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How do different data logger sizes and attachment positions affect the diving behaviour of little penguins?

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Abstract

It is crucial in any bio-logging study to establish the potential effect that attachment of loggers may have on the animal. This ensures that the behaviour monitored by the loggers has a biological relevance, as well as for ethical reasons. Evaluation of the effects of externally attached loggers shows that they increase the drag of swimming animals and increase their energy expenditure. Nevertheless, little research has been done on the effects of size or position of such loggers. In this study, we tested whether the size (i.e. large: 4.9% versus small: 3.4% of the bird's frontal area) or the place of attachment (middle *versus* lower back) affected the diving behaviour of male and female little penguins (*Eudyptula minor*). The positioning of the data logger on the middle or lower section of little penguins' back had little, if no effect, on the diving variables measured in this study. Size of the loggers, however, had strong effects. Birds with large loggers made shorter dives and reached shallower depths than those with small loggers. In addition, birds with large loggers made more dives probably to compensate for the extra cost of carrying a large logger. The measured variables also differed between the sexes, with males diving deeper and longer than females. Logger size had a sex-specific effect on the trip duration and descent speed, with males equipped with large loggers staying longer at sea than those with small loggers, and females with large loggers descending faster than those with small loggers. From our results, it appears that effects of logger position do not exist or are very small in comparison with the effects of logger size. The results of the current study indicate that the effects of size of loggers be evaluated more commonly in bio-logging research into the diving activity of free-ranging birds.

Keywords: Bio-logging; Diving performance; Penguins; External logger effects

1. Introduction

Recent advances in solid-state technology have meant that miniature data loggers can be attached to free-ranging animals to record their activity and physiology *in situ*, an approach known as bio-logging (Boyd et al., 2004; Ropert-Coudert and Wilson, 2005). Attaching devices to animals, however, is likely to affect their behaviour and fitness. For instance, brightly coloured devices can attract predators and increase antagonistic behaviour from conspecifics (Wilson and Wilson, 1989), while heavy loggers can affect flying animals (Croll et al., 1992; Phillips et al., 2003). The drag produced by these

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devices has been singled out as the factor affecting the swimming performance of streamlined, aquatic animals, such as penguins and marine mammals (Wilson et al., 1986; Kooyman, 1989; Culik and Wilson, 1991; Bannasch, 1995; Walker and Boveng, 1995). Researchers have endeavoured to use smaller loggers that have a low profile to reduce the drag caused by externally attached loggers (Culik et al., 1994) and positioned these low on the animal's back (Wilson and Culik, 1992; Bannasch et al., 1994). These suggestions, however, have been based on only a few studies; most of which have involved using model animals in air and/or water tunnels (Culik et al., 1994; Wilson and Culik, 1992; Bannasch et al., 1994).

There have been several studies that have evaluated the effects of loggers themselves, but few that have investigated the effects of the position or size of them (but see Bannasch, 1995). Loggers provide a cost-effective way of collecting information on the free-ranging behaviour of penguins, and efforts should be put into assessing the optimal positioning of loggers and evaluating whether smaller loggers are more appropriate than larger ones.

The principal difficulty of testing the effect of attaching devices on the behaviour of free-ranging animals lies in the impossibility to compare the activity of instrumented birds with that of non-instrumented ones. Some rare experiments, using birds implanted with data loggers as a control group, have shown that externally attached loggers do modify the foraging behaviour of king penguins (*Aptenodytes patagonicus*) by preventing them diving repeatedly to great depths (Ropert-Coudert et al., 2000a). Alternatively, researchers have searched for indirect cues of loggers impact, e.g., comparing the duration of the foraging trips (Croll et al., 1991; Hull, 1997; Pütz et al., 1998) and breeding success (Croll et al., 1996) between instrumented and control birds. These aspects of the ecology of free-ranging animals need to be carefully investigated, as an aerial (Wilson et al., 2004) or a flipper band (Gauthier-Clerc et al., 2004) can affect the performances and life history of seabirds.

Here, we evaluate the effects of the position and size of loggers on the diving and foraging behaviour of male and female little penguins (*Eudyptula minor*). These penguins are the smallest of all penguins and, therefore, provide a potentially sensitive test-case for logger position and size. Previous observations of captive little penguins had indicated that they were imbalanced while swimming on the surface of the water, which may have been an influence of the logger being positioned on their lower backs (Healy et al., 2004). Further experiments using accelerometers, however, did not detect any differences in the balance of the penguins swimming through a pool channel with loggers attached to either their lower or middle backs (Chiaradia et al., 2005). This experiment, however, raised the issue that little evaluation of the position of loggers has been made. Hence, we felt it was appropriate that the effects of the position of loggers on the diving performance of penguins *in situ* be assessed in order to provide a more robust evaluation of the impact that externally attached data loggers may have on the behaviour of penguins. Similarly, the loggers used currently are much smaller than those used in much earlier studies. Therefore, we wanted to test whether differences would exist between a small logger and the larger ones previously used. This test, we believed, would give us a good indication of whether our research would actually be improved (or provide a more appropriate indication of the animals behaviour) by using smaller loggers.

2. Material and methods

The study was conducted on 15 male and 16 female little penguins (3–7 years of age) between 9 and 26 November 2004. Each of these penguins was guarding at least one less than 2-week-old chick in an artificial nest box at the Penguin Parade colony on Phillip Island (38°28′S, 145°13′E), Australia (see details in Chiaradia and Kerry, 1999). Each bird was randomly selected from the group of little penguins that had been marked with transponders over the past 10 years and for which age and the details of past breeding history were known (Tiris, Texas Instruments, USA). The guard stage was ideal for our experiment because the parents make alternate daily trips to forage regardless of the environmental conditions (Chiaradia and Kerry, 1999). In addition, previous radio-tracking studies conducted in this colony have shown a limited foraging range during guard phase (Collins et al., 1999), allowing us to assume that the foraging conditions of our two groups of birds were similar. Finally, a dietary study conducted in parallel to our experiment revealed that little penguins from Phillip Island were feeding primarily on Clupeiformes this year (A. Chiaradia, unpublished results).

Diving parameters were measured using large and small loggers: "Large" loggers (4.9% of the bird's frontal area using a frontal area of 0.0055 m^2 for little penguins as calculated by Lovvorn et al., 2001) were cylindrical, two-channel depth data loggers (62 mm × 18 mm, 17 g, LTD 1200-100, Lotek Canada, Fig. 1A). "Small" loggers (3.4% of the bird's frontal area) were also cylindrical (53 mm × 15 mm, 17 g), four-channel depth-acceleration data loggers (M190-D2GT) and two-channel depth data loggers (UME-DT, Little Leonardo, Tokyo, Japan, Fig. 1B). All loggers sampled once a second and their absolute accuracy was 0.1 m. The effect of size of the loggers was tested by comparing each of the diving variables between penguins that had the large or small loggers. Different penguins were used in each treatment group.

To test the effect of positioning of the logger on a bird's diving behaviour (cf. Bannasch et al., 1994; Healy et al., 2004; Chiaradia et al., 2005), we compared each of the diving variables between penguins with loggers attached to the lower or middle back. We attached the loggers to either the point on the penguins back at the start of the tail (i.e. the "lower" position) or the top of the shoulder blades (i.e. the "middle" position, see Chiaradia et al., 2005, Fig. 1C). All loggers were attached with grey marine Tesa tape (GmbH, Kiel, Germany). The use of tape preserved the integrity of the plumage (Wilson et al., 1997) and allowed us to attach and retrieve the loggers in less than 5 min, minimising the handling time (a cause of stress for seabirds, Le Maho et al., 1992). Penguins were weighed to the nearest 1 g at the start and end of the deployment of the logger.

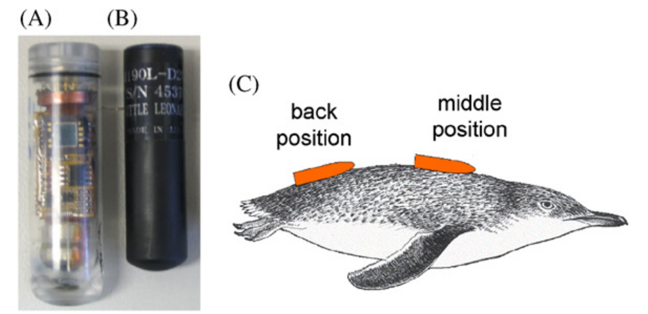

Fig. 1. Description of the two devices used in the present study: (A) the LTD 1200-100 logger (Lotek Canada) and (B) the UME-DT logger (Little Leonardo, Japan) represented the "large" and "small" loggers, respectively. In part (C), the two positions of attachment (back and middle) on the median line of the back of the little penguins are shown.

Following the trip at sea, loggers and tapes were removed from the birds and the data downloaded. Data were calibrated (including zero-alignment) with the same programme (Igor Pro—Wavemetrics Inc., ver. 4.01, USA). The start of the trip was defined as the time of the first dive >1 m and its end was defined as the time of the last dive >1 m. Several diving and foraging variables were measured and are outlined below. Bottom phase is the portion of the dive around the point of maximum depth where most of the feeding is expected to take place, as has been demonstrated in Adélie (*Pygoscelis adeliae*, Ropert-Coudert et al., 2001), king (Ropert-Coudert et al., 2000b) and little penguins (Ropert-Coudert et al., 2006). Start and end of bottom phases were defined as the first and last time the depth change rate (calculated over 1 s) became <0.25 m/s during a dive (Fig. 2), this threshold value being determined by visual inspection of the dive profile. The number of directional changes (also termed zigzag or wiggles elsewhere in the literature) also was determined (see Fig. 2).

The effects of the position of the logger and its size on the diving performance of male and female little penguins were examined using analysis of variance (ANOVA). We tested the null hypothesis that there would be no effects of these factors on the diving performance (measured variables) of the penguins. The variables considered in our analysis were the daily trip duration, the total and proportion of time spent underwater during the trip, the total number of dives, the dive rate (number of dives

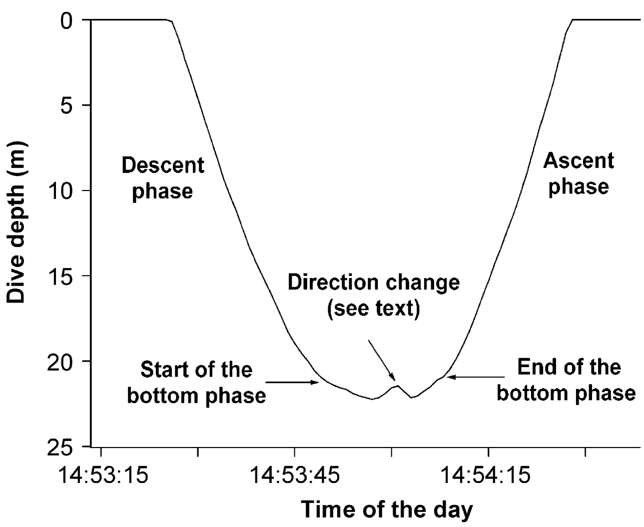

Fig. 2. A typical dive profile of a little penguin as recorded by the two types of loggers. The different phases of the dive are indicated (see the fourth paragraph in the Material and methods section for definitions).

per hour), the average maximum depth and duration of dives, the average duration of the bottom phase of dive, the proportion of time spent at the bottom phase during a dive (a good indicator of the time spent actually foraging, Wilson and Wilson, 1995), the number of direction changes in the depth profile (taken to represent prey pursuit, cf. Wilson, 1995), the amplitude of the depth changes during these direction changes in the bottom phase of the dive (an indicator of the type of feeding activity performed: demersal or pelagic corresponding to little and substantial depth change amplitudes, respectively), and the average descent and ascent rates over a dive. Comparisons of means of significant factors were analysed using Student–Newman–Keul (SNK) post hoc tests. Four different penguins were used in each combination of experimental factors (i.e. position × size × sex), except for the group of male penguins with the large logger positioned on their lower back which had only three penguins. To keep the analysis balanced, the mean of this group was used in the analysis and the degrees of freedom were appropriately adjusted (Underwood, 1997). Hence, we used a total of 31 penguins in this experiment. *A priori* we determined that four replicate penguins were adequate to provide 80% power to detect a 50% change in the total numbers of dives per trip, mean duration of the trip and mean depth in our study at the lowest level of the analysis (i.e. the interaction of position, size and sex) and a 20% change at the highest level of the analysis (i.e. position, size and sex). This level of replication was determined from power analyses (Andrew and Mapstone, 1987; Underwood, 1997) of previously collected data on male penguins without loggers (Yorke, 2003) as no prior data existed on little penguins with loggers at Phillip Island. *A posteriori* analyses also were done to calculate the levels of power for each of the tests of the main factors (specifically position) in the current study. All power calculations were done using the Java applet, "Piface" (http://www.divms.edu/~rlength/Power/).

Prior to analysis of the measured variables, the groups of penguins were evaluated for potentially confounding differences in body mass and age. There were, however, no differences either in the initial body mass or the age of the penguins between the penguins with loggers fitted on the lower or middle backs (body mass: $F_{1,18} =$, $P = 0.247$; age: $F_{1,23} =$, $P = 0.389$); or fitted with the small or large logger (body mass: $F_{1,18} =$, $P = 0.083$; age: $F_{1,23} =$, $P = 0.238$); nor were there any interactions among any of the factors. The initial body mass of the females was, however, smaller (by 11%) than those of the males ($F_{1,18} =$, $P = 0.001$). There was also no difference between the sexes in age ($F_{1,23} =$, $P = 0.347$).

3. Results

The position of the data logger on the middle or lower section of little penguins back had no direct effect on the diving variables measured in this study (Table 1). The lack of an effect was not because of a low statistical power, as the power of the tests was generally excellent to detect a 20% change in the measured variables and was even very good to detect a 5% change for a most of the variables. However, penguins with small loggers positioned in the middle backs dived deeper (almost 60% deeper, 16.1 ± 1.6 m) on average than those with the larger logger in the same position (10.1 ± 1.5 m), but no difference occurred when the logger was positioned on their lower backs (Table 1). There were also no statistically significant differences between penguins with loggers on their middle or lower backs, regardless of the size of the logger (Table 1).

Size of the loggers had many effects on the behaviour of the penguins (for all the results of this paragraph: *P*-values of tests are in Table 1 and the averages ± SD that significantly differed between size groups can be found in Table 2). Penguins with the small logger made fewer dives (37% fewer), but these dives lasted longer (16% longer) and consisted of proportionally less time spent at the bottom of the dive (16%) than those of penguins with large logger. Birds with small loggers also tended to spend less time underwater both as total underwater time and proportion of dive duration (20% less) and their diving rate was slower (36% fewer number of dives per hour). Several of the size effects differed, however, between the sexes (Table 1). Male penguins with the small logger had shorter foraging trips (almost 4%) than those with the large logger, while female penguins showed no difference in the duration of these trips. In terms of their descent during the dives, females with large loggers were the most rapid (14% more rapid), but males showed no difference in their descent. When ascending, both sexes did so most rapidly with the small logger (6.5% faster).

There were also several differences in the diving behaviour between the sexes. The dives of female

Table 1
Summary of analyses of variance of the influence of position or size of data loggers and the sex of penguins on their diving performance

Variable	Source	Position (Pos)	Size	Sex	Pos × size	Pos × sex	Size × sex	Pos × size × sex	Residual MS	Power	
	df	1	1	1	1	1	1	1	23	5%	20%
Day trip duration		0.181	—	—	0.896	0.622	**0.027**	0.066	0.22	1.000	1.000
Number of dives		0.721	**0.002**	0.118	0.646	0.663	0.236	0.944	84995	1.000	1.000
Dive rate		0.644	**0.003**	0.122	0.667	0.624	0.169	0.869	381	1.000	1.000
Dive duration		0.919	0.051	**0.001**	0.084	0.480	0.851	0.920	45.8	1.000	1.000
Average maximum depth		—	—	**0.002**	**0.050**	0.736	0.480	0.903	12.4	0.089	0.631
Average bottom duration		0.879	0.973	0.169	0.399	0.307	0.891	0.618	8.16	0.087	0.611
Average of bottom duration (% dive)		0.833	**0.049**	**0.044**	0.833	0.497	0.739	1.000	0.0044	0.081	0.538
Average descent rate		0.244	—	—	0.556	0.763	**0.013**	0.380	0.014	0.436	1.000
Average ascent rate		0.340	**0.018**	0.850	0.565	0.850	0.092	0.850	0.0082	0.781	1.000
Time underwater		0.280	**0.017**	0.147	0.243	0.992	0.492	0.794	33525699	1.000	1.000
% Time underwater		0.209	**0.022**	0.134	0.243	0.951	0.307	0.574	114.8	1.000	1.000
Average of *N* zigzag		0.282	0.926	0.650	0.929	0.181	0.856	0.717	0.1481	0.180	1.000
Average of delta depth at bottom		0.964	0.219	0.089	0.115	0.853	0.273	0.359	0.571	0.213	0.998

Each factor was fixed and orthogonal with two levels: lower or middle back; small or large and female and males (number of individuals = 3 or 4). The *P*-values are shown for each interpretable factor and interaction. Significant terms ($P \leqslant 0.05$) are shown in bold. Residual mean squares are shown to enable the full reconstruction of the ANOVA. Power is shown for each test to detect an effect of 5% and 20% at the highest level of the analysis (i.e. the factor's position, size or sex; $n = 16$).

Table 2
Average values ± SD of diving parameters that differed significantly between large and small loggers (cf. Table 1 for *P*-values)

Interaction	Parameters	Small loggers	Large loggers
Both sexes	Number of dives	617 ± 34	979 ± 95
	Dive duration (s)	34.3 ± 2.0	29.4 ± 2.1
	Bottom time duration (% of dive duration)	0.29 ± 0.02	0.34 ± 0.02
	Total underwater time (h)	5.9 ± 0.4	7.3 ± 0.4
	Underwater time (% of trip duration)	40.3 ± 3.0	49.2 ± 2.4
	Dive rate (number of dives/h)	42.3 ± 2.3	65.7 ± 6.4
	Ascent rate (m/s)	1.23 ± 0.02	1.15 ± 0.02
Males	Foraging trip duration (h)	14.3 ± 0.1	15.1 ± 0.1
Females	Descent rate (m/s)	1.14 ± 0.04	1.30 ± 0.03

penguins were shorter (by 25%, 27.3 ± 1.7 s) and shallower (by 28%, 11.1 ± 1.1 m) than that of males (duration: 36.4 ± 1.8 s; maximum depth: 15.5 ± 0.9 m). They tended, however, to spend proportionately more time at the bottom of their dives (34.2 ± 0.02% of dive duration) than the males (Table 1, 29.2 ± 0.01%). With the small logger, females tend to have longer trips (by 3%, 14.8 ± 0.2 h) than the males (Table 1, 14.3 ± 0.1 h). No difference existed between the sexes when they were carrying the large logger (Table 1) and females did not differ in the length of their trips with the large or small logger.

4. Discussion

With our experimental design, we observed statistically significant differences in the behaviour of little penguins equipped with small and large loggers. Interestingly, position of the logger (middle versus lower back) has little influence on the animal's behaviour, at least for little penguins. Hence, the use of the smallest logger available would be most appropriate, while positioning of the logger on the back of little penguin would be appropriately decided by other impinging factors (e.g., security of attachment) rather than any influence on its diving and foraging performance.

The lack of an effect of the position of the logger was surprising considering the results of a previous study (Bannasch, 1995). Experiments using penguin carcasses placed in water flumes suggested that the drag of these streamlined birds may be increased substantially by a logger placed in a middle position on the bird's back (Bannasch, 1995). There are two possible explanations for this: (1) possible artefact of using models and laboratory studies versus experiments with free-ranging animals and (2) the lower position in our experiment may have still been within the area where the flow remains relatively laminar across the penguin's back. If the latter case holds true, then the position of the logger on the little penguin's back may not affect its drag to a point where differences in the diving ability of the birds would be apparent. Indeed, Fig. 2 in Bannasch et al. (1994) indicates that a significant difference in the flow velocity distribution is observed for the most caudal position (open diamonds). From this most caudal point up to shoulder blades, modifications in the flow velocity were similar. The back of a little penguin being on average 16 cm long, we can suppose that a 53-mm-long logger would cause flow disruptions of similar amplitudes when positioned either in the lower or the middle positions, as defined in this study. In other words, for logger size used in this study, it did not matter whether the logger was placed in the middle or lower positions on the back of little penguins: both positions will have a similar effect on water flow, hence similar effects on diving behaviour.

An increase in size of the logger did significantly modify the diving behaviour of little penguins. Since we can reliably assume that birds were experiencing similar foraging conditions and targeting similar prey (cf. Material and methods), the modification in the diving behaviour of penguins with large loggers is likely to have implications on the birds foraging efficiency in comparison to those of penguins with small loggers. Probably the most important physical feature between the small and large loggers was the increase in frontal area of the logger that is likely to have increased its drag. Wilson et al. (1986) and Bannasch et al. (1994) suggested that an increase in drag will lead to an increase in the energy expended by birds to achieve the same underwater speed. If birds with a large logger expend more energy per underwater distance swum than their counterparts with small loggers, their oxygen stores will be depleted faster and their underwater diving time will be reduced. This is consistent with the observations on free-ranging individuals in the current study. Little penguins with large loggers made more dives that were of shorter duration. Dives being shorter, the greater number of dives may result from the birds with large loggers being able to perform more dives within the timeframe of their foraging trip. However, the observation in female king cormorants (*Phalacrocorax albiventer*) that increasing the diving frequency compensates for shallow-diving activity (Kato et al., 2000) suggests that the greater number of dives and greater time spent underwater at the end of the day by birds with large loggers may reflect an increase in the birds' foraging effort to compensate for the extra cost of carrying a large logger. In addition, little penguins with large loggers spent relatively longer at the bottom phase of their dives. Two reasons can be suggested to explain this: either the birds with large loggers tried to capture more prey in order to compensate for the extra energy expenditures inferred by the logger (and, therefore, spent longer at the bottom phase of their dives) or they were less efficient in capturing their prey (i.e. they spent more time at the bottom of their dives to capture a similar number of prey than birds with small loggers). Across both sexes, penguins with small loggers came up to the surface faster than those with large loggers. This is surprising as birds with large loggers increased the time spent at the bottom of dive while decreasing the dive duration. In this situation, a decrease in the transit time—i.e. an increase in the transit rate—is expected. In the case of birds with loggers on the middle of the back, the paradoxical situation is solved by the fact that birds with small loggers dived deeper. We can indeed expect these birds to try to optimise their underwater time by using a steeper ascent angle and, therefore, to ascend comparatively quicker than birds diving to shallower depths (Wilson et al., 1996; Ropert-Coudert et al., 2001). However, in the case of birds with loggers on the lower back, the observed increase in the ascent rates remains contradictory. Note that this concerns mainly the males since females probably decreased their transit time over the whole dive.

Few measures of diving performance that were related to the penguin's activity at the bottom of its dive were not influenced by the size of the logger. For instance, the bottom duration of penguins did not differ among penguins with large or small loggers; neither did the number of direction changes made at the bottom of the dive or the average amplitude of these direction changes (Table 1). This indicates that the large loggers may have caused most of their effects on the penguin descent, rather than its ability to manoeuvre at the bottom of its dive.

Differences between the male and female penguins were similar to those observed between the sexes for other seabirds. In the current study, male little penguins were heavier, dived deeper, and for longer duration than females. These differences were similar to those observed in another study on two species of cormorants (Kato et al., 1999). Diving deeper generally means that birds, such as cormorants, spend less time at the bottom phase of the dive (Kato et al., 2000), a pattern that also was observed in little penguins in the current study. These trends did not change when birds were equipped with small or large loggers. However, the size of the loggers had a sex-specific effect on the trip duration and descent rates of male and female little penguins. Males stayed longer at sea when the size of the logger increased, whereas females did not change their trip duration. In addition, females descended quicker when equipped with large loggers, while the descent rate of males was not affected. It would be surprising that the increase in the descent rate actually corresponds to an increase in the speed used by females to reach the profitable depth. Indeed, as the streamlining of the birds is affected by the logger, the drag, and consequently the cost of transport, is greater for birds with large loggers. We suspect here that females with large loggers on their backs adopt a more acute diving angle so as to decrease the transit time without increasing their speed (Wilson et al., 1996; Ropert-Coudert et al., 2001). The negative effect of using steeper angle is that the birds scan a lesser proportion of the water column. Nonetheless, it is difficult to determine how size differences in the loggers have caused these sex-specific modifications in the diving behaviour. As mentioned above, the increase in the descent rate is expected so as to reduce the transit time, and this was indeed observed in the case of females. The changes in the descent rates between females equipped with small and large loggers were even big enough to do more than compensating for the surprising decrease in their ascent rates. Males, in contrast, decreased their ascent rates and did not increase their descent rates. The reasons for this and the apparent contradiction are puzzling to us but may be an artefact from the statistical tests as the degrees of interaction between variables are substantial.

Note here that birds equipped with small loggers are not control birds. They are also carrying devices and their behaviour and performances are, therefore, also different from that of a totally undisturbed individual. However, the present study may indicate which aspects of a bird's foraging performance are the most influenced by externally attached data loggers. We demonstrated that birds with a higher level of encumbrance have to work more to maintain their efficiency (i.e. feeding rate). For one foraging trip, this probably does not have much of an influence on the overall breeding activity of birds. Gales et al. (1990) reported that the foraging efficiency (measured through isotopic water turnover) of birds equipped with devices representing 1.4–11.8% of the birds frontal area, decreased over periods of time of up to 10 days. Future research should examine the effect of carrying a logger for longer periods of time on the foraging and breeding performances.

The experimental design we used in the current study provides good evidence that the effects of logger position appear to either not exist or be very small comparison with the effects of logger size. In our experiment, the tests for position, size and sex were all equally as powerful (i.e. degrees of freedom for these tests were all 1, 23) and usually had adequate power (i.e. 80%) to detect a 20% change in the measured variables and often even a 5% change. Hence, it appears that we can be relatively confident that there were no effects of logger position that were major (i.e. $>20\%$) or in many cases even minor (i.e. 5%).

The lack of difference between the middle and lower positions therefore would mean—at least in this study—that the logger can be attached upper on the body with no apparent additional deleterious effects on the penguins diving performance. Yet, a position of attachment as close to the tail as possible would still be preferable, since the back of little penguins on land shows a pronounced curvature (Chiaradia et al., 2005). It is crucial to have the whole length of the logger in contact with the back of the bird to ensure that the device stays firmly in position. Attaching the logger in an upper position also would mean that there is a risk of the devices being entangled on land in vegetation or the top of the burrow entrance (Y. Ropert-Coudert, personal observation).

We would expect a very small effect if the loggers used in this study were deployed on larger species, such as emperor (*Aptenodytes forsteri*) or king penguins. However, with regard to the variety of logger sizes and shapes used world wide, as well as the interspecific differences in body morphometrics and ecology of spheniscids, we recommend that bio-logging researchers conduct whenever possible case-by-case determination of logger attachment on the diving activity of free-ranging birds.

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References

Andrew, N.L., Mapstone, B.D., 1987. Sampling and the description of spatial pattern in marine ecology. Oceanography and Marine Biology Annual Review 25, 39–90.

Bannasch, R., 1995. Hydrodynamics of penguins—an experimental approach. In: Dann, P., Norman, I., Reilly, P. (Eds.), The Penguins. Surrey, Beatty and Sons, Berlin, pp. 141–176.

Bannasch, R., Wilson, R.P., Culik, B., 1994. Hydrodynamics aspects of design and attachment of a back-mounted device in penguins. Journal of Experimental Biology 194, 83–96.

Boyd, I.L., Kato, A., Ropert-Coudert, Y., 2004. Bio logging science: sensing beyond the boundaries. Memoirs of the National Institute of Polar Research (special issue) 58, 1–14.

Chiaradia, A.F., Kerry, K.R., 1999. Nest attendance and breeding success in the little penguins (*Eudyptula minor*) at Phillip Island, Australia. Marine Ornithology 27, 13–20.

Chiaradia, A., Ropert-Coudert, Y., Healy, M., Knott, N., 2005. Finding the balance: the effect of positioning of external devices on little penguins. Polar Bioscience 18, 46–53.

Collins, M., Cullen, J.M., Dann, P., 1999. Seasonal and annual foraging movements of little penguins from Phillip Island, Victoria. Wildlife Research 26, 705–721.

Croll, D.A., Osmek, S.D., Bengtson, J.L., 1991. An effect of instrument attachment on foraging trip duration in chinstrap penguins. Condor 93, 777–779.

Croll, D.A., Gaston, A.J., Burger, A.E., Konnoff, D., 1992. Foraging behavior and physiological adaptation for diving in thick-billed murres. Ecology 73, 344–356.

Croll, D.A., Jansen, J.K., Goebel, M.E., Boveng, P.L., Bengtson, J.L., 1996. Foraging behavior and reproductive success in chinstrap penguins: the effects of transmitter attachment. Journal of Field Ornithology 67, 1–9.

Culik, B.M., Wilson, R.P., 1991. Swimming energetics and performance of instrumented Adélie penguins (*Pygoscelis adeliae*). Journal of Experimental Biology 158, 355–368.

Culik, B.M., Bannasch, R., Wilson, R.P., 1994. External devices on penguins: how important is shape? Marine Biology 118, 353–357.

Gales, R.C., Williams, C., Ritz, D., 1990. Foraging behaviour of the little penguin, *Eudyptula minor*: initial results and assessment of instrument effect. Journal of Zoology (London) 220, 61–85.

Gauthier-Clerc, M., Gendner, J.-P., Ribic, C.A., Fraser, W.R., Woehler, E.J., Descamps, S., Gilly, C., Bohec, C.L., Le Maho, Y., 2004. Long-term effects of flipper bands on penguins. Proceedings of the Royal Society of London Series B 271, S423–S426.

Healy, M., Chiaradia, A., Kirkwood, R., Dann, P., 2004. Balance: a neglected factor when attaching external devices to penguins. Memoirs of the National Institute of Polar Research (special issue) 58, 179–182.

Hull, C.L., 1997. The effect of carrying devices on breeding royal penguins. Condor 99, 530–534.

Kato, A., Watanuki, Y., Shaughnessy, P., Le Maho, Y., Naito, Y., 1999. Intersexual differences in the diving behaviour of foraging subantarctic cormorant (*Phalacrocorax albiventer*) and Japanese cormorant (*P. filamentosus*). Compte rendu de l'Academie des Sciences de Paris 322, 557–562.

Kato, A., Watanuki, Y., Nishumi, I., Kuroki, M., Shaughnessy, P., Naito, Y., 2000. Variation in foraging and parental behavior of king cormorants. The Auk 117, 718–730.

Kooyman, G.L., 1989. Hydrodynamics, swim velocity and power requirements. In: Burggren, W., Ishii, S., Langer, H., Neuweiler, G., Randall, D. (Eds.), Diverse Divers. Springer, Berlin, Heidelberg, pp. 129–142.

Le Maho, Y., Karmann, H., Briot, D., Handrich, Y., Robin, J.-P., Mioskowski, E., Cherel, Y., Farni, J., 1992. Stress in birds due to routine handling and a technique to avoid it. American Journal of Physiology 263, 775–781.

Lovvorn, J.R., Liggins, G.A., Borstad, M.H., Calisal, S.M., Mikkelsen, J., 2001. Hydrodynamic drag of diving birds: effects of body size, body shape and feathers at steady speeds. Journal of Experimental Biology 204, 1547–1557.

Phillips, R.A., Xavier, J.C., Croxall, J.P., 2003. Effects of satellite transmitters on albatrosses and petrels. Auk 120, 1082–1090.

Pütz, K., Wilson, R.P., Kierspel, M.A.M., Culik, B.M., Adelung, D., Charrassin, J.-B., Raclot, T., Lage, J., Le Maho, Y., 1998. Foraging strategy of king penguins (*Aptenodytes patagonicus*) during summer at the Crozet Islands. Ecology 79, 1905–1921.

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

Ropert-Coudert, Y., Bost, C.-A., Bevan, R.M., Handrich, Y., Le Maho, Y., Woakes, A.J., Butler, P.J., 2000a. Impact of externally-attached logger on the diving behaviour of the king penguin (*Aptenodytes patagonicus*). Physiological and Biochemical Zoology 74, 438–444.

Ropert-Coudert, Y., Sato, K., Kato, A., Charrassin, J.-B., Bost, C.-A., Le Maho, Y., Naito, Y., 2000b. Preliminary investigations of prey pursuit and capture by king penguins at sea. Polar Bioscience 13, 102–113.

Ropert-Coudert, Y., Kato, A., Baudat, J., Bost, C.-A., Le Maho, Y., Naito, Y., 2001. Time/depth usage of Adélie penguins; an approach based on dive angles. Polar Biology 24, 467–470.

Ropert-Coudert, Y., Kato, A., Wilson, R.P., Cannell, B., 2006. Foraging strategies and prey encounter rate of free-ranging little penguins. Marine Biology 149 (2), 139–148.

Underwood, A.J., 1997. Experiments in Ecology. Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge.

Walker, B.G., Boveng, P.L., 1995. Effects of time-depth recorders on maternal foraging and attendance behaviour in Antarctic fur seals (*Arctocephalus gazella*). Canadian Journal of Zoology 73, 1538–1544.

Wilson, R.P., 1995. Foraging ecology. In: Perrins, C., Bock, W., Kikkawa, J. (Eds.), Bird Families of the World: The Penguins Spheniscidae. Oxford University Press, Oxford, pp. 81–106.

Wilson, R.P., Culik, B.M., 1992. Packages on penguins and device-induced data. In: Priede, G., Swift, S.M. (Eds.), Wildlife Telemetry, Remote Monitoring and Tracking of Animals. Redwood Press, Melksham, pp. 573–580.

Wilson, R.P., Wilson, M.-P., 1995. Buoyancy and depth utilisation in foraging cormorants: wet feathers and that sinking feeling. Le Gerfaut 85, 41–47.

Wilson, R.P., Wilson, M.-P.T., 1989. A peck activity record for birds fitted with devices. Journal of Field Ornithology 60, 104–108.

Wilson, R.P., Grant, W.S., Duffy, D.C., 1986. Recording devices on free-ranging marine animals: does measurement affect foraging performance? Ecology 67, 1091–1093.

Wilson, R.P., Culik, B.M., Peters, G., Bannasch, R., 1996. Diving behaviour of gentoo penguins, *Pygoscelis papua*; factors keeping dive profiles in shape. Marine Biology 126, 153–162.

Wilson, R.P., Pütz, K., Peters, G., Culik, B., Scolaro, J.A., Charrassin, J.-B., Ropert-Coudert, Y., 1997. Long-term attachment of transmitting and recording devices to penguins and other seabirds. Wildlife Society Bulletin 25, 101–106.

Wilson, R.P., Kreye, J.M., Lucke, K., Urquhart, H., 2004. Antennae on transmitters on penguins: balancing energy budgets on the high wire. Journal of Experimental Biology 207, 2649–2662.

Yorke, J., 2003. Diving behaviour of little penguins *Eudyptula minor* while foraging during incubation and chick-rearing stages at Philllip Island. Honours thesis, University of Melbourne, Australia.