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Changes in body temperatures in king penguins at sea: the result of fine adjustments in peripheral heat loss?

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Schmidt, Alexander, Frank Alard, and Yves Handrich. Changes in body temperatures in king penguins at sea: the result of fine adjustments in peripheral heat loss? *Am J Physiol Regul Integr Comp Physiol* 291: R608–R618, 2006. First published April 20, 2006; doi:10.1152/ajpregu.00826.2005.—To investigate thermoregulatory adjustments at sea, body temperatures (the pectoral muscle and the brood patch) and diving behavior were monitored during a foraging trip of several days at sea in six breeding king penguins *Aptenodytes patagonicus*. During inactive phases at sea (water temperature: 4–7°C), all tissues measured were maintained at normothermic temperatures. The brood patch temperature was maintained at the same values as those measured when brooding on shore (38°C). This high temperature difference causes a significant loss of heat. We hypothesize that high-energy expenditure associated with elevated peripheral temperature when resting at sea is the thermoregulatory cost that a postabsorptive penguin has to face for the restoration of its subcutaneous body fat. During diving, mean pectoral temperature was $37.6 \pm 1.6^\circ\text{C}$. While being almost normothermic on average, the temperature of the pectoral muscle was still significantly lower than during inactivity in five out of the six birds and underwent temperature drops of up to 5.5°C . Mean brood patch temperature was $29.6 \pm 2.5^\circ\text{C}$ during diving, and temperature decreases of up to 21.6°C were recorded. Interestingly, we observed episodes of brood patch warming during the descent to depth, suggesting that, in some cases, king penguins may perform active thermolysis using the brood patch. It is hypothesized that functional pectoral temperature may be regulated through peripheral adjustments in blood perfusion. These two paradoxical features, i.e., lower temperature of deep tissues during activity and normothermic peripheral tissues while inactive, may highlight the key to the energetics of this diving endotherm while foraging at sea.

marine endotherm; *Aptenodytes patagonicus*; temperature decreases; pectoral muscle; brood patch; adjusted heat loss; energy expenditure; diving; resting

LOW AMBIENT TEMPERATURES (T_a) increase the energetic costs required for the maintenance of homeoendothermy. For some small birds, or species living in extreme environments, the metabolic rate and heat production that would be required for maintenance of core temperature reaches such levels that they adopt thermoregulatory adjustments (cyclic torpor or hypothermia) that permit energy reserves to last throughout the night or the winter season (39, 40, 46). For aquatic species, the maintenance of core temperature is even more costly because the thermal conduction of water is 25 times that of air (29, 36) and

also because of the drastic reduction of plumage insulation in water (19, 49). Logically, prevention of body cooling should, therefore, represent a substantial part of the total energy expenditure in endothermic homeotherms in water. A decrease in peripheral body temperatures well below the core temperature lowers the difference in temperature between the body shell and its surroundings and, consequently, reduces peripheral heat loss. Low peripheral temperatures result from a combination of low environment temperature, compression of air in the feathers at depth and speed, and peripheral vasoconstriction (32), whereby the warm blood bypasses the cold-exposed tissues and increases their cooling. Consequently, internal tissues are isolated, and the core temperature is maintained at minimal cost.

King penguins (*Aptenodytes patagonicus*) forage at sea with alternating long, deep dives (up to 8 min and 300-m depth) and short surface intervals (generally less than 3 min), several hours a day (12). While foraging, air-breathing species are limited in their apneic capacity by the amount of oxygen they can store and their overall metabolic rate at sea (9, 38). In king penguins, as well as in emperor and the gentoo penguins, the calculated aerobic dive limit (cADL) (32), i.e., the total usable oxygen stores divided by the rate of oxygen usage while under water, is less than the duration of up to 50% of observed dives (7, 16, 22, 33, 35). Moreover, between two long dives, the short surface intervals do not seem sufficient to permit the recovery from lactate accumulation associated with an increasing reliance on anaerobic metabolism (32). Even if the behavioral component may shorten or prolong the theoretical dive duration, the large number of dives exceeding the cADL makes this paradoxical physiological state unsustainable over several hours, as observed during common diving activity in the king penguin.

The cADL calculated from these studies must, therefore, have been underestimated, either due to overestimation of the diving metabolic rate (DMR) or erroneous assessment of available oxygen stores. However, estimation of the latter is considered to be reliable and reasonably accurate (1, 32, 37, 42). Furthermore, studies that have tried to identify possible energy-sparing strategies developed by diving birds to lower DMR have pointed to the possibility of physiological adjustments, allowing a reduction of core temperature (4, 5, 17, 25). This hypothesis is controversial, as it contradicts the classical theory

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of a highly regulated core temperature in endothermic homeotherms (9, 32, 48).

Nevertheless, temperature drops have been recorded during diving in king penguins, even in deep tissues (17, 25). In these studies, temperature sensors situated just under the liver (upper abdomen; Ref. 17) or between the liver and the apex of the heart (thoracic temperature; Ref. 24) recorded temperature drops of 12 and 2.7°C, respectively. Subsequent debate has focused on the functional significance of these temperature drops. On the one hand, they may represent core temperature and cause a reduction in overall metabolic rate via the Q_{10} effect (48). On the other hand, they may not be representative of deep tissues and may, therefore, only be exterior to the thermal core of the body. In fact, studies on emperor penguins (*Aptenodytes forsteri*) diving from an isolated ice hole reported no significant temperature changes in the inferior vena cava (43), the pectoral muscle, the stomach, or the axillary/brachial veins (44), thus indicating the maintenance of body core temperature.

Unpublished data (Y. Handrich) indicate an increase in skin temperature during the descent phase of dives in king penguins, which is unexpected in the context of the heat conservation hypothesis. Indeed, during the progression to depth, a decrease is observed in both water temperature and the air volume trapped in the feathers. Consequently, the descent to depth increases the temperature difference between the body temperature and T_a , and the effectiveness of insulation is reduced. In addition, moving through the water increases convective heat transfer. Thus swimming toward the sea bottom causes an increase in heat loss and a decrease in peripheral body temperatures. Birds showing a higher peripheral temperature when progressing to depth increase the body temperature- T_a difference and thereby undergo greater heat loss. These observations, therefore, suggest that, in some circumstances, king penguins seem to favor adjusted peripheral heat loss.

The aim of the present work is to clarify aspects of thermoregulation and the mechanisms of possible temperature and heat loss adjustments in free-ranging king penguins at sea. We examined body temperature characteristics from the scale of daily activities to the finer temporal scale of the single dive cycle in organs having opposite thermal balances. First, we examined the pectoral muscle (*Musculi pectoralis*) because of its primary contribution to overall heat production (50) and, therefore, the likelihood that this major locomotive muscle is the warmest during active swimming. Second, we examined the brood patch (*Area incubationis*), which is a bare and highly vascularized area of skin and possibly a preferential location for heat loss.

Based on the hypothesis of reduced body temperatures during sustained diving, our objectives were as follows: 1) to investigate differential thermoregulatory strategies in relation to activity at sea, i.e., the maintenance of high and stable body temperatures when resting at sea and the attainment of lowered body temperature during diving, especially at the level of a very active and energetically demanding tissue, the pectoral muscle; and 2) to investigate whether temperature reductions are regulated through active processes of peripheral adjustments in heat loss, or whether they are the passive consequences of diving in cold water.

Glossary

T_{PM}	Pectoral muscle temperature
T_{BP}	Brood patch temperature
ΔT	Temperature change (either for the brood patch, ΔT_{BP} , or the pectoral muscle, ΔT_{PM})
GI	Gradual increase of maximal dive depth
GD	Gradual decrease of maximal dive depth
MR	Metabolic rate
RMR	Resting metabolic rate
$Neg_{\Delta PM}$	Selection of dive cycles showing a final negative ΔT_{PM}
$Pos_{\Delta PM}$	Selection of dive cycles showing a final positive ΔT_{PM}
$Early_{\Delta BP}$	Selection of dive cycles showing a positive ΔT_{BP} at the beginning of the dive
$Late_{\Delta BP}$	Selection of dive cycles showing a positive ΔT_{BP} in the late descent phase of the dive

MATERIALS AND METHODS

This study was carried out at Possession Island, Crozet, Archipelago, southern Indian Ocean (46°25'S, 51°45'E) at the Grande Manchotière colony of king penguins. This colony consisted of ~28,000 breeding pairs (52), during the 2001 breeding season.

Technical Information and Measured Variables

Birds were equipped with modified Mk7 data loggers (Wildlife Computers). Due to the different characteristics of the loggers, penguins were equipped with one or two units to measure simultaneously on each bird the brood patch temperature (T_{BP}), the pectoral muscle temperature (T_{PM}), and environmental variables such as T_a and pressure. The sampling interval (SI) was 2 s for T_{BP} and 4 s for T_{PM} for birds 1, 2, 3, and 4. Birds 5 and 6 recorded body temperatures with SI = 8 s for T_{BP} and T_{PM} . These two additional birds were excluded from some of the results (bout fraction and dive cycle, see below) because the SI was inappropriate with short time scale analysis. In all birds, SI = 30 s for T_a and SI = 2 s for pressure. With this sample protocol, the 2 Mb of memory within each logger allowed recording for 18–21 days (birds equipped with two loggers in combination). The thermistor measurement ranges were 0–50°C for T_a (sea water) and 17–42°C for body temperatures; measurement accuracy was 0.2 and 0.1°C, respectively. Coated thermistors (YSI model 44017, 15 × 1 mm) had a time constant of 2.5 s (90% response in 5.7 s). The pressure sensor measurement range was –2 to 49 bars, and the sensor response was temperature corrected. Measurement precision near the surface (0–1 bar) and at depth was 0.05 and 0.2 bar, respectively. On birds equipped with two loggers, the synchronization of the units was checked according to the two depth profiles and corrected when required (<0.5 s/day).

Bird Equipment and Surgical Procedure

The capture/release and surgical procedures received the approval of the ethics committee of the French Polar Research Institute (Institut Polaire Paul Emile Victor) and of the French Ministry of the Environment. Description of the general procedure is presented in Froget et al. (22). Details concerning the use of temperature data loggers and positioning of temperature probes are given below.

On singly equipped birds, loggers were glued to lower back feathers. From the unit, two thermistor electrodes were channeled under the skin toward the pectoral muscle and the brood patch. Sensors inside the logger measured pressure and water temperature. For birds equipped with two units, one logger was implanted under the skin on the right flank, at the level of the thigh. From this logger, two

thermistor electrodes were channeled under the skin toward the pectoral muscle and the brood patch. The second logger was glued to the lower back feathers to measure pressure and T_a . The fixing of the electrode under the skin of the brood patch was undertaken without local opening of the skin. The two thermistors were located just under the epidermis of the intact brood patch and 4 cm vertically into the pectoral muscle.

Characterization of Activities and Data Analysis

All behaviors were categorized into one of three general activities.

1) Brooding on shore: birds warm the chick with their brood pouch and defend their territories.

2) Inactive period at the surface during interbout: due to increased convective heat loss when moving, even in the absence of diving events (over the limit of the sensor resolution), we hypothesized traveling and shallow diving when body temperatures were fluctuating during interbout periods. Thus inactive phases, or resting, were defined as the complete absence of diving events and the stabilization of all body temperatures during at least 1 h.

3) Dive bouts: the succession of at least three deep dives (≥ 50 m) with recovery periods at the surface of < 15 min.

The visualization of dive profiles and temperature records was achieved using specifically designed software (V46, Jensen Software). Data were analyzed using custom-made programs (FoxBase+, Fox Software). Automated programs corrected unit oscillation (pressure sensor noise) near the surface in a linear value. This correction was necessary for accurate detection of the beginning and end of dives. Programs automatically extracted the different temperatures and the pressure at various time scales and calculated their average value, absolute change (ΔT), and dynamics ($\Delta T/\text{time}$, $^{\circ}\text{C}/\text{s}$) over a period of time. During dive bouts, the variables we tested to explain body temperature changes were maximal and average depth, dive frequency, percentage of time spent under water or on the surface and the ratio of these two variables, dive bout duration, temporal index of the dive bout in the trip (e.g., 50% means that the bout starts at the middle of the trip), initial temperatures, and temperature differences between the different tissues and/or sea water. Regarding the brood patch, some dive bouts were excluded from the analysis when this tissue reached values below the thermistor range ($< 17^{\circ}\text{C}$, birds 1 and 3; $n = 4$ bouts). For the analysis of changes in temperature on a shorter time scale, the dive bout was divided into elementary components, i.e., individual dive cycles. We defined the dive cycle as a deep dive (≥ 50 m) and the following postdive period (characterized by resting at the surface or shallow dives), ending with the next deep dive. For the dive cycle analysis, we also took account of the 12 or 14 s (depending on the tissue-SI) before the first positive pressure measurement of a deep dive, to record possible events relying on the preparation of the dive (personal observations). The postdive period ended when the pre-dive period of the subsequent dive cycle started (see Fig. 1). The dive cycle was further separated into five phases (Fig. 1A): the pre-dive period, the descent to depth, the bottom time (13), the ascent to the surface, and the postdive period separating two deep dives. Initial, final, minimal, and maximal temperatures and their respective positions in time were extracted for all the different defined periods (Fig. 1B, example given for the bottom phase).

At the scale of the dive cycle, analyses were made using the temperature changes between two points. This permitted the pooling of temperature profiles showing the same trend inside the dive cycle. Therefore, initial temperatures shown on Figs. 4, 5, and 6 correspond to the mean temperature obtained from all birds.

Statistics

Reported values are means \pm SD. Data sets were verified for normality and equality of variance before test choice. Mean comparisons were followed by post hoc tests i.e., multiple-comparison Tukey test (q) for parametric data and Dunn's (different sample size)/Student

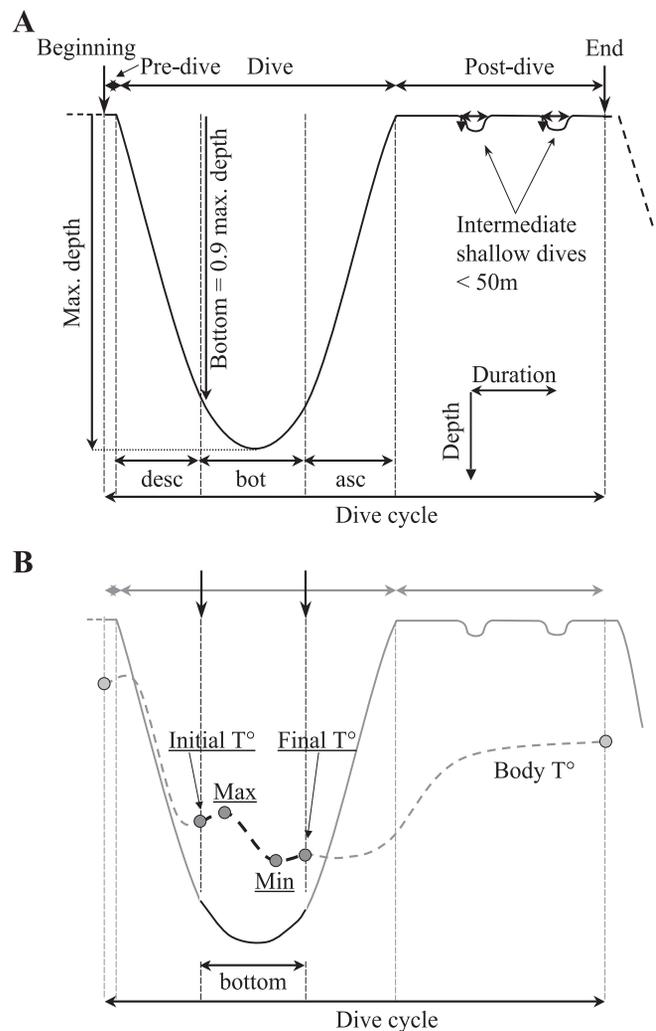


Fig. 1. A: visualization of one dive cycle with description of the 5 phases [pre-dive, descent (desc), bottom (bot), ascent (asc), and postdive]. B: example of data analysis during one of the dive phases: the bottom phase. Analyzed temperatures (T°) are initial and final temperatures and also minimum and maximum temperatures during each of the dive phase. Each temperature is associated with the time of occurrence in the dive cycle.

Newman-Keuls (same sample size) posttest (Q) for nonparametric data. Temperature changes were tested vs. the null hypothesis, a randomized data set between -0.1 and $+0.1^{\circ}\text{C}$ (confidence interval of the thermistors).

RESULTS

Because of technical problems (battery failure and broken probes) and atypical behaviors (i.e., intermediate return to shore), results presented in this study concern six birds out of the nine birds originally equipped with data loggers.

At the end of the field season, breeding was successful in six of the nine couples followed. Failures in incubation (one case) and chick rearing (two cases) were attributed, respectively, to an overextensive foraging trip, causing egg abandonment, and to extreme meteorological conditions (storm).

The six penguins accomplished foraging trips of 21.0 ± 4.6 days, which shows no difference from published results for unbanded birds from the same colony and the same year (18). As far as their behavior at sea is concerned, all dive charac-

Table 1. Summary of trip, dive bout, and dive cycle duration

Bird	Trip (day)	Bout, h			Dive Cycle, s		
		Duration	Range	n	Dive	Interdive	n
1	12	12.4±5.8	1.8–23.5	16	310±73	171±175	531
2	23	8.2±7.2	0.6–19.3	17	289±54	152±174	452
3	22	7.6±4.0	1.2–16.3	26	262±69	138±137	808
4	23	7.8±4.4	0.9–18.0	22	295±41	161±139	598
5	21	4.8±3.4	0.5–17.5	40			
6	25	9.2±4.9	0.8–18.6	34			
Average	21.0 ± 4.6	8.3±2.5	1.0–18.9		286±64	153±154	

Values are means ± SD; n, no. of birds. Values for birds 5 and 6 are not reported because of inappropriate sampling interval (see MATERIALS AND METHODS).

teristics (bimodal frequency distribution of dive depth, maximal dive depth, dive duration, number of deep dives per day) were in accordance with published results (12, 16, 34). Individual trip and bout durations are summarized in Table 1.

Body Temperatures While Brooding Onshore

The number of days for which temperatures were collected on shore ranged from 7 to 8 per penguin. Table 2 reveals that both measured body temperatures were homogenous. T_{PM} and T_{BP} on shore were not significantly different in three out of the six birds. Averaged T_{BP} among the six birds ($38.0 \pm 0.6^\circ\text{C}$) was in accordance with previous results on incubating king penguins (38.2°C ; Ref. 24).

Body Temperatures at Sea

While inactive. Inactive or resting phases at sea, as defined, mainly occurred at night, but were also recorded between two dive bouts during daylight hours (0500/2000). All measured body temperatures reached high and stable values (see Table 2). The pectoral muscle was the warmest measured tissue during these periods at $38.6 \pm 0.9^\circ\text{C}$ among the four birds. T_{BP} was $37.3 \pm 0.7^\circ\text{C}$ on average and was significantly lower ($-1.3 \pm 0.5^\circ\text{C}$) than the pectoral muscle [weakest probability among all birds (p_{\min}) = 0.002 for bird 1]. Average T_{BP} when inactive at sea was no different from that measured in the

colony (38.2°C). Resting temperatures remained constant during the entire foraging trip. Neither total time spent at sea nor sea surface temperature had any effect on resting temperatures, despite the fact that the latter varied from 7°C around the island to 4°C near the polar front.

During dive bouts. The data set analyzed here corresponds to a cumulative duration of 126 days at sea, totaling 1,264 h of deep diving activity divided into 155 dive bouts (Table 1). Dive bouts occurred only during daylight hours. Dive bouts usually started with a gradual increase (GI) and finished with a gradual decrease (GD) of maximal dive depth (from shallow to deep dives over 100 m; Ref. 34).

THE PECTORAL MUSCLE. Mean T_{PM} during dive bouts was $37.6 \pm 1.6^\circ\text{C}$ among the six birds (see range in Table 2). In five out of the six penguins, T_{PM} during diving was significantly lower than during resting in water ($P < 0.05$ for birds 1, 3, 4, 5, and 6). In bird 2, mean T_{PM} also showed a decrease during diving but was not significantly different from resting values ($Q = 1.05$, not significant). Overall mean T_{PM} during dive bouts was not different from brooding on shore, since T_{PM} was found to be lower during diving than on shore in two birds (birds 5 and 6, $P < 0.05$), not significantly different in three birds (birds 1, 3, and 4), and finally higher during diving vs. on shore in one bird (bird 2, $P < 0.05$).

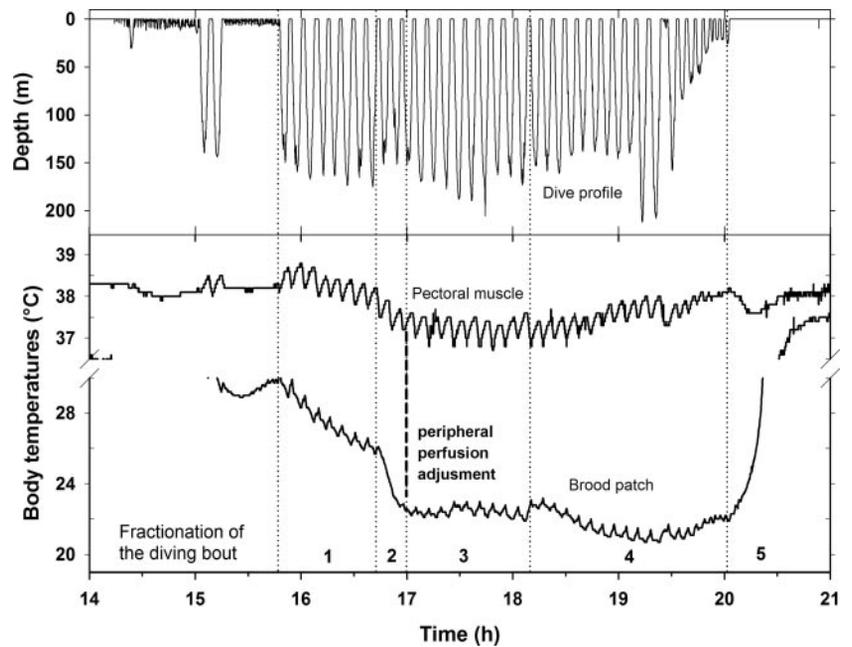
After several deep dives, T_{PM} showed significant temperature drops. The average maximal change in T_{PM} (ΔT_{PM}) when bouts and birds were pooled was $-2.0 \pm 1.3^\circ\text{C}$ (-0.5 to -4.0°C among birds). During a given bout, ΔT_{PM} was as high as -5.5°C (see Table 2). The average and maximal ΔT_{PM} during a dive bout were not correlated with bout duration. This is because the lowest T_{PM} values were rarely reached at the end of the bout due, as episodes of warming occurred at any point in time (Fig. 2). These positive ΔT_{PM} episodes lasted from 3.3 to 33.8 min (1–5 dive cycles) and ranged from $+0.1$ to $+0.7^\circ\text{C}$. We were unable to correlate these episodes of warming with any of the numerous recorded environmental or physiological parameters tested. However, the GI and GD periods of transition between shallow and deep dives at the two extremities of each bout were always characterized by episodes of positive ΔT_{PM} .

Table 2. Summary of pectoral and brood patch temperature during different activities, and maximal temperature drop for each tissue during dive bouts

Bird		Body Temperatures, $^\circ\text{C}$			Maximum Temperature Drop/Bout, $^\circ\text{C}$		
		Brooding	Resting at sea	Diving	Mean	n	Maximum
1	Pectoral muscle	36.9±0.2 ^{a†‡}	37.4±0.4 ^{a†}	36.5±0.8 ^{a‡}	1.7±1.3	16	3.3
	Brood patch	38.0±0.2 ^{b†}	37.0±0.5 ^{b‡}	27.3±4.1 ^{b*}	17.0±3.1	12	21.6
2	Pectoral muscle	37.8±0.4 ^{a†}	40.0±0.1 ^{a‡}	39.7±0.4 ^{a‡}	0.5±0.6	17	1.2
	Brood patch	38.0±0.4 ^{a†}	38.3±0.6 ^{b†}	32.5±4.5 ^{b‡}	9.2±6.9	17	18.9
3	Pectoral muscle	38.3±0.3 ^{a†}	39.1±0.2 ^{a‡}	38.5±0.2 ^{a†}	1.1±0.4	26	1.7
	Brood patch	38.3±0.2 ^{a†}	37.7±0.6 ^{b†}	33.1±2.6 ^{b‡}	15.1±5.9	22	20.8
4	Pectoral muscle	38.7±0.2 ^{a†}	39.0±0.2 ^{a‡}	38.5±0.4 ^{a†}	1.8±0.9	22	3.3
	Brood patch	38.7±0.2 ^{a†}	37.6±0.4 ^{b‡}	28.0±3.0 ^{b*}	15.8±3.9	22	20.5
5	Pectoral muscle	37.0±0.3 ^{a‡}	38.0±0.3 ^{a*}	35.9±0.5 ^{a†}	2.9±0.5	40	4
	Brood patch	37.8±0.2 ^{b‡}	36.6±0.7 ^{b‡}	28.8±2.6 ^{b*}	9.7±3.0	40	16.1
6	Pectoral muscle	37.4±0.3 ^{a‡}	38.3±0.2 ^{a*}	36.2±0.7 ^{a†}	4.0±1.0	34	5.5
	Brood patch	36.9±0.3 ^{b‡}	36.6±0.6 ^{b‡}	27.9±2.9 ^{b*}	13.2±4.2	34	18.6
Average	Pectoral muscle	37.7±0.7	38.6±0.9	37.6±1.6	2.0±1.3	6	3.2 ± 1.6
	Brood patch	38.0±0.6	37.3±0.7	29.6±2.5	13.3±3.3	6	19.4 ± 2.0

Values are means ± SD; n, no. of animals. ^{a,b}Comparison between tissues (different letters indicate a significant difference, $P < 0.05$). ^{†‡}Comparison between activities (different symbols indicate a significant difference, $P < 0.05$).

Fig. 2. Pectoral and the brood patch temperatures (T_{BP}) (time vs. temperature) are superimposed on a diving activity chart (dive profile, time vs. depth), e.g., *bird 1*, 06/03/2001. The dive bout is split according to the speed of T_{BP} change, $\Delta T_{BP}/dt$ ($^{\circ}\text{C}/\text{min}$). The dashed line at the interface between sequences 2 and 3 is the illustration of peripheral perfusion adjustment (see DISCUSSION).



BROOD PATCH. Average T_{BP} during dive bouts was $29.6 \pm 2.5^{\circ}\text{C}$ among the six birds. Typically, ΔT_{BP} throughout the dive bout was negative, and the lowest T_{BP} values were consistently reached at the end of the dive bout. Maximal ΔT_{BP} during dive bouts ranged among birds from $-9.2 \pm 6.9^{\circ}\text{C}$ to $-17.0 \pm 3.1^{\circ}\text{C}$. T_{BP} attained at the end of the dive bout was significantly, positively correlated with the cumulative time spent at depth ≥ 50 m [weakest Spearman correlation factor among all birds ($r_{\text{Spmin}} = -0.588$, $n = 22$, $P = 0.004$ for *bird 4*, illustrated in Fig. 3)].

Birds 5 and 6 were excluded from further analysis because of the SI (8 s) of body temperatures that did not permit analysis at a fine temporal resolution.

ΔT_{BP} during dive bouts usually followed an exponential decay curve. However, during the course of this decrease, the slope of ΔT_{BP} seemed to be associated with diving effort. Each dive bout was then separated into phases on the basis of the

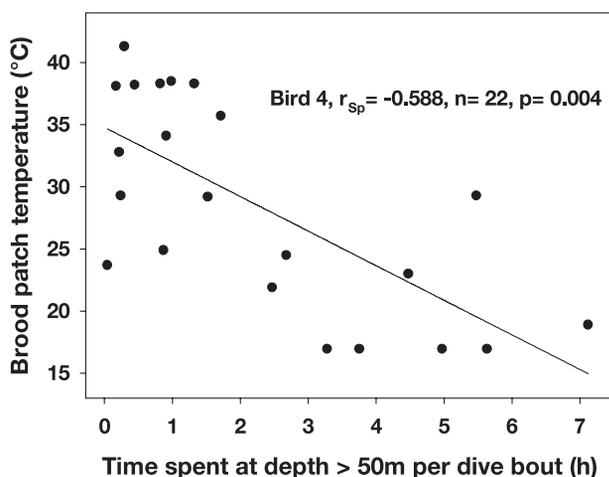


Fig. 3. Illustration on *bird 4* (lowest significance found among all birds) of the T_{BP} ($^{\circ}\text{C}$) at the end of each dive bout as a function of time spent at depth > 50 m per dive bout (h). n , No. of animals. r_{sp} , Spearman correlation factor.

speed of ΔT_{BP} ($\Delta T_{BP}/dt$, see Fig. 2). For the four birds, $\Delta T_{BP}/dt$ correlated best with the mean depth of the bout fraction (data include zero values of the surfacing period, $r_{\text{Spmin}} = -0.317$, $n = 76$, $P = 0.005$ for *bird 1*). Other variables that were significantly correlated with $\Delta T_{BP}/dt$ are, in decreasing order, percentage of time spent at depth > 50 m, time at depth > 50 m divided by time at the surface, and frequency of deep dives.

During the dive cycle. Mean duration of the dive cycles was 453 ± 185 s ($n = 2,389$), with diving and resting periods lasting 286 ± 64 and 153 ± 154 s, respectively (Table 1).

Temperature trends during a dive cycle are presented in Fig. 4 (*birds 1, 2, 3, and 4* are pooled, $n = 2,389$) and are defined

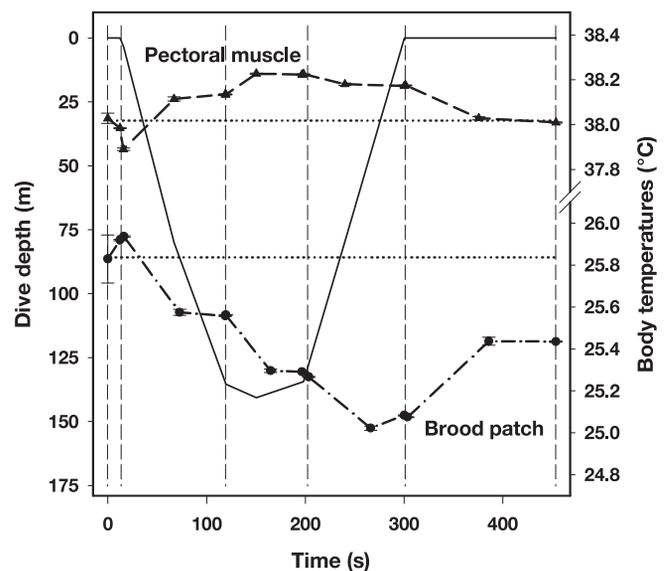


Fig. 4. Typical body temperature profile over pooled dive cycles (average on 4 penguins, $n = 2,389$). The vertical dashed lines separate the dive cycle into its different phases. Horizontal dotted lines are indicative of the initial temperature of each tissue.

as the typical trends for each tissue. The typical trend for T_{PM} was a brief decrease ($-0.14 \pm 0.32^\circ\text{C}$) during the first 15 ± 7 s of the dive cycle. Thereafter, ΔT_{PM} was positive until almost halfway through the bottom phase ($+0.34 \pm 0.46^\circ\text{C}$). At this stage, maximal T_{PM} within the dive cycle was attained. T_{PM} then remained constant until the end of the ascent phase. During the postdive period, ΔT_{PM} was negative ($-0.16 \pm 0.26^\circ\text{C}$). Finally, ΔT_{PM} over the whole dive cycle was not significantly different from zero ($-0.02 \pm 0.13^\circ\text{C}$).

The typical pattern for T_{BP} was a brief increase ($+0.11 \pm 0.24^\circ\text{C}$, lasting 15 ± 6 s) at the beginning of the dive cycle. Thereafter, ΔT_{BP} was negative throughout practically all of the duration of the dive ($-0.91 \pm 0.99^\circ\text{C}$). The end of the ascent phase and the postdive period were always characterized by a positive ΔT_{BP} ($+0.41 \pm 0.93^\circ\text{C}$). Finally, ΔT_{BP} over the whole dive cycle was a significant decrease of $-0.40 \pm 0.90^\circ\text{C}$ ($P < 0.001$).

SELECTION OF DIVE CYCLES SHOWING NEGATIVE OR POSITIVE ΔT_{PM} . Since T_{PM} was observed to decrease or reincrease progressively during dive bouts, we compared two selections of dive cycles showing either a significant negative ΔT_{PM} ($Neg_{\Delta PM}$, $-0.23 \pm 0.07^\circ\text{C}$, $n = 407$) or positive ΔT_{PM} ($Pos_{\Delta PM}$, $+0.22 \pm 0.06^\circ\text{C}$, $n = 252$). Selections are represented in Fig. 5, A and B, respectively. Between these two selections, $Neg_{\Delta PM}$ cycles showed longer dive and postdive durations than $Pos_{\Delta PM}$ (317 ± 66 vs. 282 ± 60 s, $P < 0.001$, and 185 ± 168 vs. 178 ± 207 s, $P < 0.001$, respectively). Maximal dive depth was also greater in $Neg_{\Delta PM}$ cycles (176 ± 50 vs. 147 ± 52 m, $P < 0.001$). The positive ΔT_{PM} that occurred during the descent and the bottom phase was found to be the same in both selections ($Neg_{\Delta PM}$: $+0.41 \pm 0.58^\circ\text{C}$, $Pos_{\Delta PM}$: $+0.42 \pm 0.47^\circ\text{C}$). However, during the short period of cooling that occurs within the first seconds of the dive cycle (Fig. 5), the drop in T_{PM} was twofold higher in $Neg_{\Delta PM}$ cycles than $Pos_{\Delta PM}$ cycles (-0.28 ± 0.45 vs. $-0.14 \pm 0.34^\circ\text{C}$). In addition, $Neg_{\Delta PM}$ cycles showed a decrease of T_{PM} throughout the ascent and the postdive phases (-0.15 ± 0.29 and $-0.21 \pm 0.33^\circ\text{C}$, respectively), whereas $Pos_{\Delta PM}$ cycles were characterized by a ΔT_{PM} not different from zero during the same phases. Importantly, in both selections, initial T_{PM} and T_{BP} were found to be within the whole range of temperatures measured for each tissue. Consequently, no T_{PM} or T_{BP} threshold, for example, the attainment of a minimal temperature or a minimal temperature difference between tissues and the environment, was identified to explain whether ΔT_{PM} was positive or negative after one dive cycle. In both selections, ΔT_{BP} showed no difference with the typical pattern presented in Fig. 4.

UNDERWATER EPISODES OF BROOD PATCH WARMING. Within the 2,389 analyzed dives ($n = 4$ birds), 21% of dive cycles (evenly distributed among birds) showed episodes of positive ΔT_{BP} during the descent to depth. The selection of dives cycles showing episodes of warming was made with respect to measurement precision ($\pm 0.1^\circ\text{C}$). Consequently, only temperature events showing an increase of at least $+0.2^\circ\text{C}$ were considered as significant and thus selected. These paradoxical temperature events were found to occur either at the beginning of the dive ($Early_{\Delta BP}$, $n = 293$, 12.3% of all dives) or in the second half of the descent to depth ($Late_{\Delta BP}$, $n = 199$, 8.3% of all dives, see Figs. 6, A and B, respectively). Only 19 dive cycles (0.8% of all dives) included both observed warming-up events.

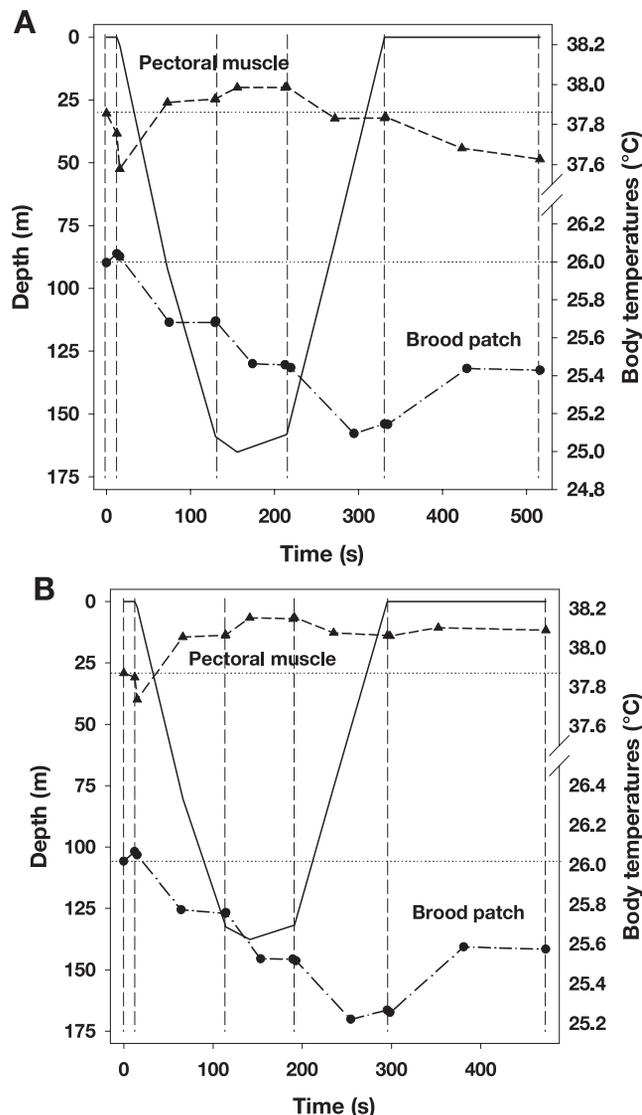


Fig. 5. Selection of dive cycles showing final negative change in pectoral muscle temperature (ΔT_{PM}) ($Neg_{\Delta PM}$, $n = 407$; A) or a final positive ΔT_{PM} ($Pos_{\Delta PM}$, $n = 252$; B) of the pectoral temperature. The vertical dashed lines separate the dive cycle into its different phases. Horizontal dotted lines are indicative of the initial temperature of each tissue.

$Early_{\Delta BP}$ cycles were characterized by a positive ΔT_{BP} that started during the pre-dive period ($+0.17 \pm 0.18^\circ\text{C}$) and continued during the first 12 ± 8 s of the immersion ($+0.26 \pm 0.10^\circ\text{C}$). Thereafter, the T_{BP} trend and final ΔT_{BP} were not different from the typical trend presented in Fig. 4. T_{PM} variation during $Early_{\Delta BP}$ cycles was characterized by a low and not significant temperature drop ($-0.07 \pm 0.16^\circ\text{C}$) at the beginning of the dive cycle and a continuous positive ΔT_{PM} until birds reached the surface. However, final ΔT_{PM} after $Early_{\Delta BP}$ cycles was not significantly different from zero.

In $Late_{\Delta BP}$ cycles, the positive ΔT_{BP} ($+0.26 \pm 0.11^\circ\text{C}$) took place after 34 ± 33 s of progression underwater, i.e., at a mean depth of 49 ± 52 m. During the bottom phase, the ascent, and the postdive phases, the T_{BP} profile and final ΔT_{BP} were similar to the general pattern presented in Fig. 4. In $Late_{\Delta BP}$ cycles, the positive ΔT_{PM} found during the descent phase and until the bird reached the bottom of the dive was $+0.40 \pm$

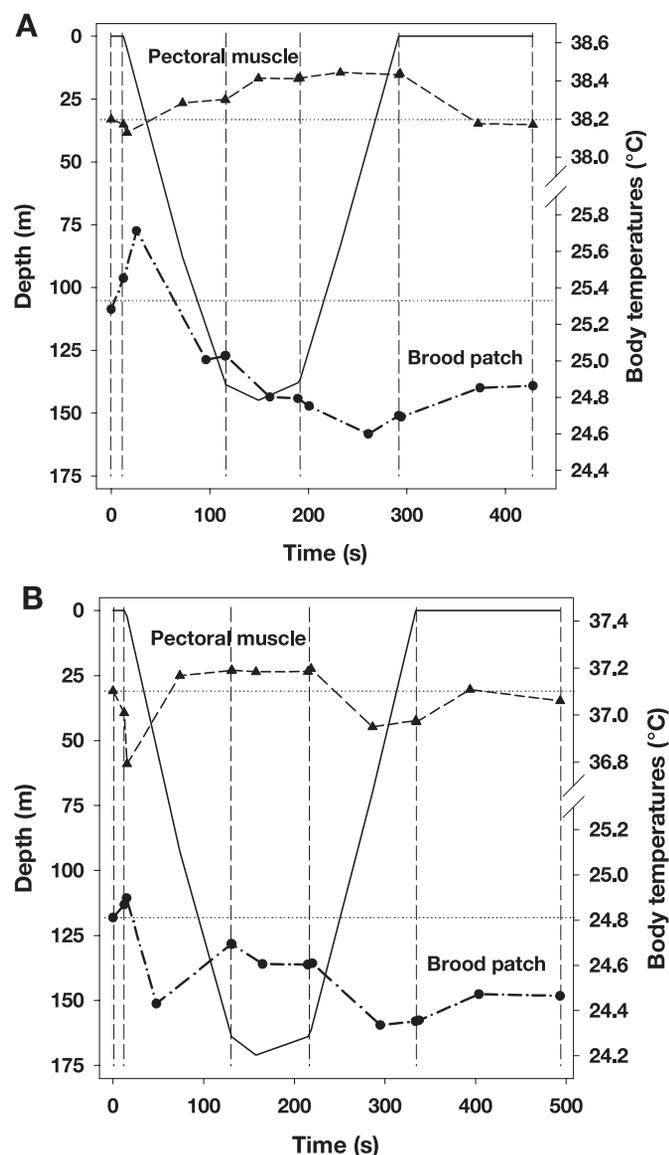


Fig. 6. Selection of dive cycles showing brood patch warming-up events. A: positive ΔT_{BP} occurring during the beginning of the dive (Early $_{\Delta BP}$, $n = 293$). B: positive ΔT_{BP} occurring during the second half of the descent to depth (Late $_{\Delta BP}$, $n = 199$). The vertical dashed lines separate the dive cycle into its different phases. Horizontal dotted lines are indicative of the initial temperature of each tissue.

0.67°C. This increase was no different from the typical temperature pattern of the muscle during diving (Fig. 4).

Regarding the dive characteristics, dive duration and maximal depth were significantly shorter and shallower for Early $_{\Delta BP}$ cycles compared with Late $_{\Delta BP}$ cycles (279 ± 52 vs. 321 ± 73 s, $P < 0.001$, and 153 ± 44 vs. 182 ± 60 m, $P < 0.001$, respectively). No difference was found in the postdive duration in Early $_{\Delta BP}$ and Late $_{\Delta BP}$ cycles, and dive cycles following these negative ΔT_{BP} selections showed no difference with the average temperature and dive profile (Fig. 4).

DISCUSSION

The findings of this study contrast with the classical model of thermoregulation proposed for diving endothermic homeotherms (32): first, because of the lowered temperature of deep

and active tissue during diving activity, and second, because of normothermic peripheral tissues during inactivity at sea. The discussions we provide concerning temperature changes are based on the change of thermal conductance. At the level of peripheral tissues, changes in thermal conductance will then be discussed with regard to Fourier's heat flux law. When measuring tissue temperature, we have the direct result of environmental and physiological cumulative effects. Thus, when taking into account 1) environmental features (water temperature, pressure), 2) the intrinsic characteristics of the tissue (being constant over the course of the temperature events we observed: e.g., fat deposit or utilization), and 3) the relative rate of heat production, then the remaining factors that could possibly influence tissue temperature are the rate of blood flow and blood temperature. Accordingly, even if blood flow or blood temperature was not directly measured in this study, temperature events discussed below can confidently be related to vascular adjustments.

Body Temperatures During Diving

T_{PM} . The pectoral muscle is the largest muscle in the king penguin (25% of total body mass at the beginning of the reproductive period) (14). In many bird species, the pectoral muscle plays a major role in thermoregulation (10). Due to low mechanical efficiency, intensive muscular work generally implies increased muscle temperature (31, 48). Therefore, we initially expected the pectoral muscle to warm up during swimming activity. However, despite the thermogenic property of muscular contraction, averaged T_{PM} was found to be normothermic over the whole dive bout, and on some occasions, T_{PM} even decreased by up to 5.5°C below inactivity values at sea.

This degree of cooling was not immediate at the onset of the dive bout. T_{PM} first increased at the beginning of each dive bout (GI phases) and then decreased systematically after several deep dives. This progressive cooling of the pectoral tissue could be attributed to the inability of the bird to repress heat loss through the periphery and to a cooling effect linked with the ingestion of prey. In this context, cooling of internal tissues would be irrepressible and passive. However, T_{PM} always stabilized before the end of the dive bouts and even exhibited episodes of warming inside the bouts. The stabilization of T_{PM} and the occurrence of warming episodes during the dive bout are illustrated by the typical T_{PM} profile during the dive cycle (Fig. 4) which shows, on average, no trend of pectoral cooling during the course of the dive bout. These episodes of warming were not correlated with less challenging dives or environmental characteristics. Furthermore, these warming episodes did not start either when attaining a given T_{PM} threshold or a minimal temperature difference between the pectoral and the brood patch or ambient. Thus, if variation of heat production/loss alone does not explicate T_{PM} changes inside the bout, variation of heat exchange via modification of heat conduction could provide an explanation.

Pectoral temperature always showed a fast drop during the pre-dive period. T_{PM} then continued to decrease in the first seconds of submersion (2.5 s on average). With regard to diving behavior and muscular activity, the pre-dive period is very similar to the ascent and the post-dive period. However, the speed of T_{PM} change ($\Delta T_{PM}/dt$) during the 12–14 s before immersion was much greater than during the post-dive and the

passive ascent phase underwater (-0.50 ± 1.15 vs. -0.08 ± 0.14 and $-0.03 \pm 0.12^\circ\text{C}/\text{min}$, respectively). We hypothesized that blood perfusion was maximal in the pectoral muscle during this short period preparing the dive. This enhancement of blood flow before the dive may be in accordance with the anticipatory tachycardia found to occur before each dive (22).

In king and emperor penguins, measurement of acceleration data has revealed the flipper stroking pattern, and thus the locomotory effort, during the different phases of the dive (47, 51). The beginning of the descent to depth, and to a lesser extent the bottom phase, are characterized by considerable flipper beating, whereas, during the last part of the ascent, king penguins stop beating their flippers and use their buoyancy to return passively to the surface. In addition, blood flow through the skeletal muscles is supposed to cease (ischemia) during submergence to preserve the circulating oxygen for strictly oxygen dependent tissue (32). This particular perfusion characteristic may presumably also occur in free-diving birds such as the king penguin (32). With the assumption that such muscle perfusion, it was expected that the heat produced by muscular activity remains stored in the surrounding tissues and thus that the T_{PM} will reflect the pattern of flipper activity during submergence. Our data seem to verify the hypotheses of a low perfusion rate in the pectoral muscle during diving, since T_{PM} profiles agree with the trends anticipated according to the variations in mechanical work (see Fig. 4): T_{PM} increases during the descent phase, then stays stationary until the end of the dive, and finally, progressively decreases during the post-dive period. An additional argument for pectoral ischemia during diving is provided by the comparison of the speed of T_{PM} change ($\Delta T_{\text{PM}}/dt$) in two phases where animals have no locomotory activity: the ascent and the postdive period. During the postdive period $\Delta T_{\text{PM}}/dt$ was threefold higher than during the ascent phase of the dive (-0.08 ± 0.14 vs. $-0.03 \pm 0.12^\circ\text{C}/\text{min}$). This suggests that blood flow through the muscle increases considerably during this recovery period and/or that blood at a lower temperature perfused the pectoral while surfacing. An increasing blood flow after the extended breath hold is coherent with the replenishment of the oxygen stores and related to a general vasodilatation, as already observed in captive seals (32). Following the reasoning on speed of temperature change at known muscular activity and insulation properties, our results call attention to the fact that, even at 5.5°C below inactivity temperature levels at sea, the pectoral muscle may still be warmer than the blood flowing into them. This in turn supports the hypothesis that the temperature of mixed blood is greatly influenced by blood returning from cold tissues and organs (e.g., limbs, skin, and digestive tracts) (17, 25). Moreover, despite the negative ΔT_{PM} during dive bouts, this organ may still be one of the warmest tissues during sustained exercise (swimming and diving). Thus our results suggest an accurate regulation of the rate of blood perfusion through the pectoral muscle to set the muscle temperature to an optimal value for a given period of diving activity.

A number of studies proposed that reduction in body temperature may allow marine species to lower their DMR (via the Q_{10} effect) (3, 5, 6, 25, 27, 38) and thus increase their breath-hold duration. Even though our results describe reductions in temperature reduction within one of the most energetically demanding tissues during swimming activity, the benefits of a lower functional temperature for muscle are still

debated and necessitate further investigation. However, counter to the possible energetic benefits, a lowered temperature may impair muscle functional properties (2, 21, 48) and thus hunting efficiency. Pectoral cooling should then be adjusted and stay within the range of normothermic temperatures to avoid declining beyond a minimal and mechanically disadvantageous value. From this point of view, variations of T_{PM} in diving king penguins may be a trade-off between an energy-sparing strategy and the maintenance of efficient locomotion.

T_{PM} has already been studied in emperor penguins diving from an isolated ice hole (44). In this study, authors reported the preservation of pectoral and core temperatures. However, trends in body temperatures in relation to diving activity reported in Ref. 38 are similar to those observed in free-ranging king penguins at the beginning of each dive bout. In both studies, the trend in T_{PM} was, first, an increase during the first 20 min of the diving activity and then a slight T_{PM} decrease (see Fig. 5 in Ref. 38, and Fig. 4 in the present study), after which emperor penguins stopped diving and rested on ice, while king penguins continued sustained diving for several hours. As subcutaneous temperature was also found to decrease (see Fig. 9 in Ref. 38), we believe that emperor penguins practicing extended durations of diving activity without leaving the water would extend the T_{PM} cooling already in progress. At the level of the dive cycle, in both studies ΔT_{PM} was initially negative before the dive and was then positive through to the bottom phase of the dive (Fig. 5 in Ref. 38). However, emperor penguins also showed a positive ΔT_{PM} during the ascent phase, which we attribute to the fact that this species does not stop flipper beats at any point when returning to the ice hole (51). Thus heat production in relation to locomotory effort may not diminish as it was assumed to do in the king penguin. Finally, conclusions proposed in both studies may not be contradictory, if we consider, in the present study, that birds start diving activity with normothermic body temperatures. Indeed, the present study revealed that several consecutive deep dives were necessary to lower pectoral temperatures.

The brood patch. The speed of swimming enhances peripheral convective heat loss (28, 32). However, the swimming speed in shallow and deep dives is equivalent (45), yet it did not influence T_{BP} in the same way. Therefore, this parameter is insufficient to explain peripheral body cooling at sea, and pressure must also be considered. Indeed, when pressure increases, the thickness of the air layer trapped in the feathers is reduced, and thermal conductivity increases. Thus, with progression to depth, the decrease of body insulation and water temperature ($1-5^\circ\text{C}$, depending on distance to the polar front) (11) favor a decrease in body temperatures (36, 53). This assumption was confirmed since ΔT_{BP} at the end of a dive bout correlated well with the time spent at depths greater than 50 m during the dive bout (Fig. 3). This trend was also shown in diving macaroni penguins, with abdominal temperature being correlated with duration and average depth of the dive bout (23). The systematic decrease of T_{BP} in the course of the dive bout is illustrated in Fig. 4, which shows an average T_{BP} drop of -0.40°C during each dive cycle.

During diving, the brood patch is protected by a fold of adjacent feathered tissue. When the king penguins swim back to the surface, the remaining air layer in the feathers, which has not been expelled under the effect of speed and pressure,

expands, and water temperature increases. Consequently, the plumage recovers, at least partly, its insulation property. Nevertheless, T_{BP} was found to decrease at the same rate during the descent and ascent phases (see Fig. 4). This observation supports the reduction of peripheral thermal conductance through limited skin perfusion (vasoconstriction) when diving, to limit peripheral heat loss, as expected (32). Warm blood bypassing the skin avoids cooling and enhances the temperature reduction of the periphery and thereby minimizes heat loss to ambient. However, a positive ΔT_{BP} was observed during the last 32 s on average before surfacing. Near the surface, the air sacs expand, and gas exchange may carry on, making available a certain quantity of oxygen. This positive ΔT_{BP} might then be an anticipatory vasodilatation, commonly occurring at the surface, to supply tissues with oxygen (32). However, because of these latter factors (perfusion rate and ambient parameters), as long as birds are under water, it is impossible to define the influence of each phenomenon on T_{BP} .

Efficient mechanisms of heat conservation and the requirement for such would imply a strong decrease of peripheral thermal conductance from the onset of a dive bout. Consequently, the brood patch should first cool rapidly to the minimum values observed and remain at this level until the end of the dive bout. Nevertheless, since T_{BP} was found to undergo different ranges of temperature drops, from a few degrees up to $>20^{\circ}\text{C}$, we hypothesize that the reduction of blood perfusion through the brood patch was not maximal at the beginning of the dive bout and that an adjusted rate of perfusion still occurred at any time during the dive bout. The perfusion of peripheral tissues permits the evacuation of heat and may contribute to the reduction of body temperatures. However, to avoid body tissues from dropping beyond a vital range of temperatures, effective heat conservation mechanisms have to take place throughout the dive bout to maintain tolerable core temperatures. With increasing vasoconstriction, the temperature difference between the skin and the water is reduced, and heat transfer is minimized. This change in perfusion rate was observed in the course of each dive bout. The hypothesis of adjusted peripheral heat loss as a response to variations in heat production is illustrated in Fig. 2, where, at a given moment (annotated "peripheral perfusion adjustment"), T_{BP} abruptly decreased while the progressive decline of T_{PM} was interrupted.

If the brood patch is used to regulate peripheral heat loss, the mechanisms involved should also fit as precisely as possible to the level of internal heat production. Therefore, we should observe dive cycles representative of periods of heat conservation or heat loss. Following the classic model of heat conservation, we have shown that a large proportion of ΔT_{BP} corresponds to a decrease in peripheral thermal conductivity. In 79% of dive cycles, T_{BP} decreased while the bird was under water. In contrast to this modal scenario, 21% of dive cycles revealed significant positive ΔT_{BP} during the descent phase (Early $_{\Delta BP}$ and Late $_{\Delta BP}$ cycles). In Early $_{\Delta BP}$ cycles, positive ΔT_{BP} occurred in the first part of the descent, while muscular effort was maximal. Related maximal heat production and possible warmer blood perfusing the brood patch could explain the temperature increase at this moment. However, the fact that this event occurred in only 12.3% of dives casts doubt on the possibility that it is a passive consequence of muscular activity and is rather an argument for vascular adjustments. Moreover,

in 8.3% of the dive cycles, positive ΔT_{BP} occurs in the second part of the descent to depth (Late $_{\Delta BP}$ cycles), when penguins progress with lowered stroking frequency but maintain a constant swimming speed (47, 54), and where peripheral thermal conductance is maximal. The positive ΔT_{BP} occurring at depth is unlikely to be related to an elevation of blood temperature. During Late $_{\Delta BP}$ cycles, T_{PM} was found to increase in a fashion similar to the typical temperature trend ($+0.4^{\circ}\text{C}$, Fig. 4), thereby rejecting the possibility of increased muscular heat release during submergence. Thus the positive ΔT_{BP} occurring at depth most probably takes place if blood perfuses the brood patch at a higher rate, i.e., after vasodilation. In this particular situation, where heat loss is enhanced, birds clearly carry out an active and adjusted thermolytic process, in contradiction to the principle of heat conservation.

Body Temperatures During Prolonged Inactivity

King penguins at sea spent time resting at the surface between dive bouts (12). At that time, muscular activity was minimal, and maximum feather insulation minimized the chill effect of the T_a . When staying inactive in cold water, penguins showed a homogenization of body temperatures between deep and peripheral tissues, all stabilized at their highest level. Even supposing effective insulation at the sea surface, the energy expenditure [resting metabolic rate (RMR)] needed to maintain this high-temperature difference between the skin and water is presumed to be important. This assumption is supported by the fact that average heart rate (indicative of MR) (8, 41) measured during resting periods in the king penguin is significantly higher than average heart rate during dive bouts (22). Heat increment of feeding (HIF) has often been suggested as the explanation of high-energy expenditure and elevated body temperature during the interbout phases. However, the duration of interbout phases largely exceeds common duration of HIF (26, 30). This paradox in energetics (diving MR $<$ RMR) may also explain why T_{PM} when inactive at sea was higher than average T_{PM} brooding on shore. If energy demand for temperature maintenance was higher, the major organ of shivering thermogenesis would require a higher metabolic rate.

Brooding king penguins have to return to sea to replenish energy stores depleted by the previous fasting period in the colony (15). Our hypothesis is that the paradoxically high temperatures and energy expenditure observed in king penguins when inactive at sea may be the counterpart for the low temperature and/or insufficient blood perfusion that the subcutaneous adipose tissues undergo during diving activity (19). Indeed, the most important tissue for accumulation of energy stores in penguins is the subcutaneous fat layer (14). Our hypothesis is that extremely low temperatures or poor oxygen supply during diving activity make the use of metabolic pathways for energy storage (fatty acids) impossible. Consequently, high blood perfusion of the periphery would be the thermoregulatory cost a postabsorptive penguin has to face for the restoration of its body reserves (20).

To conclude, our aim was to examine body temperatures and underlying physiological adjustments, as a probable trade-off between foraging behavior and environmental constraints in relation to the acquisition/assimilation of body fuel. This study highlighted thermoregulatory strategies and revealed possible vascular adjustments that may occur in king penguins at sea.

We found that temperature decreases occur in deep hyperactive and in peripheral tissue only after a succession of deep dives. The fact that the thermogenic pectoral muscle also undergoes temperature reductions raises the question as to what extent the volume of the body and the organs are involved in temperature reductions (24). Importantly, this study suggests that the progressive cooling of the pectoral muscle and the brood patch is not the result of the single and passive effect of a constraining environment. Indeed, we hypothesize accurate regulation of body temperatures via adjusted peripheral heat loss through alternating episodes of heat conservation and thermolysis. Finally, our results give new insight into thermoregulatory strategies that may be encountered in other endotherms when facing the opposite constraints of high energetic costs while foraging and the replenishment of body stores.

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