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Behavioural adaptations of the Jackass penguin, *Spheniscus demersus* to a hot, arid environment

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(With 12 figures in the text)

Penguins tend to be overinsulated for life on land. A study of the Jackass penguin *Spheniscus demersus* was undertaken to investigate the behavioural adaptations that enable the species to cope with the exigencies of a hot, terrestrial environment.

The Jackass penguin is mainly crepuscular and nocturnal at its breeding stations. The numbers of birds present on land are highest at night and lowest during the day. The majority of birds leaving a breeding colony do so just after dawn. Birds begin to return to the colony during the late afternoon. The frequency of displays is highest at dawn and from dusk to midnight. This activity cycle enables birds not engaged in incubation or chick guarding to avoid conditions promoting heat stress.

Birds remaining in the colony during the day employ strategies such as burrow-nesting, body-orientation and evaporative cooling to reduce the effects of high insolation. Compared to the ambient, the microclimate of burrows is more constant; relative humidity is higher; air temperatures fluctuate less; and wind effect is negligible. Most important, birds nesting in burrows are protected from direct insolation. Egg and nest-air temperature in a burrow are relatively constant. Burrows facing east are cooler than those facing west. However this does not influence burrow-orientation, which is determined by the slope of the ground.

Birds exposed to high insolation orientate with their backs to the sun. The lightly feathered areas of the body are shaded. This facilitates heat loss by convection and reradiation from these shaded surfaces. In this position dorsal surface temperature regularly exceeds body temperature. It is suggested that heat gain from the dorsal surface is restricted by efficient insulation, primarily an adaptation to the aquatic environment. On overcast days orientation is non-directional. In the early morning when ambient temperatures are relatively low, the birds also orientate with their backs to the sun. This is interpreted as sunbathing.

Body temperatures were significantly higher on a hot than on a cool day. The Jackass penguin appears to be relatively thermolabile. This would facilitate both energy conservation in water and resistance to heat stress on land. The overall thermoregulatory strategies of the Jackass penguin for life in two different environments are discussed.

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Introduction

The adaptations of an animal to its environment usually involve compromise between opposing selection pressures. However, animals which alternately inhabit two radically different environments presumably encounter opposing selection pressures between which compromise is not always possible. The adaptations that evolve to fit the animal successfully into both environments are therefore of interest to evolutionary biologists.

Penguins (Spheniscidae) are amongst the most aquatic of all birds. Many species probably spend more than half their life at sea, the environment from which they obtain all their nutritional requirements. Morphologically, penguins exhibit the consequences of selection pressure for locomotory efficiency in a medium denser than air. These adaptations include an elongate body, fore- and hindlimbs reduced and modified as paddles, and a stiff, waterproof and streamlined plumage (Stonehouse, 1967).

The aquatic environment is also characterized by having a thermal conductivity some 30 times greater than that of air. This capacity for increased heat loss potentially poses a substantial bioenergetic problem to endothermic animals which must maintain body temperatures considerably higher than the temperature of the environment. Penguins have largely overcome the problem by supporting thick layers of subdermal fat, a dense waterproof plumage, extensive arterio-venous associations facilitating counter-current heat exchange and probably also cardiovascular control over the peripheral blood supply (Stonehouse, 1967, 1970; Trawa, 1970; Frost, Siegfried & Greenwood, 1975). Penguins may also compensate for increased heat loss by increasing metabolic heat output, through shivering (Kooyman, 1975).

A consequence of decreased thermal conductance is that penguins tend to be over-insulated for life on land. There are certain adaptations that facilitate heat loss, such as a venous shunt bypassing the arterio-venous complex in the axilla (Frost *et al.*, 1975), dilation of peripheral blood vessels and a relative increase in the area of radiating and convective heat loss surfaces (Stonehouse, 1967, 1970). However, despite these adaptations, moderate ambient temperatures and high incident solar radiation apparently promote heat stress. This problem must be particularly acute for those penguins nesting in tropical and subtropical regions (Stonehouse, 1967).

Stonehouse (1967) concluded that nocturnal activity at breeding colonies, coupled with the use of burrows and rock fissures as nest sites, has allowed penguins to overcome the problem. However, with the exception of a recent study on the Galapagos penguin *Spheniscus mendiculus* (Boersma, 1975), there has been no quantitative information on these aspects of penguin behaviour. This paper examines the paradox of a penguin in a hot terrestrial environment, as it relates to the Jackass penguin *Spheniscus demersus*.

We discuss the microclimate available to nesting penguins, and relate the spatial and temporal variations in microclimate to the patterns of behaviour exhibited by the species.

The Jackass penguin, a subtropical species confined to the coastal waters of southern Africa (McLachlan & Liversidge, 1970), currently breeds on 18 offshore islands, predominantly along the west coast (Rand, 1963; Frost, Siegfried & Cooper, in press). This is a region of high biological productivity enhanced by the cold, nutrient-rich waters of the Benguela current (Cushing, 1971). Proximity to this cold current ensures that on the islands rainfall is low. Ambient temperatures, modified by cool sea breezes, are generally moderate. However, insulation is high, particularly during spring and summer (October–March).

Study site and methods

The work was carried out primarily on Dassen Island (33°25′S, 18°05′E), the largest (220 ha) and the most important breeding island for Jackass penguins. The island is low lying and sandy with granite intrusions. Rainfall is low (average 346 mm per year) and concentrated during the winter months (May–September) (Weather Bureau, 1952). Winds blow predominantly from the north-west during winter and south-east during summer. Perennial vegetation mainly consists of low bushes and shrubs (*Tetragonia*, *Mesembryanthemum*), while during winter large areas are covered with nettles (*Urtica*). This vegetation provides some shade for dispersed surface nesting penguins. However, the present study concentrated on the microclimate of the open breeding flats—areas of variable size in which the majority of breeding penguins burrowed. The microclimate of unoccupied burrows was compared with ambient conditions on the surface. Some birds nested in exposed situations on the surface or in collapsed burrows. The microclimates of occupied surface and burrow nests were compared.

Air, soil and soil-surface temperatures, net radiation, relative humidity and wind speed were measured inside unoccupied burrows and at the surface. Egg, nest-air, nest soil and ambient temperatures were recorded simultaneously for an occupied burrow nest and an occupied surface nest. "Black bulb" temperatures were recorded for half a day at an exposed site.

All measurements of air temperature, net radiation, relative humidity and wind speed were measured 30 cm above the ground at surface sites and 30 cm inside unoccupied burrows. Soil temperatures were measured 0·5 cm below the soil surface. Egg temperatures were measured with the probe tip resting against the inner cell membrane. Nest-air temperatures were measured inside the nest mass (dried vegetable material) approximately 1·0 cm below the eggs. Nest-soil temperatures were measured immediately underneath the nest.

Air and soil temperatures were recorded continuously during 4 days with a Grant's eight-channel thermistor thermometer. Egg and nest temperatures were recorded with a YSI model 47 telethermometer. Subsidiary temperatures were measured with mercury thermometers shielded from direct solar radiation by aluminium foil. Surface temperatures were recorded with a Barnes PRT IOL infrared radiation thermometer (field of view 2·8°, calibrated range −10°C +60°C). Night sky temperatures were obtained by offsetting the calibration 10°C. Due to non-linearity of readings below −10°C, the readings are approximate to within 10% of the true value.

Net radiation was measured with a Thornthwaite 603 miniature net radiometer, and relative humidity with a Shaw minihygrometer. Windspeeds in the open and inside burrows were measured with a vane anemometer and a Wallac-oy GGA23S thermoanemometer respectively.

Body temperatures of an adult male penguin (mass 3185 g) were recorded from an ingested temperature-sensitive radiotransmitter. The bird was housed in the open in a 9 m^2 compound. Shade was provided. The bird was allowed to recover for 12 h after ingesting the radio capsule.

The attendance pattern of birds at the colony was determined by the number of adult penguins visible on a breeding flat. During the day birds were counted every 10 min. The mean number of birds present per half hour period was computed. At night, flash-assisted photographs of the colony were taken every hour. Close agreement (less than 5% difference) was obtained between the number of birds counted at dusk and the number counted from photographs at the same time. Hence, figures obtained by the two methods are considered to be comparable.

The activity of birds in the colony was monitored from a hide. The number of "ecstatic" and "loud mutual" displays (Spurr, 1975, but see Ainley, 1975, for different terminology) were recorded visually during the day and aurally at night. The number of birds leaving for, and returning from, the beach was determined for each half hour period throughout the day. The activity of birds in a beach group was recorded as the number of birds entering and leaving, and the mean number in, the water during each half hour period of daylight.

The body orientation of 100 adult penguins loafing in the colony was recorded in a standard non-selective manner every hour from 06.30 to 16.30 hrs S.A.S.T. Due to the low number of birds present on the surface during the midday period, counting was continued into adjacent colonies in order to achieve the required sample. Sun altitude and direction were determined by measuring the length and compass direction of the shadow cast by a 40 cm high rod located in a flat area nearby.

The orientation of all burrows, occupied and unoccupied, was determined for 5 colonies throughout the island. At a sixth colony the orientation of occupied and unoccupied burrows was recorded separately. The slope and nature of the terrain at each site was noted.

Results

During our visits to Dassen Island (March 1972, December 1972, 1973, November 1974) no exceptionally hot days were recorded. Most clear days were accompanied by cooling sea breezes. Cool, overcast weather was recorded on a number of days. The results obtained represent average conditions experienced on the island in March, December and November (Weather Bureau, 1952).

TABLE I

Mean dimension (± one standard deviation) of 10 Jackass penguin burrows on Dassen Island

Depth	56·2±14·8 cm
Height at entrance	18·2± 1·8 cm
Width at entrance	32·6± 4·5 cm
Angle from horizontal	—27 ± 5°

Burrow microclimate

Average burrow dimensions are given (Table I). Overall, burrows are similar to, but smaller than those excavated by the closely related, though larger Magellanic penguin *Spheniscus magellanicus* (Boswell & MacIver, 1975).

Air temperatures inside burrows varied slightly, depending on burrow orientation (Fig. 1). Burrows facing east tended to heat up more rapidly than burrows facing west. However, after midday the latter were up to 4°C warmer than east facing burrows, and remained 2–3°C warmer for most of the night. Ambient temperature, cooler than burrow air at night, increased rapidly just after dawn. However, cooling sea breezes, which blow regularly from about 11.00 to 19.00 hrs daily, tended to depress midday ambient temperatures. Consequently temperatures in burrows were generally higher than ambient during the afternoon. Black bulb temperatures were higher than either burrow or ambient temperatures during midday, indicating the importance of solar radiation even when cooling winds were blowing.

Despite moderate surface winds of up to 3 m sec^{-1} during midday, wind movement inside burrows was negligible. Relative humidity in burrows during daylight was higher than ambient r.h. Fluctuations in the latter, effected by wind and temperature variations, were reflected in similar fluctuations in burrow r.h. There was no difference between burrow and ambient r.h. at night. Humidity was considerably higher then than on clear warm days (Fig. 2).

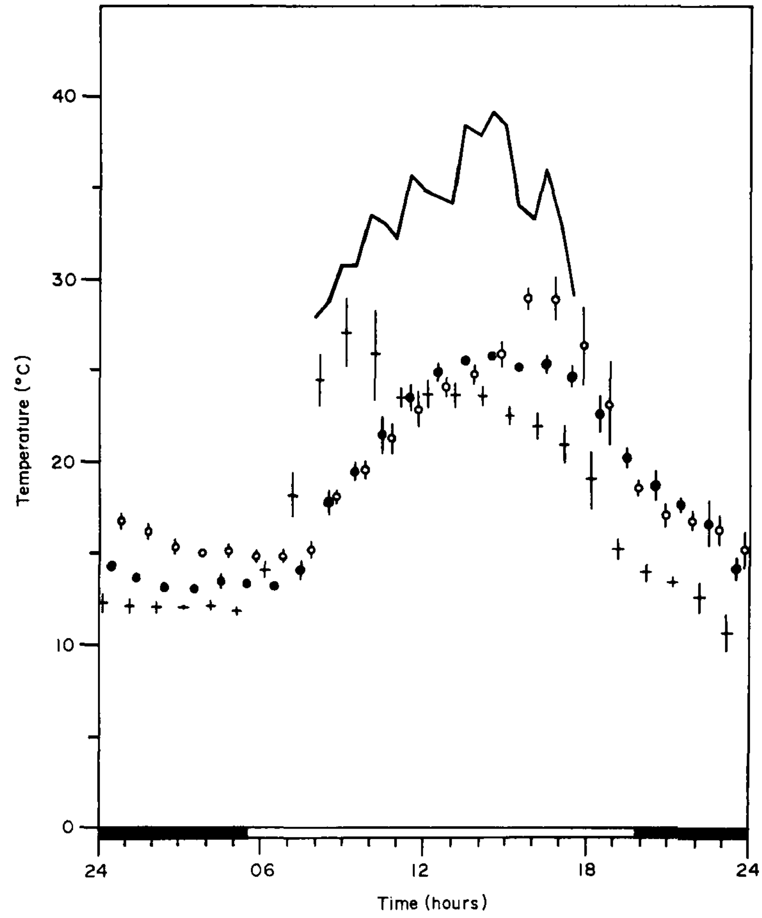

FIG. 1. Twenty-four hour records of hourly mean air temperatures at the surface and inside two unoccupied burrows on Dassen Island. (●) East-facing burrow; (○) west-facing burrow; (+) ambient; (—) "black bulb" temperature. Vertical lines each denote one standard deviation ($n = 12$). Horizontal bar indicates night (▬) and day (□).

There was a marked difference between surface and burrow soil temperature (Fig. 3). Whereas the latter varied little throughout the day, surface soil heated up rapidly during the morning to a maximum of 36°C. Surface soil temperatures would be higher on very hot days. At night, soil in burrows was warmer than exposed surface soil. The range in burrow soil temperature (17°–20°C) compared with that of the surface soil (12°–36°C) indicates the importance of burrows in affording protection from direct solar radiation during the day, and infrared reradiation at night.

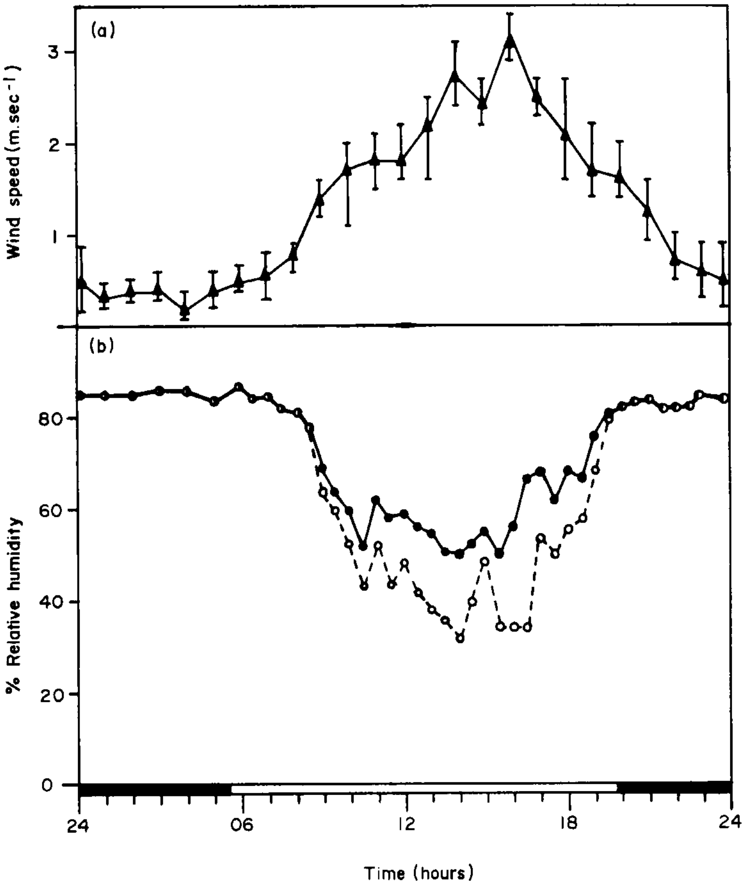

FIG. 2. Twenty-four hour record of hourly mean wind speed and relative humidity at the surface of a breeding flat and inside an unoccupied burrow. (a) Wind speed 30 cm above the soil (▲). Vertical lines each denote one standard deviation ($n = 5$). Wind movement inside the burrow was negligible. (b) Relative humidity 30 cm above the soil (○) and inside a burrow (●).

Net radiation exchange on the surface varied from +0·58 cal cm^{-2} min^{-1} during the day to −0·1 cal cm^{-2} min^{-1} at night. Inside a burrow net radiation exchange was effectively nil for most of the day and at night. However, east facing burrows in the morning, and west facing burrows during the late afternoon, received direct solar radiation. For an east facing burrow this resulted in a gain of +0.18 cal cm^{-2} min^{-1} during a brief period in the early morning (Fig. 3).

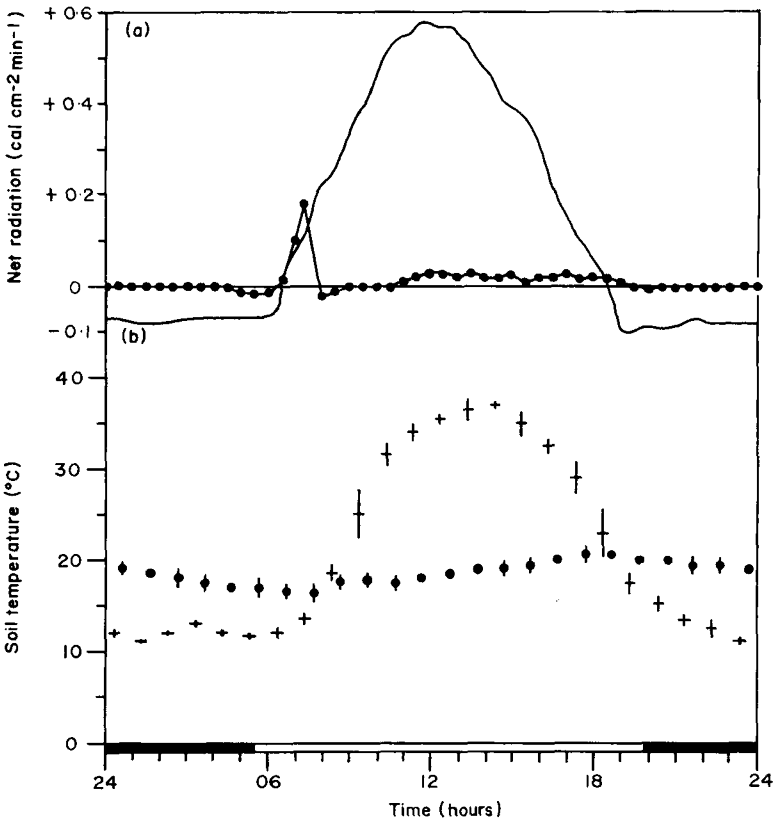

FIG. 3. Twenty-four hour record of net radiation exchange and hourly mean soil temperatures at the surface of a breeding flat and inside an unoccupied burrow. (a) Net radiation exchange at the surface (—) and inside an east facing burrow (●). (b) Soil temperatures at the surface (+) and inside an east facing burrow (●). Vertical lines each denote one standard deviation ($n = 12$).

Nest microclimate

During the day air temperatures in the exposed surface nest were up to 9·5°C warmer than in the burrow nest (Fig. 4). However, at night the burrow nest was up to 2·6°C warmer. This may be due to better insulation in the burrow against both heat loss and heat gain. The nest-air temperatures in both the burrow and the surface nest were always higher than ambient temperature (Fig. 4). These differences were least at dawn (2·2°C between ambient and surface nest, 2·8°C between ambient and burrow) and greatest just after noon (15·7°C between ambient and surface nest, 7·5°C between ambient and burrow nest).

A comparison between surface and burrow nest-soil temperatures reveals a different pattern (Fig. 5). At night the surface nest-soil was 2·3°C warmer than burrow nest-soil. During the day, with the exception of the early afternoon, there was little difference in temperature between the two. Just after midday the burrow nest-soil was 2·6°C warmer than the open nest. Nest-soil temperatures generally were higher during the day than at night. Apart from possible differences in the position and depth of the probes in the nest,

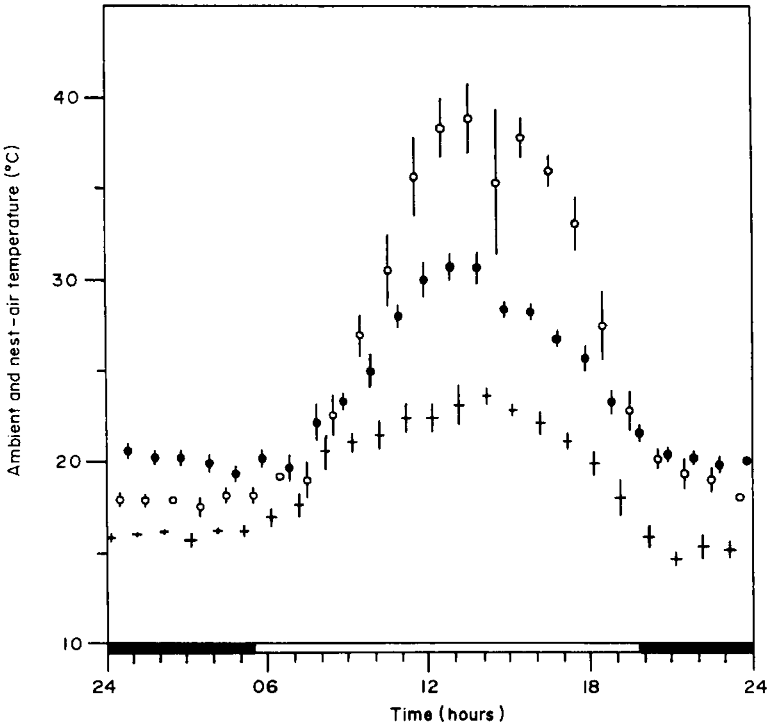
Ambient and nest-air temperature (°C)
40
30
20
10
24
06
12
18
24
Time (hours)

FIG. 4.

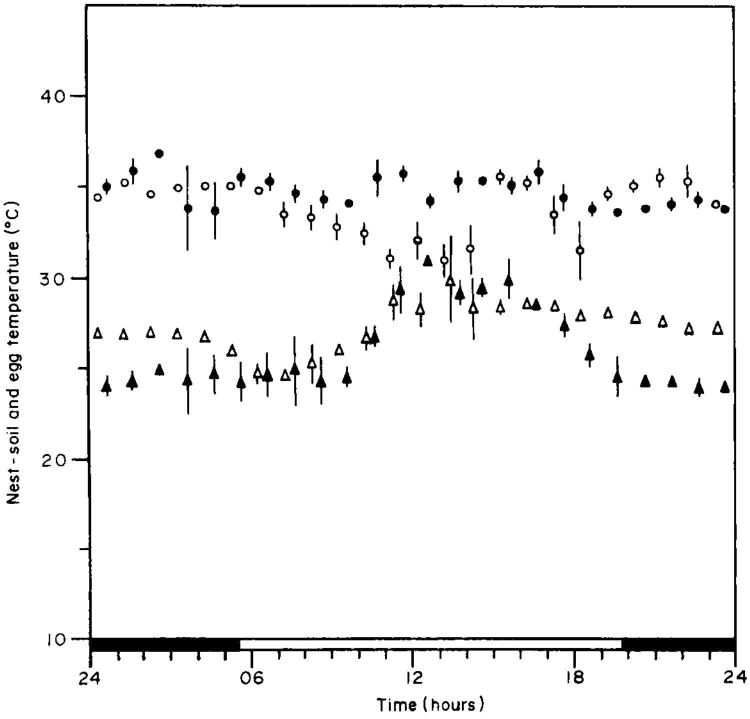
Nest-soil and egg temperature (°C)
40
30
20
10
24
06
12
18
24
Time (hours)

FIG. 5.

we cannot account for the discrepancy in the patterns of nest-air and nest-soil variation between surface and burrow nests.

Egg temperatures remained generally higher and more constant in the burrow nest than in the surface nest (Fig. 5). In the burrow, egg temperature was lowest and most variable between 03.00 and 05.00 hrs, just prior to dawn. During this period the incubating bird indulged in considerable nest building activity and this presumably affected egg temperature.

The temperature of the egg in the surface nest was lowest and most variable prior to dusk and during the early afternoon. An incubation changeover, accompanied by the birds performing displays and relatively increased nest inattentiveness, took place at dusk. The low midday temperatures of the egg were associated with the incubating bird showing symptoms of heat-stress. The bird, in addition to panting, sat upright on the nest. This posture allowed air to flow across the egg, causing it to cool.

Burrow orientation

Burrow orientation significantly departed from randomness in two out of six colonies (Table II). In both cases the preferred direction in which the burrows faced correlated well with the prevailing slope of the ground. It appears to be generally true that penguins burrow into the slope, though the presence of rock or other obstruction can also influence burrow orientation.

TABLE II

Orientation of occupied and unoccupied penguin burrows at six breeding flats on Dassen Island
x^2_{11} *value for* **P** *0·05 = 19·68*

Colony	Area (m²)	No. burrows	Slope of ground (° from N)	30° Sectors from true north												x^2	*P*
				1	2	3	4	5	6	7	8	9	10	11	12		
1	100	27	195°	1	1	0	1	0	0	0	2	7	5	7	5	34·77	<0·001
2	100	52	—	8	4	3	3	6	5	2	5	5	11	5	5	8·91	<0·8
3	100	22	150°	3	1	4	0	0	1	2	1	3	4	1	2	11·86	<0·5
4	400	105	195°	7	2	8	7	11	7	15	3	12	10	10	13	18·77	<0·1
5	100	48	15°	1	4	7	4	4	6	8	6	1	3	1	3	15·50	<0·2
6	540	158	120°	3	9	20	24	28	19	22	11	7	3	6	6	65·72	<0·001

A comparison was made between the orientation of available and occupied burrows in one colony. Individually neither set of data indicated a departure from randomness (Table III). However, a comparison between the number of burrows available and the number occupied in each 30° sector indicated an apparent preference for the 0–30°,

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FIG. 4. Twenty-four hour record of hourly mean nest-air temperatures compared with ambient temperatures. (○) Occupied surface nest; (●) occupied burrow nest; (+) ambient. Vertical lines each denote one standard deviation ($n = 12$).

FIG. 5. Twenty-four hour record of hourly mean egg and nest-soil temperatures from an occupied surface nest and an occupied burrow nest. (○) Surface nest egg; (●) burrow nest egg; (△) surface nest-soil; (▲) burrow nest-soil. Vertical lines each denote one standard deviation ($n = 12$).

TABLE III

Comparison between orientation of all burrows in colony 4 and orientation of occupied burrows only x^2_{11} *value for* P *0·05 = 19·68*

	No. burrows	30° Sectors from true north												x^2	P
		1	2	3	4	5	6	7	8	9	10	11	12		
A. Burrows available	105	7	2	8	7	11	7	15	3	12	10	10	13	18·77	<0·1
O. Burrows occupied	40	6	2	7	3	2	1	4	3	6	2	2	2	12·79	<0·5
E. Expected no. if distribution dependent only on availability of burrows	40	2·7	0·8	3·0	2·7	4·2	2·7	5·7	1·1	4·6	3·8	3·8	4·9	—	—
$(O-E)^2/E$		4·19	2·01	5·15	0·16	1·13	1·03	0·51	3·02	0·45	0·85	0·85	1·75	21·10	<0·05

30–60°, 60–90° and 210–240° sectors. This preference, within the restriction of the number of burrows available, is statistically significant (Table III).

Pattern of daily activity

Number of birds in the colony

The number of birds in the colony was highest at night and lowest during the middle of the day (Fig. 6). Numbers decreased rapidly after dawn. This was due to a movement of birds from the colony to the beach (Fig. 7). Birds started to return to the colony from 15.00 hrs. Many of the early, returning birds were adults coming back to the colony to feed chicks.

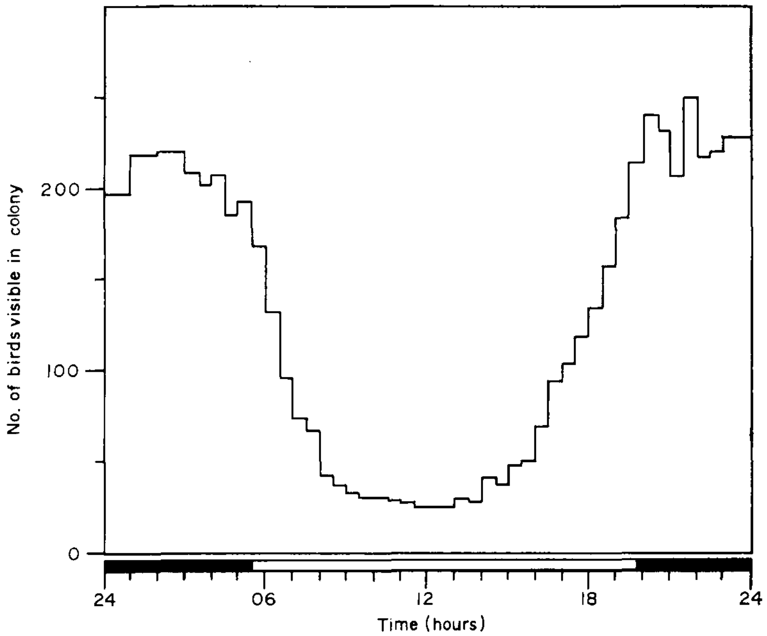

FIG. 6. Twenty-four hour record of the number of penguins visible each half hour on the surface of a breeding flat.

The pattern of movement to and from the beach (Fig. 7) shows that immediately after sunrise the number of birds leaving the colony increased. Very few birds entered the colony at this stage. However, within an hour after sunrise there was a minor peak in the number of birds returning to the colony. Subsequent observations suggest that these birds left the colony at dawn, went down to the beach to drink, bathe and preen and then returned to the colony to resume incubation or chick guarding duties.

During the midday period small numbers of birds left the colony. Many of these birds showed signs of heat stress (primarily panting) prior to departure from the colony. Observations confirmed that these birds moved to the beach to bathe, drink and presumably cool down, before returning to the colony.

Finally, there was a small peak in the number of birds leaving the colony in the late evening. Most of these birds had been relieved at the nest by a returning mate. These birds bathed and preened before returning to the colony or spending the night on the beach. Very few birds left the island in the evening.

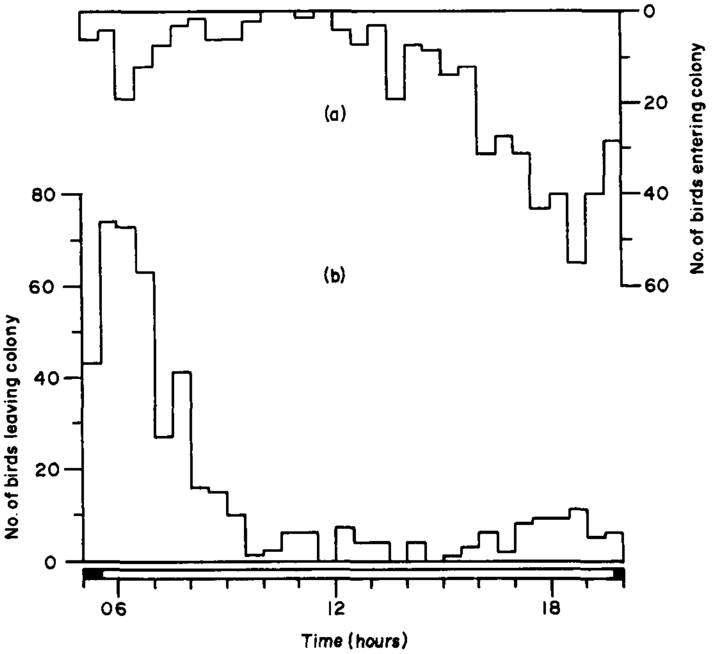

FIG. 7. Movement of penguins between a breeding flat and the beach during daylight hours. (a) Entering colony; (b) leaving colony.

The activity of birds in a beach group

The pattern of activity of penguins in a beach group reflected closely the pattern of movement of birds between the colony and the beach (Fig. 8). The number of birds entering the water was highest at dawn (Fig. 8(c)). The majority of these birds first bathed, 5–10 m from the shore, then formed into groups and gradually made their way out to sea. Minor peaks in the number of birds entering the surf occurred in the early afternoon when ambient temperature was highest (Fig. 8(a)), and in the evening when birds entered the water to bathe.

The number of birds leaving the water showed an opposite trend (Fig. 8(b)). The greatest number of birds leaving the water occurred in the late afternoon and evening. Most of these birds were returning from foraging at sea. A minor peak in the early morning consisted of individuals that had entered the water earlier to bathe and preen. These birds, after preening, either returned to the breeding colony or remained in the beach group.

The number of birds in the water accurately reflected these movements (Fig. 8(a)). Peaks occurred at dawn (when the majority of birds left the island) and at dusk (when birds were returning to the island). Birds entering the water during the middle of the day did so to drink, bathe and preen (in that order). Time spent in the water was short (non-moulting adults, $x = 278+145$ sec, $n = 15$). Moulting birds rarely entered the water and then only for very brief periods to drink (moulting adults, $x = 25\pm14$ sec, $n = 3$).

Finally it should be noted that birds loafing in a beach group experienced ambient temperatures on average 2·3°C lower than air temperatures on the breeding flats (Fig. 8(a)).

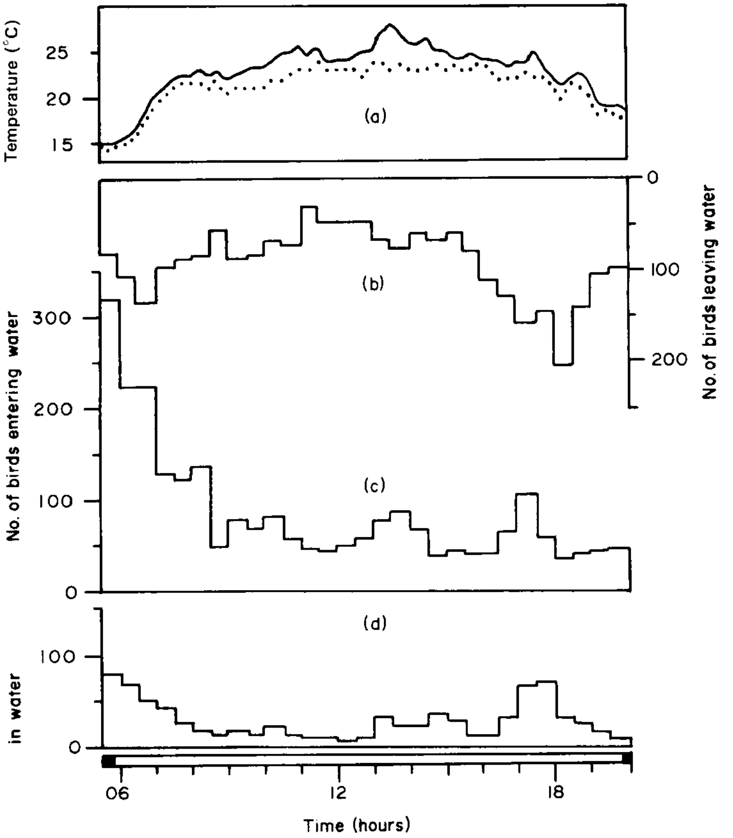

Fig. 8. Movement of penguins between a beach group and the sea during daylight hours. (a) Ambient temperature at the beach (......) and 40 m inland at a breeding flat (—); (b) number of penguins leaving water; (c) number entering water; (d) mean number in water per half hour period.

Activity of birds in the colony

Courtship behaviour, nest building and mating all appeared to be carried out primarily at dawn and dusk. This subjective impression was confirmed for "ecstatic" and "loud mutual" displays (Fig. 9). Both displays were recorded most frequently at dawn and from dusk until just after midnight.

Incubation changeovers apparently took place at dusk. Adults arriving to feed chicks did so during the late afternoon and evening.

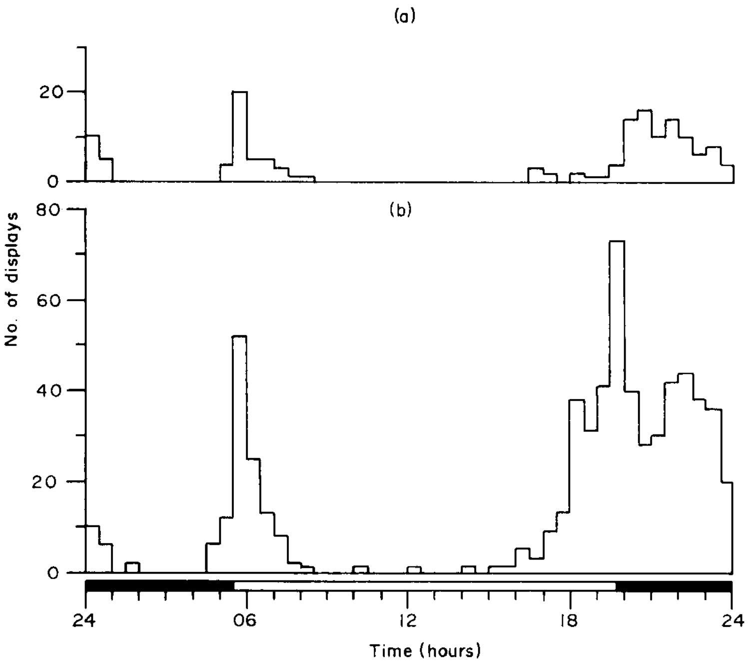
(a)
20
0
80
(b)
No. of displays
60
40
20
0
24
06
12
18
24
Time (hours)

FIG. 9.

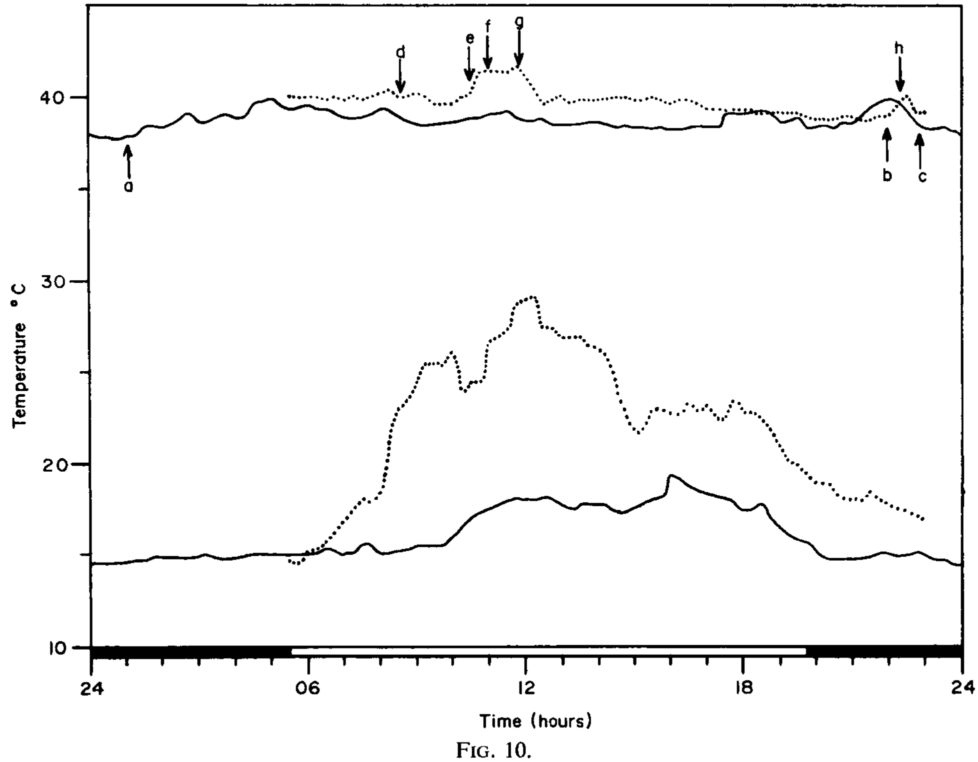
d
e
f
g
h
a
b
c
40
30
20
10
Temperature °C
24
06
12
18
24
Time (hours)

FIG. 10.

Body temperature

The deep core body temperature of an adult penguin measured on a uniformly cool day, did not reflect clearly the marked activity cycle of the species (Fig. 10). The mean temperature recorded for the period 03.00–09.00 hrs was significantly higher than the mean temperatures recorded during other periods of the day. Minor peaks in body temperature occurred from 17.30–19.00 hrs and from 21.30–22.30 hrs. No overall statistical significance was demonstrated for the six hour periods in which these peaks arose (Table IV).

Body temperatures recorded on a warm day were considerably higher than those recorded on a cool, overcast day (Fig. 10). The differences were statistically significant (Table IV). Body temperatures were significantly higher during the hot midday period, than during the relatively cooler evening period (Table IV). Periods of intense activity (in the case of the experimental bird, trying to escape from the pen) led to increases in body temperature (Fig. 10(h)). Conversely, when the overheated bird sought out and found a suitably cool microclimate (shade) body temperature rapidly decreased (Fig. 10(g)).

TABLE IV

Body temperature (T_b) data (± one standard deviation) from an adult male penguin on two contrasting days

	1.12.73 (clear)			2/3.12.73 (overcast)		
Time (hrs)	T_b (°C)	T_a (°C)	n	T_b (°C)	T_a (°C)	n
03·00–09·00	—	—		39·1 ± 0·4	15·1 ± 0·2	24
09.00–15.00	40·3 ± 0·7	26·3 ± 1·6	24	38·7 ± 0·5	17·2 ± 0·9	24
15.00–21.00	39·4 ± 0·3	21·7 ± 1·6	24	38·6 ± 0·4	17·3 ± 1·4	24
21.00–03.00	—	—		38·6 ± 0·7	14·8 ± 0·2	24

t-test (d.f. = 46)

day 1	09.00–15.00 vs 15.00–21.00	$t = 5·62$	$P<0·001$
day 2	03.00–09.00 vs 09.00–15.00	$t = 3·08$	$P<0·01$
	03.00–09.00 vs 15.00–21.00	$t = 4·17$	$P<0·001$
	03.00–09.00 vs 21.00–03.00	$t = 3·21$	$P<0·01$
day 1	09.00–15.00 vs 09.00–15.00	$t = 9·41$	$P<0·001$
vs			
day 2	15.00–21.00 vs 15.00–21.00	$t = 8·00$	$P<0·001$

Birds exposed to the midday sun had surface temperatures considerably above ambient temperature, presumably due to insolation. Birds sheltering in burrows had dorsal surface temperatures only slightly above ambient temperature (Table V).

FIG. 9. Number of displays given each half hour by penguins on a breeding flat during a 24 hour period. (a) "Loud mutual" display; (b) "ecstatic" display.

FIG. 10. Body temperature variations of an adult penguin on two different days (upper graph) and corresponding ambient temperatures (lower graph). (......) 1.12.74 clear, hot; (—) 2–3.12.74 overcast, cool. (a) Bird walking around; (b) trying to escape; (c) lying down; (d) sun on bird; (e) bird begins to pant; (f) panting heavily; (g) moves into shade; (h) bird trying to escape.

TABLE V

Mean dorsal surface temperature (T_s) (± one standard deviation) of adult penguins in the shade and in the sun, together with mean ambient temperature (T_a) and mean temperature difference (ΔT_s—T_a) at time of measurement

	n	T_s (°C)	T_a (°C)	ΔT_s—T_a (°C)
In shade	10	25·8±4·8	24·8±4·0	1·3±0·2
In sun	10	39·3±8·3	24·9±1·9	16·3±6·8

Body orientation

Some birds, not immediately involved in incubating eggs or guarding chicks, remained on the breeding flat for most of the day. These birds appeared to minimize heat uptake and maximized reradiative and convective heat loss by orientating with their backs to the sun (Table VI, Fig. 11(a)). During midday orientation was non-directional. Towards evening weak orientation occurred away from the sun.

No correlation could be found between orientation and prevailing wind. In fact on two days with opposing wind directions, orientation occurred in relation to the sun, even though on the first occasion the birds faced into the prevailing wind (Fig. 11(b), 09.30 hrs, 10.30 hrs) and on the second occasion they faced directly away from the wind (Fig. 11(a), 09.30 hrs, 10.30 hrs). There was marked orientation away from the sun in the early morning (Table IV, Fig. 11(a)). On cool overcast days with no direct sunlight orientation was non-directional (Table VII, Fig. 12).

TABLE VI

Orientation of 100 non incubating adult penguins on breeding flats at Dassen Island on two clear hot days with contrasting wind directions $x^2{}_7$ value for P 0·05 = 14·07

Date and time		Shade direction (° from N)	Wind direction (° from N)	45° Sectors from true north								x^2	*P*
				1	2	3	4	5	6	7	8		
14.11.74	06.30	320°	160°	4	7	8	7	5	30	17	22	50·08	<0·001
	07.30	305°	160°	3	6	19	4	7	31	23	7	60·80	<0·001
	08.30	295°	160°	5	7	16	8	16	15	26	6	28·96	<0·001
	09.30	280°	160°	7	3	11	4	7	21	36	10	68·48	<0·001
	10.30	270°	160°	5	6	8	7	8	15	39	12	70·24	<0·001
2.12.72	09.30	280°	345°	19	15	6	2	6	15	24	13	30·58	<0·001
	10.30	270°	345°	14	2	5	1	4	21	19	34	76·00	<0·001
	11.30	250°	345°	5	6	2	7	13	21	24	22	42·72	<0·001
	12.30	210°	345°	8	5	5	13	12	16	22	19	22·24	<0·01
	13.30	160°	345°	13	11	10	13	18	16	13	6	7·52	<0·5
	14.30	135°	345°	9	11	7	20	17	11	14	11	10·24	<0·2
	15.30	120°	345°	5	5	8	27	26	9	10	15	44·00	<0·001
	16.30	105°	345°	13	11	17	17	13	12	7	8	7·52	<0·5

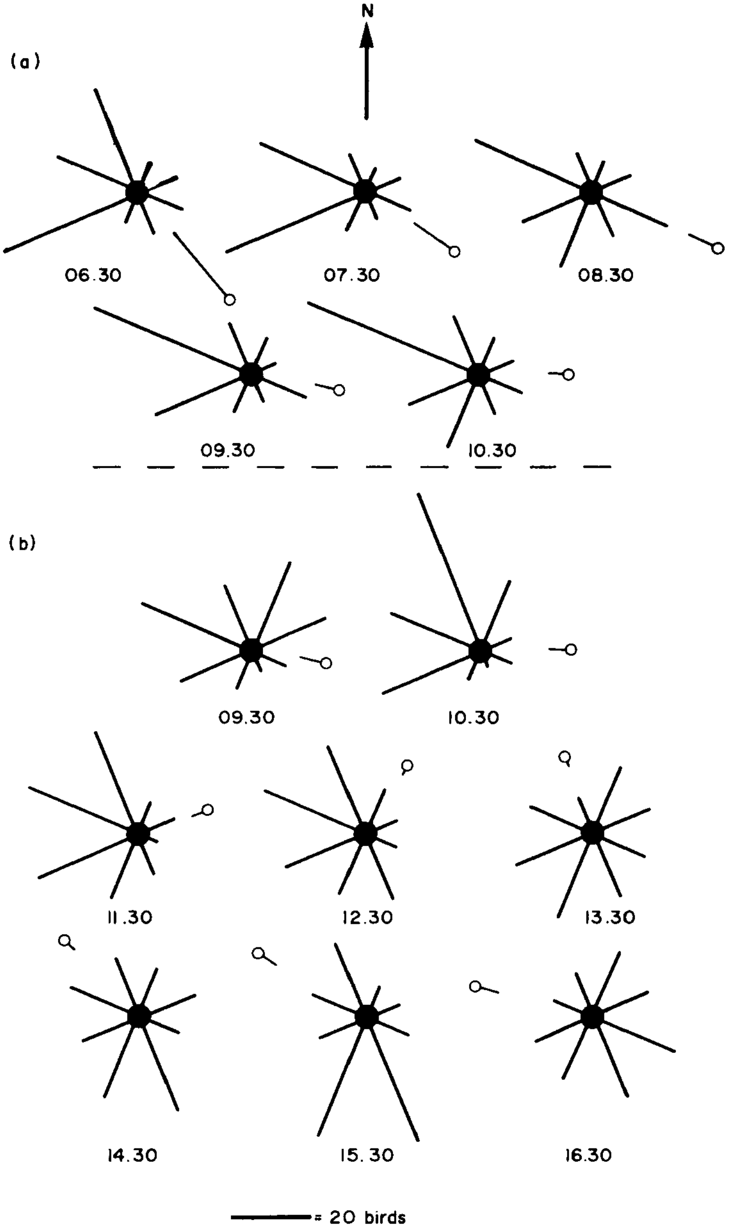

FIG. 11. Orientation of 100 non-incubating adult penguins during a clear, hot day. Length of bars proportional to the number of birds facing a particular 45° sector. (a) 14.11.74 wind blowing from 160°; (b) 2.12.72 wind blowing from 345°. (○) Horizontal angle of sun. The length of the appended bar (—) indicates the relative length and direction of the shadow cast by an adult penguin.

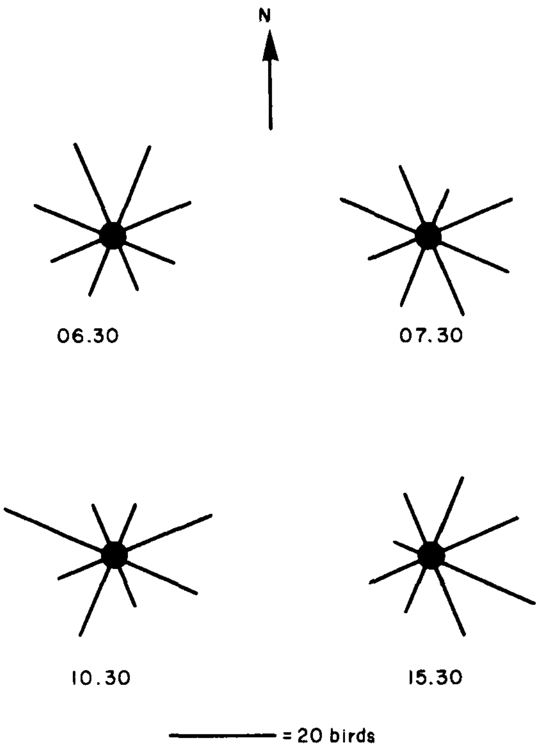

FIG. 12. Orientation of 100 non-incubating adult penguins at times during a cool overcast day. The wind was blowing from 330°. The length of the bars are proportional to the number of birds facing a particular 45° sector.

TABLE VII

Orientation of 100 non incubating adult penguins on breeding flats at Dassen Island on a cool, overcast day x^2_7 value for P 0·05 = 14·07

Date and time		Shade direction (° from N)	Wind direction (° from N)	45° Sectors from true north 1	2	3	4	5	6	7	8	x^2	*P*
4.12.72	06.30	—	330°	16	14	10	9	10	11	14	16	4·48	<0·8
	07.30	—	330°	7	15	14	14	12	10	16	12	4·80	<0·8
	10.30	—	330°	8	18	15	8	14	9	20	8	13·44	<0·1
	15.30	—	330°	14	16	20	14	11	10	5	10	11·52	<0·2

Discussion

Penguins are adapted primarily to cool aquatic environments. Enhanced insulation has evolved to counteract the effect of the high thermal conductivity of water (Stonehouse, 1967; Drent & Stonehouse, 1971; Frost *et al.*, 1975). This decrease in thermal conductance has reduced the ability of penguins to unload rapidly endogenous heat in warm terrestrial environments. Yet some penguin species successfully exploit these environments when breeding and moulting. In the Jackass penguin, behavioural and physiological adaptations are of prime importance in facilitating adjustment to the exigencies of the terrestrial environment.

Behavioural adaptations largely promote the use of favourable microclimates and the avoidance of extreme conditions. Nocturnal attendance at breeding sites ensures that the majority of birds avoid the relatively high ambient temperatures and intense solar radiation usually experienced during the day. Furthermore, ambient temperatures are invariably lower at night. Consequently, the extra endogenous heat production associated with vigorous courtship and nest building activities can be dissipated more readily.

During the day most breeding birds not immediately involved in incubation or chick guarding go to sea to forage. Non-breeding birds go to sea or retire to the beach where they gather in large groups. Here ambient temperatures are moderated by proximity to the sea. During the midday period individual birds make frequent forays into the water to drink, bathe and presumably cool down. Because of the nearness of the sea these forays can be undertaken rapidly, and involve little added energy expenditure.

The birds may benefit also from the modification of microclimate effected by the group. It appears from casual observation that the mean distance between neighbouring birds is less on warm than on cool, overcast days. This has not been quantified, but it suggests that, through crowding, individuals may benefit from shade cast by neighbouring birds.

Breeding birds, being tied to a nest site, must tolerate whatever environmental conditions occur. Many Jackass penguins (probably the majority) nest in burrows, under rocks or in shaded rock fissures, particularly during the warm spring and summer months. The incidence of surface nesting on Dassen Island appears to be higher in winter. Rain, occurring predominantly during winter, causes flooding and burrows collapse. Whether surfacing nesting is an adaptive trait or whether it is a consequence of nesting habitat destruction caused by guano and phosphatic sand removal is not known (Frost *et al.*, in press). Breeding success is significantly higher in burrow nesting birds (Cooper, in prep.). We suggest that, as an adaptive response to the pressures of the thermal environment, burrow nesting is the more typical and successful trait.

Burrow air temperatures are not always cooler than ambient temperatures during the day, but are invariably warmer during the night. Ambient temperatures are moderated by cooling sea breezes. However, these do not appear to influence burrow air temperatures, as wind penetration is minimal. Wind also affects ambient relative humidity which, during the day, is invariably lower than burrow relative humidity. At night the humidity inside burrows is similar to that of the ambient. Both are higher at night than during the day.

A major advantage of burrows appears to be the protection of incubating birds and chicks from high levels of direct solar radiation experienced during the day. Solar radiation is generally intense, especially during summer. Birds inside burrows are protected almost entirely from insolation. East and west facing burrows are insolated for a brief period during either the early morning or late afternoon. South facing burrows receive no direct sunlight while north facing burrows are partially insolated for much of the day. However the angle and depth of burrows ensures that incubating birds are almost always shaded. This influences both egg and nest temperatures. Both vary less than in exposed nests. Despite the differences in microclimate and degree of insolation, burrow orientation appears to be correlated with the slope of the breeding flat rather than with microclimate suitability. However, in one colony preference by nesting birds for those burrows that received little or no insolation, was demonstrated.

Burrows also protect the occupants from excessive radiation heat loss to the night sky. Sky temperatures, measured on a clear night, averaged −13°C ($n = 10$). As the dorsal surface of a penguin at night averaged 12·3±1·1°C ($n = 10$), a considerable gradient exists between a bird in the open and the night sky. The surface temperature of the walls of a burrow at night averaged 10·1±0·9°C ($n = 10$). A bird or chick inside a burrow would obviously lose less heat by thermal radiation during the night. While adult penguins are adapted to restrict heat flow to the environment, any saving in energy accruing through the use of burrows must be advantageous.

Burrows presumably are important also in providing an equable microclimate for young chicks. Jackass penguin chicks do not attain thermoregulatory independence until they weigh at least 400 g (Erasmus & Smith, 1974). Younger chicks (mass 200 g), despite increasing heat production more than 2·5 times, cannot maintain stable body temperatures when the ambient temperature is decreased from 35°C to 20°C (Erasmus & Smith, 1974). Jackass penguin adults can brood closely only very young chicks. However, inside a burrow where heat loss to the exterior is reduced, partial brooding by the parent may be sufficient to promote suitable conditions for chicks to channel energy into growth rather than maintenance.

In addition to providing a more constant and equable microclimate, burrows also afford considerable protection against predators. The Kelp gull *Larus dominicanus* and the Sacred ibis *Threskiornis aethopicus* prey on eggs and chicks respectively (Cooper, 1974). In the event of penguins leaving their nests because of disturbance or heat stress, surface nests would be more vulnerable to predators than burrow nests. The contents of the latter are both less visible and less accessible to predators.

Non-incubating penguins occasionally spend the day on the surface in the breeding colonies. These birds can be active breeding birds, immatures, pre-moulting or pre-breeding birds. On days when ambient temperatures exceed 33°–34°C nearly all these birds retire to the beach. On cooler days they remain in the colony where they are subject to the full effects of insolation. These birds minimize heat uptake and maximize heat loss through body orientation, posture and physiological mechanisms.

During most of the day the birds orientate with their backs to the sun. Radiation energy gain through insolation is minimized by body orientation. Dorsal surface temperatures are frequently above those of the environment. Much of the heat acquired by insolation would be radiated to the environment or lost by convective cooling. We suggest that heat transfer from the dorsal surface to the body core is restricted by the efficient insulation of the bird. In effect, those adaptations that restrict heat loss in an aquatic environment can reduce heat gain from the environment equally effectively, at least for brief periods.

Such a strategy places a premium on the effective dissipation of metabolically produced heat. This is achieved by postural adjustments that facilitate convective and radiative cooling. Facing away from the sun places the more lightly feathered surfaces of the body, the ventral surfaces of the axillae, the head and moist oral surfaces and the feet, in the shade. The birds adopt a posture designed to facilitate convective cooling. The axillae are held out from the body thereby enhancing airflow across them and the body. The axillae also serve to dissipate heat through radiation to cooler surfaces in the environment (such as the shadow cast by the bird). Conductive heat transfer to the ground may occur but usually soil temperatures are close to or above foot temperatures. Under these conditions penguins have been observed sitting on their metatarsals with their feet raised off the ground. This posture reduces heat conduction from the soil and facilitates convective cooling from the feet. Similar observations have been made on Laysan and Black footed albatrosses *Diomedia immutabilis* and *D. nigripes* (Howell & Bartholomew, 1961).

During midday body orientation is non-directional. As the sun is high overhead little shadow is cast. While the feet and ventral surfaces of the axillae are partly shaded, this effect is less dependent upon accurate orientation with respect to the sun. However high ambient temperatures and the lack of cool shaded areas with which radiation exchange can take place results in considerable heat stress during midday. It is perhaps significant that the number of birds on the surface of the colony is lowest during that period.

Jackass penguins also orientate with their backs to the sun in the early morning when ambient temperatures are relatively low. We interpret this behaviour as sunbathing. The importance of solar radiation as a supplement to metabolic heat production has been pointed out by Ohmart & Lasiewski (1971) and Hamilton (1973). The energy saving accruing through the absorption of solar energy can be considerable and may be particularly important to individuals when breeding and moulting. On cool days orientation is completely non-directional.

The physiological responses of the Jackass penguin to high ambient temperatures have not been studied fully. Penguins in the laboratory begin to pant when ambient temperature exceeds 28°C. In the field, where insolation is important, birds have been observed panting at air temperatures of 24°C. Panting is laboured and the muscular activity associated with the movement of the thoracic region, must contribute substantially to heat output. Prolonged panting results in the individual leaving the colony for the sea where it can drink and cool off.

Boersma (1975) has discussed the role of thermal lability in the Galapagos penguin. The Jackass penguin appears to be similarly thermolabile. Body temperatures varied from 37·6°C to 41·7°C. In the laboratory temperature begins to rise when ambient temperature exceeds 33°C, while in the field rapid increases in body temperature occurred when ambient temperature exceeded 27°C.

We consider both evaporative cooling and body temperature elevations to be responses designed to accommodate the animal to brief periods of thermal stress. Persistant increases in ambient temperature and insolation are not tolerated. Under these conditions the animal resorts to the behavioural strategy of retiring to the sea to dissipate excess heat.

The different strategies employed by the Jackass penguin to accommodate the opposing thermal demands of the aquatic and terrestrial environments reflect the patterns of variation in the thermal parameters of these two environments. Relative to the terrestrial environment, the aquatic environment is thermally constant. Heat loss is entirely through conduction. The optimum strategy for reducing this energy drain has been the improvement of insulation. Increases in metabolic rate, through shivering (Kooyman, 1975), may be a flexible response to short term changes in energy flux between the bird and the environment.

In contrast, the terrestrial environment is thermally complex. Energy exchange takes place through radiation, conduction, convection and evaporation (Porter & Gates, 1969). The climatic variables involved in these energy exchanges exhibit considerable spatial and temporal fluctuation. Behavioural adaptations appear to provide the optimal strategy for coping with these changes. Nocturnal activity and burrowing are habits that rely on fairly predictable features of the terrestrial thermal environment. On the other hand, body orientation, posture and associated physiological responses appear to facilitate rapid adjustment to short term, frequently unpredictable changes in energy flux.

We do not suggest that high daytime temperatures and solar radiation levels have been the only selection pressures in the evolution of burrowing and nocturnal behaviour in penguins. Both these habits are exhibited to varying degrees by certain cold temperate zone penguins (Stonehouse, 1967). In these species, burrowing or nesting under cover are probably products of selection due to habitat availability (tall tussock grass; coastal rain forest), microclimate amelioration (protection against cold wind, rain and occasionally intense insolation) and predator pressures (Stonehouse, 1967). Nocturnal activity is probably partly a consequence of the need for good visibility when foraging on fish at sea. As light intensities underwater are invariably low, piscivorous species must forage diurnally. For inshore feeding species, such as the Jackass penguin (Siegfried, Frost, Kinahan & Cooper, 1975), nocturnal activity on land becomes the logical consequence of making a daily journey to the feeding grounds.

It is suggested that these behavioural traits would have facilitated the successful colonization of warmer terrestrial habitats. None of the adaptations exhibited by the Jackass penguin are unique. Rather they appear to represent the modification of more general behavioural traits exhibited by other penguins. As Stonehouse (1967) has noted, penguins have tended to vary behaviour rather than morphology and anatomy in accommodating the demands of their terrestrial environments. The Jackass penguin is no exception. The paradox of a penguin in a hot, arid environment is apparent, not real.

Summary

Penguins are primarily adapted to an aquatic environment. The need to reduce heat loss is of major importance to all penguins. A variety of anatomical adaptations have evolved to facilitate heat conservation. A consequence of decreased thermal conductance is apparent overinsulation for life on land, to which penguins return to breed and moult. This problem is potentially more acute for tropical and subtropical breeding species. The Jackass penguin was studied in order to identify the ways in which the species is adapted to overcome this problem.

The Jackass penguin is largely nocturnal at breeding sites, where its activity is confined largely to dawn and dusk periods. Non-breeding birds go off to sea or loaf in beach groups where they take regular swims. Breeding birds nest largely in burrows which have a more equable microclimate and where the incubating bird is protected from intense solar radiation during the day. Birds remaining in the open in the colony orientate with their backs to the sun. The feet, flippers and oral surfaces are therefore shaded. This facilitates radiation and convective heat loss.

Physiological responses to heat stress include panting and moderate hyperthermia. Undoubtedly associated changes occur in the rate and distribution of blood flowing to peripheral areas of the body, though this was not investigated here. It is suggested that the Jackass penguin is adapted anatomically to its aquatic thermal environment and behaviourally to its terrestrial thermal environment. Physiological responses extend the species' zones of tolerance in both environments.

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