

Polar Biosci., 13, 101–112, 2000

Preliminary investigations of prey pursuit and capture by king penguins at sea

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Abstract: Prey pursuit and capture by king penguins (*Aptenodytes patagonicus*) were investigated with multiple data recorders in the Crozet Archipelago during the 1995/96 austral summer. Birds were fitted with a swim speed and depth data logger that sampled every second making possible fine-scale analyses of underwater behavior. Data were obtained for two birds for periods of 2.5 and 2.9 days, respectively. During each dive deeper than 30 m, the swimming speed was constant at around 2 m/s, defined as “cruising” speed. However, steep acceleration events (“dashes”) were observed. These dashes occurred in “U”, “W” and “Plateau” shaped dives. Based on their shape, these dashes were separated into “Rushes” (28% of all dash events) where penguins moved upward and increased their speed from the cruising speed; “Adjusts” (59%) where penguins swam also upward and increased their speed to return to cruising speed after a short slow-down, and “Intermediates” (13%) which were “Adjusts” events that briefly overshot the cruising speed. “Rushes” mainly occurred at the bottom phase of deep dives. They were followed by other dash events in 80% of cases. Moreover, “Rushes” lasted longer and the distance traveled during them was bigger compared to other dash events. “Adjusts” events were observed at the bottom phase and early part of the ascent phase. They were single events within a dive in 50% of cases. These results suggested that dashes, especially “Rushes” may be the main pursuit and capturing behavior performed by king penguins on patchily distributed preys in water deeper than 100 m.

key words: king penguin, Crozet Archipelago, data loggers, swimming speed, prey capture

Introduction

To detect and possibly analyze the global changes affecting the fragile polar ecosystem, the feeding and foraging behavior of marine mammals and seabirds exploiting it have to be perfectly known (Furness, 1978; Croxall *et al.*, 1985; Furness and Nettleship, 1990). The capturing behavior of prey is one important component of this foraging behavior but it remains poorly understood.

Among the key predators in sub-Antarctic, the king penguins (*Aptenodytes*

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patagonicus), one of the largest consumers of myctophid fish in the Southern Ocean (Cherel and Ridoux, 1992), cover up to 500 km in summer to reach the sub-Antarctic front, zones of maximum prey abundance (Bost *et al.*, 1997; Guinet *et al.*, 1997; Jouventin *et al.*, 1994). There, they exploit a large part of the water column, diving repeatedly to depths greater than 100 m during the day (Charrassin *et al.*, 1998). As direct observation of this foraging behavior is impossible, various types of time-series micro-recorders have been developed (Le Maho, 1994; Naito, 1997). General information about the location of feeding zones or the amount of prey ingested and approximate time of prey ingestion has been collected using satellite telemetry (Bost *et al.*, 1997) and stomach temperature recorders (Pütz and Bost, 1994; Wilson *et al.*, 1992, 1995), respectively.

New studies should focus on fine scale behavior and more complex interaction between the predator and its prey. Indeed, little is known about how king penguins locate and capture their main prey, myctophids fish (Cherel and Ridoux, 1992) in the dark deep-sea environment. Penguins are assumed to rely mainly on vision for hunting, based on anatomical studies (Sivak, 1976; Howland and Sivak, 1984; Martin and Young, 1984; Bowmaker and Martin, 1985; Suburo and Scolaro, 1988; Suburo *et al.*, 1991) and to a less extent, behavioral studies (Cannell and Cullen, 1998). Although, at first sight, the light level might be too low for detecting prey visually, king penguins still seem to be able to capture prey at high rates (Pütz and Bost, 1994). To investigate the detection, approach and capturing behavior performed by this bird, fine-scale multiple data recording was needed. Thanks to constant technological progress, it has become possible to increase the memory capacity of loggers and the number of parameters recorded.

In the present study, depth utilization and swimming speeds were sampled on free-ranging king penguins at a high sampling rate in order to determine accurately the birds' fine-scale underwater swimming and hunting behavior. Using these data, preliminary assumptions on the mechanisms of pursuit and capture of prey by king penguins are discussed.

Materials and methods

The study was conducted at a king penguin colony of approximately 45000 breeding pairs (Weimerskirch *et al.*, 1992), located in *La Baie Du Marin*, Possession Island, Crozet Archipelago (46° 25'S; 51° 45'E) from February to March 1996.

Five breeding king penguins were equipped with depth and swim speed data loggers (KS-400PDT, Little Leonard, Tokyo, Japan). These cylinder-shaped recorders measured 25 mm (32 mm at the thickest part of the recorder) in diameter for a total length of 110 mm and weighed around 81.5 g. The depth and swim speed data were recorded every second. The depth resolution of the recorders was 0.1 m between depths of 0 to 400 m. Speed was calculated from the number of revolutions of a propeller per second, which was converted into flow speed (m/s) using a regression line obtained by calibration experiments. These calibration experiments were made *in situ* by pulling the recorder in the water over a known distance at three different speeds using an electric fishing reel. The revolutions per distance relationship was linear at tow speeds of 0.3 to

2.5 m/s with the coefficient of determination for each recorder being greater than 0.98. To confirm these results, the methods of Fletcher *et al.* (1993) and Blackwell *et al.* (1999) were used.

The birds were captured as they departed the colony to go to sea. Each bird was weighed prior to being equipped with a recorder. The devices were fixed on the bird's back in a median position along the axis of the vertebral column, using TESA tape and cable ties to limit the impact of the attachment on the feathers (Wilson *et al.*, 1997). Penguins were individually recognized by a colored band of TESA tape on their flipper. While the adults were at sea, the presence or absence of their mates in the colony and the status of their chicks were checked every day. After their return from one foraging trip, the equipped birds were captured and the recorders were retrieved. The data were downloaded to a computer and analyzed using appropriate software (IGOR, Wavemetrics, U.S.A.).

Previous studies indicated that 83% of the fishing behavior of king penguins occurs during deep dives (Pütz and Bost, 1994). A bimodal distribution of the maximum depth frequencies is classically observed in king penguins and is used to separate shallow from deep dives (Kooyman *et al.*, 1992). Consequently, further analysis was performed only on dives to depths >30 m, this value representing the trough in the bimodal distribution of the maximum depth frequencies.

During the analysis, the role of dives classically judged from their shape or profile (Wilson, 1990, 1995) was used. This criterion separates the dives into three categories: "U" and "V" shaped (spike) dives that may be exploratory dives (Wilson, 1995; Kooyman *et al.*, 1992) and "W" shaped dives characterized by depth oscillations or "wiggles" occurring around the maximum depth, which are assumed to be associated with feeding activity (Wilson, 1990, 1995). In the present analysis, the "W" shape dives were defined as those with wiggles ≥ 2 m.

Bottom times, the times spent at depths $>90\%$ of the maximum depth of each dive, were calculated to provide estimates of hunting time (Kirkwood and Robertson, 1997). An assumption in the parameter is that prey are most likely to be found at or near the maximum depth of each dive. Finally, the statistical threshold was fixed at the 5% level.

Results

Two of the five devices deployed were recovered with reliable data, on birds PF141 and PF161. The high frequency of sampling and the limited data storage capacity in the devices restrained the duration of the recording periods to 2.9 days (19–22 February) and 2.5 days (16–19 February) for birds PF141 and PF161 respectively. These sample periods occurred early in the foraging trips. Trip spans were February 14th to March 4th and February 16th to March 13th for the respective birds. Nevertheless, 262 and 156 dives deeper than 30 m were recorded for birds PF141 and PF161 respectively. The average maximum depths of dives were 125 ± 53 m for PF141 and 169 ± 59 m for PF161.

During each deep dive, the speed increased rapidly from 0 m/s when at surface to a constant value of approximately 2 m/s, defined hereafter as "cruising speed" (Fig. 1,

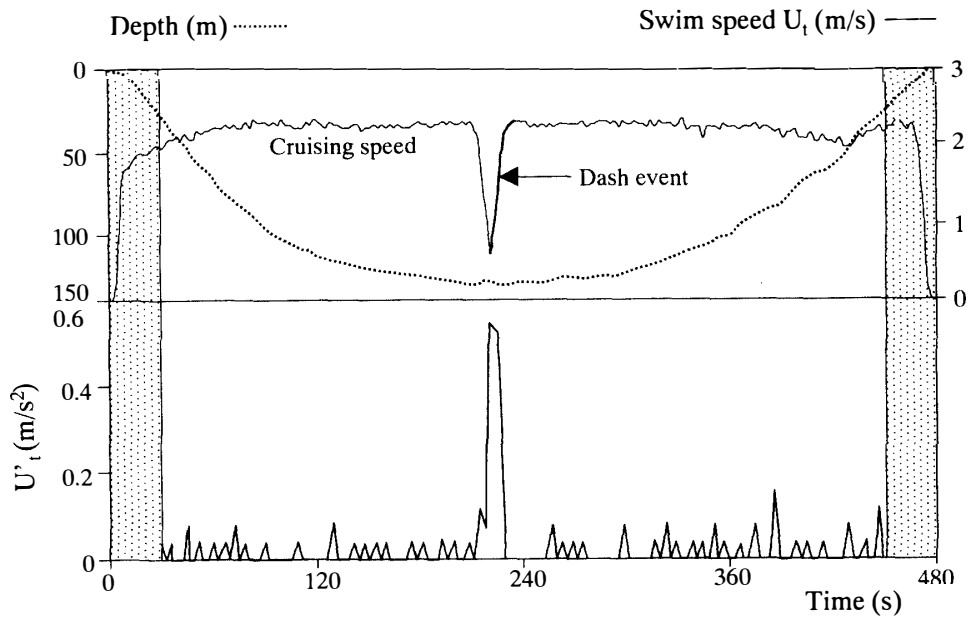


Fig. 1. Depth and swimming speed data during a dive (top) and the function U'_t derived from the evolution of the swim speed U_t as a function of time (bottom).

top). Penguins maintained this cruising speed until the last 30 s of the dive (Fig. 1, top) when a short acceleration (up to 2.5 m/s) was observed followed by a rapid deceleration to 0 m/s when the bird emerged at the surface. The mean cruising speed was higher for bird PF161 (2.01 ± 0.11 m/s) than for bird PF141 (1.80 ± 0.05 m/s, Student $t_{32764df} = 233.72$, $P < 0.0001$).

Interrupting the constancy of the cruising speed, steep accelerations of speeds termed “dashes” were observed (Fig. 1, top). In order to distinguish these pronounced dash events, a mathematical method was applied. The speed was first changed into accumulated values of acceleration using the following formulae:

$$U'_t = U'_{t-1} + (dU/dt), \quad \text{if } (dU/dt) \geq 0$$

$$U'_t = 0, \quad \text{if } (dU/dt) < 0$$

where U_t is the function describing the evolution of the cruising speed as a function of time (t). The function U'_t highlighted only the acceleration events (Fig. 1, bottom). Thus, for all dives, the acceleration peaks were counted for different thresholds ranging from 0 to 1 with a step of 0.02 on U'_t (Fig. 2). At first, the number of peaks was very high reflecting the noise due to variability. This number showed a sharp decrease before remaining constant after reaching a threshold value around 0.2. This stabilization corresponded to the detection of pronounced accelerations that were distinct from the variability. However, the limit between noise and clear peaks was difficult to estimate for all dives, as no clear break point was observed (Fig. 2). Thus, this operation was repeated dive by dive, giving a threshold for each dive. Finally, the time of all peaks above a specific threshold indicated the position of the steep acceleration events in each dive, allowing accurate determination of dashes.

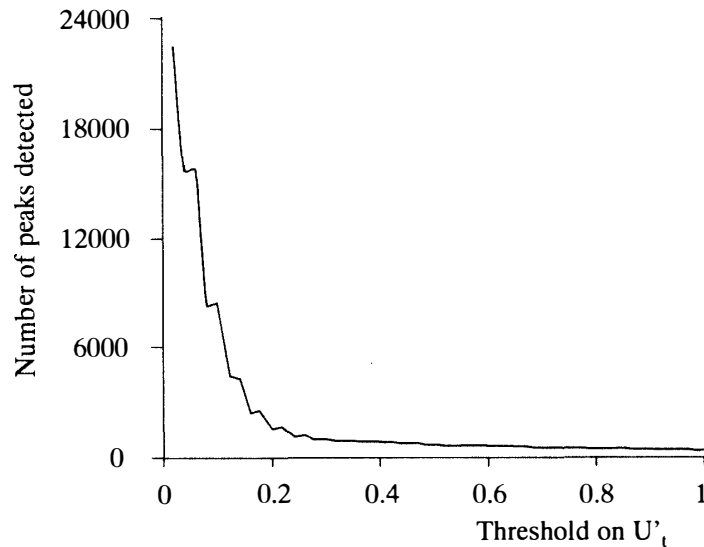


Fig. 2. Evolution of the number of peaks detected as a function of different thresholds of U'_t for all dives.

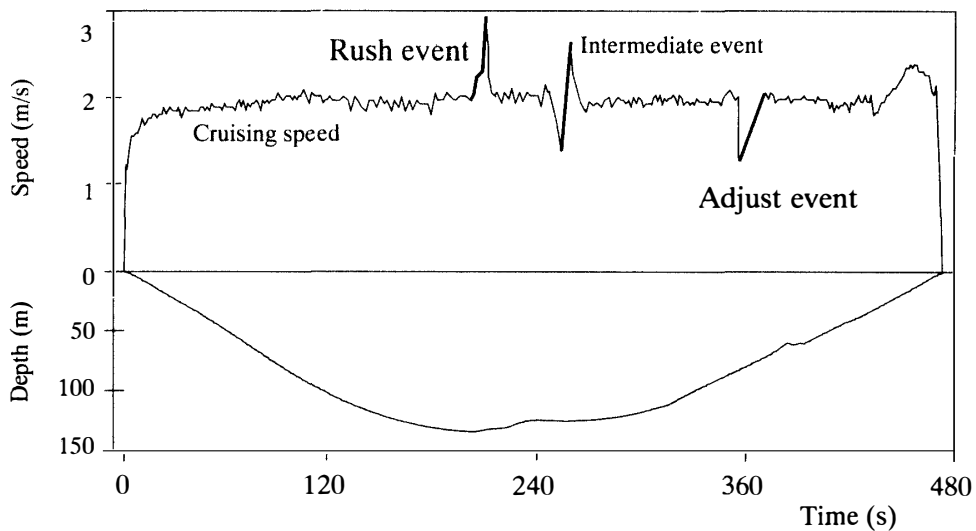


Fig. 3. The three types of dash events observed on the swimming speed (top) and a diagram of a "Plateau" shaped dive (bottom).

The dashes were separated into three categories based on their starting and ending values (Fig. 3, top). In 28% of all the dashes, these drastic accelerations arose from the cruising speed and were termed "Rush" events. In 59% of cases, following a brief deceleration, the dash events represented accelerations to return to the cruising speed and thus were termed "Adjust" events. Finally, there were "Intermediate" events (13% of the dashes) which were "Adjusts" that reached speeds greater than the cruising speed. No other combinations or profiles were observed within the recorded periods of the two birds.

Based on the depth profile of dives, a new category called "Plateau" dives was added to the three classical ones: "V", "U" and "W" shaped dives (Wilson, 1990, 1995).

Table 1. Categorization of king penguin dives based on both their depth profile and the presence (DDE) or absence (DW) of rapid acceleration events (“dashes”) during the dives. See the text for description of the dive types.

Categories of dives	Sub-categories	Detailed percentages		Mean number of dash events for the 2 birds (\pm SD)
		PF141	PF161	
DW	“V” shape	1.5 %	2.6 %	–
	“U” shape	40.8 %	24.4 %	–
	“W” shape	0.4 %	1.3 %	–
	“Plateau” shape	3.8 %	0.6 %	–
DDE	“U” shape with “Adjust” only	13.4 %	30.8 %	1.5 (\pm 1.0, $N=83$)
	“U” shape	11.8 %	4.5 %	2.5 (\pm 1.3, $N=38$)
	“Plateau” shape	9.2 %	14.1 %	2.8 (\pm 2.7, $N=46$)
	“W” shape	14.9 %	18.6 %	5.0 (\pm 3.6, $N=68$)
Unclassified dives		4.2 %	3.2 %	–

The “Plateau” dives had a portion of the ascending phase during which the depth remained constant (± 2 m, Fig. 3, bottom).

Dives were categorized as being with (DDE) and without (DW) “dash” events, then sub-categorized according to their depth profile (Table 1). There were three types of “U” shaped dives, those without dashes (33% of dives), those with only “Adjusts” dashes (22%) and those with the three types of dashes combined together (8%). No dashes were performed during “V” shaped dives. On the other hand, three “W” shaped dives without dashes ($N=71$) and 11 “Plateau” shaped dives without dashes ($N=56$) were observed for the two birds. The number of dashes per dive category increased gradually from the “U” shaped dives that had only “Adjusts” to the “W” shaped dives.

76% of dash events (85, 80 and 71% for “Intermediates”, “Rushes” and “Adjusts”, respectively) were performed at depths > 100 m. Moreover, half of the dashes detected at depths < 100 m occurred during dives with maximum depths < 100 m. Additionally, no clear dashes were observed during dives shallower than 30 m. “Rushes” and “Intermediates” occurred mainly during the early ascent phase of dives (Fig. 4). “Adjust” events were most prevalent during the ascent phase of dives, but generally were also performed later in the ascent than the other types of dashes. Finally, birds performed few dashes during the descending phase of dives.

Overall, 65% of dashes corresponded to a movement of birds directed upward (Table 2). However, 58% of the “Intermediates” corresponded to downward movements.

The dashes were separated into “straight” (continuous increase in the speed) and “non-straight” (the acceleration was briefly interrupted by a small deceleration) events (Fig. 5, top left). “Straight” events generally were shorter (2.7 ± 1.9 s, $N=560$) in duration than were “non-straight” events (7.2 ± 8.9 s, $N=65$, Mann-Whitney U-test, $U=1914.5$, $P<0.001$, Fig. 5). Additionally, “straight” events were “Rushes” in 80% of cases. Correspondingly, the mean distance traveled during “straight” events was less than the distance traveled during “non-straight” events (5.6 ± 3.1 m, $N=560$ and 17.3 ± 8.8 m, $N=65$, respectively; Mann-Whitney U-test, $U=2401$, $P<0.001$). There was a

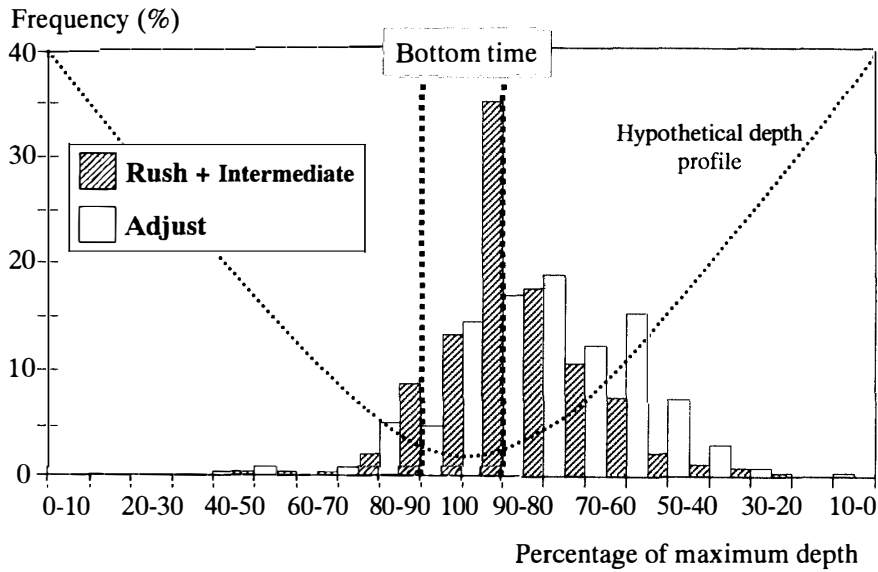


Fig. 4. The frequency of occurrence of dash events in relation to the maximum depth of dives, in categories that represent 10% intervals of the maximum depth. The “Intermediate” events were included in the “Rush” events as their distribution was similar.

Table 2. Directions followed by king penguins during dash events.

Per dash type	Upward	Downward	No depth changes
“Rush” events	65 %	26 %	9 %
“Adjust” events	74 %	15 %	12 %
“Intermediate” events	28 %	58 %	14 %
All dash type together	65 %	24 %	11 %

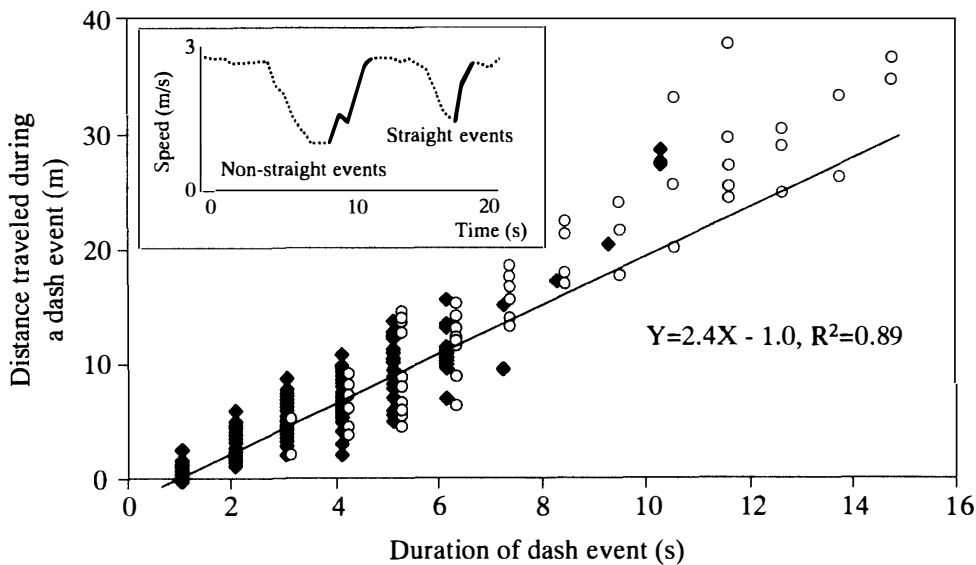


Fig. 5. Relationship between the distance traveled during dash events and their duration. Closed squares indicate the “straight” events and open circles, the “non-straight” events. For the definition of “straight” and “non-straight” events, see text and the speed diagram at the top left of the figure.

Table 3. Duration of the three types of dash events and rates of acceleration by the penguins during the events. Although the data were non-parametric and tested as such, they are presented as means (\pm SD) for ease of comparison between data sets.

	Duration (s)	Acceleration (m/s ²)
“Rush”	4.1 (\pm 3.3)	0.35 (\pm 0.3)
“Adjust”	2.9 (\pm 1.3)	0.39 (\pm 0.2)
“Intermediate”	2.8 (\pm 1.7)	0.58 (\pm 0.3)

linear relationship between the distance traveled during dashes and their duration ($Y = 2.4X$, $R^2 = 0.87$).

“Rushes” were of longer duration than the other types of dashes (Kruskall-Wallis $H_{2df} = 6.08$, $P < 0.048$) whereas the penguins’ rate of acceleration was greatest during “Intermediates” (Kruskall-Wallis $H_{2df} = 60.74$, $P < 0.0001$, Table 3).

Within a dive, 80% of “Rushes” were followed by another dash (“Rush”, “Adjust”, “Intermediate” or a combination). In one third of the cases, a “Rush” was followed by an “Adjust” while “Adjusts” represented single events in 48% of cases.

Discussion

During most of each foraging dive, the penguins maintained constant speeds of approximately 2 m/s, which may correspond to an optimal velocity at which the energetic cost of transport is at a minimum. Measurements of energetic and swim velocity performed on pygoscelids (Culik and Wilson, 1991a, b; Culik *et al.*, 1991) and king penguins (Culik *et al.*, 1996) in artificial swim canals have suggested that penguins did possess this optimal speed. An optimal speed for king penguins was estimated to be around 2.2 m/s (Culik *et al.*, 1996), which is comparable with the mean “cruising” speed recorded in our field study.

Penguins departed from the cruising speed to perform discrete dashes, which we postulate to be prey pursuit, capture and eventually recovery or swallowing events. Some dashes may indicate escapes from predators. However, the main predator of king penguins while at sea is the killer whale, *Orcinus orca*, whose hunting seems to occur near the sea surface rather than at depths > 100 m (Guinet, 1991), where the majority of dashes were performed.

Previous studies of penguins foraging based on time and depth alone have characterized “W” dives as feeding dives and “V” or “U” dives as exploratory dives (Wilson, 1990, 1995). Assuming that dashes represent hunting events, the role of dives based on both their shape and the presence of these dash events, can be better understood. “W” shaped dives do seem to represent active feeding dives. Also “V” shaped dives included no dashes and probably were exploratory dives. A new category of dive types, previously undefined, has been observed in our data: the “Plateau” shaped dive. In this dive type, the depth remained constant during a portion of the ascending phase. Their role remains unclear although 80% of them might have been feeding dives. In this dive type, dashes occurred mainly during the constant portion of the ascent phase. Thus, this constant depth portion probably corresponds to an alternative

bottom phase. More observations are required to elucidate the exact role of "Plateau" shaped dives. Perhaps the most important observation, however, was the presence of dashes during 53% of the "U" shaped dives, suggesting that they were not limited to exploration but were also feeding dives.

Few dashes were performed at shallow depths. When this happened, these shallow dashes occurred during dives performed at the beginning and end of each day. The maximum depth of these dives increases and decreases at dawn and dusk respectively, following the vertical migration of prey (Wilson *et al.*, 1993).

The prey of king penguins in the Crozet Archipelago are mainly mesopelagic, myctophid fish, particularly *Krefflichthys andersonii* and *Electrona carlsbergi* (Cherel and Ridoux, 1992). These are schooling fish species that exhibit diurnal vertical migrations and patchy distributions (Gjosaeter and Kawaguchi, 1980; Zasel'slyi *et al.*, 1985; Torres and Somero, 1988). The fine temporal scale of our recordings (one second interval) allows speculating on the actual detection, pursuit and capturing strategies of these prey by king penguins.

Penguins are assumed to detect their prey by sight (Sivak, 1976; Howland and Sivak, 1984; Martin and Young, 1984; Bowmaker and Martin, 1985; Suburo and Scolaro, 1988; Suburo *et al.*, 1991). As such, prey recognition is dependent on their visibility at the depths where the penguins hunt. This visibility will vary with degrees of light penetration and characteristics of the prey such as bioluminescence. A dash was initialized once a potential prey was detected within a potential hunting range and ended once this prey was caught, in case of a successful capture. Therefore, in our study, the distance of prey detection by the king penguins might equate to the distance traveled during constant acceleration ("straight") dashes, which ranged between 1 and 7 m. This would be true except if the prey starts an escape using the same direction as the predator's attack. On the other hand, the "non-straight" events may represent active pursuits of either a single prey escaping in more than one direction or several trials of capture on more than one prey.

Most of the dashes performed by king penguins corresponded to the ascent phase of the penguin's dives, suggesting that the penguins swam down to a depth where they expected to find prey, then foraged both at that depth and during the ascent back toward the surface. Moreover, two-thirds of the dashes were associated with upward movements, suggesting that most prey were detected and approached from below. Since an animal's eye looking upward in the sea would receive about 100 times more intense ambient flux light than an eye directed downward (Clarke and Denton, 1962), observed from below, the prey would be silhouetted against a bright background, making them easier to locate. Adoption of an upwardly focused hunting strategy has been observed in Weddell seals (*Leptonychotes weddelli*) that were equipped with infrared cameras (Davis *et al.* 1999). Additionally, king penguins' prey are probably standing head-down in a torpid attitude during the day (Barham, 1966). Therefore, an approach of the bird from below may prevent the fish from escaping. Indeed, the fish would have to change its heading direction to start an escape.

However, using the counter-shade effect may be highly dependent on the light available at different depths, which would depend on the time of day, cloud cover and water clarity. A more recent study focusing on the vision of little penguins underwater

(Cannell and Cullen, 1998) has revealed the existence of a relationship between the light level and the efficiency of prey hunting. Similarly, the bioluminescence of the myctophid fish would limit the use of the counter-shading effect, as these two mechanisms are antagonistic (Hastings, 1971; Tett and Kelly, 1973). These fish possess photophores on their ventral surfaces (Tett and Kelly, 1973), which would blur the periphery of the fish. On the other hand, since one third of dashes were performed while the birds were swimming downward or horizontally, king penguins probably rely occasionally on bioluminescence to detect their prey as suggested by Martin (1999). This may be the case when the light level at the depths where prey are encountered decreases below the limit where the counter-shading effect can be used. However, the higher proportion of movements directed upward indicates that the counter-shading effect may play a more important role than bioluminescence for king penguins' hunting behavior in deep water (> 100 m).

Based on the variety of dashes distinguished, king penguins may have several prey approaches and capture techniques. "Rushes" were the most common dashes performed and probably represented spontaneous movements toward a prey upon its detection. "Rushes" occurred singly, perhaps indicating a single prey capture, or in a series, which could reflect multiple prey captures or several unsuccessful "Rushes" prior to a successful capture.

"Adjusts" also were either single events or occurred within a series of other dashes. Single "Adjusts" may indicate the catching of a motionless prey such as torpid myctophids (Barham, 1966). The bird would sight the prey from a distance, slowing down so as to approach the prey undetected, and the "Adjust" would be a dash forward to capture the prey. When they occur within a series of other dashes, "Adjusts" may indicate returns to cruising speed following changes in direction (in which velocity was lost) or brief pauses to handle and/or swallow prey. "Intermediates" may have been "Adjusts" that over-shot cruising speeds or "Adjusts" that turned into "Rushes" as further pursuit was required to capture the prey.

This study reveals much about the possible hunting strategies of king penguins but is limited to just two penguins and a total of just over two days of foraging early on in summer foraging trips by these birds. King penguins may vary their hunting strategies through foraging trips (Bost *et al.*, 1997), between foraging trips at different times of the year and other penguins may have different prey approaches to those suggested by the current data. Further studies with time-depth-speed recorders are required to better understand prey capture by king penguins and other seabirds.

Acknowledgments

The authors wish to express their gratitude to the Institut Français pour la Recherche et la Technologie Polaires (I.F.R.T.P.) and the Terres Australes and Antarctiques Françaises (T.A.A.F.) for their financial and logistical support during the experiments. This work was also financially supported by the Grant-in-Aid for International Scientific Research from the ministry of Education, Science, Sports and Culture of Japan. Many thanks to all the members of the 32nd mission in the Crozet Archipelago, especially Guillaume Froget for his help in the fieldwork and Aziz the cook

for dealing with people living more often on the beach than in the base. We are especially thankful to Frank Pattyn for his help in the mathematical determination of dash events. Finally, we are sincerely grateful to two unknown referees who provided constructive comments and helped to improve the readability of the text.

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