Impact of Externally Attached Loggers on the Diving Behaviour of the King Penguin

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ABSTRACT

The impact of relatively small externally attached time series recorders on some foraging parameters of seabirds was investigated during the austral summer of 1995 by monitoring the diving behaviour of 10 free-ranging king penguins (Aptenodytes patagonicus) over one foraging trip. Time-depth recorders were implanted in the abdominal cavities of the birds, and half of the animals also had dummy loggers attached on their backs. Although most of the diving behaviour was not significantly affected by the external loggers ($P > 0.05$), the birds with externally attached loggers performed almost twice as many shallow dives, between 0 and 10 m depth, as the birds without external loggers. These shallow dives interrupted more frequently the deep-diving sequences in the case of birds with external loggers (percentage of deep dives followed by deep dives: 46% for birds with implants only vs. 26% for birds with an external attachment). Finally, the distribution pattern of the postdive durations plotted against the hour of the day was more heterogeneous for the birds with an external package. In addition, these penguins had extended surfacing times between two deep dives compared to birds without external attachments ($P < 0.0001$). These results suggest the existence of an extra energy cost induced by externally attached loggers.

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Introduction

In recent years, the use of electronic recorders to monitor the behaviour and physiology of diving mammals and birds at sea has consistently improved our understanding of their foraging ecology and energetics (Kooyman 1989a; Butler and Jones 1997). However, the devices used in such studies are often attached to the backs of these animals, thereby compromising their streamlined shape (Bannasch et al. 1994). Some experiments on penguins have demonstrated that externally attached data loggers create additional drag, which might affect the bird's swimming speed and energy expenditure (Wilson et al. 1986; Kooyman 1989b;Wilson and Culik 1992; Bannasch 1995). Most of these experiments, however, were conducted on penguins equipped with dummy loggers in water tanks and did not, therefore, reflect the conditions that exist in the wild. This lack of information is mainly because it has been impossible to record the diving behaviour of unencumbered birds and compare it with that from individuals equipped with externally mounted devices.

Thus, until now, the evaluation of the effect of carrying a device has been limited to the comparison between externally equipped birds and control birds of parameters measured at the departure and the return of the birds to their colony. The most common parameters measured are the duration of foraging trips, the mass of meals brought to the offspring, or the body mass gain of the adults (e.g., Croxall et al. 1988; Croll et al. 1991; Williams et al. 1992a, 1992b; Chappell et al. 1993; Croxall et al. 1993; Pütz and Bost 1994; Croll et al. 1996; Davis et al. 1996; Watanuki et al. 1997). Thus, the parameters used to compare equipped and nonequipped birds do not directly reflect the impact of an external data logger on the swimming and diving behaviour (Wilson and Culik 1992) and the energetic (Hull 1997) of free-ranging birds.

The development of implantation techniques in recent years (Butler and Woakes 1979; Stephenson et al. 1986; Bevan et al. 1994; Bevan et al. 1995; Woakes et al. 1995) has meant that the diving behaviour of free-ranging animals can be studied without any external attachment. The aim of our study was to determine the impact of an externally attached logger on the diving performances of king penguins (Aptenodytes patagonicus). This was achieved by comparing the diving behaviour obtained from a group of birds with implants only with those from a group that also had dummy loggers attached externally.

Material and Methods

The experiments were conducted from January 25 to March 4, 1995, on a king penguin colony of approximately 45,000 breeding pairs (Weimerskirch et al. 1992) located in La Baie Du Marin, Possession Island, Crozet Archipelago ($46°25'S$, $51°45'E$).

Twelve king penguins brooding small chicks 2–3 wk old were implanted with miniaturized time-depth recorders (MK5, Wildlife Computers, Redmond, Wash.). These devices measured 6.4 x 3.8 x 1.3 cm and weighed 50 g. The range of depth measured was 0–500 m, and the resolution was 2.0 m (with an accuracy of ± 2 m so that only the dives deeper than 4 m were taken into account for the comparisons). The MK5 were programmed to start recording after the first dive deeper than 10 m in order to optimize the memory usage and to ensure that a full foraging trip would be recorded. The depth data were then sampled every 3 s.

The devices, encapsulated in wax and silicone rubber, were inserted into the abdominal cavity under halothane anaesthesia (for the implantation procedure, see Stephenson et al. 1986; Bevan et al. 1994). They were placed under the abdominal muscle layer approximately level with the brood patch, toward the tail end of the bird, and sutured into position by black silk thread (see Handrich et al. 1997 for details).

During these experiments, care was taken to minimize stress due to the surgery. The implantation surgery was planned so that it took place approximately 7 d before the implanted bird departed to sea. This gave the tissues sufficient time to recover from the surgical procedures and decreased the stress of the implantation procedures. Previous studies with implanted devices stated that the birds showed physiological signs of recovery after 1–2 d (Bevan et al. 1995, 1998). Every bird that underwent an operation continued to raise its chick normally, and all birds were seen at the next moulting period. This study covered a single foraging trip for each bird during the brooding period, when the foraging activity is the highest (Charrassin et al. 1998). The birds were identified by a picric acid dye-specific mark on their chest and weighed before release.

Of the 12 penguins implanted, six were also equipped with a dummy silicone-built logger identical in size (6.4 x 3.8 x 1.3 cm) and similar in weight (around 50 g) to the internal MK5 recorder (which corresponds to a frontal area of 4.9 cm²). The externally fixed dummies were shaped to minimize the hydrodynamic drag (Wilson and Wilson 1989; Bannasch et al. 1994) and were attached to the birds' backs using TESA tape (Bannasch et al. 1994), in a median position near the tail, because this position has been noted to produce the least hydrodynamic drag (Bannasch et al. 1994). Thus, two groups were defined: the "internal" group composed of six king penguins that were only implanted with a data logger and the "external" group that consisted of six king penguins with both an implanted data logger and an externally mounted dummy MK5.

On the return of the implanted birds to the colony after a single foraging trip, the penguins were recaptured, weighed, and anaesthetized, and the implanted loggers and externally attached dummies were removed. Among the internal group, one MK5 did not provide reliable data and could not, therefore, be used for the subsequent analysis. Consequently, the internal group would have been limited to five birds versus six birds for the external group. Thus, one bird from the six composing the external group was randomly excluded from the analysis so that an equal number of birds could be compared between the two groups.

Afterward, the birds were released, and their attendance behaviour and reproductive success were checked every day until the moulting period. The data stored in the MK5s were downloaded to a computer and analysed by Wildlife Computers software. The dive parameters, that is, maximum dive depth, dive durations, time spent at the maximum depth, and vertical ascent and descent rates, were extracted. These parameters were compared between the two groups of birds.

The foraging bout — defined as periods during which a bird dived repeatedly to similar depths with minimal surface interval (Chappell et al. 1993) and usually observed in the diving behaviour of king penguins (Pütz et al. 1998) — was impossible to determine in our study, even by applying various methods (Naito et al. 1990; Williams et al. 1992a, 1992b; Watanuki et al. 1993; Boyd 1996; Mori 1997). This inability to separate bout events from each other might have been caused by the high variability between each dive within individuals.

Finally, five other king penguins that were at the same breeding stage were used as a control group to check the effect of the implantation method by comparing their foraging-trip duration with those of the implanted birds. The birds in this control group had nothing implanted or attached externally.

During the analysis, to avoid statistical difficulties induced by the interindividual variability that is attributed to the differences in the foraging areas and/or the prey availability encountered by each bird (Bost et al. 1997), the comparison of the dive parameters between the two groups was confined to a restricted part of their foraging trip. Sequences lasting 48 h (midnight on day n to midnight on day n + 2) were chosen so that n + 2 was 2 d before the arrival of the birds back at the colony. At this time of the year, such a period corresponds to the location of the penguins at the polar and sub-Antarctic fronts where most of the foraging time (i.e., deep diving) is spent, according to satellite-tracking studies performed in Crozet Archipelago (Bost et al. 1997).

The statistical tests were performed using SYSTAT 7.0 software (SYSTAT, USA). The statistical threshold was fixed at the 5% level. In the following analysis, the term "SD" is used for standard deviation. We used nested (hierarchical) analysis of variance (ANOVA; Zar 1984) to compare both inter- and intragroup variation, the factor "birds being nested" within the

Table 1: Results for the comparisons of the dive parameters that showed no statistical differences between the two groups of birds

Dive Parameters	Internal		External		Statistics
Percentage of time spent at various depths	...		...		$\chi^2 = .5$, 3 df, $P > .9$
Percentage of diving activities compared between day and night	...		...		$\chi^2 = 1.4$, 4 df, $P > .75$
Time spent at the maximum depth (s)	89.1	$\pm$ 30.0	91.9	$\pm$ 30.6	Groups: nA, $F_{1,8} = 2.3$, $P = .13$ Individuals: nA, $F_{1,8} = 80.0$, $P < .0001$
Vertical ascent rate (m s^{-1})	$-1.34 \pm$	.47	$-1.33 \pm$	.42	Groups: nA, $F_{1,8} = .06$, P = .81 Individuals: nA, $F_{1,8} = 1.91$, P = .06
Vertical descent rate (m s^{-1})	1.38 $\pm$	.42	1.38 $\pm$	.41	Groups: nA, $F_{1,8} = 0.03$, P < .86 Individuals: nA, $F_{1,8} = 1.69$, P = .096

Note. nA = nested ANOVA test,

factor "groups." Proportions were compared between the two groups by using a χ^2 test.

Results

All 5,027 dives deeper than 4 m were recorded during the 2 d selected within the foraging trip, according to the method described above. Among these dives, 2,466 were recorded for the internal group, with a mean number of dives per trip = 493 ± 205 dives (±SD), versus 2,561 dives for the external group, with a mean number of dives per trip = 512 ± 36 dives.

The duration between the time of departure from the colony observed visually and the time when the logger started recording (first dive deeper than 10 m) was, on average, 12.2 ? 3.3 h for internal birds and 13.28 ± 5.2 h for external birds. These two durations were not significantly different from each other (Student's t-test, $t = -1.48$, 8 df, $0.2 > P > 0.1$) and represented the time birds spent ashore before departing or resting at sea.

The mean overall foraging-trip durations were also not statistically different between the two groups (internal = 6.70 ± 0.82 d; external = 6.16 ± 0.37 d; Student's t-test, t = 0.51, 8 df, P > 0.5). Finally, the foraging-trip durations compared between the internal group and the control group did not differ significantly (control = 7.8 d; Student's t-test, $t = 1.00$, 8 df, $0.5 > P > 0.2$).

The form and shape of the dives showed no clear differences between the birds. Thus, the percentage of U- and W-shaped dives versus V-shaped dives (Wilson 1990, 1995) were not different between the two groups (U and W shapes represented 90% and 91% for the internal and external birds, respectively), as well as compared to the value observed in a previous study (88% in Kooyman et al. 1992). No differences were observed for the proportion of time spent at the surface versus time spent underwater (1.16 for the internalvs. 1.06 for the external). The diving behaviour compared between the two groups of birds mostly showed no statistical differences at the 5% level

(Table 1) in terms of the percentage of time spent at various depths at day and night, time spent at the maximum depth of dives, and vertical ascent/descent rates.

In contrast, there were statistical differences between the two groups of birds in the frequency distribution of the maximum depth reached (Fig. 1). This was compared between the two groups at 20-m intervals ($\chi^2 = 143.5$, 18 df, P < 0.0001). The bimodal distribution of the depth allowed us to define two categories of dives: the shallow dives above 50 m and the deep dives below 50 m (Pütz et al. 1998). A significant difference was also found for the proportion of deep and shallow dives between the two groups of birds ($\chi^2 = 21.4$, 1 df, P < 0.0001) because the external birds performed more shallow dives than did the internal birds (64% vs. 58%, respectively).Additionally, the mean maximum depth of deep dives was significantly different within the two groups of birds (nested ANOVA, F =
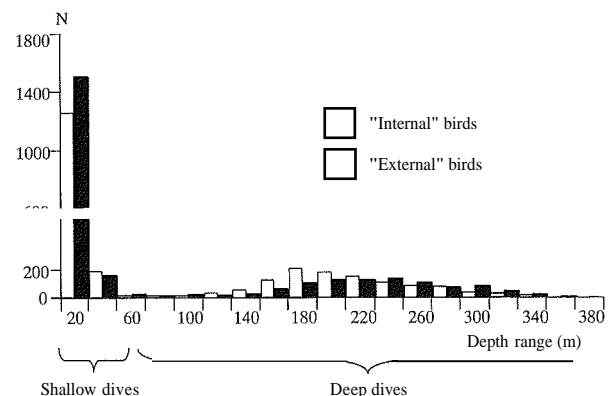

Figure 1. Frequency of maximum depth reached per dives for "internal" and "external" groups. The upper limit for the definition of shallow dives is 50 m.

32.96, 8 df, $P < 0.0001$) and between the two groups of birds (nested ANOVA, $F = 69.99$, 1 df, $P < 0.0001$). The external birds dived deeper, on average, compared to the internal birds (214.7 ± 59.2 m vs. 196.8 ± 50.9 m, respectively).

Likewise, there were statistical differences between the frequency distributions of dive durations ($\chi^2 = 243.7$, 15 df, $P < 0.0001$) that reflected the differences seen in the maximum depth frequencies. This was because the external birds performed more shallow dives of 1–2-rain durations than the internal birds.

The larger number of shallow dives for the external birds implied a decrease in the numbers of a deep dive following another deep dive, or in other words, the deep-dive sequences were more frequently interrupted in external birds compared with internal birds (Fig. 2).

The postdive time, which can represent the time needed to recover from the preceding dive, was calculated first between two consecutive dives (PD1), then between two deep dives (PD2), excluding the duration of the shallow dives that occurred between these two deep dives, and finally, between two deep dives (PD3), including the duration of the shallow dives that occurred between the deep dives. Indeed, the shallow dives, inserted between two deep dives, could represent recovery phases without interruption of the foraging activity (Kooyrnan et al. 1992). There were statistical differences between the two groups for the PD1, PD2, and PD3 (Table 2). Additionally, the PD3 was placed as a function of the hour of the day (Fig. 3). According to the ephemeris, sunrise occurred at 5:00 A.M. in early January and at 7:00 A.M. in late March, whereas the sunset occurred at 9:00 P.M. in January and 6:00 P.M. in late March (local times). However, the deep-diving behaviour started throughout this period at 7:00 A.M., and the last deep dives were observed around 6:00 P.M. On this basis, the distribution pattern of the postdive times appeared slightly different between the internal and external groups. As shown in Figure 3 and in the value of the SD, the distribution pattern of the PD3 was more heterogenous for the external birds compared with that of the internal birds, for which the PD3 mainly concentrated around the average value.

Discussion

Until now, the effects of externally attached data loggers on the foraging behaviour of free-ranging diving birds remained poorly understood. This study reveals the impact of an externally attached relatively small-sized logger on the behaviour of a large diving bird, the king penguin. In the present study, most of the dive parameters were not significantly different between the two groups of birds, except for the maximum depth frequency, the proportion of deep versus shallow dives, the dive succession, and the postdive times.

In accordance with previous studies on king penguin at Crozet Archipelago (Kooyman et al. 1992) and at South Georgia
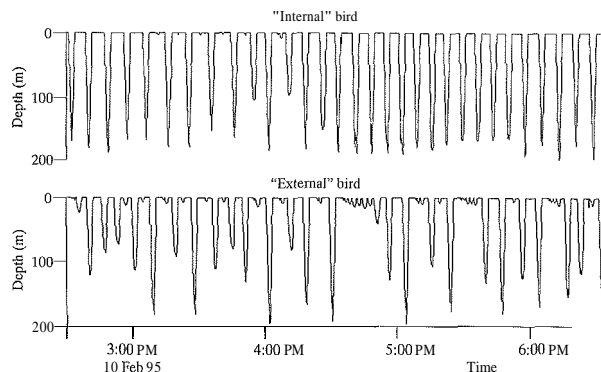

Figure 2. Diagram of the depth profile showing the succession of deep and shallow dives in the external birds (top) and the internal birds (bottom).

Island (Kooyman et al. 1992), the duration of a single foraging trip was not affected by carrying either an externally attached device or an implanted device.

As the two groups of instrumented birds (internal and external) foraged during the same period, their access to prey can be considered essentially comparable. In addition, king penguin prey is presumably abundant during this period of the reproductive cycle (Foxton 1956; Koslov et al. 1991; Cherel and Ridoux 1992) so that prey availability should not be a limiting factor. Thus, the change in the dive successions and the increase in the postdive durations may reflect an increase in the energy expenditures during diving for the external birds. If so, more oxygen is used for a given dive, and the recovery time is longer. This is in accordance with the findings from previous studies on captive birds swimming in water tanks—that an externally attached logger causes an extra energy cost as a result of the extra drag (Wilson and Wilson 1990; Culik and Wilson 1991, 1992; Culik et al. 1994). This extra cost would compromise the capacity of the birds to perform deep dives in a consecutive series.

As no clear foraging bouts were defined within our data, it is difficult to distinguish clearly the significance of these prolonged postdive times. They might represent either periods of subsurfacing traveling from one prey patch to another or extended resting periods at sea on surface. However, the numerous extended PD3, associated with the difficulty for the external birds to follow deep dives with deep dives, further suggests that there was an increase in the energy expenditure caused by the externally attached logger. The large number of extended postdive times could be interpreted as both a consequence of this increase in the energy cost while performing deep dives, as well as a strategy to compensate for this cost by performing longer rests more often during a succession of deep dives.

Table 2: Comparison of postdive times of types 1, 2, and 3 (PD1, PD2, and PD3, respectively) between the two groups of birds

Postdive Time (s)	Internal	External	Results of Nested ANOVA
PD1	65 ± 68.0	59 ± 49.0	Groups: $F_{1,8} = 77.2$, $P < .0001$
			Individuals: $F_{1,8} = 50.4$, $P < .0001$
PD2	112 ± 57.2	132 ± 64.3	Groups: $F_{1,8} = 166.3$, $P < .0001$
			Individuals: $F_{1,8} = 38.1$, $P < .0001$
PD3	179 ± 170.6	206 ± 190.4	Groups: $F_{1,8} = 28.7$, $P < .0001$
			Individuals: $F_{1,8} = 7.5$, $P < .0001$

The large proportion of shallow dives that accompany the increase of the mean maximum depth for external birds could be interpreted in light of a recent hypothesis of Kooyman and Ponganis (1998). These authors suggested that these shallow dives, interspersed among deep dives, may act as decompression stages that would avoid the bends. However, the number of deep dives did not differ between the two groups, and it appeared to be difficult to explain the consistent increase of shallow dives in external birds as only a consequence of the slight importance of deeper dives by contrast to internal birds. Thus, regarding the other data obtained, another hypothesis can be proposed.

Indeed, the deep dives represent the most efficient dives with regard to the hunting behaviour of king penguins because 83% of the myctophid (or simply, fish) prey appears to be caught during dives below 50 m (Pütz and Bost 1994). Dives shallower than 50 m may also represent subsurface traveling dives during the day and probably hunting dives during the night (17% of total prey catch). However, these shallow dives, interrupting a succession of deep dives, may also be interpreted as a way for the birds to recover from these deep dives (Kooyman et al. 1992). Indeed, the different values of the aerobic dive limit (ADL), which is defined as the diving duration beyond which blood lactate concentration increases above resting levels (Kooyman et al. 1983) and calculated ADL (cADL; Butler and Jones 1997) for deep divers such as king penguin (Burns and Castellini 1996; Ponganis et al. 1997a, 1997b, 1997c), remain problematic because these calculations rely on estimates of usable oxygen stores and theoretical assumption of the field metabolic rate (FMR) of free-ranging divers (Boyd 1997; Butler and Jones 1997). On the basis of the estimated rate of oxygen usage and usable oxygen stores, almost 25% of the deep dives of a king penguin should then exceed the cADL (Kooyman et al. 1992). However, this value might have been overestimated because the substantial drop in body temperature in the lower abdomen of king penguins (Handrich et al. 1997) indicates a reduction in the metabolic rate of some tissues that would lead to an increase in the cADL so that most of the dives of king penguins would remain aerobic.

Because the present data suggest an increase in the metabolic rate resulting from the externally attached logger, the cADL will be reduced. This could force the bird either to rely on anaerobic metabolism for deep dives, especially during a consecutive sequence of deep dives, or to increase the number of longer resting periods and of shallow dives. These latter strategies could, therefore, be a way for the bird to decrease the level of lactate in its blood after a series of deep dives, as has been infrequently observed on Weddell seals *Leptonyckotes weddellii* (Castellini et al. 1988). Indeed, when dives remain within the ADL, the rate of blood lactate accumulated during deep dives continues to decrease as quickly as if the seals remained on the surface (Castellini et al. 1988). At the same time, such subsurface traveling dives could be considered as more profitable than simply resting on the surface in terms of avoidance of predation, as well as they could be a source of heat production.

Apart from this extra energy cost, it should be added that there could have been an increase in the time spent by the birds preening and trying to remove the device from their back while resting on the surface. Such behaviour might have influenced the onset of diving.
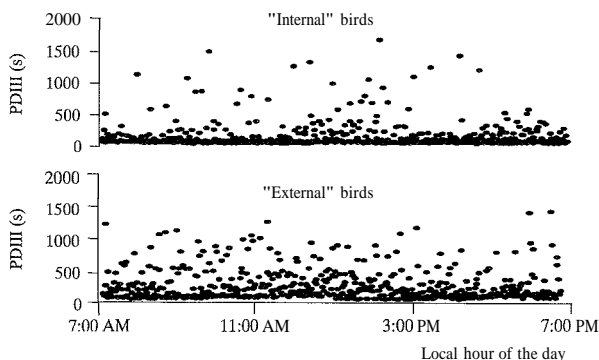

Figure 3. Changes in the postdive duration of type 3 in relation to the time of day. The postdive-duration type 3 represents the time spent surfacing between two consecutive deep dives, including the duration of shallow dives (shallower than 50 m).

Previous results defined the chick-rearing period as highly constraining for seabirds in terms of energy expenditures (Ricklefs 1983; Gales and Green 1990; Weimerskirch et al. 1993). In king penguins, recent studies have shown that higher constraints are observed during the period when the bird has to provide food for large chicks before the winter fast (Charrassin et al. 1998). Marine resources are then located further from the colony, a condition that is exacerbated by the large amounts of food required by the chick to face the winter fast (Charrassin et al. 1998). The inferred extra energy cost during the period of maximum food abundance in external birds, therefore, suggests that the penguin's foraging efficiency would be more affected during the period of rearing big chicks.

To summarize, on the basis of our data, externally attached loggers, even of a relatively small size, induce subtle changes in the diving behaviour of king penguins. These changes in the birds' behaviour were probably related to the increased drag caused by the logger, which consequently increased the energy expended during diving, as externally equipped birds performed fewer deep dives in a consecutive series.

That most of the other dive parameters measured were not affected might be explained by the fact that the measurements were conducted over a single foraging trip and during the period of the season when there is maximum abundance in the marine resources. Indeed, the effect measured in the present study would presumably have been stronger and would have led to a greater impact on the birds' behaviour and energetics if the deployment had been conducted over several consecutive foraging trips or over the winter when there is a lack of marine resources (Adams and Klages 1987; Hindell 1988). Indeed, due to a cumulative effect of the logger, this might lead to a decrease in the reproductive success of the bird. The latter point could be even more pronounced in smaller bird species or when the relative size of the logger is greater. Previous studies have already pointed out that an increase in the frontal area of loggers can affect the foraging behaviour of diving birds (Hull 1997), and O^{18} doubly labeled water turnover measurements performed on free-ranging northern fur seals (Callorkinus ursinus) showed that individuals carrying Meer Instruments' photomechanical TDRs externally attached by the means of a harness had a consistent increase in their energy consumption when compared to themselves (Costa and Gentry 1986).

Therefore, future studies should accurately quantify the impact of externally attached loggers by combining similar logger implantation with heart rate recording and estimates of metabolism (Butler et al. 1995). Finally, despite its invasive nature, the implantation method would appear to open a new field of investigation by recording the diving behaviour of birds without increasing their hydrodynamic drag. The logger deployment on the animals could be extended to several consecutive foraging trips, and the monitoring could cover periods of the annual cycle that have not been possible until now, such as the pre-moulting period.

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