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## DIVING PATTERN AND STOMACH TEMPERATURES OF FORAGING KING CORMORANTS AT SUBANTARCTIC MACQUARIE ISLAND<sup>1</sup>

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*Key words:* King Cormorant; diving; stomach temperature; food ingestion.

Logging stomach temperature in marine endotherms has enabled the determination of when and how much food has been ingested by free-ranging seabirds (Weimerskirch and Wilson 1992, Wilson et al. 1992, Grémillet and Plöts 1994, Pütz and Bost 1994). While considerable errors in mass estimates caused by factors such as position of the loggers and activity of the animal can occur using this technique, the timing of prey ingestion can generally be determined accurately (Wilson et al. 1995).

We simultaneously recorded the diving depth and stomach temperatures of free-ranging King Cormorants (*Phalacrocorax albiventer*) using micro data loggers with the goal of quantifying the variability between the top and bottom stomach temperatures and comparing methods to estimate meal mass in free-ranging seabirds. Here we report on the advantage of using two temperature sensors on the top and bottom of the loggers, and the problems in determining the feeding activities of seabirds from their stomach temperature.

### MATERIALS AND METHODS

The study was conducted at the Handspike Point colony on subantarctic Macquarie Island (54°30'S, 158°57'E) in January 1994. Two micro data loggers (0.5

Mbytes memory size, Little Leonardo Co. Ltd., Tokyo) were used for each bird: a time depth logger (TDL) and a stomach temperature logger (STL). The TDL had a cylindrical shape, 75 mm long and 19 mm in diameter, with a domed top and weighed 35 g including battery. It included a pressure sensor which measured depth with accuracy of 1.0 m and resolution of 0.1 m. The STL had a cylindrical shape, 90 mm long and 19 mm in diameter, with a domed top and bottom and weighed 35 g including battery. Single sensors at the top and bottom of the STL each measured temperature with an accuracy of 0.1°C. Both loggers were programmed to sample temperature or depth every 6 sec. TDLs were attached on the back of the King Cormorants with cable ties and quick-set epoxy glue. Birds were then induced to swallow STLs. Both TDLs and STLs were deployed on five breeding males that were then released at the colony. Three birds were recaptured after a single foraging trip and the loggers were successfully recovered. The other two birds returned to the colony without their STLs. We believe they were regurgitated earlier, and only their TDLs were recovered. At the time of retrieving the loggers, stomach regurgitations were collected; details of the collection and analysis of regurgitations are described in Kato et al. (1996).

Data from the loggers were downloaded onto computer for analysis. For each dive deeper than 1 m, maximum depth, duration, bottom time (time spent at depth greater than 85% of maximum dive depth), descent rate, ascent rate, and surface duration were determined. Stomach temperature drops often coincided with diving events (Fig. 1a). For each stomach temperature drop that exceeded 0.2°C (because the

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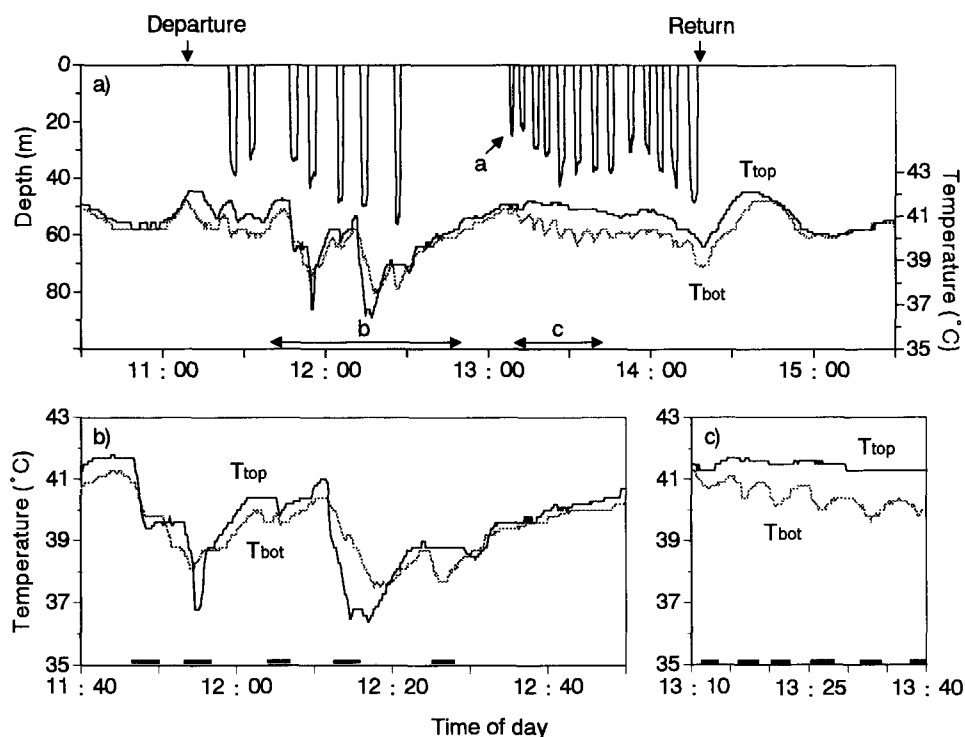


FIGURE 1. Example of diving record and top and bottom stomach temperature change ( $T_{top}$ ,  $T_{bot}$ ) of a male King Cormorant (#2) during one foraging trip between 11:10 and 14:20 on 11 January 1994 (a). Arrow a shows a bounce dive and other dives are bottom dives. Arrows b and c show the parts that are enlarged. Bars at the bottom of b and c indicate when the bird was diving.

accuracy of temperature sensor was  $\pm 0.1^{\circ}\text{C}$ ), the duration and extent of temperature decrease were measured, and the rate of temperature decrease was calculated. Statistical analyses were carried out using JMP statistical software (SAS Institute Inc.).

## RESULTS

The two birds that returned without STLs made only two or three shallow dives in 1–2.5 hr away from the colony. For the other three birds, 20–43 dives were

recorded by the TDLs during 3–5 hr foraging trips (Table 1). Typically the three birds descended rapidly to a depth where they remained for 53–66% of the dive duration (bottom time) and then ascended rapidly. The birds also made bounce dives without remaining at the bottom (Fig. 1a, arrow a). The first dive occurred 4–11 minutes after leaving the colony and the birds returned to the colony 5–46 minutes after the last dive.

Stomach temperatures fluctuated between  $36^{\circ}\text{C}$  and  $43^{\circ}\text{C}$ . Generally it decreased after birds started diving

TABLE 1. Dive depth, duration, bottom time, descent rate, ascent rate and surface duration of three male King Cormorants at Macquarie Island. Values are medians with ranges in parentheses.

Measurement	#1	#2	#3
Body mass (kg)	3.0	3.1	3.2
Trip duration (hr)	5.2	3.2	4.1
Time at nest (hr)	2.9	3.3	1.7
Number of dives	43	20	35
Dive depth (m)	27.1 (1.4–46.7)	37.8 (23.0–56.2)	39.3 (22.5–66.2)
Dive duration (sec)	90 (6–180)	146 (89–203)	150 (72–198)
Bottom time (sec)	48 (0–120)	96 (42–150)	96 (12–132)
Descent rate ( $\text{m sec}^{-1}$ )	1.1 (0.03–1.5)	1.7 (0.7–1.8)	1.3 (0.5–1.6)
Ascent rate ( $\text{m sec}^{-1}$ )	1.6 (0.3–2.0)	1.3 (0.6–1.4)	1.6 (0.4–1.8)
Surface duration (sec)	126 (6–3,130)	229 (109–2,413)	348 (144–1,512)

TABLE 2. Top and bottom stomach temperatures ( $T_{top}$ ,  $T_{bot}$ ) and the difference between them at the nest and during a foraging trip, the number of the precipitous temperature drops (exceeding  $0.1^{\circ}\text{C}/6$  sec), the number of fish and estimated individual fish mass in regurgitations of three male King Cormorants at Macquarie Island. Values of temperature are medians with ranges in parentheses. The differences between  $T_{top}$  and  $T_{bot}$ , and between at nest and during trip were examined by paired Wilcoxon signed rank test. Statistical significance is indicated by \* ( $P < 0.001$ ).

Measurement		#1	#2	#3
<b>Stomach temperature (<math>^{\circ}\text{C}</math>)</b>				
Nest	$T_{top}$	40.7 (40.2–41.7)	40.9 (39.6–43.0)	40.9 (40.0–42.8)
	$T_{bot}$	40.4 (40.0–41.3)	40.7 (38.8–42.1)	40.7 (39.9–42.6)
	$T_{top}$ vs. $T_{bot}$	*	*	*
Trip	$T_{top}$	41.2 (36.5–43.0)	41.0 (36.4–42.1)	40.4 (38.6–42.8)
	$T_{bot}$	40.3 (37.6–42.1)	40.2 (37.5–41.5)	40.3 (38.4–42.6)
	$T_{top}$ vs. $T_{bot}$	*	*	*
<b>Difference between <math>T_{top}</math> and <math>T_{bot}</math> (<math>^{\circ}\text{C}</math>)</b>				
Nest		0.3 (–0.4–0.7)	0.2 (–0.5–2.3)	0.2 (–0.4–0.5)
Trip		0.8 (–3.6–2.3)	0.6 (–2.7–1.6)	0.3 (–2.0–2.1)
	Nest vs. Trip	*	*	*
No. of precipitous temperature drops		4	4	5
No. of fish		2	10	4
Individual fish mass (g)		54, 18	21, 20, 13, 4, 4, 4, 4, 1, 1	48, 33, 22, 2

and then increased after a series of dives ended (Fig. 1a). The temperature tended to be higher at the top of the logger ( $T_{top}$ ) than at its bottom ( $T_{bot}$ ) (Table 2); this difference reversed when a steep temperature drop occurred (Fig. 1b). The difference between  $T_{top}$  and  $T_{bot}$  was greater during foraging trips than when the birds were at their nests (Table 2).

Stomach temperature drops exceeding  $0.2^{\circ}\text{C}$  coincided with dives on 40 of 98 dives for  $T_{top}$ , and on 63 of 98 dives for  $T_{bot}$  (Fig. 2).  $T_{bot}$  usually started to decrease after the birds started diving and before  $T_{top}$ . Most temperature decreases were extended temperature drops between  $0.2$  and  $1.5^{\circ}\text{C}$ , with rates between

$0.0$  and  $0.1^{\circ}\text{C}/6$  sec (Fig. 2). Precipitous temperature drops (decrease rates  $> 0.1^{\circ}\text{C}/6$  sec) were recorded during 13 dives with  $T_{top}$  and during 6 dives with  $T_{bot}$  (Fig. 2b).

Two to 10 bottom fish, *Paranotothenia magellanica* and *Harpagifer georgianus* with estimated mass of 1 to 54 g, were found in the regurgitated food (Table 2). The estimated total mass of food was 72–105 g.

DISCUSSION

There is evidence that the position of the temperature sensing device in the stomach affects the temperature measurement (Wilson et al. 1995). The position of the

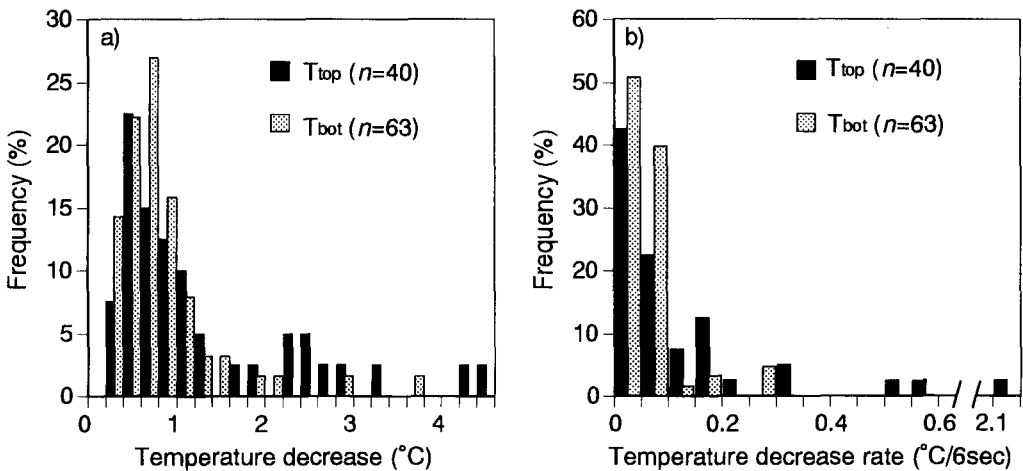


FIGURE 2. Frequency distributions of stomach temperature decrease exceeding  $0.2^{\circ}\text{C}$  and the temperature decrease rate of male King Cormorants. Data from three birds were combined.

device within the stomach of King Penguins (*Aptenodytes patagonicus*) was monitored using a x-ray, and did not change during simulated diving (Pütz and Bost 1994). Similarly, Grémillet and Plös (1994) reported that prey stuck to the bottom of the device and it did not change relative position in the stomach of Bank Cormorants (*Phalacrocorax neglectus*) during foraging trips. In our study, the temperature obtained by the top sensor was always higher than those obtained by the bottom sensor during both descent and ascent phases, suggesting that the logger did not reverse position in the stomach. Thus the top temperature sensor always stayed close to the entrance of the stomach and would be expected to react more sensitively to food ingestion than the bottom sensor. Precipitous temperature drops ( $>0.1^{\circ}\text{C}/6$  sec) were recorded more frequently by the top temperature sensors (Fig. 2) and were assumed to be associated with food ingestion.

The bottom temperature was lower than the top temperature and the extended temperature drops ( $\leq 0.1^{\circ}\text{C}/6$  sec) that coincided with dives were typically recorded by the bottom sensor before the top sensor (Fig. 1, Fig. 2b). These temperature drops were not assumed to have resulted from food ingestion. The top sensor stayed closer to the body core temperature, while the bottom sensor was closer to the body surface temperature. Bradycardia and body temperature decrease associated with dives are known for several species of marine mammals and birds (Jones and Larigakis 1988, Kooyman 1989). Extended temperature drops are assumed to reflect the change of the body temperature distribution which might be a physiological response to diving; it would correlate with redistribution of blood within the body (Jones et al. 1979). Body temperature of seabirds is dependent on activity (Wilson et al. 1992, Wilson et al. 1993, Grémillet and Plös 1994). The difference between the top and bottom of the temperature sensors was greater during foraging trips than when birds were at the nest, suggesting the body temperature distribution was influenced by the birds' activity. Furthermore, the body temperature of King Cormorants gradually decreased during a series of dives and started to increase at the end of the dives. Resting metabolic rate of Adélie Penguin (*Pygoscelis adeliae*) increased after the ingestion of cold food as the result of heating ingested food to body temperature within the stomach (Wilson and Culik 1991). Similarly, metabolic rate of King Cormorants is likely to increase during the period of stomach temperature increase after a series of dives.

To determine the number of food ingestion events from the stomach temperature record, temperature drops that resulted from food ingestion and those from diving activity need to be separated. Most temperature decrease rates were lower than  $0.1^{\circ}\text{C}/6$  sec for  $T_{\text{bot}}$  (Fig. 2b) and these extended temperature drops were assumed to be the result of diving activity rather than food ingestion, while precipitous temperature decreases ( $>0.1^{\circ}\text{C}/6$  sec) recorded with  $T_{\text{top}}$  could be taken as a food ingestion. But the number of food ingestion events recorded by the stomach sensor differed from the number of fish in the regurgitation (Table 2). Factors that could contribute to this difference are that the regurgitations are unlikely to contain all prey items caught during the previous foraging trip and that small prey items are less likely to induce stomach tempera-

ture drop because of their small heat capacity (they could be rapidly heated before reaching the stomach). Thus, small temperature drops associated with ingestion of small prey items would be difficult to separate from temperature drops resulting from diving activity. Temperature occasionally decreased stepwise and this could result either from serial ingestion of prey (Grémillet and Plös 1994) or from movement of prey in the stomach. Therefore temperature drops are not accurate even to determine the timing of food intake. Major prey size of male King Cormorants were 0–5 g and 15–25 g; although fish smaller than 15 g composed about 30% by number, small fish were not important prey because of their small mass (Kato et al. 1996). If a temperature decrease greater than  $0.1^{\circ}\text{C}/6$  sec was associated with ingestion of a fish larger than 15 g per dive, then King Cormorants successfully caught fish larger than 15 g on four or five dives, or 9.3–20% of the total number of dives (Table 2).

Logging stomach temperature in free-ranging seabirds has also been used to determine the mass of ingested prey (Weimerskirch and Wilson 1992, Wilson et al. 1992, Grémillet and Plös 1994, Pütz and Bost 1994). Mass estimation assumes a homogenous temperature in the stomach (Wilson et al. 1995) and is calculated from the integral of the curve below the asymptote (Wilson et al. 1992). In our study, the stomach temperature of King Cormorants differed between the top and bottom, which meant it was not homogenous. Stomach temperature drops were not always followed by exponential rise, and often the temperature did not rise to the initial level before the next dive (Fig. 1b). Furthermore, the fluctuation of the stomach temperature was too large to detect the start and end point of the temperature drops. In laboratory experiments, Wilson et al. (1995) noted that the lower regions of a simulated stomach were somewhat warmer than the upper regions when prey were serially ingested. The stomach temperature at the bottom was synchronous with those at the top in the early stage of foraging trips (Fig. 1a). However, food might stick to the bottom sensor later, making it less sensitive to temperature change. Grémillet and Plös (1994) reported that prey remained stuck to the bottom of the device in the pellet of Bank Cormorants after the experiment. Thus it is possible that even the top temperature sensor could become less sensitive after a certain amount of food had been ingested.

Although the concurrent recording of stomach temperatures and dive depth is a very useful method to determine feeding activities of seabirds, problems still exist in determining the timing of food ingestion and estimating the prey mass, especially for animals feeding on small prey items. Moreover, logging temperatures at both the top and bottom of the stomach helps to determine changes in stomach temperature that reflect either food intake or body temperature change. More research is needed to measure the temperature of other parts of the abdomen (not only the stomach), and to follow changes of body temperature distribution during various activities.

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## COLONIAL SEABIRD NESTING IN DENSE AND SMALL SUB-COLONIES: AN ADVANTAGE AGAINST AERIAL PREDATION<sup>1</sup>

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**Key words:** colony size; Audouin's Gull; *Larus audouinii*; Peregrine Falcon; *Falco peregrinus*; Ebro Delta; Spain.

Nesting in colonies is a form of social behavior in birds that is modified by adaptive pressures, with costs and benefits for the colony members (see review in Wittenberger and Hunt 1985). Seabirds have been widely studied to assess the importance of colony density on predation (Gotmark and Anderson 1984, Velarde 1992, Anderson and Hodum 1993). Lack (1968) asserted that breeding near conspecifics is a mode of nest defense in birds, and that the use of habitat may be influenced by potential predation risks (Wiens 1989). However, Anderson and Hodum (1993) stated that the importance of nesting near other birds for protection against predators is still not clear because results do not always agree. Moreover, the size of a colony is another factor

that could influence the distance between nests (e.g., Brown et al. 1990).

The predation behavior of Peregrines (*Falco peregrinus*) on breeding Audouin's Gulls (*Larus audouinii*) is examined here with respect to density and size of the different sub-colonies within a colony. Quantitative variation of the two factors are considered among the sub-colonies to test how they influence aerial predation by Peregrines.

#### STUDY AREA AND METHODS

The Audouin's Gull colony is located on the Punta de la Banya, Ebro Delta, NW Mediterranean (40°37'N, 00°35'E). This colony was established in 1981 and since then has grown dramatically, now holding about 70% of the total world population (Pedrocchi and Ruiz 1995). The habitat is a sandy, flat peninsula of 2,500 ha with small dunes covered by halophilous vegetation. Audouin's Gulls only breed on these dunes, although not all the dunes are occupied by breeding gulls. Each dune occupied by breeding Audouin's Gull was considered

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