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Diel shift of king penguin swim speeds in relation to light intensity changes

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ABSTRACT: It is generally expected that animals, including marine organisms, travel at speeds achieving the minimum energetic cost of transport. However, several factors cause variation in speeds within the energetically acceptable range. Light intensity is known to affect movement speeds in some flying and walking insects, which reduce speeds at low light levels. This is explained as compensation for degraded temporal resolution of vision in dim light by maintaining the rate of information gained per unit of travelling distance. Such a relationship between ambient light intensity and movement speeds is expected for any visual system in principle, but has not been examined in any marine species. As a mesopelagic forager, king penguins *Aptenodytes patagonicus* regularly commute between their breeding colonies and productive foraging areas over several hundreds of kilometres. During these trips, they experience a wide variation in light intensity between day and night, as well as within daylight hours, as dives often reach deeper than 100 m. The present study investigated diel patterns in the swim speeds of king penguins in relation to light intensity experienced within dives. King penguins gradually decreased their cruising speeds around dusk and increased them again around dawn. This resulted in consistently slower speeds in nocturnal dives. Correspondingly, the underwater light levels estimated were always higher in diurnal dives, even at depths greater than 100 m. The slower swim speeds after dusk may facilitate travelling and occasional prey detection in the dark. These results suggest that a common behavioural response to ambient light levels has evolved in different taxa of animals.

KEY WORDS: Bio-logging · Diel cycle · Diving behaviour · Foraging · Movement · Penguins · Vision

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INTRODUCTION

For animals travelling in the marine environment, speed is one of the parameters that should be optimized for energetically efficient movements. However, there are likely to be some factors causing variation of speeds within the energetically acceptable range. Among terrestrial organisms, some insects are known to change their flight/walking speeds depending on light intensity; they reduce speeds under low light conditions (Menzel 1981, Spiewok &

Schmolz 2006, Narendra et al. 2013, Reber et al. 2015). This is explained in relation to the temporal summation of neural responses in visual systems. Under dim light, where the absolute number of photons is small, temporal resolution of vision decreases because animal visual systems are thought to temporally integrate visual signals to improve the signal-to-noise ratio. One of the solutions to this is to slow down movement speeds, which enables the animals to maintain the rate of information gained per unit of travelling distance (Spiewok & Schmolz

2006, Reber et al. 2015). Such a relationship between ambient light intensity and movement speeds is expected for all visual systems in principle (cf. Warrant 1999, Warrant & Lockett 2004; but also see Baird et al. 2015).

Diving seabirds, such as penguins, are generally considered to be visually guided in their foraging (Wilson et al. 1993, Cannell & Cullen 1998, Zimmer et al. 2008, Regular et al. 2011), although some seabirds may use non-visual information according to circumstances (White et al. 2007, Regular et al. 2011, Martin & Crawford 2015). Dive depths of seabirds are often reported to present diel changes, i.e. deep in diurnal dives and shallow in nocturnal dives, associated with ambient light intensity at depth and/or diel vertical migration of prey resulting from changes in underwater light conditions (e.g. Wilson et al. 1993, Regular et al. 2010). Thus, diving behaviours of seabirds are directly or indirectly affected by ambient light conditions. However, other fine-scale behavioural adjustments between diurnal and nocturnal dives are not yet fully understood.

The king penguin *Aptenodytes patagonicus* is a large avian diver often foraging at depths greater than 100 m (Williams 1995). Additionally, as central place foragers, they regularly commute between their breeding colonies and productive foraging areas such as frontal zones over several hundreds of kilometres (Bost et al. 1997, Pütz et al. 1998). Because these foraging trips can last for more than 1 wk during brooding periods (Bost et al. 1997, Charrassin & Bost 2001), they spend both day and night at sea. A strong diel pattern of dive depth has been reported in king penguins; they rarely dive deeper than 40 m during nighttime, while often diving deeper than 100 m during daytime (Kooyman et al. 1992, Bost et al. 2002). Thus, they experience a wide variation in light intensity between diurnal and nocturnal dives,

as well as within diurnal dives, of more than 5 orders of magnitude (Martin 1999, Bost et al. 2002). In the present study, we investigated diel changes of behaviours within dives in king penguins, using novel data sets of swim speed, acceleration and dive path. We analysed the change in swimming behaviours during diving in relation to the ambient light intensity experienced within each dive. We show how king penguins may adjust their underwater cruising speeds within a range reasonable for cost-efficient transit, depending on ambient light conditions.

MATERIALS AND METHODS

Field study

Field experiments were performed at Possession Island (46° 25' S, 51° 45' E), Crozet Archipelago, South Indian Ocean, from late January to early March in 2011. Chick-rearing king penguins were spotted at their nesting site and caught at the edge of the colony (Baie du Marin, Grande Manchoitière, 16 000 pairs) just before departing for the sea after the return of their partner. We used a hooked pole to capture birds and a hood to decrease the stress of capture. Multi-channel data loggers (W1000L-3MPD3GT, 166 mm in length, 26 mm in diameter, 132 g in air; Little Leonardo) were deployed on the lower back of the birds (N = 9) with waterproof tape (Tesa tape, 4651; Tesa), stainless steel cables (4.5 mm in width, STB-360S; HellermannTyton) and instant glue (Loctite, 401; Henkel) to record diving behaviours during foraging trips at sea. The data loggers recorded depth based on ambient pressure (m), ambient temperature (°C), swim speed (m s^{-1}), 3-axis magnetism (nT) at 1 Hz, and 3-axis acceleration (m s^{-2}) at 8 Hz for 2 birds and 16 Hz for the other birds (Table 1). For

Table 1. Summary of bio-logging data for instrumented king penguins *Aptenodytes patagonicus* at Crozet. Dates given as dd/mm/yy

Bird ID	Date and time (h)			Trip length (d)	Data length (d)	Data length/ trip length	No. of dives	Longest dive (min)	Deepest dive (m)	Dive path	Notes
	First dive	Recapture	Last recording								
K1	27/01/11 01:00	08/02/11 12:00	02/02/11 18:00	12.5	6.7	0.54	1252	7.8	244.0	Yes	
K2	29/01/11 05:00	12/02/11 15:00	05/02/11 06:00	14	6.7	0.48	1311	7.0	241.5	No	
K3	30/01/11 13:00	21/02/11 19:00	05/02/11 23:00	22.3	6.4	0.29	1208	7.6	205.8	Yes	GPS logger
K4	29/01/11 19:00	09/02/11 12:00	06/02/11 03:00	10.7	7.3	0.68	1695	7.5	259.8	Yes	
K5	31/01/11 05:00	22/02/11 17:00	06/02/11 14:00	22.5	6.1	0.27	1654	5.1	182.0	Yes	GPS logger
K6	12/02/11 04:00	23/02/11 19:00	23/02/11 19:00	11.6	11.6	1.00	3346	8.4	318.0	Yes	Acc. at 8 Hz
K7	–	–	–	–	–	–	–	–	–	–	No trip
K8	18/02/11 12:00	03/03/11 14:00	25/02/11 18:00	17.0	7.3 ^a	0.43	1395	7.6	272.8	No	Oesophagus logger
K9	17/02/11 16:00	04/03/11 09:00	02/03/11 13:00	14.7	12.9	0.88	3648	9.7	366.2	Yes	Acc. at 8 Hz

^aRecording started 96 h after deployment

2 birds, a GPS data logger (CatTrack, recustomized with a 1500 mAh lithium-iron phosphate battery and a deep depth casting; final size was ca. $60 \times 40 \times 25$ mm, 50 g in air) was also deployed on the upper back (Table 1). These GPS tracking data were not used in this paper. For another bird, an oesophageal temperature logger was also deployed in addition to the multi-channel data logger, of which a temperature sensor was placed in the oesophagus and the body of the logger itself was inserted into the stomach (see methods in Charrassin et al. 2001) (Table 1). After deploying the loggers, all birds were released at the beach from which they departed. The birds were recaptured after their return from foraging at sea, and the data loggers and attachment tape were removed.

Data processing

Data were analysed using IGOR Pro (WaveMetrics) with the program package Ethographer (Sakamoto et al. 2009) and R (R Core Team 2014).

Dives were defined as submerging deeper than 2 m for longer than 30 s, and shallow dives corresponded to dives <40 m depth (Charrassin et al. 2002). Nocturnal dives were defined as dives that started during periods between 1 h after sunset and 1 h before sunrise. Sunrise and sunset times, which are defined as times of day when the top of the sun is on the horizon, were downloaded from the Hydrographic and Oceanographic Department of Japan Coast Guard website (www1.kaiho.mlit.go.jp/KOHO/automail/sun_form3.html). For sunset and sunrise times, those at the breeding colony for the corresponding dates were used because it was not possible to estimate accurate positions of king penguins at sea from our data sets. As variations of sunrise/sunset times within a potential range of trips are less than 20 min (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m561p233_supp.pdf), we consider that the use of data for the geographic position of the colony did not influence the results.

Swim speeds relative to water were recorded as the number of rotations of an external propeller on the data logger (rev s^{-1}), which was converted to absolute speeds (m s^{-1}) using a constant value. The value of the constant was chosen so that depth profiles calculated from swim speeds and pitch angles at each time became consistent with actual depth profiles measured by a pressure sensor (Shiomi et al. 2008). Resolution of swim speed data corresponding to 1 rotation of the propeller ranged from 0.019 to 0.025 m s^{-1} .

After the data conversion, mean swim speed within a dive was calculated. Because the rotation of the propeller seemed to slow or stop in some dives, which was seen as inconsistent with acceleration data presenting continuous strokes, dives with mean swim speed below a threshold of 1.0 m s^{-1} were excluded from the further analyses. The threshold was determined by visually checking a plot of average swim speed against stroke rate within a dive.

Three-dimensional dive paths were calculated with a customized macro available online (Narazaki & Shiomi 2010, Shiomi et al. 2010) using the data of magnetism, acceleration derived from gravity, swim speed and depth (Johnson & Tyack 2003, Shiomi et al. 2008). For that purpose, gravitational components of acceleration were extracted by a low-pass filter with a threshold value of 0.5 Hz. From the reconstructed dive paths, horizontal travel distance and straight-line distance from the start to the end points of each dive were calculated.

King penguins performed flipper stroke-and-glide swimming. As an index of muscle workload during a dive, the number of strokes was calculated using the longitudinal acceleration data (cf. van Dam et al. 2002, Williams et al. 2004). First, by removing the component of gravitational acceleration from the longitudinal acceleration data, it was possible to obtain the dynamic part of the acceleration caused by body movements and changes of swimming speed. Then, total number of strokes per dive was measured by counting regular peaks in the dynamic acceleration data on the longitudinal axis, which reflect stroking activity associated with the change of propulsive forces (Shiomi et al. 2012). We defined a set of up- and down-beats as 1 flipper stroke.

Data from the oesophageal temperature logger on bird K8 were used to measure feeding activities during shallow dives. Decreases in oesophageal temperature are considered a reliable index of feeding events (Charrassin et al. 2001). Defining a change of $-0.06^\circ\text{C s}^{-1}$ in oesophageal temperature as a threshold to extract the feeding events (cf. Charrassin et al. 2001), the number of feeding dives was counted in bird K8. We defined abrupt drops of swim speed by values $<-0.4 \text{ m s}^{-2}$ (cf. Ropert-Coudert et al. 2000) as related to feeding events (see 'Results').

Statistical analyses

To examine whether diving behaviours were different between day and night, mixed model approaches were applied. Two models with and with-

out day/night effect as a fixed factor were fitted to each combination of parameters from each individual. In all models, date of each dive was included as a categorical random factor. Then, a parsimonious model was determined by comparing Akaike's information criterion (AIC) values of the 2 models. Parameters and types of applied models are listed in Table 2. We used the lmer and the glmer functions in R package 'lme4' (Bates et al. 2014) for linear mixed model and generalized linear mixed model analyses, respectively; for non-linear mixed model analyses, the non-linear mixed effect (nlme) function in R package 'nlme' (Pinheiro et al. 2014) was used.

Diel change in diving behaviours

To quantitatively investigate the diel changes in swim speeds, a double-sigmoid model (see Eq. 1) was fitted to mean swim speeds (S_{mean}) against times of day at the start of each dive (T) using the nlme function in R package 'nlme' (Pinheiro et al. 2014):

$$S_{\text{mean}} = s_n + s_d / \{1 + \exp[(t_1 - T)/c_1]\} - s_d / \{1 + \exp[(t_2 - T)/c_2]\} \quad (1)$$

where s_d is the asymptotic height, corresponding to an estimate of the difference of mean swim speeds between nocturnal and diurnal dives, s_n is the mean swim speed in nocturnal dives, t_1 and t_2 are the times during the day at which mean swim speed reaches the middle values between nocturnal and diurnal speeds, and c_1 and c_2 are the steepness factors, corresponding to the time elapsed between reaching 1/2 and 3/4 of s_d . This model is modified from the one used by Bunnefeld et al. (2011). For comparison, the same model was also applied to dive depths (D_{max}) against T :

$$D_{\text{max}} = d_n + d_d / \{1 + \exp[(t_3 - T)/c_3]\} - d_d / \{1 + \exp[(t_4 - T)/c_4]\} \quad (2)$$

where d_d is the asymptotic height, corresponding with an estimate of the difference in mean dive depths between nocturnal and diurnal dives, and d_n is the mean dive depth in nocturnal dives. Coefficients t_3 , t_4 , c_3 and c_4 have the same meaning as t_1 , t_2 , c_1 and c_2 , respectively. Note that only dives deeper than 40 m were used for twilight and daylight periods in this regression analysis, because changes of the upper limit of dive depth around dawn and dusk were the focus of this study.

Diel change in light intensity

To study vertical and temporal variation in light levels experienced in each dive, underwater light intensity was estimated by an astronomical model, following Regular et al. (2011). This model was based on Iqbal (1984) for estimation of solar irradiance and on Jensen et al. (2001) for estimation of lunar and star irradiance at night. Results of this model calculation were previously validated with data of light intensity measured by a light sensor on diving birds (Regular et al. 2011). In the present study, the light level at the maximum depth reached within each dive was calculated as a function of date, time of day and depth. We used an attenuation coefficient of 0.03, which was the average value measured by light sensors on southern elephant seals at sea around Kerguelen Island, i.e. near our field site (Jaud et al. 2012). The coefficient to include effects of atmospheric absorption of light was determined as 0.25, which means that 1/4 of the light above the atmosphere is assumed to reach the Earth's surface. This coefficient affects absolute values of estimation but not relative relationships of values between diurnal and nocturnal dives. Note that because the model does not cope with twilight periods, only diurnal and nocturnal dives were used for this analysis.

Table 2. Summary of the models fitted to examine differences between diurnal and nocturnal diving behaviours. Estimated coefficients are presented as a and b . All models include day/night as a fixed effect and date as a random factor for coefficient b

Model ID	Dependent variable (Y)	Fixed effect (X)	Type of model
Model 1	Mean swim speed		Linear mixed model ($Y = b$)
Model 2	Total no. of strokes		Generalized linear mixed model (error distribution = Poisson, log link function, offset = $\ln(\text{dive duration})$) ($Y = \exp(b + \text{offset})$)
Model 3	Dive duration	Dive depth	Non-linear mixed model ($Y = aX^b$)
Model 4	Straight-line distance	Travelled horizontal distance	Non-linear mixed model ($Y = aX^b$)

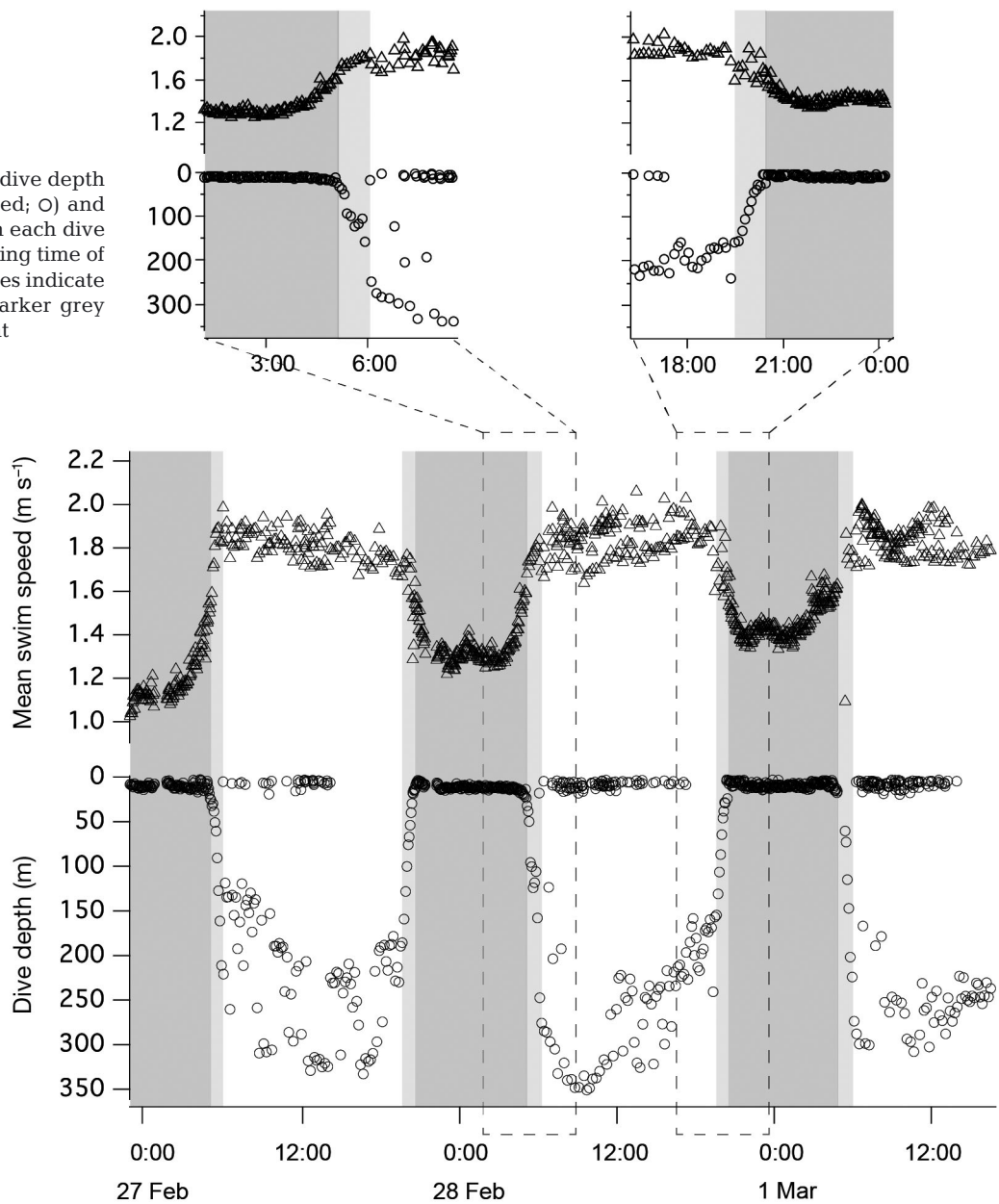
RESULTS

For 6 of the 9 instrumented birds, all the parameters were successfully recorded; for 2 other birds, all the data except magnetism were obtained, i.e. dive paths could not be calculated; another bird did not leave the colony and was excluded from the dataset (Table 1). The data from 1 bird (K6) covered a whole trip, while those from the other birds covered around 30 to 90% of the foraging trip (Table 1). One of the birds (K9) recorded both the longest (9.7 min) and the deepest (366.2 m) dives among those reported for this species in summer.

Diel change in diving behaviours

Of all dives recorded during the 24 h diel cycle, $71 \pm 11\%$ (mean \pm SD, $N = 8$ birds) of dives in each bird were diurnal, $20 \pm 11\%$ nocturnal and $9 \pm 2\%$ during twilight periods. During the night, the mean diving depth of each bird was 5.6 to 19.9 m, and all except for a few dives were shallower than 40 m. During the day, there were dives both deeper and shallower than 100 m; most of the latter were shallower than 40 m, similar to nocturnal dives (Fig. 1). Dive depths gradually increased during dawn and decreased during dusk (Fig. 1).

Fig. 1. Example data of dive depth (maximum depth reached; \circ) and mean swim speed (Δ) in each dive plotted against the starting time of the dive. Light grey zones indicate twilight periods, and darker grey indicates night



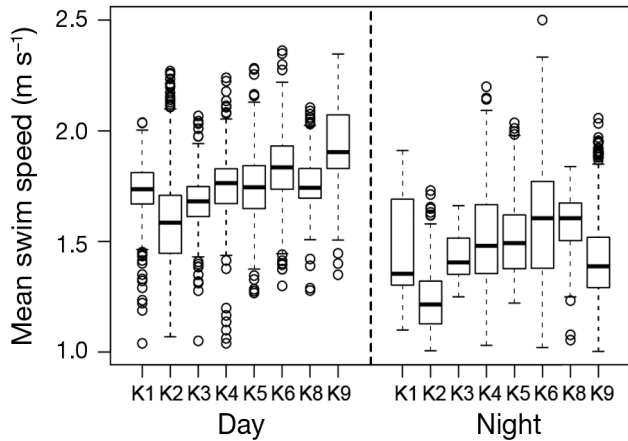


Fig. 2. Box plots of mean swim speeds in diurnal shallow and nocturnal shallow dives for each individual ($N = 8$ birds, see Table 1). Bottom and top of each box correspond to lower and upper quartile values, respectively. Black horizontal line within each box represents the median. Whiskers represent 1.5 times the interquartile range, and circles indicate outliers beyond this range

Swim speeds also showed diel patterns (Fig. 1). Swim speeds within a shallow dive were relatively constant, while those in deep dives dramatically varied at depth (see Ropert-Coudert et al. 2000 for details). Therefore, only shallow dives were used when comparing day and night behaviours. Mean swim speed in each shallow dive was lower at night than in the day for all birds (mean difference: $0.3 \pm 0.10 \text{ m s}^{-1}$; grand mean speed: $1.7 \pm 0.07 \text{ m s}^{-1}$ vs. $1.4 \pm 0.10 \text{ m s}^{-1}$; Fig. 2, Table 3, Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m561p233_supp.pdf). Swim speeds gradually increased towards the daytime and decreased towards nighttime, respectively (Figs. 1 & 3).

The double-sigmoid models showed temporal patterns of both mean swim speeds and dive depths: both parameters increased around sunrise

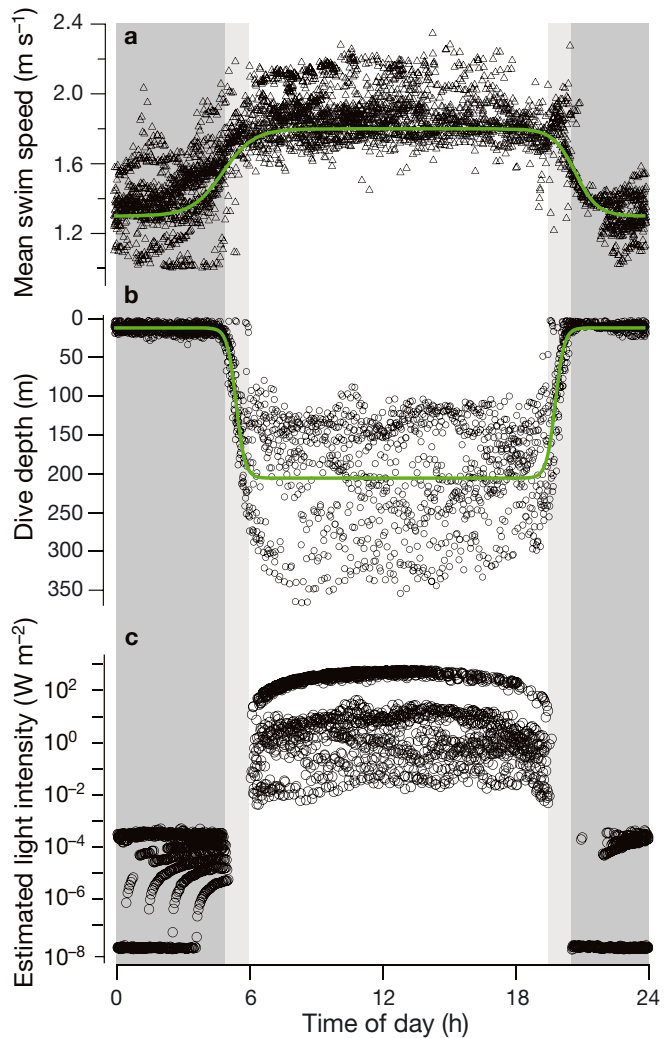


Fig. 3. (a) Mean swim speeds, (b) dive depths and (c) estimated light intensity at the maximum depth in each dive plotted against time of day for bird K9. Light grey zones indicate twilight periods, and dark grey indicates night. Green lines represent the double-sigmoid models fitted by a non-linear mixed model approach. Note that for diurnal and twilight dives in (b), only dives deeper than 40 m were used, because the upper limit was the main focus

Table 3. Swim speed and stroke rate estimated with mixed models for each individual. Swim speeds were estimated as the intercept of Model 1, and stroke rates as the slope of Model 2 (see Table 2, Fig. 4a)

Bird ID	Body mass (kg)	No. of dives			Swim speed (m s^{-1})			Stroke rate (Hz)	
		Deep day	Shallow day	Shallow night	Deep day mean	Shallow day mean	Shallow night mean	Shallow day	Shallow night
K1	12.1	135	893	45	1.8	1.7	1.4	0.79	0.64
K2	10.9	326	554	182	1.8	1.6	1.3	0.70	0.55
K3	9.3	317	669	99	1.7	1.6	1.4	0.84	0.64
K4	11.5	529	560	411	1.8	1.8	1.4	0.76	0.60
K5	10.3	249	994	243	1.8	1.7	1.5	0.94	0.76
K6	10.7	654	1519	918	1.8	1.8	1.5	0.83	0.68
K8	8.9	794	204	283	1.9	1.7	1.6	0.83	0.72
K9	11.3	1104	889	1377	1.8	1.8	1.4	0.91	0.59
Mean	10.6				1.8	1.7	1.4	0.82	0.65

Table 4. Estimates of coefficients obtained by fitting double-sigmoid models to mean swim speeds and dive depths against time of day (see Fig. 3a,b). Blanks mean that it was not possible to estimate coefficients due to lack of data for some times of day. Note that the number of dives analysed differs between mean swim speed and dive depth because different numbers of dives were excluded from each analysis, due to stalling of a propeller for swim speeds and shallow dives during daylight and twilight periods for dive depths (see text for details)

Bird ID	No. of dives	Mean swim speed						No. of dives	Dive depth						
		s_n	s_d	t_1	t_2	c_1	c_2		d_n	d_d	t_3	t_4	c_3	c_4	
K1	1140							251							
K2	1202	1.2	0.5	4.5	21.3	0.2	0.1	702	10.6	131.2	4.8	20.7	0.2	0.2	
K3	1207	1.4	0.3	4.6	21.4	0.2	0.2	503							
K4	1658							1081	10.9	157.5	4.8	20.6	0.2	0.2	
K5	1651							535	5.8	97.2	5.4	20.8	0.5	0.2	
K6	3319	1.4	0.4	4.5	21.6	0.4	0.8	1727	11.8	176.8	5.3	20.2	0.2	0.2	
K8	1390	1.4	0.5	5.2	20.6	0.4	0.4	1168	17.8	140.4	5.2	20.0	0.2	0.3	
K9	3613	1.3	0.5	4.9	20.8	0.7	0.5	2682	12.1	193.5	5.5	19.9	0.2	0.2	
Mean		1.3	0.4	4.7	21.2	0.4	0.4		11.5	149.4	5.2	20.4	0.3	0.2	

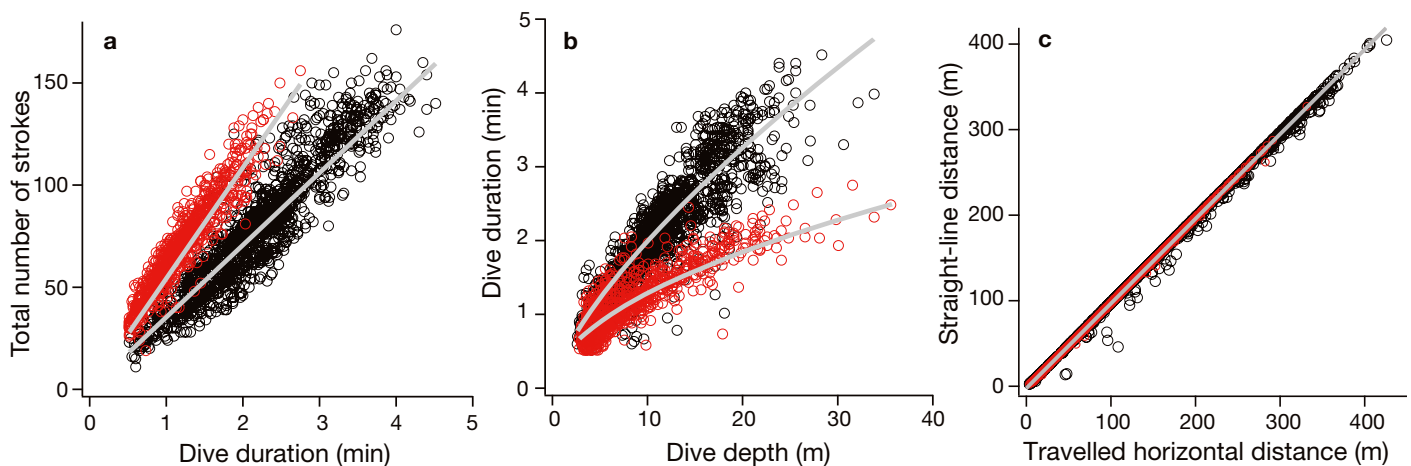


Fig. 4. Relationships between (a) total number of strokes in a shallow dive and dive duration, (b) dive duration and dive depth, and (c) straight-line and travelled horizontal distance from the start to the end of each dive for bird K9. Diurnal shallow dives (○) and nocturnal shallow dives (○) are shown. Grey lines show fitted models for each relationship (see Table S2 in the Supplement at www.int-res.com/articles/suppl/m561p233_supp.pdf)

and decreased around sunset, respectively (Fig. 3a,b, Table 4). However, swim speeds started to increase earlier and to decrease later than dive depth, according to the estimated coefficients t_{1-4} (Table 4). In most cases, rates of change during these transition periods (coefficients c_{1-4}) were smaller in the models for swim speeds (Table 4).

Characteristics of flipper stroke activities during diurnal and nocturnal shallow dives corresponded with those of swim speeds. Thus the total numbers of strokes during dives were smaller at night (for a given dive duration), indicating a lower stroke rate (Fig. 4a, Table 3). For all except 1 individual, dive durations to a given depth were longer in nocturnal dives (Fig. 4b, Tables S1 & S2).

Dive paths and oesophageal temperature in shallow dives

Estimated dive paths of the 6 birds during shallow dives showed that the maximum horizontal distance king penguins could travel in a typical shallow dive was around 400 m (Fig. 4c). Estimated exponents of the mixed models for the relationship between straight line and travelled distance were nearly equal to 1.0 (range 0.92 to 0.96; Table S2), which means that the birds swam horizontally on a nearly perfect straight line. A significant effect of day/night was not found, except for 1 bird (Table S1).

In dives of the bird for which oesophageal temperature was recorded (K8), drops of temperature,

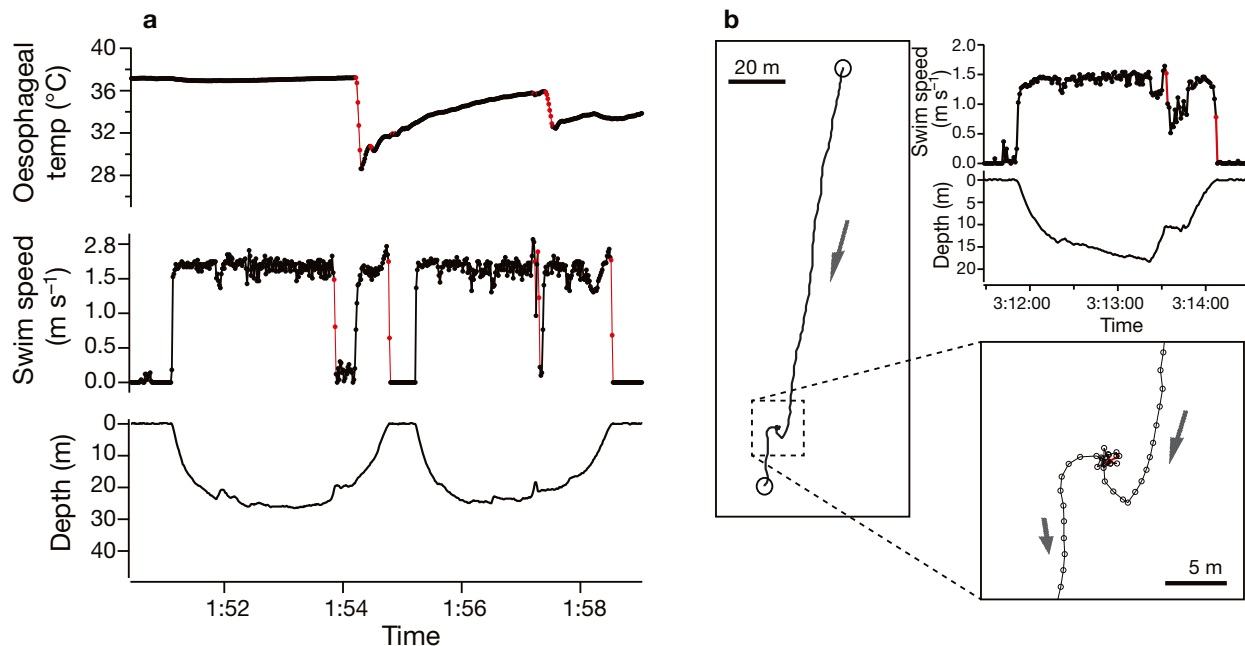


Fig. 5. (a) Time-series data of oesophageal temperature, swim speed and depth in bird K8 and (b) horizontal paths and time series data of swim speed and depth in a nocturnal dive of bird K9 when rapid decrease in swim speeds occurred. In (b), circles indicate the start and end points of the dive, arrows indicate travelling direction and red points indicate the data where rate of changes in swim speeds was below -0.4 m s^{-2}

i.e. the signal of feeding events, were observed in some shallow dives (Fig. 5a). Of the 17 shallow dives in which such temperature decreases occurred, 14 were nocturnal. The dives associated with oesophageal temperature decreases for this bird corresponded to 4.9% of all the nocturnal dives recorded during its foraging trip. Among these 14 dives, 13 also showed rapid and short drop in swim speed (Fig. 5a). Such drops in swim speed occurred in 12.7% (36 dives) of the nocturnal dives in bird K8, while swim speeds were basically kept constant within nocturnal dives as well as diurnal shallow dives. Rapid decreases in swim speeds were also observed in 2.0 to 12.6% of nocturnal shallow dives in the other individuals. On the few nocturnal dives where that occurred, dive paths concurrently became tortuous (Fig. 5b).

Diel change in estimated light intensity

According to the astronomical model, light intensity experienced in each dive varied from 10^{-8} to 10^{-3} W m^{-2} at night and from 10^{-2} to 10^3 W m^{-2} in the day (Fig. 3c). In deep dives during daylight hours, even to >300 m, light intensities were still higher than those in nocturnal shallow dives.

DISCUSSION

The present study revealed strong diel patterns in diving behaviours of king penguins, not only in dive depth but also in swim speed, stroke rate and dive duration. The nocturnal dive depths were limited to shallow water, in agreement with previous studies (Kooyman et al. 1992, Bost et al. 2002), and the birds swam more slowly with a lower stroke rate at night for longer dive durations. Some diving mammals have been reported to decrease their swim speeds in nocturnal dives, but the differences were observed during the bottom phases, i.e. foraging (e.g. Baikal seals, Watanabe et al. 2004; sperm whales, Aoki et al. 2007). These changes were, therefore, interpreted as optimization of foraging behaviour following a diurnal shift of prey species and/or changes in prey density, based on a theoretical model (Wilson et al. 2002). In king penguins, a decrease in swim speeds is likely to be attributable to a different reason. Their swim speeds were indeed lower at night compared to those during the day, not only during the bottom phase but throughout the entirety of a nocturnal dive. In addition, horizontally straight paths in their shallow dives indicated that the main function of these dives was transit rather than foraging, both in the day and at night.

As the main foraging area of king penguins is the Polar Front Zone, about 400 km from their colony (Bost et al. 2009), they are expected to have a strong motivation for horizontal movements between the destination of the foraging trips and the breeding island. The number of feeding events recorded as rapid changes in oesophageal temperature and/or swim speeds showed that they caught prey during nocturnal shallow dives, but only occasionally. Previous studies presented similar evidence that feeding in shallow water occurs in only a small proportion of nocturnal dives (Pütz & Bost 1994). The bulk of king penguin diet consists of myctophid fish during the summer season (Cherel & Ridoux 1992), and these small, mesopelagic fish are known to perform diel vertical migration (Perissinotto & McQuaid 1992, Collins et al. 2008). During daylight hours, they aggregate and rest mostly at great depths, i.e. >100 m. At night, myctophids actively disperse to near-surface waters in large numbers (Perissinotto & McQuaid 1992, Collins et al. 2008), although prey species of king penguins occupy only a small part of fish biomass in shallow water at night (0.2%; Bost et al. 2002). The main prey fish for king penguins is likely to have photophores (Bost et al. 2002), but it is expected to reduce intensity of bioluminescence during the night because the main function of photophores in myctophids is to camouflage their bodies from below by counter-illumination (Case et al. 1977). This high activity and low visibility of prey at night are probably the reasons why feeding in nocturnal shallow dives is rare in king penguins and why they mainly forage in diurnal deep dives (Pütz & Bost 1994, Bost et al. 2002).

King penguins have eye structures adapted to the dim light experienced at depth and at night, as their eye size is relatively large and their pupil can expand 300 times larger in the dark than the smallest size during the daylight (Martin 1999). However, as light levels experienced in nocturnal dives were estimated to be much lower than those in diurnal dives, even when reaching 100 to 300 m depth, additional behavioural adjustments should be adaptive. The difference in mean cruising speeds between diurnal and nocturnal shallow dives (1.7 vs. 1.4 m s⁻¹ on average in this study) means that, when the birds swam at night, it took about 1.2 times longer to travel a given distance than when swimming during the day. During travelling and opportunistic feeding in darkness, lower swim speeds would be beneficial, maintaining the rate of information gained per unit of travelling distance despite the temporal integration of visual signals.

Gradual decreases and increases in mean swim speeds, as well as differences in underwater light intensities between day and night, support the hypothesis that changes in swim speeds are linked with ambient light conditions. To date, such temporal transitions in swim speeds have not been documented in any aquatic animals. Swim speeds did not start to shift at the same time as the dive depths, but started to increase earlier in the morning and to decrease later at night than did dive depths. Thus, it would appear that light intensity, either via a threshold or an intensity-linked mechanism, might modulate both swim speeds and dive depths. For example, light intensity itself and diel vertical migration of prey following changes in light intensity may trigger the observed shift of swim speeds and dive depths, respectively. In either case, these temporal patterns indicate that king penguins adjust their swim speeds in response to changes in ambient light conditions.

The lower stroke rate found in nocturnal shallow dives further confirmed king penguins actively changed their locomotion patterns between day and night, resulting in a difference in swim speeds. As an additional effect of the slower swimming at night, the lower mechanical cost per unit of time with the lower stroke rate could prolong dive duration (cf. Hindell et al. 2000). Thus, the longer depth-specific dive durations of night dives (in 6 of the 8 studied birds) seem to stem from reduced power costs due to the lower swim speeds (Culik et al. 1996), which themselves may compensate for the shorter travelling distance per second with lower swim speeds under the limited light conditions. In the congeneric emperor penguin *Aptenodytes forsteri*, the durations until starting to return to the water surface are also longer when the penguins swim at lower stroke rate (Shiomi et al. 2012). These data indicate a trade-off between dive duration and rate of energy consumption in avian air breather foragers with limited oxygen stores.

To conclude, this study showed diel shifts in swim speeds of king penguins. They may adjust their swim speeds within a range reasonable for cost-efficient transit, depending on ambient light conditions. To date, this phenomenon has not been studied in any marine diving animals, although it is well known in some insects. Future studies may provide evidence that this behaviour is common in other marine taxa.

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