

BODY TEMPERATURES OF FREE-LIVING AFRICAN PENGUINS (*SPHENISCUS DEMERSUS*) AND BANK CORMORANTS (*PHALACROCORAX NEGLECTUS*)

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Summary

Two free-living seabirds (the African penguin *Spheniscus demersus* and the bank cormorant *Phalacrocorax neglectus*) were equipped with stomach temperature-loggers to study body temperature changes during foraging. Body temperature in these endotherms was environmentally and activity-dependent and varied in the case of the cormorant by over 5 °C. Considerations of heat flux show that such flexibility confers considerable energetic advantages: by allowing body temperature to drop when the heat loss to the environment is high, such as in water, birds may save the energy that would normally be necessary to compensate for this drop. It appears that, in cormorants, low body temperature resulting from extended time in water can subsequently be elevated using

solar energy when the birds return to land in a manner similar to that of ectotherms. In the better-insulated penguins, muscle-generated heat during swimming is used to re-elevate low body temperature. Continued swimming eventually causes body temperature to rise above normal resting levels so that metabolic rate could theoretically be dramatically reduced immediately post-exercise when the temperature drops to some critical level before any increase in metabolism is necessary to correct it.

Key words: African penguin, *Spheniscus demersus*, bank cormorant, *Phalacrocorax neglectus*, body temperature, thermoregulation, energetics, foraging.

Introduction

The maintenance of high body temperatures has allowed endotherms to become fast-reacting, effective predators while living in colder areas of the earth where ectotherms become sluggish (see, for example, Heinrich, 1977). Typically, body temperature in endotherms shows diel periodicity (e.g. Aschoff, 1981) and may additionally vary as a function of animal activity (Dawson and Hulbert, 1970) although, apart from species which engage in torpor, body temperature in many endotherms does not usually vary by more than 1–2 °C (e.g. Bezzel and Prinzinger, 1990; Schmidt-Nielsen, 1995). A quite radical departure from this scheme has been demonstrated in some endotherms subject to extreme heat or cold stress whereby energy and water can be saved simply by allowing body temperature to change. Schmidt-Nielsen's (1963) pioneering work with the camel (*Camelus dromedarius*) is an example of this. Such flexibility is expected to confer an advantage to any endotherm living in thermally extreme environments.

The maintenance of a body temperature different from that of the environment is facilitated by insulation, e.g. fur, feathers or fat, which can be altered to some degree to maintain body temperature as heat production through activity and heat loss to the environment occur. Most endotherms have to contend

with heat loss that is seasonally and diurnally variable. One of the most extreme cases of variability in the thermal environment, however, is found in endotherms such as seabirds that regularly move between water and air, because water has a thermal conductivity that is some 25 times that of air. This poses particular problems for temperature regulation since potential differences in heat loss between water and air differ by orders of magnitude. This situation is particularly extreme for those species that inhabit upwelling regions which generally have a warm climate but are characterized by abnormally cold water rising to the sea surface owing to offshore winds (Eckman, 1905).

We used remote-sensing logging units to study changes in body temperature as a function of activity in breeding bank cormorants (*Phalacrocorax neglectus*) and African penguins (*Spheniscus demersus*) in an upwelling system. In this paper, we present results which allow us to determine energy expenditure as a function of activity, and we examine how the efficiency of foraging birds is dependent on their activity and their capacity to regulate body temperature within limits.

Both seabird species are medium-sized (bank cormorant, 1950 g; African penguin, 3000 g; Cooper, 1972, 1985) pursuit divers (*sensu* Ashmole and Ashmole, 1967) which breed

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throughout the year on South Africa's west coast (Cooper, 1981; Rand, 1960). Here, the Benguela upwelling current maintains water temperatures at approximately 13.4°C (Walker *et al.* 1984) although air temperatures may reach 35°C (Schulze, 1965). In air, both the cormorants and penguins are likely to be in their thermoneutral zone. In water, the situation is more complex since cormorants and penguins have very different thermoregulatory capacities owing to substantial differences in insulation. Cormorants have little plumage air (Wilson *et al.* 1992b) because of a family-specific feather structure which leads to feather wetting (Rijke, 1968). The lack of large quantities of trapped air minimizes energy expenditure during swimming by reducing upthrust, although heat loss is believed to be high (Wilson *et al.* 1992b). Penguins do not have wettable feathers but also have little plumage air. These birds are, however, not considered to experience high heat loss while under water because of insulation from a thick dermis and subcutaneous fat (Wilson *et al.* 1992b; Drent and Stonehouse, 1971).

Materials and methods

All field work was conducted at Dassen Island (33°25' S, 18°05' E), South Africa, where both bank cormorants and African penguins breed. African penguins *Spheniscus demersus* Linnaeus were studied during June 1991 and bank cormorants *Phalacrocorax neglectus* Wahlberg during October 1992.

Body temperature

Bird body temperature was recorded using gastric temperature-logging units which were ingested by the birds and retained in the stomach for periods of several hours to several days before being actively regurgitated in the form of pellets (all cormorants and some penguins) or retrieved by stomach pumping (Wilson, 1984). Two different temperature-logging units were used. Penguins were fed 'Einkanalige Automatische TemperaturLogger' (EATLs) (Elkutec GmbH, D-85386 Eching bei München, Germany) which consisted of a 32 kbyte logging unit with eight-bit resolution housed within a titanium capsule with outside dimensions of 93 mm×21 mm (length×diameter) and a mass of approximately 80 g. With these units, temperature can be determined to a relative accuracy of 0.1°C and an absolute accuracy of better than 0.8°C (no drift). All units were calibrated in a waterbath before use. During deployment, stomach temperature measurements were recorded every 8 or 16 s. EATLs are described in detail by Wilson *et al.* (1992a, 1995). Cormorants were fed similar temperature-logging units except that they were much smaller (72 mm×17 mm; mass approximately 17 g). These units (single-channel unit processors, SICUPs; Driesen and Kern GmbH, Am Hasselt 25, D-24576 Bad Bramsted, Germany) had a memory of 128 kbytes and recorded temperature every 16 s (Wilson *et al.* 1995).

Both EATLs and SICUPs were connected to an interface before being started by portable computers shortly before being deployed. Data from recovered units were transferred to computer in a similar manner.

Cormorants were caught at the nest in the early morning (06:00–07:00 h) before they left to forage. SICUPs were given to them inside a prey item (mullet, Mugilidae). The birds were then released and watched continuously, where possible, until nightfall precluded further observation. The precise time when the equipped birds left the nest to forage as well as when they returned was noted. In addition, at all times when equipped birds were visible, all behaviour was recorded immediately on a Husky field computer. Behaviours noted were flight, standing, sitting, sleeping, preening, gular flutter, nest building, feeding chicks and interactions with other birds. SICUPs regurgitated as pellets during the night were recovered the following day from within the colony. Nineteen cormorants were equipped with SICUPs.

African penguins leave their breeding sites to forage in the early morning around dawn and generally spend a single day at sea before returning to feed their chicks at dusk. The partner of a foraging bird generally remains at the nest at this time (Wilson and Wilson, 1990). At dusk, the roles are reversed. In order to minimize disturbance, penguins were caught around mid-day before being induced to swallow the EATLs. The nests were then left undisturbed until the following day at approximately 10:00 h when they were checked to ascertain that the equipped birds had gone to sea. Nests were then revisited at approximately 22:00 h on the same day to recover the EATLs. Ten birds were successfully equipped with EATLs in this way.

Penguin activity

The activity of EATL-carrying penguins was ascertained by means of a multi-channel logger (MCL) (Driesen and Kern GmbH, Am Hasselt 25, D-24576 Bad Bramsted, Germany). The unit measured 99 mm×54 mm×20 mm (mass 160 g) and consisted of a 64 kbyte memory logger which recorded swim speed (to the nearest 0.1 km h⁻¹ for speeds in excess of 0.3 km h⁻¹), dive depth (to the nearest 0.3 m) and swim heading (to the nearest 2°) at intervals of between 2 and 5 s. Swim speed was measured by counting the number of rotations of a paddlewheel per second. The unit was calibrated by setting it to record swim speed every second and attaching it to African penguins which were allowed to swim in a shallow pool (6 m×6 m×0.8 m). The birds were filmed from above against a grid on the bottom of the pool and the time of the logger was exactly matched against the time mixed onto the film. We could not correct for potential effects of paddlewheel turning variability as a function of turbulence in the water since all our measurements were made in essentially still water in the pool. The MCL was programmed and data were accessed *via* computer in a similar manner to those of the temperature-measuring units. An extensive description of this unit is given in Wilson *et al.* (1993).

MCLs were attached using adhesive tape (Wilson and Wilson, 1989) to the dorsal mid-line of the penguin and, following the recommendations of Bannasch *et al.* (1994), were attached as posteriorly as possible so as to minimize hydrodynamic drag. Units were attached at the same time as

birds were fed EATLs (around mid-day) and were recovered approximately 34 h later at the same time as the EATLs.

Prey ingestion

The timing and amount of prey ingested were indicated by the stomach temperature loggers. Since cormorant and penguin prey are ectothermic, ingestion of prey leads to a precipitous temperature drop in the stomach, followed by an exponential rise as the prey is warmed to body temperature (termed a PDER event, precipitous drop with exponential rise, as defined by Wilson *et al.* 1992a). After suitable calibration, the mass of the prey ingested can be calculated by integrating the area under the temperature asymptote since such area measurements correct automatically for stomach fullness, which is not the case if the absolute temperature drop is considered (for details, see Wilson *et al.* 1992a, 1995).

Where penguins were stomach-pumped, prey were sorted and measured immediately. For those individual fish whose caudal length could not be measured directly, the otoliths were removed and their length measured. This value could then be converted into fish caudal length measures from standard otolith length/fish length regressions (Laugksch, 1989). Regurgitated pellets were collected from the bank cormorants and were analysed for otoliths and crustacean exoskeleton remains.

Results

A total of 132 h of bank cormorant stomach temperatures was recorded, 22 h of which came from birds actively foraging during a total of 17 foraging trips. Seven temperature-logging units were regurgitated away from the breeding site and were never recovered.

A total of 284 h of penguin stomach temperatures was recorded, of which 134 h was time spent at sea. Two EATLs were regurgitated away from the nest and were never recovered.

Body temperature changes versus activity in penguins

African penguins had a fairly constant overall swim speed with a mean of $1.83 \pm 0.5 \text{ m s}^{-1}$ (s.d., $N=924$) interspersed with interdiving rests which varied between 2 and 630 s (mean 15.5 s, $N=111$). Mean dive duration was $77 \pm 36 \text{ s}$ (s.d., $N=507$).

Body temperature of African penguins, as measured with the stomach temperature-loggers, varied between 37.3°C , at approximately 01:00 h when the birds were sleeping on land, and 40.8°C during bursts of high-speed swimming. Excluding PDER events due to prey ingestion, the fastest rates of change of temperature occurred when birds were in the water. Stomach temperature is most useful for the examination of rapid rates of change in body temperature when the stomach is empty since the addition of food, which acts as a passive insulator, will tend to slow down the response of the EATLs to changes in body temperature. For our assessment of rates of change of body temperature, we considered only those cases for which penguin stomachs were known to be empty, i.e. at the beginning of the foraging period before any PDER events had

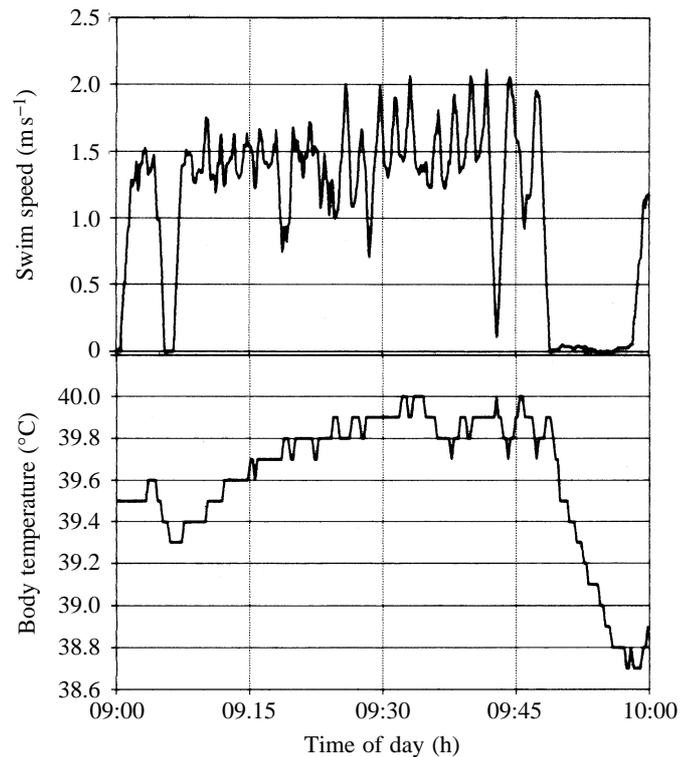


Fig. 1. Example recordings of changes in body temperature of an African penguin *Spheniscus demersus* in relation to swimming activity.

been recorded. Overall, body temperature increased when the birds swam and decreased again when the birds rested on the water's surface (Fig. 1), the rate of change of body temperature being highest immediately following a change in activity, i.e. resting after swimming or swimming after resting (Fig. 1). When birds rested after a period of swimming during which body temperature had stabilized, body temperature (T_b) decreased as a function of time since the change in activity (t) according to: $T_b = -0.00355t + 2.218 \times 10^{-6}t^2 + 40.04$ ($r^2=0.96$, $P<0.001$ for eight events) (Fig. 2A). T_b increased during swimming after resting according to: $T_b = 0.00178t - 6.172 \times 10^{-7}t^2 + 38.67$ ($r^2=0.98$, $P<0.001$ for two events) (Fig. 2B). The rates of change of temperature, ΔT , at $t=0$ are therefore $0.00355^\circ\text{C s}^{-1}$ and $0.00178^\circ\text{C s}^{-1}$, for resting after swimming and swimming after resting, respectively.

Body temperature changes versus activity in cormorants

Body temperature of bank cormorants showed similar trends to those of African penguins, being more variable when the birds were in water (range $36.8\text{--}42.0^\circ\text{C}$, excluding PDER events) than on land (range $37.4\text{--}40.0^\circ\text{C}$) (Fig. 3). Just before birds left the nest to forage, body temperature increased linearly over $485 \pm 287 \text{ s}$ (s.d., $N=11$) by a mean of $0.00333 \pm 0.00083^\circ\text{C s}^{-1}$ (s.d.) to a mean maximum of $41.35 \pm 0.74^\circ\text{C}$ (s.d.). This increase in body temperature occurred even though bird activity at the nest did not appear to change. After the birds had begun diving, body temperature

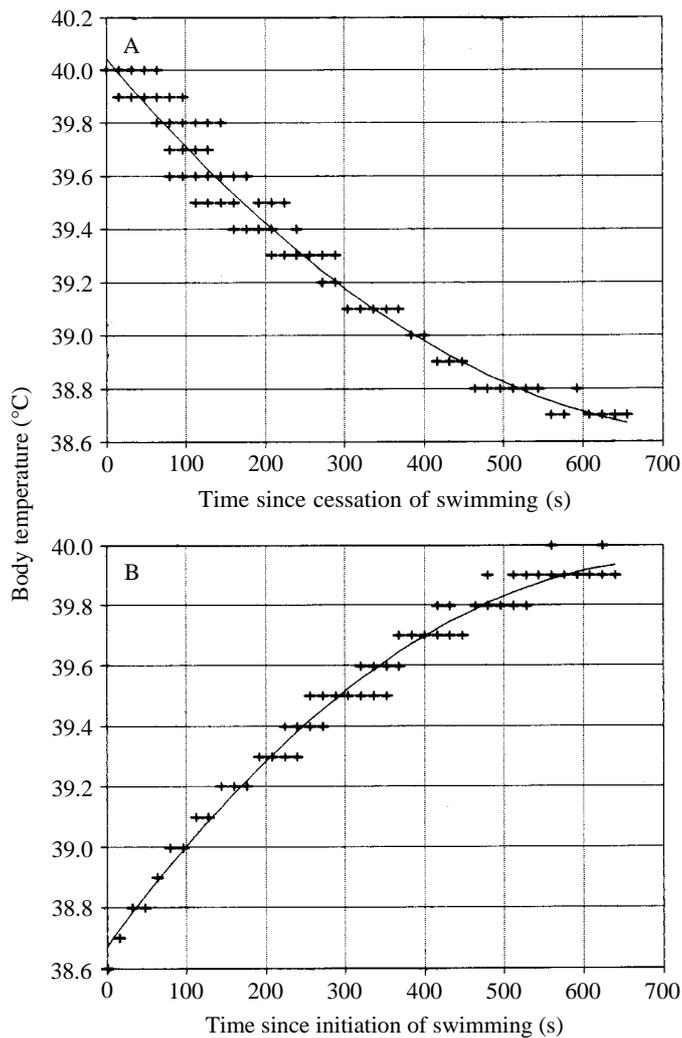


Fig. 2. (A) Overall change in body temperature (T_b) as a function of time (t) since cessation of swimming in African penguins *Spheniscus demersus* ($N=8$) resting after body temperature had stabilized during an extended swimming period. The curve fit is $T_b = -0.00355t + 2.218 \times 10^{-6}t^2 + 40.04$ ($r^2=0.96$, $P<0.001$). (B) Overall change in body temperature as a function of time since initiation of swimming in African penguins ($N=2$) that began swimming after body temperature had stabilized during an extended rest period. The curve fit is $T_b = 0.00178t - 6.172 \times 10^{-7}t^2 + 38.67$ ($r^2=0.98$, $P<0.001$).

initially stabilized for a mean of 540 ± 61 s (s.d., $N=4$; only four individuals did not ingest prey before body temperature began to drop) before dropping linearly at a rate of 0.002 ± 0.00117 °C s⁻¹ (s.d., $N=18$) for a mean period of 2092 ± 1646 s (s.d., $N=18$) (e.g. Fig. 3). Overall rates of temperature drop were unaffected by the ingestion of cold prey, which only induced short-term temperature drops in the stomach (Fig. 3). After birds left the water, body temperature rose by 0.0045 ± 0.00133 °C s⁻¹ (s.d., $N=7$).

Rate of food ingestion

During a total of 134 h at sea, African penguins ingested a total of 12.254 kg of food, giving a mean ingestion rate of

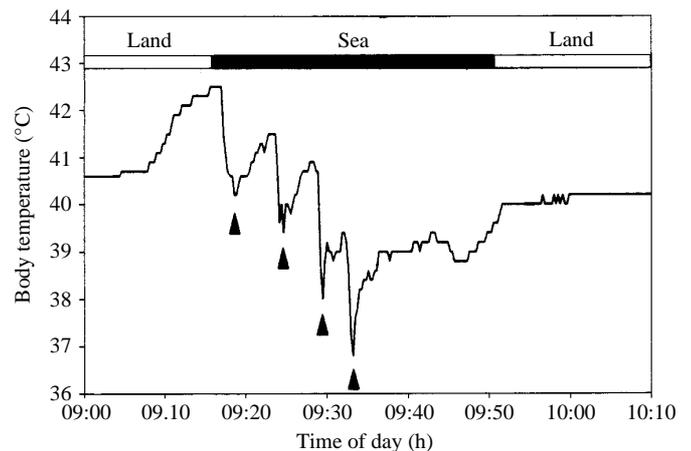


Fig. 3. Example of changes in body temperature of a bank cormorant *Phalacrocorax neglectus*. The black bar at the top of the graph shows when the bird was absent from the nest and, for the most part, foraging. Arrowheads show when (cold) prey items were ingested.

0.025 g s⁻¹. All identified prey consisted of pelagic school fish, principally anchovy *Engraulis capensis*. During 22 h at sea, bank cormorants ingested a total of 1410 g of food, giving a mean ingestion rate of 0.018 g s⁻¹. Prey consisted of rock lobster (*Jasus lalandii*), pilchard (*Sardinops ocellatus*) and horse mackerel (*Trachurus trachurus capensis*).

Discussion

Changes in body temperature

Changes in body temperature occur as a result of a combination of factors. Heat is lost by the bird to the environment because of the temperature difference between the bird and the environment. However, the rate at which heat is lost may be extensively controlled by the bird using a variety of mechanisms which affect the bird's effective insulation, e.g. gular flutter, plumage thickness, etc. (Whittow, 1986). Heat production occurs as a consequence of metabolic activity, which may also be changed by the bird when necessary. Under normal circumstances, body temperature may be maintained within narrow boundaries by appropriate changes in both heat production and/or heat loss. During intense activity, such as swimming, it may be necessary for birds to reduce their effective insulation extensively so as to maintain body temperature within reasonable limits. Conversely, during periods of inactivity in water, heat loss may be too high to be counteracted by changes in insulation alone. In this case, body temperature can only be maintained by an increase in metabolic activity. One striking feature of our results, however, is the high variability in stomach temperature which, in the absence of prey ingestion, is likely to reflect body temperature.

Variability in body temperature

The energetic advantage of having a flexible body temperature (T_b) can be illustrated by modelling heat loss and

heat production in birds with and without a flexible T_b . In order to achieve this, we have to consider the metabolic consequences for a seabird stopping an activity for which the heat produced is very high and when body temperature (T_b) has reached its maximum permissible value. This is likely to be the case when an African penguin rests after an extended swimming period. At the instant that the penguin begins to rest, its metabolic rate need only reflect a minimal resting metabolic rate (RMR) because no extra metabolism is required to maintain body temperature. If such a drop in metabolic rate indeed occurs, it will not be evident using gas respirometry because oxygen utilization immediately post-exercise is certain to be high as a result of the oxygen deficit in the blood and muscles. This oxygen deficit arises from the metabolism during the preceding exercise rather than from the actual metabolism by the resting animal at the time that oxygen consumption is being measured. As penguin T_b drops, it is to be expected that the bird will increase its body insulation and, as T_b approaches a lower critical level, increase its metabolic rate so as to counter heat loss fully. The RMR of African penguins at sea is 33.8 W, which is 2.3 times higher than the 14.4 W RMR of birds on land (Nagy *et al.* 1984), demonstrating that these penguins cannot cope with the substantial difference in the thermal environments of land and sea solely by altering their body insulation.

African penguins

For our model, we will simplistically assume that at the time the bird stops swimming the metabolic rate drops instantly to the RMR of a penguin on land (14.4 W) until body temperature reaches exactly half the value between $T_{b,max}$ and $T_{b,min}$, when metabolic rate is assumed to rise instantly to the RMR of a penguin at sea (33.8 W). We further assume that African penguins allow body temperature at sea to vary between 38.7 and 40.0 °C and that the rate of change of body temperature as a function of activity follows a pattern identical to that measured by us: resting after swimming leads to a body temperature drop that changes as a function of time according to $T_b = -0.00355t + 2.218 \times 10^{-6}t^2 + 40$ and that T_b during swimming after resting changes according to $T_b = 0.00178t - 6.172 \times 10^{-7}t^2 + 38.7$ (Fig. 2). Since penguins at rest cool at a faster rate than they heat up by swimming, the relationship between swim time and rest time for which T_b always achieves a specific value at the end of the swimming phase generally has a longer swim period than rest period (Fig. 4). However, if birds rest for so long that T_b falls to its lowest permissible value, then the swim period necessary for recovery becomes constant. Assuming a normal swimming speed of 1.8 m s⁻¹, the cost of transport (energetic expenditure per unit distance travelled) varies according to the swim:rest ratios (Fig. 5A), with costs becoming particularly high if birds rest for so long that T_b falls below 39.35 °C increasing RMR from 14.4 to 33.8 W. The alternative strategy, that penguins hold T_b absolutely constant (at say 39.4 °C), thereby incurring continuous swimming costs of 48 W and continuous resting costs of 33.8 W, irrespective of the swim:rest ratio, leads to

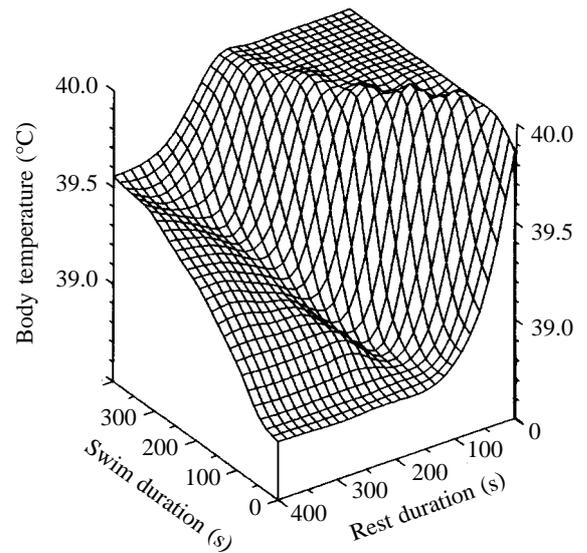


Fig. 4. Body temperature of African penguins *Spheniscus demersus* as a function of different swim and rest durations. The temperature represented is that just after completion of the swim phase. See text for details of model and assumptions.

higher costs of transport overall (Fig. 5B), for all cases except continuous swimming, where transport costs exactly equal those of birds with flexible body temperatures. It is particularly important that transport costs be low in penguins since prey are only encountered during active underwater swimming (R. P. Wilson and M.-P. Wilson, in press).

A measure of the foraging efficiency (see Nagy *et al.* 1984) of penguins can be calculated by examining the energetic gain acquired by prey ingestion in relation to the costs incurred for different swim:rest ratios. This efficiency can further be modelled for birds with, and without, flexible body temperatures. African penguins feed principally on Cape anchovies (Duffy *et al.* 1987), which provide 5.13 kJ g⁻¹ wet mass (Nagy *et al.* 1984). At sea, hunting African penguins ingest an average of 0.025 g s⁻¹ and thus gain energy at a rate of 128 J s⁻¹. Birds in our study spent 28% of their total time at sea resting and 72% of their sea time swimming. Thus, the energy gain which actually takes place during swimming amounts to 178 kJ s⁻¹, while no energy is gained during rest periods. Integration of this information together with the costs of transport for birds with and without fixed body temperatures indicates that for given swim:rest durations penguins with flexible body temperatures are more efficient than birds with fixed body temperatures in all cases except during continuous swimming or continuous resting (Fig. 6A,B). Typical dive and rest durations of 76 s and 15 s, respectively (as observed by us), led to higher foraging efficiencies in birds with flexible body temperatures by approximately 10% compared with birds with fixed body temperatures.

Bank cormorants

In bank cormorants, the situation is somewhat different. First, the steady drop in T_b during periods in water, and rise during periods on land, means that, even though cormorant T_b

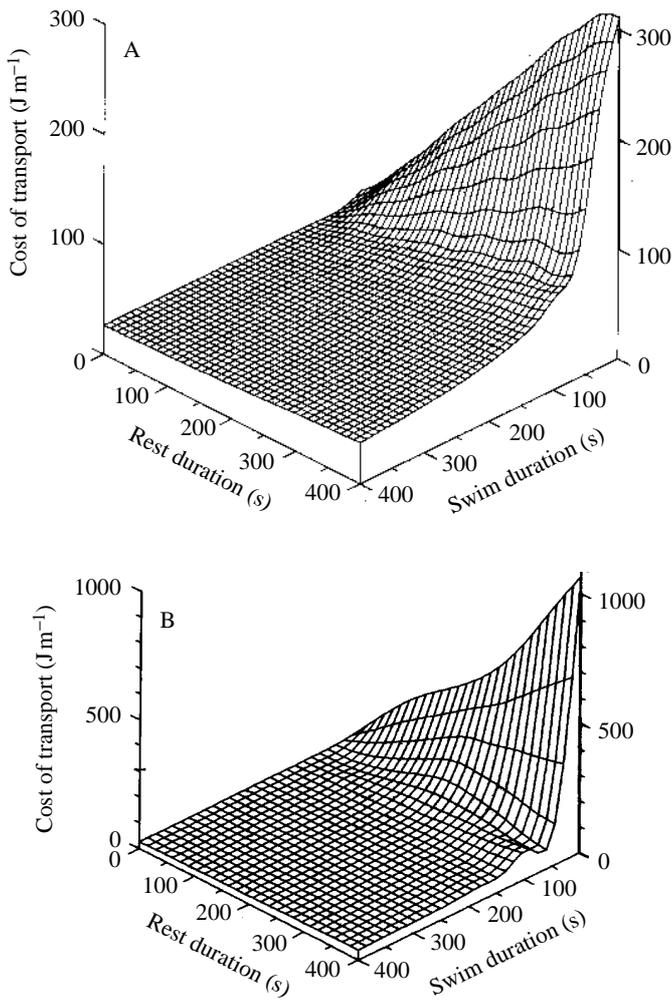


Fig. 5. (A) Calculated cost of transport (COT) in African penguins *Spheniscus demersus* (with flexible body temperatures) as a function of swim and rest durations. (B) Calculated cost of transport in African penguins, if the birds were to maintain body temperature constant, as a function of swim:rest duration. See text for details of model and assumptions.

is remarkably plastic, overall time in the water is restricted and must be followed by appropriate periods on land (Fig. 7). The drop in T_b in actively foraging bank cormorants indicates either that the birds are poorly insulated and/or that they are extremely efficient swimmers so that the heat generated during swimming is less than the heat loss to the water. By assuming that stomach temperature is equivalent to body temperature, that birds have a specific heat capacity of $3.48 \text{ J } ^\circ\text{C}^{-1} \text{ g}^{-1}$ and that approximately 75% of the energy expended during muscular activity is released as heat (Schmidt-Nielsen, 1982), we can calculate changes in stored energy levels in foraging cormorants. Cormorants of mass 2000 g, such as the bank cormorant, are likely to expend approximately 7.4 W during swimming (Hennemann, 1983). This means their heat production is $7.4 \times 0.75 = 5.6 \text{ W}$. Since T_b falls by $0.002 \text{ } ^\circ\text{C s}^{-1}$ after the first 540 s in the water (which is presumably the time it takes for water to penetrate the feathers), birds incur an

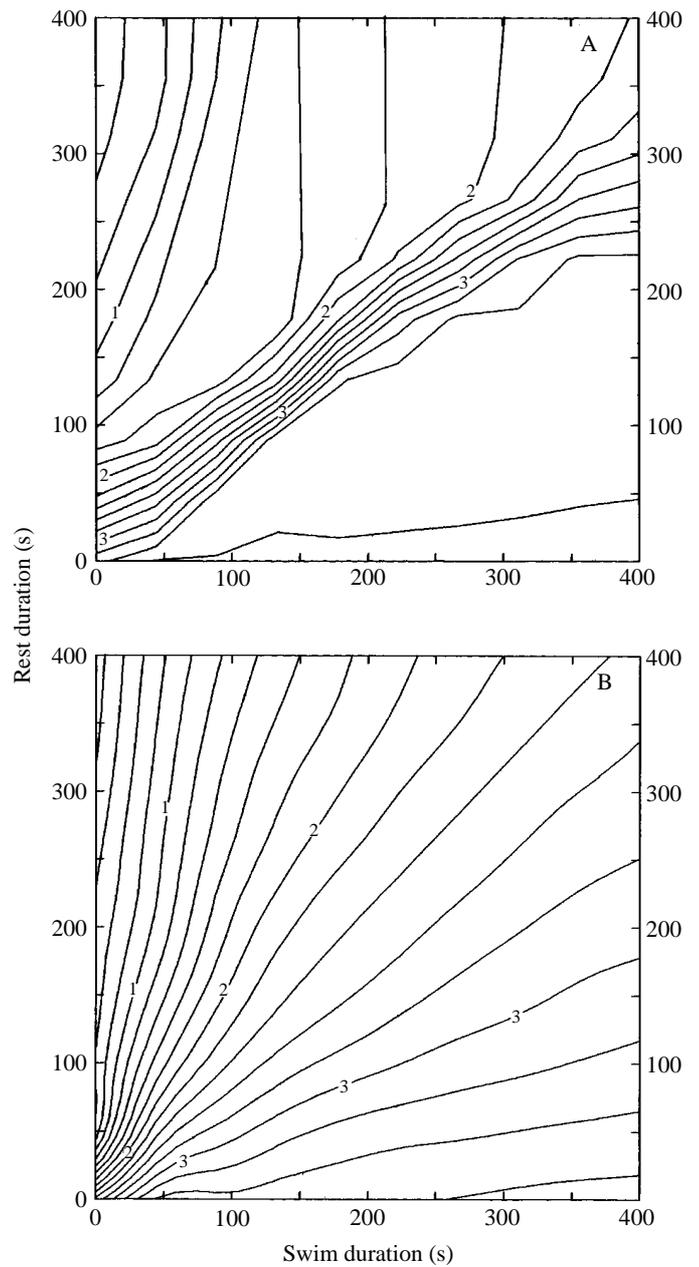


Fig. 6. (A) Calculated foraging efficiency (energy gain per unit time/energy loss per unit time) of African penguins *Spheniscus demersus* (with flexible body temperatures) as a function of swim and rest durations (see text). The numbers on the lines refer to efficiency values. Non-numbered lines differ from adjacent lines by a value of 0.2. (B) Calculated foraging efficiency in African penguins, if the birds were to maintain body temperature constant, as a function of swim and rest durations. The numbers on the lines refer to efficiency values. Non-numbered lines differ from adjacent lines by a value of 0.2. See text for details of model and assumptions.

overall heat loss of $5.6 + (0.002 \times 2000 \times 3.48) = 19.5 \text{ W}$. Were body temperature to be maintained constant, bank cormorants would have a much higher metabolic rate in water of $19.5 \times 1.33 = 25.9 \text{ W}$, or approximately $7.2 \times \text{SMR}$ (standard metabolic rate; data derived from Hennemann, 1983).

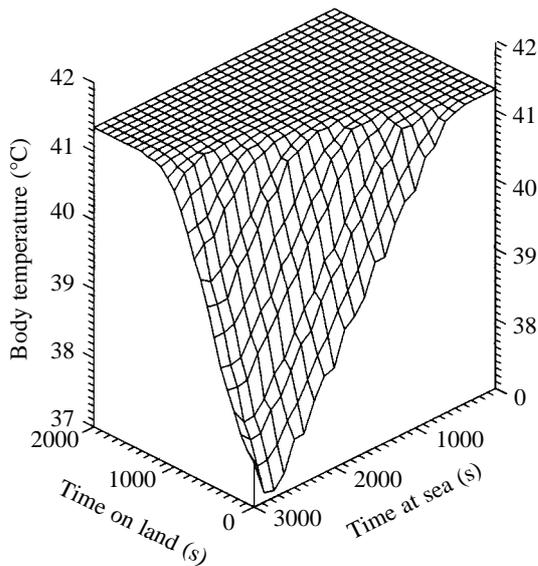


Fig. 7. Body temperature in bank cormorants *Phalacrocorax neglectus* (immediately following the land phase) as a function of time at sea and on land. Areas where the temperature falls below 41.3 °C indicate land:sea durations which could not be maintained for extended periods without the body temperature dropping to unacceptable limits. See text for details of model and assumptions.

Post-foraging bank cormorants on land are likely to expend energy at a rate of 8.5 J s^{-1} (Hennemann, 1983) which leads to a heat production of only 6.4 W. Our temperature measurements, however, show that at this time birds heat up at a rate of $0.0045 \text{ }^\circ\text{C s}^{-1}$, which necessitates a heat energy input of $0.0045 \times 2000 \times 3.48 = 31 \text{ W}$, of which apparently a remarkable $31 - 6.4 = 24.6 \text{ W}$ must be derived from the environment and, in particular, from the high insolation.

Again, the efficiency of flexible and fixed body temperatures may be modelled for cormorants if prey capture rates are known. Bank cormorants ingest prey at a mean rate of 0.018 g s^{-1} , which leads to an energy gain of 92 J s^{-1} when the birds are at sea (prey energy values are taken to be identical to those of the Cape anchovy). Efficiencies for birds with T_b values that vary between 37 and $42 \text{ }^\circ\text{C}$ thus lie between 0 and approximately 10 and are dependent on the sea:land durations (Fig. 8A). Certain sea:land duration combinations are, however, not possible without T_b falling below lower critical limits. Although cormorants with fixed body temperatures could exploit such sea:land durations, fixed- T_b birds would be overall much less efficient than their flexible- T_b counterparts (Fig. 8B). During normal foraging bouts of approximately 50 min during which bank cormorants allow their body temperature to vary by up to $5.2 \text{ }^\circ\text{C}$, they are up to 150 % more efficient than they would be if body temperature were not allowed to vary.

Despite rigid lower T_b limits, cormorants could also extend the duration of foraging bouts by allowing T_b to rise to particularly high levels just before a foraging trip. The duration of the period in the water could then be extended by $\Delta T/0.002 \text{ s}$,

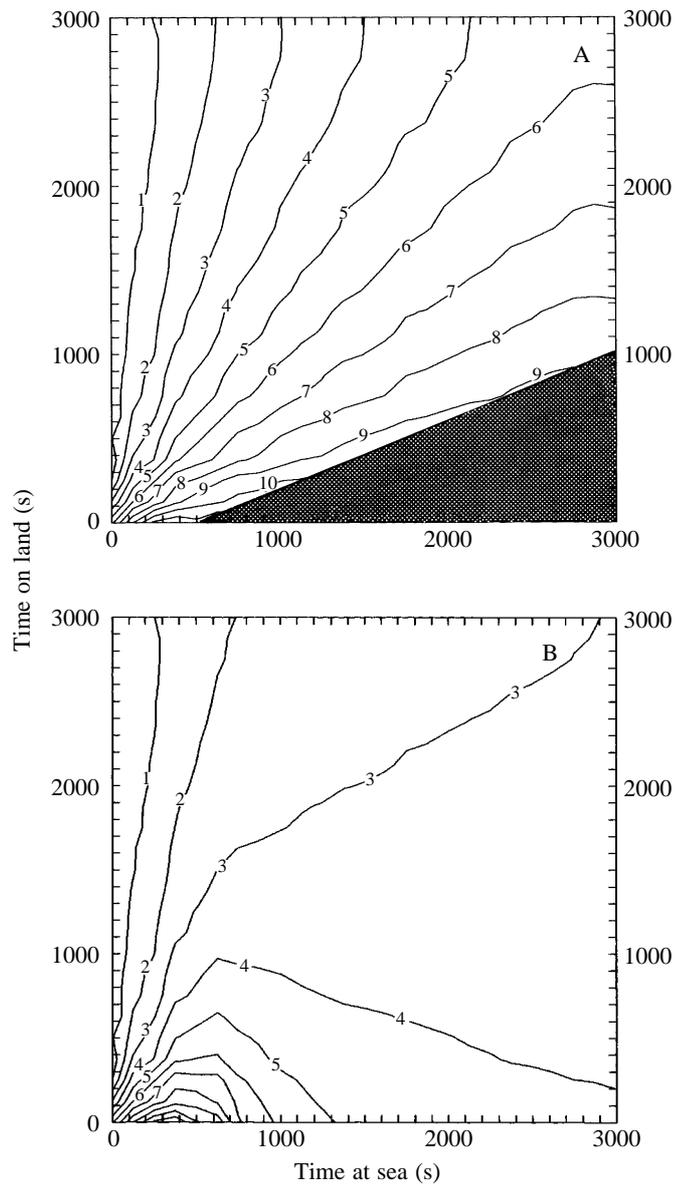


Fig. 8. (A) Calculated foraging efficiency (energy gain per unit time/energy loss per unit time) in bank cormorants *Phalacrocorax neglectus* (with flexible body temperatures) as a function of time at sea and on land. The numbers on the lines refer to efficiency values. The hatched area indicates foraging rhythms which could not be adhered to without the body temperature dropping to unacceptable limits. (B) Calculated foraging efficiency in bank cormorants, if the birds were to maintain body temperature constant, as a function of time at sea and on land. The numbers on the lines refer to efficiency values. See text for details of model and assumptions.

where ΔT is the incurred temperature rise prior to foraging. In this context, it is interesting to note that birds underwent a mean temperature rise of $1.6 \text{ }^\circ\text{C}$ just before departing to forage without any apparent change in activity. Such temperature changes could be brought about by a reduction in heat loss, such as cessation of gular flutter, rather than by increased heat production. A comparable, though less radical, situation

apparently occurs in beavers (*Castor canadensis*). These animals exhibit immersion hypothermia of between 1.0 and 1.5 °C but show an increase in mean body temperature of between 0.2 and 0.6 °C immediately prior to entering the water (Dyck and MacArthur, 1992).

There are many cases of endothermic animals living in extreme environments allowing body temperature to vary by a number of degrees in order to save energy or water. An example of an endotherm exposed to excessive heat is that of the camel which, when dehydrated, allows rectal temperature to vary by up to 7 °C (Schmidt-Nielsen, 1963). In contrast, willow tit (*Parus montanus*) body temperature may vary by up to 10 °C during the sub-zero temperatures experienced in Norway during winter (Reinertsen and Haftorn, 1986). In both cases, the problem experienced by the animals is that of temperatures that are consistently much higher or lower than those of the body. The case of the two seabirds in the present study reflects a thermal environment that is itself highly variable, stemming primarily from the substantial difference in thermal conductivity between water and air. Many marine endotherms living at high latitudes have remarkably constant body temperatures (e.g. Gallivan, 1979). Others, such as fur seals (*Arctocephalus gazella*) and gentoo penguins (*Pygoscelis papua*), have relatively constant body temperatures on land which then decrease by over 7 °C when the animals go to sea (Woakes *et al.* 1992, 1995). Marked hypothermia is also shown in some partially aquatic animals such as muskrats (*Ondatra zibethicus*) on exposure to cold water (Sherer and Wunder, 1979; Dyck and MacArthur, 1992). It is not clear, however, the extent to which such temperature drops serve primarily to save energy in the long term or whether they allow increased dive duration by cooling body tissues so that metabolic rate slows while the animals are under water (Culik *et al.* 1996).

African penguins and bank cormorants also have relatively flexible body temperatures, which accord closely with their lifestyle and which probably help to reduce energy expenditure. It seems likely that both penguins and cormorants are in their thermoneutral zone when dry on land, although penguins, being apparently better insulated, may have to engage in a number of specific behaviours to minimize energy expenditure to prevent overheating when insolation is high (Frost *et al.* 1976). This better insulation means that penguins may rest essentially indefinitely at sea but benefit most from body temperature flexibility when foraging by maintaining particular dive:rest ratios. Cormorants are poorly insulated and thus are restricted in the time they can spend at sea. However, by allowing body temperature to sink by over 5 °C and by using the substantial energy from the sun, birds can heat up when on land and forage efficiently at water temperatures that would otherwise necessitate exorbitant energy expenditure.

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