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Changes in dive profiles as an indicator of feeding success in king and Adélie penguins

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Abstract

Determining when and how deep avian divers feed remains a challenge despite technical advances. Systems that record oesophageal temperature are able to determine rate of prey ingestion with a high level of accuracy but technical problems still remain to be solved. Here we examine the validity of using changes in depth profiles to infer feeding activity in free-ranging penguins, as more accessible proxies of their feeding success. We used oesophageal temperature loggers with fast temperature sensors, deployed in tandem with time-depth recorders, on king and Adélie penguins. In the king penguin, a high correspondence was found between the number of ingestions recorded per dive and the number of wiggles during the bottom and the ascent part of the dives. In the Adélie penguins, which feed on smaller prey, the number of large temperature drops was linearly related to the number of undulations per dive. The analysis of change in depth profiles from high-resolution time-depth recorders can provide key information to enhance the study of feeding rate and foraging success of these predators. Such potential is especially relevant in the context of using Southern marine top predators to study change in availability of marine resources.

Keywords: Bio-logging; Diving; Foraging; Penguins; Prey capture

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1. Introduction

Quantifying the ingestion rate and food consumption of diving birds at sea is of prime importance to understanding their foraging behaviour, their role in marine food webs, and their use as monitors of change in prey availability (Croxall and Lishman, 1987; Bost and Le Maho, 1993; Ropert-Coudert et al., 2001). Penguins are an important element in the Southern ocean food webs, where they represent up to 90% of the avian biomass (Woehler, 1995). However, considerable uncertainties exist about their annual prey consumption. In addition, penguins are remarkable models for theoretical studies of foraging (Wilson, 1995), but most of the predictions relating to their

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energy intake as a function of the time spent in a foraging patch still need to be tested (Charrassin et al., 2002). Determining how and when penguins feed indeed remains a challenge despite technical advances (see Ropert-Coudert and Wilson, 2005, for examples). Penguins forage at sea during trips extending from several hours to several weeks (Croxall and Davis, 1998). Deep dives, such as those undertaken by king penguins (*Aptenodytes patagonicus*), are associated with fluctuations in their abdominal temperature, which complicate the use of records of stomach temperature to detect ingestion events (Pütz and Bost, 1994; Handrich et al., 1997; Charrassin et al., 2001). Penguins usually feed on small, patchily distributed prey (Wilson, 1995). Thus, monitoring their ingestion rate and prey mass by recording drops of stomach temperature is less reliable than for other avian predators such as albatross feeding on large ectothermic prey (Weimerskirch et al., 1994). Finally since the stomachs of penguins fill up during periods of high feeding rate, the stomach sensor may be prevented from detecting additional ingestion of small prey (Wilson et al., 1995).

Recently, several ingenious and promising systems have been developed to tackle these problematic issues. To date, two types of systems are able to record rate of prey ingestion with a good level of accuracy. The first one involves recording oesophageal temperature. A fast response sensor in the upper oesophagus, linked to a data logger with a suitably fast recording rate, enables the ingestion of small prey (i.e. 0.4 g) to be detected (Ancel et al., 1997; Ropert-Coudert et al., 2001; Charrassin et al., 2001). The second system records beak-opening activity by the use of a Hall sensor glued to one mandible of the beak that senses the magnetic field produced by a magnet glued onto the other mandible (cf. Wilson et al., 2002a). The change in sensor voltage is proportional to the distance between the sensor and the magnet, which, with appropriate calibration, allows researchers to allude to the angle of beak opening. These changes are recorded in a data logger fitted to the back of the bird. Such a system enables the recording of a variety of activities that involve the opening of the mouth, i.e. breathing rate (Wilson et al., 2003), feeding activity (Wilson et al., 2002a; Takahashi et al., 2004a; Ropert-Coudert et al., 2004), calling, preening, etc. (Wilson et al., 2002a). These two systems offer considerable potential for inferring and quantifying the foraging success of penguins. However, results from field studies suggest that these technologies, including the methods for attaching them to the birds, still need substantial improvement before they can be routinely used to successfully obtain worthwhile data on prey ingestion. Additionally, a correct interpretation of the data as recorded by these systems necessitates rigorous calibration on captive individuals before deploying the loggers and sensors on free-ranging animals (Ropert-Coudert et al., 2000a; Charrassin et al., 2001; Wilson et al., 2002a; Takahashi et al., 2004a). Because of the difficulties associated with using these systems in the wild, there is considerable interest in more accessible proxies of feeding success and prey distribution, such as, for instance, changes in the profiles of diving (Takahashi et al., 2004a), speed (Ropert-Coudert et al., 2000b, 2001) and/or acceleration (Ropert-Coudert et al., 2006). In these approaches, the feeding recorder systems described above were deployed on birds in tandem with conventional time-depth or speed recorders.

In the present paper, we examine the reliability of using changes in depth profile (wiggles) to infer feeding activity in free-ranging penguins. For this purpose, we used the data obtained from dive profiles and oesophageal temperature recorders, sampled at high frequency in king and Adélie penguins (*Pygoscelis adeliae*). Additional swimming speed data obtained in relation to dive depth in the Adélie penguin also were considered. These two penguin species employ different foraging behaviours when feeding on distinct prey types and sizes. These data allowed us to better test the reliability of the approach along with its limitations.

2. Study models and methods

2.1. King penguin

King penguins are pelagic foragers that feed mostly during the day on myctophid fish (Cherel and Ridoux, 1992; Bost et al., 1997, 2002). These small pelagic fish usually occur in dense monospecific shoals (Hulley, 1981; Zasel'sliy et al., 1985) and are patchily distributed deep within the water column (Perissinotto and Mc Quaid, 1992). The field study was carried out during the summer 2002/2003 at La Grande manchotière colony (30,000 pairs), Possession Island (46.42°S, 51.86°E), Crozet archipelago, south Indian Ocean. Seven brooding king penguins leaving their colony to forage at sea were instrumented with an oesophageal temperature recorder and a time-depth recorder. The fast-response temperature sensor was surgically implanted under anaesthesia in the lumen of the oesophagus (Charrassin et al., 2001). Multi-channel behavioural data loggers (64 Mb, 1 Hz recording frequency, 12 bit resolution) were implanted into the abdomen and the cables linking the temperature sensor to the logger were tunnelled under the skin. Oesophageal temperature and depth were recorded with a resolution of 0.01 °C and 0.1 m, respectively. Experiments on captive birds showed that the use of a fast-response temperature sensor was sensitive enough to allow detection of prey smaller than the smallest fish usually caught by the free-ranging penguins (1.8 g) (Charrassin et al., 2001).

All the instrumented penguins were released in good condition and recaptured at the colony after one foraging trip that lasted between 12 and 23 days. Three complete records of foraging trips were obtained after the removal of the equipment (Table 1). Most of the technical failures were the result of broken cables, probably caused when the penguins extended the neck. All the birds continued to breed after the removal of the equipment.

2.2. *Adélie penguin*

Adélie penguins are Antarctic foragers. Their diving activity depends to a large extent on sea-ice conditions and they perform both benthic and/or pelagic dives. These medium sized penguins target small prey, such as krill (*Euphausia superba*, *E. chrystallorophias*) and occasionally small fish (Ridoux and Offredo, 1989; Ropert-Coudert et al., 2002). Sixteen penguins breeding in Adélie Land (66.7°S, 140.0°E) were instrumented with two different data-loggers, one device recording swimming speed and depth, and a second device recording oesophageal temperature only. Detailed information about instruments, and deployments are given in Ropert-Coudert et al. (2000a; 2001). Briefly, depth and swimming speed were measured every second with a 3-channel UWE-PDT logger (Little Leonardo, Tokyo, Japan). These loggers recorded data with 12 bit resolution and had 16 Mb of memory. The speed and depth logger were attached to the back of brooding birds departing to sea for a single foraging trip. The body of the oesophagus logger (12 bit resolution, 68 × 15 mm cylinder, 30 g in weight, 1 Hz recording frequency) was placed in the stomach of birds by gently inducing each bird to swallow the logger. The cable emerging from the head of the logger was attached to a multi-stranded thread, which was long enough to emerge from the mouth of the penguin. The thread was then glued on the feathers of the back of the head so that the temperature sensor at the end of the cable was held suspended in the oesophagus lumen. Quantitative data were available from three birds still carrying the oesophageal temperature recorder and speed–depth data logger upon their return to the colony (Table 2).

Experiments on hand-fed, captive birds, as well as feeding experiments conducted in aquariums, indicated that ingestion of the dominant prey species of Adélie (i.e. *E. superba*, 0.8–1.5 g mean mass) were likely to be detected reliably (Ropert-Coudert et al., 2000a). Overall the detection rate of ingestion among captive birds was high (70%) for isolated prey weighing >0.4 g. This detection rate became lower for smaller items and when prey were ingested sequentially at a high frequency.

2.3. *Data analysis*

In both penguin species, wiggles were defined as deviations >2 m of depth with a vertical speed getting through 0. The bottom phase was defined as

Table 1
Characteristics of feeding dives reported from three complete records obtained for king penguins, Possession Island, summer 2003

	Trip duration (d)	Number of foraging dives	Maximal depth (m)	Mean maximal depth (m)	Total number of temperature drops	Total number of feeding events	Total number of wiggles		Maximal number of feeds per dive
							Bottom	Ascent	
Bird 1	22.4	1914	261	131.7±42.5	7436	6953	3257	3139	15
Bird 2	12.2	1189	255	134.6±35.8	6122	5520	2680	1944	15
Bird 3	23.1	1676	227	113.5±38.5	7661	6879	3073	3280	12

Table 2
General information on the foraging trip, dives and oesophageal temperature for three equipped Adélie penguins, Dumont D'Urville summer 1997

	Parameters	Bird 24	Bird 28	Bird 07
Trip	Time spent at sea (h)	15	29	22
Dive	Total number of dives	400	947	877
	Maximal depth (m)	93.2	67.0	58.4
	Mean maximal depth (m)	23.9±26.6	24.8±31.1	18.3±22.3
Oesophagus temperature	Basal temperature[a] (°C)	38.3±0.4	39.8±1.1	37.8±1.1
	Total number of drops	269	565	548
	Number of drops per hour	22.1±37.8	22.6±28.7	19.5±24.0
	Minimal temperature (°C)	22.7	18.7	10.2

[a] Temperature recorded before the departure to sea.

the time between the first and last points below 90% of maximum depth, and as the time elapsed between the first and last wiggle in a dive for king and Adélie, respectively. In king penguins, temperature drops in the oesophagus were considered to correspond to a prey ingestion when the temperature decreased by $\geqslant 0.06\,^{\circ}\mathrm{C\,s^{-1}}$ (for details see Charrassin et al., 2001). In Adélie penguins, a mathematical method was applied to detect outliers in the distribution of the temperature drops (cf. Ropert-Coudert et al., 2000a for details).

Data were analysed using Jensen System Software programs (Laboe, Germany), custom-made Matlab (Mathworks Inc., Natick, MA, USA) and Igor (Wavemetrics, Oregon, USA) programs. Statistics analysis was performed using Systat (9.0 @, SPSS, Chicago) and StatView (Abacus concepts, USA, version 4.57, 1996). For all statistical tests, the significance threshold was taken to be $P<0.05$.

3. Results and discussion

3.1. King penguins

As seen in Fig. 1, '*V*' *dives* are symmetrical dives, with no bottom phase. Few or no feeding events are associated with these dives (as indicated by the absence of steep accelerations or 'dashes' *sensu* Ropert-Coudert et al., 2000b), which is in agreement with previous suggestions that these are exploratory dives rather than feeding dives (Wilson, 1995; Ropert-Coudert et al., 2000b; Pütz and Cherel, 2005).

'*U*' *dives* are deep dives that include a short bottom phase without wiggles. The oesophageal records indicate that U dives were also associated with very low feeding events (2.7% of U dives included ingestions). Feeding occurred mostly during '*ragged bottom dives*', which are symmetrical dives with several wiggles at the bottom showing both ascent and descent segments (76.9% of ingestions occur during such dives). Additionally some ingestions were observed during '*asymmetrical plateau dives*' (10.3% of ingestions), in which depth remained fairly constant during a portion of the ascending phase (Ropert-Coudert et al., 2000b). The significance of this last category of dives has not yet been elucidated. The plateau period may correspond to the pursuit of prey detected during the beginning of the ascent part of the dive. Finally, '*asymmetrical ragged dives*' are characterised by a distinct descent phase and a ragged ascent phase with wiggles (10.0% of the ingestions). Overall, most of the dives with wiggles (84.7%) are successful dives with one or more prey ingested regardless of the type of dive.

Data obtained previously with swim speed recorders on king penguins suggested that wiggles are associated with intensive prey pursuits, with a gradual increase in the number of steep events ('dashes') from 'U' dives to 'ragged bottom' dives (Ropert-Coudert et al., 2000b). In the present study, the analysis of simultaneous dive and oesophageal temperature records demonstrates that the number of ingestions recorded per dive (i.e. the feeding success) was significantly related to the number of wiggles occurring during the bottom and the ascent part of the dives (Fig. 2). A high correspondence was found for bird 2 and bird 3 with a slope of the regression line close to 1 and a intercept close to

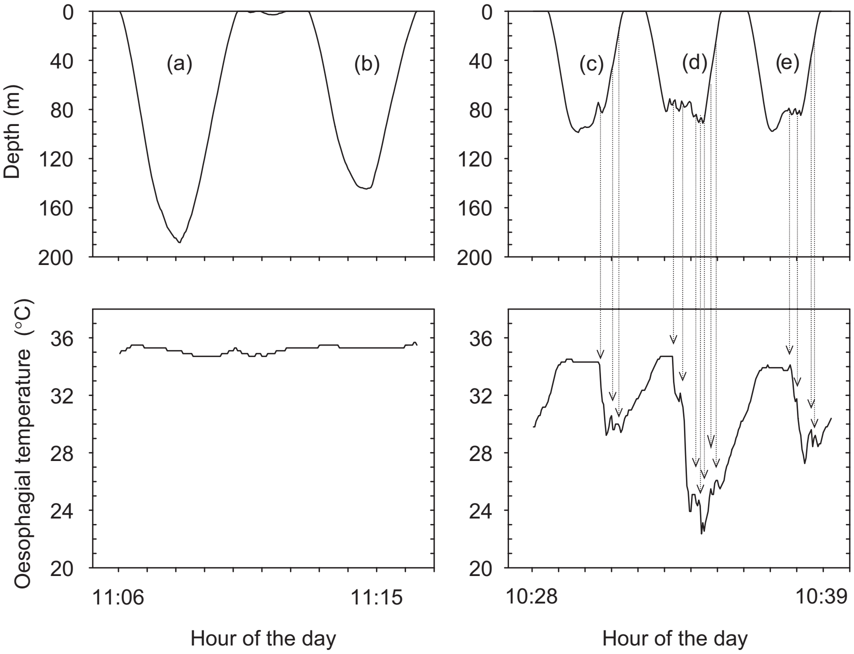

Fig. 1. Changes in ingestion rate from oesophageal temperature records in a free-ranging king penguin in relation to different dive profiles. The arrows indicate the occurrence of ingestion events. See Section 3.1. for details concerning the characteristics of the dives profiles. a: 'V' dive; b: 'U' dive; c: 'asymmetrical ragged' dive; d: 'ragged bottom' dive; e: 'asymmetrical plateau' dive.

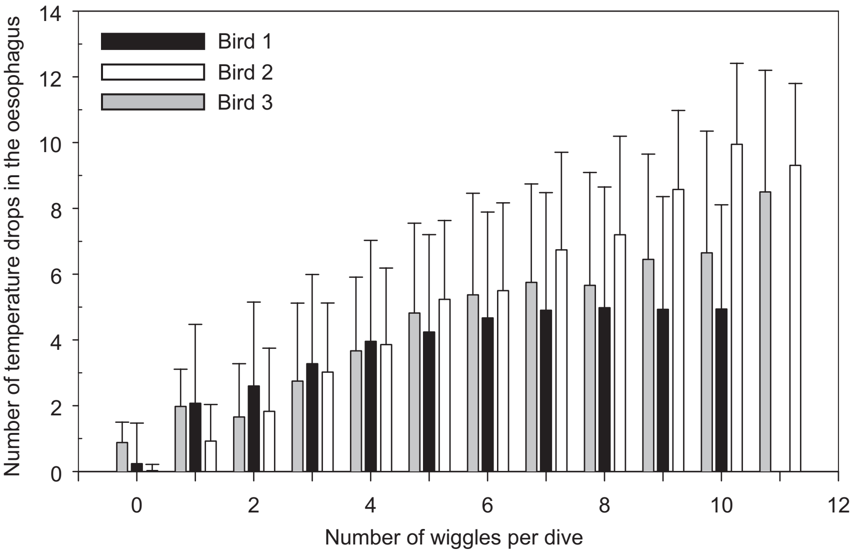

Fig. 2. Mean number of feeding events (*Nf*) per dive (with SD) in relation to the mean number of wiggles (*W*) per foraging dive for three king penguins. The best fit regressions are as follows: *All wiggles per dive considered*: Bird 1: $Nf = 0.68^{*}\ W+0.41$, $R^2 = 0.36$, $F_1 = 3523$, $P<0.001$; Bird 2: $Nf = 0.94^{*}\ W+0.03$, $R^2 = 0.76$, $F_1 = 14273$, $P<0.001$; Bird 3: $Nf = 0.77^{*}\ W+0.12$, $R^2 = 0.62$, $F_1 = 15481$, $P<0.001$; combined data: $Nf = 0.79\ W+0.18$, $R^2 = 0.58$, $F_2 = 26729$, $P<0.0001$. *Dives including 0–6 wiggles*: Bird 1: $Nf = 0.84^{*}\ W^{*}0.77+0.33$, $R^2 = 0.48$, $F_1 = 3253$, $P<0.001$; Bird 2: $Nf = 0.96^{*}\ W^{*}0.686+0.41$, $R^2 = 0.71$, $F_1 = 10100$, $P<0.001$; Bird 3: $Nf = 0.90^{*}\ W+0.08$, $R^2 = 0.58$, $F_1 = 12287$, $P<0.001$.

zero for bird 2. The slopes of the regression lines for bird 2 and bird 3 were, however, significantly different (ANCOVA $F_1 = 240.9$, $P<0.0001$). Bird 1 had a feeding rate quite different from that of the other birds. For this bird, a clear correspondence between wiggles and ingestions was observed from zero wiggles to a mean value of 6 wiggles per dive; however, beyond this value the mean number of ingestion per dive remained constant as the number of wiggles increased (Fig. 2).

3.2. Adélie penguins

During diving, most of the temperature drops in the oesophagus clearly occurred when the birds were close to their maximal depth and during an undulatory phase that corresponds to about 90% of the maximum depth of the dive. Overall, there was a significant ($F_{1,396} = 141.1$, $P<0.001$), positive, linear relationship between the number of wiggles recorded during the dive and the number of temperature drops but the coefficient of determination explained only 26% of the variability in the relationship. On a bird-by-bird basis, the relationships were all significant and the coefficient of determination ranged from 0.09 to 0.29 (Fig. 3). The mean swimming speed during the undulatory phase of feeding dives was lower ($1.7\,\mathrm{m\,s^{-1}}$) than during the ascent and descent phases ($2.03\,\mathrm{m\,s^{-1}}$), indicating that Adélies penguins reduce their swimming speeds once a patch has been detected. The abrupt deceleration occurs when the penguins perform their first undulation. Thereafter, there are rapid accelerations and decelerations during the remainder of the undulatory phase (Ropert-Coudert et al., 2001). The low swimming speed at the undulatory phase, which contrasts to the steep acceleration events (‘dash events’) recorded in king penguins (Ropert-Coudert et al., 2000b), may correspond to the catching and processing of numerous small prey (cf. Wilson et al., 2002b) that display escape speeds much lower than the hunting speed of Adélie penguins (Kanda et al., 1982).

4. Conclusion

We believe that the analysis of the change in depth profile is a simple yet powerful tool to quantify the feeding success at depth by at least some species of pelagic penguin. Overall, a strong linear relationship was found between the mean number of wiggles per dive and the mean number of ingestions of king penguins, although there were also substantial variations unaccounted for, within as well as between individual penguins. In contrast, the relationships were weak in the case of Adélie penguins feeding on slow-moving prey. The feeding technique of Adélie penguins implies that a large number of prey items are ingested per dive. Prey may be gathered in the mouth before being swallowed (cf. Ropert-Coudert et al., 2000a), thus preventing the detection of single ingestion events

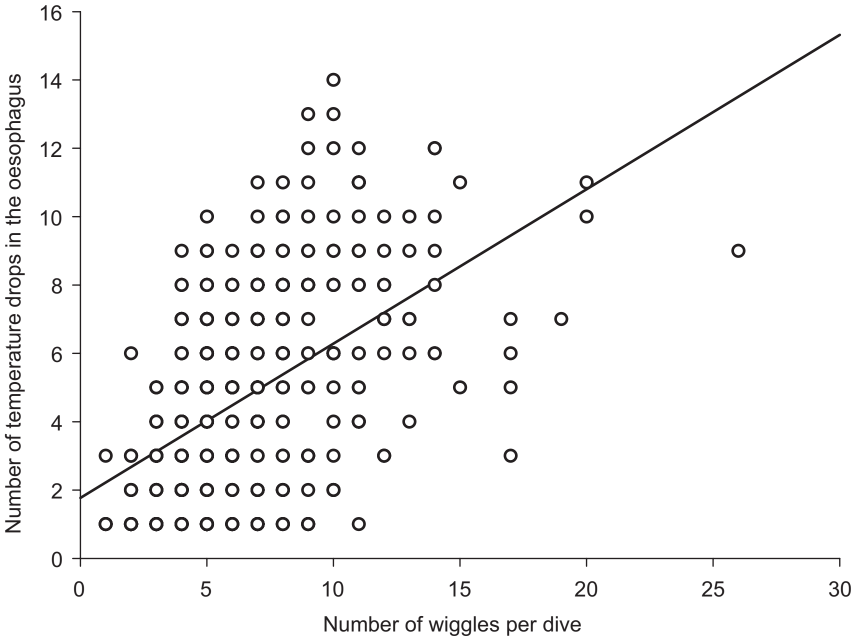

Fig. 3. Relationship between the number of wiggles per dives and the ingestions recorded by the oesophageal temperature recorder in the Adélie penguin ($n = 3$ birds). Number of temperature drops = 0.45 * number of wiggles + 1.77, $R^2 = 0.26$, $F_2 = 141.07$, $P<0.001$.

by the oesophagus temperature sensor. If this is so, the number of wiggles may be greater than the number of detected events. Besides the limitations due to the hunting strategies of penguins, technical limitations also may have prevented the accurate detection of change in depth profiles and high feeding rates. The 2 m amplitude used to define wiggles may miss some small pursuit attempts at depth. High feeding success may be underestimated because of the thermal inertia of the oesophageal temperature sensor.

Nonetheless, wiggles recorded in a dive appear as reliable proxies of feeding success even in penguins eating small prey, as a preliminary study on a krill-eating chinstrap penguin (*Pygoscelis antarctica*) suggested (Takahashi et al., 2004a). The chinstrap penguin studied here was simultaneously instrumented with a beak-angle recorder and a time-depth recorder. The good correspondence between prey ingestion and wiggles also may be due to the fact that beak-angle data recorders provide a more accurate picture of the number of small prey ingested over time (as each beak opening corresponds to one ingestion).

Importantly, the analyses of change in depth profiles of diving penguins can provide key information about their foraging success at different depths. Such analysis can be performed at spatial scales intermediate to those of a single dive and entire trips to sea. This would be particularly relevant when using marine top predators to study changes in availability of marine resources (Reid and Croxall, 2001). However, generalising this approach to other penguin species requires extensive studies to be undertaken both in captivity and in the field. This has to be done using suitable feeding recorders together with depth/speed recorders at a relevant sampling frequency. It has been shown, for instance, that hunting speeds vary between penguin species and appear to be linked to prey escape speed and optimum rate of prey-processing (Wilson et al., 2002b). Similarly, acceleration signals can be recorded many times per second allowing for a fine-scale analysis of prey pursuit (Ropert-Coudert et al., 2006). Future studies should examine the possibility of employing such indices to accurately quantify the behaviours relating to foraging success per dive in penguins. In this regard, the recent development of miniaturised cameras and still-pictures loggers (e.g., Takahashi et al., 2004b) appear particularly promising in determining the foraging behaviour of these fascinating deep divers.

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References

Ancel, A., Horning, M., Kooyman, G.L., 1997. Prey ingestion revealed by oesophagus and stomach temperature recordings in cormorants. Journal of Experimental Biology 200, 149–154.

Bost, C.A., Le Maho, Y., 1993. Seabirds as bio-indicators of changing marine ecosystems: new perspectives. Acta Oecologica 14, 463–470.

Bost, C.A., Georges, J.Y., Guinet, C., Cherel, Y., Pütz, K., Charrassin, J.B., Handrich, Y., Zorn, T., Lage, J., Le Maho, Y., 1997. Foraging habitat and food intake of satellite tracked king penguins during the austral summer at Crozet archipelago. Marine Ecology Progress Series 150, 21–33.

Bost, C.A., Zorn, T., Le Maho, Y., Duhamel, G., 2002. Feeding of diving predators and diel vertical migration of prey: King penguins' diet versus trawl sampling at Kerguelen islands. Marine Ecology Progress Series 227, 51–62.

Charrassin, J.B., Kato, A., Handrich, Y., Sato, K., Naito, Y., Ancel, A., Bost, C.A., Gauthier-Clerc, M., Ropert-Coudert, Y., Le Maho, Y., 2001. Feeding behaviour of free-ranging penguins determined by oesophageal temperature. Proceedings of the Royal Society of London B 268, 151–157.

Charrassin, J.B., Le Maho, Y., Bost, C.A., 2002. Seasonal changes in the diving parameters of king penguins. Marine Biology 141, 581–589.

Cherel, Y., Ridoux, V., 1992. Prey species and nutritive value of food fed during summer to king Penguin (*Aptenodytes patagonica*) chicks at Possession Island, Crozet Archipelago. Ibis 134, 118–127.

Croxall, J.P., Davis, L.S., 1998. Penguins: paradoxes and patterns. Marine Ornithology 26, 1–12.

Croxall, J.P., Lishman, G.S., 1987. The food and feeding ecology of penguins. In: Croxall, J.P. (Ed.), Seabirds Feeding Ecology and Role in Marine Ecosystems. Cambridge University Press, Cambridge, pp. 101–131.

Handrich, Y., Bevan, R., Charrassin, J.-B., Butler, P.J., Pütz, K., Lage, J., Woakes, A., Le Maho, Y., 1997. Hypothermia in foraging king penguin. Nature 388, 64–67.

Hulley, P.A., 1981. Results of the research cruises of FRV "Wather Herwig" to South America. LVIII. Family Myctophidae (Osteichtyes, Myctophiformes). Archiv für Fishereiwissenschaft 31 (1).

Kanda, K., Takagi, K., Seki, Y., 1982. Movement of the larger swarms of Antarctic krill (*Euphausia superba*) off Enderby Land during the 1976–77 season. Journal of Tokyo University on Fish 68, 24–42.

Perissinotto, R., Mc Quaid, C.D., 1992. Land-based predator impact on vertically migrating zooplankton and micronekton advected to a Southern Ocean archipelago. Marine Ecology Progress Series 80, 15–27.

Pütz, K., Bost, C.A., 1994. Feeding behavior of free-ranging king penguins (*Aptenodytes patagonicus*). Ecology 75, 489–497.

Pütz, K., Cherel, Y., 2005. The diving behaviour of brooding king penguins (*Aptenodytes patagonicus*) from the Falkland Islands: variation in dive profiles and synchronous underwater swimming provide new insights into their foraging strategies. Marine Biology 147, 281–290.

Reid, K., Croxall, J.P., 2001. Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. Proceedings of the Royal Society of London B 268, 377–384.

Ridoux, V., Offredo, C., 1989. The diets of five summer breeding seabirds in Adélie Land, Antarctica. Polar Biology 9, 137–145.

Ropert-Coudert, Y., Wilson, R.P., 2005. Trends and perspectives in animal-attached remote-sensing. Frontiers in Ecology and the Environment 3 (8), 437–444.

Ropert-Coudert, Y., Baudat, J., Kurita, M., Bost, C.A., Kato, K., Le Maho, Y., Naito, Y., 2000a. Validation of oesophagus temperature recording for detection of prey ingestion on captive Adélie penguins (*Pygoscelis adeliae*). Marine Biology 137, 1105–1110.

Ropert-Coudert, Y., Sato, K., Kato, A., Charrassin, J.B., Bost, C.A., Le Maho, Y., Naito, Y., 2000b. Preliminary investigations of prey pursuit and capture by king penguins at sea. Polar Bioscience 13, 101–112.

Ropert-Coudert, Y., Kato, A., Baudat, J., Bost, C.A., Le Maho, Y., Naito, Y., 2001. Feeding strategies of free-ranging Adélie penguins (*Pygoscelis adeliae*) analysed by multiple data recording. Polar Biology 24, 460–466.

Ropert-Coudert, Y., Kato, A., Bost, C.A., Rodary, D., Sato, K., Le Maho, Y., Naito, Y., 2002. Do Adélie penguins modify their foraging behaviour in pursuit of different prey? Marine Biology 140, 647–652.

Ropert-Coudert, Y., Kato, A., Liebsch, N., Wilson, R.P., Müller, G., Baubet, E., 2004. Monitoring jaw movement: a cue to feeding activity? Game & Wildlife Science 21, 1–19.

Ropert-Coudert, Y., Kato, A., Wilson, R.P., Cannell, B., 2006. Foraging strategies and prey encounter rate of free-ranging Little Penguins. Marine Biology 149, 139–148.

Takahashi, A., Dunn, M.J., Trathan, P.N., Croxall, J.P., Wilson, R.P., Sato, K., Naito, Y., 2004a. Krill-eating behaviour in a chinstrap penguin (*Pygoscelis Antarctica*) compared with fish-eating in magellanic penguins (*Spheniscus magellanicus*): a pilot study. Marine Ornithology 32, 7–54.

Takahashi, A., Sato, K., Naito, Y., Dunn, M., Trathan, P.N., Croxall, J.P., 2004b. Penguin-mounted cameras glimpse underwater group behaviour. Proceedings of the Royal Society of London B 271, S281–S282.

Weimerskirch, H., Doncaster, C.P., Cuénot-Chaillet, F., 1994. Pelagic seabirds and the marine environment: foraging patterns of wandering albatrosses in relation to prey availability and distribution. Proceedings of the Royal Society of London B 255, 91–97.

Wilson, R.P., 1995. Foraging ecology. In: Williams, T.D. (Ed.), The Penguins. Oxford University Press, Oxford, pp. 81–106.

Wilson, R.P., Pütz, K., Grémillet, D., Culik, B., Kierspel, M., Regel, J., Bost, C.A., Lage, J., Cooper, J., 1995. Reliability of stomach temperature changes in determining feeding characteristics of seabirds. Journal of Experimental Biology 198, 1115–1135.

Wilson, R.P., Steinfurth, A., Ropert-Coudert, Y., Kato, A., Kurita, M., 2002a. Lip-reading in remote subjects: an attempt to quantify and separate ingestion, breathing, and vocalisation in free-living animals. Marine Biology 140, 17–27.

Wilson, R.P., Ropert-Coudert, Y., Kato, A., 2002b. Rush and grab strategies in foraging marine endotherms: the case for haste in penguins? Animal Behaviour 63, 85–95.

Wilson, R.P., Simeone, A., Luna-Jorquera, G., Steinfurth, A., Jackson, S., Fahlman, A., 2003. Patterns of respiration in diving penguins: is the last gasp based on an inspired tactic? Journal of Experimental Biology 206, 1751–1763.

Woehler, E.J., 1995. Consumption of Southern Ocean resources by penguins. In: Dann, P., Norman, I., Reilly, P. (Eds.), The Penguins: Ecology and Management. Surrey Beatty and Sons, Chipping Norton, Australia, pp. 267–291.

Zasel'sliy, V.S., Kudrin, B.D., Poletayev, V.A., Chechenin, S.C., 1985. Some features of the biology of *Electrona carlsbergi* (Tanning) (Myctophidae) in the Atlantic sector of the Antarctic. Journal of Ichtyology 25, 163–166.