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Foraging strategies and prey encounter rate of free-ranging Little Penguins

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Abstract There is little information on the effort put into foraging by seabirds, even though it is fundamental to many issues in behavioural ecology. Recent researchers have used changes in the underwater cruising speed of penguins to allude to prey ingestion since accelerations are thought to reflect the encounter and pursuit of prey. In this study, we attached minute accelerometers, to determine flipper beat frequency as a proxy for prey pursuit, to Little Penguins *Eudyptula minor* foraging in shallow waters in Western Australia. During diving, Little Penguins flapped continuously and at a regular pace of 3.16 Hz while descending the water column and throughout the bottom phase of most dives. However, the frequency and amplitude of wingbeats increased transitorily, reaching 3.5–5.5 Hz, during some dives indicating prey pursuit. Pursuit phases lasted a mean of 2.9 ± 3.3 s and occurred principally during the bottom phases of dives (75.4%). Most dives in all birds (86%) had a clear square-shaped depth profile indicating feeding activity near the seabed in the shallow waters of the bays. Hourly maximum depth, time spent underwater, percentage of dives with pursuit events and catch per unit effort showed an overall increase from zero at ca. 0500 h to a maximum during the hours around mid-day before decreasing to zero by 1900 h. During pursuit phases, Little Penguins headed predominantly downward, probably using the seabed to assist them in trapping their prey. In the light of our results, we discuss depth use by Little Penguins and their allocation of

foraging effort and prey capture success as a function of environmental conditions.

Introduction

Feeding and activity patterns are central themes to studies of life-history evolution (Stearns 1992). The rate of energy acquisition via feeding determines how energy can be allocated to the exclusive processes of growth or reproduction (Levins 1968). Seabirds are central place foragers, which gather food at sea but reproduce on land. Their feeding is thus limited by the time they spend at sea, and their foraging efficiency constrained by prey encounter rate and their hunting and prey processing abilities (Ropert-Coudert et al. 2004a). The constraints imposed on seabirds make them interesting models for behavioural ecology work, recently enhanced by recent advances and miniaturization of electronics that can continuously monitor their activity at sea (cf. Naito 2004 for details).

Little Penguins *Eudyptula minor* are largely visual hunters (Cannell and Cullen 1998), a capacity that limits foraging to daylight hours. However, little is known about their actual foraging effort. The few studies that have investigated the at-sea activity of Little Penguins in Western Australia have revealed that during breeding, these birds forage almost exclusively within 15–20 km of the colony, where waters are shallow (seabed at a maximum depth of ca. 17 m, Klomp and Wooller 1988). Time-depth recorders mounted on Little Penguins have shown that they recurrently exploit specific depth zones from trip to trip (Ropert-Coudert et al. 2003). Dietary studies indicate that these birds eat primarily small, schooling fish such as sandy sprat (*Hyperlophus vittatus*), pilchard (*Sardinops sagax*), garfish (*Hyporhamphus melanochir*), blue sprat (*Spratelloides robustus*), anchovy (*Engraulis australis*) and occasionally squid (*Idiosepius notoides*) (Klomp and Wooller 1988; Wienecke et al. 1995). Aside from this, nothing is known about prey

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encounter rates and the portion of underwater time devoted to feeding and travelling.

Measurement of speed in free-ranging penguins has shown that individuals swim at a roughly constant speed during the majority of their dives and during all travelling phases of dives (Wilson et al. 2002; Ropert-Coudert et al. 2001a; Bethge et al. 1997). Departures from this cruising speed have therefore been thought to reflect the encounter and pursuit of prey (Ropert-Coudert et al. 2000; Wilson et al. 2002) and, in keeping with this, Little Penguins have been observed to accelerate when capturing fish prey in both shallow and deep waters and when capturing either a solitary fish or one from a shoal (Schulz 1987; Cannell 1994). Therefore, measurement of changes of swimming speed of Little Penguins should help elucidate their foraging strategies and prey encounter rate. Since reliable swim speed recorders are generally too large for such a small animal (0.6–1.4 kg, but see Bethge et al. 1997), we used minute accelerometers that record simultaneously the body posture and the dynamic motion of animals (Yoda et al. 2001; Ropert-Coudert et al. 2004b, c; Watanuki et al. 2003) to determine flipper beat frequency as a proxy for acceleration.

This study aimed to reconstruct the time/activity budget of free-ranging Little Penguins from Penguin Island, Western Australia as they foraged in the shallow waters of Comet Bay. Using acceleration as an index of prey pursuit, we provide a first attempt to describe the foraging strategies of this bird and its rate of prey encounter. Based on the rate of prey encounter and the birds' diving activity, we discuss prey availability and Little Penguins foraging efficiency and how both might vary according to environmental conditions.

Materials and methods

Data-loggers were fitted to four Little Penguins in August 2002. All birds were nesting on the central part of Penguin Island, Rockingham (32°16'S, 115°21'E), Western Australia, in rectangular, wooden nest-boxes (see Klomp et al. 1991 for details), allowing easy capture of the adults and checking of the chicks. Nautical dusk and dawn for the study period were taken to be 0550 h and 1848 h (local time), respectively, (<http://lychnis.imcce.fr/cgi-bin/levcou.cgi>). Birds were captured at their nest site, either at night or before departure for sea early in the morning. The sex (determined from the bill depth; Gales 1989), breeding status and the mass of both the adult and its chicks were noted. Loggers were then attached using waterproof (Tesa) tape (Wilson et al. 1997a) on the median line of the birds' back, near the tail so as to minimize drag (Bannasch et al. 1994). The attachment of the logger was completed in < 5 min and birds were released at the entrance of their nest-box.

Time-budgets and activity patterns of birds were recorded using miniaturized, cylindrical, four-channel data loggers (M190-D2GT, 12 bit resolution, 52×15 mm, 16 g, Little Leonardo, Tokyo, Japan). The absolute

accuracy for the depth sensor was 0.1 m. The devices simultaneously monitored depth (1 Hz) and acceleration (16 Hz) along the longitudinal (surging) and dorso-ventral (heaving) axes of the birds. The units contained sensors capable of measuring both dynamic acceleration (e.g. vibration) and static acceleration (gravity). In the absence of movement, values of static acceleration ranged from +1 to –1 G. For instance, a vertically upright logger would correspond to values of 0 G on the heaving axis and –1 or +1 G on the surging axis, depending on whether the logger was head-up or head down, respectively, (see Yoda et al. 1999 for technical details).

Equipped birds were recaptured after one foraging trip at sea. The instruments and tape were removed, and the penguins were reweighed and released. The status of the birds was then checked weekly until the next moulting period.

Calibration sessions were conducted at the Perth Zoo, Western Australia. One Little Penguin was equipped with an accelerometer, attached using tape in same position as used on free-ranging individuals. This bird was then released in the pool where it swam with conspecifics. The behaviour of the bird was filmed using a digital video-camera (Handycam, Sony Ltd., 30 frames/s) while it fed on dead pilchards *S. sagax*. An exhibit window comprising one complete side of the pool allowed us to track the bird for the whole period it was submerged. These video sessions were subsequently used to confirm the relationship between the signals recorded by the logger and the posture and activity of the birds.

Data were downloaded into a computer and analysed using IGOR Pro (Wavemetrics Inc., USA, 2000, Version 4.01). A dive started when birds departed from the water surface and ended when they returned to it. Only dives > 1 m were analysed. The bottom phase of dives was considered to have started and ended the first and last times that the rate of change of depth did not exceed 0.25 m/s. All depth changes occurring within this bottom phase are subsequently termed undulations (see Wilson 1995; Simeone and Wilson 2003).

Since surging acceleration was recorded along the main body axis of the birds, the static component of this acceleration channel was the most sensitive to changes in body orientation and was consequently used to calculate dive angle. Body angle was defined using the method described by Watanuki et al. (2003). Briefly, we used a low-pass filter (Tanaka et al. 2001) to separate the component of the gravity acceleration along the surging axis from the high frequency component resulting from wing beat activity. Body angle (θ) was then calculated using the following equation:

$$\theta = a \sin(A/g) - \alpha,$$

where A is gravity acceleration along the surging axis, g is gravity and α is logger attachment angle. Attachment angle was calculated assuming that body angle was 0 when birds were at the sea surface between two dives.

The accurate start time of the foraging trip was inferred from body angle values since the birds' body angles differed between standing on land and swimming at sea, with distinctive acceleration values of ca. 0 G and ca. +0.4 G, respectively, on the surging axis.

Flipper beats were apparent in the acceleration signals as an oscillating pattern present simultaneously on both axes, with each propulsive stroke recorded on the heaving axis resulting in a forward acceleration recorded on the surging axis. This oscillating pattern has been identified as limb beating in several studies using similar loggers on a variety of birds' species (Yoda et al. 2001; Sato et al. 2002; Watanuki et al. 2003; Ropert-Coudert et al. 2004b, c; Weimerskirch et al. 2005). All parts of the Little Penguin dives lacking these distinctive oscillating patterns were considered to be passive swimming phases where birds use buoyancy to ascend (cf. Sato et al. 2002). The amplitude and frequency of each wingbeat were analysed using the heaving acceleration signal (the most sensitive to undulation in the birds body resulting from flipper beats).

Hourly irradiation data measured by a solar panel (with 0° of inclination and a reflectivity of 0.1) were downloaded from the web page of the Australian National University (<http://solar.anu.edu.au/Sun/Irrad/Irradiation.html>) for Perth, Western Australia during August.

Flipper beat frequencies were calculated using a Power Spectrum Density analysis (Igor Procedure Version 1.1, LH 971028, Wavemetrics Inc., USA, 2000, Version 4.01). Simple regression was used to highlight trends between variables. Comparisons of dive parameters were conducted using the Student's *t*-test. All statistical tests were performed using Statview (Version 4.57, Abacus Concepts Inc., Berkeley, CA, USA, 1996) following Sokal and Rohlf (1969). When data did not follow a normal distribution, non-parametric tests were used. The statistical threshold was 0.05. Values are presented as means \pm SD.

Results

Three of four Little Penguins foraged over a single day, restricting their diving activity to daylight hours (Fig. 1a). Birds entered the water between 0330 h and

0400 h and exited the water between 1745 h and 1930 h. The last bird (B18) entered the water relatively late, at 0517 h, and foraged throughout the day but stayed at sea overnight, resuming its activities on the next day. For this bird, we only analysed the diving activity on the first day because the accelerometer's memory was full before the end of the second day. Three penguins started to dive about 2 h after entering the water but B18 began diving 4 h after entering the water (Table 1). The time spent by the penguins underwater varied according to the time of day, with birds spending a higher percentage of their time underwater during the mid-day period than they did closer to dawn or dusk (Fig. 4a). Most dives (86%) had a clear square-shaped depth profile (Fig. 1b).

Little Penguins flapped continuously and at a regular frequency while descending the water column. They maintained this pace throughout the bottom phase of most dives, before progressively reducing their wingbeat frequency towards the beginning of the ascent (Fig. 2a). Penguins stopped beating their flippers completely during the ascent phase, a mean of 5.69 ± 4.55 m (vertical distance from the surface) before surfacing, i.e. at $56 \pm 29\%$ of the maximum depth of their dives ($n=2,114$ dives for all birds, Table 2). We applied a power spectrum density analysis on the heaving acceleration signals during diving phases only. We found that about a main wing-beat frequency peak of 3.16 Hz there were two clear points of inflection located at 2.25 and 3.94 Hz (Fig. 2b). Inspection of the dives showed that values below the lower threshold of 2.25 Hz corresponded to decelerations preceding the final gliding phase when the penguins were returning to the surface (cf. Sato et al. 2002—see later). Values above the upper threshold of 3.95 Hz generally occurred in discrete groups. We assumed that all frequencies exceeding 3.94 Hz for more than three consecutive wing beats were due to prey pursuit. Note that we assume that any 'encounter' with a prey during the course of a dive will result in a pursuit of this prey, and that this is illustrated by an increase in the flipper beat frequency as defined. Frequencies < 2.25 Hz were subsequently termed 'decelerations'. Overall, birds beat their flippers between 87.3 and 97.6% of their underwater time swimming, 86% of this flapping time at the cruising frequency between 2.25 and 3.94 Hz.

Based on the presence or absence of pursuits, dives were separated into pursuit and cruising dives,

Fig. 1 Diving activity (*top*) of a free-ranging Little Penguin and the corresponding acceleration profiles recorded on the heaving (*middle*) and surging (*bottom*) axes for a complete foraging trip

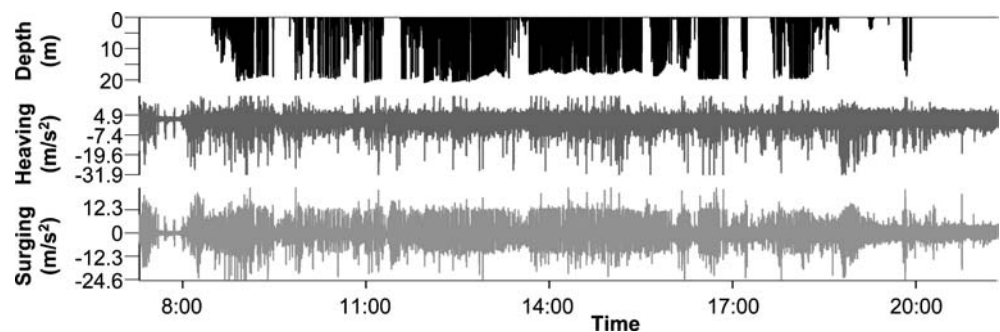


Table 1 Foraging dates and characteristics of the foraging trip and dives of Little Penguins breeding on Penguin Island, Western Australia in August 2002

Sex	B18 Male	B19 Male	B35 Male	B65 Female
Body mass at departure (g)	1,470	1,300	1,450	900
Foraging dates	23 Aug	23 Aug	17 Aug	24 Aug
Foraging trip duration (h)	16.1 + overnight	14.8	14.4	17.1
Time before first dive (> 1 m) (h)	4.46	2.16	1.97	2.54
Total underwater time (> 1 m, h) (% of trip)	3.9	5.5 (37%)	5.4 (37.5%)	7.1 (41.5%)
<i>N</i> dives > 1 m	428	416	527	693
Mean maximum depth (m)	12.9 ± 6.7	10.8 ± 5.8	8.9 ± 3.9	9.0 ± 2.5
Mean dive duration (s)	31.3 ± 16.8	46.7 ± 17.1	35.4 ± 15.3	37.1 ± 12.6
Mean descent angle (°)	-21.7 ± 15.2	-19.6 ± 6.8	-31.3 ± 13.3	-30.4 ± 9.1
Mean bottom phase duration (% of dive duration)	40.2 ± 23.3	56.6 ± 19.5	55.3 ± 19.7	58.2 ± 15.9
Mean Ascent angle (°)	39.5 ± 15.7	17.2 ± 6.9	27.7 ± 13.3	40.5 ± 13.5

respectively. Overall, the ratio of cruise to pursuit dives was 1.16 ± 0.57 but this ratio was highly variable among birds (Table 3). However, this ratio changed systematically during the day as the proportion of pursuit dives increased in the morning to peak around mid-day before decreasing again in the late afternoon (Fig. 4c). Long, uninterrupted successions of cruising dives were mainly observed at the beginning and end of foraging trips. Prey encounter rates were similar for the four birds although rates were notably lower for B19 than in conspecifics (Fig. 3). Catch per unit effort, a measure of the ease with which birds encountered prey (Wilson et al. 1994; Grémillet 1997), was derived by dividing the number of pursuits per time interval by the total time spent underwater during that time interval. This calculation showed an overall increase from zero at ca. 0500 h to a maximum during the hours around mid-day before decreasing to zero by 1900 h (Fig. 4c). A sixth order polynomial fit of the data ($y = -18.24x^6 + 56.17x^5 - 61.31x^4 + 27.17x^3 - 3.91x^2 + 0.12x + 0.002$; $R^2 = 0.71$) showed a peak at mid-day and 90% limits between 0540 h and 1840 h (Fig. 4d).

Little Penguins performed 2.17 ± 1.53 pursuit phases per pursuit dive (maximum = 11 distinct accelerations in one dive, Table 2). These pursuit phases lasted a mean of 2.9 ± 3.3 s (range 0.19–31.6 s, $n = 4$ birds), with 86% of the pursuits lasting < 5 s. They occurred principally during the bottom phases of dives (75.4% of all dives on all birds, range 67.4–82.9%) and only occasionally during the descent (13.7%) and ascent (10.9%) phases. During pursuit phases, Little Penguins headed predominantly downward (Fig. 3b) but, overall, the amplitudes of depth changes during pursuit phases were extremely small, being on average 0.74 ± 1.71 m (max. 11.8 m, $n = 457$ pursuits) and 0.73 ± 0.94 m (max. 8.0 m, $n = 935$ pursuits) during upward and downward pursuit phases, respectively. The distribution of the depth at which acceleration occurred revealed intra-specific variability in the way Little Penguins use the water column with individuals apparently exploiting rather narrow depth bands (Fig. 5).

The descent angle of a dive was significantly more acute when a pursuit had occurred during the course of

the previous dive in all birds (Fig. 6) although there was substantial inter-individual variability in the way descent angles changed. This variability was probably related to the differences in the maximum depth reached during the foraging trip by birds.

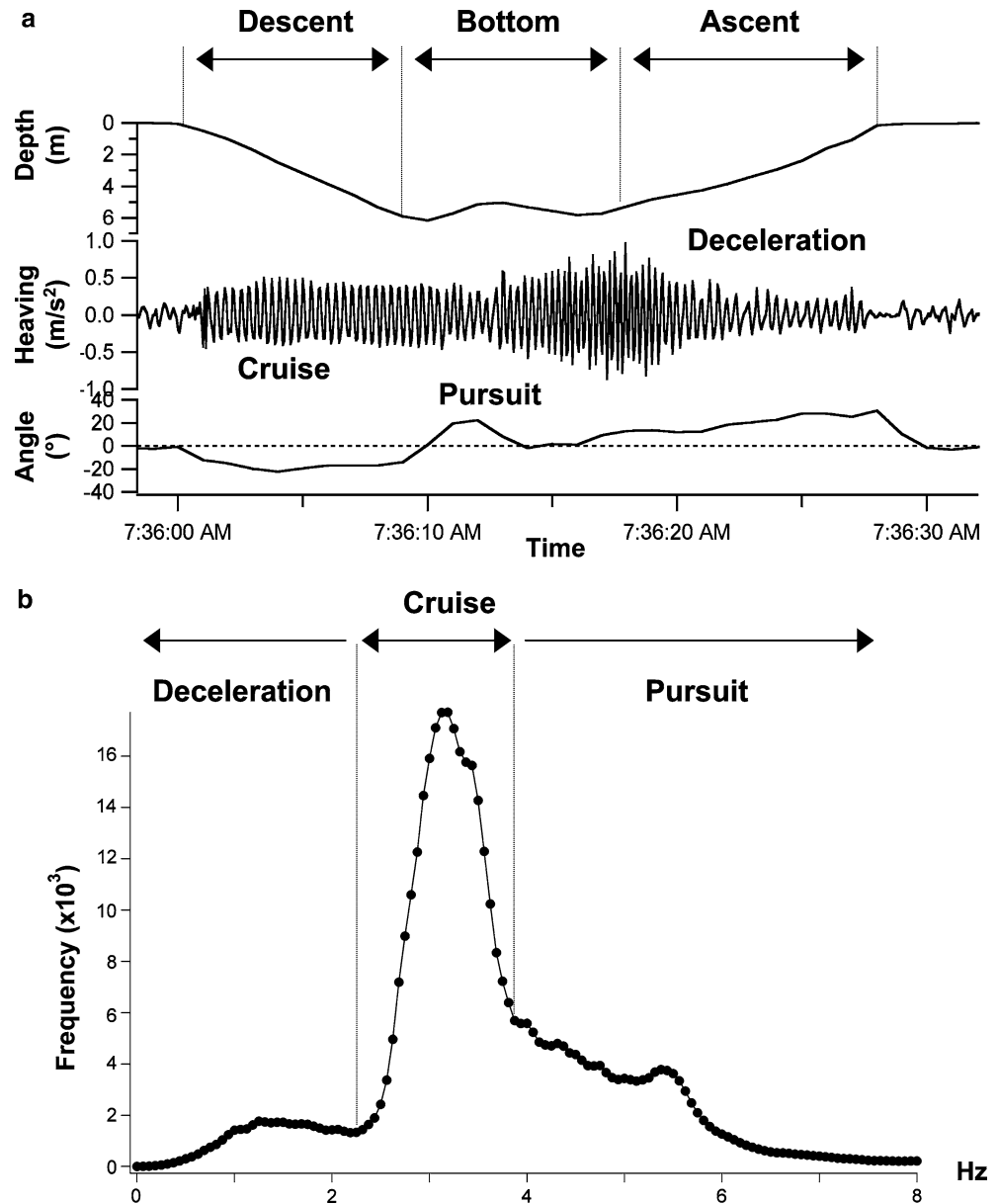
Discussion

Our data represent, to our knowledge, the first account of the fine-scale time budget of Little Penguins, with a detailed description of the species' underwater activities (but see also Bethge et al. 1997; Gales et al. 1990). This study also provides the first report of the diving angle for this species. Although our sample size was too small to allow us to be too specific about the quantitative aspects of the foraging efficiency of Little Penguins, we have highlighted general trends in the foraging activity and strategies of the smallest of all the Spheniscids.

Assumptions about flipper beat frequency being a proxy for prey pursuit

One critical assumption in this study is that Little Penguins that occasionally depart from their cruising flipper-beat frequency during the course of a dive do so in order to increase their speed to pursue prey. Such observations have been made by one of the authors during feeding experiments of Little Penguins in captivity (B.L. Cannell, unpublished data). We expect free-living Little Penguins to behave similarly when they encounter prey in the wild, although we cannot define the extent to which such pursuits were successful. However, data from Magellanic penguins (*Spheniscus magellanicus*) fitted with speed and flipper beat frequency/amplitude sensors in tandem with beak angle sensors show that most (>90%) sudden increases in acceleration result in prey capture (R.P. Wilson, unpublished data). We cannot exclude the possibility that birds accelerated to avoid predators or as a result of agonistic behaviour from conspecifics. We believe, nonetheless, that should this occur, it would only reflect a

Fig. 2 a Dive depth, smoothed heaving acceleration data and dive angle illustrated during the course of one dive; and **b** distribution curve resulting from a Power Spectrum Density analysis (*PSD*) applied to the heaving acceleration signals recorded during the dive phases of all Little Penguins. The main flipper beat frequency of Little Penguins was 3.16 Hz. All frequencies below 2.25 and above 3.94 Hz were termed deceleration and pursuits, respectively. These three frequencies are also visible on the heaving acceleration data in **a**



very small proportion of the acceleration events recorded in our study. The very short accelerations observed (0.75–1 s) may correspond to either very short pursuits or chases abandoned quickly. In both cases, accelerations should still generally reflect a prey encounter but do not necessarily represent prey capture and ingestion.

Depth use by Little Penguins

The increase in mean maximum depth from dawn to mid-day and decrease from mid-day to dusk shown by our equipped penguins (Fig. 4b) typifies general patterns of depth use by other penguin species (Wilson et al. 1993; Ropert-Coudert et al. 2004a, etc.). Diel changes in

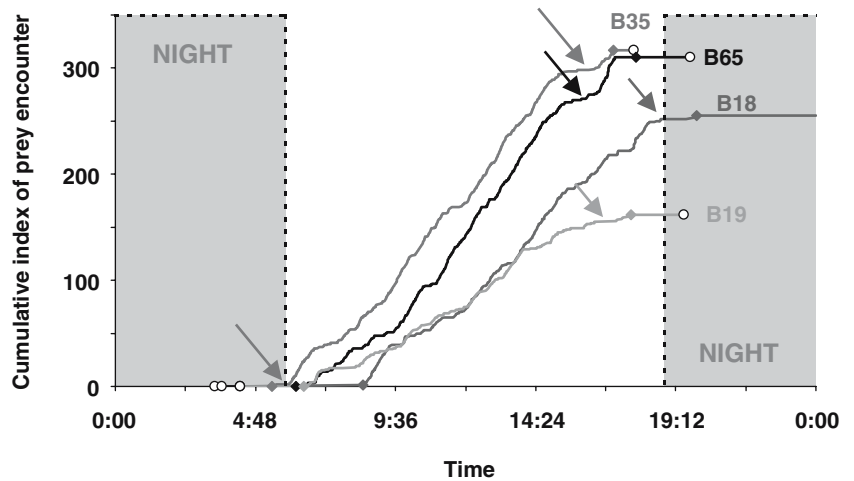
Table 2 Characteristics of the pursuit events (i.e. the transient increase in the flipper beat frequency, see text) occurring within the course of dives of Little Penguins

	B18	B19	B35	B65
<i>N</i> pursuit per trip	1,162	319	928	537
<i>N</i> pursuit > 1 s per trip	833	213	554	359
Mean <i>N</i> pursuit per dive	2.38 ± 1.55	1.97 ± 1.30	2.51 ± 1.81	1.71 ± 1.05
Mean depth of last wingbeat (m)	4.4 ± 4.8	7.7 ± 6.2	4.5 ± 3.5	6.3 ± 3.1
Mean % of maximum depth at which last wingbeat occurred	38.4 ± 29.8	65.7 ± 24.8	49.1 ± 26.8	68.0 ± 25.3

Table 3 Numbers and ratio of cruise and pursuit dives (i.e. dives without and with pursuit events, respectively)

Dive type	B18		B19		B35		B65	
	Cruise	Pursuit	Cruise	Pursuit	Cruise	Pursuit	Cruise	Pursuit
<i>N</i> dives	195	233	255	161	212	315	420	273
Ratio Cruise:Pursuit	0.84		1.58		0.67		1.53	

Fig. 3 Cumulative index of prey encounter (see Results for details) as a function of the time of day for birds B35, B65, B19 and B18. *Arrows* indicate substantial sequences of cruising dives. *White circles* show the departure from and arrival at the colony. *Losanges* on the curves indicate the first and last dive > 1 m, respectively



the vertical distribution of prey may play some role in this. However, a primary determinant of maximum dive depth in penguins seems to be the availability of light since these birds rely primarily on vision to hunt (Wilson et al. 1993; Pütz and Bost 1994; Cannell and Cullen 1998) and this would appear to be the case in our study (Fig. 4e). However, a notable difference between our study birds and other penguin species is the difference in the absolute values of the depth maxima as a function of time of day (and therefore light intensity). Little Penguins do not dive as deep as other species (maximum depth so far recorded: 69 m, Montague 1985) at any time of the day even though the general diel pattern is apparent. Aside from the general allometric relationship between maximum dive depth and body mass (e.g. Kooyman and Davis 1987; Wilson et al. 1997b), this implies that something is different for Little Penguins. They may have, for instance, poorer vision at low light intensity than other species (e.g. the special anatomical adaptation of the eye of the deeper diving king penguins *Aptenodytes patagonicus*, Martin 1999). In addition, the water turbidity is markedly higher in our study area than in areas where studies have been conducted on other species. This would lead to more rapid reduction in light intensity with increasing depth. Although there is indeed evidence that waters in the Perth area result in more rapid light attenuation with depth than many sub-Antarctic and Antarctic sites where other penguin species forage (Jerlov 1968), bottom topography may compound the observed patterns. The square ‘U-shaped’ dive profiles (see Le Boeuf et al. 1988 for general defi-

inition) and the consistency between maximum depths in adjacent dives makes it highly likely that the dives are made close to the sea bed (cf. also Tremblay and Chérel 2000). This is given further credence by the fact that water depths in the foraging areas of these birds generally concur closely with maximum dive depths (which are around 15–20 m in Cockburn Sound, Warnbro Sound and Shoalwater Bay). Thus, Little Penguins leaving their breeding site and moving out into deeper waters during the day before reversing the process towards evening, will have a depth use pattern that should approximate that shown in Fig. 4b. The depth limits at any time will thus be defined by the movements of the birds and the bottom topography. The apparent correlation of depth with light may be a consequence of this and the general penguin condition of needing light to forage (Cannell and Cullen 1998).

Allocation of foraging effort and prey capture success

In tandem with diel changes in maximum dive depth (Fig. 4b), the apparent foraging success of the birds also increased, as evidenced by their CPUE (Fig. 4c) and this, in turn, was paralleled by an increase in the proportion of time that the birds spent underwater (Fig. 4a). The clear, apparently light-dependent, patterns need to be considered in a hierarchical manner so that proper dependencies can be ascertained. As discussed earlier, the absolute maximum dive depth, ultimately, is likely to be dependent on light levels

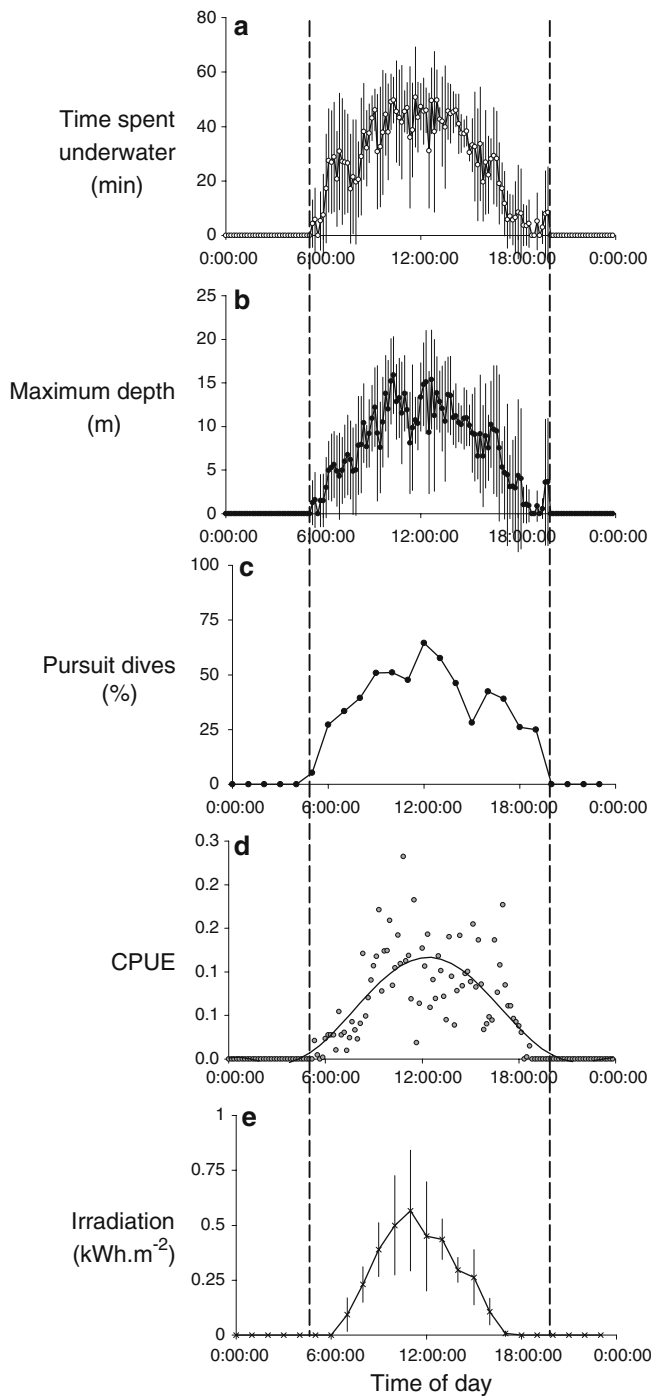


Fig. 4 **a** Hourly time spent underwater, **b** mean maximum dive depth per 10 min, **c** proportions of pursuit dives, **d** Catch per Unit Effort (CPUE, calculated as the proportion of the underwater time spent engaged in prey pursuit over a 10 min interval) and **e** average irradiation recorded in the Perth region in August, all against time of day. Vertical bars show SD

because Little Penguins are visual hunters (Cannell and Cullen 1998). The fact that Little Penguins encounter more prey over mid-day (Fig. 4c) may be due to greater light at depth, which would enhance visual capacities and increase the probability of prey being perceived, or

simply because it is at this time, roughly half way through the foraging trip, that the birds have moved to the areas of greatest prey abundance. The final, ostensibly light-related, pattern of percentage time spent underwater (Fig. 4a) may simply be a correlate of prey abundance, with penguins working harder in areas where prey are most encountered. This behaviour is a well-known feature of animal foraging (Krebs 1978; Schoener 1971; Pyke 1984) and has obvious advantages.

Specifics of prey capture

Little penguins apparently pursued most prey during the bottom phase of the dives. Pursuit of prey during bottom phases of dives in penguins that forage in the water column has been noted for Magellanic Penguins (cf. Simeone and Wilson 2003). Benthic or demersal feeding has already been noted in emperor *Aptenodytes forsteri* (Rodary et al. 2000), chinstrap *Pygoscelis antarctica* (Takahashi et al. 2003), gentoo *P. papua* (Croxall et al. 1988; Wilson et al. 1991; Robinson and Hindell 1996), rockhopper *Eudyptes chrysocome* (Tremblay and Chérel 2000) and Adélie penguins *P. adeliae*, although in this last species benthic dives are extremely rare (Ropert-Coudert et al. 2001b). It is, therefore, little surprising that benthic diving activity was also observed in the Little Penguin. Interestingly, penguins foraging in the mid-water, i.e. king penguins *A. patagonicus* (Ropert-Coudert et al. 2000) and Adélie penguins for most of their diving activity (Ropert-Coudert et al. 2001a) tend to capture prey from the underneath. In contrast, Little Penguins headed downward for most of their pursuits. This, together with the small amplitude of the depth changes during pursuit, suggests that birds use the seabed to trap prey. The overall picture, therefore, is one where birds encountered most of their prey in the demersal zone, a few meters above the seabed, and force them down closer to the seabed to reduce the prey's escape field. A similar, but reverse effect, has been noted for auks manoeuvring prey against the sea surface (Duffy et al. 1987).

Interestingly, descent angles were more acute when a prey had been encountered in the previous dive than when no prey was encountered. In Adélie penguins, this has been regarded as a strategy to reduce transit times between the surface and the prey patch without having to depart from the COT_{min} speed (Wilson et al. 1996; Ropert-Coudert et al. 2001b). Such a strategy is not expected to occur in the case of benthic diving activity since the profitable depth here is the seabed. Indeed, benthic divers are expected to use the same angle to reach the seabed whether the presence of prey at the bottom is certain or not. In our study, although Little Penguins dived substantially close to the seabed, an appreciable proportion of their dives terminated in mid-water. This, together with the purported 25% of prey catches occurring during transit warrant the change in angle observed. The predominant dependence on

Fig. 5 Frequency distribution of the depth at which pursuit events occurred (depth zones where >90% of the pursuits occurred are indicated by *pale cylinders*)

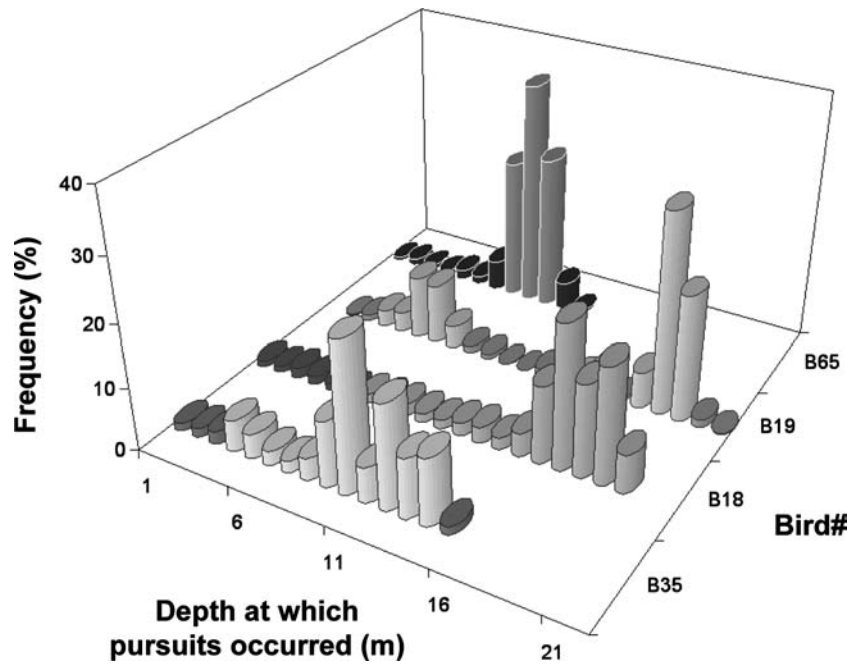
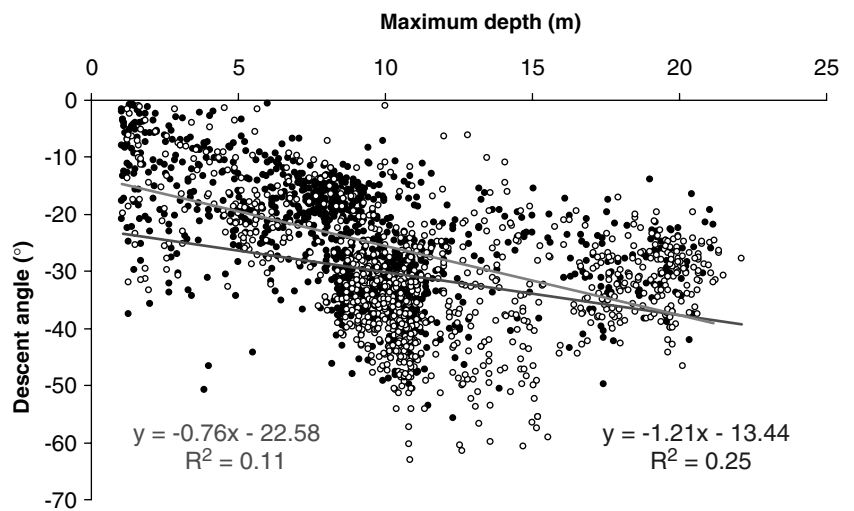


Fig. 6 Descent angles of cruise (*black circles*) and pursuit dives (*white circles*) as a function of the maximum depth of the dives. Regression lines, equations and coefficient of determination for cruise (*dark grey*) and pursuit dives (*light grey*) are shown



near-bottom-dwelling fish, however, may account for the fact that the difference in dive angles is small.

The use of miniature accelerometers has allowed us access to the fine-scale underwater activity and to allude to prey encounter rate in free-ranging Little Penguins. The possibility of inferring prey-predator interactions from the analysis of the behaviour of the predators means that we are now potentially able to assess the foraging efficiency of individuals. Future studies should focus on verifying the extent to which our use of accelerometry is justified as a measure of prey encounter so that large numbers of similar datasets could subsequently be collected.

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