicularis* were warmed significantly more than the elytra of *O. bicolor* (Fig. 7a, Table 6a). However,thoracic and abdominal temperatures differed only slightly between the species, with *O. bicolor* being the warmer (Table 6b & c). As in all previous experiments, wind speed was a significant factor, with higher winds forcing beetle temperatures close to air temperature (Fig. 7, Table 6). At the highest wind speeds, beetle temperatures were not more than a few degrees above air temperature (Table 6). At slow wind speeds and still air, beetle temperature was tens of degrees above air temperature (Fig. 7, Table 6).

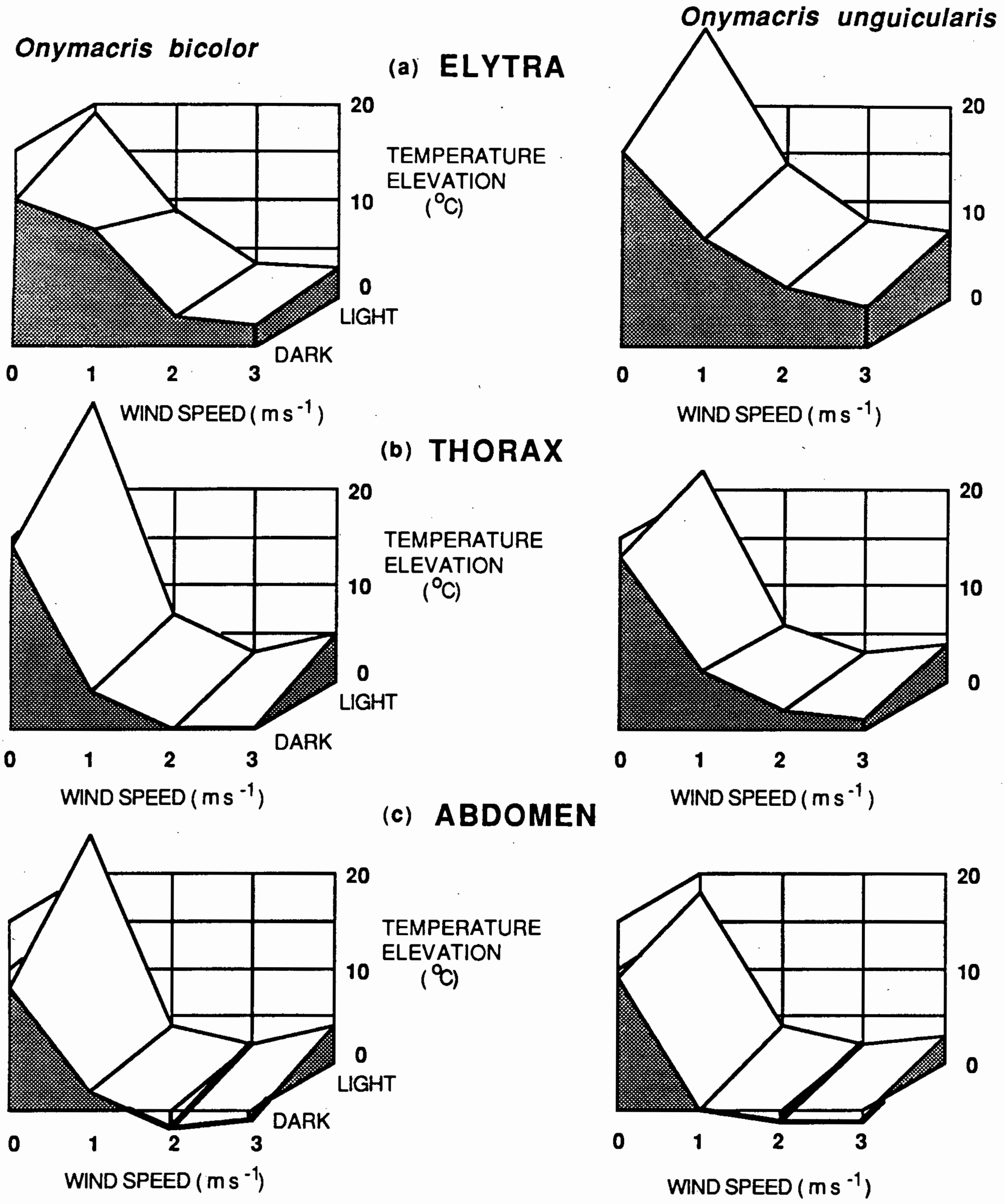


Fig. 7. Equilibrium temperatures of two Namib tenebrionids exposed to "natural" conditions of visible radiation, heated sand and wind. Temperature elevations are as defined in Fig. 5. Points are the least-squares means, corrected for variation of ground temperature by analysis of covariance. Four wind speeds (0,1,2 and 3 m s^{-1}) and two substrata (light sand and dark sand) are the independent variables. (a) Elytral temperature, (b) Thoracic temperature and (c) Abdominal temperature.

Table 6. Analysis of covariance for elevation of (a) elytral, (b) thoracic, and (c) abdominal temperature above air temperatures during natural sand experiments. Main effect means and the least significant difference (L.S.D.) are presented below.

	(a)			(b)			(c)		
Factor	F	p>F	r^2	F	p>F	r^2	F	p>F	r^2
Main Effects									
Ground Temp.	14.84	**<0.001**	0.092	384.35	**<0.001**	0.405	69.85	**<0.001**	0.192
Species	15.09	**<0.001**	0.093	3.80	0.057	0.004	0.20	0.655	0.001
Wind Speed	24.75	**<0.001**	0.458	136.10	**<0.001**	0.431	57.99	**<0.001**	0.478
Substratum	2.64	0.111	0.006	56.94	**<0.001**	0.060	47.00	**<0.001**	0.129
Interactions									
Species X Wind Speed	1.36	0.265	0.016	4.35	**0.009**	0.014	1.37	0.263	0.011
Species X Substratum	1.01	0.319	0.025	8.73	**0.005**	0.009	2.35	0.132	0.006
Substratum X Wind Speed	0.78	0.509	0.015	5.08	**0.004**	0.016	3.87	**0.015**	0.032
Species X Wind Speed X Substratum	0.26	0.855	0.005	3.50	**0.023**	0.011	2.51	0.070	0.021

	(a) Main Effect Means	L.S.D.	(b) Main Effect Means	L.S.D.	(c) Main Effect Means	L.S.D.
Species						
O. bicolor	8.02	2.22	8.45	0.91	11.17	2.14
O. unguicularis	12.21		7.38		10.49	
Wind Speed						
0	17.12	3.14	18.49	1.28	23.88	3.02
1	12.83		6.95		10.95	
2	6.44		3.55		5.10	
3	4.06		2.66		3.40	
Substratum						
Dark Sand	9.72	2.22	6.62	0.91	8.60	2.14
Light Sand	10.50		9.21		13.06	

Table 7. Analysis of variance for time constants (s) for warming of (a) elytral, (b) thoracic, and (c) abdominal temperatures during natural sand experiments. Main effect means and the least significant difference (L.S.D.) are presented below.

		(a)			(b)			(c)	
Factor	F	p>F	r^2	F	p>F	r^2	F	p>F	r^2
Main Effects									
Species	10.21	**0.003**	0.088	0.82	0.370	0.004	3.12	0.084	0.020
Wind Speed	16.03	**<0.001**	0.415	51.76	**<0.001**	0.736	32.16	**<0.001**	0.615
Substratum	3.63	0.063	0.031	<0.01	0.994	<0.001	1.64	0.206	0.010
Interactions									
Species X Wind Speed	1.64	0.192	0.042	0.84	0.478	0.012	1.16	0.237	0.028
Species X Substratum	<0.01	>0.999	<0.001	0.24	0.625	0.001	1.03	0.314	0.007
Substratum X Wind Speed	0.96	0.418	0.025	1.17	0.333	0.017	0.54	0.659	0.010
Species X Wind Speed X Substratum	<0.01	>0.999	<0.001	0.23	0.872	0.003	0.39	0.763	0.007

	(a) Main Effect Means	L.S.D.	(b) Main Effect Means	L.S.D.	(c) Main Effect Means	L.S.D.
Species						
O. bicolor	116	18.7	104	15.1	168	27.0
O. unguicularis	86		97		144	
Wind Speed						
0	142	26.3	171	21.2	256	37.8
1	124		111		165	
2	87		69		113	
3	60		49		83	
Substratum						
Dark Sand	96	19.2	100	15.5	148	27.6
Light Sand	115		100		165	

Sand temperature was a significant component of variation in beetle temperature, in the case of thorax temperature, explaining as much of the variance as did wind speed (Table 6). The lamp warmed the dark sand more than the light sand (46 vs. 43 °C). Despite this, beetles over light sands were warmer than beetles over dark sands (Table 6). For thoracic and abdominal temperature, the time constant did not differ between species (Table 7). The time constant for the elytra of *O. unguicularis* was significantly shorter than for *O. bicolor*. The time constant varied with wind speed, as expected from Experiment 1. Sand colour had no discernible effect on any of the time constants (Table 7).

DISCUSSION

In a relatively "natural" situation, *i.e.* a beetle illuminated by bright light while it is over a warmed surface, colour seems to have little impact on temperature. As expected (Experiment 2), the elytra of *O. unguicularis* were warmer than than those of *O. bicolor*. However, this does not translate into higher temperatures elsewhere in the beetles, as equilibrium temperatures of the thorax and abdomen differed little between the species, with *O. bicolor* being the warmer. A possible explanation for this is that, in the absence of other factors, more energy absorbed by the black elytra translates into higher temperatures throughout the beetle (Fig. 5, Table 4). However, it appears that while *O. unguicularis* absorbs more heat from overhead illumination, *O. bicolor* receives more heat from the heated sand below. Consequently, the total energy budgets are identical for the two species, but for different reasons.

Sand colour has an interesting effect on beetle temperature. The dark sands were warmed more by the lamp than light sands. Nevertheless, the beetles over the light sands were warmed more than the beetles over the dark sands. Presumably, the light sands added a reflected component to the radiation impinging on the beetles, and increased their temperatures. This supports the findings of Experiment 2, which showed that reflected radiation increased beetle temperatures at all wind speeds. The reflected component thus raises beetle temperatures more than the added infrared component emitted by hotter sands.

As with the equilibrium temperature, the time constant for the elytra differed significantly between species (it was smaller for *O. unguicularis*), but the time constants for the abdomen and elytra did not. Likewise, time constants do not differ between light and dark sands. Wind speed was a significant component of the variation of time constant. These beetles have time constants of the order of minutes (Table 7). Therefore, they have the capacity to tolerate environmental temperatures that would be lethal if they came to equilibrium, provided the exposure time is short. This may occur if a beetle crosses an extremely hot and brightly illuminated patch of sand on its way from one shady patch to another.

The time constant alone does not express the length of exposure a beetle could tolerate in a hot environment. It merely describes a first-order transient (Turner 1987), and designates the time taken for the temperature of an object to change by a set fraction (e^{-1}) of the object's total temperature excursion during the transient. In an equation, this may be expressed:

$$\frac{T_t - T_\infty}{T_0 - T_\infty} = e^{-t/t} \qquad (1)$$

where T_t = temperature at any time t
T_∞ = equilibrium temperature
T_0 = temperature at time 0

Using this equation, it is possible to estimate the time, t∗, it will take for the temperature to reach some specified value, T∗:

$$t* = -t \;.\; \ln\left[\frac{T_* - T_\infty}{T_0 - T_\infty}\right] \qquad (2)$$

If T∗ is the maximum temperature the beetle can tolerate, *i.e.* its lethal temperature (T_l), it will allow us to estimate how long a beetle can endure a radiative heat load. In order to calculate T_l, the equilibrium temperature (T_∞), the starting temperature (T_0) and the time constant (t) must be known.

Equation 2 may be simplified, first by taking advantage of the fact that both T_∞ and t are functions of the wind speed, U (m s^{-1}), as shown in Experiment 4:

$$t_1 = -t\ (U)\ .\ \ln\left[\frac{T_1 - T_\infty(U)}{T_0 - T_\infty(U)}\right] \tag{3}$$

As wind speed increases, t decreases (Table 7). From equation (3), the maximum length of exposure is lessened by increasing wind speed. However, the equilibrium temperature also declines with increasing wind speed, and this lengthens the maximum tolerable length of exposure. The actual exposure time is determined by whether the time constant or the equilibrium temperature is most affected by changes of wind speed.

In order to examine the temperature dynamics of the abdominal temperature, we turn first to the time constant. As shown in Table 7, wind speed is the only significant factor explaining the variation in t. If the data is lumped appropriately, the best description of t as a function of U is:

$$t = 10^{(2.39 - 0.16U)} \tag{4}$$

With respect to the abdomen's equilibrium temperature, it was evident that wind speed and colour of the sand were the only significant factors explaining its variation. If the data is lumped appropriately again, the best descriptions for T_∞ as a function of U are, for light sand:

$$T_{\infty,\,l} = T_{air} + 10^{(1.43 - 0.29U)} \tag{5a}$$

and for dark sand:

$$T_{\infty,\,d} = T_{air} + 10^{(1.24 - 0.28U)} \tag{5b}$$

Using these equations and light sand as an example, equation (3) may be rewritten:

$$t_1 = -10^{(2.39 - 0.16U)}\ .\ \ln\left[\frac{T_1 - T_{air} - 10^{(1.43 - 0.29U)}}{T_0 - T_{air} - 10^{(1.43 - 0.29U)}}\right] \tag{6}$$

and if one assumes, for simplicity, that the beetle always starts its transient equal to air temperature, the equation further simplifies to:

$$t_l = -10^{(2.39 - 0.16U)} . \ln \left[\frac{(T_l - T_{air}) - 10^{(1.43 - 0.29U)}}{-10^{(1.43 - 0.29U)}} \right] \quad (7)$$

Thus, the time it takes for a beetle to reach lethal temperature is a function of two variables, the wind speed U, and the difference in temperature between the air temperature and lethal temperature ($T_l - T_{air}$). The value of the coefficients in this equation will be different for dark sand.

Some estimates of exposure time are plotted in Fig. 8. At higher wind speeds, the tolerable duration of exposure is longer. Additionally, the exposure time is shorter if the beetle starts off warm *i.e.* if the surrounding air is warm. The maximum tolerable exposure is shorter over light sand than over dark sand, not as a result of different time constants (Table 7), but because the equilibrium temperatures differ (Table 6). The tolerable exposure time can be quite short. In still, hot air, a beetle crossing light sand will be able to tolerate 20 s or less of exposure. The running speeds of these beetles are unknown. However, another Namib tenebrionid of similar size, *Physadesmia globosa*, has a running speed of about 23 cm s^{-1} (Nicolson *et al.* 1984). Assuming similar speeds for *O. unguicularis* and *O. bicolor*, a "dash" for cover would have to be less than 5 m. In very high winds, if the air is hot, the exposure time is 45-100 s, which translates into a longer "dash" length of 10-23 m.

DOES COLOUR HELP NAMIB BEETLES SURVIVE IN AN EXTREME ENVIRONMENT ?

Experiments 1-4 have shown that, in Namib beetles, only one avenue of heat exchange, *i.e.* the absorption of visible radiation from above, is influenced by beetle colour. Predominantly white beetles incur a smaller heat load than black beetles when exposed to radiation in the visible range. However, the colour of the beetles is irrelevant to other aspects of their thermal energetics. Colour is not relevant to the absorption of shortwave radiation reflected from below. White beetles are warmed more by heated ground than are black beetles, but our evidence indicates that difference in colour is not the reason for this. Heat loss by convection is not affected by colour at all. When these different modes of heat exchange combine, an increased heat load as a result of colour may

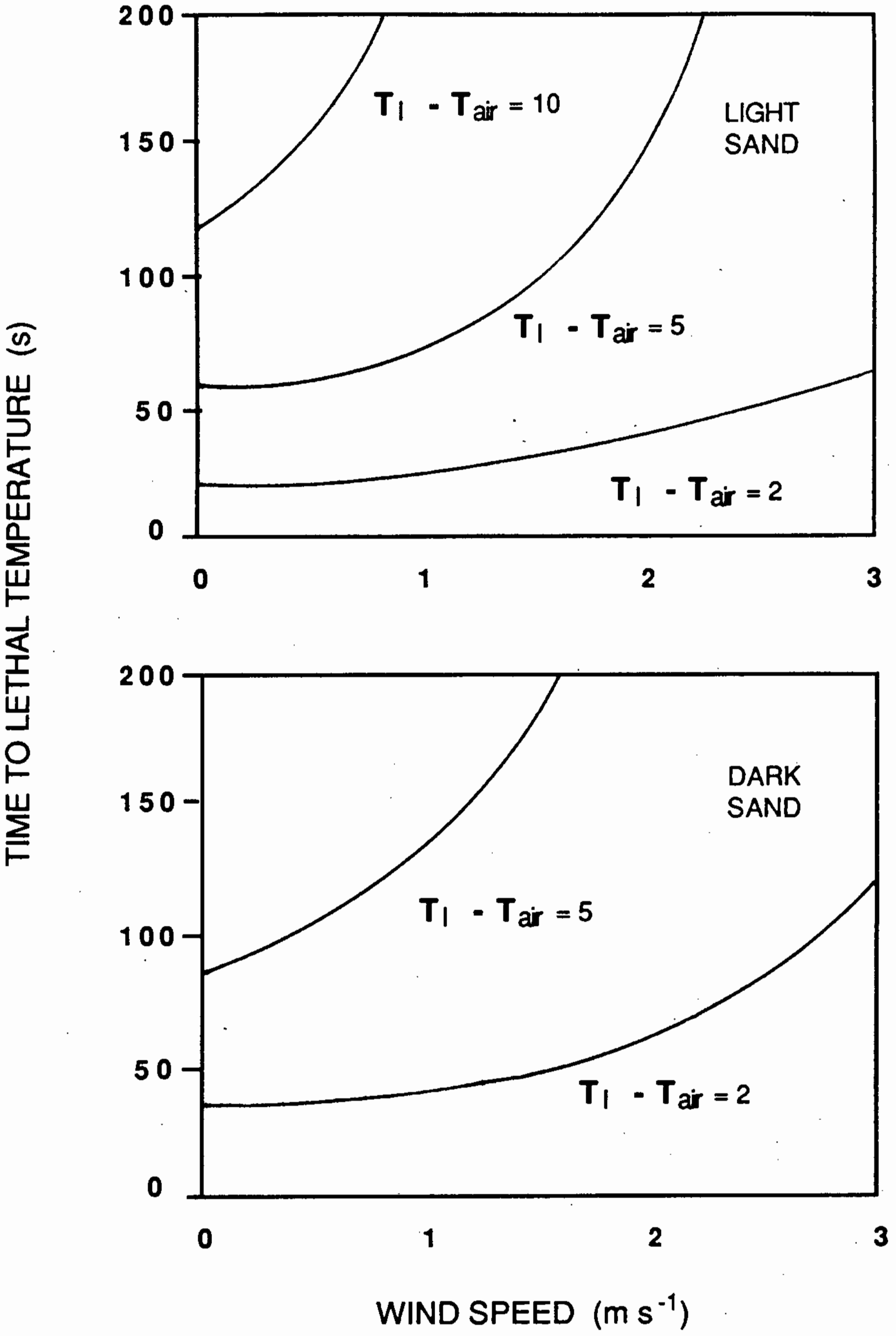


Fig. 8. Maximum tolerable exposure times for Namib Desert beetles. Simulations are for two sands (light , dark) and three starting temperatures ($T_l - T_{air} = 2$, 5 and 10 °C).

be ameliorated or even negated by other modes of heat exchange, as shown by the natural sand experiments. Even though the black beetles absorbed more heat through visible radiation, as shown by their warmer elytra, both species had identical body temperatures. Presumably, while the black beetles absorbed more heat from above, the white beetles absorbed more heat from the heated ground below.

Additionally, the thermal effect of colour may be small compared with other factors. Our experiments showed that variation of wind speed was always the most important factor in the beetles' temperatures. In the semi-natural conditions of Experiment 4, beetle colour was unimportant, whereas wind speed and ground temperature were very important. Indeed, sand colour proved to be a more important influence on beetle temperature than did beetle colour. However, the beach sand used in these experiments was far whiter, and had a much higher reflectance, than the pale Namib (Unjab) sand which is the natural home of *O. bicolor* . If Unjab sand had been used instead of beach sand, one would expect similar beetle temperatures over both Unjab and Gobabeb sands, since Fig. 11 (Chapter 3) shows that the reflectances of these sands are almost identical.

The results presented here suggest that authors who support the view that the colour of Namib tenebrionids has a thermoregulatory value (Bolwig 1957, Edney 1971b, Hamilton 1973), as well as those who claim that these colours are cryptic or aposematic (Cloudsley-Thompson 1978), could both be correct. However, the true answer depends very strongly upon both the thermal environment the beetles live in (*i.e*. the variation in wind speed, the intensity of solar radiation, the colour of the sand), and how the experiments are performed. For example, Edney (1971b) made many careful measurements of beetle temperature in field conditions and ensured that beetles were exposed to circumstances as natural as possible. However, he concentrated on the beetles' radiative thermal exchanges, and minimised the ameliorating effects of wind. His measurements were taken during only calm periods, because even slight winds caused the temperatures to vary considerably. Hamilton (1973) did likewise for his experiments, noting that variations of wind speed made his measurements unrepeatable. Given the very important effects of wind found by the present study, it is difficult to draw a firm conclusion about the thermal effects of colour. Clearly, colour is sometimes, and in some conditions, thermally relevant, as shown by Edney (1971b) and Hamilton (1973). At other times, and in other conditions, colour is not, as shown by us.

Our experiments also address certain misconceptions about the factors which determine temperatures of small animals, like beetles. It is often assumed that small, ground-dwelling animals live in a "boundary layer", a layer of still air next to the ground. In this layer, temperature can be very high, and any animal living there cannot benefit from variations of wind speed. We do not doubt that animals that live close to the ground are in a very different environment from those that live well off the ground. Nevertheless, variation of wind speed was a very important factor in the thermal energetics of the beetles tested here. This result supports the measurements of Digby (1955) on a variety of other ground-dwelling arthropods.

An additional assumption is that small animals incur a very heavy radiative load from heated ground and rocks (Hadley 1970, Edney 1971b, Cloudsley-Thompson 1978). In contrast, we found that infrared radiation from the ground is a negligible component of the radiative heat load the beetles incur. Rather, beetles incur a heat load from the ground by conduction from the ground through the air, and by reflection of visible radiation. Both are important only in still air, and they are essentially eliminated even in very slow winds. Both Parry (1951) and Digby (1955) provide similar results.

In summary, we found that three factors are important in the thermal biology of two tenebrionids from the Namib Desert: wind speed, ground temperature and ground colour (although the latter factor may be negligible, as previously discussed). Beetle colour is relevant to only one aspect of the beetles' thermal biology, the absorption of visible radiation. Other factors, where colour is irrelevant, predominate. Nevertheless, colour can be important where inputs of energy from direct solar radiation predominate and other factors, like wind speed, are minimised. Thus, in answer to the question regarding differential heating effects in beetles under visible or infrared radiation, one must conclude that species differences are not apparent in infrared conditions, whereas species differences are apparent under visible radiation, in limited circumstances. Lastly, differences in elytral temperatures between species do not result in differences in thoracic or abdominal temperatures.

CHAPTER THREE

COMPARATIVE BEETLE TEMPERATURES: FIELD EXPERIMENTS

INTRODUCTION

In its natural habitat, an active beetle exchanges heat with its environment via radiation, convection and conduction. The results of the previous chapter show that beetle colour affects only the absorption of visible incident radiation. In addition, differences in beetle temperatures (resulting from differential absorption of visible radiation by black or white colours) occur only at low wind speeds. Convective heat loss was shown to explain most of the variance in beetle body temperatures. These results could only be achieved under controlled laboratory conditions, which allow one to quantify separately the contributions of the various modes of heat exchange to the beetles' thermal budgets. However, it is also necessary to ascertain if beetles in their natural environment (a) respond to heating like the beetles in the "natural sand" experiments in Chapter 2, and (b) experience significant amounts of convective heat loss.

This chapter attempts to answer the following five questions: (i) What are the reflectances of: beetle elytra and abdomens; sands from the beetles' natural habitats; and sands used in the laboratory experiments in the previous chapter ? (ii) What effect does wind speed have on elytral temperatures of *O. bicolor* and *O. unguicularis* ? (iii) What are the temperatures of the elytra, thoraxes and abdomens of freshly killed beetles of both species in the field, when exposed to visible or infrared radiation ? (iv) What are the temperatures of tethered live beetles under similar conditions (including natural wind) ? (v) What are the temperatures of free-ranging beetles in the field ?

The results of this and the previous chapter are compared. However, an interpretation of these results is only achieved in the following chapter (Chapter 4), which examines the microclimatic conditions to which the beetles are naturally exposed during their diurnal activity periods.

EXPERIMENT (1): REFLECTANCES OF BEETLE CUTICLES AND DESERT SANDS

RATIONALE

In the previous chapter, laboratory experiments showed that reflected visible radiation from the sand significantly increased beetle temperatures, and that sand colour was more important to beetle temperatures than beetle colour was. However, the beach sand used in these experiments was far whiter than the desert sands to which *O. bicolor* and *O. unguicularis* are naturally exposed. It was thus postulated that differences in the colours of pale (Unjab, Rooibank) and dark (Gobabeb) desert sands (Fig. 2, Plate 2) may not be sufficient to have a significant effect on beetle temperature. In this experiment, reflectances (in the visible range) of desert and beach sands are measured, and their differential role in contributing to the reflected radiation component experienced by the two beetle species is discussed. Reflectances of beetle elytra and abdomens are also reported.

PROCEDURE

Beetles were collected from Rooibank (*O. unguicularis*) and the Skeleton Coast National Park (*O. bicolor*) in the Namib Desert (Fig. 2) and taken to the National Physics Research Laboratory of the Council for Scientific and Industrial Research (CSIR) in Pretoria. Sand samples were collected from each of the above sites, as well as Gobabeb, the Kalahari Gemsbok Park (dark red sand) and a beach on the Cape Peninsula (Scarborough). Beetle and sand reflectances were measured with an apparatus which was modified from equipment originally designed to measure the reflectance of small diamonds (Fig. 9). Measurements of the spectral reflectances of sand samples and wax blooms in five other species of Namib tenebrionids were previously calculated with the same apparatus by McClain *et al.* (in prep.). However, the glass lenses used by these authors to focus the light beam were removed in the present study, and replaced by a series of concave and convex mirrors. This allowed measurements to be taken at shorter wavelengths, since glass lenses absorb most of the ultraviolet radiation. An attempt was made to measure reflectances in the infrared

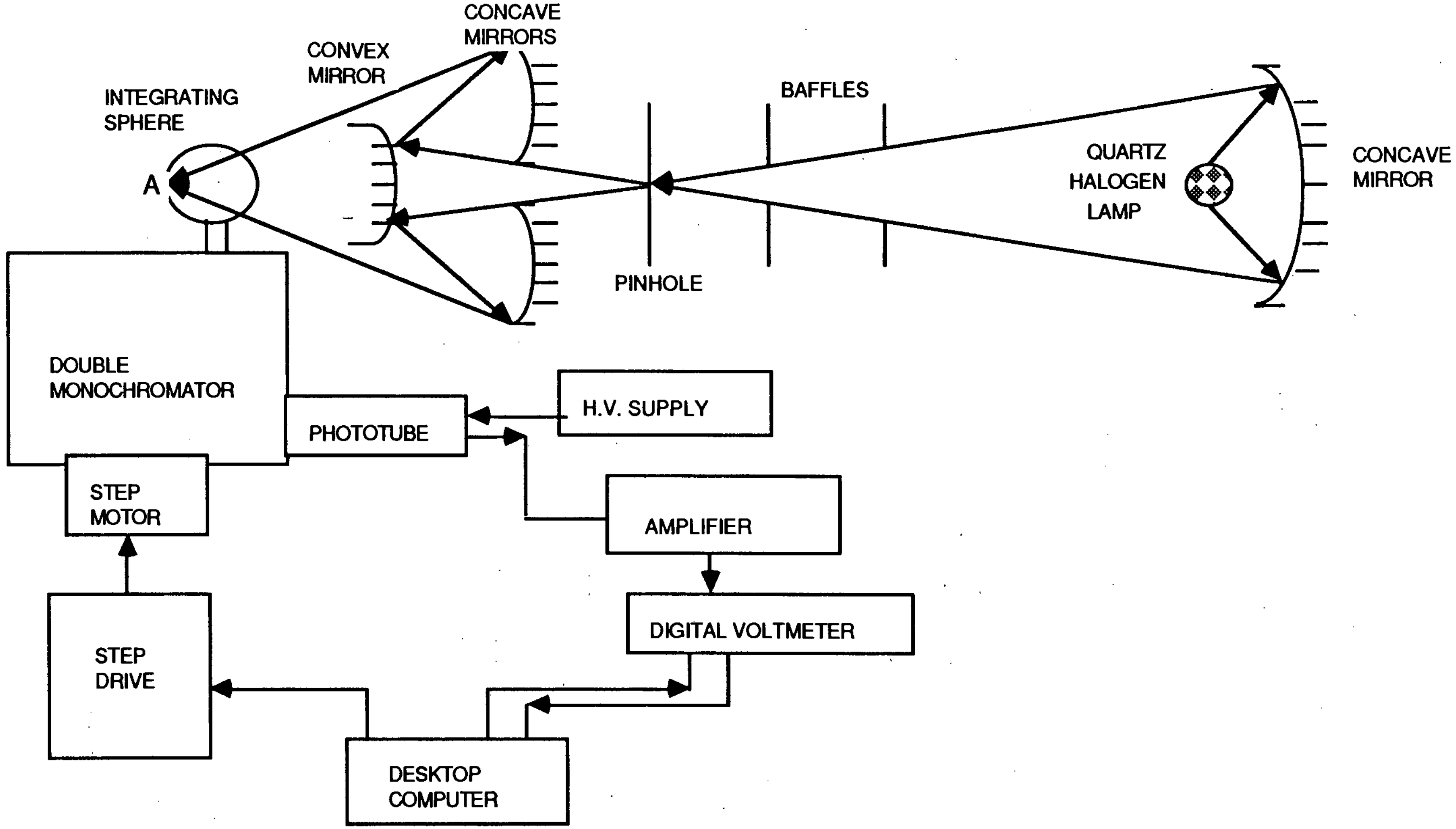


Fig.9. Schematic diagram of the equipment used to measure beetle and sand reflectances. Live beetles and sand samples were placed at position A on the integrating sphere.

region, but limitations of the spectrophotometer prevented this. The remaining equipment and method of calculating the spectral reflectances of beetle cuticles and sand samples are described in detail by McClain *et al.* (in prep.). However, the procedure of the present study differed in two further respects: spectrophotometric measurements were made between 320-800 nm (instead of 380-750 nm), and live beetles were used.

Spectral reflectances were measured for the elytra of four individuals of each species, and the ventral abdominal regions of two individuals of each species. One reflectance profile was measured for each of the five sand samples.

RESULTS

Reflectance profiles for the two beetle species and the five sand samples are shown in Figs. 10 and 11 respectively. Standard deviations of the beetle data ranged between 0.21-9.17 (*O. bicolor*) or 0.13-6.60 (*O. unguicularis*), and are not included in Fig. 10. Reflectances of the white elytra of *O. bicolor* increase from 23 % at 320 nm to a maximum of 78 % at 790 nm. The black elytra of *O. unguicularis* show a flat reflectance profile between 320-800 nm, and reflectance values lie between 4-5 % in this range. Profiles of the black abdomens of both species are similar to the profile of the *O. unguicularis* elytra, showing a slight increase at the longest wavelengths. Reflectance values for the abdomen of *O. bicolor* lie between 4-5 % from 350-750 nm, reaching a maximum of 7 % at 800 nm. The abdomen of *O. unguicularis* reflects 3 - 5 % between 320-800 nm, reaching a maximum of 5 % at 800 nm.

Sand reflectances also increase with increasing wavelength (Fig. 11). Beach sand, which appears visibly lighter than the other sand samples, reaches a peak reflectance of 45 % at 790 nm. Reflectance values increase most rapidly (5-25 %) between 320-370 nm. The remaining profile shows a relatively constant increase throughout the visible range. This profile is predictable from the white appearance of the sand. The reflectances of the desert sands are similar to one another. Values increase most between 520- 600 nm in all four profiles. Peaks are also reached in the longer wavelengths (780-790 nm), with Kalahari sand being the most reflective (max. 33 %), followed by Rooibank sand (30 %), Gobabeb sand (26 %), and Unjab sand (max. 22 %).

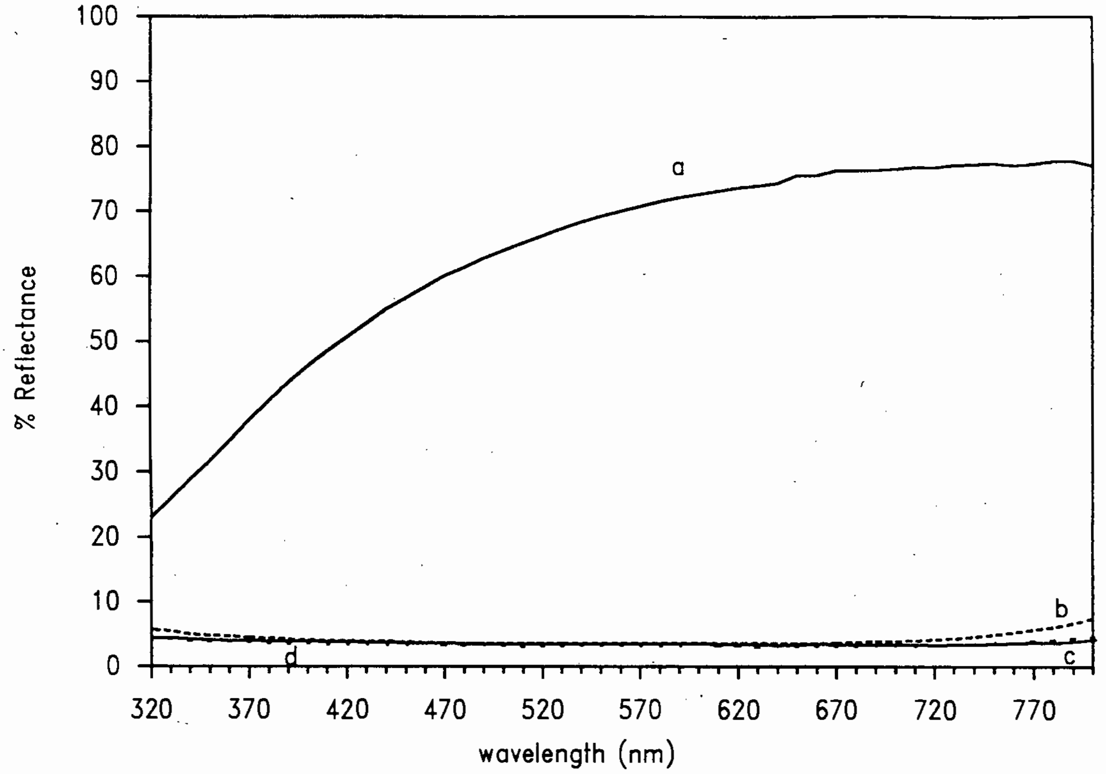


Fig. 10. Reflectance profiles of a) *Onymacris bicolor* elytra —, b) *O. bicolor* abdomen ---, c) *O. unguicularis* elytra — and d) *O. unguicularis* abdomen — —.

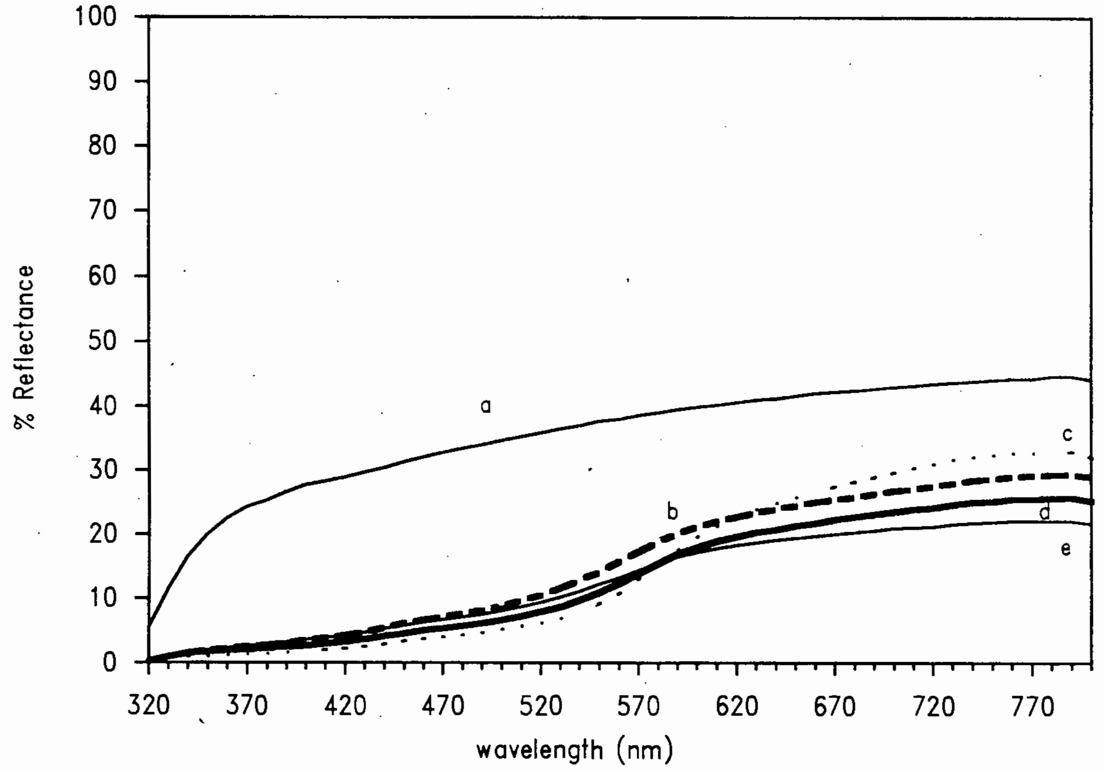


Fig. 11. Reflectance profiles of the five sand types used during laboratory and field experiments. a) Beach —, b) Rooibank ▬ ▬, c) Kalahari ----, d) Gobabeb ▬, e) Unjab —.

However, below 600 nm, the situation is reversed, and Rooibank sand proves the most reflective, followed by Unjab sand, Gobabeb sand and then Kalahari sand. Although the reflectances of the desert sands do not differ by more than 12 % at any wavelength, the visible appearances of the sands differ markedly (Plate 2). Kalahari sand is dark red (which explains its higher reflectance in the longer wavelengths), Gobabeb sand is a paler red, Rooibank sand is a pale fawn colour, and Unjab sand is slightly paler than Rooibank sand. It was thus expected that Rooibank and Unjab sands would have flatter profiles with higher values in the visible range than the other two sands, but the curves are not flat and the pale sands show higher reflectances only below 580 nm. However, the differences between the two pale sands and the two darker sands are never larger than 5 % in this range.

Plate 2. Three different desert sands: Unjab sand from the Skeleton Coast (left), Kalahari sand (right) and Gobabeb sand from the central Namib (background).

DISCUSSION

Reflectances of black insect cuticles presented here are in close accordance with those in the literature. The black elytra of *O. unguicularis* and the black abdomens of both *O. unguicularis* and *O. bicolor* reflected between 3-5 % of visible radiation. Reflectance values of 2-5 % have been reported for black insect cuticles by Henwood (1975b), Willmer & Unwin (1981) and McClain *et al.* (1986). In the present study, the white elytra of *O. bicolor* reflected between 23 % (380 nm) and 78 % (790 nm). The latter value is similar to the reflectance of 79 % quoted for *O. bicolor* by Edney (1971b).

These results are all expected, and emphasize that white elytra do gain less energy from visible radiation (in still conditions), and that reflected visible radiation from the sand will affect the black abdomens of both species similarly. It could be argued that the white elytra, which extend to the lateral parts of *O. bicolor*, may reflect a significant amount of reflected visible radiation from the sand, thereby reducing heat gain from this source. However, experiment (2) in Chapter 2 showed that both *O. bicolor* and *O. unguicularis* are affected similarly by a reflected radiation component from the substratum.

Table 8 shows that the reflectance results for Gobabeb and Rooibank sands compare favourably with those available in the literature. Gobabeb and Kahane sand reflectances may be directly compared because the Kahane site is very close to Gobabeb and the sands do not differ visibly. Close agreement between the Gobabeb sand reflectances measured by the present study, and by Savage *et al.* (1984), render the higher values obtained by McClain *et al.* (in prep.) questionable.

Table 8. Reflectances of desert sands.

Sand type	Wavelength (nm)	% Reflectance	Authors
Gobabeb	400	2.8	present study
	720	24.2	"
	400	11	McClain *et al.* (in prep.)
	720	35	"
Kahane	400	5	Savage *et al.* (1984)
	720	20	"
	daylight	20	Nott & Savage (1985)
Rooibank	400	4.2	present study
	720	28.2	"
	400	7	Savage *et al.* (1984)
	720	29	"
	daylight	24	Nott & Savage (1985)

As shown in Fig. 11, the reflectances of Rooibank, Unjab and Gobabeb sands differ minimally in the visible range. The much higher reflectance of the white beach sand explains why beetle temperatures were significantly affected by differences in sand colour in experiment 2 (Chapter 2). However, in the light of the similarity amongst the reflectances of the three types of desert sands, it seems unlikely that any difference exists in the proportion of reradiated infrared or reflected visible radiation experienced by beetles exposed to the three sand types.

EXPERIMENT (2): TEMPERATURES OF BLACK AND WHITE ELYTRA

RATIONALE

Although black insects have a much higher absorbance in the visible range than white insects (experiment 1), a lot of the heat absorbed at the surface of a black insect may be reradiated or lost by convective heat loss. Digby (1955) found that naturally dark insects had higher temperatures before they were painted black, owing to a deeper level of penetration of radiant energy in the unpainted insects. In addition, conduction of heat from surrounding parts of an insect's body may override the differential heating effects caused by colour variations in the elytra. Thus, any reduced temperatures experienced by *O. bicolor* owing to its white elytra may be negated by conducted heat from its black head, thorax and abdomen. This complicates the determination of the effects of colour alone on beetle temperatures.

In this experiment, the elytra were removed from freshly killed beetles, to determine the temperatures reached by isolated elytra, and the effect of forced convection on elytral temperatures was determined.

PROCEDURE

The elytra of *O. bicolor* and *O. unguicularis* were removed from freshly killed beetles of similar sizes. A 30 Ga Type T thermocouple was secured to the upper surface of one elytron of each species by a droplet of wax (which covered ± 5 % of the elytron surface). Elytra were then suspended side by side, by fine hair, and placed about 30 cm above the ground, in natural sun and wind conditions, at the field station at Gobabeb. Temperatures were recorded every 0.25 s by two Bat-12 (Bailey Instruments Inc.) digital thermocouple readers, connected to a BBC desktop computer. Wind speed was monitored with a Mike Cotton Systems (MCS, Cape Town) 101 field logger and an MCS 177 cup anemometer, placed adjacent to the elytra. The minimum measureable wind speed for this anemometer is ± 0.2 m s^{-1}. Ambient temperature was measured with a white tipped 23 Ga Type T thermocouple, connected to an analog-digital (A/D) converter and Radio Shack (TRS-80 Model 100) field computer. Temperature elevations of elytra were calculated by subtracting air temperature readings from elytral temperatures. The temperature elevations of the elytra of both species, at five different wind speeds, were then compared.

RESULTS

Temperature elevations reached by the white and black elytra of *O. bicolor* and *O. unguicularis* respectively are shown in Fig. 12. Figures in parentheses refer to the number of experimental runs at each wind speed, not the different number of elytra used. Elytra were removed from one beetle of each species, and had masses of 0.029 mg (*O. bicolor*) and 0.031 mg (*O. unguicularis*).

Fig. 12 shows that differences between the two elytra diminish with increasing wind speed. However, elytral temperatures of *O. unguicularis* were significantly higher than *O. bicolor* at all wind speeds (t tests, $p<0.05$), and increasing wind speeds significantly decreased temperature elevations in both species (ANOVA, $p<0.05$). Temperature elevations at 0 and 1 m s^{-1} were higher than those at 2,3, and 4 m s^{-1} in *O. unguicularis*, whereas temperatures at 0 m s^{-1} were higher than those at 1 m s^{-1} and above in *O. bicolor* (Tukey's test). The elytra of *O. unguicularis* maintained a positive temperature elevation at all wind speeds, whereas the elytra of *O. bicolor* maintained temperatures below ambient at wind speeds over 1 m s^{-1}. This result is difficult to explain. It is unlikely that the thicker gauge of thermocouple used to measure air temperature was responsible for conducting heat to the thermocouple junction (thereby maintaining higher air temperatures), considering that the thermocouple was well insulated throughout its length. A more likely explanation is that the calibration of the A/D converter - Radio Shack system used to measure air temperature was a fraction of a degree inaccurate when compared with the Bailey-Bat - BBC system used to measure elytral temperatures. Nevertheless, it seems that the black elytra of *O. unguicularis* were more affected by wind speed: between 0-4 m s^{-1}, average temperature elevations decreased by 6.2 °C, whereas *O. bicolor* showed a decrease of only 1.9 °C.

DISCUSSION

As was found in experiment (1), the absorption of incident radiation by beetle elytra is affected by colour. The present experiment has confirmed that the greater absorbance in the visible range of black elytra results in black elytra reaching higher temperatures than white elytra, especially at low wind speeds. In still wind conditions, black elytra can be 5 °C warmer than white elytra (Fig. 12). As wind speed increases, differences between black and white elytra diminish, but black elytra are

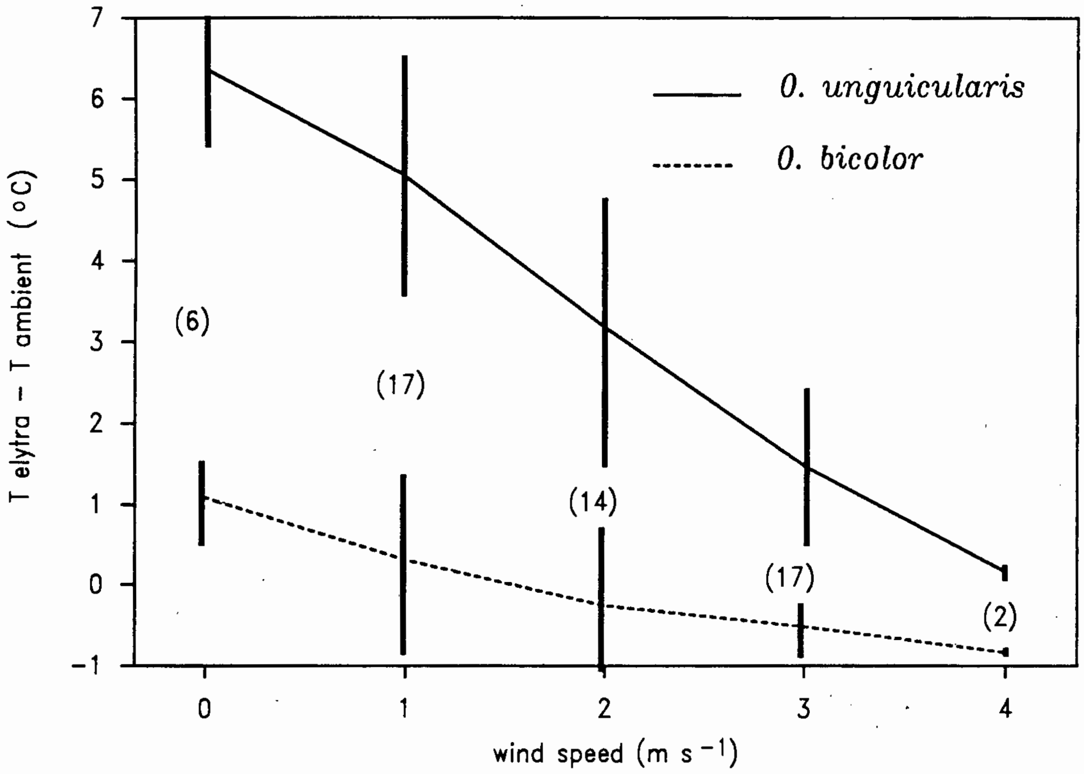


Fig. 12. Effect of wind speed on the difference between elytral temperature and air temperature in two species of Namib tenebrionids. Figures in parentheses indicate the number of experimental runs at each wind speed. Vertical bars indicate one standard deviation above and below the mean.

still significantly warmer at wind speeds up to 4 m s^{-1}. Forced convection does, however, affect black elytra more than white elytra.

Large temperature differences at the surfaces of elytra may not necessarily result in large temperature differences below the elytra. Firstly, if a large proportion of absorbed heat is lost by reradiation and convection in black elytra, less will be available to penetrate the cuticle into the beetle's abdomen. Secondly, the insides of *O. bicolor* 's white elytra are lined with a brown chitinous layer, and any radiation which does penetrate the cuticle may be effectively absorbed by this layer. Thirdly, a sub-elytral air space exists between the beetle's abdomen and its elytra in these tenebrionid beetles, and as suggested by Cloudsley-Thompson (1964) and Slobodchikoff & Wismann (1981), this air space may act as a thermal buffer, owing to the low conductivity of air. These effects are tested in experiments (3) and (4), which measure the sub-elytral, thoracic and abdominal temperatures of beetles under varying conditions of radiative, conductive and convective heat exchange.

EXPERIMENT (3): TEMPERATURE TRANSIENTS OF DEAD BEETLES

RATIONALE

The temperature dynamics of dead beetles exposed to infrared radiation, and simulated natural radiation conditions, were determined in the previous chapter. In this experiment, temperatures of dead beetles were measured under both visible and infrared conditions in the field. A comparison of these results with those reported in Chapter 2 provides useful information about the extrapolation of the laboratory results to the field.

Owing to the negligible contribution of metabolic heat production and evaporative water loss to the thermal budgets of small insects (Parry 1951, Digby 1955), temperature measurements should differ minimally between dead and live beetles. Nonetheless, experiments were repeated with live beetles to test these findings (see experiment 4). The use of dead beetles in experiments has the advantage that equilibrium temperatures may be directly recorded. These equilibrium temperatures can then be compared with those calculated by the method of Bakken (1976b).

PROCEDURE

O. bicolor and *O. unguicularis* were collected at the Unjab River and at Rooibank respectively (Fig. 2), and were kept in terraria at Gobabeb until used. Beetles were weighed, killed by freezing, and then secured posteriorly to a short plastic rod. Two Type T thermocouples (23 Ga) were implanted in each beetle, one in the prothorax (henceforth referred to as the thorax) and one in the sub-elytral air space. The thermocouples were held in place by a droplet of cyanoacrylate adhesive. Experiments were always conducted with two beetles (one of each species) placed 3 cm apart, and approximately 5 mm above the ground (this approximates their natural position). Ambient temperature was measured with a white tipped 23 Ga Type T thermocouple placed next to the beetles, at the same height above the ground. Temperatures were recorded every 4 s from two Bailey Bat-12 digital thermocouple readers. Each reader was connected to a five channel thermocouple switching device.

Micrometeorological conditions at the base of dunes and adjacent to the beetles were monitored during experiments. An MCS cup anemometer, connected to an MCS 101 field logger, was placed at beetle height to monitor wind speed. A Wallac oy thermo-anemometer hand-held at beetle height provided more sensitive wind speed data. Direct and reflected radiation were measured with a double pyranometer (Middleton & Co.) and a Fluke 73 digital multimeter, and infrared radiation from the ground (^{o}C) was measured with a Barnes infrared thermometer.

Owing to the difficulty of separating the various components of heat transfer under field conditions (as was achieved in the laboratory), experiments were conducted under only two different thermal regimes: (i) visible and (ii) infrared radiation. (i) In the visible radiation set of experiments, beetles were allowed to equilibrate to ambient temperatures in the shade on cool sand. Thereafter, they were placed on to hot sand in sunlight for 12 min. Following this, they were returned to the shade and allowed to cool for 12 min. They were then returned to sunlight and hot sand for a final 12 min. These experiments thus measured temperature transients of beetles subjected to visible radiation from above, reflected radiation from the sand, infrared radiation and conduction from the hot sand, and convection heat loss (*i.e.* their natural thermal environment).

(ii) In the infrared set of experiments, beetles were allowed to equilibrate in the shade on cool sand, and were then placed on to hot, shaded sand. This sand had previously been exposed to sunlight, but was then shaded for the duration of the experiment. Temperatures were measured for 7 min., and then beetles were returned to cool sand and shade for 7 min. Thereafter, beetles were replaced on to hot, shaded sand for a final 7 min. The radiation impinging on the beetle was thus predominantly infrared, as beetles were shaded from visible radiation by a white styrofoam board (55 x 55 cm). Beetles also experienced conduction from the hot sand, and convective heat loss, as in the previous experiment. During experiments, the sand temperatures remained sufficiently unchanged to allow beetles to warm to temperatures significantly greater than air temperature.

Experiments were always conducted in the beetles' natural habitats (*i.e.* at the base of dune slipfaces), between 09h30 and 15h00 under cloudless conditions. Both sets of experiments were repeated four times at Gobabeb (on the dark sand) and four times at Rooibank (on the pale sand). A total of eight fresh pairs of beetles was used for 16 experiments. Beetles in an experimental pair were chosen for similarity in mass, the average difference being 65 mg.

As described in Chapter 2, equilibrium temperatures and time constants were calculated from the temperature transient, using the method of Bakken (1976b). However, temperature equilibria were also estimated directly from temperature transients, which all ran to equilibrium temperatures.

RESULTS

(i) Visible radiation

The additional heat absorbed by the black elytra of *O. unguicularis* results in sub-elytral temperatures which are significantly warmer than those under the white elytra of *O. bicolor* (Fig. 13, Table 9). Henceforth, "sub-elytral" temperatures will be referred to as "elytral temperatures". *O. unguicularis* elytra were, on average, 2.5 °C warmer than *O. bicolor* elytra. Thoracic temperatures of the two species did not differ significantly (Fig. 13, Table 9). The white elytra of *O. bicolor* averaged only 0.5 °C less than the black thorax, but this difference was not significant (t-test, $p<0.05$). Equilibrium temperatures averaged 41.2 - 41.7 °C for *O. bicolor*, and

42.2-43.7 °C for *O. unguicularis* (calculated from the temperature transient by the method of Bakken 1976b). Average equilibrium temperatures calculated directly from the temperature transient differed by an average of +0.3 °C from those calculated above.

The effect of wind speed on equilibrium temperatures could not be calculated, because wind speeds fluctuated too much during the experiments for a meaningful average to be chosen. However, wind speeds were generally very close to 1 m s^{-1}. Readings from the cup anemometer compare well with those taken by the hot wire anemometer, since readings seldom differed by more than 0.5 m s^{-1}. Substratum type had no significant effect on either elytral or thoracic temperatures, and as a result, the species by substratum interactions were also not significant (Table 9).

The time constant for the elytra of *O. unguicularis* was significantly shorter than for *O. bicolor*, whereas time constants of the thoraxes were not significantly different between species (Table 10). Time constants were shorter on Gobabeb sand for both elytra and thoraxes, but these differences were not significant at the $p=0.05$ level (Table 10).

(ii) Infrared radiation

Equilibrium temperatures of elytra and thoraxes of both species, on both substrata, were statistically indistinguishable from air temperatures (t-tests, $p<0.05$). Temperatures reached by *O. bicolor* were not significantly different from those of *O. unguicularis* (Fig. 14, Table 11). Substratum type had a significant effect on both elytral and thoracic temperatures (Table 11). Beetles were warmer on Rooibank than on Gobabeb sand. This was not due to higher sand temperatures at Rooibank, since Gobabeb and Rooibank sand temperatures, measured with the infrared thermometer, did not differ significantly (t-tests, $p<0.05$). Both species were affected similarly by substratum, as shown by the species by substratum interactions, which were not significant (Table 11).

Average equilibrium temperatures were 36.7-37.1 °C for *O. bicolor* and 37.0-37.2 °C for *O. unguicularis*. During experiments, ambient temperatures averaged 38.5 °C over Gobabeb sand and 34.7 °C over Rooibank sand, whereas sand temperatures averaged 39.5 °C for Gobabeb sand and

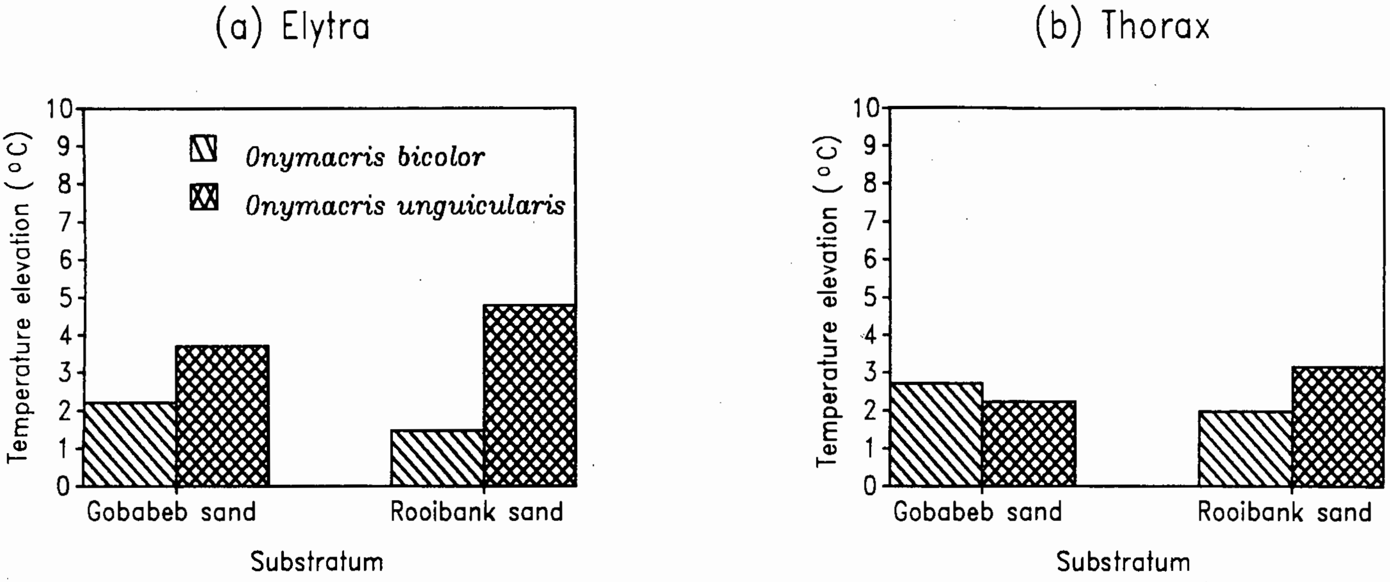


Fig. 13. Equilibrium temperatures of two Namib tenebrionids exposed to natural radiation in the field. Temperature elevation is the difference between beetle temperature and air temperature. Substratum is the independent variable. (a) Elytral temperature and (b) Thoracic temperature.

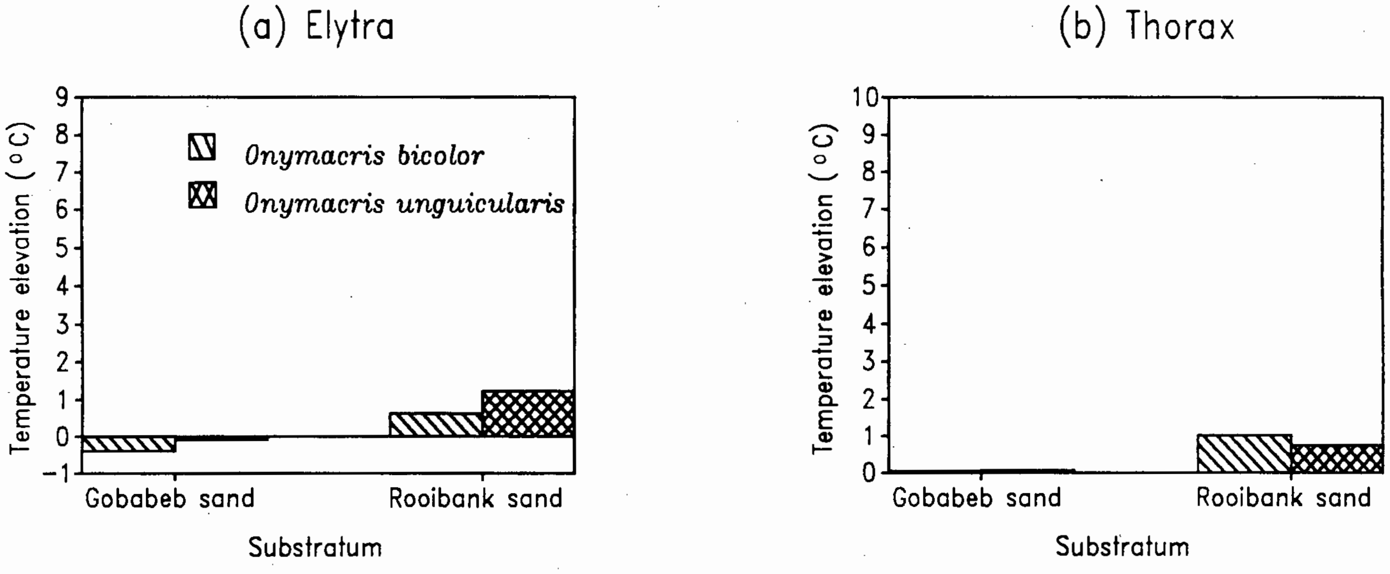


Fig. 14. Equilibrium temperatures of two Namib tenebrionids exposed to infrared radiation in the field. Temperature elevations are as defined in Fig. 13. Substratum is the independent variable. (a) Elytral temperature and (b) Thoracic temperature.

Table 9. Analysis of variance for elevation of (a) elytral and (b) thoracic temperature above air temperatures during field experiments with dead beetles, under visible radiation. Main effect means and standard errors (S.E.M.) are presented below.

	(a) Elytra			**(b) Thorax**		
Factor	F	p>F	r^2	F	p>F	r^2
Main Effects						
Species	13.21	**0.002**	0.423	1.19	0.290	0.055
Substratum	0.05	0.829	0.002	0.01	0.936	<0.001
Interactions						
Species X Substratum	1.71	0.210	0.055	3.61	0.075	0.165

	(a) Elytra		**(b) Thorax**	
	Main Effect Means	S.E.M.	Main Effect Means	S.E.M.
Species				
O. bicolor	1.82	0.51	2.31	0.28
O. unguicularis	4.33	0.44	2.79	0.36
Substratum				
Gobabeb	2.85	0.44	2.50	0.29
Rooibank	3.26	0.73	2.56	0.34

Table 10. Analysis of variance for time constants (s) for warming of **(a)** elytral and **(b)** thoracic temperatures during field experiments with dead beetles, under visible radiation. Main effect means and standard errors (S.E.M.) are presented below.

	(a) Elytra			**(b) Thorax**		
Factor	F	p>F	r^2	F	p>F	r^2
Main Effects						
Species	5.55	**0.029**	0.199	0.26	0.790	0.003
Substratum	3.54	0.075	0.127	0.43	0.525	0.020
Interactions						
Species X Substratum	0.21	0.656	0.008	1.70	0.207	0.080

	(a) Elytra		**(b) Thorax**	
	Main Effect Means	S.E.M.	Main Effect Means	S.E.M.
Species				
O. bicolor	196	16	173	15
O. unguicularis	151	13	167	14
Substratum				
Gobabeb	156	17	163	16
Rooibank	191	13	177	12

Table 11. Analysis of variance for elevation of (a) elytral and (b) thoracic temperature above air temperatures during field experiments with dead beetles, under infrared radiation. Main effect means and standard errors (S.E.M.) are presented below.

	(a) Elytra			**(b) Thorax**		
Factor	F	p>F	r^2	F	p>F	r^2
Main Effects						
Species	2.95	0.102	0.070	0.22	0.653	0.008
Substratum	19.21	**<0.001**	0.455	9.07	**0.007**	0.318
Interactions						
Species X Substratum	0.35	0.567	0.008	0.31	0.590	0.011

	(a) Elytra		**(b) Thorax**	
	Main Effect Means	S.E.M.	Main Effect Means	S.E.M.
Species				
O. bicolor	0.06	0.24	0.50	0.27
O. unguicularis	0.57	0.26	0.41	0.17
Substratum				
Gobabeb	-0.24	0.13	0.07	0.11
Rooibank	0.94	0.25	0.88	0.24

40.7 °C for Rooibank sand. The average equilibrium temperatures calculated for both species by the method of Bakken (Table 11) differ by an average of 0.2 °C from those estimated directly from the temperature transients.

DISCUSSION

(i) Visible radiation

In natural field conditions, the black elytra of *O. unguicularis* result in sub-elytral temperatures which are 2.5 °C warmer than those of *O. bicolor*. This value differs little from the value of 4 °C calculated in experiment 4, Chapter 2, bearing in mind that the variations in wind speed produced in the laboratory were not present in the field. Both values lie within the range of 1-4 °C, reported by other studies, for the difference in temperature between black and white tenebrionids (Table 1, Chapter 1). In experiment (2), it was shown that black elytra are about 4.5 °C warmer than white elytra, at a wind speed of 1 m s^{-1}, whereas in this experiment, the average difference between sub-elytral temperatures of beetles was about 2.5 °C. This confirms the assumptions that black cuticles may loose a substantial amount of absorbed heat to convection, and that the sub-elytral air space may act as a thermal buffer.

Variations in elytral colour explained 42 % of the variance in elytral temperature in the field, but only 9 % in the laboratory. Once more, this may be due to the lack of wind speed data for the field, as the contribution of wind to beetle temperatures could not be analysed. Elytral colour did not affect thoracic temperatures, which were similar in both species. This confirms the results of the laboratory experiments. Gobabeb and Rooibank sands had no significant effect on beetle temperatures. This is to be expected, considering that both sands have similar reflectances in the visible range (experiment 1).

Equilibrium temperatures (calculated by the method of Bakken 1976b) reached by both species ranged between 41 and 44 °C. These experiments confirmed that equilibrium temperatures calculated by this method differ, on average, by less than 0.5 °C from equilibrium temperatures estimated directly from temperature transients. The equilibrium temperatures calculated in this experiment are the operative temperatures that beetles would reach if they were active for indefinite periods, at wind speeds of about 1 m s^{-1}, under insolation of 996 W m^{-2}, with no access to shade and no behavioural thermoregulation. These equilibrium temperatures are also about 10 °C higher than the temperatures of free-ranging beetles, of the same species, measured by Seely *et al.* (1988). Owing to the minimal dune vegetation in the habitats of both species, beetles must either: (a) be active at ambient temperatures below 39 °C (this was the average ambient temperature during the visible radiation experiments), or (b) be active at wind speeds over 1 m s^{-1}, or (c) employ some method of behavioural thermoregulation, or (d) employ some combination of factors (a)-(c). These possibilities are discussed further in Chapter 4.

The time constant for warming of elytra was shorter for *O. unguicularis* but did not differ between species for thoraxes, and did not differ on the two substrata. This supports the laboratory results. However, time constants in the field were 27-72 s longer than in the laboratory. This means that the times to lethal temperature calculated in Fig. 8, Chapter 2, are underestimations. Time constants calculated from live beetles in the field are presented in the following experiment, and these are also 23-82 s longer than those in Chapter 2. Nevertheless, the equilibrium temperatures reached by beetles were 4-8 °C lower than the maximum temperatures reached by beetles in a laboratory gradient, as found by Seely *et al.* (1988). Thus, beetles would not be in danger of overheating even if they did reach equilibrium temperature in the radiation conditions of this experiment. However, it is not certain how long a beetle can be exposed to its maximum temperature without suffering some physiological heat damage.

(ii) Infrared radiation

Both the field and laboratory results confirm the findings of Parry (1951) and Digby (1955), that infrared radiation contributes minimally to the thermal budgets of small arthropods. Equilibrium temperatures of beetles in the field were indistinguishable from ambient temperatures, thus *O. bicolor* was not warmer than *O. unguicularis*, as was found in the laboratory. However, beetle temperatures were higher on Rooibank than on Gobabeb sand. This effect cannot be explained by differences in sand temperature, and it seems unlikely that the emissivities of the sands differ, owing to the similar results shown by the infrared thermometer for both sands. As found in the visible radiation experiments, equilibrium temperatures calculated by the method of Bakken and those estimated directly off temperature transients, differed by a negligible amount. This supports the use of Bakken's method of determining equilibrium temperatures from transients which do not reach equilibrium.

EXPERIMENT (4): TEMPERATURE TRANSIENTS OF LIVE BEETLES

RATIONALE

Although metabolic heat production and evaporative water loss may have little effect on beetle temperatures, temperature transients were remeasured with live beetles in the field. The primary reason for this was to ascertain if the physical properties of dead beetle cuticles differed from those of live beetles, and if so, did this difference affect heat exchange in dead beetles?

PROCEDURE

O. bicolor and *O. unguicularis* were collected on the Skeleton Coast and at Rooibank respectively, and kept in terraria at Gobabeb until used. Beetles were weighed and secured posteriorly to a short plastic rod. Three 30 Ga Type T thermocouples were implanted in the beetle; one in the thorax, one in the sub-elytral air space, and one in the abdomen between legs two and three. Thermocouples were held in place by small droplets of wax. As in experiment (3), heating and cooling curves were conducted with beetles of each species placed 3 cm apart, and 5 mm above the sand. Ambient temperature was monitored by a white tipped 23 Ga Type T thermocouple placed adjacent to the beetles, whereas ground temperature was measured with a similar, unpainted thermocouple, placed just below the sand surface. Temperatures were recorded with an A/D converter and a field microcomputer (Radio Shack). Data were then downloaded onto a BBC desktop computer at the field station for further analysis. Wind speed was measured with the MCS field logger and anemometer as described in experiment (3).

Experiments were conducted under visible and infrared conditions, as described in experiment (3). However, beetle temperatures were not allowed to exceed 50 °C, and consequently heating transients under visible radiation conditions were often terminated before equilibrium temperatures were reached. All experiments were conducted in the field at Gobabeb, at the base of dune slipfaces. Experiments were run on three different sand types: Gobabeb, Unjab and Kalahari. The latter two sands were overlayed on the background Gobabeb sand for experimentation (Plate 2). During visible radiation experiments, 23 experiments were run on Gobabeb sand, 24 on Unjab sand and 6 on Kalahari sand. Under infrared conditions, 16 experiments were run on Gobabeb sand, 15 on Unjab sand and 5 on Kalahari sand. During some experiments, a shelter was built to keep wind off the beetles, as gusty conditions yielded data which were unrepeatable (Plate 3). Once again, beetles in an experimental pair were chosen for similarity in size, and their masses differed by an average of 59 mg. As previously described, equilibrium temperatures and time constants were calculated by the method of Bakken (1976b).

Plate 3. Equipment used to measure temperatures of live beetles in the field.

RESULTS

(i) Visible radiation

Elytral colour has a definite consequence for beetle temperature. Temperature elevations of the subelytral air spaces of *O. unguicularis* averaged 4.3 °C higher than for *O. bicolor* (Fig. 15, Table 12). It seems that this temperature difference may have contributed to increased temperatures in the thorax and abdomen of *O. unguicularis*, because these latter two temperatures were also significantly greater in *O. unguicularis* than in *O. bicolor*. Equilibrium temperatures reached by *O. bicolor* averaged 40.1-41.8 °C, and 43.0-45.4 °C for *O. unguicularis*. Wind speed significantly decreased equilibrium temperatures of only the elytra (Fig. 15). At a wind speed of 2 m s^{-1}, the thorax and abdomen of both species reached similar temperatures, although the elytra of *O. unguicularis* were still 3 °C warmer (Fig. 15). Equilibrium temperatures of the three segments did not differ significantly in *O. unguicularis*, whereas the abdomen of *O. bicolor* was significantly warmer than its thorax or elytra (Table 12). The white elytra of *O. bicolor* averaged only 0.2 °C less than the black thorax. Beetle temperatures were not affected by the different substrata, and no interactions of species with either wind speed or substratum had a significant effect on beetle temperature (Table 12), signifying that both species respond similarly to wind speed and substratum types. Interactions between wind speeds and substrata could not be statistically tested, owing to the lack of variation in wind speed encountered during Unjab and Kalahari sand experiments.

Neither species, wind speed nor substratum had any significant effect on time constants for warming of beetles (Table 13). The trends noted in the previous experiment, and in Chapter 2, are however borne out by the data in Table 13: the average time constant decreases with wind speed, and the time constant for the elytra of O. unguicularis is a little shorter than that of *O. bicolor*.

(ii) Infrared radiation

Beetle temperatures were statistically indistinguishable from air temperatures, except for the abdomen of *O. bicolor* and the elytra of *O. unguicularis*, which warmed significantly over hot sand (T-tests, $p<0.05$). Temperatures reached by the two species did not differ significantly (Table 14), although *O. bicolor* was always warmer at 0 m s^{-1} than *O. unguicularis* (Fig. 16). Equilibrium temperatures reached by the two species averaged 38.1-38.5 °C (*O. bicolor*) and 38.3-38.5 °C (*O. unguicularis*). Air temperature averaged 36.6 °C overall.

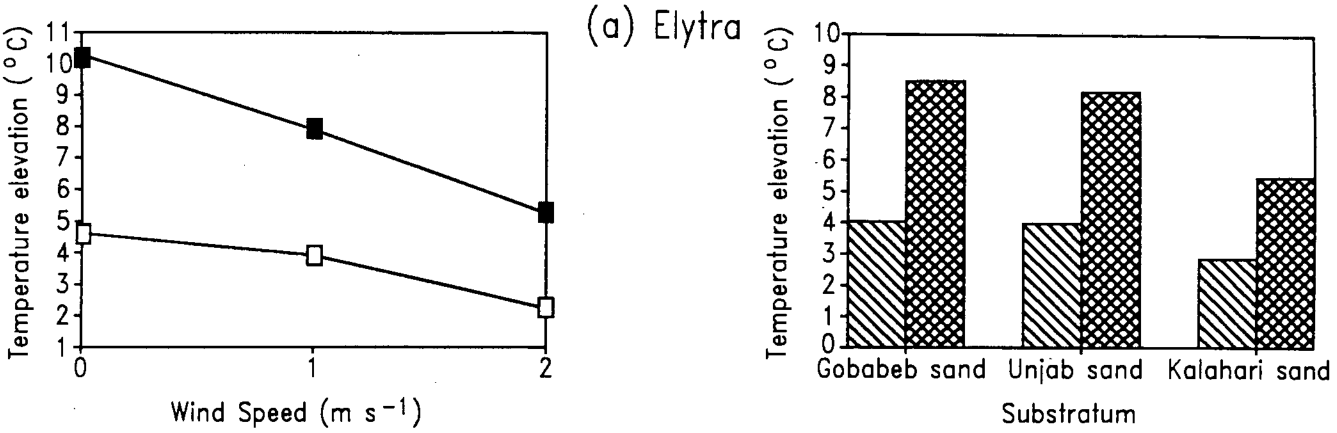
Equilibrium temperatures did decrease with increasing wind speed, but this effect was only significant for abdominal temperatures of pooled species (Fig. 16, Table 14). Owing to unbalanced sample sizes, the effect of wind speed was also tested with a non-parametric analysis of variance (*i.e.* Kruskall-Wallis, $p<0.05$), and the results were the same as those calculated in Table 14. Substratum type had a significant effect on elytral temperatures, which were similar on Gobabeb and Unjab sand, but lower on Kalahari sand. This was not due to decreased sand temperatures on Kalahari sand, because sand temperatures did not differ among the three substrata (ANOVA, $p<0.05$). As a result, sand temperature was not used as a covariate in the ANOVA tests in Table 14. Sand temperatures averaged 43.1 °C (Gobabeb sand), 44.7 °C (Unjab sand) and 42.3 °C (Kalahari sand).

DISCUSSION

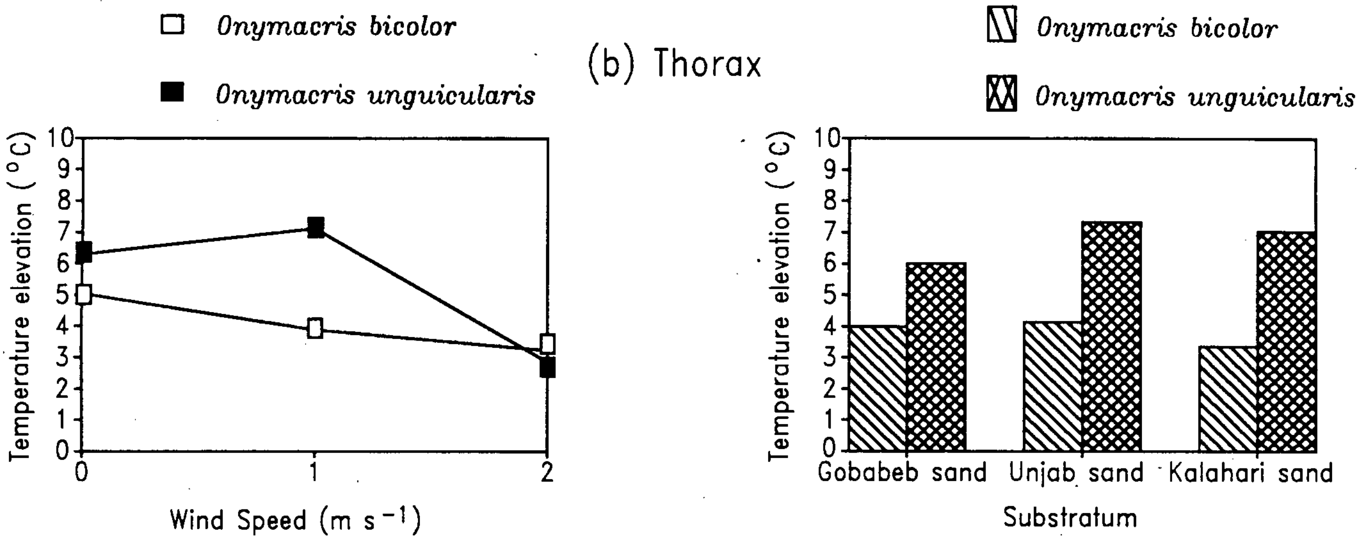
(i) Visible radiation

Elytral coloration has a definite consequence for beetle temperatures in the field. Variation in colour explains 34 % of the total variation in elytral temperatures, 18 % of thoracic temperature variation and 23 % of abdominal temperature variation. Although the thoraxes and abdomens of both species are black, it seems that reduced temperatures under white elytra serve to reduce overall temperatures in *O. bicolor*. However, the average difference in equilibrium temperatures of the two species is 3.5 °C, and this difference disappears at a wind speed of 2 m s^{-1} (Fig. 15), except for the elytra, which were always warmer in *O. unguicularis*. Thus, colour only affects beetle temperatures at wind speeds under 2 m s^{-1}. Although wind speed explained most of the variance in beetle temperatures in the laboratory experiments, wind speed in the field explained only 1-4 % of beetle temperature variation. This result must be interpreted with the following in mind: in the field, wind speed is not constant, and the wind speed data presented here are only estimations of

(a) Elytra



(b) Thorax



(c) Abdomen

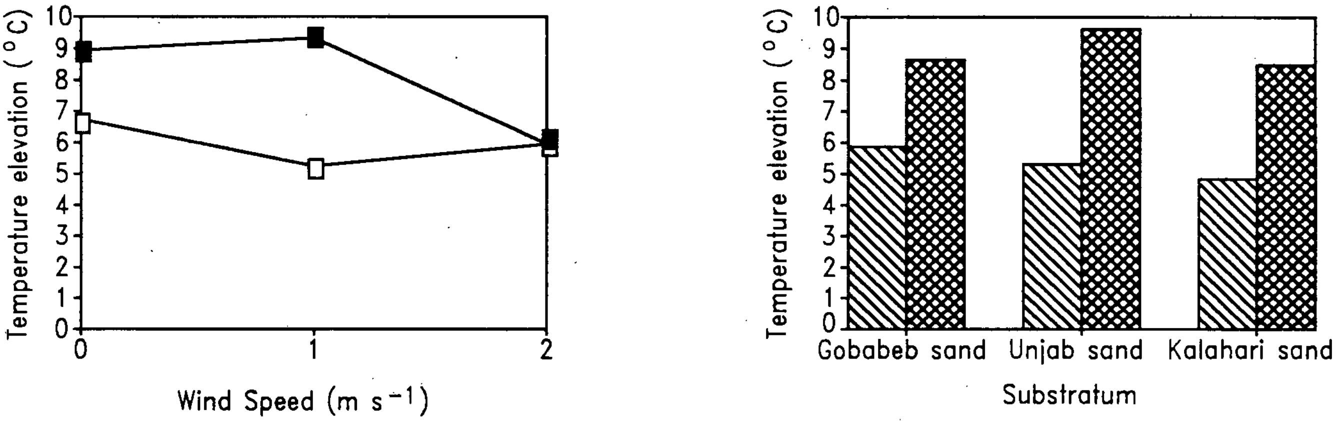
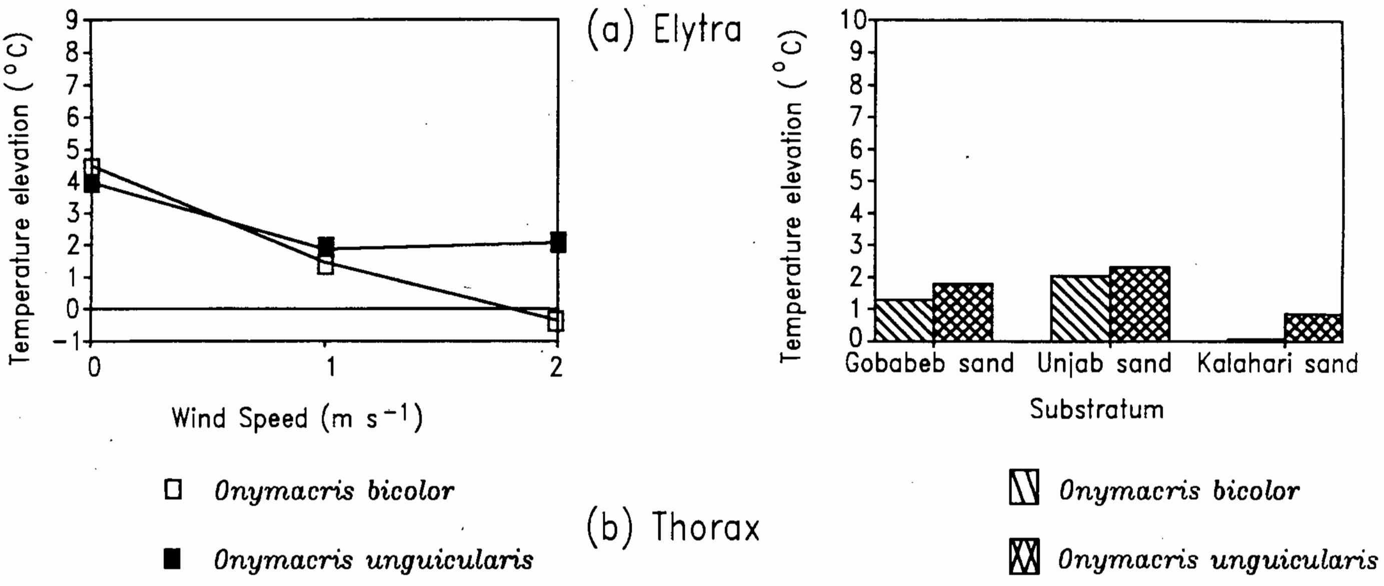
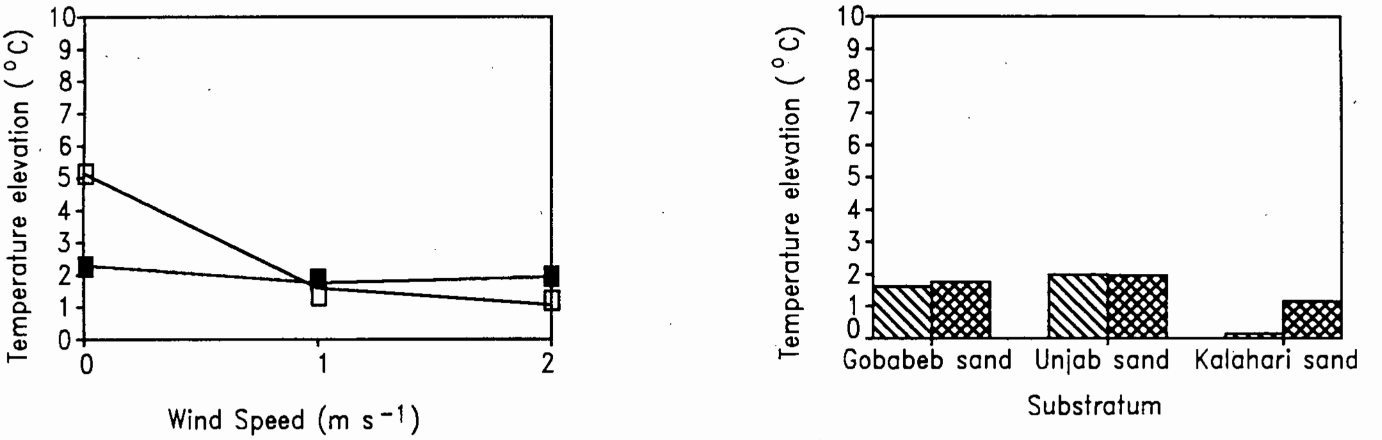


Fig. 15. Equilibrium temperatures of two live Namib tenebrionids exposed to natural radiation in the field. Temperature elevations are as defined in Fig. 13. Windspeed is the independent variable in the line graphs, whereas substratum is the independent variable in the histograms. (a) Elytral temperature, (b) Thoracic temperature and (c) Abdominal temperature.

(a) Elytra



(b) Thorax



(c) Abdomen

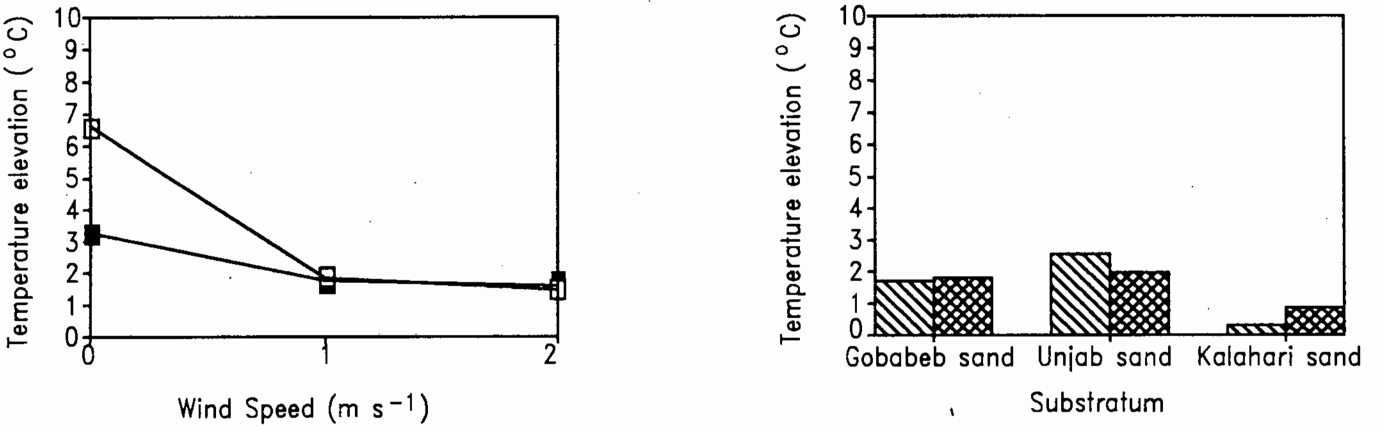


Fig. 16. Equilibrium temperatures of two live Namib tenebrionids exposed to infrared radiation in the field. Temperature elevations are as defined in Fig. 13. Windspeed is the independent variable in the line graphs, whereas substratum is the independent variable in the histograms. (a) Elytral temperature, (b) Thoracic temperature and (c) Abdominal temperature.

Table 12. Analysis of variance for elevation of (a) elytral, (b) thoracic, and (c) abdominal temperature above air temperatures during field experiments with live beetles, under visible radiation. Main effect means, standard errors (S.E.M.) and sample sizes (N) are presented below.

	(a) Elytra			**(b) Thorax**			**(c) Abdomen**		
Factor	F	p>F	r^2	F	p>F	r^2	F	p>F	r^2
Main Effects									
Species	51.70	**<0.001**	0.339	20.06	**<0.001**	0.179	25.06	**<0.001**	0.231
Wind Speed	3.12	**0.049**	0.041	1.08	0.345	0.019	0.51	0.604	0.009
Substratum	0.98	0.379	0.013	0.52	0.595	0.010	0.08	0.927	0.001
Interactions									
Species X Wind Speed	0.53	0.588	0.007	1.20	0.305	0.021	1.06	0.351	0.020
Species X Substratum	0.49	0.612	0.007	0.85	0.433	0.015	0.55	0.579	0.010

	(a) Elytra			**(b) Thorax**			**(c) Abdomen**		
	Main Effect Means	S.E.M.	N	Main Effect Means	S.E.M.	N	Main Effect Means	S.E.M.	N
Species									
O. bicolor	3.85	0.39	51	4.00	0.30	50	5.55	0.39	45
O. unguicularis	8.10	0.44	48	6.71	0.54	46	9.11	0.58	44
Wind Speed									
0	7.26	0.87	15	5.61	0.51	15	7.77	0.58	15
1	5.92	0.41	76	5.46	0.41	74	7.29	0.47	70
2	3.54	1.34	7	3.07	0.97	5	5.95	2.26	4
Substratum									
Gobabeb	6.26	0.55	44	4.98	0.45	43	7.27	0.51	42
Unjab	6.02	0.54	45	5.70	0.53	45	7.41	0.65	43
Kalahari	3.87	0.88	10	4.74	1.12	8	6.65	1.28	4

Table 13. Analysis of variance for time constants (s) for warming of (a) elytral, (b) thoracic, and (c) abdominal temperatures during field experiments with live beetles, under visible radiation. Main effect means and standard errors (S.E.M.) are presented below.

	(a) Elytra			**(b) Thorax**			**(c) Abdomen**		
Factor	F	p>F	r^2	F	p>F	r^2	F	p>F	r^2
Main Effects									
Species	0.31	0.588	0.003	0.93	0.349	0.010	1.85	0.177	0.021
Wind Speed	1.92	0.153	0.038	0.56	0.572	0.012	0.37	0.691	0.008
Substratum	1.73	0.183	0.034	0.15	0.859	0.003	0.80	0.454	0.018
Interactions									
Species X Wind Speed	0.42	0.663	0.008	0.68	0.508	0.015	0.46	0.631	0.011
Species X Substratum	0.26	0.772	0.005	0.15	0.863	0.003	0.15	0.857	0.003

	(a) Elytra		**(b) Thorax**		**(c) Abdomen**	
	Main Effect Means	S.E.M.	Main Effect Means	S.E.M.	Main Effect Means	S.E.M.
Species						
O. bicolor	175	12	147	8	191	9
O. unguicularis	168	16	161	11	210	10
Wind Speed						
0	201	14	167	15	207	13
1	174	12	155	8	200	8
2	103	28	129	39	183	25
Substratum						
Gobabeb	189	17	158	12	206	9
Unjab	168	12	155	8	198	11
Kalahari	108	23	121	23	167	29

Table 14. Analysis of variance for elevation of (a) elytral, (b) thoracic, and (c) abdominal temperature above air temperatures during field experiments with live beetles, under infrared radiation. Main effect means, standard errors (S.E.M.) and sample sizes (N) are presented below.

	(a) Elytra			(b) Thorax			(c) Abdomen		
Factor	F	p>F	r^2	F	p>F	r^2	F	p>F	r^2
Main Effects									
Species	1.47	0.231	0.021	0.12	0.738	0.002	0.28	0.602	0.004
Wind Speed	2.30	0.110	0.067	1.95	0.153	0.062	4.73	**0.013**	0.130
Substratum	3.62	**0.034**	0.106	1.61	0.209	0.051	2.60	0.084	0.071
Interactions									
Species X Wind Speed	0.52	0.596	0.015	1.32	0.297	0.042	1.22	0.303	0.034
Species X Substratum	0.09	0.910	0.003	0.17	0.847	0.005	0.30	0.740	0.008

	(a) Elytra			(b) Thorax			(c) Abdomen		
	Main Effect Means	S.E.M.	N	Main Effect Means	S.E.M.	N	Main Effect Means	S.E.M.	N
Species									
O. bicolor	1.50	0.31	32	1.63	0.26	32	1.94	0.29	32
O. unguicularis	1.95	0.23	32	1.78	0.21	32	1.79	0.19	32
Wind Speed									
0	4.23	0.26	2	3.72	1.41	2	4.96	1.66	2
1	1.67	0.20	58	1.67	0.17	58	1.81	0.17	58
2	0.86	1.21	2	1.50	0.42	2	1.55	0.06	2
Substratum									
Gobabeb	1.55	0.25	30	1.67	0.22	30	1.75	0.23	30
Unjab	2.18	0.31	28	1.96	0.28	28	2.26	0.28	28
Kalahari	0.45	0.41	6	0.66	0.25	6	0.60	0.23	6

the average wind speed during warming experiments. In addition, unbalanced sample sizes at the three different wind speeds skew the data towards 1 m s^{-1}, as sample sizes for this wind speed are over 5 times greater than for 0 and 2 m s^{-1} (Table 12). It follows from this that at an average wind speed of 1 m s^{-1}, beetle colour explains 18-34 % of the variation in beetle body temperature, and this figure may be as high as 42 %, as calculated in experiment (3).

Although all the previous experiments found that differences in elytral temperatures between species did not translate into higher temperatures elsewhere in *O. unguicularis*, the present experiment revealed that the additional heat absorbed by the black elytra of *O. unguicularis* may well result in increased temperatures throughout the beetle's body. A possible explanation is that in live beetles, circulating haemolymph in the abdomen is continuously exposed to the high temperatures in the sub-elytral air space, thereby warming the whole body. Nonetheless, these differences do disappear at a wind speed of 2 m s^{-1} (Fig. 15).

Once again, substratum type had no significant effect on beetle temperatures. The only substratum that affected beetle temperature under visible radiation was the white beach sand used in experiment 4, Chapter 2. However, Namib tenebrionids do not encounter such white sands in their natural habitat, and are generally found on sand types similar to those in this experiment. It must thus be concluded that substratum colour does not influence Namib Desert beetle temperature.

The equilibrium temperatures calculated for live beetles ranged between 40.1 and 45.4 °C. These temperatures are similar to the range reported for dead beetles (41-44 °C), and thus seem to be an accurate estimation of the maximum temperatures beetles would reach under cloudless conditions and fairly low wind speeds (average 1 m s^{-1}). As previously mentioned, the maximum temperatures of beetles in the laboratory range up to about 49 °C: it thus seems unlikely that beetle activity is severely limited by thermal stress at high temperatures.

The commonly held view that black coloration is an advantage to beetles in that it allows them to attain their preferred temperatures more quickly than white beetles, thereby extending their foraging activity, must be questioned on the following grounds: the time constants of the black *O. unguicularis* and the predominantly white *O. bicolor* do not differ in field experiments with live beetles. Although the laboratory experiments and the field experiments with dead beetles found that the time constant was shorter for the warming of *O. unguicularis* elytra, it was also found that elytral temperatures did not affect thoracic and abdominal temperatures. It thus seems unlikely that *O. unguicularis* would heat up faster than *O. bicolor* in its natural habitat.

(ii) Infrared radiation

Although *O. bicolor* was always warmer than *O. unguicularis* in windless conditions, the overall temperatures of beetles exposed to infrared radiation were similar. Once again, beetle temperatures were not greatly affected by the presence of a hot substratum, with the exception of *O. unguicularis* elytra and *O. bicolor* abdomens. It is difficult to explain why the elytra of *O. unguicularis* were significantly warmer than air temperature, but the abdomen of *O. bicolor* does seem to warm far more (3 °C) than that of *O. unguicularis*, in still conditions. This may be due to an increased surface area for the absorption of heat conducted from the substratum, owing to the difference in shape between the two species, as postulated in Chapter 2.

In conclusion, it seems that the major difference between body temperatures of dead and live beetles in the field is that live beetles reach higher temperature elevations. A possible explanation for this is that the reflective properties of dead beetles are higher than for live beetles, resulting in lower equilibrium temperatures in dead beetles. Henwood (1975a) measured the reflectance of two Namib tenebrionids (*Onymacris plana* and *Cauricara phalangium*) and found that reflectances averaged 8-15 % higher in dead beetles. It thus seems possible that the reflective properties of beetle cuticles are altered upon death, although the exact physical or chemical changes involved have not been ascertained. It is also possible that the reflectances of black elytra increase more than white elytra upon death. This would explain why the average difference in temperature elevation between *O. bicolor* and *O. unguicularis* was 1.5 °C for dead beetles, and 3.5 °C for live beetles, with *O. unguicularis* being the warmer in both cases.

Of the three factors which could be responsible for differences in body temperatures between dead and live beetles, namely metabolic heat production, evaporative water loss (EWL) and changes in reflectance, it seems that the latter is the most likely. An increased metabolic rate in the live beetles is unlikely to have caused the higher temperature elevations, because activity was limited to minimal leg movements by tethering the beetles posteriorly, and EWL would have reduced the temperatures of live beetles, instead of increasing them.

EXPERIMENT (5): INSTANTANEOUS TEMPERATURES OF BEETLES IN THE FIELD

RATIONALE

Although controlled laboratory and field conditions allow one to estimate the temperatures beetles would reach under different thermal regimes, allowances are not made for behavioural thermoregulation. In addition, beetles which are active during their preferred activity time are not necessarily subjected to the same thermal environments tested in experiments (3) and (4). It is useful to know the temperatures of free-ranging beetles in the field, firstly, to compare temperatures between white and black species, and secondly, to ascertain the range of body temperatures over which the beetles are active.

PROCEDURE

Thoracic temperatures of both *O. bicolor* and *O. unguicularis* were obtained in the field. Temperatures were measured from naturally active *O. bicolor* along the dunes of the Skeleton coast, whereas temperatures of *O. unguicularis* were obtained from beetles in the Rooibank dunes. A 23 Ga Type T thermocouple, embedded into the tip of a 21 Ga hypodermic syringe needle with insulative adhesive, was placed into the thorax of an active beetle. Care was taken to obtain a reading immediately after capture, with mimimal handling of the beetle, and without adpressing the beetle to the hot sand. Temperatures were recorded from both digital (Bailey Bat-12) and analog (Bailey Bat-4) thermocouple readers. Readings were taken at times of peak population activity. Measurements of *O. bicolor* were taken at different times, on three different days, whereas measurements of *O. unguicularis* were taken at different times on one day.

RESULTS

Thoracic temperatures recorded from free-ranging *O. bicolor* and *O. unguicularis* are shown in Table 15.

Table 15. Mean body temperatures (°C, ± 1 S.D.) of two free ranging Namib tenebrionids.

species	N	mean	range
O. bicolor	10	33.7 ±3.7	27.9 - 38.5
O. unguicularis	5	30.7 ±5.1	25.4 - 36.8

The values reported here are in close agreement with similar readings taken by Seely *et al.* (1988), who measured average field temperatures of 34.4 °C for *O. bicolor*, and 32.2 °C for *O. unguicularis*. *O. bicolor* thus had higher mean temperatures in both studies. The ranges of body temperature over which both species are active are similar: 10.6 °C for *O. bicolor*, and 11.4 °C for *O. bicolor*.

DISCUSSION

The data presented in Table 15, and similar figures given by Seely *et al.* (1988) for beetle temperatures, illustrate four important points. (i) Beetles do not attempt to regulate their body temperatures at levels just under their tolerable maxima of 38-40 °C, calculated by Hamilton (1975), (ii) free-ranging beetles do not attain the equilibrium temperatures calculated for either dead or live experimental beetles in the field, (iii) beetles of both species are active over a similar wide range of body temperatures and (iv) *O. bicolor* has higher mean body temperatures in the field than *O. unguicularis*. Although these conclusions are based on small sample sizes in the present study, the same conclusions would be drawn from the results of Seely *et al.* (1988), which are based on sample sizes of 20 for each species.

According to Hamilton (1975), the upper lethal temperatures of *O. bicolor* and *O. unguicularis* are 48.7 and 47.6 °C respectively. Maximum temperatures measured in the laboratory for both species range between 48-50 °C. If beetle temperatures in the field can range from 25-39 °C (Table 15), it does not seem that beetles are attempting to regulate body temperatures at levels just under their tolerable maxima. Hamilton (1975) postulated that these maxima are 43.0 °C for *O. bicolor* and 42.6 °C for *O. unguicularis*. However, it is also evident that beetles are choosing their periods of activity to ensure that they do not reach the equilibrium temperatures of 40-45 °C calculated for beetles in experiments (3) and (4). The range of body temperatures over which beetles are naturally active is rather wide (about 10 °C). This may result in a certain flexibility or tolerance to prevailing environmental conditions during a particular day, suggesting that beetle activity may not be limited primarily by temperature. The fact that *O. unguicularis* does not attain higher temperatures than *O. bicolor* in the field could mean either that the thermal budgets of *O. bicolor* and *O. unguicularis* are similar and thus unaffected by colour, or that the beetles are choosing to be active during different environmental heat loads. Chapter 4 reports the environmental conditions to which beetles are exposed, and discusses this suggestion further.

DOES COLOUR HELP NAMIB BEETLES SURVIVE IN THEIR NATURAL ENVIRONMENT?

The results of this chapter have confirmed two of the conclusions drawn from the literature review in Chapter 1: firstly, that the differential heating effects of black versus white beetles are small (under 5 °C) and secondly, the preferred temperatures of beetles cover a wide range. Both these points suggest that the thermal consequences of beetle coloration may play a minimal role in the ecology of Namib beetles. This is further supported by the similarity of black and white beetle temperatures at wind speeds of 2 m s^{-1}, the similarity in the body temperatures of free-ranging beetles of both species, and the similarity in the ranges of body temperatures over which beetles are active. Although one cannot determine the separate contributions of all avenues of heat exchange to the thermal load of beetles in the field, it is evident that coloration affects only the absorption of incident visible radiation, and this only at low wind speeds. However, additional heat absorbed by black elytra is more easily dissipated by convection, and the sub-elytral air space may act as a thermal buffer, ameliorating the differential effects of coloration on beetle body temperature.

There is no evidence that black beetles warm faster than white beetles, although Hamilton (1973) proposed that black colour allowed beetles to warm up faster in the morning, and maintain heat longer in the evening, thereby extending their activity periods.

It now remains to determine the environmental conditions in which beetles choose to be active, especially the wind speeds to which beetles are exposed. This is achieved in the following chapter, which presents data on the activity patterns and concurrent micrometeorological conditions of both *O. bicolor* and *O. unguicularis* in the field.

CHAPTER FOUR

ACTIVITY PATTERNS OF BEETLES IN THE FIELD

INTRODUCTION

The seemingly hostile environment of the Namib Desert supports a diversity of endemic tenebrionid beetles which is unparalleled in any similar ecosystem (Koch 1962, Seely 1978). Namib tenebrionids are abundant in all three of the major habitat types: dune fields, dry river beds and gravel plains. Most species are specific to a particular habitat, and the timing of periods of activity differs among species. Activity may be diurnal, crepuscular or nocturnal (Louw & Hamilton 1972, Wharton 1980), and may vary daily or seasonally, depending on changing microclimatic parameters (Holm & Edney 1973, Hamilton 1975).

Numerous explanations exist regarding the ecological or physiological constraints which delimit times of activity. The need to maintain body temperature at some physiological optimum may be responsible for confining activity to particular times of day. Hamilton (1973) developed the "maxithermy" hypothesis, which postulates that desert insects function optimally at a preferred temperature close to their upper lethal limits, and attempt to maintain this physiological optimum for as long as possible. Evidence for this hypothesis is provided by Dreisig (1980) and Morgan (1985), who showed that predatory tiger beetles forage more successfully at their preferred temperatures, and time their activity accordingly. Many tenebrionids exhibit a seasonal shift in activity, *e.g.* from diurnal to nocturnal, in order to maintain body temperatures within some preferred range (Ahearn 1971, Kenagy & Stevenson 1982, Whicker & Tracy 1987).

Instead of timing activity so as to achieve a preferred body temperature, beetles may limit activity to times when temperature extremes can be avoided. Sand temperatures of 70 °C and over have been recorded in the Namib dunes (Robinson & Seely 1980). Numerous studies of Namib beetles have concluded that activity patterns are related to avoiding temperature extremes, either by burrowing during the hotter times of day, or by crepuscular or nocturnal activity. Many diurnal

Namib beetles show a bimodal activity pattern on hot days, and a unimodal pattern on cooler days when midday activity is permitted due to lower surface temperatures (Hamilton 1971, 1975, Holm & Edney 1973, Wharton 1980, Louw & Seely 1982).

Factors other than temperature may, however, be responsible for the timing of activity in beetles. Preferred body temperatures may not be directly related to some physiological optimum, but may be indirectly determined by food availability for predators (Dreisig 1980, Morgan 1985), or detritivores (Seely 1983, Seely & Mitchell 1987). Many detritivores rely on wind-blown detritus, and activity patterns have been shown to be wind facultative in numerous species of Namib beetles (Louw & Hamilton 1972, Hamilton 1975, Seely & Mitchell 1987). Louw & Hamilton (1972) demonstrated that tenebrionid activity may be controlled by endogenous rhythms. Yet other studies have related activity patterns to a need to minimise water loss (Ahearn & Hadley 1969, Edney 1971a), or to avoid predation (Cloudsley-Thompson 1979, Wharton 1980). It is clear that activity patterns of beetles correlate well with numerous meteorological and ecological variables, but the causal nature of these correlations is often unclear, as are the inter-relationships of various causal factors.

Both *O. bicolor* and *O. unguicularis* are diurnal Namib tenebrionids which inhabit dune slipfaces and emerge to feed on wind-blown detritus. If one assumes that both species wish to maximise the time spent on the surface where feeding and mating take place, and that temperature extremes do limit their activity, and that coloration may influence their thermal balance and thus their activity times, then one may expect to find differences in their timing of activity. In this chapter, the activity patterns of *O. bicolor* and *O. unguicularis* are examined, with the concurrent meteorological data, in an attempt to ascertain if activity patterns differ between species, if the differences can be related to thermal constraints, and if coloration affects these thermal constraints.

PROCEDURE

Activity patterns of *O. bicolor* and *O. unguicularis* were determined by noting the number of beetles active on specified dunes, from sunrise to sunset, at 10, 15 or 20 minute intervals. Activity of *O. bicolor* was monitored on the Skeleton Coast (Fig. 2) for 1 day in March 1986, 3 days in September 1987 and 5 days in January 1988. A total of 12 different dunes were monitored during this time. Activity patterns of *O. unguicularis* were recorded at Rooibank (Fig. 2) for 1 day in April 1986 and 4 days in January 1988. Additional readings were obtained for 5 days in January 1988 on the Skeleton Coast, where the ranges of *O. bicolor* and *O. unguicularis* overlap. A total of 17 different dunes was monitored.

Concurrent micrometeorological variables were measured at the base of dune slipfaces, where beetles of both species are active. Ambient temperatures were recorded with a white tipped MCS temperature probe, and a 28 Ga Cr-Al thermocouple shielded with aluminium foil and an Omega 871 digital thermometer. Black-bulb temperatures were measured with a black tipped MCS temperature probe, and a globe thermometer, of 15 cm diameter and 0.56 mm thickness (Yaglou 1968), placed just above the sand surface of the slipface. Sand temperatures were measured with an MCS probe, and with a 23 Ga Type T thermocouple and a Sensortek model Bat-12 digital thermocouple reader. Wind speed at beetle height was monitored by an MCS cup anemometer. Additional readings were taken with a Wallac oy thermo-anemometer at 1 cm and 2 m above the ground. A tube solarimeter measured direct and diffuse radiation. Relative humidity was measured with a whirling psychrometer and an MCS humidity probe. Changes in cloud cover and fog were monitored continuously. All MCS probes, and the solarimeter, were connected to an MCS 101 field logger, which recorded data at 10, 15, 20, 30 or 60 min. intervals, depending on the variable.

In order to estimate the equivalent blackbody temperatures (T_e) of beetles, two methods were used. T_e is defined as the "temperature of a black body cavity (having wall temperature equal to air temperature) that will provide the same radiant and convective exchange as is present in the animal's natural environment" (Campbell 1977). The first method of measuring T_e involved placing two dead specimens of *O. unguicularis* at the base of the slipface where meteorological data were being monitored, during the activity study at Rooibank in January 1988. The elytra of one beetle were coated with white enamel paint, and this beetle served as a model for *O. bicolor*. Thoracic temperatures of these two beetles were noted throughout the day. The second method of calculating T_e involved the use of a biophysical model, which describes the T_e reached by an active beetle in direct sunlight:

$$T_e = T_a + \frac{r_e}{p\,c_p}(R_{abs} - e\,o\,T_a^4)$$

The model is derived from Campbell (1977) and is developed in Appendix 1. The calculation of T_e allows a convenient method of quantifying the combined effects of meteorological variables on beetle body temperatures.

RESULTS

Beetle T_es, both measured and calculated, are shown for a day at Rooibank in January 1988 (Fig. 17). Ambient temperatures, and black-bulb temperatures measured with the globe thermometer, are included for comparison. The number of beetles active throughout the day are shown by the histogram. Table 16 shows the differences between temperatures of *O. bicolor* and *O. unguicularis,* when body temperatures of dead beetles are measured (a), or calculated by the model (b).

Table 16. Thoracic temperature differences between *O. unguicularis* and *O. bicolor*, for two days in Jan. 1988, when temperatures of dead beetles were measured (a), or calculated with a biophysical model (b).

		Temperature difference (°C) (*O. unguicularis* - *O. bicolor*)	
Date		range	mean
14 Jan.	(a)	-3.4 - 3.5	0.5
	(b)	0 - 2.6	1.3
15 Jan.	(a)	0.1 - 2.1	1.1
	(b)	0.1 - 2.7	1.3

Fig. 17 shows that T_es calculated with the model underestimate T_es of dead beetles by an average of 3.5-4.5 °C. Reasons for this are discussed later. However, differences in T_e between black and

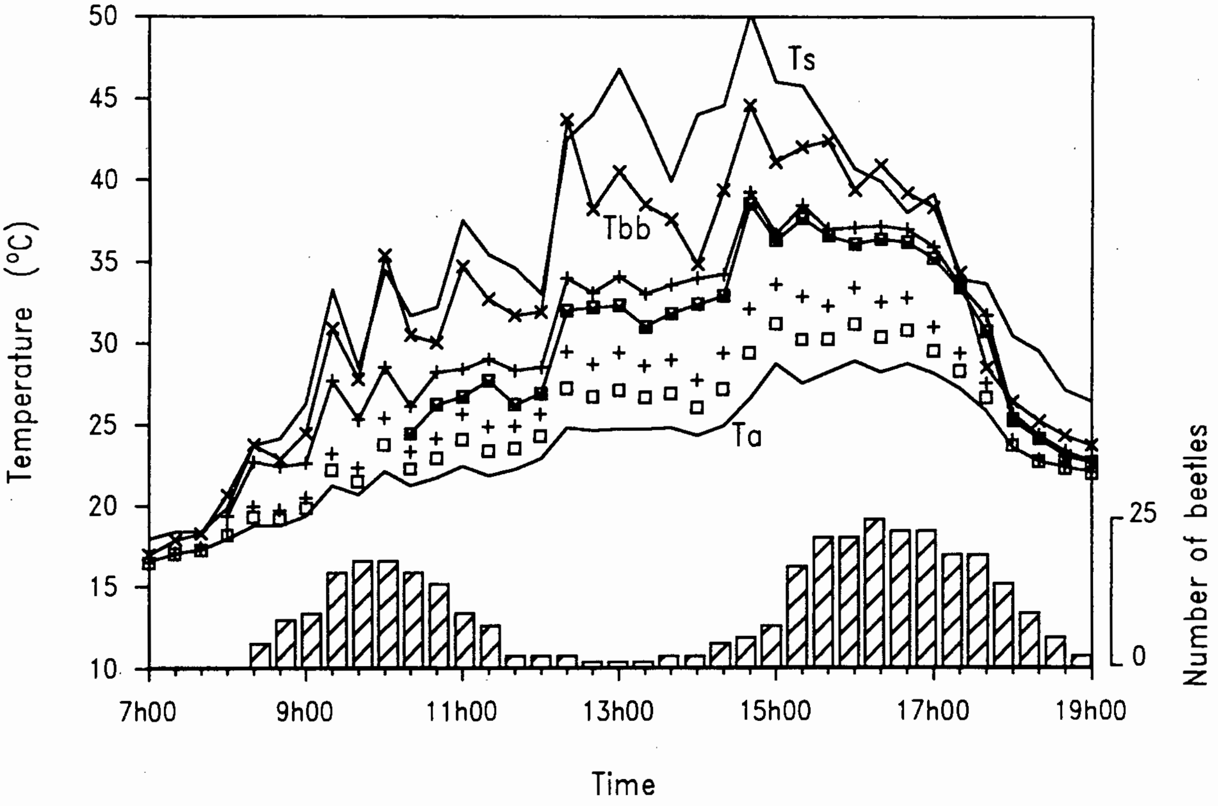


Fig.17. Equivalent temperatures (T_e) of *O. unguicularis* (+), and *O. unguicularis* with painted, white elytra (□), during a day at Rooibank in January 1988. T_e was measured using two methods : (1) thoracic temperatures of dead beetles were measured (—+— —□—), and (2), T_e was calculated with a model (+ □). Concurrent black-bulb (Tbb), ambient (Ta) and sand (Ts) temperatures are included. Activity of *O. unguicularis* is depicted by the histogram.

white beetles differ by similar amounts, whether T_e is measured, or calculated with the model (Table 16). Owing to the lack of measured T_es for most days during which activity data were gathered, the model T_es are used here for comparative purposes. Fig. 17 also shows that black-bulb temperatures (Tbb) measured with the globe thermometer overestimate measured T_es by 1-10 ^{o}C, thus activity patterns of *O. bicolor* and *O. unguicularis* are not compared with reference to Tbb. The globe thermometer has a diameter 2 orders of magnitude larger than the beetles' diameters, and consequently reaches far higher temperatures. The parameters which are most frequently thought to limit beetle activity are beetle body, and sand surface temperatures. Activity patterns of *O. bicolor* and *O. unguicularis* are thus compared here with reference to sand temperatures, and T_es predicted by the model.

Activity patterns and meteorological data for a single dune slipface, on the Skeleton Coast, on January 6 1988, are presented in Fig. 18. Although greater numbers of *O. bicolor* were active on this day, it is evident that the unimodal activity peaks of both species overlap. The major difference is that *O. bicolor* becomes active earlier, and reaches peak activity about 30 mins after *O. unguicularis*. The sand temperatures and T_es over which both species were active are shown in Table 17.

Table 17. Sand and equivalent blackbody temperatures experienced by *O. bicolor* and *O. unguicularis*, during activity on a single dune, on January 6, 1988. Ranges during activity depict the temperature at onset of activity, to the maximum at midday, followed by the temperature at which beetle activity ceased.

Species	before activity	during activity	after activity	at maximum activity
		Sand temperature (^{o}C)		
O. bicolor		37 - 49 - 35	35 - 31	40
O. unguicularis	37 - 45	45 - 49 - 35	35 - 31	47
		Equivalent blackbody temperature (^{o}C)		
O. bicolor	30	31 - 35 - 32	32 - 25	33.5
O. unguicularis	33 - 36	37 - 33	33 - 25	36.5

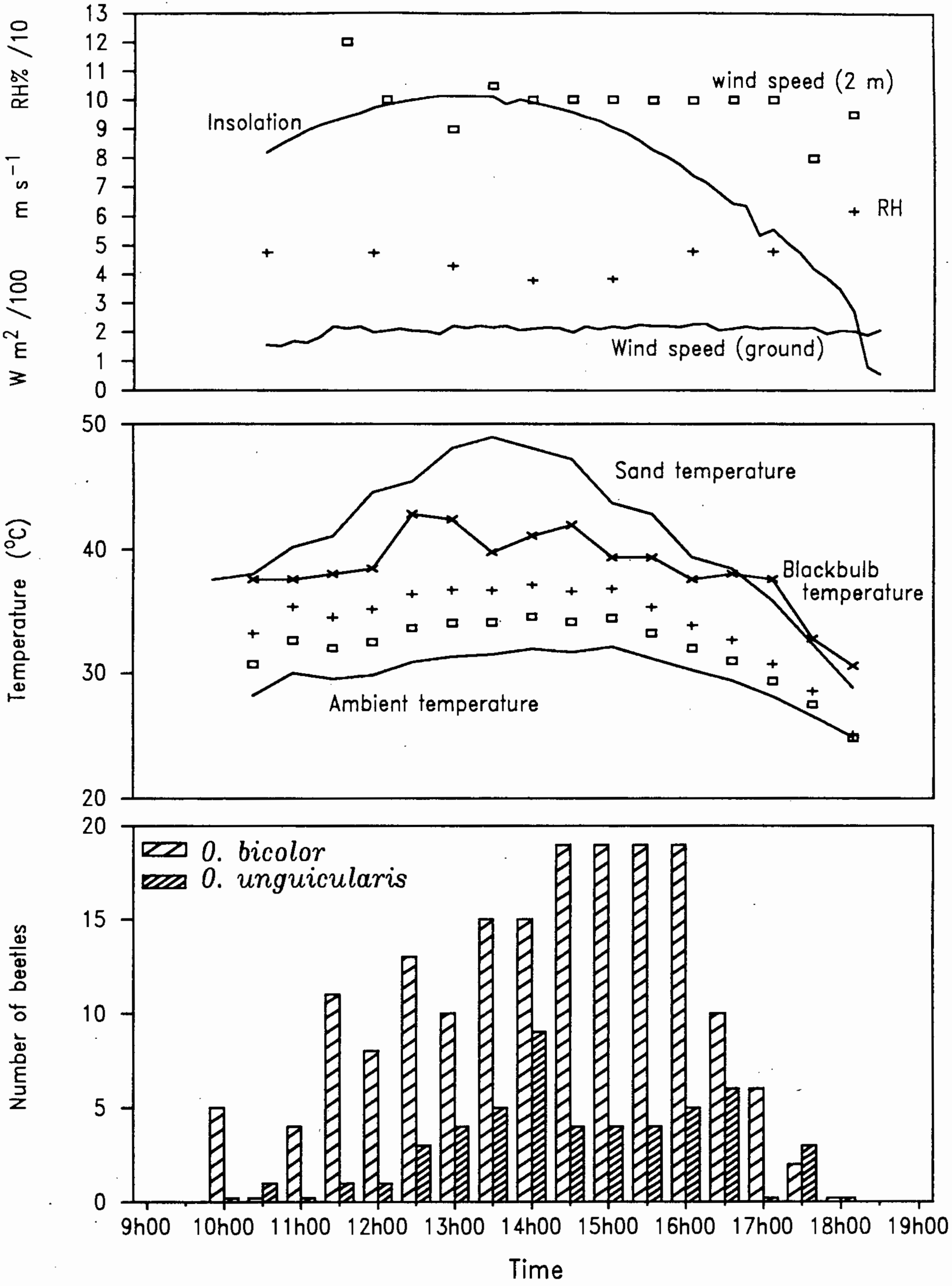


Fig. 18. The daily activity patterns and equivalent blackbody temperatures (T_e) of *O. bicolor* (□) and *O. unguicularis* (+), with concurrent meteorology, on January 6, 1988. Data were collected along a single dune slipface on the Skeleton Coast.

Conclusions to be drawn from Fig. 18 and Table 17 are as follows:- Both beetle species show a unimodal, overlapping activity pattern. The two species do not partition their activity in order to avoid competition for either space or food resources. *O. unguicularis* is active at higher sand temperatures than *O. bicolor*. The maximum activity of *O. bicolor* occurs as sand temperatures begin to decline below 49 °C. In addition, *O. bicolor* becomes active at lower sand temperatures and T_es in the morning. Activity of both species is terminated when sand temperatures and T_es decline below 35 °C and 23 °C respectively. Activity of *O. unguicularis* is not limited by sand temperatures up to 49 °C, and a T_e of 35 °C is within their range of tolerance.

Meteorological data for January 5-9 1988, on the Skeleton Coast, are shown in Table 18. The hottest days are listed first, followed by increasingly cooler days. Ranges in sand temperature and T_e for each day are shown on the left. Temperatures prevailing at maximum activity, as well as the maximum number of beetles present on a particular day, are also listed. Wind speeds at beetle height, and at 2 m above the ground, appear on the right. The data in Table 18 refer to the activity of *O. bicolor* only. The total number of *O. unguicularis* sighted on all days (excluding the 6th), was only three. Activity patterns were unimodal on all days, with a peak occurring in the morning, midday or afternoon.

Table 18. Meteorological data for unimodal activity patterns of *O. bicolor* for 5 days in January 1988, on the Skeleton Coast.

Date	Daily temperature range		Temperature at maximum activity		Maximum number of beetles active	Wind speed (m s^{-1})	
	sand	equivalent (Te)	sand	Te		beetle height	2 m
9	30-53	28-34	48	31.5	2	1-2.5	8-10
5	33-54	28-36	42	33.5	5	1.5-2	-
6	31-49	25-35	40	33.5	19	1.5-2.5	10-12
8	27-45	26-31	45	30	5	1.5-2.5	5-10
7	25-45	26-31	41	30	9	2-2.5	7-10

The ranges of sand temperature and T_e which were available to beetles, and the ranges of temperature over which beetles were active, during the period 5-9 January 1988, are shown in Figs. 19 & 20 (unimodal, *O. bicolor*). With reference to *O. bicolor,* the conclusions reached from these data are the following: sand temperatures over 50 °C, and below 34 °C, are avoided, whereas activity is concentrated towards temperatures of 40 °C. T_es up to 36 °C do not limit activity, but beetles are not active below a T_e of 28 °C. The preferred T_e is 33 °C.

All activity data gathered in April 1986 (1 day) and September 1987 (3 days) for *O. bicolor* showed the characteristic bimodal activity pattern frequently observed in diurnal Namib tenebrionid beetles, where morning and afternoon peaks of activity occur. It is evident from Figs. 19 & 20 that daily sand temperatures and T_es were much lower in these two months than in Jan. 1988. No conclusions can be drawn regarding the temperature extremes which limit activity because beetles were active at all available temperatures (except below sand temperatures of 18 °C). Beetles were active over sand temperatures from 18-39 °C, but concentrated their activity in the range 20-33 °C. T_es experienced during activity ranged from 16-31 °C, with peaks at 17-25 °C. Temperature data for the bimodal activity patterns of *O. unguicularis* are also shown in Figs. 19 & 20. Data were collected at Rooibank during April 1986 (1 day) and January 1988 (3 days). Beetles were active over higher sand temperatures than *O. bicolor,* although this comparison is influenced by the fact that *O. bicolor* was not exposed to the high temperatures that were available to *O. unguicularis.* Sand temperatures over 54 °C do limit beetle activity, and few beetles remain active over 49 °C. At sand temperatures below 23 °C, activity ceases. Peaks of activity occurred over a wide range of temperatures (28-44 °C). *O. unguicularis* is active over a similar range of T_es to *O. bicolor* (17-34 °C), although the preferred temperature is higher in *O. unguicularis* (28 °C). It could be interpreted from the data in Fig. 20 that *O. unguicularis* activity is limited over T_es of 34 °C. However, the unimodal data show that beetles can be active up to 37 °C.

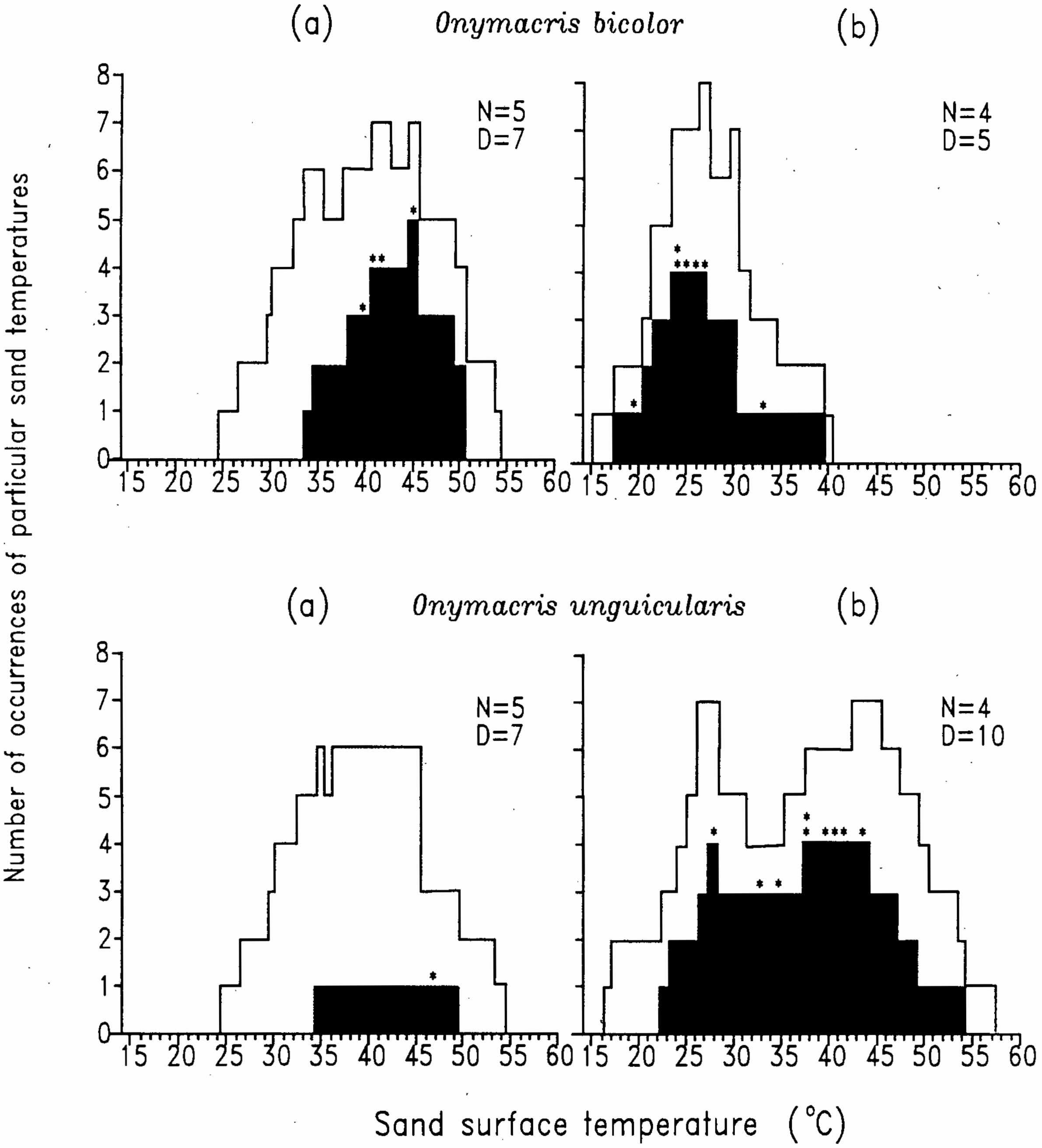


Fig. 19. Frequency distributions of the number of occurrences of a particular sand temperature (□), and the number of these occurrences during which beetles were active (■). Figures on the left show data for unimodal activity patterns (a), whereas right hand figures show data for bimodal patterns (b). Stars (*) indicate the temperatures which prevailed at maximum activity on each day. Data in each figure are pooled for the total number of days sampled (N), and the total number of dunes sampled during those days (D).

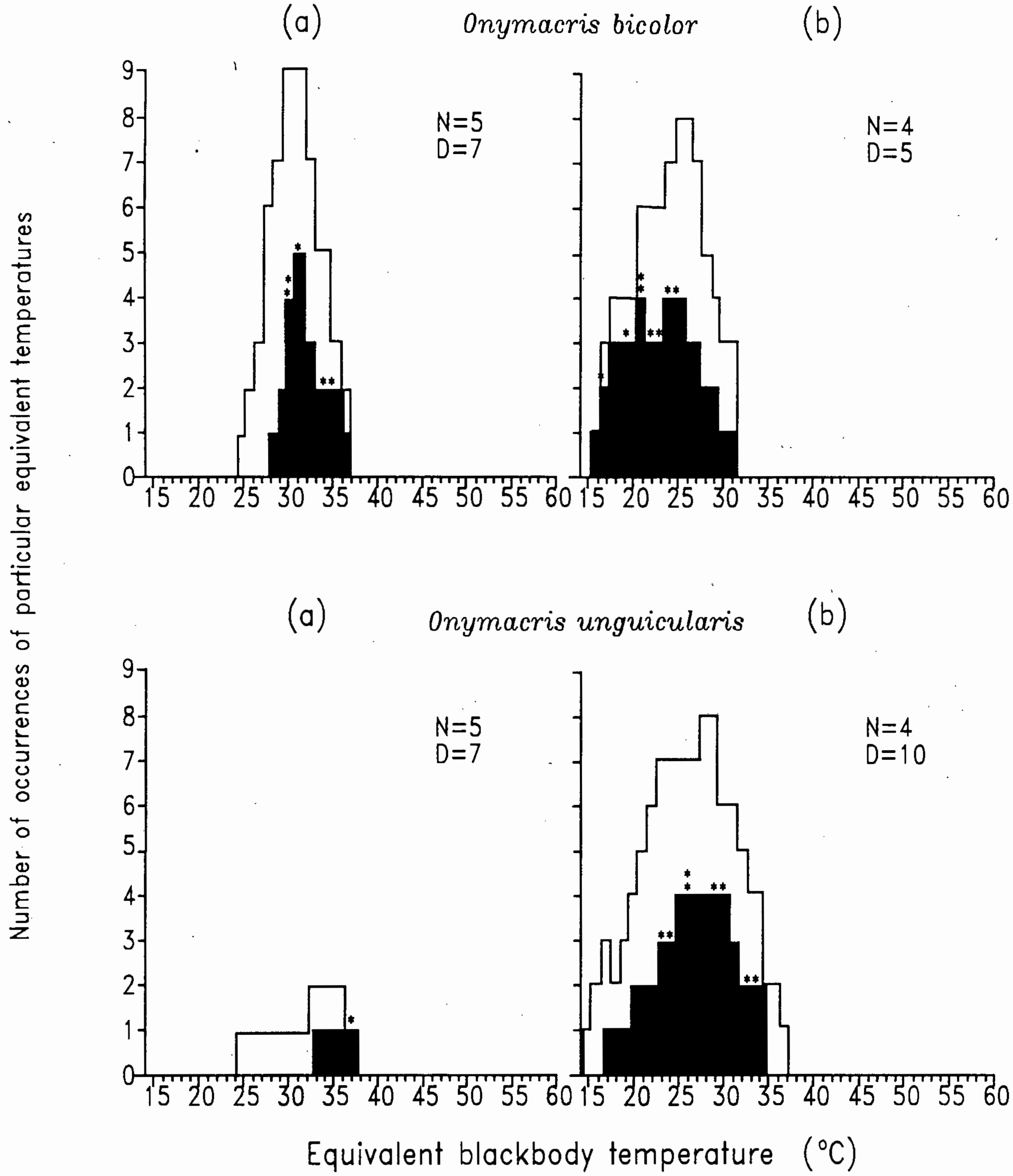


Fig. 20. Frequency distributions of the number of occurrences of the equivalent blackbody temperatures that beetles could reach (□), and the number of these occurrences during which beetles were active (■). Figures on the left depict data for unimodal activity patterns (a), whereas right hand figures depict data for bimodal patterns (b). Stars (*) indicate the temperatures which prevailed at maximum activity on each day. Data in each figure are pooled for the total number of days sampled (N), and the total number of dunes sampled during those days (D).

DISCUSSION

The timing of activity in tenebrionid beetles is often attributed to environmental fluctuations in temperature, namely ground or ambient temperatures. Comparisons among studies are complicated by the fact that these temperature measurements are frequently taken with different instrumentation, which is placed at varying levels above the ground. The most reliable parameter which facilitates comparisons among different studies to date, is ground temperature, but this does not provide an estimate of beetle temperature. The latter is seldom measured continuously during activity studies, and various models have been developed to predict the equivalent blackbody temperature (T_e) of a beetle exposed to a particular suite of environmental variables (Henwood 1975a, Kenagy & Stevenson 1982). It is evident from the present study that black-bulb temperatures (Tbb), depending on how they are measured, may be meaningless to an insect's body temperature (Fig. 17). Nevertheless, thermoregulatory behaviour in animals is often related to Tbb. Black-bulb temperatures, do however, provide a measure of the integrated effects of radiation and convection in a particular habitat, and if a standard apparatus is used in all future studies concerning similar groups of animals (*e.g.* tenebrionid beetles of similar size), the ambient conditions to which these animals are exposed could be successfully compared. In order to measure the T_e of an insect, either a dead model of the insect, or a biophysical model which accurately predicts measured body temperatures, should be used (due to the difficulty of monitoring body temperatures of naturally active insects).

As previously noted, the biophysical model used in this study underestimates the measured T_es of dead model beetles by about 4 °C (Fig. 17). However, the body temperatures of active live beetles in the field may be closer to the calculated T_es than the measured values, owing to the inability of the dead models to behaviourally regulate their body temperatures, either by forced convective cooling achieved by movement (Hamilton 1975), stilting (Seely 1983), or by orientation with respect to the sun (Edney 1971b). Nonetheless, the differences found between body temperatures of *O. bicolor* and *O. unguicularis* were similar (whether measured in dead beetles or calculated by the model). The average difference was 0.5-1.3 °C, with *O. unguicularis* being the warmer (Table 16). It should be noted that the temperatures measured of dead beetles were thoracic temperatures, but the model calculates an overall body temperature for a white or a black beetle, due to the absorption term in equation (7) (Appendix 1). The model seems to predict the differences found in measured thoracic temperatures accurately, and T_es calculated by the model are thus reliable for determining and comparing the thermal constraints which may be placed on the activity patterns of the two species.

The results presented in this and previous chapters, show that *O. unguicularis* reaches higher body temperatures than *O. bicolor,* but only when wind speeds are under 2 m s^{-1}, and that these differences are generally 2.5-3.5 °C. Hamilton (1975) examined the activity patterns of a black and white species pair of Namib tenebrionids, which also inhabit dune slipfaces (*O. unguicularis,* and *O. brincki,* which has white elytra). He found that body temperatures were similar in both species during the course of a day. Diurnal activity times did not differ between species, but *O. unguicularis* was far more abundant in windy conditions. A second comparison, between the black *Physosterna globosa* and *O. langi* which has pale elytra, revealed that both species exhibit bimodal, diurnal activity patterns, which differ slightly in their onset and termination (Hamilton 1975). Hamilton suggests that the paler species extended its activity into the hotter midday more than the black species (perhaps because it reflected more solar radiation and enjoyed a tolerable body temperature), whereas the black species was active earlier in the morning and later in the evening (perhaps because a greater absorption of solar radiation afforded high enough body temperatures). The data presented in Fig. 18 do not support these predictions. The white *O. bicolor* became active earlier, and at lower temperatures, than the black *O. unguicularis* (Table 17). Both species were active throughout the day, with *O. unguicularis* achieving peak activity at the hottest period during midday. *O. bicolor* was most abundant as temperatures began to decline, and evening activity was terminated simultaneously in both species. *O. unguicularis* showed maximum activity at higher sand temperatures and T_es than did *O. bicolor* (Table 17). Thus coloration does not appear to affect activity patterns of this black and white species pair.

Beetle coloration is less likely to influence timing of activity if a factor other than temperature is the primary cue for activity. Data in Fig. 16 show that activity of *O. unguicularis* on a particular day in Jan. 1988 was not related to either sand temperature or T_e. The contribution of wind to activity is displayed in Table 18. During the five sampling days in January 1988, *O. unguicularis* was active on one day only, and *O. bicolor* was active in very small numbers (<9) on all days except January 6, when the maximum number active was 19. Sand temperatures and potential T_es on this day were intermediate, compared with the other days, and the preferred sand temperatures and T_es during activity on the 6th were available to beetles on all other days. Wind speeds at beetle height did not differ markedly among days, but wind speed at 2 m was far greater, and more constant on the 6th, especially during the morning (Fig. 18). On other days, wind speed increased only towards midday. A facultative response to wind in *O. unguicularis* has been noted previously (Hamilton 1975, Seely 1983), and this may explain why *O. unguicularis* was active only on the 6th. This implies that wind, rather than temperature, may determine activity patterns in *O. unguicularis,* and possibly *O. bicolor,* and that beetles are able to sense macroclimatic wind speeds, while remaining buried. Although Dreisig (1980) suggests that beetle emergence may be governed by soil temperature gradients, Hamilton & Seely (1976) have shown that *O. unguicularis* is able to respond to vapour pressure gradients in the soil. These beetles emerge to condense water from cool, advective fogs, which may occur at night or early morning, a time when beetles are normally buried at depths of up to 20 cm (Seely *et al.* 1983).

Further evidence for wind as a primary cue for activity is that both species feed on wind-blown detritus, which collects on dune slipfaces. The consequence of the wind facultative response is that differences in beetle temperature due to colour, are negated, and Table 18 shows that even at beetle height, wind speeds averaged 2 m s^{-1}, which is sufficient to negate temperature differences due to colour (Chapters 2 & 3). Although these wind speeds were measured with a cup anemometer, additional readings taken with the more sensitive hot wire anemometer provided similar (and often higher) results.

It could be argued that the black *O. unguicularis* is more wind facultative then the white *O. bicolor,* because it relies on convective cooling to keep its higher body temperature below lethal limits. However, as previously stated, temperature differences between *O. bicolor* and *O. unguicularis* are generally under 3.5 °C, and the data from the present study show that *O. unguicularis* selects higher sand temperatures and T_es for maximal activity, than does *O. bicolor.* In addition, a strong facultative wind response exists in the diurnal dune beetle *Zophosis fairmairei,* which has pale elytra with black markings (Seely 1983). Also, Louw & Hamilton

(1972) and Louw & Seely (1982) observed a strong wind facultative response in two dune beetles, *Lepidochora argentogrisea,* and *L. discoidalis,* which are both nocturnal. Louw & Hamilton (1972) also noted that activity varied among dunes, and related this to variations in wind direction, caused by the different orientations of dunes. These observations support the argument that wind is the primary cue regulating the timing of activity in detritivores which inhabit slipfaces.

A seasonal shift in activity of Namib tenebrionids has been observed by Holm & Edney (1973). The data in Figs. 19 & 20 show that both unimodal and bimodal activity patterns were observed in *O. bicolor* and *O. unguicularis,* but whether these patterns are seasonally related in unclear. Unimodal activity was observed in *O. unguicularis* on one day only, in the dunes of the Skeleton Coast, on a hot, windy day in January 1988. Bimodal activity prevailed at Rooibank during the same month (Fig. 17). Sand temperatures were higher during midday at Rooibank, and Fig. 19 shows that temperatures above 50 °C prevented midday activity in *O. unguicularis.* This is in agreement with the findings of Hamilton (1975), Louw & Seely (1982) and Seely *et al.* (1983) who found that high midday sand temperatures resulted in bimodal activity in many Namib tenebrionids.

O. bicolor, on the other hand, shows a curious seasonal response. Fig. 19 shows that a unimodal pattern prevailed during 5 days in Jan. 1988, when sand temperatures were high. However, for 1 day in April 1986 and 3 days in September 1987, a bimodal pattern prevailed when sand temperatures were far lower. In addition, preferred sand temperatures were lower than the maximum available temperatures during these cooler periods (Fig. 19). This phenomenon is difficult to explain, and can not be attributed to a wind response because on these days wind was either constant, or increased in the afternoon. Nonetheless, the important points which are illustrated in Figs. 19 & 20 are that *O. unguicularis* prefers to be active at sand temperatures of 42 °C (unimodal) or 37-44 °C (bimodal), whereas *O. bicolor* prefers 39-45 °C (unimodal) or 24-27 °C (bimodal). When the two species are sympatric, *O. unguicularis* prefers the higher temperature (Table 17). With respect to T_e, *O. unguicularis* prefers 37 °C (unimodal) and 25-31 °C (bimodal), whereas *O. bicolor* prefers 31 °C (unimodal) and 17-25 °C (bimodal). Thus the black *O. unguicularis* prefers to be active during higher temperatures than does the white *O. bicolor,* confirming that black coloration places no additional thermal constraints on black beetles. The ranges of sand temperatures over which *O. bicolor* and *O. unguicularis* are active are 18-50 °C and 23-55 °C respectively. *O. bicolor* can be active at T_es over 16-36 °C, whereas *O. unguicularis* is able to tolerate 17-37 °C. Thus colour does not extend the upper or lower temperature limits of either species during activity.

As regards Hamilton's (1973) theory of maxithermy, the activity data presented here neither support nor refute this theory. Beetles do usually prefer the upper ranges of the T_es available to them (Fig. 20), but whether the preferred temperatures of 37-41 °C quoted by Hamilton (1973) are ever attained is questionable. Table 15 (Chapter 3), and data presented by Seely *et al.* (1988), reveal that body temperatures of *O. bicolor* and *O. unguicularis* are generally between 30-34 °C. This is far below the "maxithermal" temperatures quoted by Hamilton (1973).

DO BLACK AND WHITE COLORATION HAVE A THERMAL VALUE IN NAMIB DESERT BEETLES ?

If black and white coloration in beetles is an "adaptation to maximise the mean interval of potential activity at elevated body temperatures" (Hamilton 1975), one must expect differences between body temperatures and activity patterns of black and white beetles. This study shows that this is not the case, and that wind, and not temperature, may be the primary cue to which many Namib tenebrionids respond. However, extreme surface temperatures at midday do limit activity, and a secondary response to temperature is evident. If white colour does allow beetles to extend their activity over midday, one would expect to find more white beetles in the hotter inland areas of the Namib, but most pale beetles occur in cooler coastal areas (Penrith 1975).

Seely & Mitchell (1987), and the present study have noted that Namib tenebrionids do not surface daily, even when surface microclimatic conditions fall within preferred ranges. This could imply that beetles respond to some macroclimatic parameter which is necessary for activity to be profitable, or that beetles are not sufficiently stressed energetically to need to maximise the time spent actively foraging on the surface, or both. Data in Table 18 show that macroclimatic changes in wind speed at levels 2 m above the ground may indeed be responsible for determining the onset of activity, and in windy conditions, beetle colour is thermally irrelevant. Alternatively, if beetles are not energetically stressed (*i.e.* if food availability is not limiting), then any small extension in the length of daily activity afforded by a particular colour, would be irrelevant. One could argue that natural selection would act on colour only during times of stress, such as food shortage. However, three factors mitigate against this. Firstly, Seely & Louw (1980) and Seely & Mitchell (1987) suggest that energy availability is not a limiting factor in the Namib. Secondly, population numbers in the Namib are greatly affected by rainfall (Seely & Louw (1980), and it is possible that the survival of beetle larvae in the sand is more affected during dry periods than survival of the adults. If so, adult coloration would have little bearing on the propagation of a particular species. Thirdly, Henwood (1975a) points out that maxithermy would not be profitable during food shortages. If coloration is an adaptation to achieve maxithermy, the very time when coloration could be exposed to selection would be the time at which its selective advantage would be unprofitable.

Regarding the original hypothesis of this study, which postulates that the white elytra of *O. bicolor* provide a selective advantage by allowing beetles to extend their daily foraging periods over the hotter midday periods, the following conclusions can be drawn (these conclusions are best discussed by answering the questions posed in Chapter 1, pp. 13):

1) Coloration affects beetle body temperatures only when the thermal environment is dominated by visible radiation.
2) However, wind speed and behavioural mechanisms (such as the timing of activity), can and do override these differential effects.
3) Activity patterns are determined primarily by wind, and the body temperatures attained by species differ in an unexpected way: the black *O. unguicularis* has the lower body temperature in the field, and prefers to be active at higher sand temperatures and T_es.

The proposed hypothesis must thus be rejected. The data presented here support the predictions reviewed in Chapter 1 (pp. 12), that:

a) Body temperature differences between black and white beetles are usually restricted to the sub-elytral air-space, whereas thoracic and abdominal temperatures seldom differ. The average temperature differences of sub-elytra were: 4 °C, (laboratory experiments) and 3.4 °C (field experiments).

b) Behavioural and environmental factors (such as activity patterns and wind) influence body temperatures more than colour does.

c) Preferred temperatures cover a wide range, rendering small temperature differences due to colour negligible (Table 15). Also, temperatures of both species in the field are usually close to 30 °C, and T_es of up to 36 °C are acceptable to both species (Fig. 20).

d) Preferred temperatures may be ecologically, rather than physiologically, determined.

With reference to d), preferred temperatures have been reported for beetles from many different habitats (Dreisig 1980, Kenagy & Stevenson 1982, Slobodchikoff 1983, Morgan 1985, Whicker & Tracy 1987, Seely *et al.* 1988). Not all of these studies could attribute temperature preferences to a physiological optimum, and Seely *et al.* (1988) suggest that high temperatures in Namib tenebrionids may be determined by the aseasonality of the environment, and the presence of a constant thermal refuge (the sand). Like Heinrich (1974), they argue that beetles prefer the temperatures which are easiest to maintain in a particular habitat. It follows that beetles in exposed environments prefer higher temperatures than those who have access to shade. Evidence for this is presented by Nicolson *et al.* (1984), who showed that *O. plana* (exposed slipface habitat) prefers body temperatures of 36-37 °C, whereas *P. globosa* (shaded river-bed habitat) prefers 21-30 °C. It is thus suggested that beetles prefer body temperatures that allow them to extend foraging activity for as long as possible, throughout the year, and that beetles do not prefer temperatures at which physiological processes function at an optimum (as suggested by Hamilton in his "maxithermy" hypothesis). Kenagy & Stevenson (1982) support this argument with evidence of low preferred body temperatures in 8 species of tenebrionids in a temperate environment, and Whicker & Tracy (1987) show that preferred body temperatures ranged seasonally in 7 different tenebrionid species, allowing them longer periods of activity in spring and fall. It thus seems likely that preferred temperatures are ecologically determined, and support for the maxithermy hypothesis is provided mainly by predatory tiger beetles (Dreisig 1980, Morgan 1985) and Namib beetles living in exposed habitats which lack shade (Henwood 1975a, Nicolson *et al.* 1984). It is interesting that body temperatures of free-ranging *O. bicolor* and *O. unguicularis* are close to 30 °C (Table 15), and that sand temperatures at 30 cm under the sand remain constant between 22-32 °C yearly. It is thus possible that 30 °C is the most easily maintained temperature in these beetles, which do bury to depths of over 20 cm (Seely *et al.* 1983).

In conclusion, question 4 posed in Chapter 1 (pp. 13) can be dealt with as follows: environmental and body temperatures only pose physiological constraints on beetles at temperature extremes, and black and white beetles are affected equally. Colour does not provide a selective advantage by allowing either black or white beetles to extend their activity periods. If colour has no thermal value, what is its function? Although Cloudsley-Thompson (1979) and Wharton (1980) suggest that pale colour in Namib tenebrionids may be cryptic, Seely (1985) suggests that predation is not an important selective pressure in the Namib, owing to the lack of behavioural or morphological adaptations in beetles for predator evasion, and the conspicuous nature of the colour, and activity, of diurnal black and white tenebrionids. If temperature and predation are not responsible for beetle coloration, several other factors could have selected for the ofsetting advantages of black coloration previously mentioned: increased mechanical protection, protection against UV radiation, reduced permeability, or Mullerian mimicry, owing to the supposed hard and distasteful nature of tenebrionids. Black and white coloration in a single beetle could be aposematic, or it could play a role in intra-specific communication, either to allow species recognition in bicoloured beetles which are sympatric with other black species, or to enhance social facilitation in active beetles (Louw & Hamilton 1972). The latter authors noted that activity in the Namib tenebrionid *Lepidochora argentogrisea* in captivity was facilitated by dense population concentrations, and concluded that these slipface beetles may be gregarious under natural conditions. It has also been suggested that black colour is an evolutionary legacy (Buxton 1924), arising from wetter and more vegetated periods, and maintained owing to being neutrally adaptive. Evidence provided in this and other studies discounts the thermal value of coloration, and the most reasonable conclusion is that some combination of the abovementioned factors is responsible for coloration in Namib tenebrionids.

SUMMARY OF SECTION I

1. Laboratory experiments show that although *O. unguicularis* reaches higher sub-elytral temperatures, *O. bicolor* gains more heat from the substratum. Consequently, both beetles experience similar thermal loads, and their thoracic and abdominal temperatures do not differ significantly.
2. Field experiments show that when temperature differences occur between *O. bicolor* and *O. unguicularis,* these differences are generally less than 3.5 °C. Considering the range of temperatures over which beetles are active (over 10 °C), these differences are small.
3. Temperature differences between beetles occur only at low wind speeds (< 2 m s^{-1}). Field data show that beetles choose to be active in high wind speeds, possibly because of the nature of their food source, which is wind-blown detritus.
4. Coloration in *O. bicolor* and *O. unguicularis* does not appear to be of thermal value, thus the occurrence of black beetles in the Namib does not present a paradox, and the presence of white elytra in many coastal species is not an adaptation to extend surface activity during the hotter parts of the day.
5. Coloration in Namib beetles may be a neutrally adaptive evolutionary legacy, an adaptation for predator avoidance or intra-specific communication, or in the case of black beetles, a by-product of some physiological advantage of melanin which is unrelated to any possible thermal implication.

SECTION II

THE ROLE OF BLACK AND WHITE COLORATION IN MARINE BIRDS

(*Phalacrorax capensis* and *Morus capensis*)

CHAPTER FIVE

COLOUR AND THERMOREGULATION IN ENDOTHERMS

Thermal budgets of endotherms are complicated by insulating layers of feathers or fur (henceforth referred to collectively as coats). Factors, other than colour, which affect temperature exchange across coats include coat thickness (Øritsland & Ronald 1973), density (Tregear 1965, 1966, Chappell 1980a), skin colour beneath the coat (Ohmart & Lasiewski 1971), and the level of penetrance (P) of radiation into the coat. Coat structure and the optical properties of individual feathers and hairs together determine P (Øritsland 1971, Cena & Clark 1973, Cena & Monteith 1975a, Øritsland & Ronald 1978). Surface measurements of absorbance or reflectance of coats are almost independent of the absolute values of these optical properties, and heat transfer processes through an insulating coat layer have been shown to depend largely on P (Kovarik 1964, Hutchinson & Brown 1969, Cena & Monteith 1975a, Walsberg 1983). As discussed for ectotherms, heat absorption in endotherms is affected by behavioural responses (Lustick 1983), and environmental factors such as convective properties (Walsberg *et al.* 1978, Walsberg 1983), the angle of incident radiation (Lustick *et al.* 1980) and the spectral energy distribution of the radiation (Øritsland 1970, 1971). These factors may sometimes override the physical properties of the animal surface in the determination of heat absorption. Consequently, coloration alone does not enable us to predict the heat load upon an endotherm.

The importance of solar heat gain to the thermal budgets of endotherms is well documented. A reduced cost for the maintenance of endothermy in birds and mammals at temperatures below the thermoneutral zone (TNZ) has been demonstrated by researchers since the 1940s. Examples include the following: Adolph & Molnar (1946) investigated the physiological effect of radiation on nearly nude men at moderately low temperatures. They calculated that the men saved 20-25 % of their total energy output when resting in sunshine as opposed to shade. The findings of Morton (1967) revealed that white-crowned sparrows significantly reduced their food intake at a temperature of 7 °C when irradiated. De Jong (1976) then quantified the metabolic effect of insolation on white-crowned sparrows, and calculated that the TNZ was shifted down by about 15 °C in irradiated birds at low temperatures. Over 30 °C, irradiation imposed a thermal stress and served to increase metabolic rate. Ohmart & Lasiewski (1971) showed that roadrunners can save up to 41 % of their standard metabolism by sunning in temperatures below the TNZ. Lustick *et al.* (1979) calculated that at low ambient temperatures, juvenile herring gulls can reduce their energy expenditure by 29 % by basking in the sun. Eastern chipmunks can depress their metabolic rates by 20.6 % below the TNZ when irradiated (Neal & Lustick 1974), and Thiessen *et al.* (1982) calculated that Mongolian gerbils can acquire 14-15 % of their daily energy requirements by being exposed to solar radiation.

Since the mid 1960s, research done mainly on birds, goats and cattle has led to the development of a controversy regarding whether light or dark coats are better absorbers of solar radiation. The rationale behind this controversy encompasses two hypotheses: the conventional "black heats better" hypothesis, which postulates that black coats absorb more visible radiation, and the "white heats better" hypothesis which can be summarized as follows (refer to Fig. 21): visible radiation can penetrate coats by multiple diffuse reflection and this is enhanced by white or bright coloration (Øritsland 1970, 1971). This radiation may be scattered into the coat and absorbed below the surface, helping to heat the skin. Thus low absorbance (high reflectance) occurs at the coat surface, coupled with relatively low surface temperatures, but the radiation that is absorbed penetrates deeply into the white coat, owing to the high reflectance within the coat. As a result, convective heat loss does not affect white coats very greatly, because radiation is absorbed deep within the coat where convective forces have less effect (Walsberg *et al.* 1978). It follows that white coats may be advantageous in cold, sunny, windy environments. Conversely, black coats have a high absorption at the surface, coupled with high surface temperatures and a shallow penetration of radiation into the coat (Kovarik 1964, Hutchinson & Brown 1969, Cena & Monteith 1975a). This occurs because the high surface temperatures reradiate much of the absorbed energy as infrared radiation, and the high surface temperatures increase the temperature gradient between the coat and the environment, facilitating heat loss to the environment (Priestley 1957). As a result, convective heat loss has a greater effect on black coats, because absorption occurs closer to the surface. Thus black colour may reduce heat gain and the need for evaporative water loss, and it may be an advantage in a hot, sunny, windy environment.

An examination of the ecological distribution of endotherm coloration reveals many white Arctic species and many black desert species. Stullken & Heistand (1953) and Svihla (1956) noted that many Arctic animals have white coats in winter and darker coats in summer, *e.g*. Arctic foxes, ptarmigans, snowshoe hares, collared lemmings and weasels. Crypsis is generally offered as the adaptive advantage of these colour changes, but a thermal role for the coloration of Arctic animals was postulated as early as the 1930s by Hesse *et al*. (1937) and Hamilton (1939). They suggested that white coloration affords improved heat conservation due to lower emissivity. This incorrect view is discussed in detail in section (ii) of this chapter.

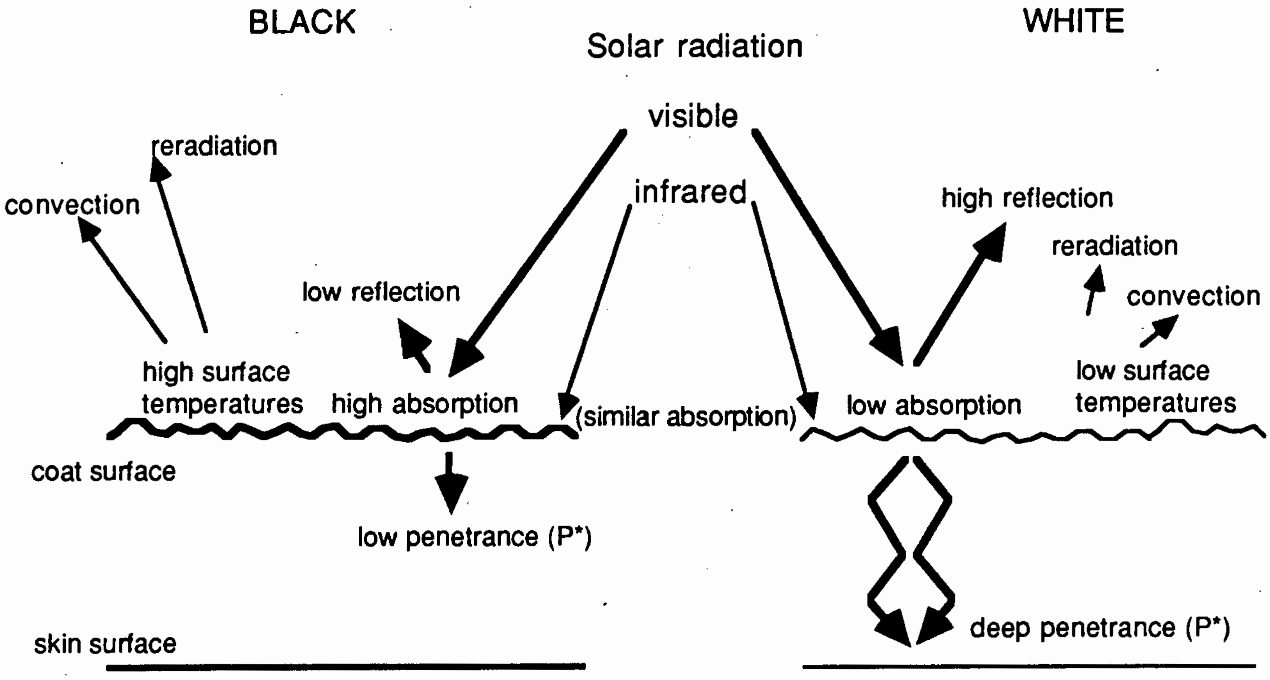


Fig. 21. Effect of coat colour on the absorption of solar radiation.

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* The value P refers to the depth of the coat at which absorption takes place. Attempts to measure P were made by Hutchinson & Brown (1969) and Cena & Monteith (1975a), who calculated the values Ip and *p* respectively. Ip is defined as the thermal insulation of that portion of the coat through which radiation is supposed to penetrate before reaching the level at which absorption takes place, whereas *p* is defined as the interception function, and refers to the fraction of radiation intercepted by a unit depth of coat.

Buxton (1924) remarked that many black birds are found in the Great Palaearctic Desert, *e.g.* ravens, wheatears and chats. He notes that black is not ancestral in the latter two groups which are rarely black outside of deserts. Buxton could not explain this coloration pattern which he deemed paradoxical owing to the assumed increased absorption of radiation by black coloration, and he suggested that black coloration in these birds was inherited or neutrally adaptive. Meinertzhagen (1954) noted that no white birds inhabit the Arabian desert (although pale coloured birds are present), and Burtt (1981) claimed that the predominance of black coloration in desert birds renders plumages more resistant to abrasion. Howell *et al.* (1974) noted that the darkest gull species nest in arid terrains and hot climates.

If one assumes a thermoregulatory function for black and white coloration, the ecological distribution of endotherm colour morphs seems to support the "white heats better" hypothesis. However, many authors have shown that, at temperatures below thermoneutrality, irradiated black animals can reduce their metabolic rates and the cost of endothermy to a greater extent than white animals. This supports the "black heats better" hypothesis. Experimental evidence supporting both facets of the controversy is examined below in sections (i) and (ii).

(i) "Black heats better" in endotherms

In 1925, Cartwright & Harrold postulated that avian metabolism is greatly affected by the absorption of radiant energy. Since then, black coloration has been shown to absorb more visible radiation than white coloration in the uninsulated areas of many birds and mammals. Burtt (1986) demonstrated the thermal significance of coloration in the uninsulated legs of warblers. He calculated that dark legs absorb more solar energy than light legs. He suggests that dark-legged birds are thus at a thermal advantage in that they have a more northern winter distribution across North America and can delay migration into the colder temperatures during fall. Ohmart & Lasiewski (1971) suggested that sunning roadrunners expose a naked patch of black dorsal skin in order to absorb solar radiation directly. Blum (1961) calculated that in human skins, black coloration can absorb 30 % more visible radiation than white coloration.

However, as previously mentioned, heat flow is complicated by insulation, and a quantification of the radiation absorbed at the surface of a coat does not necessarily predict the heat flow towards the skin, and the resulting heat load experienced by the animal. Nevertheless, a suite of experiments supports the fact that irradiated black animals can reduce their metabolic energy expenditure below the TNZ significantly more than white animals. These experiments were initiated by Hamilton & Heppner (1967), who showed that white zebra finches, exposed to artificial sunlight at temperatures below thermoneutrality, used 22.9 % less energy once dyed black. They concluded that black coloration maximised the absorption of solar energy. Lustick (1969) repeated these experiments with dark cowbirds, albino finches and dark-grey zebra finches and found a 26 % reduction in the metabolic rate of dark birds when exposed to artificial radiation, as opposed to a 6 % reduction in white birds. Results also showed that the lower limit of the thermoneutral zone had shifted from 35 °C to 25 °C. He concluded that sunning behaviour of dark birds at temperatures below thermoneutrality presented a saving of metabolic energy.

This decrease in metabolic rate below thermoneutrality has been ascribed to a decrease in conductive heat loss, brought about by a decreased temperature gradient between the skin and the coat surface (Cowles *et al.* 1967, Heppner 1969, Heppner 1970, Neal & Lustick 1975, Dmi'el *et al.* 1980). Lustick *et al.* (1970) also confirmed that exposure to insolation decreased temperature gradients within the plumage of redwinged blackbirds in temperatures below the lower critical temperature (T_{lc}). They also found that at temperatures above the T_{lc}, the thermal gradient was reversed with a net flow of heat into the birds. This suggests that black coloration could impose a thermal stress on endotherms at high ambient temperatures.

However, working with black and brown cowbirds and grey and albino zebra finches, Lustick (1971) found no significant difference in energy conservation amongst black, brown or grey birds which were exposed to artificial insolation at 10 °C. He concluded that black has no thermal advantage over the other dark colours in terms of heat conservation at low temperatures, and agreed with Cowles *et al.* (1967) that thermoregulation could be only one of the numerous selective pressures acting on plumage coloration. In retrospect, the findings of Morton (1967) confirm this view because he showed that insolation can be a significant factor in the energy metabolism of white-crowned sparrows, which are dark but not black.

Research on mammals also supports the "black heats better" hypothesis. Finch & Western (1977) showed that the heat stress on black cattle was 16 % more than on brown cattle and 58 % more than on white cattle. Finch *et al.* (1980) quantified that solar heat gain was twice as great in black Bedouin goats as in white goats. Further research on black and white Bedouin goats by Dmi'el *et al.* (1980) supported the results of Finch *et al.* (1980) and concluded that the increased heat load imposed by black coloration places black goats at a thermal disadvantage on hot summer days. However, the black goats are able to maintain constant body temperatures by dissipating the excess heat through panting and sweating (Dmi'el & Robertshaw 1983). Moreover, at ambient temperatures of 12.2 °C, under sunny conditions, black goats are able to reduce their metabolic rates significantly more than white goats, thus enjoying an energetic advantage during cold, sunny winter days.

As previously mentioned, dark coloration can impose thermal stresses on animals at high ambient temperatures (Lustick *et al.* 1970, De Jong 1976, Dmi'el *et al.* 1980, Finch *et al.* 1980). In addition, Lustick *et al.* (1978) and Ellis (1980), working on Herring gulls and dark and white herons respectively, reached the same conclusion. However, the interacting effects of behavioural changes and convective properties were found to minimise heat stress in these two studies.

The effect of colour on irradiated animals at temperatures below the T_{lc} thus seems to be well documented; dark coats absorb more solar radiation, and decreased temperature gradients in the coats reduce conductive heat loss and enable dark animals to reduce their metabolic rates more than white animals. However, metabolic research is most conveniently pursued under laboratory conditions, or controlled field conditions. It is important to note that this applies to all the research quoted above in support of the "black heats better" hypothesis. As a result, the effects of convection, angle of insolation, level of P, and changes in posture and orientation on heat gain have often been neglected. Experiments dealing with these effects are reviewed later in this chapter. However, it may be stated here that enough evidence exists to show that the results obtained under laboratory conditions can not always be extrapolated to natural conditions, and "black may not heat better" in the field.

(ii) "White heats better" in endotherms

Earlier experiments by Stullken & Heistand (1953) suggested that white coloration may afford improved heat conservation at low temperatures, owing to its lower emissivity. These experiments were conducted with naturally black, black-dyed and white mice, and results revealed that black mice had higher metabolic rates at low temperatures than white mice. However, an examination of Kirchoff's law reveals that the authors interpreted their results incorrectly: Kirchoff's law states that emissivity is equivalent to absorption only at the same wavelength of the electromagnetic spectrum. According to Wien's displacement law, the radiation emitted by a body is a function of the absolute temperature of the body, thus biological tissues, which are at temperatures between approximately 0-50 °C, emit radiation in the middle infrared. Hammel (1956) and Barnes (1963) calculated that light and dark Arctic homeotherms, and human skins, act as black body absorbers in the middle infrared (4000-20 000 nm) and have emissivities of approximately 0.98 in this range. Thus, the fact that a black surface absorbs most visible radiation (400-700 nm) provides no estimate of the emissivity of the surface in the middle infrared.

An alternative explanation for the results obtained by Stullken & Heistand (1953) is provided by Heppner (1970), who noted that the strain of black mice used by Stullken & Heistand is a very active strain, and that this strain may become more active at lower temperatures, showing higher metabolic rates. In addition, he suggested that the insulating properties of the coat of the black-dyed mice may have been affected by the dye, causing a greater heat loss through the coat. Heppner (1970) also calculated that the emissive properties of black and white feathers in the infrared region are nearly the same. In addition, Svihla (1956) showed experimentally that coloration in white and black-dyed rats had no effect on coat reradiation or heat conservation, and Kelly *et al.* (1954) reported no difference in emissivity between black and white swine in wavelengths over 3000 nm. Thus the arguments which claim that white coloration increases heat conservation owing to decreased emissivity are incorrect, and other answers must be found to explain the occurrence of white coats in cold areas.

A possible answer emerged with a mathematical model which investigated the radiant flux in an irradiated coat (Kovarik 1964). The model revealed that absorption in dark coats occurred close to the surface, thereby reducing the depth of penetration of radiation. A large amount of surface radiation was lost by reradiation, and the coat itself provided insulation against the flow of heat to the skin. In light coats, absorption of radiation occurred further into the coat owing to deeper penetration of radiation and lower surface absorbance. Heat flow generated within the coat was divided between the animal and the environment, and Kovarik calculated that heat loads at skin level would be greatest for some intermediate colour, neither very dark nor very light. Experimental verification of this model was provided by Macfarlane *et al.* (1956) and Hutchinson & Brown (1969). Macfarlane *et al.* (1956) calculated that skin temperatures in shorn Merino sheep (white fleece exposed) reached higher values than skin temperatures in unshorn sheep. The fleece of the latter was three times as thick and contained dark tips where most of the radiation was absorbed, thus more heat was lost to the environment than to the animal. Working with dark and light cattle coats, Hutchinson & Brown (1969) calculated that radiation penetrated deeper into white coats than dark coats. In addition, convection increased heat loss of black coats more than white coats. In still conditions, heat loads at skin level were greater for dark coats, while at wind speeds between 0-7 m s^{-1}, the effect of colour on heat load was reduced, white coats sometimes resulting in greater heat loads.

Although Kovarik and Hutchinson & Brown demonstrated that radiation may penetrate deeper into white coats, neither study can be used to predict heat loads at skin level of animals in the field. As noted by Cena & Monteith (1975a), Kovarik's model incorporated artificial boundary conditions which preclude a direct comparison between his results and field measurements, and the experiments of Hutchinson & Brown did not demonstrate a consistent relationship between coat colour, radiation and heat load.

Agreement between theoretical equations and direct measurements of radiative transfer in coats was provided by Cena & Monteith (1975a). The main parameters of their equations were the length, number and radiative properties of individual hairs and the reflectance of the skin. Using sheep's fleece, they predicted and measured that a short white coat and a dark skin would be the most effective trap for solar energy. In a second paper (Cena & Monteith 1975b), they emphasized the danger of using laboratory measurements of coat thermal conductivity to test the heat balance of animals under natural conditions, owing to the interacting effects within coats of molecular conduction, and previously neglected effects of free convection (induced by temperature gradients) and radiation transfer between hairs.

The "white heats better" hypothesis is further supported by experimental work on harp seals, *Pagophilus groenlandicus*. For adult harp seals, solar heating per unit incident radiation was greater for light parts of the coat than for dark parts (Øritsland 1970,1971). This occurs because radiation is transmitted to the skin by diffuse scattering, and the white hairs act as optical fibres guiding radiation towards the skin (Øritsland 1971, Øritsland & Ronald 1973, Grojean *et al.* 1980). Solar heat load at skin level was also related to air temperature, wind speed, solar radiation, and the angle of insolation and wind direction to the pelt surface (Øritsland 1971, Øritsland & Ronald 1973), but the authors could not quantify the combined effects of these parameters on heat load. Øritsland (1970,1971), also demonstrated the effect of spectral energy distribution on the reflectance of pelt surfaces. Reflectance increased in both light and dark pelts between 300-1000 nm, with the greatest differences (30 %) in the near infrared (750-900 nm). Thereafter, Øritsland & Ronald (1978) showed that heat load at skin level was positively correlated with both hair transmittance and coat reflectance. Their pioneering calculations of hair transmittance show that it can no longer be assumed that transmittance has a negligible effect on heat loads at skin level. They suggested that the methods of calculating the interception fraction *p* , developed by Cena & Monteith (1975a), would possibly have to be revised. Øritsland & Ronald (1978) also suggested that the combined effects of high pelage and individual hair reflectance, and the relatively thick fur, would act as a "heat trap" (owing to absorption occurring at levels close to the skin. This absorbed heat is "trapped" by the pelage, which acts as a barrier to reradiation in the long wavelengths). Ray & Smith (1968) measured both skin and fur temperatures in insolated pelts of the Weddell seal *Leptonychotes weddelli,* and found that they rose at faster rates and to higher equilibrium temperatures than black-bulb temperatures. The authors suggested that these seal furs also acted as "heat traps".

It has also been suggested that Arctic plants such as pussywillow catkins and Arctic cotton grass may warm by "trapping" absorbed heat (Krogg 1955). Willow catkins have shiny, transparent hairs which may allow light to pass through to the dark centre of the catkin, but may be opaque to infrared radiation coming off the centre, thus forming a heat trap. The shiny bracts which cover spikelets of cotton grass may function in the same way. These observations are in agreement with Cena & Monteith's (1975a) prediction that a white coat and dark skin is the most efficient trap for solar energy.

The research reviewed thus far has demonstrated that white coats may acquire greater heat loads than black coats owing to a greater penetrance of radiation into light coats and the greater effect of convection on heat loss in dark coats. Heat flow through coats was also shown to depend on the optical properties of individual hairs, and transmittance was shown to be more important than previously suggested. As mentioned in the conclusion of section (i), further experimental analysis has shown that wind speed, the angle of the incident radiation and behavioural responses can negate the differential heating effects of dark and light coloration, and may even reverse these effects, causing greater heat loads in white coats. Experiments which have dealt directly with these effects are discussed below.

A detailed analysis of radiative heat loads in black and white pigeon plumages revealed that in depressed plumages, the radiative heat gain was always greater in black plumages. However, differences between black and white plumages converged with increasing wind speed (Walsberg *et al.* 1978). At wind speeds over 3 m s^{-1}, erected black plumages acquired lower heat loads than erected white plumages. This was due to the greater effect of convective heat loss upon black plumages, which absorbed most of the incident radiation in the surface layers, and thus conducted less heat to the skin. The authors concluded that plumage depression in black birds could reduce cold stress on cold, sunny, windy mornings, and plumage erection could reduce heat stress on hot, sunny, windy afternoons. Consequently, black birds may be at a thermal advantage in hot desert regions. Howell *et al.* (1974) suggested that grey gulls *Larus modestus* thermoregulate in the same way by controlling ptiloerection. These results are supported by Shkolnik *et al.* (1980), who calculated that the heat loads gained by men wearing black or white Bedouin robes in the desert were equal. Although surface temperatures were higher in insolated black robes, skin temperatures were the same under both coloured robes. The results could be explained by a "chimney effect", which occurs on the inside of the black robe as a result of free convection caused by the rising of a boundary layer of warmer air at the surface of the robe. A study by Marder

(1973b) on the brown-necked raven *Corvus corax ruficollis* showed that black plumage surfaces heated up more than light coloured feathers when insolated, but skin temperatures remained similar. He attributed this to the increased convective loss in black plumages, and the possible increased penetrance of visible radiation into light feathers. Marder calculated that forced convection, brought about by normal flight, could serve to dissipate any excess heat gained by birds, by decreasing or even reversing the temperature gradient through the plumage.

The angle of incident radiation greatly affects the penetration of solar radiation into fur (Skuldt *et al.* 1975), and Monteith (1973) noted that the reflectance of natural surfaces increases at angles of incidence over 45°, regardless of colour. The latter effect has been demonstrated for cattle (Riemerschmid & Elder 1945), ungulates (Hofmeyr 1981) and birds (Lustick *et al.* 1980). Lustick *et al.* (1980) showed how the angle of insolation affected heat loads in grey and white plumages of bicoloured herring gulls *Larus argentatus*. Absorptivities of the grey and white areas were 50 % and 15 % respectively, and when the angle of insolation was 90°, grey plumages transmitted four times as much heat as white plumages. However, over 160°, no significant differences existed in heat transfer between the two plumages. The authors concluded that postural adjustments could render a dark bird thermally white with regard to radiative load.

Mechanisms of behavioural thermoregulation which minimise the differential heating effects of coloration thus include flight (forced convection, Marder 1973b) and postural adjustments (Lustick *et al.* 1980). The importance of ptiloerection in determining heat flow has been demonstrated by Walsberg *et al.* (1978). The combined effects of orientation and postural adjustments were shown to reduce heat gain in herring gulls (Lustick *et al.* 1978). By orienting towards the sun, birds exposed only the white breast to direct sunlight, and the surface area exposed to sunlight was reduced. Furthermore, Lustick *et al.* (1979) demonstrated the importance of microhabitat selection in reducing the effects of radiation in juvenile herring gulls. Lustick (1983) concluded that vertebrates are in a genetic trap with respect to coloration, *i.e.* coloration as a response to thermal environmental stress cannot change very fast. This may be untrue for some vertebrates, such as lizards, who are able to alter their coloration with changes in ambient temperature (see Chapter 1). However, Lustick stated that the complex behavioural patterns of vertebrates can override the thermal consequences of coloration, and animals can rapidly adjust to their thermal environments by employing behavioural shade seeking, postural adjustments, changes in orientation, ptiloerection, evaporative water loss (panting and sweating), and microhabitat selection.

Thus, in conclusion, sufficient evidence exists to suggest that "white does heat better" under certain environmental conditions, and behavioural mechanisms are able to control some of the variables which determine heat flow through coats, thereby rendering dark and light coats thermally similar. However, if convective properties are removed and behavioural mechanisms are disallowed, black coats usually gain greater heat loads (harp seals may be an exception), but these unrealistic conditions do not always apply to animals in the field. It thus seems that the "white heats better" hypothesis may explain the occurrence of white polar and black desert animals. However, the selective advantages of crypsis in white polar animals and the possible resistance to abrasion in black desert plumages are examples of other factors which should not be neglected. This emphasizes the need for an integrated approach in the analysis of the selective advantages of coat and plumage coloration.

This study tests the hypothesis that black and white coloration in two species of marine birds has been selected for its thermal implications. Cape gannets and Cape cormorants were chosen as experimental animals for the following reasons: Cape gannets possess a predominantly white plumage, whereas Cape cormorants are totally black (Plate 4). Neither species displays sexual dimorphism in size or coloration. The two species nest adjacent to one another on Bird Island, Lamberts Bay (South Africa) (Fig. 2, Plate 5), and thus experience similar macrometeorological conditions, although the micrometeorological conditions of their preferred nesting sites do differ. During the breeding season, birds are confined to their nests and thus present an ideal opportunity to compare the thermal consequences of colour for their heat budgets. The hypothesis of the study is tested by attempting to answer the following questions:

1. Do black or white plumages acquire greater heat loads at skin level?
2. How do convection and the angle of insolation affect these heat loads?
3. How do coloration, behavioural thermoregulation and environmental variables interact in determining the heat loads?
4. If coloration does not have thermal advantages, which other forces may have selected for coloration in these two species?

As outlined in the general introduction, the questions were dealt with as follows:

Questions 1 & 2: The reflectances of bird plumages were measured at different angles of incident radiation. The effect of convection on temperature gradients set up across irradiated plumages was calculated in the laboratory. A model was developed for predicting heat flow across plumages (Chapter 6).

Questions 3 & 4: Behavioural thermoregulation was monitored with concurrent body temperatures (measured with radio-transmitters), and micro-meteorological conditions. The thermal role of plumage coloration, and other factors which could select for black and white coloration in these birds, are discussed (Chapter 7).

Plate 4a. The Cape gannet, *Morus capensis*.

Plate 4b. The Cape cormorant, *Phalacrocorax capensis*.

Plate 5. Nesting Cape gannets and Cape cormorants on Bird Island, Lamberts Bay.

CHAPTER SIX

PHYSICAL PROPERTIES OF CAPE GANNET AND CAPE CORMORANT PLUMAGES

INTRODUCTION

The amount of solar energy gained by a coat is dependent on the optical, structural and insulative properties of the coat, as well as the optical properties of the individual feathers or hairs, and the skin colour beneath the coat (Chappell 1980a, Ohmart & Lasiewski 1971, Øritsland & Ronald 1973, Walsberg 1988a, 1988c). Walsberg (1988a) calculated that two desert squirrels of similar colour (*Ammospermophilus harrisi* and *Spermophilus tereticaudus*) differed in their solar heat gain by 40 %, owing to differences in fur structure and hair optics. In addition, microenvironmental variables such as angle of insolation and wind speed have been shown to negate the differential heating effects in dark and light coloured birds (Lustick *et al.* 1980, Walsberg *et al.* 1978). Thus heat gain at skin level cannot be predicted by surface colour alone.

It is the purpose of this chapter to quantify the additional heat load, resulting from solar radiation, which is placed upon breeding birds with differently coloured plumages. Plumage reflectance is measured in experiment (1), and an integrated mean effective absorbance is calculated for birds exposed to varying angles of incidence of solar radiation. In experiment (2), the effect of convection on plumage temperature gradients is examined in the laboratory. Finally, a biophysical model is developed in section (3). The model predicts the additional heat load placed on differently coloured birds in the field, and presents these loads as percentages of field metabolic rates (FMR). The model integrates the effects of environmental variables (air temperature, radiation intensity, wind speed), and variables defined by the animals themselves (body temperature, plumage coloration and depth, mass and surface area), on heat loads.

(1) REFLECTANCE

INTRODUCTION

In this experiment, the reflectance of the plumage surface of the Cape gannet and Cape cormorant is measured at varying angles of incidence to solar radiation. The resulting reflectances at each angle are integrated into a mean effective absorbance, which is then compared with the absorbance measured at an angle normal to solar radiation. Assuming that absorbance = 1 - reflectance, the total amount of solar energy impinging upon a bird of a particular size and colour is calculated. Resulting values are compared later (in section 3) with results predicted by the model, which recognizes that energy which is not reflected by a plumage is not necessarily absorbed, and may be reflected, or transmitted, within the plumage towards the skin. The calculations of the model require the reflectance term which is measured in this section.

PROCEDURE

Plumages used for reflectance measurements were obtained from the dorsal surfaces of freshly killed adult birds of each species. The birds were skinned and their untreated plumages frozen until use. All readings were taken within two months of skinning. No sexual dimorphism occurs in the plumages of either species, thus male and female plumages were pooled within species for experiments.

The method used to measure reflectance was adapted from the technique developed by Hofmeyr (1981). A double pyranometer (Middleton & Co.), calibrated under solar radiation and certified by the C.S.I.R.O. of Australia, and a Fluke 73 digital multimeter were used for all radiation measurements. The outer glass bulb of the pyranometer measured 4 cm in diameter and the black, inner sensitive surface measured 2 cm (Fig. 22). Four thin, steel legs of 5 cm lengths were added to the base of the bulb to ensure that the distance between the black sensitive surface and the plumage would be kept constant during readings. If the bulb of the pyranometer remained unrestricted, 100 % radiation could be received from only an infinitely flat surface. However, the sections of plumage used for measurement were approximately 11 X 12 cm because this was the

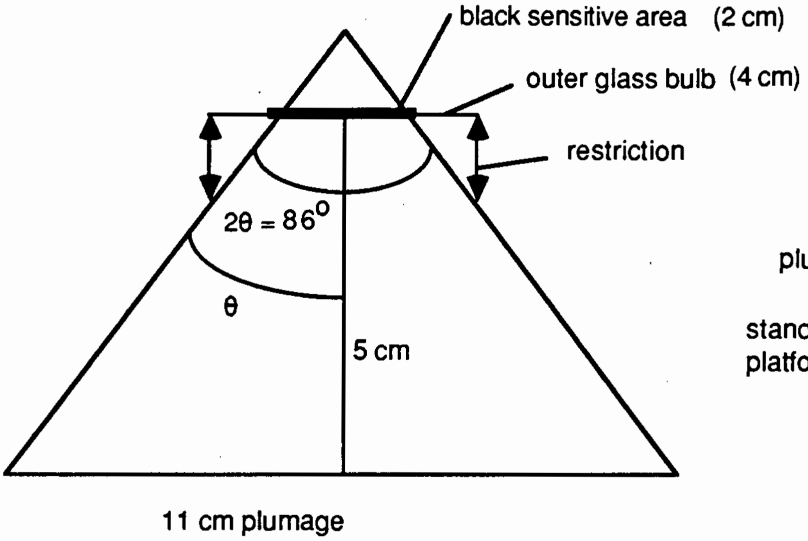


Fig. 22. Pyranometer restriction.

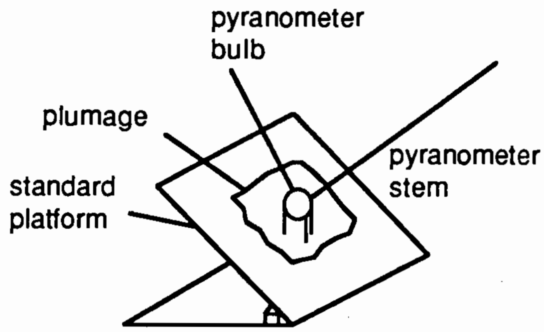
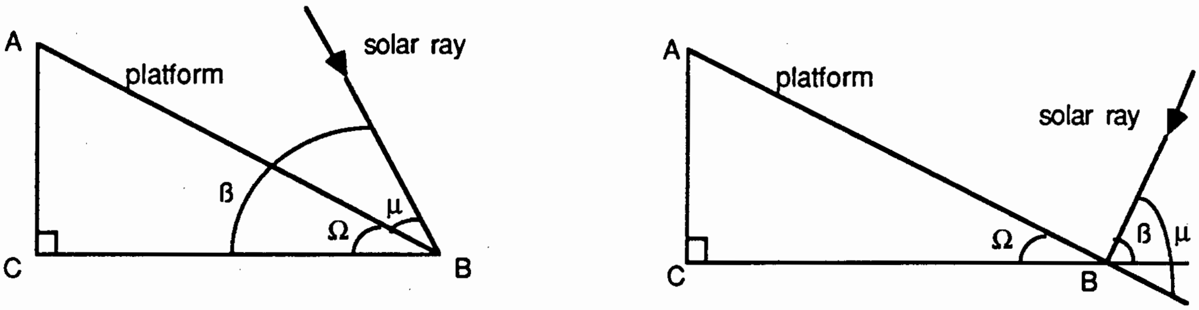
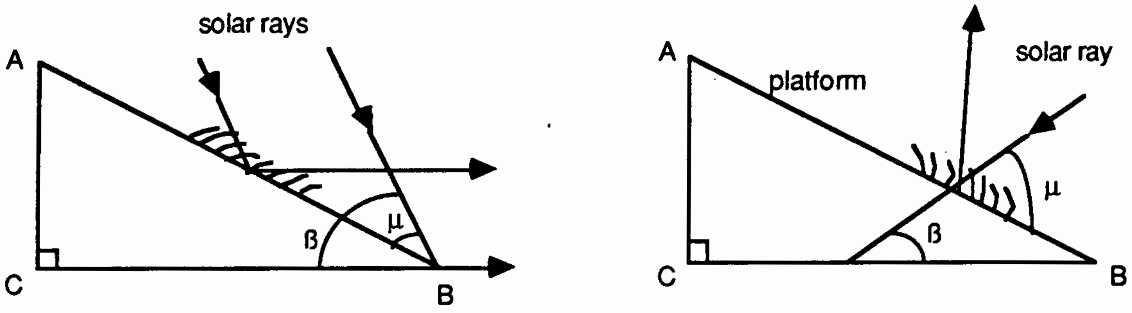


Fig. 23. Adjustable platform.


(a)

(b)

Fig. 24. Angles of incidence (μ), platform (Ω) and solar altitude (ß).


(a)

(b)

Fig. 25. Relationship between direction of feathers, angle of incidence (μ) and solar altitude (ß).

largest section that would remain flat when mounted on a platform. The radiation received from a plumage, as a percentage of that received from an infinitely flat surface, can be calculated from the following equation:

$$\% = 100 \sin^2\theta \qquad (1)$$

where 2θ is the angle of acceptance of the pyranometer (Hutchinson *et al.* 1975). Thus, a value of 86° for 2θ ensured that 100 % of the radiation received by the pyranometer was from the plumage (Fig. 22). In order to vary θ, strips of black insulating tape of pre-calculated widths were placed at the base of the glass dome. Trigonometry was used to calculate these widths.

At a particular time, the curved surfaces of a bird will receive direct solar radiation from many different angles of incidence. The total solar radiation reflected from a live bird will thus be an integrated value of the reflectances of solar rays impinging on the bird at many different angles. Reflectance values were thus measured at seven different angles of incidence (5°, 15°, 30°, 45°, 60°, 75° and 90°) at various times throughout the day. This was achieved by mounting the plumages on an adjustable platform which could be positioned at any angle between the horizontal and the vertical (Fig. 23). Care was taken to ensure that each plumage was mounted in a "normally" depressed state (*i.e.* the feathers were allowed to lie in a natural state, and were not artificially erected). Fig. 24a shows the relationships among angle of incidence (μ), angle of platform (Ω) and solar altitude (β), where the latter is the angle of the sun above the horizon. Solar altitude at a particular time was calculated from the following standard equations :

$$\sin \beta = \sin \varnothing \sin \partial + \cos \varnothing \cos \partial \cos t \qquad (2)$$
$$t = 15(\text{SAST} - 2\text{ hr} + E + \lambda_E) \qquad (3)$$

where $\varnothing$ = Latitude (degrees, - for South)
∂ = Declination (degrees, - for South)
t = local hour angle of sun (degrees)
SAST = South African standard time (hours)
E = GHA - UT (hours)
GHA = Greenwich hour angle
UT = Universal time (GMT)
λ_E = Longitude (hours)

The values E and ∂ were obtained from the Star Almanac for Land Surveyors (1984). Once β was known, the desired value for μ was achieved by calculating the distance AC with the formula AC

$= AB \sin (\beta - \mu)$ or, when μ exceeded β, $AC = AB \sin (\mu - \beta)$ (Fig. 24b). Plumages were mounted with the feathers facing 180° away from the sun's azimuth (Fig. 25a). When μ exceeded β, both the plumage and the platform were placed facing 180° away from the sun's azimuth (Fig. 25b).

Reflectance values were calculated as follows. The platform was set to the desired angle and the pyranometer was clamped into position above and parallel to it (Fig. 23). The platform was coated with white matt paint, which had a reflectance of 0.95 in the visible range and served as a standard. The total direct solar radiation incident on the platform was measured with the upper, unrestricted bulb of the solarimeter. Diffuse radiation from the sky was measured by shading the solarimeter and platform with a black shield held approximately 1 m above the platform. The total radiation reflected from the standard and the plumage was measured with the restricted, bottom bulb of the solarimeter. The diffuse component of the total reflected radiation was measured only at $\mu = 5^\circ$, 15° and 30°. According to Riemerschmid & Elder (1945), while the sun is at higher altitudes, too large a part of diffuse sky radiation is obscured when the plumage is shaded. Thus the mean reflectance for diffuse radiation at angles 5°, 15° and 30° was used to calculate the diffuse component of the total reflected radiation for the higher angles of incidence. Plumage reflectance at each angle of incidence was calculated using the following equation :

$$\text{Reflectance} = \frac{\text{TRP} - \text{DRP}}{\text{TRS} - \text{DRS}} \times 0.945 \qquad \textbf{(4)}$$

where TRP = Total radiation reflected from plumage

DRP = Diffuse radiation reflected from plumage

TRS = Total radiation reflected from standard

DRS = Diffuse radiation reflected from standard

Fifteen sets of measurements were taken at each angle of incidence of a total of five cormorant plumages. Twelve sets of measurements were taken of four gannet plumages. Average reflectance values were established for each species at each angle of incidence.

MEAN EFFECTIVE ABSORBANCE (*a*)

An estimate of the amount of visible energy absorbed by a bird's plumage can be calculated as a function of the intensity of the incident radiation, the surface area (and corresponding projected area) of the plumage exposed to the radiation and the angle at which the radiation strikes the plumage. This angle affects the percentage radiation absorbed by the plumage. The mean effective absorbance for the entire plumage exposed to solar radiation is thus an integrated value of the absorbances of all the different areas of the plumage exposed to different angles of incidence. In order to calculate this mean, each bird was considered as a circular cylinder of length L and radius r, placed at right angles to the incoming radiation (Fig. 26). The arc XY (Fig. 26) was then divided into 50 equal angles, and the total E absorbed over the 50 respective projected areas of these angles was calculated as follows:

Over the arc XY, and along the length of the cylinder (Fig. 27a), the projected area (PA) is:

$$PA = L \cdot r \ \sin ß_i \ (m^2)$$

The energy (W) absorbed over XY along the length of the cylinder is thus:

$$\begin{aligned} q_{abs\,XY} &= (1-p\,(ß_i))\, q_{inc} \cdot PA \\ &= (1-p\,(ß_i))\, q_{inc} \cdot L \cdot r \ (\sin ß_i) \qquad (5) \end{aligned}$$

where q_{inc} = incident radiant flux density $(W\ m^{-2})$

$p\,(ß_i)$ = reflectance as a function of $ß_i$

If the angle $ß_i$ is decreased by some decrement $\Delta ß$, the new angle will be $(ß_i - \Delta ß)$ (Fig. 27b). The projected area of the arc AY along the length of the cylinder is then:

$$\begin{aligned} PA(1) &= PA - PA(2) \\ &= (L \cdot r \ \sin ß_i) - (L \cdot r \ \sin (ß_i - \Delta ß)) \end{aligned}$$

The energy absorbed over AY along the length of the cylinder is thus:

$$\begin{aligned} q_{abs\,AY} &= (1-p\,(ß_i))\, q_{inc} \cdot PA(1) \qquad (6) \\ &= (1-p\,(ß_i))\, q_{inc} \cdot L \cdot r \ \left[(\sin ß_i) - (\sin (ß_i - \Delta ß))\right] \end{aligned}$$

The energy absorbed over the arc XY along the length of the cylinder, as calculated in equation (6), can thus be recalculated with $ß_i$ = 50 different angles. This allows the integration of the absorbances at each of these different angles. Fig. 27c shows how the projected area of the arc AB can be calculated by a further decrement in angle by $\Delta ß$. Thus, in Fig. 27c, the projected area of the arc XY along the length of the cylinder is:

$$\mathrm{PA} = \mathrm{PA}(1) + \mathrm{PA}(4) + \mathrm{PA}(5)$$

which is represented by the following summation equation:

$$\mathrm{PA} = L \, . \, r \sum_{i=\Delta ß}^{\Pi/2} \left[\sin ß_i - \sin (ß_i - \Delta ß)\right]$$

The energy absorbed over XY along the length of the cylinder is thus:

$$q_{\mathrm{tot\,XY}} = q_{\mathrm{inc}} \, L \, . \, r \sum_{i=\Delta ß}^{\Pi/2} \left[\sin ß_i - \sin (ß_i - \Delta ß)\right]\left[1 - p\,(ß_i)\right] \qquad (7)$$

which can be written:

$$q_{\mathrm{tot\,XY}} = q_{\mathrm{inc}} \, L \, . \, r \sum_{i=\Delta ß}^{\Pi/2} \left[\sin ß_i - \sin ß_i \cos \Delta ß + \cos ß_i \sin \Delta ß\right]\left[1 - p\,(ß_i)\right] \qquad (8)$$

The mean effective absorbance of each plumage is given by the summation factor:

$$a = \sum_{i=\Delta ß}^{\Pi/2} \left[\sin ß_i - \sin ß_i \cos \Delta ß + \cos ß_i \sin \Delta ß\right]\left[1 - p\,(ß_i)\right] \qquad (9)$$

in equation (8). Equation (8) does not calculate the heat load on the bird, only the visible radiation absorbed by the surface layers of the plumage.

The energy absorbed over the hemicylinder XZ (*i.e.* an incubating bird with half its surface area exposed to insolation) is simply $2q_{\mathrm{tot\,XY}}$ watts. Values of percentage reflectance for angles of incidence between 0° and 90° were calculated from polynomial equations fitted to the reflectance data obtained for the seven angles previously listed. Percentage reflectance was previously plotted

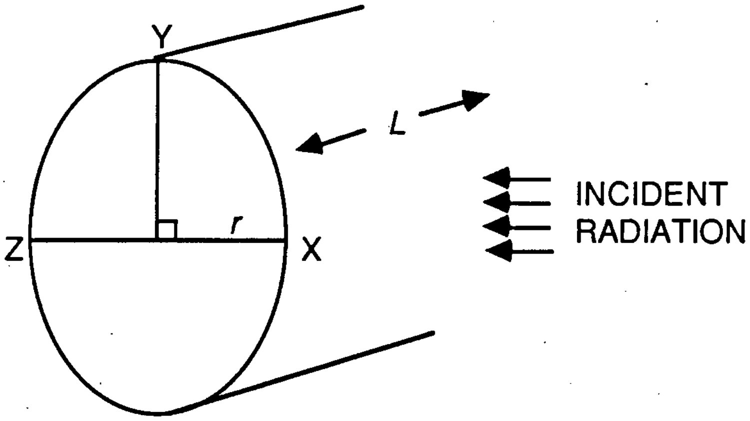


Fig. 26. Cylinder used to calculate the mean effective absorptance of bird plumages.

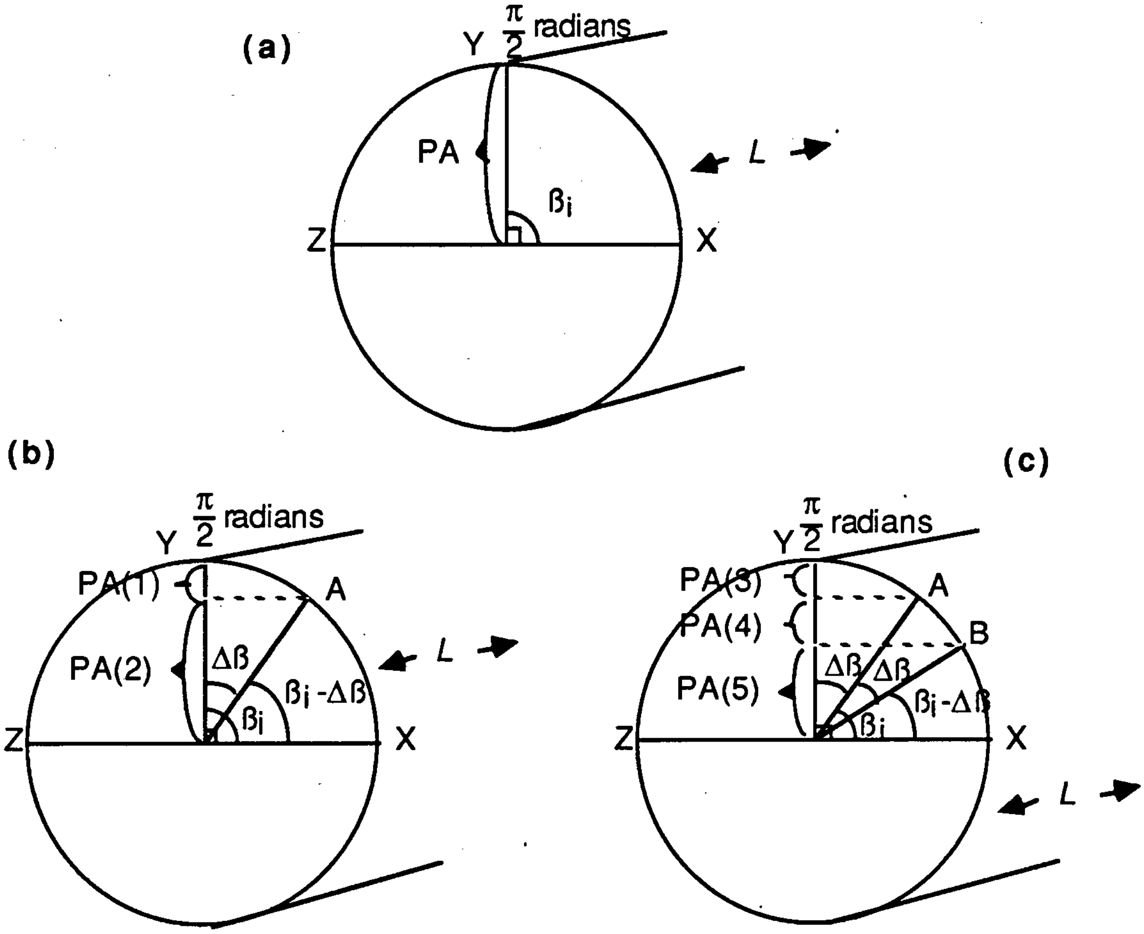


Fig. 27. Angles used to calculate projected area of cylinder.
See text for explanation.

against q_{inc} at each angle of incidence and was found to be independent of q_{inc}. Values of r for both species were calculated by the method of Mitchell (1976). Average bird masses used in these calculations were: gannets 2.645 kg (Jarvis 1971) and cormorants 1.227 kg (Berry 1976). The resultant values of r were 0.069 m (gannets) and 0.054 m (cormorants). Length (L) was measured from the base of the neck to the end of the tail (excluding the tail-feathers). Resultant values averaged from three adults of each species were 0.310 m (gannets) and 0.230 m (cormorants).

RESULTS

Reflectance values for gannet and cormorant plumages as a function of angle of incidence to solar radiation are shown in Fig. 28. Gannet plumage reflectances increased from 77.7 % to 95.3 % with decreasing angles of incidence, whereas a marked increase in reflectance occurred at only 5° for cormorant plumages. Mean absorbances (1 - mean reflectance) and mean effective absorbances (integrated approach) for both species are listed in Table 19. Absorbances at 90° are included in the table for comparison. As previously explained, these absorbance values all represent maximum values, because radiation may also be transmitted through the plumage or reflected towards the skin. It is evident from Table 19 that the mean absorbance calculated from an average of six to seven angles of incidence underestimates the mean effective absorbance calculated with equation (9) by only 0.9 % (gannets) and 1.5 % (cormorants). However, the absorbance at 90° overestimates the mean effective absorbance by 6.4 % in gannets and underestimates it by only 0.5 % in cormorants.

The maximum amount of visible solar radiation absorbed by plumage surfaces of birds of a particular size can be calculated from equation (8) (*i.e.* $2q_{tot\ XY}$). The mean maximum incident radiation during the December 1987 research season was approximately 950 W m^{-2}, thus the plumage of a gannet of dimensions $L = 0.310$ m and $r = 0.069$ m would absorb a maximum of 6.5 W, whereas the plumage of a cormorant of dimensions $L = 0.230$ m and $r = 0.054$ m would absorb a maximum of 20.4 W (Table 19). Table 19 also lists the amount of energy which would

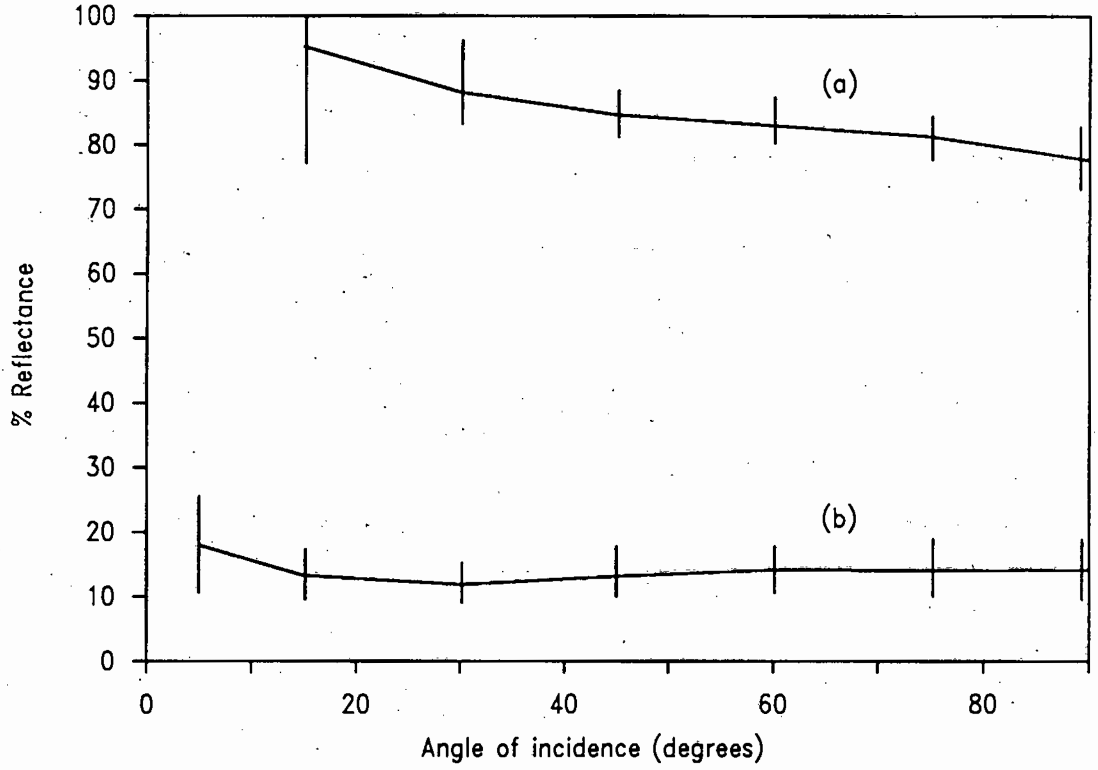


Fig. 28. Reflectance values of Cape gannet (a) and Cape cormorant (b) plumages at different angles of incidence to solar radiation. Vertical lines indicate one S.D. above and below the mean.

Calculations using the mean effective absorbance reveal that the amount of energy absorbed at the plumage surface of gannets is 0.73BMR and 0.27FMR, whereas cormorant plumages may absorb 4.04BMR and 1.49FMR. However, these values are substantially lower at skin level, since all the energy absorbed at the plumage surface is not transmitted to the skin. The energy values reported here are compared in section (3) with the results of the biophysical model.

DISCUSSION

Walsberg (1980), Riemerschmid & Elder (1945), Hutchison *et al.* (1975) and Hofmeyr & Louw (1987) found that reflectance values increased with decreasing angles of incidence in bird plumages, and cattle, large mammal and African ungulate coats respectively. Hutchinson *et al.* (1975) and Walsberg (1980) attribute the increase in reflectance to an increase in effective glossiness at lower angles of incidence, which results in an increase in specular as opposed to diffuse reflection. The plumage data presented here support this argument.

Walsberg (1980) suggested that the percentage change in a bird's net heat flux, owing to angular effects, would be negligible when compared with other avenues of heat exchange. He also concluded that in the passerine *Phainopepla nitens*, absorbance values calculated from near-normal angles of incidence resulted in heat loads which differed from those calculated with the mean effective absorbance by only 4-6 % of the BMR. Similar figures resulting from the present study indicate that this value may increase to 29 % of BMR (or 11 % of FMR) in gannet plumages. However, using an absorbance figure obtained by averaging absorbances at 6 to 7 angles of incidence results in energy loads which differ from those calculated using the mean effective absorbance by only 5-7 % of BMR or 2-3 % of FMR. Therefore, it seems that a reflectance value taken only at a near-normal angle of incidence may not always adequately represent the mean effective absorbance of a bird's plumage, whereas averaging (without integrating) the reflectances over six or seven angles of incidence between 0° and 90° may yield a satisfactory value for an integrated mean absorbance, as the present study has shown.

Calculations show that the potential absorbance at the plumage surface of a white gannet and a black cormorant results in gannet plumages gaining an additional heat load of 0.27FMR, whereas cormorant plumages can absorb up to 1.49FMR, owing to the higher absorbance of black coloration. However, these values are overestimates of the extra heat load at skin level (especially with respect to cormorants), since energy absorbed at the surface of a plumage may be lost by convection, or reradiated in the long wavelengths, before it reaches the skin. Nevertheless, coloration results in plumage surfaces of white gannets and black cormorants differing in potential absorbance of energy by a ratio of 1 : 5.5 % FMR. However, the model in section (3) is needed to quantify the proportion of energy to reach the skin.

(2) PLUMAGE TEMPERATURE GRADIENTS: LABORATORY MEASUREMENTS

INTRODUCTION

The reflectance of a plumage surface is determined largely by coloration, but many additional factors are responsible for heat flow across plumages. Plumage properties such as thickness and density are independent of colour. However, the level of penetrance of radiation into plumages is dependent upon coloration in such a way that dark and light plumages have low and high penetrance values respectively. As reviewed in Chapter 5, many researchers have shown, both mathematically and experimentally, that a greater level of penetration of radiation into light pelages is often responsible for light coloured animals reaching higher skin temperatures and experiencing greater heat loads than dark animals (Kovarik 1964, Hutchinson & Brown 1969, Øritsland 1971, Cena & Clark 1973, Cena & Monteith 1975a, Øritsland & Ronald 1978). The "white heats better" hypothesis outlined previously, predicts that absorption occurs close to the surface in dark pelages, where generated heat is exposed to convective heat loss. However, deeper penetration of radiation into light pelages results in heat generation at levels closer to the skin. These deeper levels are insulated by the pelage from surface convection.

The effect of wind speed on plumage temperature gradients, and net heat fluxes through pigeon plumages, was investigated by Walsberg *et al.* (1978). They found that depressed, and erected white plumages gained greater heat loads than erected black plumages, as wind speed increased. Their experiments confirmed that black plumages lose more heat by convection, and that skin temperatures below irradiated black or white plumages are similar, despite the higher surface temperatures of black plumages.

In the present experiment, excised plumages of Cape gannets and Cape cormorants were artificially irradiated in a wind tunnel in the laboratory, to ascertain the effect of convection on surface temperatures, and to calculate the temperature gradients of plumages at different wind speeds.

PROCEDURE

Temperature gradients across plumages were measured from the same plumage sections used to calculate reflectance. Samples were mounted in an open flow wind tunnel (Fig. 29) and irradiated with a 300 W quartz-halogen lamp. The radiation incident on each plumage was 1000-1300 Wm^{-2}. Constant wind speeds of up to 8 $m\ s^{-1}$ were generated by a fan connected to a regulated DC power supply. The plumages were mounted over an open ended cylinder of acrylamide gel and placed in the test section of the wind tunnel. The feathers lay parallel to, and facing 180° away from, the wind direction. This ensured that the same degree of plumage depression was maintained throughout the experiments. Acrylamide gel was used because its thermal diffusivity is similar to that of animal tissue, owing to its high water content. Two 28 gauge Type T thermocouples were mounted in the centre of the plumage samples, one at the plumage surface and one at skin level. The thermocouples were held in place by a movable rod, attached to a rack-and-pinion scale and mounted on top of the wind tunnel. Each thermocouple was connected to a Bat-4 (Bailey Instruments Inc.) analog thermocouple thermometer which was in turn connected to a Pederson dual pen strip chart recorder.

Plumage temperature gradients were determined at wind speeds of 0, 2, 4, 6 and 8 $m\ s^{-1}$. Heating curves were initiated by switching the lamp on after the system had equilibrated at each particular wind speed. Readings were recorded for an average of 11 minutes. Wind speed was measured with a hand-held Wallac oy thermo-anemometer. All measurements were made inside a constant environment cell where the ambient temperature was kept constant at 15 °C (± 0.5 °C) and

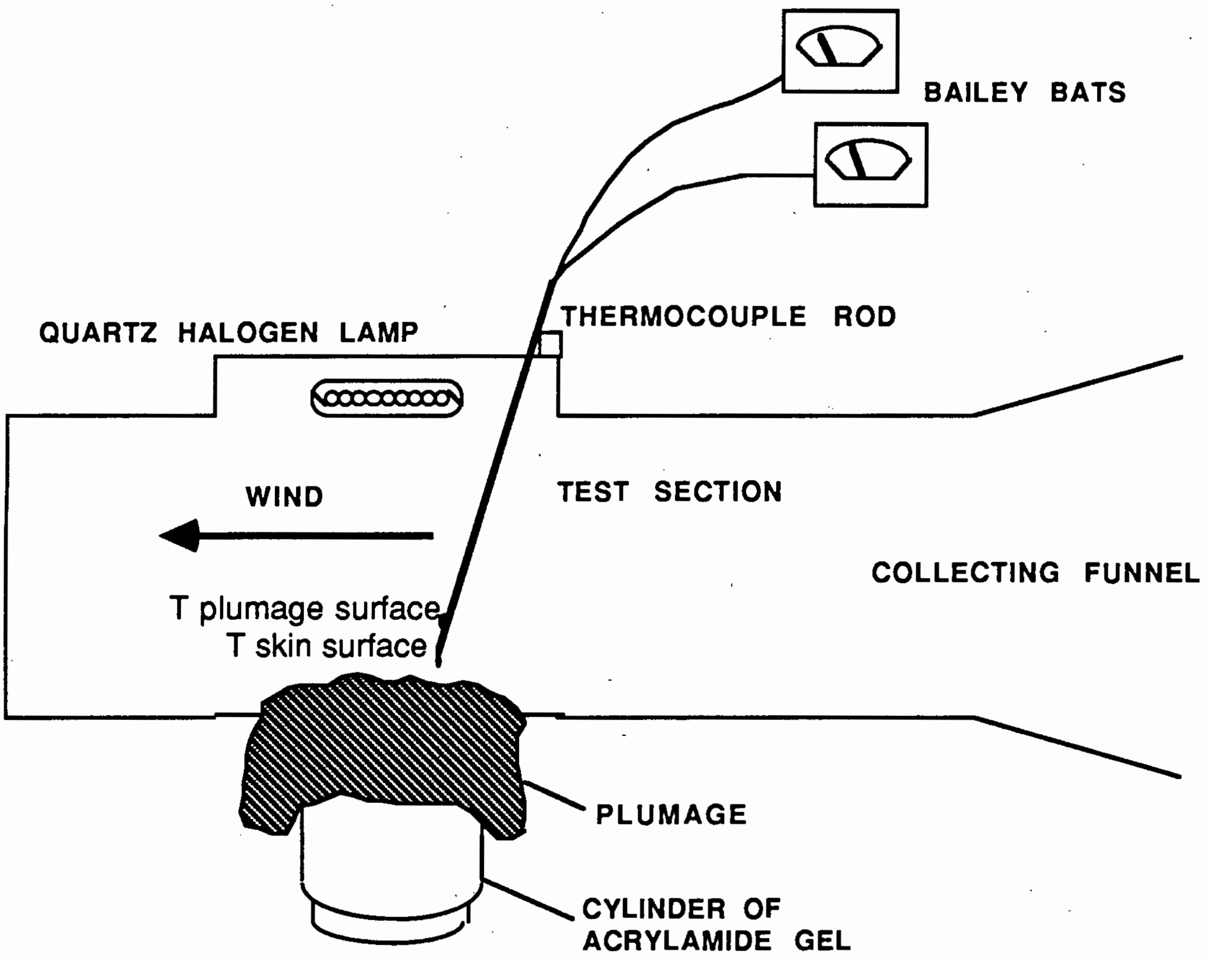


Fig. 29. Schematic diagram of wind tunnel and experimental apparatus. See text for explanation.

the relative humidity at 70 % (± 2 %). At each wind speed, readings were taken from either three or four plumage samples of each species.

Plumage depths were measured by placing a light, thin, wooden rod into plumages, which were laid flat in the same state of feather depression as the plumages used for reflectance and temperature gradient measurements. Measurements were taken from the rod with Vernier calipers. A total of 15 readings were averaged from three cormorant plumages and 10 readings were averaged from two gannet plumages.

RESULTS

Fig. 30 shows the effect of wind speed on the equilibrium temperatures (T_E) reached by the plumage and skin surfaces of each species. Each data point presented in Fig. 30 is an average obtained from three or four plumages. Standard deviations are not included in the figure but ranged between 1.07 - 4.62 °C (only 5 of these values were over 3 °C). It is evident from Fig. 30 that convection decreases the T_E reached by each sample. These effects are most pronounced at wind speeds under 4 m s^{-1}. Between 4-8 m s^{-1}, the percentage changes in T_E of all samples were notably smaller, and very small differences were found between plumage surface and skin temperatures both within and between species. Fig. 30 also shows that cormorant plumage and skin temperatures were affected more by increased convection than gannet plumage and skin temperatures. In still conditions and at 2 m s^{-1}, cormorant plumage surfaces reached significantly higher T_E values than gannet plumage surfaces (t tests, 0 m s^{-1} : $P<0.002$, 2 m s^{-1} : $P<0.1$), and cormorant skin temperatures were also significantly higher than gannet skin temperatures (0 m s^{-1} : $P<0.001$, 2 m s^{-1} : $P<0.05$). However, the gradients set up across the plumages were similar for both species.

Fig. 31 shows that plumage temperature gradients were similar for both species at all wind speeds, and decreased with increasing wind speed. However, once a wind speed of c. 4 m s^{-1} was reached, little further change in plumage temperature gradient was displayed. Over wind speeds of 4 m s^{-1}, a reversed gradient was set up in gannet plumages, where skin temperatures were higher than plumage surface temperatures. These effects were also shown by individual plumages, before

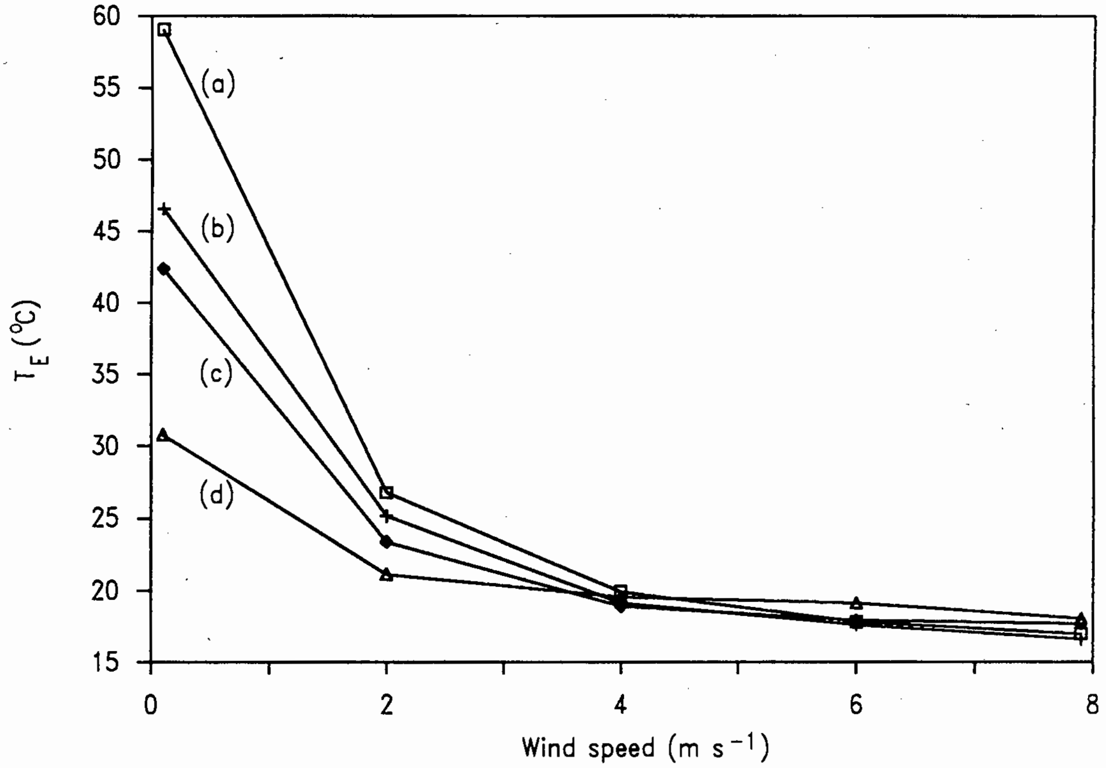


Fig. 30. Equilibrium temperatures of irradiated cormorant plumage surfaces (a) and skins (b), and gannet plumage surfaces (c) and skins (d), as a function of wind speed.

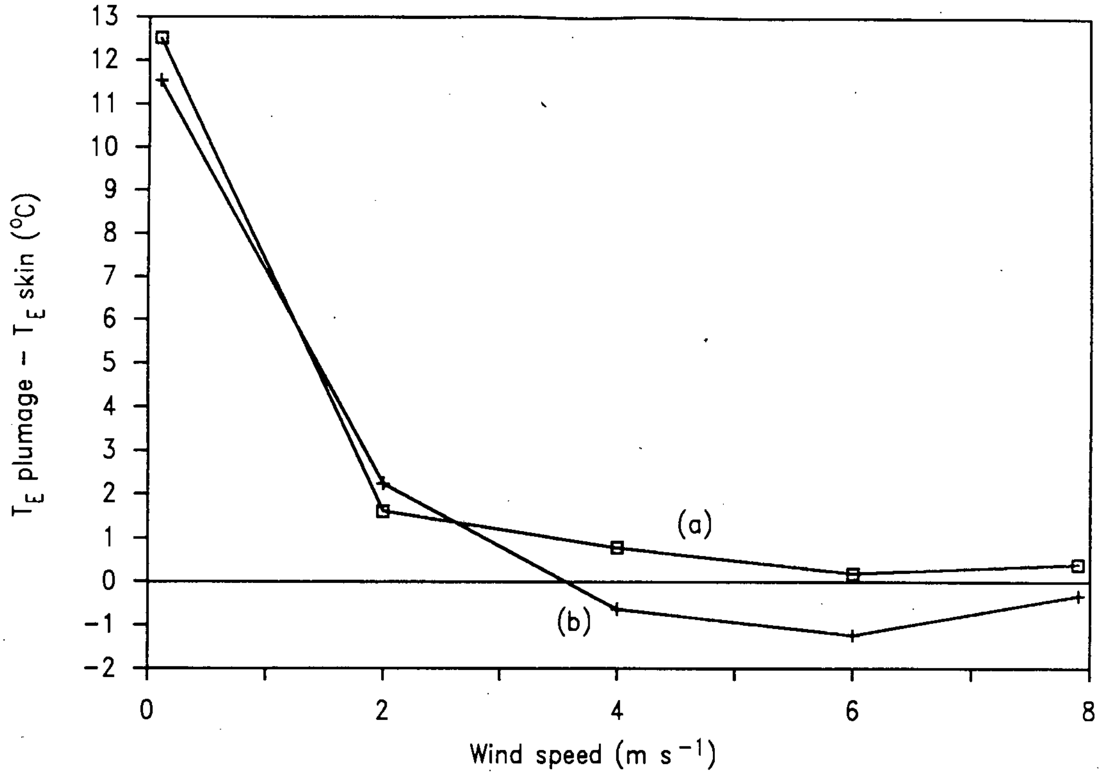


Fig. 31. Temperature differentials across cormorant (a) and gannet (b) plumages as a function of wind speed.

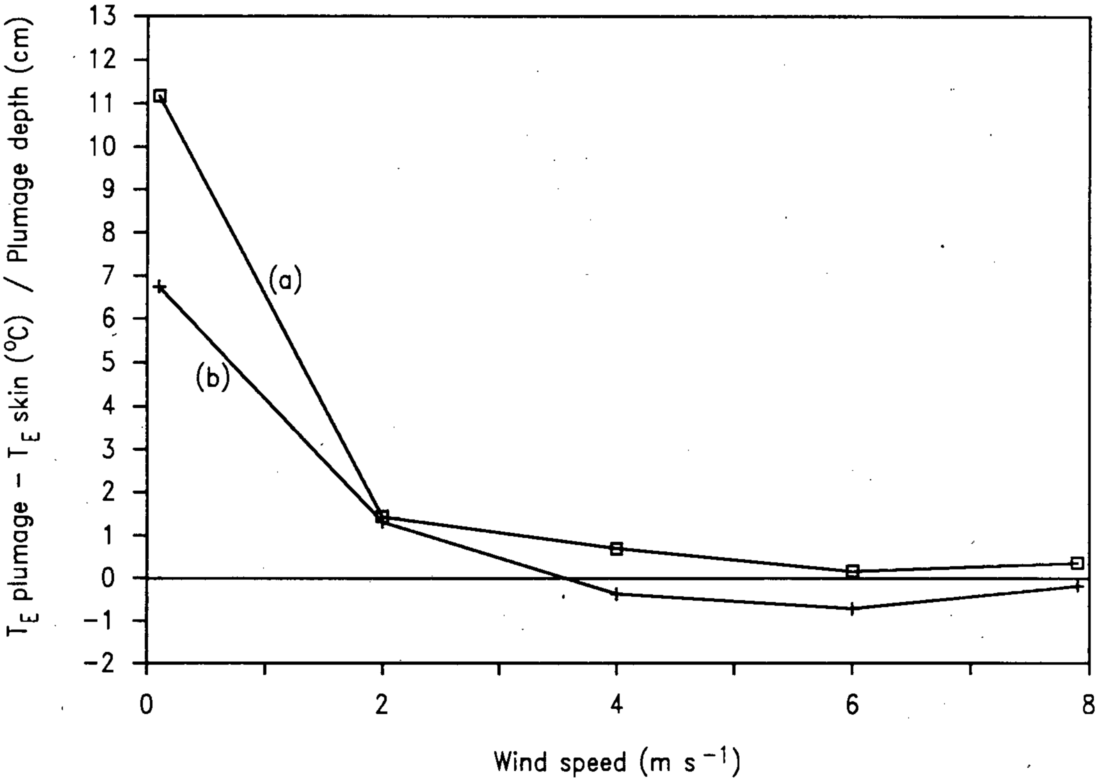


Fig. 32. Temperature differentials per cm depth of cormorant plumages (a) and gannet plumages (b), as a function of wind speed.

the data were averaged. However, these reversed gradients were small (<1.3 °C) and the differences between skin and surface temperatures were not statistically significant.

The average depths of "normally" depressed cormorant and gannet plumages were 1.1 cm (N=15; S.D.=0.1 cm) and 1.2 cm (N=10; S.D.=0.1 cm) respectively. Fig. 32 shows temperature differentials per cm plumage depth, as a function of wind speed. The only notable differences occurred in still conditions, where cormorant plumages displayed a significantly higher temperature differential per cm plumage depth (t test, $P<0.01$). At wind speeds of 2 m s^{-1} and over, very little difference was shown between the two species.

DISCUSSION

It is evident from Fig. 30 that, in still conditions, irradiated black plumages may reach temperatures up to 17 °C higher than irradiated white plumages, and a similar difference may exist between the temperatures of the underlying skins. However, increased convection decreases equilibrium temperatures of plumages and skins, and at a wind speed of 2 m s^{-1}, black plumages (and the underlying skins) may be only 2-3 °C warmer than white plumages and skins. Over 4 m s^{-1}, the differential heating effects of colour are negated by convective heat loss, and all plumages and skins reach similar temperatures. Fig. 30 also illustrates that black plumages lose a greater percentage of heat than white plumages, as wind speed increases. These data are consistent with the measurements made by Walsberg *et al.* (1978) of pigeon plumages and skin temperatures. They found that as wind speed increased from 0.25-9 m s^{-1}, black plumage surfaces cooled from 63-38 °C, whereas white plumages cooled from 44-35 °C. These and the present results confirm the findings of Kovarik (1964), Hutchinson & Brown (1969) and Cena & Monteith (1975a) that absorption occurs closer to the surface of dark pelages, where a large proportion of heat is subsequently lost by convection.

Although the heat load experienced by a bird of a particular colour cannot be calculated from plumage and skin temperatures alone, it is evident from the present study that, at wind speeds as low as 2 m s^{-1}, coloration may no longer affect the heat load experienced by birds. Heat loads of pigeons were quantified in the study by Walsberg *et al.* (1978), and their results are compared with the results of the model in section (3). However, Walsberg *et al.* (1978) found that at wind speeds over 3-5 m s^{-1}, white plumages (either erect or depressed) gained greater heat loads than erected black plumages, but experienced lower heat loads than depressed black plumages at all wind speeds. They also found that in temperature gradients across erect white plumages, skin temperatures were higher than plumage temperatures at wind speeds over 1 m s^{-1}. Date from the present study (Fig. 31) support these results, and reveal that at wind speeds over 2 m s^{-1}, gannet skins were warmer than gannet plumages. Although cormorant plumages were always warmer than cormorant skins, temperature gradients across cormorant plumages decreased to 0 as wind speed increased. Walsberg *et al.* (1978) found similar results for black pigeon plumages, where skin temperatures exceeded plumage temperatures only at wind speeds over 5 m s^{-1}.

(3) HEAT LOADS ON GANNETS AND CORMORANTS: A MODEL

INTRODUCTION

Birkebak (1966) and Porter & Gates (1969) initiated a widespread interest in the quantification of the energy exchange between free-living animals and their environments. Since then, studies of energy exchange in endotherms have concentrated on two areas of research: a) The quantification of the relative contributions of radiation, conduction and convection to heat flow (Hammel 1955, Davis & Birkebak 1975, Skuldt *et al.* 1975, Cena & Monteith 1975a, 1975b, Walsberg 1988b): results of these studies are seldom in agreement, and the only study involving bird plumages was that of Walsberg (1988b). b) The measurement of the standard operative temperature (T_{es}) of an animal in its microenvironment, where T_{es} is defined by Bakken (1976a) as "the temperature of a standard reference metabolism chamber in which an animal with a given, constant body temperature requires the same effective net metabolism heat production to maintain body temperature as it does in the complex environment". T_{es} is then used as an index of sensible heat flow (*i.e.* flow by radiation, conduction and convection, excluding the latent heat of vaporisation of water) between the animal and its environment. The numerous methods employed to calculate T_{es} include the use of invertebrate exoskeletons, painted models of naked animals, heated taxidermic models covered with the relevant pelages, or biophysical heat transfer models (Bakken & Gates 1975, Bakken 1976a, Robinson *et al.* 1976, Bakken 1980, Bakken *et al.* 1981).

In this study, a heat transfer model of heat exchange across avian plumages is developed for the Cape gannet and the Cape cormorant. The advantage of a model is that it allows manipulation of its component variables (*e.g.* reflectance, size, wind speed, solar radiation), and is thus ideally suited to comparing the excess heat loads from solar radiation which may impinge on animals of different colours and sizes, exposed to varying wind speeds and solar radiation intensities. The model developed here integrates the effects of environmental variables (air temperature, solar radiation, wind speed), and properties of the birds themselves (mass; surface area; plumage reflectance, penetrance depth and conductivity; body temperature; conductance through body) on heat flow, and predicts the additional energy gained by birds of both species, under varying environmental conditions.

PROCEDURE: THE MODEL

A model of the components of heat flow across a plumage is developed in Appendix 2. Heat balance equations are derived for nodes at the plumage-air interface (T_{pl}), and the skin-plumage interface (T_{sk}) (see Fig. 47, Appendix 2). The model was used to predict plumage surface and skin temperatures of Cape gannets and Cape cormorants exposed to wind speeds of 0.5, 1, 2, 3, 4, 6, 8 m s^{-1}, air temperatures (T_{air}) of 10 and 25 °C, and solar radiation of 950 and 550 W m^{-2}. (The mean maximum radiation intensity during the 1985-1987 breeding seasons on Bird Island was 950 W m^{-2}, whereas T_{air} averaged between 9-27 °C).

RESULTS

Once plumage and skin temperatures were established, the net heat gain or loss (q) experienced by birds was calculated as follows:

$$q\ (\mathrm{W\ m^{-2}}) = K\ (T_{sk} - T_b) \tag{11}$$

where K = conductance ($\mathrm{W\ m^{-2}\ {}^{o}C^{-1}}$)
T_{sk} = skin temperature (^{o}C)
T_b = body temperature (^{o}C)

In order to calculate the heat exchange across one half of the surface area (SA) of a bird (it is assumed that approximately one half of the SA of an incubating bird is exposed to solar radiation at any particular time), results of equation (11) were expressed in watts (per SA/2), where

$\mathrm{SA} = 0.09\ W^{0.74}\ \mathrm{m^2}$ (W = mass in kg, Peters 1983)
$= 0.18\ \mathrm{m^2}$ (gannets)
$= 0.10\ \mathrm{m^2}$ (cormorants)

Results are presented in Fig. 33. Data in Fig. 33 were then recalculated for hypothetical black gannets and white cormorants. This was achieved by interchanging the colour terms of the model (*p* and a) between species (Fig. 34) (where *p* = plumage reflection, and a = fraction of radiation to penetrate plumage).

In all figures, values > 0 indicate an additional heat load imposed by solar radiation, whereas values < 0 indicate a net heat loss to the environment. It is evident that black coloration is responsible for placing greater heat loads on birds than is white coloration. However, heat loads, and the difference between heat loads experienced by black and white birds, decrease as wind speed increases, and solar radiation decreases. In naturally coloured birds (Fig. 33a), both species experience heat loads at 950 W $\mathrm{m^{-2}}$ solar radiation and T_{air} above 10 ^{o}C, but when solar radiation decreases to 550 W $\mathrm{m^{-2}}$, both species experience heat losses at T_{air} of 10 ^{o}C (Fig. 33b). It is evident that wind speed and T_{air} may affect the energy balance of birds in such a way that heat loads in the two species could be equal if incubating gannets are exposed to lower wind speeds and higher air temperatures than incubating cormorants. This possibility is investigated in Chapter 7. Although increased wind speed decreases net heat gain in both species, cormorants lose more heat by convection than gannets (Fig. 33).

Fig. 34a shows that at 950 W $\mathrm{m^{-2}}$, a black gannet would gain 8-25 W more energy than a white gannet, and a white cormorant would gain 5-13 W less than a black cormorant. The larger mass of

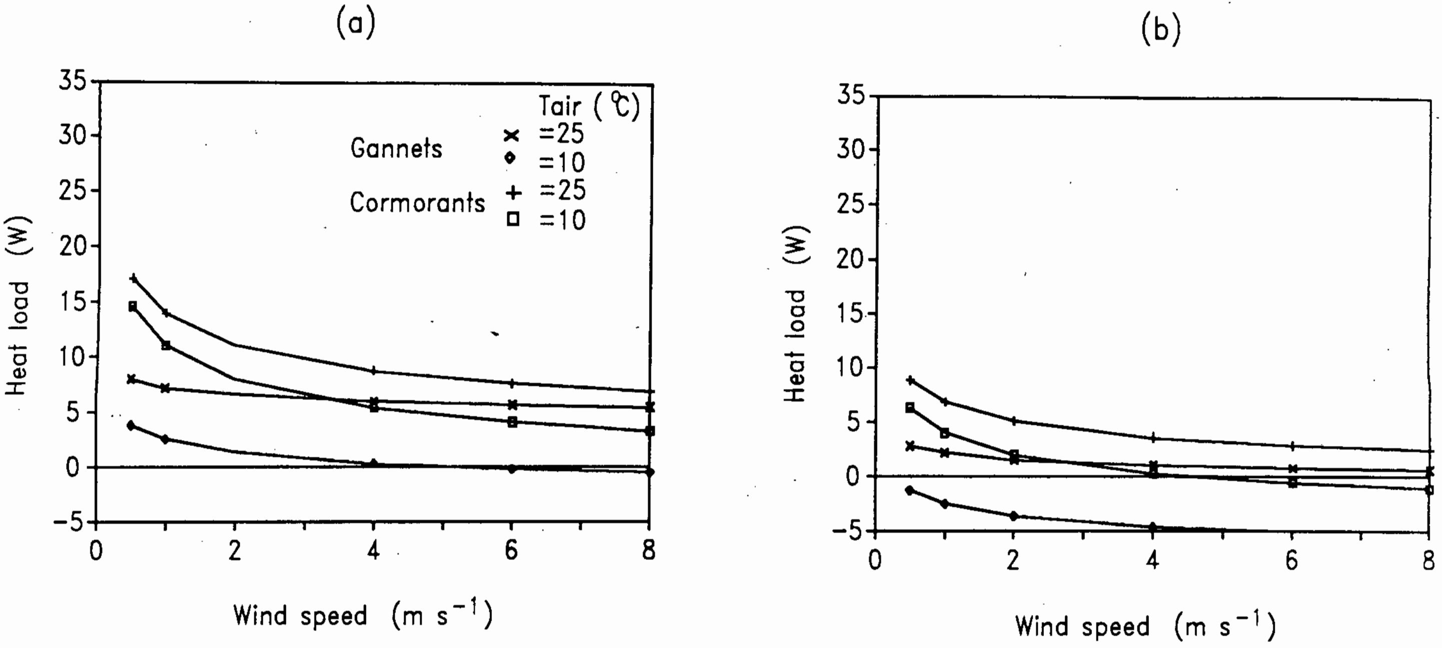


Fig. 33. The effect of wind speed and air temperature on the additional heat load (positive values) or net heat loss (negative values) experienced by Cape gannets and Cape cormorants exposed to (a) 950 and (b) 550 W m^{-2} of solar radiation.

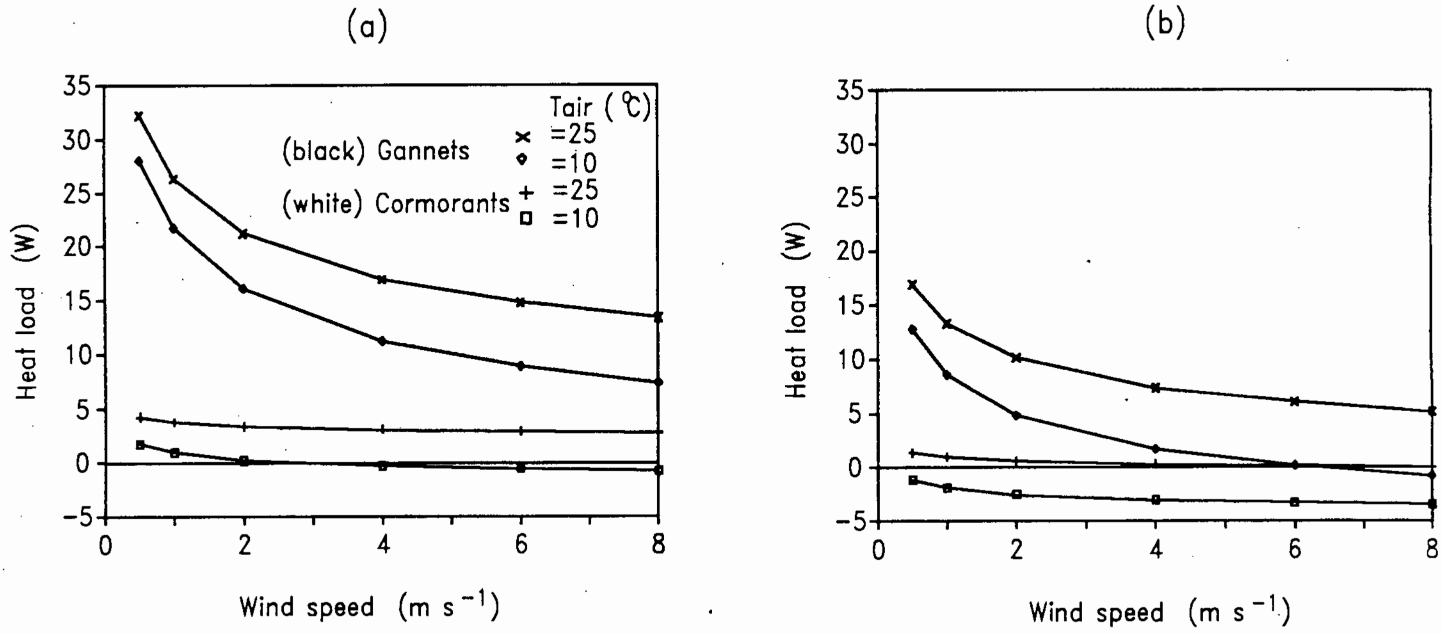


Fig. 34. The effect of wind speed and air temperature on the additional heat load (positive values) or net heat loss (negative values) experienced by hypothetical black gannets and white cormorants exposed to (a) 950 and (b) 550 W m^{-2} of solar radiation.

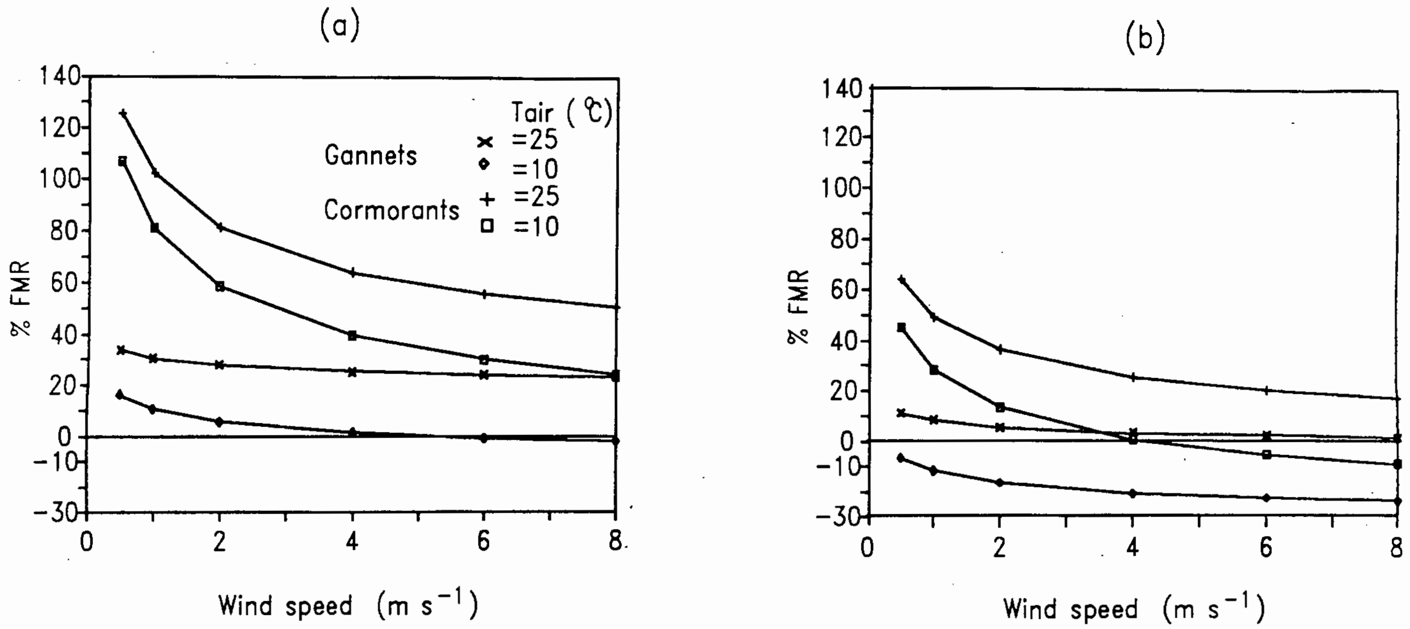


Fig. 35. The effect of wind speed and air temperature on the additional heat load (positive values) or net heat loss (negative values) experienced by Cape gannets and Cape cormorants exposed to (a) 950 and (b) 550 W m^{-2} of solar radiation. Values are expressed as a percentage of field metabolic rate (FMR).

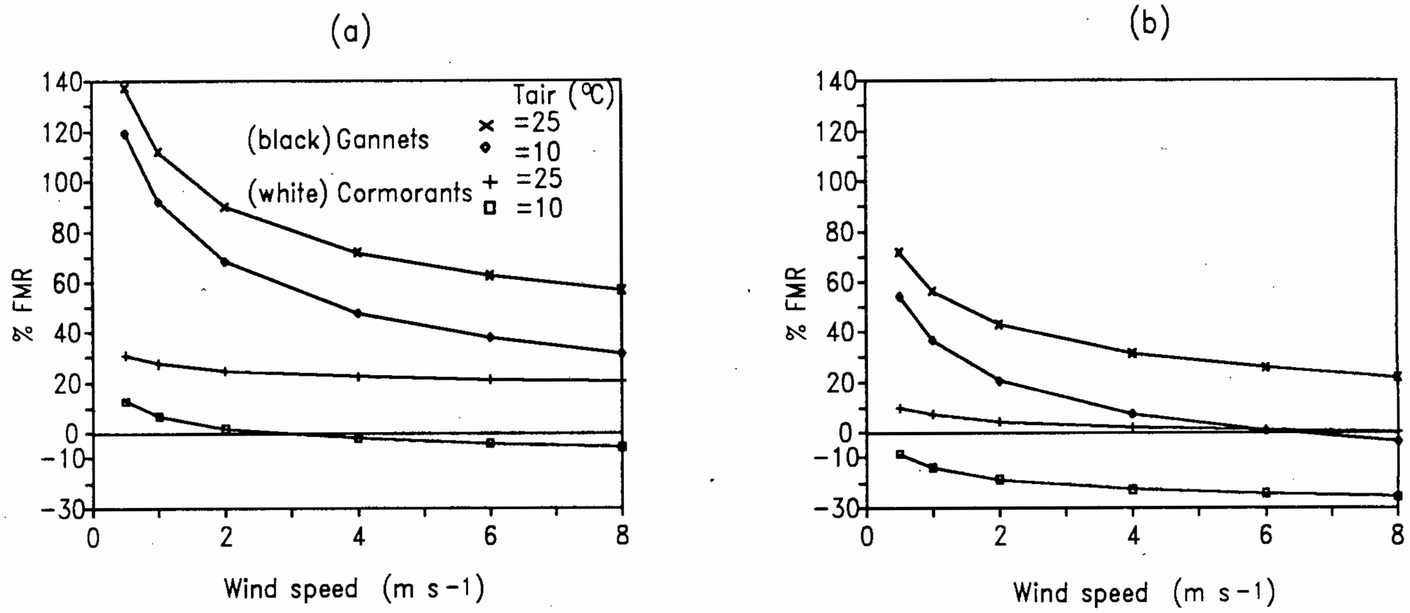


Fig. 36. The effect of wind speed and air temperature on the additional heat load (positive values) or net heat loss (negative values) experienced by hypothetical black gannets and white cormorants exposed to (a) 950 and (b) 550 W m^{-2} of solar radiation. Values are expressed as a percentage of field metabolic rates (FMR).

the gannet results in heat gains of 2-16 W more than those experienced by the smaller black cormorant. At 550 W m^{-2} (Fig. 34b), differences in heat gain between species decrease, but are still larger than differences which occur between naturally coloured birds (Fig. 33b).

Figs. 35 & 36 show the results of Figs. 33 & 34 expressed as percentages of field metabolic rates of each species. Field metabolic rates (FMR) were calculated from Nagy (1987), as described on pp. 123.

Fig. 35a shows that at low wind speeds and solar radiation of 950 W m^{-2}, cormorants may experience heat loads of 1.1-1.3xFMR, whereas gannets would experience heat loads of 0.2-0.4xFMR. These differences decrease with wind speed, and at 4 m s^{-1}, cormorants gain 0.4-0.7xFMR, whereas gannets gain 0-0.3xFMR, depending on T_{air}. Fig. 35b shows that as solar radiation decreases, gannets lose 5-25 %FMR to the environment at 10 °C, whereas cormorants lose 0-10 %FMR at the same temperature if wind speed is over 4 m s^{-1}. Fig. 36 shows that exchanging the colour terms between species results in heat loads (or losses) which are very similar for birds of the same colour (*i.e.* a black gannet would gain a similar amount of heat (%FMR) to a black cormorant). This is due to the relatively larger FMR of the larger gannet, which balances the effect that size has on heat gain (*i.e.* larger animals gain more heat).

DISCUSSION

In experiment (1), the amount of solar radiation intercepted by an incubating gannet and cormorant was calculated, using the measured reflectance value only. It was concluded that at 950 W m^{-2} of incident radiation, a cormorant and gannet would intercept 20.4 and 6.5 W respectively. These values translate to 1.49 and 0.27 %FMR, which represents a ratio of 5.5 : 1. Alternatively, the results of the model predict that, at 950 W m^{-2}, 25 °C and 0.1 m s^{-1}, cormorants and gannets receive 25.3 and 9.9 W respectively, which translates into 1.85 and 0.42 %FMR (a ratio of 4.4 : 1). A direct comparison between these two sets of results is impaired by the fact that in experiment (1) the amount of heat intercepted by the plumage surface is calculated, and no provision is made for the effect of plumage insulation on heat flow to the animal itself. In addition, air temperature and wind speed are not accounted for in the calculations. Nonetheless, the similarity between the two sets of results (both in absolute and ratio form) verifies the predictive and comparative value of the model, and it may thus be concluded that under average midday conditions at the breeding site (950 W m^{-2} and 25 °C), breeding birds experience heat loads which are of a ratio of 4.4-5.5 : 1 (cormorants : gannets), in terms of %FMR.

The maximum additional heat load a cormorant could experience at wind speeds above 0.5 m s^{-1}, and maximum solar radiation, was 1.1-1.3xFMR, whereas gannets would experience 0.2-0.4xFMR in similar conditions. The question lies in whether cormorants are able to dissipate the additional heat load, or whether they experience severe heat stress in these conditions. Firstly, it is relevant that the heat loads calculated in experiments (1) and (3) both represent maximum possible amounts of energy gained, in that both models assume maximal absorbance at flat black or white surfaces. Research by Marder (1973a) on the brown-necked raven showed that at air temperatures of 50 °C, panting birds were able to dissipate 167 % of their metabolic rates by evaporative water loss, whereas at the upper level of their thermoneutral zone (TNZ) (38-40 °C), 100 % of the metabolic heat production was dissipated. It thus seems reasonable to assume that at low wind speeds, the additional heat load (130 % of the FMR) placed on cormorants by solar radiation could similarly be dissipated by panting. Air temperatures causing the onset of panting in breeding birds of both species are investigated in the following chapter. It seems that the heat load of 40 % of the FMR of gannets is adequately compensated for by the panting mechanism of evaporative cooling, and that gannets suffer less thermal stress during midday than cormorants. Thus, if the results of Marder (1973a) can be extrapolated to the present study, panting may be the primary method of heat dissipation in gannets and cormorants (see Chapter 7), since it may be able to dissipate 100 % of metabolic heat, as well as any additional heat load caused by solar radiation, in both species.

However, an additional cooling mechanism exists which may override the differential heating effects of black and white plumages, and may render heat loads on black plumages lower than those on white. This mechanism is ptiloerection, and coupled with increasing convection in the form of wind, erected black plumages may gain lower heat loads then either erect or depressed white plumages. This was confirmed in a study by Walsberg *et al.* (1978), whose results appear in Fig. 37. Over 3 m s^{-1}, it is evident that an erect black plumage gains a lower heat load than white plumages. The results of the present study are included in Fig. 37 for comparison, and the

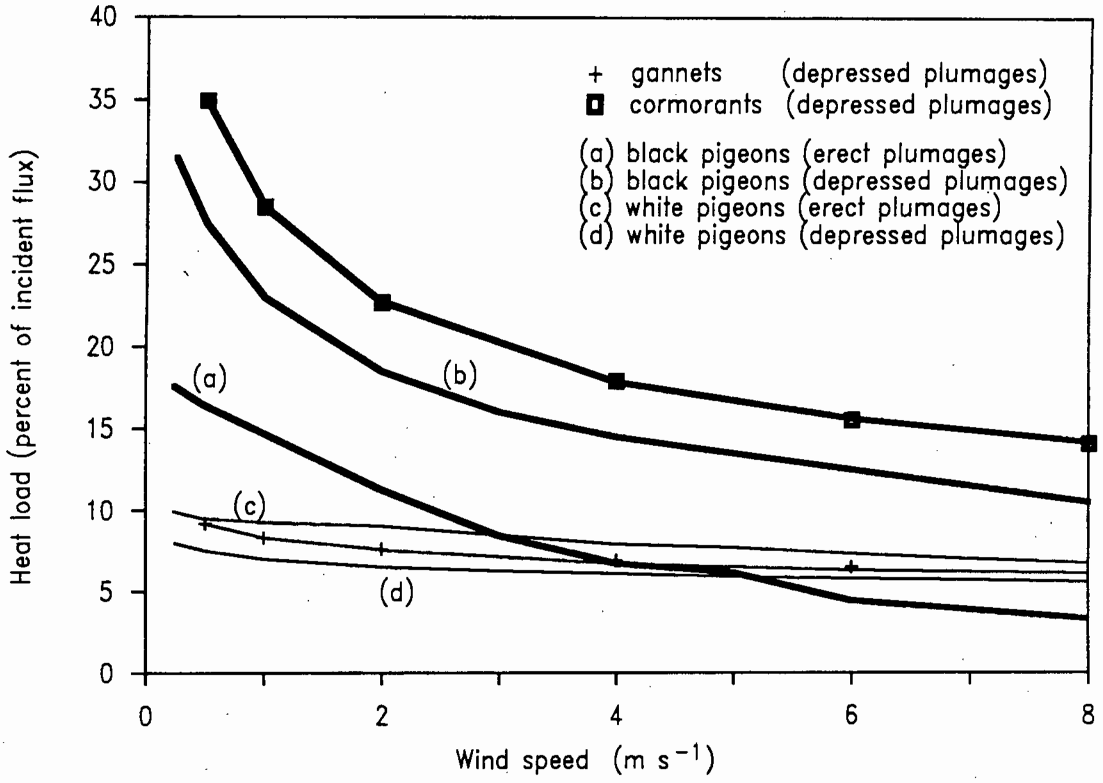


Fig. 37. Comparison of radiative heat load in plumages of Cape gannets, Cape cormorants, and black and white pigeons. Data for gannets and cormorants were calculated by the heat transfer model, whereas data for pigeon plumages are from Walsberg *et al.* (1978).

similarity between the two sets of data further supports the predictive value of the model used in this study. It should be noted that the model calculated heat loads in depressed plumages only, and that heat flow through erect plumages should be quantified empirically, owing to the lack of understanding of the relative contributions of conduction, convection and radiation to the heat transfer processes through erect plumages.

Although black plumages experience greater heat loads during still conditions and intense solar radiation, the effects of increased wind speed and reduced insolation on decreasing heat loads in black plumages are well illustrated in Figs. 33 & 35. Heat loads in white plumages do not diminish at the same rate. This confirms the predictions of Kovarik (1964), Hutchinson & Brown (1969), Cena & Monteith (1975a) and Walsberg (1988a) that heat is absorbed nearer the surface of dark pelages, where it is subsequently lost by convection, whereas insolation penetrates deeper into light pelages before absorption occurs.

The results of the present model indicate that heat loads on black and white plumages converge as wind speed increases. They also show that in cooler conditions (Fig. 35b), cormorants may be at a thermal advantage owing to the small but positive heat loads they experience due to their black coloration. Gannets would have a net heat loss to the environment (5-25 %FMR) at 550 W m^{-2} insolation and 10 °C air temperature, as opposed to the positive heat loads cormorants would experience at wind speeds under 4 m s^{-1} (0-45 %FMR). In fact, a hypothetical white cormorant exposed to the same conditions would lose between 8-22 %FMR, thus the black coloration of cormorants results in a saving of up to 22 %FMR at wind speeds under 4 m s^{-1} (Fig. 36b).

As opposed to the net heat loss quoted above for a white gannet in cool conditions (5-25 %FMR), a black gannet would gain 0-55 %FMR (Fig. 36b). Thus black colour in a hypothetical gannet would result in a saving of up to 25 %FMR (provided that thermoregulation is a large component of the total energy budget). These energy saving figures are in close agreement with figures from the literature reviewed in Chapter 5, for the energy savings of basking animals. At temperatures below the TNZ, white crowned sparrows, roadrunners, juvenile herring gulls and various mammals were shown to save between 7-41 % of standard metabolism when exposed to insolation (Morton 1967, Ohmart & Lasiewski 1971, Lustick *et al.* 1979, Neal & Lustick 1974, Thiessen *et al.* 1982). Hamilton & Heppner (1967) showed that below the TNZ, white zebra finches used 22.9 % less energy when dyed black. This figure is similar to the energy savings of 22-25 % predicted by the model for black cormorants and gannets exposed to cool conditions.

WHAT IS THE THERMAL IMPLICATION OF COLOUR TO ENERGY BALANCES OF GANNETS AND CORMORANTS ?

In experiment (1), simplified calculations of heat load, based on reflectance values only, predicted that black cormorants would experience a heat load 5.5 times greater than that of white gannets. This ratio represents a load of 20.4 W for cormorants and 6.5 W for gannets. In experiment (2), it was shown that at a wind speed of 2 m s^{-1}, plumage temperatures do not differ between the two species, and it was predicted that increasing wind speed ameliorates (or may negate) the differential heating effects of black and white plumages. The heat loads which were predicted by the model in experiment (3) were similar to those calculated in experiment (1) (*i.e.* at low wind speeds and high levels of insolation). However, the model calculated heat loads for depressed plumages only, and the similarity between the results of this study and those of Walsberg *et al.* (1978) (for heat loads in depressed plumages of black and white pigeons), allows one to assume that erect cormorant plumages may act in a similar way to the erect pigeon plumages investigated by Walsberg *et al.* (1978). In addition, ptiloerection may result in cormorants gaining lower heat loads than gannets as wind speed increases. It may be concluded that ptiloerection and microhabitat selection may interact to negate the differential heating in differently coloured plumages in hot conditions, but at temperatures below the TNZ, cormorants may be at a thermal advantage due to their black coloration, since the higher plumage surface temperatures would retard heat loss to the environment, as suggested by Cowles *et al.* (1967). However, if the prevailing ambient temperatures at a site 0° 45' South of the breeding site of Cape gannets and Cape cormorants are investigated, it is apparent that the average daily minimum temperature, between the years 1936-1984, ranged between 9.8-13.5 °C during the summer months (August-March), whereas average maximum temperatures ranged between 16.3-21.1 °C (Weather Bureau, Pretoria). Thus breeding birds are not exposed to severe temperature fluctuations, and evaporative water loss (panting) may be adequate to dissipate any extra heat load imposed on black cormorants during ambient temperatures up to 25 °C. During the coldest conditions (± 10 °C), the maximum amount of heat loss experienced by a gannet is predicted to be 25 %FMR. Since low temperatures are reached mostly at night when insolation cannot affect heat loads, black and white birds would differ in terms of their heat loss only because of size differences.

From data in this chapter, it can be predicted that postural adjustments (as a form of behavioural thermoregulation) will be secondary to panting, as a mechanism of heat dissipation, in both species (pp. 135). It is also predicted that neither species will show behavioural adaptations to ameliorate severe thermal stress (either heat or cold), owing to the temperate nature of their breeding environment. These factors are investigated in the following chapter, which also examines the degree of microhabitat selection by both species for breeding sites. This information will reveal if the thermal implications of coloration in the two bird species are further diminished by the possible selection of windy and cooler nesting sites by the black cormorants.

CHAPTER SEVEN

MICROHABITAT SELECTION AND BEHAVIOURAL THERMOREGULATION IN CAPE GANNETS AND CAPE CORMORANTS

INTRODUCTION

It has been well documented that birds are able to influence their heat exchange with the environment by employing various behavioural adjustments of posture, orientation and microhabitat selection. At temperatures below their TNZ, numerous species are able to reduce their metabolic costs of endothermy by orientating so as to maximise the surface area exposed to insolation (Ohmart & Lasiewski 1971, roadrunners; Storer *et al.* 1975, Ryan & Heagy 1980, grebes; Hennemann 1982, 1983, anhingas and double-crested cormorants). Many other species utilise changes of posture and orientation as a means of dissipating excess heat (Howell & Bartholomew 1961, Whittow 1980, albatrosses; Bartholomew 1966, masked boobies; Shallenberger *et al.* 1974, red-footed boobies; Jefford & Urban 1970, white-breasted cormorants; Frost *et al.* 1976, Jackass penguins; Bartholomew & Dawson 1979, Heermann's gulls; Mahoney *et al.* 1985, frigate birds). Many of these authors have concluded that dark plumages may gain more energy from solar radiation than light plumages, but only if the dark plumage is depressed (as opposed to erect) and the environment is sunny and windless. However, after considerable research on Herring gulls (Lustick *et al.* 1978, 1979, 1980), Lustick (1983) concluded that microhabitat selection and behavioural thermoregulation can override the consequences of colour in the thermal budgets of birds.

The biophysical model of heat transfer in the previous chapter predicted that black cormorants experience greater heat loads from solar radiation than white gannets, and that these differences are due to plumage coloration. However, these predictions may be valid only if both plumages are depressed (as opposed to erect), if birds of both species adopt similar thermoregulatory postures and orientations, and are exposed to the same microclimatic conditions. The influence of microhabitat selection and behavioural thermoregulation were not considered in the model, and these factors are investigated in this chapter.

The purpose of this study was to record the behavioural responses and body temperatures of Cape gannets and Cape cormorants simultaneously, as ambient temperature increased, in order to determine if any differences exist in the thresholds of panting, the postural responses, orientational changes or body temperatures of the two species as their heat loads increase. This comparison is facilitated by the fact that these species nest adjacent to each another on Bird Island (Fig. 2), and thus respond to the same macro-environmental variables (*e.g.* sun and wind direction) at any particular time.

PROCEDURE

STUDY AREA

Bird Island (32° 05' S, 18° 18' E) on the west coast of South Africa (Fig. 2) is used by seven species of seabirds for breeding purposes. However, Cape gannets and Cape cormorants are the dominant species, together contributing to over 99% of the total breeding population (Jarvis & Cram 1971). The island, which has an area of 3.2 ha, consists of two rocky outcrops and a large, central, artificially paved area from which guano is scraped. Cape gannets utilise this flat, central area for nest building purposes whereas the Cape cormorants prefer the low rocky outcrops (1- 3 m in height).

Behavioural thermoregulation of gannets and cormorants was monitored daily for selected periods during three breeding seasons: October 1985 (7 days), January 1987 (12 days) and December 1987 (8 days). During all three seasons, the study site comprised a hide placed in an area between the gannet and cormorant colonies (Plate 5). Nests of both species were situated adjacent to one another in this area and thus experienced similar macroclimates. This facilitated the comparative analysis of the thermoregulatory behaviour of the two species.

METEOROLOGICAL DATA

An MCS 101 field logger placed within the hide collected meteorological data over each 24 hour period at 15 minute intervals. Instantaneous and average values were obtained from each sensor. Ambient temperature was measured with an MCS 153 temperature probe coated with white enamel paint at the tip. The probe was either shielded from direct sunlight with aluminium foil, or left unshielded (Christian & Tracy 1985). Two MCS temperature probes (151 and 153), coated with black enamel paint, were used to measure black-bulb temperature. All temperature probes were previously calibrated to 0.2 °C against an SABS (South African Bureau of standards) standardised mercury thermometer.

Wind speed and wind direction were measured with an MCS 177 cup anemometer and an MCS 176 wind vane respectively. A hand held Wallac oy thermo-anemometer was used to measure wind speed profiles above the ground. An MCS 174 relative humidity meter monitored changes in humidity. Additional humidity readings were calculated from wet and dry bulb temperatures measured with a Zeal whirling psychrometer. Direct solar radiation was measured with a Delta-T Device tube solarimeter. Finally, fog and cloud were recorded by dividing the sky into fractions of eight. The ambient and black-bulb temperatures, wind speed, wind direction and relative humidity were all measured at 20 cm above ground level. All micrometeorological parameters were measured within 5 m of the nests under observation.

SPHERICAL MODELS

Owing to size differences between species, spherical models of different sizes were placed in the gannet and cormorant colonies, in order to measure three components of the micrometeorological environment: (1) black spheres to integrate radiative and convective properties, (*i.e.* to measure radiative temperature) (2) silver spheres to measure air temperature, and (3) white spheres, which were kept wet, to integrate the air temperature, humidity and convective properties of the microenvironment (Plate 6). The spheres were all hollow and were constructed with "Plaster of Paris". Black spheres were coated with matt black paint, silver spheres were covered with aluminium foil and white spheres retained the natural white colour of the "Plaster of Paris". These white spheres were wet at hourly intervals with distilled water. Spheres in the cormorant and gannet colonies had diameters of 10.6 and 13.7 cm respectively. These diameters were calculated using the method of Mitchell (1976). This method allows one to calculate the diameter of a sphere which will have the same convective properties as an animal of a defined mass. Although the spheres were designed to measure differences in micrometeorological conditions experienced by birds of different sizes, the data generated by these spheres must be interpreted in the light of the findings of Paw U (1987). He calculated (by partial differential analysis) that operative temperatures measured with spherical models may differ from temperatures measured with accurate mounts of experimental animals by up to 7°C.

Temperatures of spheres were measured at 5 min. intervals by MCS 151 and 153 temperature probes connected to the MCS 101 field logger, or by 28 Ga Cr-Al thermocouples and an Omega 871 digital thermometer. Each temperature probe (or thermocouple) was placed in the centre of the sphere, through a small hole in its base.

Plate 6. Spherical models in the gannet colony (a) and the exposed cormorant colony (b).

Nest temperatures (*i.e.* temperatures adjacent to incubating birds) of both species were measured with black spheres (as described above) which were suspended from a movable rod. Measurements were made randomly during one day in the Dec. 1987 sampling period, in order to ascertain the variability of nest temperatures.

BEHAVIOURAL THERMOREGULATION

During the three breeding seasons when field data were collected, ten nests of each species were chosen for observation. These nests occurred within a 5 m radius from the centrally placed hide (Plate 5) and contained either eggs or newly hatched chicks. This ensured that breeding adults were easily visible and that only one parent would be present on the nest during most of the day. Breeding pairs of both species without eggs or chicks, or with older chicks, were not confined to their nests or to incubating postures and were thus unsuitable for observation. During 1987, a sample of 10 gannet chicks was also observed. The chicks were fully feathered and were almost the same size as the adults, but were still confined to their nest sites. Gannet chicks of this size possess a black plumage, which is later replaced by the white plumage of the adults.

Birds under observation were marked with dots of enamel paint on their heads, necks or wings. The birds were surveyed throughout the day at 30 minute intervals and the activity, thermoregulatory posture (including panting) and orientation relative to the sun and wind, of each bird, was noted. Nest attendance spells were monitored for each pair of birds under observation.

Orientations of birds were monitored as follows: the angle between magnetic north and (a) the sun's azimuth, (b) wind direction, and (c) the long axis of the bird's body, were calculated for each reading (using the bird's head as the direction of the long axis). A hand-held Suunto compass was used for all measurements. The sun's azimuth was measured from the shadow cast by a vertical rod and wind direction was measured either from a wind vane or from a flowing streamer. Meteorological data were recorded as described earlier. Data were then analysed using the computer programme DIRECT, developed by Mimmack *et al.* (1980) for the statistical analysis of two-dimensional directional data (see Appendix 3). The programme calculates a modal vector for the mean direction of orientation in a particular sample of 10 birds, and tests for randomness of the mean. Each resultant modal vector is then statistically defined as indicating either a random, or a preferred orientation of birds in the sample. Each sample tested consisted of 10 birds (rarely 8 or 9) of a particular species.

BODY TEMPERATURE

Birds were induced to swallow Elvax-coated, temperature sensitive radio transmitters, previously calibrated to 0.1 °C against an SABS standardised mercury thermometer. Calibrations measured the time taken for the transmitter to emit 20 pulses at a particular temperature. When possible, transmitters were retrieved from regurgitations and recalibrated. Radio signals from the transmitters were monitored by a Lafayette model HA-420 transceiver. Transmitters remained in birds for the lengths of their attendance spells (± 3 hours in cormorants, ± 30 hours in gannets). The behaviour of each bird containing a transmitter was monitored continuously.

RESULTS

THE MICROENVIRONMENT

Micrometeorological temperatures measured by the spherical models are shown in Fig. 38. Temperatures were measured in two different parts of the cormorant colony: exposed nests and sheltered nests (*i.e.* with respect to wind). Sheltered nesting sites were occupied only when no exposed sites were available, thus exposed sites may be considered as preferred (pers. obs.). Figs. 38a & b show that cormorants on exposed nests experience lower radiative (max. 32 °C) and air temperatures (max. 26 °C) than cormorants on sheltered nests (max. 43 and 30 °C respectively). This results in lower heat loads for exposed cormorants, and this is reflected by lower incidences of panting (see histograms). Gannets are exposed to lower radiative heat loads (max. 36 °C) than sheltered cormorants, but greater heat loads than exposed cormorants (Fig. 38a) (although these heat loads are subject to the complicating effects of plumages). Nevertheless, gannets show lower incidences of panting than both groups of cormorants (see histograms). Gannets and sheltered

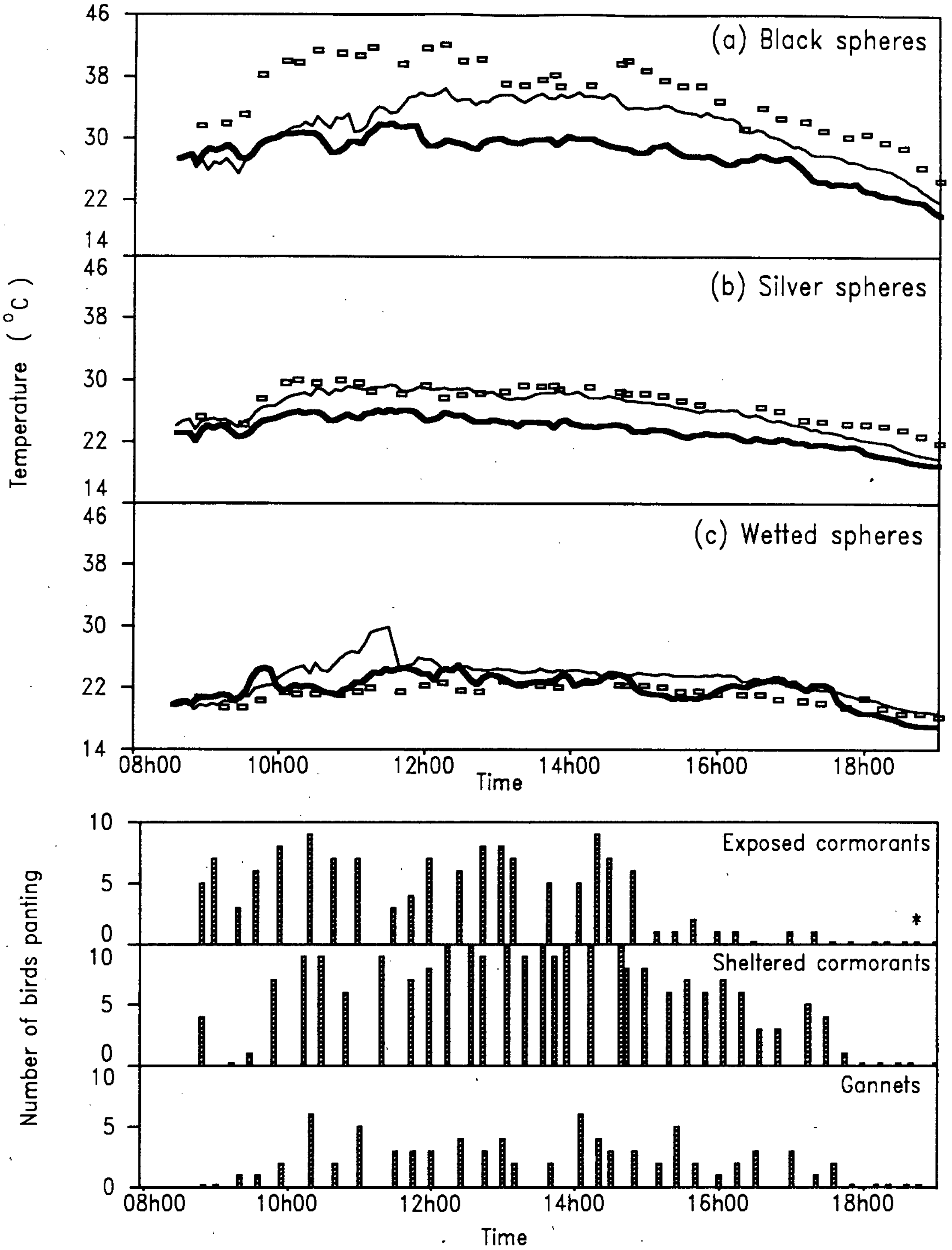


Fig. 38. Micrometeorological temperatures experienced by nesting Cape cormorants (▬ exposed nests, ☐ sheltered nests) and Cape gannets (—) during a day in Dec.1987. Temperatures were measured by three types of spherical models: (a) black, (b) silver and (c) wetted (see text for explanation). Histograms depict the number of panting birds of each species (in a sample of 10), at various times throughout the day. Times at which no birds were panting are indicated by the shortest bars (see *).

cormorants experience similar air temperatures, and temperatures measured by white spheres were similar for all birds (Fig. 38b & c). Henceforth, any reference to cormorants implies cormorants on exposed nests, as these were the nests which occurred adjacent to the gannet colony. Cormorants on sheltered nests were only present for one study period (Dec. 1987), and insufficient data were collected from these birds to facilitate a comparison between their thermoregulatory behaviours and those of gannets.

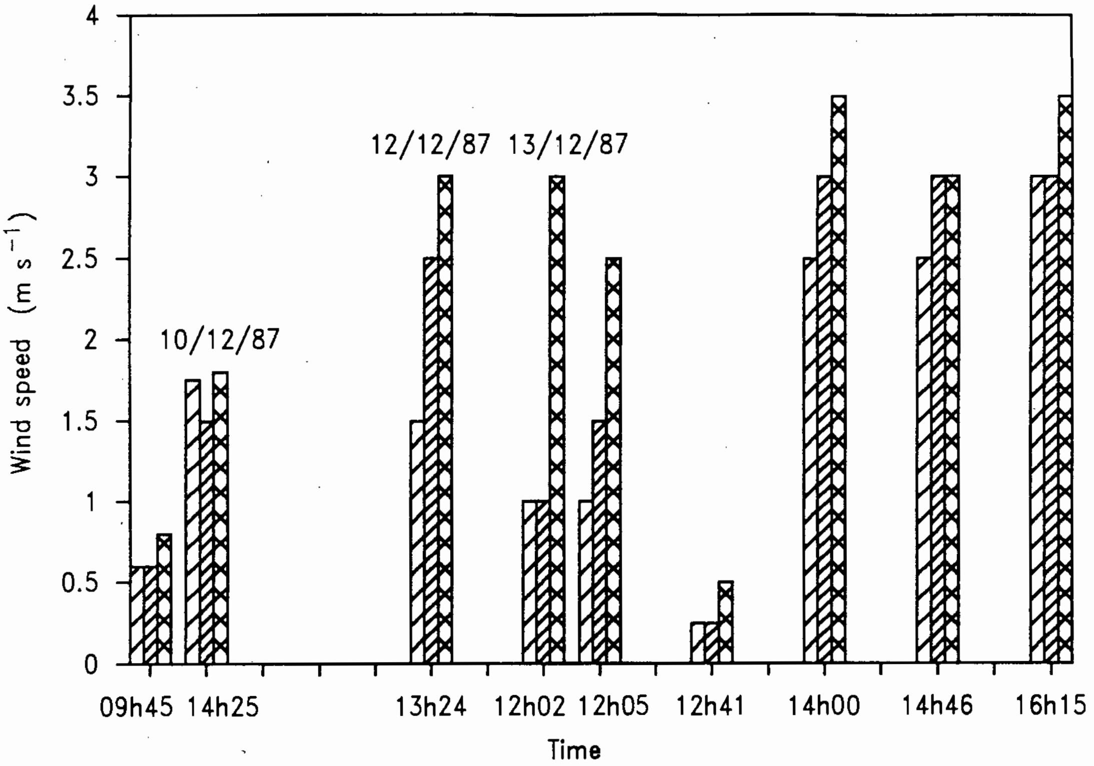
Wind speeds measured adjacent to nesting gannets and cormorants are depicted in Figs. 39a & b respectively. Wind speeds within the first 30 cm above ground level were seldom less than 1 m s^{-1}. During a typical day, wind speeds experienced by nesting birds averaged between 1-3.5 m s^{-1}. This figure may be substantially higher for cormorants on exposed sites because their nests are between 1-3 m above the ground level where wind speed was measured.

Results of random measurements of nest temperatures on the 14 Dec. 1987 are shown in Fig. 40. It is evident that nest temperatures ranged widely within the colonies of both species (cormorants: 25-38 °C, gannets: 27-42 °C), and the average temperature of gannet nests (34.1 °C ±2.9) was higher than that of cormorant nests (31.2 °C ±3.6). During nest temperature measurements it was noted whether the nest's occupant was panting. Fig. 41 shows that cormorants began to pant at nest temperatures between 29-30 °C, whereas gannets began to pant only at 36 °C.

PANTING THRESHOLDS AND POSTURAL ADJUSTMENTS

The threshold of panting was defined as the time when 50 % of the birds in a sample were panting. Mean values were calculated of the meteorological conditions (air temperature, black-bulb temperature) which prevailed at panting thresholds of both species, on each day of observation (Table 20). Sample sizes ranged from 16-23 for all data. The thresholds of cormorants occur at lower temperatures than for either gannet adults or chicks (ANOVA, $P<0.001$, homogeneous groups were calculated by Tukey's test).

(a) CORMORANT COLONY



(b) GANNET COLONY

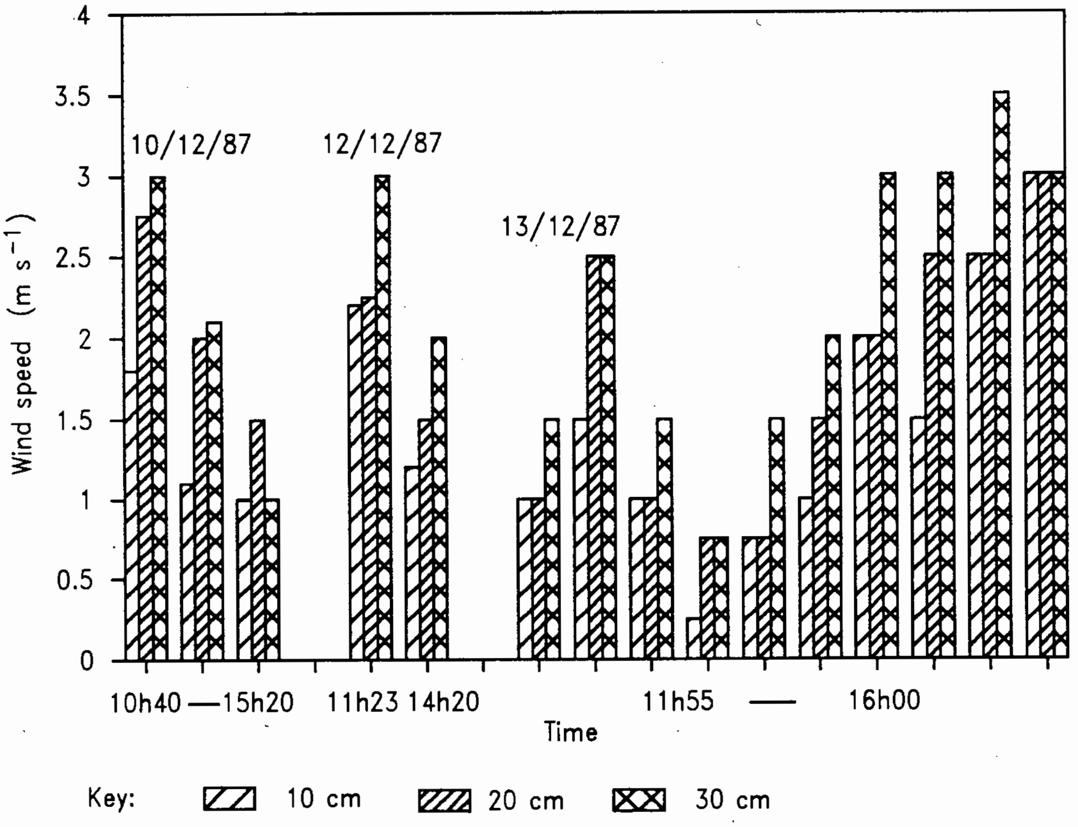


Fig. 39. Wind speed at 10, 20 and 30 cm above the ground within (a) Cape cormorant and (b) Cape gannet colonies on Bird Island for three days in December 1987.

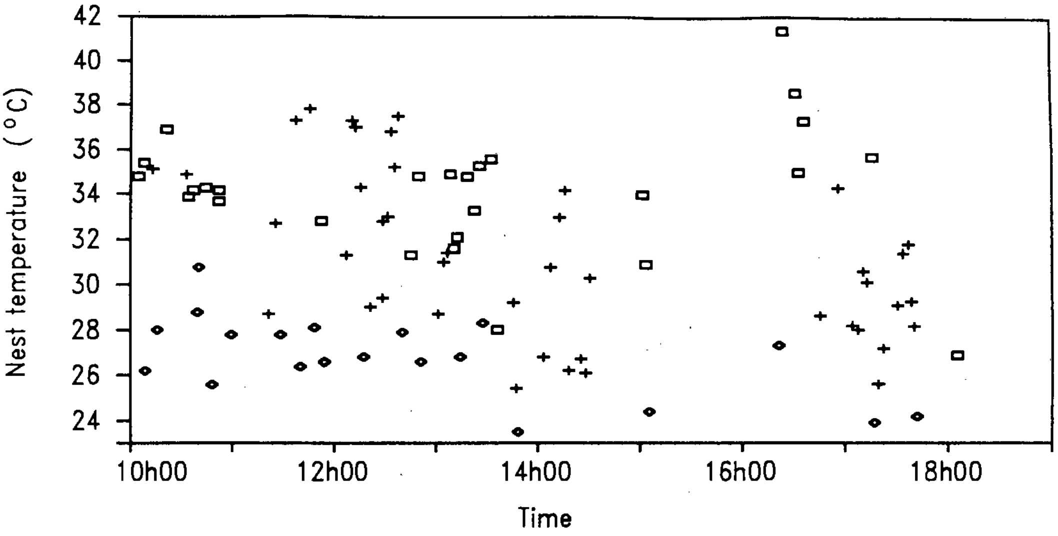


Fig. 40. Nest temperatures of breeding Cape cormorants (+) and Cape gannets (□) during the 14 Dec. 1987. Temperatures measured in the free stream above nesting birds are included in the figure (◇).

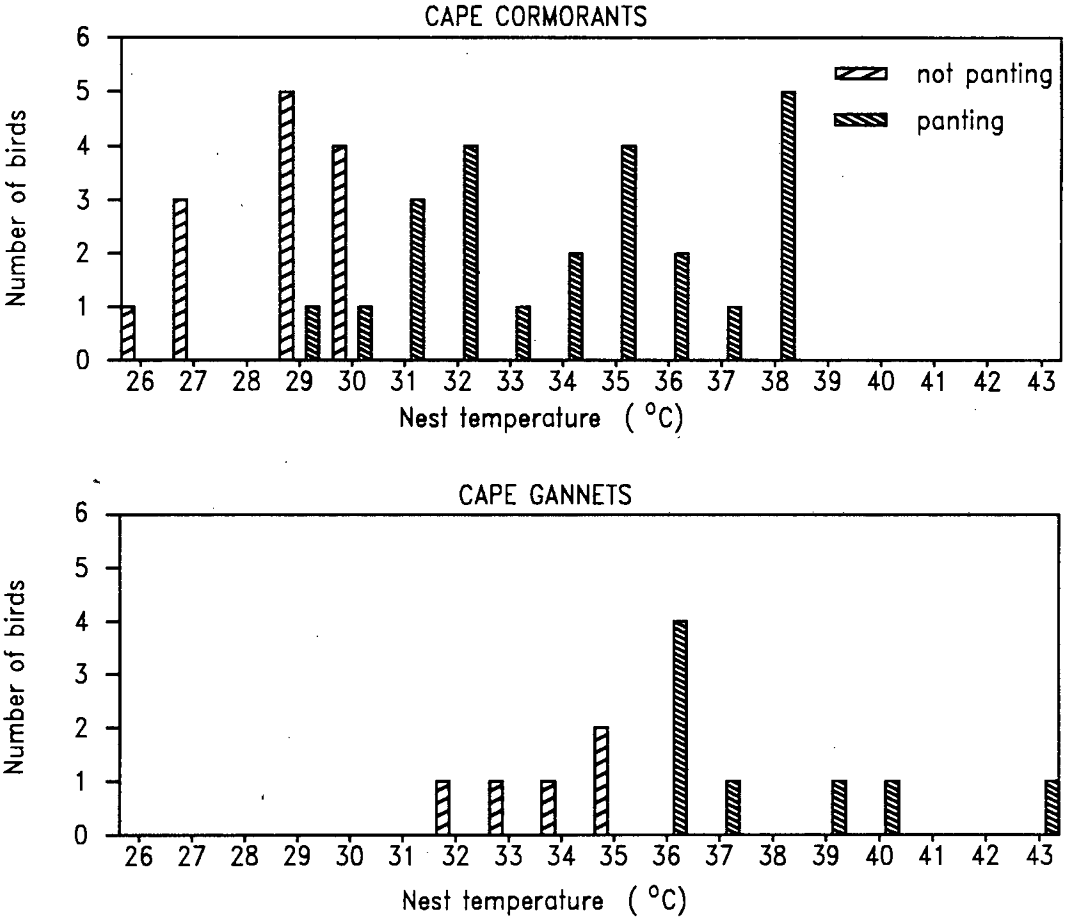


Fig. 41. Frequency distribution of the number of Cape cormorants and Cape gannets panting at different nest temperatures during the 14 Dec.1987.

Table 20. Meteorological data defining panting thresholds in nesting Cape gannets and Cape cormorants. Values quoted are averages (± 1 S.D.). Asterisks (*) indicate homogeneous groups. (See text for explanation).

	Air temperature (°C)		Black-bulb
Species	Sun	Shade	temperature (°C)
Gannet			
adults	*23.5 (±1.8)	*21.8 (±1.3)	*26.3 (±1.9)
chicks	*23.5 (±1.5)	*21.8 (±1.5)	*25.6 (±1.8)
Cormorant			
adults	21.0 (±2.0)	19.2 (±1.7)	22.8 (±1.8)
ANOVA	$p<0.001$	$p<0.001$	$p<0.001$

Panting thresholds were also calculated using the temperatures measured by the three types of spherical models. Results appear in Table 21. Once again, thresholds of cormorants occurred at significantly lower temperatures in all three instances. Sample sizes for all means were 21 (cormorants) and 23 (gannets).

Table 21. Micrometeorological temperatures (°C) which define panting thresholds of breeding Cape cormorants and Cape gannets. Black spheres integrate the radiative and convective environment, silver spheres measure air temperature, and white (wet) spheres integrate air temperature, humidity and convection.

	Black sphere	Silver sphere	Wetted sphere
Gannets	36.7 (±2.7)	28.9 (±1.2)	24.4 (±1.1)
Cormorants	28.5 (±2.0)	25.0 (±1.8)	21.8 (±0.9)
Student's t test	$p<0.001$	$p<0.001$	$p<0.001$

As regards the thermoregulatory postures of both species, the various postures observed during the three study periods on Bird Island are defined in Table 22.

Table 22. Thermoregulatory postures adopted by Cape gannets and Cape cormorants.

Species	Posture	Description
Cape gannet Cape cormorant	Incubating	Bird adopts a typical incubating (or brooding) position with breast feathers touching nest, feet not visible, wings folded. (Gannet chicks also adopt this posture, although they are neither incubating nor brooding).
Cape cormorant	Squat	Bird squats on tarsi, with breast feathers raised off nest (feet not visible owing to construction of nest).
Cape gannet	Semi-squat	Bird squats on tarsi, with breast feathers raised off nest, tips of feet visible.
Cape gannet	Full-squat	Bird squats on tarsi, with breast feathers raised off nest, feet entirely visible.
Cape gannet Cape cormorant	Standing-squat	Bird stands, tarsi off ground, breast parallel to ground.
Cape gannet Cape cormorant	Stand	Bird stands in "normal" position, with breast at an angle of ± 45 ° to ground.

As air temperature increases, the sequence of postural adjustments in both species follows the order in Table 22 (from incubating to standing), but cormorants commence panting while in the incubating position, whereas gannets begin to pant in any one of the other thermoregulatory postures. Panting generally accompanies the thermoregulatory postures in cormorants, but may be replaced by intermittent panting, or may cease for limited periods, while the bird is occupied with other other non-thermoregulatory behaviours.

During the hottest days, both species were observed to hold their folded wings slightly away from their bodies. However, this behaviour was difficult to score in cormorants, owing to possible confusion with instances when the wings were held in positions which would shade the chicks. Finally, the most heat stressed cormorants would raise their scapular and dorsal feathers. This behaviour was not observed in gannets.

Data in Fig. 42a show the percentage of birds in a sample employing a particular posture, during the hottest day in the Jan. 1987 sampling period. Air temperature has been included in the figure to show how postural adjustments vary with changing temperatures. Fig. 42b shows the percentage of birds panting in each of the above samples. Fig. 42 shows that cormorants reached panting thresholds at air temperatures of about 20 °C, whereas thresholds were reached between 23-25 °C in gannet adults and chicks. This confirms the figures quoted in Table 20. In addition, cormorants maintained panting for longer periods during the day, and only ceased to pant as temperatures declined again to 20 °C. During the day, more gannet chicks than adults were panting at any particular time, but both adults and chicks ceased to pant as temperatures decreased again to 23-25 °C.

The postural responses to increased thermal stress shown in Fig. 42 reveal the following: (a) the sequences of the various postures occur as listed in Table 22; (b) although cormorants pant to a greater extent than gannets, gannet adults engage in thermoregulatory postures to a greater extent than cormorants; (c) gannet chicks prefer to stand during both warm and cool conditions, which suggests that chicks do not stand in response to increased thermal stress.

BODY TEMPERATURE

Body temperatures and thermoregulatory behaviours during 13 and 16 Dec. 1987 are shown in Fig. 43. On 13 Dec., body temperatures were obtained for two cormorants and one gannet, whereas on the 16 Dec. measurements were obtained for one bird of each species. Body temperatures of cormorants ranged from 40-41.5 °C, whereas gannets had lower temperatures of 39.3-41 °C. Gannet temperatures also declined towards evening. Concurrent behavioural data confirm that gannets relied more on postural thermoregulation than cormorants: at high body and ambient temperatures, gannets engaged in standing-squats, and then gradually changed to full and semi-squats as temperatures declined. Panting was observed at body temperatures of over 41 °C. The cormorants did not appear to rely as much on postural changes as a method of thermoregulation, and were found in either standing-squats or incubating positions at body

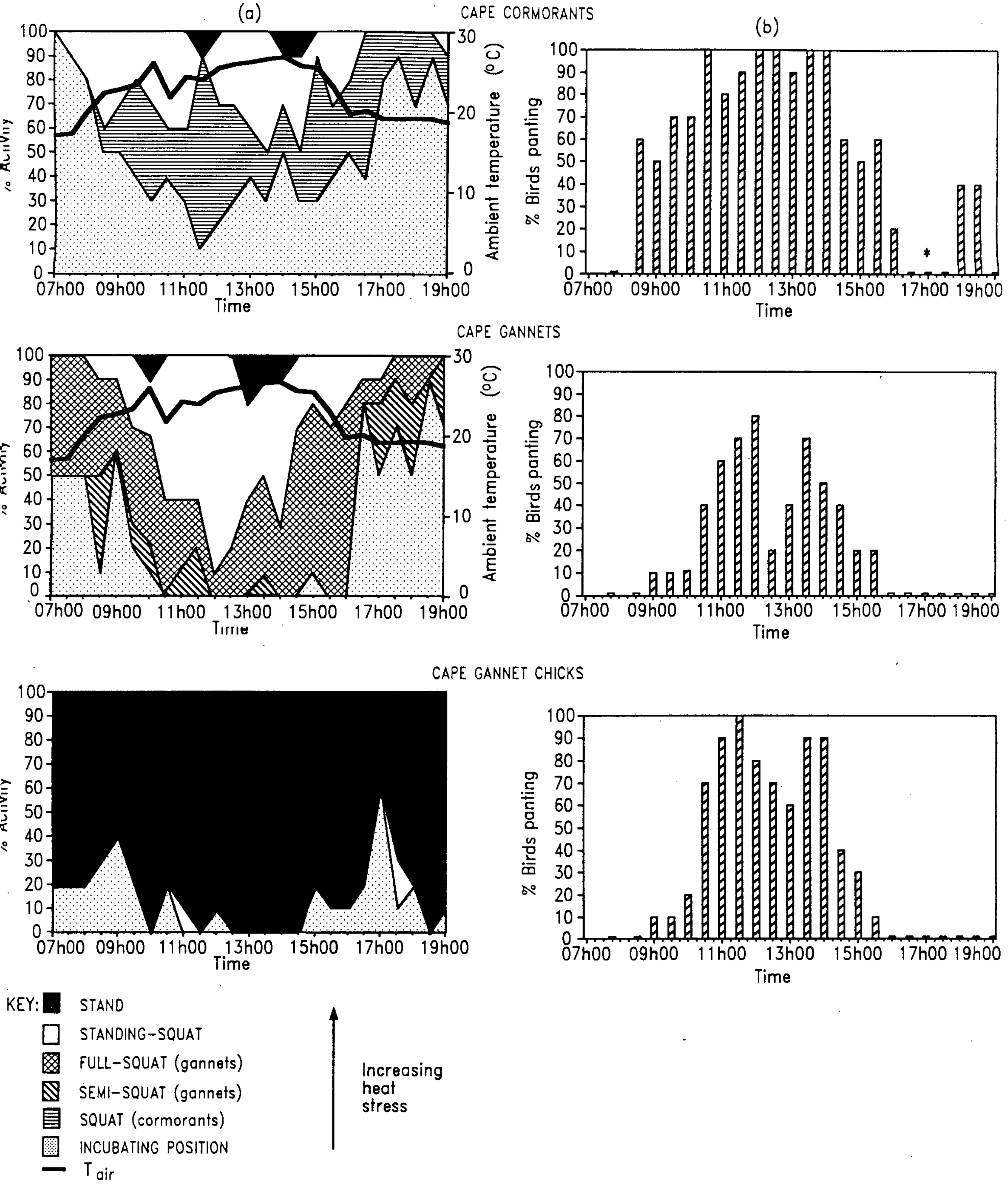


Fig. 42. Percentages of birds (in a sample of 10) engaged in thermoregulatory postures (left hand figures) or panting (right hand figures), during the hottest day in the Jan. 1987 sampling period. Times at which no birds were panting are indicated by the shortest bars (see *).

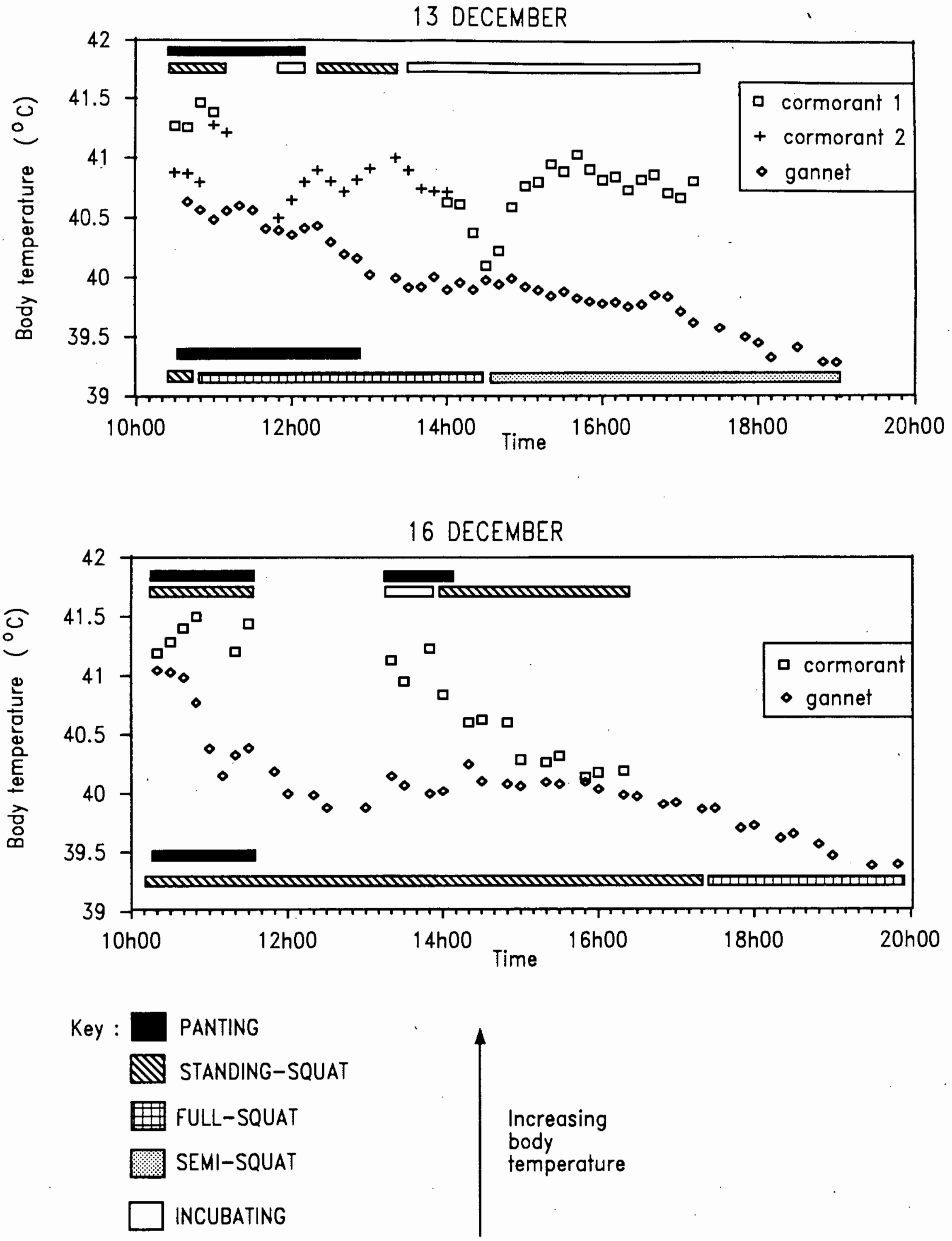


Fig. 43. Body temperatures of Cape cormorants (□, +) and Cape gannets (◇) during two days in December 1987. Thermoregulatory behaviours (see key) are included for both species: cormorant behaviours appear at the top of both figures, whereas gannet behaviours are shown below.

temperatures of 40-41 °C. However, cormorants began to pant at lower body temperatures than gannets (± 40.1 °C).

ORIENTATION

Table 23 lists the total number of samples recorded, and the number of samples showing preferred orientations, for Cape gannet adults and chicks, and Cape cormorants, during all conditions (a), conditions of heat stress (b), and cool conditions (c). ("Preferred orientation" was defined on pp. 148). Conditions of heat stress represent all the samples in which a minimum of one bird was panting, and cool conditions represent samples in which no birds were panting. A ratio of the number of gannet adults: gannet chicks: cormorant adults showing preferred orientations is also listed in Table 23.

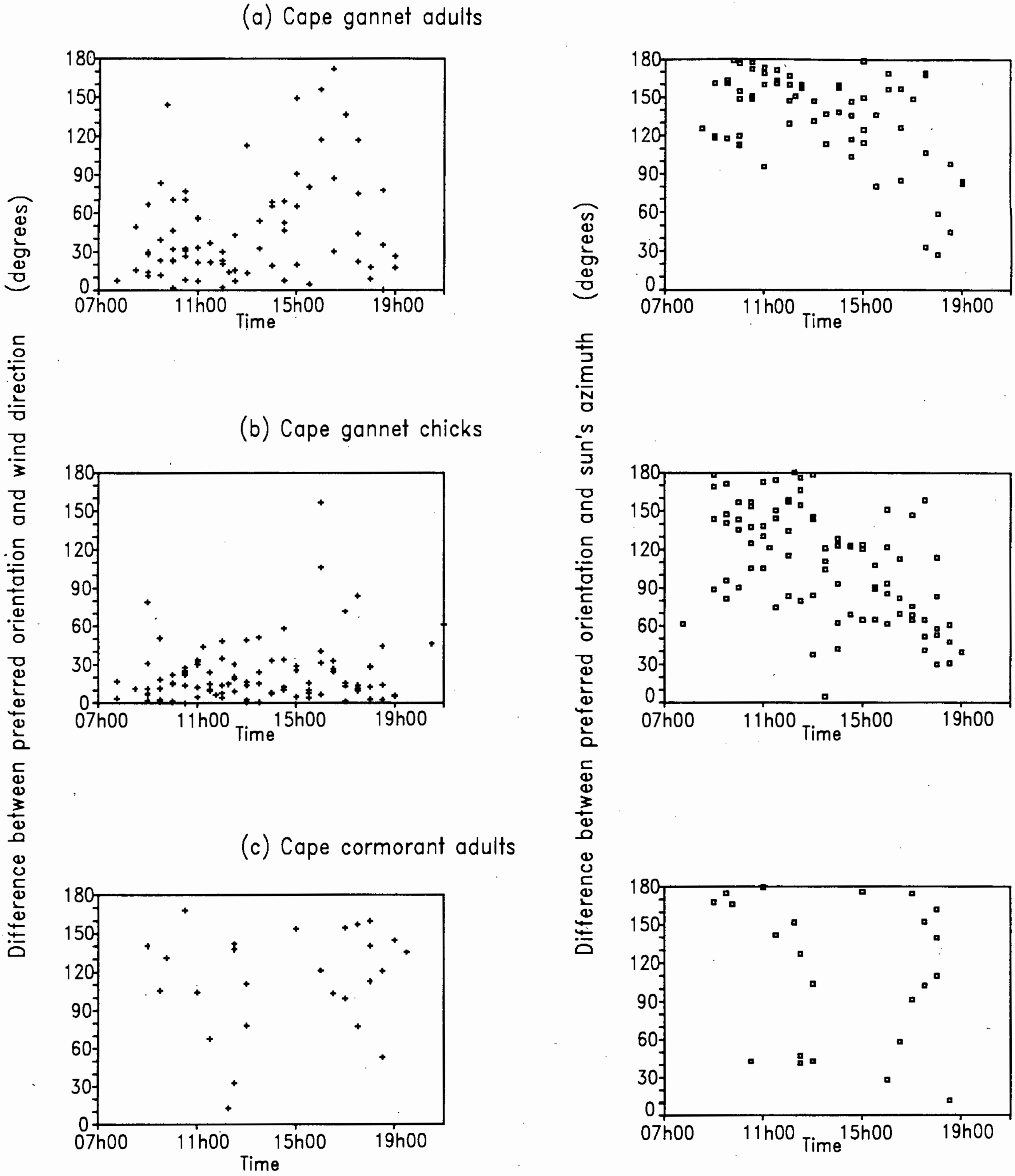
Table 23. Numbers of samples of gannets and cormorants showing preferred orientations in a) all conditions, b) conditions of heat stress and c) cool conditions.

Species	Total number of samples	Number of samples with preferred orientations	% of samples with preferred orientations	Ratio
		a) All conditions		
Gannet adults	241	124	51	3
Gannet chicks	133	100	73	4.4
Cormorant adults	247	42	17	1
		b) conditions of heat stress		
Gannet adults	111	54	49	3.4
Gannet chicks	67	55	82	5.8
Cormorant adults	198	28	14	1
		c) cool conditions		
Gannet adults	130	70	54	1.9
Gannet chicks	66	45	68	2.4
Cormorant adults	49	14	29	1

On average, gannet chicks showed the greatest tendency to orientate in a particular direction (73 % of all samples showed preferred orientations), followed by gannet adults (51 %) and then by cormorant adults, who showed little tendency (17 %) to orientate in a preferred direction. This trend was maintained in both warm and cool conditions (Table 23).

Fig. 44 shows how birds orientated with respect to wind (left hand figures) and sun (right hand figures), during the Jan. 1987 sampling period. All modal vectors indicating preferred orientations were pooled, and plotted against a common axis denoting daily time. These modal vectors were compared with wind direction and the direction of the sun's azimuth at the time at which the sample was taken (where sun's azimuth is the horizontal angle between the sun and magnetic north). The differences, in degrees, between the modal vectors and the wind and sun angles, were calculated. A small difference indicates a preferred orientation into the wind or sun, whereas a large difference (180°) indicates an orientation directly away from the wind or sun.

It is evident from Fig. 44 that gannet adults and chicks orientate in preferred directions far more frequently than cormorants. In addition, the few preferred orientations of cormorants have no discernible pattern, whereas gannet adults and chicks prefer to orientate to within 60° and 30° of the prevailing wind, respectively. The relationship between bird orientation and sun's azimuth is best described by Fig. 45, which relates the orientation of birds with respect to the sun, to the angle between the sun's azimuth and wind direction. If birds orientate into the wind throughout the day, one would expect a positive correlation between the dependent and the independent variables. This is indeed the case for all the gannet data. Linear regressions showed that a significant ($p<0.01$), and positive correlation exists between the dependent and independent variables in Figs. 45a & b, 46a & b). Cormorants showed no preferred orientation with respect to the sun (Fig. 45c). Similar data for a hot day in Jan. 1987 are shown in Figs. 46a & b. Once again, a significant ($p<0.01$) and positive correlation exists between the dependent and independent variables, indicating that 76-83 % of the variation in orientation of gannet adults and chicks is explained by a tendency to face into the wind.


(a) Cape gannet adults

(b) Cape gannet chicks

(c) Cape cormorant adults

Fig. 44. Occurrences of preferred orientations relative to wind direction (+), and sun's azimuth (□), for (a) gannet adults, (b) gannet chicks and (c) cormorant adults, during 6 days in January 1987. Date for the 6 days are pooled in each figure.

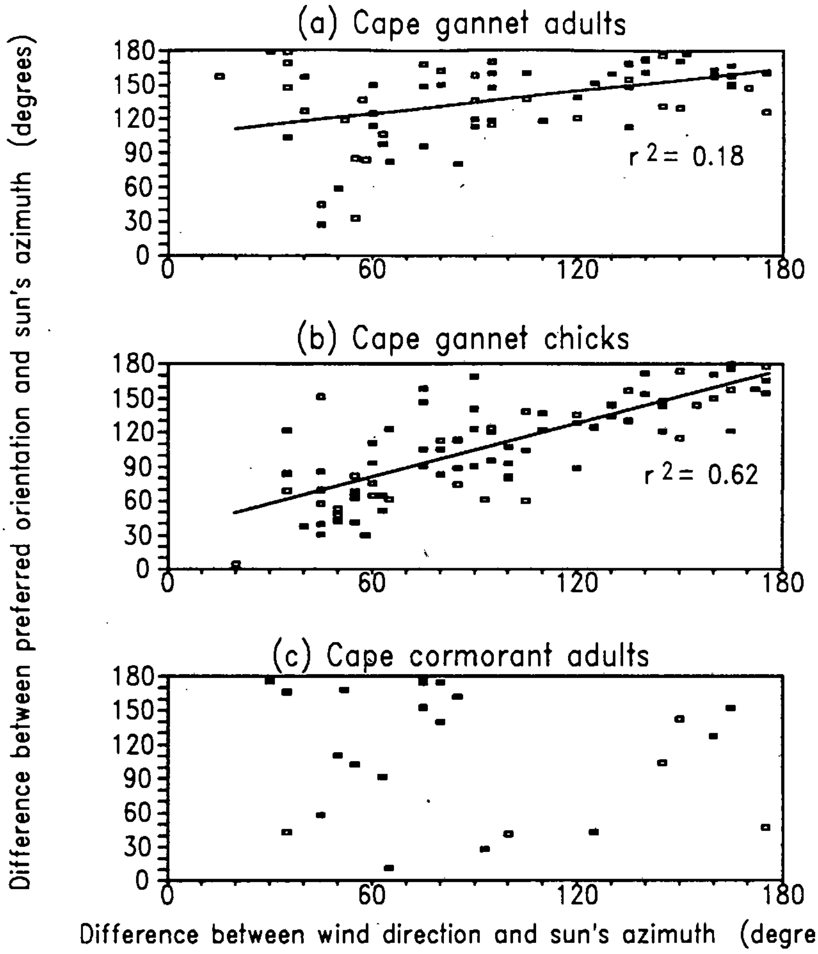


Fig. 45. The relationship between the preferred orientations of (a) gannet adults, (b) gannet chicks and (c) cormorant adults to the sun, and the angle between the sun's azimuth and wind direction, for 6 days in January 1987. The r^2 values of linear regressions appear on the figures.

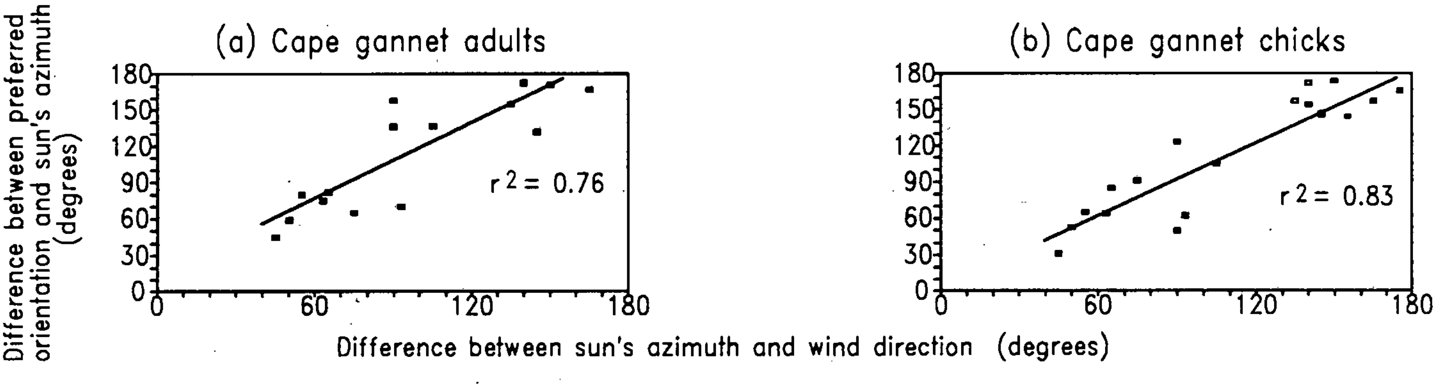


Fig. 46. The relationship between the preferred orientations of (a) gannet adults and (b) gannet chicks to the sun, and the angle between the sun's azimuth and wind direction, for a hot day in January 1987. The r^2 values for the linear regressions appear in the figures.

DISCUSSION

THE MICROENVIRONMENT

In the previous chapter it was concluded that the black plumages of cormorants would lead to greater heat loads than white gannet plumages, but that selection of cool and windy nesting sites by cormorants would decrease (or negate) any differential heating effects between the two species. Yearly observations on Bird Island (1985-1988) revealed that cormorants do prefer to nest in areas which are exposed to wind, and sheltered nest sites (*i.e.* sites similar to those on which gannets nest) are occupied only when exposed sites are no longer available. Data collected in 1987 confirm that exposed cormorants do experience lower radiative temperatures than sheltered cormorants, and the lower incidences of panting among exposed cormorants suggest that they are subjected to lower heat loads than the sheltered birds. Nevertheless, any additional heat loads experienced by sheltered cormorants appear to be effectively dissipated by panting. Thus, heat stress in cormorants may result in a preference for certain nesting sites, but it does not seem to limit the range occupied by breeding birds on the island (pers. obs.).

Further examination of the microenvironment reveals that wind speeds measured at ground level adjacent to breeding birds of both species range between 1-3.5 m s^{-1} on a typical day. This may be a conservative estimate for the exposed cormorants, since wind speeds may be substantially greater at a height of 3 m where the nests occur. In the light of the findings of Walsberg *et al.* (1978), these winds, coupled with ptiloerection of cormorant plumages, may be sufficient to negate differences in heat loads between the exposed cormorants and the gannets on adjacent nests.

It is now relevant to ask (a) whether exposed cormorants experience cooler microenvironmental conditions than adjacent gannets and (b) which species demonstrates greater levels of heat stress. Spherical models showed that the radiative, air and nest temperatures were higher in the gannet colony than in the exposed cormorant colony, but that cormorants appeared to experience greater heat stress, as was revealed by the greater prevalence of panting in the cormorant colony. Additional evidence for greater heat stress among exposed cormorants as opposed to gannets is provided by behavioural thermoregulation of the two species. Firstly, cormorants were observed to erect their dorsal feathers during hot midday periods, whereas gannets failed to do so. Secondly, cormorants began to pant at significantly lower temperatures than gannets (whether one considers air, radiative or nest temperatures). Finally, cormorants had body temperatures which were between 0.1-1 °C higher than gannet body temperatures. This could reflect an ability of cormorants to allow their body temperatures to rise by c. 0.5 °C during times when excess heat can no longer be dissipated by panting, although it could also be a result of species-specific differences in body temperature, or the greater thermal inertia of the larger gannets.

It can thus be concluded that exposed cormorants experience cooler microenvironments than gannets. Nevertheless, cormorants experience greater levels of heat stress than gannets, and the interacting effect of wind and ptiloerection in cormorants may decrease this heat stress, but does not negate the differential heating between the two species.

POSTURAL ADJUSTMENTS

Behavioural data suggest that heat loads in gannets may often be low enough to be dissipated by changes in posture alone (*i.e.* by standing to expose the well-vascularised webbed feet to convective heat loss). Panting becomes necessary only when radiative temperatures exceed ± 37 °C. The thermoregulatory value of standing and squatting in gannets is demonstrated in Fig. 42 which shows that as air temperatures drop in the evening, the majority of gannets abandon their various squatting positions and resume the incubating position; panting ceases simultaneously. Behavioural data in Fig. 43 also reveal that as environmental temperatures decline towards evening, the order of thermoregulatory postures assumed by gannets can be predicted.

Postural adjustments appear to be insufficient to dissipate excess heat in cormorants, and the order of postures assumed by a particular cormorant can not be predicted during a rise or decline in environmental temperature (Fig. 43). Panting in cormorants begins at radiative temperatures as low as ± 29 °C, and during the hottest parts of the day cormorants may squat, stand or maintain incubating positions, while panting. The secondary role played by postural adjustments may be partly due to the nest structure of cormorants. Nests are constructed from dried kelp and other debris, and the walls may be several cm high. A cormorant standing in such a nest will not expose its webbed feet and uninsulated legs to convective heat loss, whereas the shallow guano nests of gannets do not provide similar protection. For this reason, postural adjustments may be more effective in dissipating excess heat in gannets.

Behavioural thermoregulation in gannet chicks provides an interesting comparison with the adults. As previously mentioned, just prior to fledging, gannet chicks possess a black plumage. Behavioural data show that chicks prefer to stand during the day, even during the early morning and late evening when conditions are cool (air temperatures < 20 °C). Standing is thus not considered to be method of heat dissipation in these chicks. However, during hot conditions, incidences of panting are greater in gannet chicks than the adults (this was also observed by Jarvis 1971), and it is possible that this reflects greater heat stress in chicks, and that this heat stress is due to their black plumages (these chicks have a similar mass to the adults). Once again, the evidence provided here suggests that black coloration results in greater heat stress.

ORIENTATION

(a) Gannet adults

During daylight hours, the sample of 10 adult gannets under observation chose to orientate in a preferred direction in approximately 50 % of all samples, under both warm and cooler conditions. These gannets usually faced to within 60° of the wind. Owing to the consistent preference of gannets for facing the wind during both hot and cool conditions, it is difficult to propose a thermoregulatory advantage of this orientation that would operate under both conditions. Storer *et al.* (1975) noted a universal tendency for birds to face into wind, and Gibson-Hill (1948) noted that during courtship, Cape gannets faced into the wind, unless it was very light.

It is also apparent that gannets usually orientate perpendicularly to, or away from, the sun. In order to separate the two variables of wind and sun as the primary cues for orientation, the covariation of wind and sun must be taken into account. Data collected on a hot day show that as the angle between wind and sun increases, so does the angle between birds and sun, showing that the apparent tendency of birds to face away from the sun may be a consequence of their tendency to face into the wind. In addition, during late evening, when the strength of solar radiation is minimal (0-400 W m^{-2}), and during midday, when the sun is directly overhead, birds continue to orientate into the wind.

(b) Gannet chicks

Gannet chicks displayed the strongest tendency to orientate in a preferred direction (72 % of all the samples taken). Chicks usually oriented to within 30° of the wind direction, and seldom faced more than 60° away from wind. The orientation of chicks relative to the sun is best described by Figs. 45b & 46b, where 62-83 % of the variation in orientation is explained by the tendency of chicks to face into the wind. Chicks do not appear to orientate relative to the sun, unlike Laysan and black-footed albatross chicks, who balance on their heels and simultaneously shade their well vascularised feet, thus losing heat by convection and reradiation (Howell & Bartholomew 1961, Whittow 1980). This may reflect the temperate nature of the environment, and suggests that gannet chicks did not experience severe heat stress during the periods of observation.

(c) Cormorants

Table 23 shows that cormorants orientated in preferred directions in only 17 % of all samples taken. However, changes in orientations were not made relative to either the sun or the wind. The low occurrence of preferred orientations in cormorants may be due to the nature of nest building, nest defence and bird movement within the cormorant colony. As previously mentioned, cormorants build their nests from debris such as dried kelp, feathers etc. Strong competition exists for nest material and birds continuously protect their nests against neighbours or other cormorants moving through the colony. In addition, bird movement within the colony can be intense, since breeding pairs bear from 2-5 young, and attendance spells average only 2.8 hrs. In contrast, gannets build their nests from guano scraped into a mound, and no competition exists for nest material once the breeding colony is established. Bird movement within the colony is limited to birds attempting to leave their nests, after attendance spells of c. 36 hrs. In addition, each nest has only one chick, further limiting numbers and disturbances within the colony. Thus, nest defence occupies less time for gannets than it does for cormorants. Berry (1976) concluded that Cape cormorants do not employ orientation relative to the sun as a means of thermoregulation, because birds are too involved in nest defence. These findings are in agreement with those of the present study. It thus seems that orientational changes are not vital to the thermoregulation of cormorants, although possible thermoregulatory advantages could still be gained if birds were freed from nest defence and could orientate relative to the wind or sun. An illustrative example is provided by Bartholomew & Dawson (1979) who found that in Heermann's gulls, adults shade their gular areas by orienting with their backs to the sun when heat stressed, but incubating birds remain randomly oriented. The authors suggested that it is too much trouble for incubating birds to keep changing their orientation, because of the need to change the position of the egg to keep it under the brood patch.

Thus, orientation relative to the wind or sun does not appear to be used as a form of behavioural thermoregulation in either gannets or cormorants, owing to the fact that gannets orientate into the wind during both warm and cool conditions, and nest defence overrides any orientational preferences of cormorants.

ATTENDANCE SPELLS

Nest attendance spells of breeding Cape gannets and Cape cormorants are determined primarily by feeding ecology (although breeding stage and clutch size play secondary roles, in that older, and more numerous chicks, have greater feeding requirements, and thus serve to decrease the attendance spells by increasing the fishing excursions of the adults). As regards feeding ecology, both species feed mainly on pelagic shoaling fish (Crawford & Shelton 1978). However, their similar food resources are exploited by different methods, which are related to the degree of water repellency of their plumages. Gannet plumages are highly water resistant (Rijke 1970), whereas cormorant plumages exhibit lower degrees of water repellency (Rijke 1968, Casler 1973). Consequently, gannets plunge dive for fish and roost on offshore islands or at sea (Jarvis 1971). They are essentially offshore feeders, seldom moving close inshore to feed like Cape cormorants (Rand 1959). Consequently, periods of nest attendance (and thus periods of absence from the nest) during breeding average as much as 39.4 hrs (Jarvis 1970) or 36.0 hrs (present study).

Owing to the lower water repellency of their plumages, cormorants swim on the surface and dive underwater in pursuit of prey, and usually return to land in order to rest and dry their plumages. They are thus able return more frequently to their nesting sites during the breeding season, and consequently nest attendance spells are relatively short (1.25-3.5 hrs, Berry (1976); or 1.7-3.3 hrs, this study).

The thermal consequences of the feeding ecology (and thus the lengths of attendance spells) in the two species are twofold. A direct consequence is that gannets are confined to their nests for longer periods (± 1.5 days), whereas cormorants are free to leave their nests ± every 3 hrs in order to dissipate excess heat by seeking cooler microenvironments or bathing in the sea. This avenue of heat loss, which is unavailable to attentive gannets, has been shown to be important in breeding gulls (Chappell *et al.* 1984, Lustick 1983) and penguins (Frost *et al.* 1976). However, this form of heat loss will be important only in the transient state. For steady state heat losses, heat dissipation should average out to similar levels for both gannets and cormorants. The second, indirect consequence, of feeding ecology is that cormorants have a continuous need to dry their wet plumages. It was shown in Chapter 6 that black plumages reach higher surface temperatures than white plumages in still conditions, and these higher surface temperatures aid evaporative water loss from plumages. Siegfried *et al.* (1975), Berry (1976) and Hennemann (1983) propose that the characteristic spread-winged posture of Cape and double-crested cormorants facilitates wing drying. Black colour may thus provide a thermal advantage to seabirds which forage underwater, and have plumages with low water repellencies.

DO BLACK AND WHITE COLORATION IN CORMORANTS AND GANNETS HAVE A THERMOREGULATORY VALUE ?

Evidence provided in this chapter suggests that cormorants experience greater heat loads than gannets during hot days, and that these heat loads are not a result of cormorants being exposed to warmer microclimates. In fact, it is evident that cormorants select exposed areas for nesting, with cooler microenvironments than those occupied by gannets. In addition, the black gannet chicks appear to experience greater heat loads than the white adults. These factors suggest that, owing to black coloration, cormorants and gannet chicks experience greater heat loads than gannet adults. The prevalence of wind on Bird Island, as well as ptiloerection in exposed cormorants, may interact to reduce heat loads in cormorants, but behavioural data show that cormorants employ thermoregulatory behaviours at much lower environmental temperatures than gannets. However, in order to measure relative heat loads incurred by gannets and cormorants, their water budgets should be measured. The difference in evaporative water loss between the two species would provide an estimate of the extra heat load imposed on cormorants owing to their black coloration.

Answers to the predictions of the previous chapter regarding the effects of microhabitat selection and behavioural thermoregulation on thermal budgets can be summarized as follows: panting is the primary method of heat dissipation in cormorants, and postural adjustments play a secondary role. In gannets, postural adjustments are employed to a greater extent, and may assume equivalent importance to panting as a means of heat dissipation. Microhabitat selection does decrease the differences in heat loads between black and white birds, but black birds have greater heat loads even though they nest in cooler, more windy, microenvironments. Owing to a temperate climate, black coloration does not limit the distribution of breeding birds, but results in a preference for cooler nesting sites.

Further evidence for the temperate nature of the environment is provided by the fact that, during the three periods of observation, neither species employed thermoregulatory behaviours associated with severe heat stress. Cape cormorants and Cape gannets have been noted to droop their wings, or hold them horizontally, during periods of extreme heat stress (Cooper & Siegfried 1976, Berry 1976). In addition, urohidrosis and subsequent paddling in the excreta have been noted in heat-stressed Cape gannets (Cooper & Siegfried 1976). Masked boobies, red-footed boobies and frigate birds also droop their wings and ptiloerect during extreme heat (Bartholomew 1966, Shallenberger *et al.* 1974, Mahoney *et al.* 1985). Lastly, orientation relative to the wind or sun as a thermoregulatory response does not appear to be necessary in either species. The only thermal implication of colour which appears to have a selective advantage is that the black plumage of cormorants may facilitate wing-drying.

The hypothesis that black and white coloration has been selected for its thermal implications in Cape gannets and Cape cormorants can be reviewed by answering the questions posed in Chapter 5 (pp. 111):

1) Black plumages do acquire greater heat loads, especially in still conditions, but wind and ptiloerection may reduce these differences.
2) Increased convection decreases heat loads in both species, but neither convection nor angle of insolation seems sufficient to negate the differences in heat absorption between black and white plumages.
3) Behavioural thermoregulation and selection of cooler microhabitats by cormorants decreases the differential heating between black cormorants and white gannets, but black cormorants and gannet chicks display greater heat loads than gannets during hot conditions.

In conclusion, question 4 posed in Chapter 5 ("which forces other than thermoregulation may have selected for coloration ?") can be answered as follows: coloration does have thermal consequences for both Cape gannets and Cape cormorants. Black cormorants gain greater heat loads during the breeding season, and the consequence is that they prefer cooler nesting sites. However, thermal stress does not limit the distribution or success of breeding birds on the Island, and panting is adequate to dissipate any excess heat. Owing to the temperate nature of the environment, coloration is not likely to provide a selective advantage to either species during either hot or cold conditions, where white and black coloration respectively would be advantageous to thermal energy budgets. The most significant thermal advantage of colour is gained by cormorants from their black plumages. Black coloration provides elevated surface temperatures in relatively still conditions, and these aid evaporative water loss from their wet plumages. The water repellent nature of gannet plumages eliminates the need for gannets to dry their plumages.

It thus appears that microhabitat selection and behavioural thermoregulation may not always override differences in heat gain between black and white birds, and that black coloration may provide a thermal advantage to Cape cormorants. However, white coloration may be neutrally adaptive in Cape gannets, or it may provide a slight thermal advantage to breeding gannets on hot days. Nevertheless, a black gannet would most likely be able to dissipate its heat load by panting and postural adjustments, considering that black gannet chicks coped adequately with heat stress in this way.

Thus far, this study has considered only the thermal implications of colour to Cape gannets and Cape cormorants. A further examination of the feeding ecology of both species reveals, however, that their coloration may be a result not only of the degree of water repellency of their plumages, but also the degree of sociality of their feeding patterns. As was noted by Simmons (1972), seabirds can be broadly categorised into three plumage types: (1) mostly dark, (2) dark above and pale below and (3) mostly white. Simmons concluded that feeding ecology is the primary selective force in seabird coloration, and the selective advantages of the above three plumage categories are as follows: (1) social inconspicuousness and hunting camouflage, (2) inconspicuousness to predators, competitors or pirates from above, inconspicuousness to prey from below and (3) social conspicuousness and hunting camouflage. Simmons suggests that dark coloration is advantageous to birds which are skilled solitary feeders (cormorants), and wish to remain cryptic to prey which are captured underwater, or to competitive con-specifics when food resources are limited (brown boobies and the grey adult phases of red-footed boobies). He also suggests that dark colour is advantageous to "pirate" birds such as the latter two species, and that Cape gannet juveniles may be dark for this reason, owing to undeveloped feeding efficiency. On the other hand, light coloration (with limited black markings) is thought to be socially conspicuous, and facilitates congregations of birds which exploit patchy resources (Armstrong 1946, Murton 1971, Simmons 1972). These birds are also plunge divers as opposed to swimmers, and their light colour is thought to be cryptic against the pale sky when viewed from below (Tinbergen 1953, Phillips 1962, Simmons 1972).

Thus, it appears that the colours of Cape gannets and Cape cormorants are best explained by their feeding patterns, and that the thermal implications of colour to both species are as follows: white gannets experience a thermal advantage during the breeding season in that they receive lower heat loads than cormorants, but this advantage may be minimal owing to the temperate nature of the environment. Black cormorants experience greater heat loads during breeding but are adequately able to dissipate any excess heat by microhabitat selection and behavioural thermoregulation, and black coloration may provide a thermal advantage to cormorants by facilitating evaporative water loss from their wet plumages between feeding excursions.

SUMMARY OF SECTION II

1. Field measurements show that the mean effective absorbances (a) of gannet and cormorant plumages are 0.159 and 0.863 respectively. The mean absorbance of six angles of incidence (between 0-90 °) is a good estimate of a, but the absorbance measured at 90 ° over-estimates a in gannets.
2. Laboratory experiments using excised plumages show that, in still conditions, cormorant plumages may be up to 17 °C warmer than gannet plumages. However, at 2 m s^{-1} wind speed, cormorant plumages and skins are only 2-3 °C warmer than gannet plumages and skins. At 4 m s^{-1}, plumages and skins of both species all reach similar temperatures.
3. A biophysical model of heat transfer predicts that in still, warm, sunny conditions, cormorants may gain up to 185 % of their field metabolic rate (FMR) from insolation, whereas gannets would gain 42 % of their FMR. In cooler conditions (10 °C, 550 W m^{-2}), cormorants may gain 0-45 % of their FMR, whereas gannets would lose 5-25 % of their FMR.
4. Field observations of behavioural thermoregulation show that black gannet chicks and cormorants experience greater heat loads than white gannet adults, even though the chicks are exposed to the same microenvironments as the gannet adults, and the microenvironments of cormorants are cooler than those of gannets.
5. The thermal implications of coloration to both species are as follows: (1) cormorants may have a lower cost of endothermy at temperatures below their TNZ, but are more heat stressed than gannets during warm conditions, (2) microhabitat selection (of cool, windy nest sites) and behavioural thermoregulation allows cormorants to dissipate any excess heat gained owing to their black plumages, (3) at wind speeds less than 2 m s^{-1}, higher surface temperatures of black cormorant plumages may aid evaporative water loss from their wet plumages.
6. The thermal implications of colour are negligible in both species, considering the temperate nature of their breeding environment.
7. Coloration in seabirds is best explained by feeding ecology: white coloration enhances congregations at patchy food resources, and is cryptic when viewed from below; black coloration reduces conspicuousness of solitary feeders, and is cryptic when viewed underwater.

GENERAL CONCLUSIONS

A thermal role, and associated selective advantages, have frequently been postulated for black and white coloration in animals. Research in this thesis has shown that black and white colour in Namib Desert beetles, and marine birds, has not been selected for its thermal implications, although coloration does have thermal consequences for marine birds. In an attempt to identify the thermal value of coloration, this study has yielded the following major conclusions:

(1) The thermal significance of coloration in animals must be analysed in a realistic physical context, where the combined effects of all naturally occurring modes of heat transfer are investigated. This approach has shown that in Namib beetles, coloration affects only the absorption of visible radiation; that heat exchange in beetles is dominated by modes of heat transfer which are independent of coloration; and that other factors such as differences in beetle shape, may be responsible for differential absorption of heat from a hot substratum. It is concluded that body temperatures of black and white beetles do not differ in their natural environment, and that coloration does not have a thermal value in the biology of these beetles.

(2) Once the thermal environment of an animal is understood, the other factors which complicate heat transfer must be analysed, *e.g.* wind, behavioural thermoregulation and the presence of an insulating layer of fur or plumage. This study has shown that wind speeds between 1-2 m s^{-1} are sufficient to negate differential heating effects between black and white beetles; that ptiloerection and wind may interact to reduce heat loads in black birds; and that behavioural thermoregulation such as the timing of activity (in beetles) or microhabitat selection (in birds) further negate the possible thermal effects of coloration.

(3) The selective advantage of black and white coloration may not be related to a thermal role, but to some other component of the animal's biology. Black coloration in Namib beetles has many possible advantages, *e.g.* increased resistance to abrasion, protection against ultraviolet radiation, and reduced permeability. These advantages can also apply to black beetles with white elytra. Bicoloured beetles may have the added advantage of increased conspicuousness in the sand dune environment, which may enhance feeding or mating encounters. In marine

birds, feeding ecology seems to explain coloration in Cape gannets and Cape cormorants, although cormorants do appear to experience greater heat stress than gannets, owing to their black coloration. The consequences of black coloration in cormorants are that they prefer nesting sites which are exposed to wind, they engage in evaporative water loss (*i.e.* panting) to a greater extent than the white gannets, and they may experience an advantage in that black coloration enhances wing-drying.

Thus, no evidence can be found for a thermal role for black and white coloration in Namib tenebrionids or marine birds. It is suggested that coloration in these species has adaptive values which are related to other factors such as abrasion resistance, reduced water permeability, and feeding ecology.

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SYMBOLS

Symbols and abbreviations used in Appendices 1 & 2:

Appendix 1

A	total area of sphere (m^2)
A_p	projected area of sphere (m^2)
a_s	shortwave absorptance = 0.50 (*Onymacris bicolor*) = 0.95 (*Onymacris unguicularis*)
c_p	specific heat of air at 25 °C = 1010 $J\ kg^{-1}\ k^{-1}$
d	diameter of sphere (m)
D_H	thermal diffusivity ($m^2\ s^{-1}$)
e	emissivity of beetle = 0.99
$\bar{e}_s$	average emissivity of surrounds
H	heat flux density ($W\ m^{-2}$)
Nu	Nusselt number
Pr	Prandtl number
R_{abs}	absorbed long and shortwave radiation ($W\ m^{-2}$)
Re	Reynolds number
r_e	equivalent parallel resistance of r_{Ha} and r_r ($s\ m^{-1}$)
r_{Ha}	heat transport resistance of the air boundary layer ($s\ m^{-1}$)
r_r	"resistance" to longwave radiation transfer ($s\ m^{-1}$)
$\bar{S}_d$	mean diffuse radiation ($W\ m^{-2}$)
S_p	direct radiation ($W\ m^{-2}$)
T_a	ambient temperature (°C)
T_a^4	ambient temperature (K)
T_e	equivalent blackbody temperature (°C)
T_s	surface temperature (°C)
U	wind speed ($m\ s^{-1}$)
o	Stefan-Boltzmann constant = $5.67 \times 10^{-8}\ W\ m^{-2}\ K^{-4}$
p	density of air at 25 °C = 1.183 $kg\ m^{-3}$
μ	dynamic viscosity of air
ν	kinematic viscosity of air ($m^2\ s^{-1}$)

Appendix 2

A	surface area of bird = 0.09 $W^{0.74}$ (m^2)	(Peters 1983)
c_p	specific heat capacity (KJ kg^{-1} °C^{-1})	
d	thickness of plumage (m)	
F	frequency of pulse (s^{-1})	
h_c	convection co-efficient (W m^{-2} °C^{-1})	
K	conductance (W m^{-2} °C^{-1})	
k_{air}	conductivity through air = 0.02624 W m^{-1} °C^{-1} (temperature = 300 K)	(Thomas 1980)
K_{bl}	conductance by blood flow (W m^{-2} °C^{-1})	
k_{pl}	conductivity through plumage (W m^{-1} °C^{-1})	
K_s	conductance through body shell (W m^{-2} °C^{-1})	
k_{sh}	conductivity of shell (W m^{-1} °C^{-1})	
$\dot{m}$	mass flow rate (kg s^{-1})	
Nu	Nusselt number	
Pr	Prandtl number = 0.708 (temperature = 300 K)	(Thomas 1980)
q_{abs}	absorbed radiation (W m^{-2})	
$q_{cond, b}$	conduction through body shell (W m^{-2})	
$q_{cond, pl}$	conduction through plumage (W m^{-2})	
q_{conv}	convective heat loss (W m^{-2})	
q_{inc}	incident radiation (W m^{-2})	
q_{pene}	penetrating radiation (W m^{-2})	
q_{refl}	reflected radiation (W m^{-2})	
r	radius of shell (m)	
Re	Reynolds number	
t	thickness of shell (m)	
T_{air}	air temperature (°C^{-1})	
T_b	body temperature (°C)	
T_{pl}	plumage surface temperature (°C)	
T_{sk}	skin temperature (°C)	
U	wind speed (m s^{-1})	
V_s	stroke volume (ml)	
W	mass of bird (kg)	
∂	diameter of disc or shell (m)	
p	relectance of plumage	
p_{bl}	density of blood (kg ml^{-1})	
v	kinematic viscosity of air = 15.68 x 10^{-6} m^2 s^{-1} (temperature = 300 K)	(Thomas 1980)

APPENDIX 1

The equivalent blackbody temperature of beetles: a model

The equivalent blackbody temperature (T_e) calculated in this study is derived from Campbell (1977):

$$T_e = T_a + \frac{r_e}{\rho c_p}(R_{abs} - e \sigma T_a^4) \tag{1}$$

To calculate r_e:

$$r_e = \frac{r_{Ha} r_r}{r_{Ha} + r_r} \tag{2}$$

To calculate r_{Ha}:

Heat flux density at the surface of an organism is expressed as

$$H = \rho c_p \frac{T_s - T_a}{r_H} \tag{3}$$

but $$Nu = \frac{Hd}{\rho c_p D_H (T_s - T_a)} \tag{4}$$

where

$$d = \left(\frac{\text{mass of beetle}}{\text{density of beetle}}\right)^{1/3}$$
$$= 0.00843 \text{ m}$$

combining (3) and (4) gives

$$Nu = \frac{\rho c_p (T_s - T_a) d}{r_H \rho c_p D_H (T_s - T_a)} = \frac{d}{r_H D_H}$$

therefore

$$r_H = \frac{d}{Nu D_H}$$

From Whitaker (1976), the Nu number for flow over a sphere is

$$Nu = 2 + \left(0.4 Re^{1/2} + 0.06 Re^{2/3}\right) Pr^{0.4} \left(\frac{u_\infty}{u_0}\right)^{0.25}$$ assume $\left(\frac{u_\infty}{u_0}\right)^{0.25} = 1$ at 25 °C

from Campbell (1977) $Re = \frac{Ud}{\nu}$

and $$Pr = \frac{\nu}{D_H}$$

$$= \frac{15.5 \times 10^{-6}}{22.2 \times 10^{-6}} \text{ at } 25\,^{\circ}C$$

therefore

$$r_{Ha} = \frac{d}{D_H\left[2 + \left(0.4 Re^{1/2} + 0.06 Re^{2/3}\right) Pr^{0.4}\right]}$$

$$= \frac{0.00843}{22.2 \times 10^{-6}\left[2 + \left(0.4\left(\frac{Ud}{\nu}\right)^{1/2} + 0.06\left(\frac{Ud}{\nu}\right)^{2/3}\right) Pr^{0.4}\right]}$$

$$= \frac{d \times 10^{6}}{44.4 + 1954\,(Ud)^{1/2} + 1856(Ud)^{2/3}}$$

$$= \frac{8430}{44.4 + 179.407\,U^{1/2} + 76.877U^{2/3}} \tag{5}$$

To calculate r_r:

$$r_r = \frac{\rho c_p}{4 e \sigma Ta^3} = \frac{1194.83}{22.453 \times 10^{-8}\,Ta^3} \text{ s m}^{-1} \tag{6}$$

To calculate R_{abs}:

$$R_{abs} = a_s\left(\frac{A_p}{A} S_p + \bar{S}_d\right) + \bar{e}_s \sigma T_a^4 \tag{7}$$

where

$$\frac{A_p}{A} = \frac{\pi r^2}{4\pi r^2} = 0.25$$

assume $\bar{S}_d = 0.2\,S_p$

assume $\bar{e}_s = 0.95$

Equation **(1)** (T_e) is then calculated by combining **(2)** with **(5)**, **(6)** and **(7)**.

Field variables necessary for the calculation of T_e include :

T_a (ambient temperature)

U (wind speed)

S (total incident radiation = direct + diffuse radiation)

The shortwave absorptance (a_s) of beetles was calculated in Chapter 3 (experiment 1). Absorptance of *O. bicolor* was estimated as follows: the reflectance of the white elytra at 500 nm (the peak spectral emittance of sunlight) is c. 65 %. The reflectance of the black thorax is c. 5 %. If the thorax contributes c. 0.25 of the surface area exposed to solar radiation, then the resultant reflectance (or absorptance) of the beetle is c. 50 % (*i.e.* a_s= 0.5). The reflectance of *O. unguicularis* was 5 %, thus a_s= 0.95.

APPENDIX 2

Heat exchange across plumages: a model

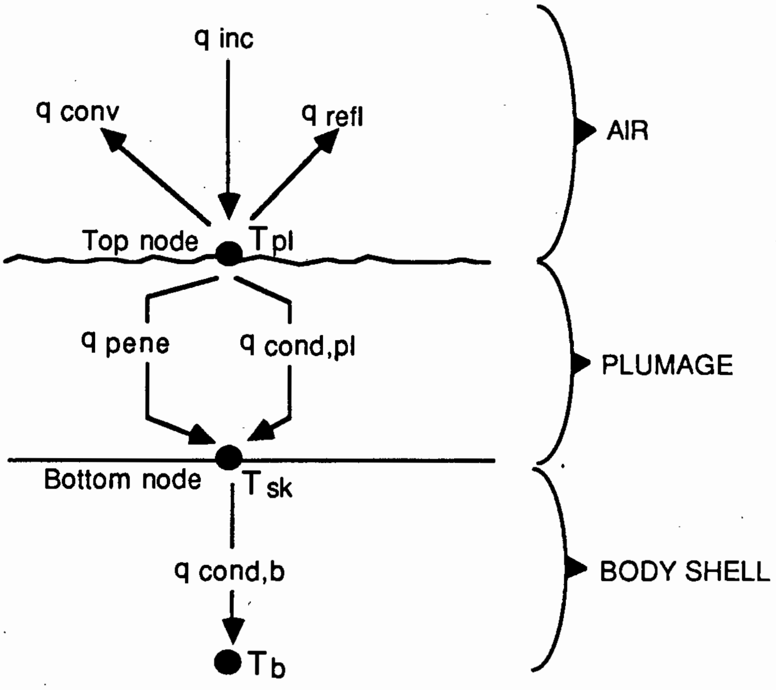

Fig. 47. Basic model of heat exchange across a plumage.

Heat balance equation for top node:

$$q_{inc} - q_{refl} - q_{pene} - q_{conv} - q_{cond,pl} = 0 \qquad \textbf{(1a)}$$

and $q_{inc} - q_{refl} - q_{pene} - q_{abs} = 0$ (where $q_{abs} = q_{conv} + q_{cond,pl}$)

thus $q_{inc} - p\,(q_{inc}) - q_{pene} - q_{abs} = 0$

$q_{abs} = (1 - p)q_{inc} - q_{pene}$

but $q_{abs} = q_{conv} + q_{cond,pl}$

∴ **for top node:**

$$q_{abs} + q_{conv} + q_{cond,pl} = 0 \qquad \text{(where } q_{conv} \text{ and } q_{cond,pl} < 0) \qquad \textbf{(1b)}$$

However, $q_{conv} = h_c(T_{air} - T_{pl})$ ($q_{conv} < 0$ when $T_{pl} > T_{air}$)

$$q_{cond,pl} = \frac{k_{pl}\,(T_{sk} - T_{pl})}{d}$$

($q_{cond,pl} < 0$ when $T_{pl} > T_{sk}$)

therefore, from (1b) :

$$q_{abs} + q_{conv} + q_{cond,pl} = 0$$

$$q_{abs} + \left[h_c(T_{air} - T_{pl})\right] + \left[\frac{k_{pl}(T_{sk} - T_{pl})}{d}\right] = 0$$

$$q_{abs} + h_c T_{air} - h_c T_{pl} + \frac{k_{pl}}{d} T_{sk} - \frac{k_{pl}}{d} T_{pl} = 0$$

$$q_{abs} + h_c T_{air} + \left[-h_c - \frac{k_{pl}}{d}\right] T_{pl} + \frac{k_{pl}}{d} T_{sk} = 0$$

$$\left[-h_c - \frac{k_{pl}}{d}\right] T_{pl} + \frac{k_{pl}}{d} T_{sk} = -q_{abs} - h_c T_{air} \qquad \text{units: (W m}^{-2}\text{)} \qquad (2)$$

Heat balance equation for bottom node:

$$q_{pene} + q_{cond,pl} - q_{cond,b} = 0 \qquad (3)$$

$$q_{pene} + \frac{k_{pl}(T_{pl} - T_{sk})}{d} + K(T_b - T_{sk}) = 0$$

$$q_{pene} + \frac{k_{pl}}{d} T_{pl} - \frac{k_{pl}}{d} T_{sk} + KT_b - KT_{sk} = 0$$

$$q_{pene} + \frac{k_{pl}}{d} T_{pl} + KT_b + \left[\frac{-k_{pl}}{d} - K\right] T_{sk} = 0$$

$$\frac{k_{pl}}{d} T_{pl} + \left[\frac{-k_{pl}}{d} - K\right] T_{sk} = -q_{pene} - KT_b \qquad (4)$$

from (2) for top node:

$$\left[-h_c - \frac{k_{pl}}{d}\right] T_{pl} + \frac{k_{pl}}{d} T_{sk} = -q_{abs} - h_c T_{air}$$

from (4) for bottom node:

$$\frac{k_{pl}}{d} T_{pl} + \left[\frac{-k_{pl}}{d} - K\right] T_{sk} = -q_{pene} - KT_b$$

these equations can be solved by matrix algebra as follows:

$$\begin{bmatrix} -h_c - (k_{pl}/d) & k_{pl}/d \\ k_{pl}/d & -(k_{pl}/d) - K \end{bmatrix} \begin{bmatrix} T_{pl} \\ T_{sk} \end{bmatrix} = \begin{bmatrix} -q_{abs} - h_c T_{air} \\ -q_{pene} - KT_b \end{bmatrix} \qquad (5)$$

solving the above:

1) to calculate h_c

for a flat disc:

$$Nu = 0.66\, Re^{1/2} Pr^{1/3}$$

$$Nu = \frac{h_c \partial}{k_{air}}$$

$$Re = \frac{U\partial}{\nu}$$

to solve for h_c:

$$h_c = \frac{Nu\, k_{air}}{\partial}$$

$$h_c = \frac{(0.66\, Re^{1/2} Pr^{1/3}) k_{air}}{\partial}$$

$$= \frac{0.66 \dfrac{U^{1/2} \partial^{1/2}}{\nu^{1/2}} (0.708^{1/3})\ (0.02624)}{\partial}$$

$$= \frac{(0.66)\ (0.708^{1/3})\ (0.02624)}{(15.68 \times 10^{-6})^{1/2}} \cdot \frac{U^{1/2} \partial^{1/2}}{\partial}$$

$$= (3.8980) \frac{U^{1/2} \partial^{1/2}}{\partial}$$

$$= (3.8980) \frac{U^{1/2}}{\partial^{1/2}}$$

from Mitchell (1976):

$$\partial = \left[\frac{\text{mass of bird (kg)}}{\text{density of bird (kg m}^{-3}\text{)}} \right]^{1/3}$$

use 1 g cm^{-3} = 1000 kg m^{-3}

$$\text{therefore} \quad \partial = \frac{W^{1/3} kg^{1/3}}{(10^3 kg\, m^{-3})^{1/3}}$$

$$= \frac{W^{1/3} kg^{1/3}}{10\, kg^{1/3} m^{-1}}$$

$$= \frac{W^{1/3}}{10}\ m$$

$$= (3.898)\,\frac{U^{1/2}\sqrt{10}}{W^{1/6}} \qquad \text{therefore} \quad \partial^{1/2}\,\mathrm{m} = \frac{W^{1/6}}{10^{1/2}}\,\mathrm{m}$$

$$h_c = 12.3267\,U^{1/2}W^{-1/6} \quad \text{units: W m}^{-2}\,{}^{\circ}\mathrm{C}^{-1} \qquad (6)$$

2) to solve for k_{pl} :

from Gates & Schmerl (1975):

$$\begin{aligned} k_{pl} &= 0.009 \ \mathrm{cal\ cm^{-1}\ min^{-1}\ {}^{\circ}C^{-1}} \qquad (1\ \mathrm{J} = 0.2388\ \mathrm{cal}) \\ &= 0.0628 \ \mathrm{W\ m^{-1}\ {}^{\circ}C^{-1}} \qquad (7) \end{aligned}$$

This figure is in agreement with the values of thermal conductivity of avian plumages calculated by Walsberg (1988b) (0.0339-0.0796 $\mathrm{W\ m^{-1}\ {}^{\circ}C^{-1}}$).

3) to calculate K (conductance through body):

$$K = K_s + K_{bl}$$

a) to calculate K_s:

$$q_{condK_s} = \frac{k_{sh}}{t}(T_{sk} - T_b)$$

for cylinder:

$$t = \frac{1}{4}r \quad , \quad r = \frac{\partial}{2}$$

therefore $$t = \frac{1}{8}\partial$$

but $$\partial = \frac{W^{1/3}}{10}$$

therefore $$t = \frac{W^{1/3}}{80}$$

therefore $$K_s = \frac{k_{sh}}{t} = \frac{0.412\ \mathrm{W\ m^{-1}\ {}^{\circ}C^{-1}}}{W^{1/3}/80 \ \ \mathrm{m}}$$

(Bowman *et al.* 1975)

$$= 32.96\,W^{-1/3}\ \mathrm{W\ m^{-2}\ {}^{\circ}C^{-1}}$$

b) to calculate K_{bl}:

$$q_{cond,bl} = \frac{\dot{m}c_p}{A}(T_{sk} - T_b)$$

$$\dot{m} = F\ V_s\ p_{bl}$$

From Peters (1983):

$$F = 2.60\ W^{-0.23}\ s^{-1}$$
$$V_s = 0.66\ W^{1.05}\ ml$$

assume $p_{bl} = 0.001\ kg\ ml^{-1}$

therefore $\dot{m} = 2.60\ W^{-0.23}\ 0.66\ W^{1.05}\ 0.001\ ml\ s^{-1}\ kg\ ml^{-1}$

$$= 0.00172\ W^{0.82}\ kg\ s^{-1}$$

therefore $\dot{m} = 0.00172\ W^{0.82}\ 4200\ J\ s^{-1}\ {}^{o}C^{-1}$ (where: c_p=4200 J $kg^{-1}\ {}^{o}C^{-1}$)

$$= 7.224\ W^{0.82}\ J\ s^{-1}\ {}^{o}C^{-1}$$

$$= 7.224\ W^{0.82}\ W\ {}^{o}C^{-1}$$

therefore $K_{bl} = \frac{\dot{m}c_p}{A} = \frac{7.224\ W^{0.82}}{0.09\ W^{0.74}}\ \frac{w\ {}^{o}C^{-1}}{m^2}$

i.e. $K_{bl} = 80.267\ W^{0.08}\ W\ m^{-2}\ {}^{o}C^{-1}$

therefore $K = K_s + K_{bl}$

$$= 32.96\ W^{-1/3} + 80.267\ W^{0.08}\ W\ m^{-2}\ {}^{o}C^{-1} \tag{8}$$

4) to solve for q_{abs}:

let $q_\infty = (1 - p)\ q_{inc}$
$= q_{abs} + q_{pene}$

and $q_{pene} = aq_\infty$
$= a\ (1 - p)\ q_{inc}$ (9)

where a = fraction of q_∞ to
penetrate plumage
(a < 1)
assume a = p

and $q_{abs} = (1 - a)\ q_\infty$
$= (1 - a)\ (1 - p)\ q_{inc}$ (10)
$= (1 - a - p + ap)\ q_{inc}$

this is consistent with equation **(1b)** where:

$$\begin{aligned}
q_{abs} &= (1 - p)\, q_{inc} - q_{pene} \\
&= (1 - p)\, q_{inc} - [a(1 - p)\, q_{inc}] \\
&= (1 - p)\, q_{inc} - (a - ap)\, q_{inc} \\
&= q_{inc} - p\, q_{inc} - aq_{inc} + ap\, q_{inc} \\
&= (1 - a - p + ap)\, q_{inc}
\end{aligned}$$

to solve for (5):

for both species:

$h_c = 12.327\, U^{1/2} W^{-1/6}$ W m^{-2} °C^{-1} from **(6)**
$k_{pl} = 0.0628$ W m^{-1} °C^{-1} from **(7)**
$K = 32.96\, W^{-1/3} + 80.267\, W^{0.08}$ W m^{-2} °C^{-1} from **(8)**
$q_{pene} = a\,(1 - p)\, q_{inc}$ from **(9)**
$q_{abs} = (1 - a)\,(1 - p)\, q_{inc}$ from **(10)**

for:	<u>gannets</u>	<u>cormorants</u>	
	$W = 2.6$ kg	$W = 1.2$ kg	(Jarvis 1971, Berry 1976)
	$p = a = 0.841$	$p = a = 0.137$	(experiment 1)
	$d = 0.0117$ m	$d = 0.0112$ m	(experiment 2)
	$T_b = 40.1$ °C	$T_b = 40.4$ °C	(see Chapter 7)

APPENDIX 3

Application of the computer package DIRECT (Mimmack *et al.* 1980).

DIRECT is a computer programme for the analysis of two-dimensional, unimodal directional data. The programme was applied to the orientation data collected in the present study, in order to ascertain if birds displayed a statistically significant preferred direction of orientation at any one time. The programme refers to this as a single sample test, as opposed to additional multi-sample tests which were not used in this study. The single sample test calculates a modal vector (a circular mean) for each sample and tests for randomness with the following null hypothesis:

$$H_o : x = 0$$

where x is the dispersion parameter of the modal vector and indicates the degree of variance in the data. The null hypothesis states that there is no preferred direction shown in the sample, whereas the alternative hypothesis, H_1, states that a preferred direction of orientation is displayed. DIRECT is designed for sample sizes over 20. In this case, H_o is rejected at the level α if

$$2R^2/N > \chi^2_{2(\alpha)}$$

where R = length of modal vector

N = sample size

χ^2 = chi-square

However, for sample sizes ≤ 10 (as in the present study), H_o is tested as follows: H_o is rejected at the level α if

$$R/N > 0.540 \ (p < 0.05)$$

or

$$R/N > 0.687 \ (p < 0.01)$$

for N = 10. These values were obtained from Table 56 (Pearson & Hartley 1972), which lists the percentage points of R/N (on a circle), for a given N and x. Similar values are listed for sample sizes from 5 - ∞.

DIRECT produces a results sheet which lists each single sample separately, with the modal vector and the confidence interval for the angle of the modal vector. Confidence limits are only printed for single samples in which H_0 has been rejected. However, for sample sizes of $N \leq 10$, the values R/N on the results sheet must be manually compared with the previously mentioned values in Table 56, in order to ascertain which modal vectors represent statistically significant preferred orientations.