Assessing performance constraints in penguins with externally-attached devices

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ABSTRACT: Externally-attached transmission and logging devices have greatly helped elucidate the biology of free-living animals over the last 50 yr. However, such devices may hinder animals so that the behaviour monitored is not representative of unequipped conspecifics. We suggest that if animals are equipped with devices of varying size, the change in recorded parameters with size can be used to extrapolate to the condition in unencumbered animals. Use of this approach with Adélie penguins *Pygoscelis adeliae* showed that unequipped birds are predicted to range farther, swim faster, dive deeper and be more efficient underwater than equipped birds. The derived data not only set baseline information for the species concerned but also allow us to put the deleterious effects of the devices into perspective.

KEY WORDS: Data-logger impact · Bio-logging · Spheniscids · Adélie penguins · *Pygoscelis adeliae* · Swim speed · Diving performance · Foraging

INTRODUCTION

The attachment of transmitting or recording devices to animals, either as transmitters or recorders, has already proved pivotal in elucidating the biology of a large number of species that are difficult to observe directly (cf. Ropert-Coudert & Wilson 2005). Indeed, advances in solid-state technology have been so rapid over the last 2 decades that animal-attached loggers are currently transforming our knowledge of the behaviour, physiology and ecology of animals in the wild more than ever before (for reviews, see Cooke et al. 2004, Ropert-Coudert & Wilson 2005). The benefits of this approach range from conservation (e.g. Shimazaki et al. 2004) to elucidation of optimised foraging strategies (e.g. Wilson et al. 2005) and make a compelling case for the use of such devices.

The considerable advantages that such methods have for studying animals in the wild, away from the confines of the laboratory, are, however, marred by the potential that the devices have for modifying the behaviour of their carriers. Since the emergence of device-attached sensing, the generic problem of measurement affecting performance (Wilson et al. 1986) has led to workers increasingly attempting to document the effects of devices (for review, see Calvo & Furness 1992). For instance, attaching a device to the body of a penguin alters its streamlining, which in turn affects its swim speed (Wilson et al. 1986). Since the time penguins can remain underwater depends on body oxygen stores and the rate at which they are used up (Butler & Jones 1997), this latter being a direct function of energy expenditure (Schmidt-Nielsen 1972), it is to be expected that altered streamlining will affect dive durations. Penguins with attached devices should dive less efficiently, which may impact dive depths (cf. Ropert-Coudert et al. 2000) and/or foraging range. Such limitations would have a drastic influence on the ability of penguins to collect food, since ca. 73% of food items are captured during the bottom phase (i.e.
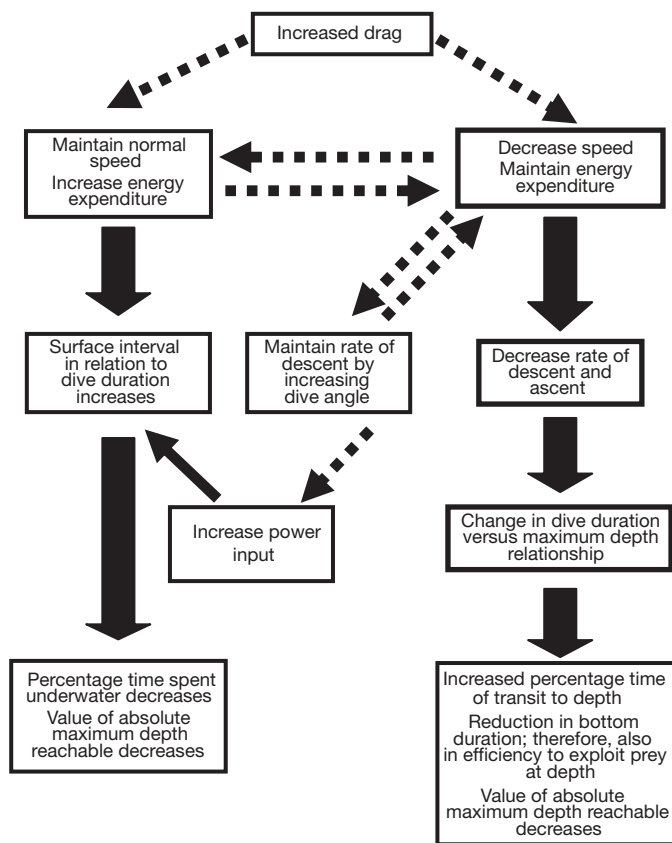
Fig. 1. *Pygoscelis adeliae.* Schematic diagram of how the attachment of external devices to penguins may affect their foraging. Dotted arrows show options open to the birds while solid arrows show consequences

Understanding of the cascade is important because it helps elucidate the behaviour of both equipped and unequipped animals (Wilson et al. 1986, Ropert-Coudert et al. 2000, Wilson & McMahon 2006), which is critical because measurements made from device-equipped animals are intended to exemplify the norm (cf. Moorhouse & Macdonald 2005). In this regard, researchers should adopt an approach that aspires to estimate the activity that would be expected from an unencumbered animal.

In this work, we examined the effect that externally-attached devices of 2 different sizes have on the diving behaviour and body mass gain of a diving endotherm, the Adélie penguin *Pygoscelis adeliae*, and put our findings into context by attempting to derive the behaviour that defines the species 'norm'. For this, we regressed (device-measured) performance against device size for animals equipped with devices of varying sizes so that the value at the intercept could be derived (Wilson et al. 1986, Wilson & McMahon 2006). This procedure is particularly apt where animals carrying devices might expend extra energy for locomotion, such as in birds flying with added mass (Obrecht et al. 1988) or marine animals subject to extra drag (Bannasch et al. 1994). Although we used data from a study that was not originally primarily designed to test for the effects of devices on penguins, i.e. we only used 2 different device sizes, the devices did comprise different percentage cross-sectional areas compared to those of the carriers so we expected to see corresponding variation in diving performance (cf. Bannasch et al. 1994).

around the point of maximum depth) of dives (Ropert-Coudert et al. 2001). This has profound implications on the energy allocation by birds to their survival and their reproduction.

Although the proximate (e.g. reduction in swimming speed; Wilson et al. 1986) and ultimate consequences (e.g. a reduction in the breeding success; Ballard et al. 2001) of modifying the streamlining of a bird have been highlighted in some studies (see above), our understanding of the decision-making process of individual birds in facing these impediments is still fragmentary. However, we propose that penguins may adopt 1 of 2 likely scenarios when equipped with external devices; they may maintain normal speeds with increased power requirements, or maintain normal power requirements by decreasing speed (Fig. 1). From this initial decision, a cascade of reactions is to be expected, but the detailed process of this cascade has not been examined with regard to the consequences that it may have on the foraging and breeding efficiency of penguins.

MATERIALS AND METHODS

The study was conducted from 18 December 2001 to 04 January 2002 on breeding Adélie penguins in Dumont d'Urville, Adélie Land (66.7° S, 140.0° E), Antarctica. In total, 14 birds, raising 1 or 2 small chicks (guard phase), were equipped with 2 different types of data-loggers. One group (n = 7 birds) was fitted with small loggers (hereafter referred as the SMALL group) and the other one (n = 7 birds) with large loggers (the BIG group). BIG loggers consisted of cylindrical, 3-channel W200-PDT loggers (102×22 mm, 50 g, Little Leonardo) which measured speed and depth at 1 Hz, while SMALL loggers consisted of miniaturised, cylindrical, 4-channel, M190-D2GT data loggers (53×15 mm, 17 g, Little Leonardo), which recorded depth (1 Hz) and acceleration (16 Hz) along the longitudinal and dorso-ventral axes of the birds (see Yoda et al. 2001).

Device deployments occurred in 3 sessions with BIG and SMALL birds being equally represented during

December 2001 and January 2002. Birds were weighed to the nearest gram, and the head and bill length and flipper width and length were measured (to 1 mm) along with maximum thorax circumference (to the nearest 1 cm) to enable determination of the bird cross-sectional area, assuming a perfect circle at this point. Body condition index was calculated by dividing the body mass by the flipper length (Numata et al. 2000). Loggers were attached on the median line of the bird's back (Bannasch et al. 1994) using tape (Wilson et al. 1997). A group of 7 other birds that carried no data-loggers, identified with picric acid dye marks on the chest, was used as a control group, and their foraging trip duration was compared to that of birds from the SMALL and BIG groups.

After one foraging trip, devices were removed and the birds were reweighed before being stomach lavaged using water off-loading (Wilson 1984). The stomach contents were drained before being weighed to the nearest gram. Data downloaded from the loggers were analysed using IGOR software (Wave-metrics, version 5.0). Based on the resolution of the loggers, only dives ≥0.5 m were included in the analysis. A dive is classically considered to comprise 3 main phases: descent, bottom and ascent phases (e.g. Le Boeuf et al. 1986). The start and end of bottom phases were defined as the first and last time the rate of change of depth became <0.25 m s^{-1} during a dive. In the case of the BIG group, speed was measured via the number of rotations of a propeller mounted at the front end of the logger. The number of rotations per second was further converted into actual flow speed (in m s^{-1}) following the method of Blackwell et al. (1999), where the number of revolutions of the propeller per second is regressed against change in depth measured by the pressure sensor of the logger. A non-linear, least-squares (using the Levenberg-Marquardt algorithm; Press et al. 1988) equation relating the lowest number of rotations per second to the changes in depth was determined for each animal. Swim speed in the SMALL group was determined by examining dive angle with respect to the rate of change of depth (cf. Watanuki et al. 2003, Kato et al. 2006). First, body angle was calculated from the surge acceleration after removing the high frequency component of the acceleration signal by applying a 2-band, low-pass filter (0.5/1.0 Hz) to the data (IGOR Filter Design Lab, Wave-Metrics, Version 4) and correcting for the angle of logger attachment on the bird's body (cf. Watanuki et al. 2005, Kato et al. 2006). Body angle was thus re-sampled at 1 Hz, and swim speed (v) was calculated as:

$$v = r/\sin\theta \qquad (1)$$

where θ is the body angle and r is the rate of depth change, calculated as:

$$r_n = (d_n - d_{n-1})/(t_n - t_{n-1}) \qquad (2)$$

where d is depth and t is time over 1 s.

Note that swim speed and descent rates were calculated only during the descent phase of a dive because bird body angles do not necessarily represent trajectories during the ascent (cf. Blackwell et al. 1999).

A series of standard parameters was used to define diving. Durations of the descent, bottom and ascent phases, the swim speed of the descent phases as well as the duration of the surface pauses between dives were compared between SMALL and BIG groups. In addition, means of dive duration were calculated for each depth bracket (in ranges of 10 m). The duration values for each 10 m depth bracket from each bird were then used in a series of regressions against the cross-sectional area of the corresponding device as a percentage of the bird carrier (hereafter referred to as 'device size').

We used the residual maximum likelihood analyses (REML, Patterson & Thompson 1971) with individual as random effect in order to control for potential pseudo-replication. Simple regression was used to highlight trends. Slopes of regression lines were compared between the 2 groups with a General Linear Model. The statistical threshold was 0.05. Statistical tests were conducted using JMP and Systat (SAS Institute Inc., versions 5.1.1J and 10, respectively), as well as Statview (Abacus Concept, 4.57, 1996).

RESULTS

All birds were recaptured after one foraging trip and none had lost devices. The morphometric measurements of the birds from the SMALL group did not differ from those of birds from the BIG group, and neither did the initial body mass and body condition (Table 1). The mean frontal area of birds was 84.4 ± 3.1 cm^2, so that SMALL and BIG loggers accounted for 0.8% and 1.4% of the maximum cross-sectional area. In the following analysis, the percentage of the logger's cross-sectional area as a function of the bird's cross-sectional area was calculated for each individual penguin.

Trip duration. The duration of the foraging trip of birds ranged from 18.1 to 71.1 h (mean = 36.5 ± 13.7 h, n = 14 birds), and there was no significant difference between the SMALL, BIG and control groups (Table 1). After departing and before returning, birds with loggers of different sizes spent similar amounts of time outside of the colony without diving, performed a similar number of dives per trip and spent a similar amount of time underwater (Table 1).

Dive depth and duration. The average dive duration was not different between the 2 groups ($F_{1,14} = 0.02$, p =

0.89, BIG: 60.8 ± 20.0 s; SMALL: 59.6 ± 12.5 s). However, birds from the BIG group dove significantly shallower than those from the SMALL group (11.7 ± 5.2 m and 18.6 ± 5.1 m, respectively; $F_{1,14}$ = 6.37, p = 0.03),

with the maximum depth reached by the birds ranging from 51.4 to 136.4 m (SMALL) and 35.2 to 112.8 m (BIG). In both groups, dive duration increased significantly with maximum depth (SMALL group: $F_{1,65}$ =

Table 1. *Pygoscelis adeliae.* Comparisons of the morphometric measurements and parameters of the foraging trip between Adélie penguins equipped with BIG and SMALL loggers

	SMALL (n = 7)	BIG (n = 7)	Control (n = 7)	Statistical results
Morphometrics				
Body mass before the trip (kg)	4.69 ± 0.55	4.56 ± 0.69		t_{11} = 0.37, p = 0.72[a]
Body mass after the trip (kg)	5.01 ± 0.39	4.84 ± 0.59		t_{12} = −0.31, p = 0.76
Body mass change (kg)	0.28 ± 0.35	0.28 ± 0.14		t_{11} = −0.02, p = 0.98[a]
Body condition (g mm^{-1})	25.0 ± 2.8	24.8 ± 1.8		t_{11} = 0.13, p = 0.92[a]
Head and bill length (mm)	140.7 ± 11.1	135.7 ± 11.2		t_{12} = 0.85, p = 0.41
Flipper length (mm)	187.9 ± 5.6	183.2 ± 9.5		t_{12} = 0.39, p = 0.70
Flipper width (mm)	63.0 ± 2.1	64.0 ± 4.7		t_{12} = −0.52, p = 0.61
Foraging trip				
Duration (h)	37.5 ± 19.1	35.6 ± 4.8	32.9 ± 4.3	H_2 = 1.04, p = 0.60
Meal mass (g)	361.7 ± 315.7	401.1 ± 127.4		Z = −0.32, p = 0.75
Time to first dive (h)	3.8 ± 2.8	2.1 ± 2.1		t_{12} = 1.26, p = 0.23
Time from last dive (h)	6.0 ± 5.6	5.5 ± 2.8		t_{12} = 0.22, p = 0.83
Total number of dives	803.9 ± 597.1	852.7 ± 313.1		t_{12} = −0.19, p = 0.85
Total underwater time (h)	13.1 ± 9.9	13.8 ± 4.5		t_{12} = −0.16, p = 0.87

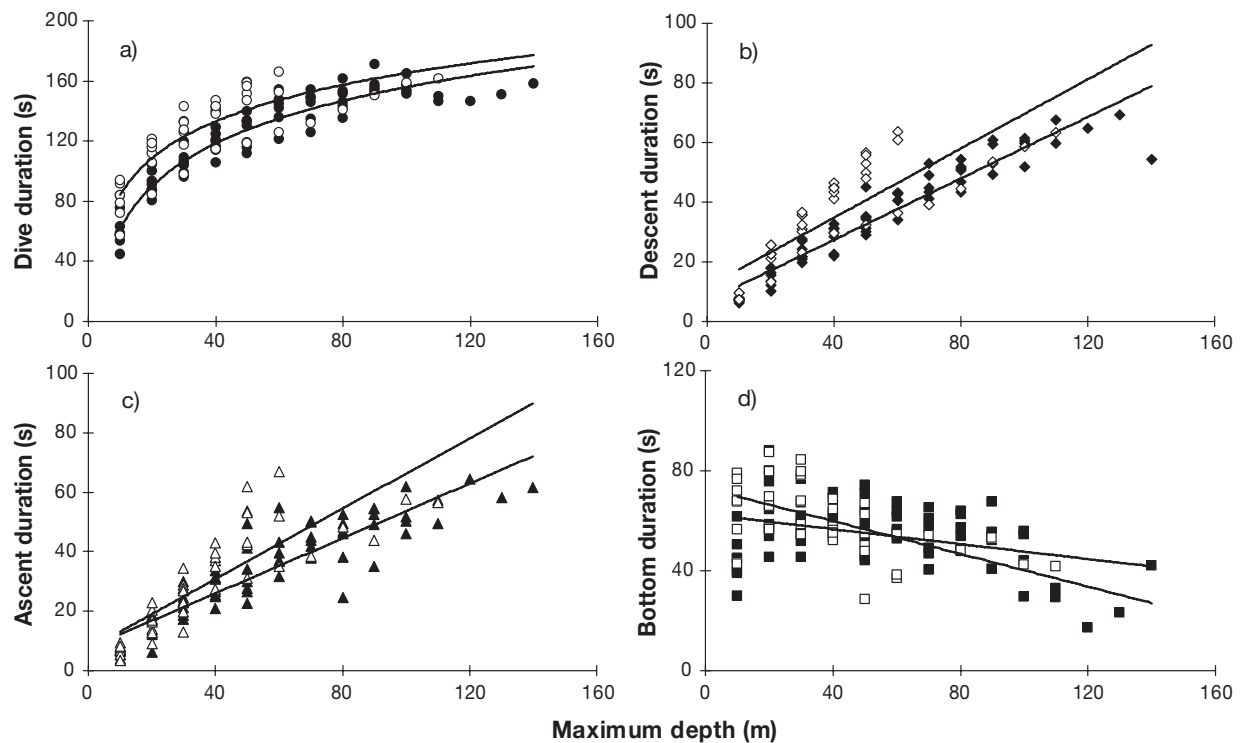[a]The body mass of one SMALL bird was not collected before the trip (n = 6)

Fig. 2. *Pygoscelis adeliae.* Relationship between the maximum depth (*x*) and the duration of the (a) dive (BIG: *y* = 35.19Ln[*x*] + 3.22, R^2 = 0.76; SMALL: *y* = 40.79Ln[*x*] − 32.75, R^2 = 0.91), (b) descent (BIG: *y* = 0.58Ln[*x*] + 11.62, R^2 = 0.70; SMALL: *y* = 0.51Ln[*x*] + 6.78, R^2 = 0.91), (c) ascent (BIG: *y* = 0.59Ln[*x*] + 7.15, R^2 = 0.69; SMALL: *y* = 0.46Ln[*x*] + 7.54, R^2 = 0.83) and (d) bottom (BIG: *y* = −0.15Ln[*x*] + 62.57, R^2 = 0.14; SMALL: *y* = −0.33Ln[*x*] + 72.96, R^2 = 0.35) phases for BIG (open symbols) and SMALL (closed symbols) group penguins
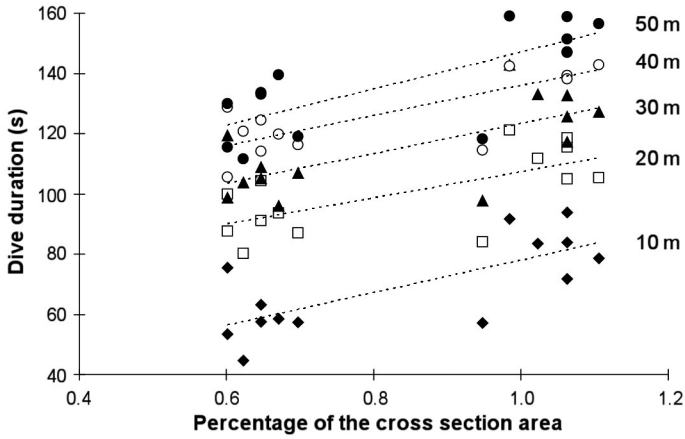
Fig. 3. *Pygoscelis adeliae*. Relationship between total dive duration (each point shows a mean from an individual penguin within the depth range specified) and device size (for more details, see Table 2). Depth ranges: ◆ (10 m); □ (20 m); ▲ (30 m); ○ (40 m); ● (50 m)
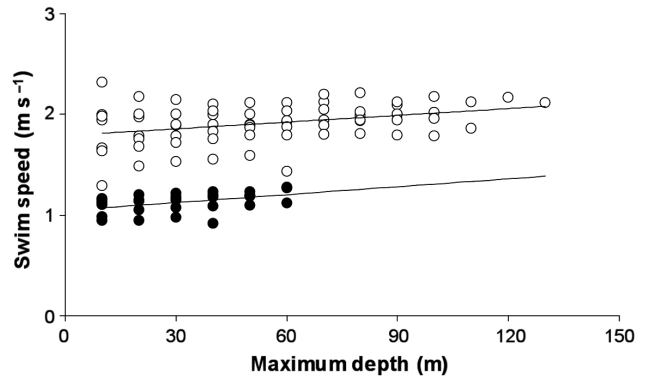

Fig. 4. *Pygoscelis adeliae*. Swim speed calculated during the descent phases of dives as a function of the maximum depth for penguins of the SMALL group (●; $y = 0.002x + 1.79$, $R^2 = 0.12$) and the BIG group (○; $y = 0.003x + 1.05$, $R^2 = 0.20$)

670.8, p < 0.0001; BIG group: $F_{1,39} = 123.5$, p < 0.0001) and was best-fitted by a log function (curve fits: duration = 40.97 Ln [Depth] – 32.75, $R^2 = 0.92$; and duration = 35.2 Ln [Depth] – 3.22, $R^2 = 0.76$ for birds from the BIG and SMALL groups, respectively, Fig. 2a). Here, the slopes of the regressions did not differ ($F_{1,104} = 3.27$, p = 0.07), but the intercept was larger for birds from the BIG group than for birds from the SMALL group ($F_{1,105} = 43.2$, p < 0.001). The duration of the transit phases were also positively and linearly related to the maximum depth of the dive (descent duration of SMALL and BIG groups: $F_{1,65} = 673.5$, p < 0.0001 and $F_{1,39} = 90.28$, p < 0.0001, respectively; ascent duration of SMALL and BIG groups: $F_{1,65} = 313.67$, p < 0.0001 and $F_{1,39} = 86.4$, p < 0.0001, respectively; Fig. 2b,c). The regression slopes of the descent duration were parallel ($F_{1,104} = 1.49$, p = 0.23), but the intercept of the BIG group was significantly larger than that of the SMALL group ($F_{1,105} = 26.11$, p < 0.001). In contrast, the slopes of the regression lines of the ascent duration vs. maximum depth were different ($F_{1,104} = 4.57$, p = 0.04) but the intercepts were not ($F_{1,104} = 0.02$, p = 0.90). While the transit phases became longer as the diving depth increased, the time spent at the bottom of the dive decreased significantly with depth (SMALL group: $F_{1,65} = 10.7$, p = 0.002; BIG group: $F_{1,39} = 20.65$, p < 0.0001; Fig. 2d). Here, both the slopes ($F_{1,104} = 4.18$, p = 0.04) and intercepts ($F_{1,104} = 5.29$, p = 0.02) of the regression lines differed between the 2 groups.

In each 10 m depth bracket, total dive duration was significantly related to the cross-sectional area of the device as a percentage of that of the animal carrying the device (Fig. 3). The positive linear regressions showed that larger devices impacted the birds more than small devices (Fig. 3, Table 2). Finally, there was no difference between the 2 groups of birds in the extent of the post-dive surface pause in relation to the duration of the previous dive (paired *t*-test: t = 2.02, p = 0.08).

Swim speed. The swim speed during the descent phase was significantly different ($F_{1,96} = 6.39$, p = 0.01) between the 2 groups of birds. Birds of the BIG group swam at lower speeds (1.30 ± 0.51 m s⁻¹) than those from the SMALL group (1.87 ± 0.23 m s⁻¹). Although the descent speed was significantly related to the maximum depth reached (Fig. 4), the slopes of the regressions were very small (0.002 and 0.003). In other words, the regression indicated that the swim speed increased by less than 0.4 % from a shallow dive near the surface to a 100 m deep dive. In this respect, the slopes of the regression lines of the birds from the BIG and SMALL groups were not significantly different

Table 2. *Pygoscelis adeliae*. Linear regressions of mean dive durations (s) by individual Adélie penguins (y-axis) as a function of device size (% cross-sectional area, x-axis) for dives terminating at different depths. Depths were only considered when visited at least 5 times by all birds

Depth (m)	Parameter	Intercept	Slope	R^2	$F_{1,12}$	p
10	Total dive duration	23.96	54.16	0.54	13.86	p = 0.003
20	Total dive duration	64.05	43.34	0.46	10.07	p = 0.008
30	Total dive duration	73.82	49.56	0.47	10.62	p = 0.007
40	Total dive duration	86.22	49.82	0.61	17.13	p = 0.002
50	Total dive duration	86.43	60.66	0.56	13.89[a]	p = 0.003

[a]The degrees of freedom for the 50 m depth bracket was $F_{1,11}$

from each other ($F_{1,96} = 0.04$, p = 0.85) but the intercepts were ($F_{1,97} = 381.3$, p < 0.001).

Body mass changes. At the group level, birds with BIG loggers put on less weight during their trip at sea than birds with SMALL loggers (Table 1) but this was the result of substantial inter-individual variation. Indeed, body mass change (BMC, in kg) was not different between the 2 groups and was significantly (R^2 = 0.53; $F_{1,11} = 12.52$, p = 0.005) related to the duration of the foraging trip (TD, in h), such that BMC = 0.014(TD) – 0.21.

All birds fed successfully. Antarctic krill *Euphausia superba* was the dominant prey item in all samples. Birds from the BIG and SMALL groups brought back the same amount of food for their chicks (Table 1), which was 381.4 ± 232.2 g (mean ± SD, n = 14 birds). The mass of the meal (MM, in g) was positively and significantly (R^2 = 0.75, $F_{1,12} = 35.92$, p < 0.0001) related to the duration of the foraging trip: MM = 14.6(TD) – 152.7.

DISCUSSION

Strategy adopted by penguins with increasing impediments (Fig. 1)

An earlier study documented that African penguins *Spheniscus demersus* swim slower with increasing device size (Wilson et al. 1986); the Adélie penguins also did this. This reduction in speed apparently did not increase power (and therefore oxygen) requirements, because post-dive surface duration in relation to dive duration was not significantly different between the birds from the BIG and SMALL groups (i.e. if birds of the BIG group had used more oxygen per unit time underwater than those from the SMALL group, they should have had longer surface durations to replenish oxygen reserves).

Although power output did not apparently vary between the 2 groups of birds, the necessary reduction in speed that this entails has drastic consequences for foraging capacity. Firstly, slower-swimming birds will range less widely in a given amount of time. Birds from BIG and SMALL groups could travel mean maximum distances of 17.4 and 25.1 km (mean underwater time multiplied by mean swim speed), respectively, in the 13.4 h underwater time available to them (Table 1). This may have consequences with regard to optimal foraging zones and rates at which the chicks can be provisioned (Trivelpiece et al. 1987, Takahashi et al. 2003). However, it is in depth exploitation that the consequences of device size are most far-reaching, since the decreased swim speed restricts the depth that the birds can reach in a given amount of time; this is

reflected in our results (Table 2). However, even if equipped birds were to maintain normal swim speeds, they would still be depth-restricted because their higher rate of oxygen consumption would necessitate that they surface sooner (Fig. 1).

Beyond the matter of simple ability to reach particular depths, the change in swim speed actually impacts the allocation of time to activity of penguins underwater, reducing foraging efficiency at all attainable depths. We consider the bottom phase to be critical in foraging success, reflecting either the birds remaining at a particular depth to feed (73% of all food items are caught by Adélie penguins during this phase; Ropert-Coudert et al. 2001) or the depth at which prey are most likely to be encountered (Wilson et al. 1996). Thus, the definition of foraging efficiency used by Kooyman et al. (1992) for king penguins *Aptenodytes patagonicus* (i.e. efficiency = bottom phase duration/ dive cycle duration) is appropriate for our birds. Here it is clear that the increased duration in transit between the surface and the preferred foraging depth makes penguins with larger devices increasingly inefficient with depth (Fig. 5).

Why then, is this discrepancy in foraging efficiency not reflected in the amounts of food brought back by the 2 bird groups, or at least in terms of foraging trip duration? The mean time spent away by the equipped birds was ca. 36 h, during which time the overall body mass increased by about 300 g, although the mass of food in the stomach was 400 g (Table 1). Given that complete gastric emptying in penguins that are not provisioning chicks occurs within several hours (Wilson 1985, Wilson et al. 1989), the stomach may have
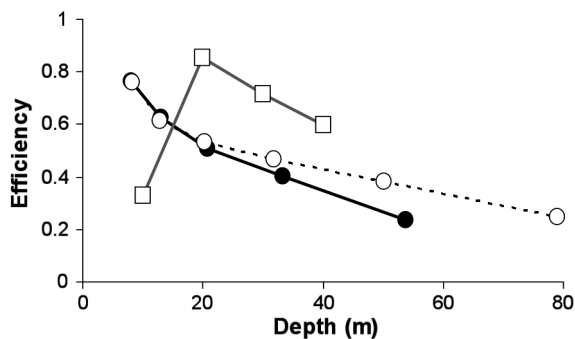

Fig. 5. *Pygoscelis adeliae*. Relationship between calculated efficiency (see text for definition) of Adélie penguins and depth for birds wearing BIG (○) and SMALL (●) devices as well as extrapolated efficiency for unequipped birds (□). Note that the apparent low efficiency for unequipped penguins is due to the extremely low predicted dive durations of unequipped penguins, something that may be related to an increased tendency for unencumbered Adélie penguins to engage in travelling, rather than foraging, behaviour during shallow dives

been filled and emptied a number of times during the foraging trip. We suggest that, overall, birds from the BIG group did acquire less food than those from the SMALL group. This affected the use of their own body reserves, although in such a short time the effect would not be substantial. Furthermore, since penguins suspend digestion at a particular point during their foraging trip so as to acquire and store food for their chicks (Gauthier-Clerc et al. 2000), all equipped birds catered to their brood needs, but likely bore the shortfall in overall needs in their own body condition where mass differences were less obvious and hidden in the variance of stomach meal mass. The apparent correlation between meal mass and time spent foraging may be nothing more than adults ensuring an appropriate provisioning rate to the brood, which would necessitate a greater meal delivery for birds that had been absent for longer. In other words, we suggest that birds equipped with SMALL devices were better able to bring the necessary amount of food to ensure the normal growth of their chicks, while acquiring food for themselves and digesting it before returning to their nests. In contrast, birds with BIG loggers were able to acquire the food for their chicks but may have acquired relatively less food for themselves. Thus, the primary mass factor was related to the food brought ashore for the chicks, and this did not differ between groups, as it only represented the chick meal. Body mass loss (rather than stomach content) over a single foraging trip is not expected to be high, even in individuals that did not feed for themselves. However, decreases in adult body mass would be expected if birds were equipped for longer. Also, since the study was conducted early in the chick-breeding season, chick demands were not yet at their peak. We suspect that later in the season, we may have observed an actual decrease in the body mass of the birds equipped with BIG devices even after a single trip.

While Adélie and African penguins apparently adopt a similar strategy in response to an increase in the drag, it is noteworthy that little penguins *Eudyptula minor* use the reverse approach. It has recently been shown that little penguins rearing chicks and instrumented with devices of 2 different sizes dive shallower but also for shorter duration when carrying a bigger device (Ropert-Coudert et al. 2007). If we refer to the scenarios proposed in Fig. 1, this would imply that little penguins do not decrease their swim speed in response to a greater drag. Such a discrepancy in the strategy adopted by penguins suggests that the appropriate response to a greater impediment may be species-specific, if not situation-specific. There is a need for similar studies to be conducted in the future to clearly assess what determines the choice of one response over another, both inter- and intra-specifically.

Derivation of the norm

Our experimental protocol for derivation of the Adélie penguin norm was not particularly rigorous since few birds were equipped, we used only 2 device sizes (although relative device size shows more variance due to differing bird size), there were likely differences in the hydrodynamics of the 2 devices beyond simple cross-sectional area, and because a linear interpolation between device size and the variables may not be entirely appropriate (but see data in Wilson et al. 1986, where extended variance in device size beyond 2 major groups augurs for a linear interpolation between device cross-sectional area and normal swim speed). Nonetheless, we believe that even with these misgivings, it is instructive to attempt to derive the norm for future studies, especially since this has rarely been done in the past.

Regression of the 2 constants describing the relationship between total dive duration and maximum depth for the 2 groups (see 'Results') against mean device size gave intercepts leading to a predicted total duration equation for unequipped birds (Fig. 6): duration =
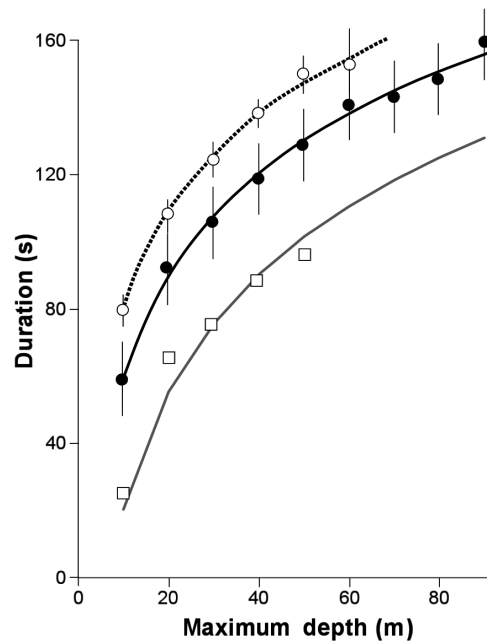

Fig. 6. *Pygoscelis adeliae*. Relationship between the grand-mean of the dive duration for penguins of the BIG group (○) and the SMALL group (●). The dotted line shows the predicted dive duration for unequipped birds, derived by regressing the constants in the log curve fits (see Fig. 2) for BIG and SMALL birds against percentage device cross-sectional area and extrapolating to zero before using these values in a third log curve. (□) Maximum dive durations for unequipped birds derived by regressing all individual bird values for mean duration at a specific depth against percentage cross-sectional area (see Fig. 3 for data sets where N = 14 birds) and then extrapolating to the intercept

50.42(Ln depth) – 95.8, which corresponds well to the durations predicted from the regressions of device size versus maximum depth reached for the different individuals (Fig. 3 and open squares in Fig. 6). Assuming that this regression holds true, and if equipped and non-equipped birds are considered to show the same distribution of dive durations (see comparison between BIG and SMALL groups documented earlier), then 10 % of dives made by non-equipped birds would exceed 110 m, 5 % would exceed 139 m and 1 % would exceed 199 m. This latter figure comes close to the 175 m found for Adélie penguins by Whitehead (1989) using minute capillary depth gauges. While the example above deals specifically with depth, the same principle should apply to any parameters of the diving behaviour.

The shorter overall dive durations of unequipped birds to specific depths presumably stem from the faster swim speeds (predicted to be 2.4 m s^{-1}) resulting in reduced transit durations. This would mean that bottom durations could be consequently maintained at higher values at greater depths (cf. bottom durations of BIG and SMALL groups in Fig. 2). Indeed, if we assume that bottom duration in non-equipped penguins is similar to those of equipped birds and use the mean values for birds of the BIG and SMALL groups, the derived efficiency of a non-equipped bird substantially exceeds that of birds from either BIG or SMALL groups (Fig. 5).

Overall, equipping birds with devices of different sizes helps define the extent to which the units affect behaviour. Our example shows that this effect in Adélie penguins is substantial, even though the difference in the devices used was relatively small. The difference between measured and derived performance is cause for concern because it implies that inter-locality comparisons should at least be conducted using standard-sized devices.

Researchers should always attempt to use the smallest, lightest or most streamlined devices to investigate the activity of free-ranging individuals, bearing in mind that despite this, the behaviour of an animal carrying an externally-attached data logger will likely differ from that of an unimpaired individual. Our work, however, indicates that one way to access the diving behaviour and performance of unencumbered animals is to equip individuals with differently-sized devices and to extrapolate. Implicit in this is that some of the study subjects will be exposed to more device-induced stress than previously considered necessary, which raises ethical issues. We would argue that such experiments are justified when the animal concerned can behave in a manner that approximates what is considered normal. We note that researchers should consider that unless we understand the extent to which devices affect animals, we have no measure of the value of our results. Adoption of such an approach necessitates careful thought in consideration of the sample size of animals exposed to the differing-sized devices (in this regard, the use of power analysis would prove extremely useful; cf. Andrew & Mapstone 1987, Underwood 1997), as well as to the actual size variance and the wearing time so that the animals are minimally impacted.

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