Management and Conservation Article

Flipper Bands Modify the Short-Term Diving Behavior of Little Penguins

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ABSTRACT Flipper banding has long been the primary method to identify individual penguins, despite studies indicating that it may be detrimental to breeding success and survival. Our objectives were to measure the effects that flipper bands may have on diving performance of little penguins to determine whether the bands may be detrimental. We studied short- and long-term direct effects of flipper banding on diving behavior of free-ranging little penguins (*Eudyptula minor*) by comparing diving behavior before and after banding and by comparing diving performance of unbanded birds to those that had carried flipper bands for several years, respectively. Recently banded birds displayed increases in multiple variables following banding. Long-term banded penguins did not exhibit differences to their unbanded counterparts in most variables examined. Our findings are useful to those considering or reviewing the use of bands in penguin study and management. (JOURNAL OF WILDLIFE MANAGEMENT 73(8):1348–1354; 2009)

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Banding is widely used as an effective method to identify birds for long-term monitoring. Unlike other bird groups, in which bands are typically placed around the leg, the shape of the penguin knee joint renders leg bands unsuitable (Froget et al. 1998), thus bands are applied to the proximal end of the flipper. Flipper banding has taken place for over half a century (Jackson and Wilson 2002) and thousands of penguins are banded every year (Gauthier-Clerc et al. 2004). However, a number of studies have shown that banding may have negative effects on body condition and performances that may contribute to a reduction in reproductive fitness and survival rates (Froget et al. 1998, Jackson and Wilson 2002, Gauthier-Clerc et al. 2004, Le Bohec et al. 2008). One of the main problems associated with flipper banding is that, although a well-designed band is less likely to directly result in death or injury, it may still increase the drag of a swimming penguin, reducing its hydrodynamic efficiency and making foraging energetically more expensive (Bannasch 1995). Research into effects of other externally attached devices on penguins, such as data loggers, have shown that devices protruding from the body create flow separation (Bannasch 1995), affect swim speed (Wilson et al. 1986, Ropert-Coudert et al. 2007*b*), and alter diving behavior (Ropert-Coudert et al. 2000). Because penguins may spend up to 40% of their daily energy expenditure foraging at sea (Culik et al. 1993), an increase in energetic cost may influence their chances of surviving (Ainley et al. 1983, Gauthier-Clerc et al. 2004, Le Bohec et al. 2008).

Previous studies examined the hydrodynamic impact of devices using captive birds or carcasses placed in flow tanks (Culik et al. 1993, Bannasch et al. 1994, Bannasch 1995), situations that may not accurately represent live birds in natural conditions. Other studies have investigated the effects of banding on large-scale factors, such as breeding biology, survival rates, and population size. These investigations yielded variable results. For instance, bands were found to alter the demographic parameters of penguins in their first year of breeding (Gauthier-Clerc et al. 2004), but did not seem to have a similar effect on older birds (Hindell et al. 1996). This discrepancy probably stems from the fact that all the aforementioned studies occurred at different time scales and there has been no investigation of the effects of flipper bands on free-ranging penguins concurrently at short- and long-term scales. For instance, it is unknown whether newly banded penguins try to compensate for extra drag when diving and swimming by increasing the amount of time foraging or by expending more energy without modifying their diving performances (Ropert-Coudert et al. 2007*a*). There is also no information on possible habituation of penguins to the presence of a band in terms of their diving performance. This lack of information is mainly due to the difficulty of monitoring the activity of free-ranging animals. In this regard, the development of electronic recording devices provides the means to monitor and reconstruct the precise activity of animals (reviewed by Ropert-Coudert and Wilson 2005) in order to examine these effects. Additionally, previous studies examined a number of band types (Petersen et al. 2005), differing in material and size depending on the species on which they were used.

Little penguins (*Eudyptula minor*) are the smallest (900–1,300 g) penguin species and are a suitable model for such investigations, because their diving energy requirements are greater than those of all other species of penguin (Bethge et

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al. 1997). The energetic expenditure of little penguins at sea increases from 3.1 × FMR (field metabolic rate) to 5.2 × FMR in late chick-rearing (Butler and Jones 1997). This suggests that this species should be particularly sensitive to externally attached devices and if there is an effect of banding it is likely to occur during a time of increased energy demand, such as the chick-rearing period.

Our objectives were to measure and understand the possible short- and long-term effects that flipper bands may have on diving performance of little penguins, and to determine whether the practice of banding negatively affects the diving performance of these animals and possibly other penguin species. Ultimately, we sought to assess whether banding is an acceptable marking technique for penguins.

STUDY AREA

We studied little penguins in a colony at Phillip Island, Victoria, Australia (38°30′30″S, 145°09′00″E). Birds nested in artificial nest boxes among the coastal vegetation behind the primary dunes (details in Chiaradia and Kerry 1999).

METHODS

From 1968 to 2004, thousands of penguins in the Phillip Island colony were each identified with a single stainless steel band (54.2 mm long × 6.3 mm wide × 7 mm thick) applied to the right flipper (Sidhu et al. 2007). This type of band has been widely used in the study of little penguins (Dann and Cullen 1990). Following the end of wide-scale banding of penguins at this site, we implanted both unbanded and banded birds with electronic transponders as a marking technique (Chiaradia and Kerry 1999, Sidhu et al. 2007). We did not remove flipper bands from banded birds and over half of the birds recorded in our study site still carried bands at the time of the study. We carried out this study with ethics approval number 2.2004 from Phillip Island Nature Park Animal Ethics Committee and research permit number 10003419 from the Department of Sustainability and Environment, Victoria, Australia.

We conducted the diving experiment described below using 21 female little penguins in guard stage (i.e., the stage of breeding when parents alternate with each other to remain with the chick for a day, Chiaradia and Kerry 1999) between November and December 2005. We used females because they are more susceptible to changes in diving behavior when impaired by external devices (Ropert-Coudert et al. 2007*a*). Guard stage was an ideal period because parents typically forage for 1 day before returning to the colony (Chiaradia and Kerry 1999, Chiaradia and Nisbet 2006), thus facilitating the recovery of data loggers.

We assigned each female to 1 of 3 groups: an unbanded control group (unbanded, $n = 7$), a banded control group that had been carrying bands for a number of years (banded, $n = 7$), and a treatment group of unbanded birds that we banded on one foraging trip specifically for this experiment (treatment, $n = 7$). We monitored the diving activity of birds from each group over 2 consecutive foraging trips, with each trip starting when the birds headed out to sea before dawn and ending when they returned after sunset of the same day. The mean age of the banded birds was 11 years and the mean age of the unbanded and treatment birds was 5 years.

To measure short-term effect, we recorded dives on 2 consecutive foraging trips of 1 day each for all 3 groups. We collected diving data from the first foraging trip of the treatment group when they did not carry bands, then banded them and collected dive data from a second foraging trip, after which we removed the bands. We compared dive variables collected from treatment birds on the foraging trip before banding with those same variables collected on the foraging trip after treatment birds were banded. To control for individual and daily variability at foraging, we used unbanded and banded as control groups to compare diving data between trips 1 and 2.

To measure long-term effects, we collected diving data from banded birds and compared them with dive variables from unbanded birds for the first foraging trip. We included data of treatment birds (i.e., before they were banded) with those of the unbanded group since penguins from both groups were not banded during the first foraging trip. For the second foraging trip, we compared dives between the banded and unbanded groups only.

We monitored diving activity using cylindrical, 12-bit resolution UME-D2GT data loggers (Little Leonardo, Tokyo, Japan) measuring 53 × 15 mm, and weighing 16 g in air. These loggers simultaneously recorded depth and temperature every second, as well as acceleration along 2 planes: across the dorso–ventral axis (heave) and along the longitudinal axis (surge) of the bird at a frequency of 32 hertz (Ropert-Coudert et al. 2006). Absolute accuracy for depth and temperature sensors were 0.1 m and 0.1° C, respectively. We attached loggers to the feathers of the lower back using Tesa tape, following the procedure described in Ropert-Coudert et al. (2006). We deployed individuals from each group evenly throughout the duration of the experiment to account for seasonal effects, and recorded no bird for more than one set of 2 foraging trips.

We downloaded logged data and analyzed them using a custom program in Igor Pro (Wavemetrics Inc., v. 5.0.4.8, Portland, OR). We divided each dive into the descent, bottom, and ascent phases, followed by a postdive period at the surface of the water. During the descent phase, little penguins use flipper propulsion to descend through the water column, maintaining a relatively constant flipper stroke frequency. In contrast, most of the ascent is passive, with birds using their buoyancy to rise to the surface with low energy expenditure (Kato et al. 2006). We defined the bottom phase to begin and end the first and last time the descent and ascent rates became <0.3 m/second, respectively. It is during this phase that behavior is most influenced by the presence of prey, with over 75% of short increases in flipper stroke amplitude and frequency (indicative of prey pursuit) observed within this stage (Ropert-Coudert et al. 2006). Finally, postdive duration represents both recovery time from the preceding dive and preparation time for the forthcoming one (Wilson 2003). We applied a Power Spectrum Density analysis to the result of the difference between the heave signal and a low-pass filtered heave signal, to determine the dominant flipper stroke frequency (FSF in hertz, see Ropert-Coudert et al. 2006, Kato et al. 2006 for details).

We statistically tested 10 diving variables: maximum depth (m), dive duration (sec), descent and ascent rate (m/sec), duration of bottom phase (sec), postdive duration (sec), number of dives per trip, FSF, dive efficiency defined as bottom phase duration/(dive duration + post dive duration) in seconds (Ydenberg and Clark 1989), and diving effort defined as the cumulative time spent underwater during the day. We excluded dives <5 seconds duration and postdive durations >100 seconds from the analysis, because most dive variables cannot be accurately measured in such short dives (Kato et al. 2006) and because postdive durations >100 seconds represented interbout periods rather than recovery time (Chiaradia et al. 2007).

To determine whether there were any short-term effects of attaching a flipper band, we compared the values of trip 1 to those of trip 2 within all groups. All variables except the number of dives per day, the dive effort, and the FSF, are autocorrelated measurements (corresponding to the different dives made by each bird during one trip). Because we aimed at comparing trip 1 and trip 2 for each group, we had to take into consideration the longitudinal structure of our data in which each dive was not independent. Therefore, we used a General Linear Model (GLM) with the dependent variables and groups as fixed factors and individuals as random factors (to account for pseudo replication effects). This model takes into consideration the special dependence structure of our data even without applying a Kenward and Roger's adjustment on degrees of freedom (Kenward and Roger 1997). The large degrees of freedom led to a powerful test able to detect small differences, but because we used the 2 control groups (unbanded during both trips and banded during both trips), we offer that these differences are biologically meaningful.

To measure long-term effects of banding, we compared diving behavior during the first trip of banded birds to the first trip of the unbanded and treatment groups. Here, we used a GLM with a different linear model design from our previous analysis. We aimed to compare the performance of different individuals rather than a change in the dive characteristics of the same individuals under change in the experimental design (unbanded then banded). As a result, we included individuals as a random factor and nested them to the fixed factor (i.e., the banded or unbanded group). This resulted in smaller degrees of freedom according to the Fisher–Snedecor distribution (Kenward and Roger 1997) and allowed us to interpret the results directly without having to reference to control groups.

We performed statistical analyses using SYSTAT (version 10; SPSS Inc., Chicago, IL) and JMP (version 6.0; SAS Institute, San Francisco, CA) with the significance level set at $P < 0.05$. We presented data as mean $\pm$ one standard deviation unless stated otherwise. We log-transformed data, except for the dive efficiency data, which were arcsine transformed. We compared those variables that had only one value per bird per day using paired *t*-tests and 2-way *t*-tests for the immediate and long-term effect experiments, respectively.

From the start of October 2005 to the end of January 2006, we monitored flippers of banded and unbanded little penguins (5 M and 6 F in each group) for changes in feather wear. For each penguin, we photographed the right flipper (which carries the band) approximately every 20 days, depending on their presence at the nesting site. We took the initial photographs before breeding began and continued until we no longer found birds in the colony during the day, usually at the start of the postguard stage of rearing young. We took photographs in the shade during daylight and without the use of a flash using a 3.2-mega pixel digital camera (Pentax, Tokyo, Japan) mounted on a tripod that held the lens 280 mm away from the platform on which we laid the flipper flat.

We examined digital images to detect any changes in the area of the white feathers on the trailing edge of the flipper. We cropped the flipper from the background, then isolated the white feathers of the trailing edge from the dark blue feathers of the flipper by using a function of Adobe Photoshop (Adobe Systems Inc., San Jose, CA) to select areas of similar color and recolor them in plain white. We then used the pixel count function to count the number of white pixels in the image and compared the number of pixels in the first and last photos taken for each bird to measure the percentage change (arcsine transformed) in white pixel area as our measure of change in white feather area. We determined statistical differences using an analysis of variance with the presence or absence of a band as a factor.

RESULTS

Our experiments did not appear to affect breeding activity and all birds continued to raise their chicks. We successfully retrieved all data loggers, but data from one logger deployed on a banded bird were corrupted and not used. The resulting samples were 6 banded birds, 7 unbanded birds, and 7 treatment birds.

Within the treatment group, diving effort, number of dives made per trip, and the FSF were the only variables that did not differ between trip 1 (no flipper band) and trip 2 (flipper band present; Table 1). For all other diving variables, differences between trip 1 and trip 2 differed statistically (in all cases, the risk of a type I error was <0.1%). In the unbanded and banded groups, we found differences for only 3 and 4 of these variables, respectively (with a risk of a type I error ranging between 1% and less than 0.1%; Table 1). This implies that the cost of diving for birds from the banded and treatment groups was less during the first trip, whereas that for birds from the unbanded group did not differ between trips.

Only one diving variable recorded during the first trips of the banded birds was different (Table 2) from that of the unbanded birds. Birds in the banded group spent on average 2.69 seconds longer at the bottom than those in the unbanded groups.

Table 1. Immediate effects of a flipper band on the diving activity of little penguins on Phillip Island, Victoria, Australia. Measurements were made using a General Linear Model (GLM) and paired *t*-test to compare dives of 7 birds (Treatment group) just before (trip 1) and just after (trip 2) applying a band to the right flipper. In parallel, we also compared dives during trip 1 and 2 of 2 other control groups of 7 birds each, which were either banded during both trips (Banded control group) or unbanded during both trips (Unbanded control group). We recorded all data over a single day trip during the guard stage of the 2005 breeding season. Values are presented as the grand mean ± one standard deviation. Significant differences are highlighted in bold.

Diving variables	Trip 1 ($n = 7$)	Trip 1 SD	Trip 2 ($n = 7$)	Trip 2 SD	Statistics	*P*
Treatment group (unbanded during trip 1 and banded during trip 2)						
Diving depth (m)	9.54	3.44	10.05	3.57	**GLM: $F_{1,10949} = 76.8$**	**$\leq$0.001**
Diving duration (sec)	23.87	8.93	26.22	7.43	**GLM: $F_{1,10949} = 182.0$**	**$\leq$0.001**
Bottom phase duration (sec)	8.70	2.60	9.77	2.48	**GLM: $F_{1,\ 10183} = 151.3$**	**$\leq$0.001**
Descent rate (m/sec)	1.41	0.17	1.30	0.10	**GLM: $F_{1,10950} = 222.1$**	**$\leq$0.001**
Ascent rate (m/sec)	1.31	0.07	1.35	0.08	**GLM: $F_{1,10878} = 25.6$**	**$\leq$0.001**
Postdive duration (sec)	18.20	5.58	22.20	5.70	**GLM: $F_{1,10950} = 144.4$**	**$\leq$0.001**
Dive efficiency	0.219	0.04	0.216	0.06	**GLM: $F_{1,10950} = 20.7$**	**$\leq$0.001**
No. of dives per trip	587.17	197.13	810.64	392.37	paired-*t*: $t_6 = 1.76$	0.13
Dive effort (sec)	17,970	5,591	16,818	4,734	paired-*t*: $t_6 = 0.79$	0.46
Flipper stroke frequency (hertz)	3.21	0.28	3.20	0.43	paired-*t*: $t_6 = -0.17$	0.87
Banded control group (banded during both trips)						
Diving depth (m)	11.68	2.25	11.48	4.48	GLM: $F_{1,6760} = 0.02$	0.88
Diving duration (sec)	31.04	5.29	28.82	9.98	**GLM: $F_{1,6764} = 12.5$**	**$\leq$0.001**
Bottom phase duration (sec)	10.73	2.22	9.69	2.53	**GLM: $F_{1,\ 6371} = 9.7$**	**0.002**
Descent rate (m/sec)	1.27	0.07	1.26	0.14	GLM: $F_{1,6755} = 1.8$	0.17
Ascent rate (m/sec)	1.31	0.09	1.27	0.09	**GLM: $F_{1,6735} = 6.1$**	**0.014**
Postdive duration (sec)	25.75	3.99	26.48	6.60	GLM: $F_{1,6764} = 12.5$	0.15
Dive efficiency	0.211	0.03	0.193	0.05	**GLM: $F_{1,6764} = 11.7$**	**$\leq$0.001**
No. of dives per trip	587.17	197.13	540.83	270.23	paired-*t*: $t_5 = 0.38$	0.72
Dive effort (sec)	17,970	5,591	14,900	6,797	paired-*t*: $t_5 = 1.21$	0.28
Flipper stroke frequency (hertz)	3.17	0.29	3.27	0.22	paired-*t*: $t_5 = 0.92$	0.40
Unbanded control group (unbanded during both trips)						
Diving depth (m)	10.66	5.74	9.97	4.10	**GLM: $F_{1,10745} = 7.3$**	**0.007**
Diving duration (sec)	24.13	11.33	23.23	9.16	GLM: $F_{1,10745} = 0.22$	0.64
Bottom phase duration (sec)	7.39	2.86	7.42	2.03	GLM: $F_{1,\ 9793} = 0.04$	0.85
Descent rate (m/sec)	1.37	0.19	1.34	0.20	GLM: $F_{1,10745} = 1.51$	0.22
Ascent rate (m/sec)	1.29	0.09	1.40	0.17	**GLM: $F_{1,10745} = 25.7$**	**$\leq$0.001**
Postdive duration (sec)	25.61	8.03	22.64	6.47	**GLM: $F_{1,10745} = 20.0$**	**$\leq$0.001**
Dive efficiency	0.166	0.04	0.175	0.02	GLM: $F_{1,10745} = 1.84$	0.17
No. of dives per trip	696.43	344.19	839.57	389.01	paired-*t*: $t_6 = -1.60$	0.16
Dive effort (sec)	14,598	4,898	16,784	2,313	paired-*t*: $t_6 = -1.24$	0.26
Flipper stroke frequency (hertz)	3.32	0.29	3.34	0.28	paired-*t*: $t_6 = 0.26$	0.80

Banded birds had a higher rate of wear on flipper feathers than unbanded birds over one breeding season. There was a significant difference between banded and unbanded birds in the percent change between the initial and final white pixel areas (analysis of variance of arcsine-transformed data, $F_{1,20} = 9.20$, $P = 0.007$) determined from the digital images of the right flipper (Fig. 1). In the banded group, there was a 10% decrease in the white pixel area (mean

Table 2. Long-term effects of a flipper band on the diving activity of little penguins on Phillip Island, Victoria, Australia. Measurements were made using a General Linear Model (GLM) and 2-sample *t*-test to compare dives of birds that have been banded for several years (trip 1 of the Banded group) with those of a group of birds that had never been banded (trip 1 of the Unbanded and Treatment groups). We recorded all data over a single day trip during the guard stage of the 2005 breeding season. Values are presented as the grand mean ± one standard deviation. Significant differences are highlighted in bold.

Diving variables	Banded birds (banded group; $n = 6$)	Banded SD	Unbanded birds (unbanded and treatment groups; $n = 14$)	Unbanded SD	Statistics	*P*
Diving depth (m)	11.68	2.25	10.10	4.59	GLM: $F_{1,18} = 0.78$	0.39
Diving duration (sec)	31.04	5.29	24.00	9.81	GLM: $F_{1,18} = 2.78$	0.11
Bottom phase duration (sec)	10.73	2.22	8.04	2.71	**GLM: $F_{1,18} = 5.54$**	**0.03**
Descent rate (m/sec)	1.27	0.07	1.39	0.17	GLM: $F_{1,18} = 3.65$	0.07
Ascent rate (m/sec)	1.31	0.09	1.30	0.08	GLM: $F_{1,18} = 0.44$	0.52
Postdive duration (sec)	25.75	3.99	21.90	7.68	GLM: $F_{1,18} = 1.84$	0.19
Dive efficiency	0.211	0.03	0.192	0.04	GLM: $F_{1,18} = 0.25$	0.63
No. of dives per trip	587.17	197.13	810.64	392.37	2-*t*: $t_{18} = -1.31$	0.21
Dive effort (sec)	17,970	5,591	16,818	4,734	2-*t*: $t_{18} = 0.86$	0.34
Flipper stroke frequency (hertz)	3.17	0.11	3.27	0.08	2-*t*: $t_{18} = 0.74$	0.47

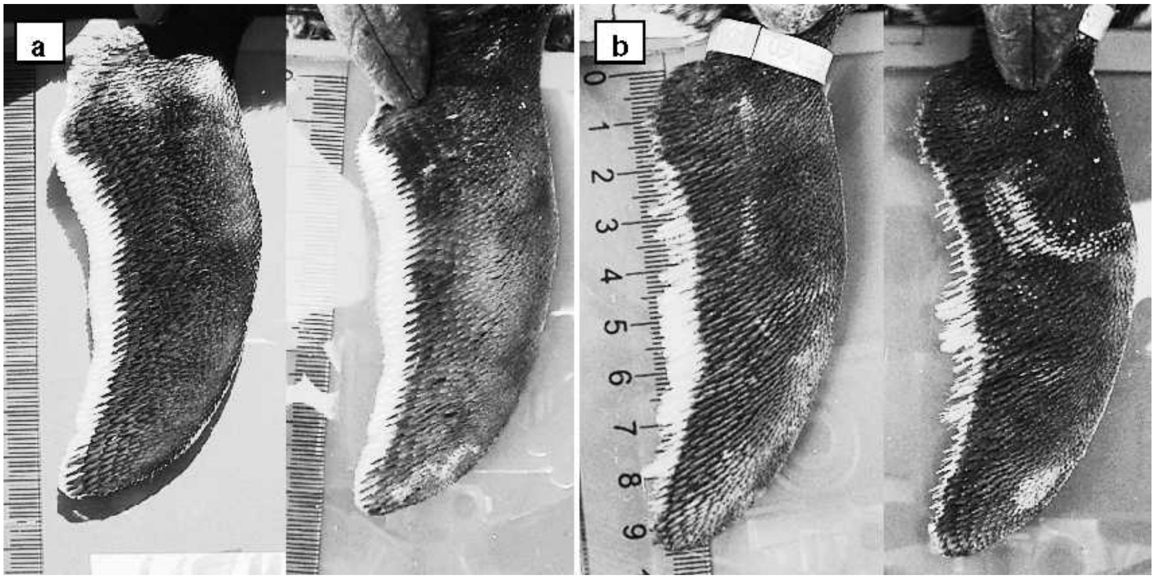

Figure 1. Flipper wear of little penguins on Phillip Island, Australia. We measured the degree of wear of the white feathers of the trailing edge for (a) an unbanded and (b) a banded bird. Left and right photos in (a) and (b) were taken in October 2005 and January 2006, respectively.

initial area = 5,029 ± SE 409 pixels, mean final area = 4,567 ± SE 440 pixels). In contrast, the unbanded group showed a 13% increase in the measured white pixel area (mean initial area = 5,277 ± SE 321 pixels, mean final area = 5,956 ± SE 280 pixels). The amount of feather wear observed on the unbanded (left) flipper was visually similar to that of the right flipper of banded birds.

DISCUSSION

We detected immediate effects of wearing a band on the diving behavior of little penguins, but we did not detect any long-term effects. We detected the immediate differences in the diving activity of birds from the control groups (birds that were either unbanded both trips or banded both trips) and birds from the treatment group (birds that were unbanded during the first trip and banded for the second trip). We expected some differences because birds from these groups did not forage on the same day and thus would have modified their diving behavior according to the environmental conditions they encountered. However, the variability between trip 1 and 2 was higher in the treatment group than in the control groups. When comparing dives on day 1 (not banded) with day 2 (banded) for the treatment group, several variables changed. On day 2, birds dived deeper, for longer, spent more time in the bottom phase, ascended more quickly, descended more slowly, and had longer surface pauses between dives. In contrast, the diving behavior of the unbanded control group did not differ between the 2 trips. Our findings from free-ranging penguins agree with those of Culik et al. (1993), who examined immediate effects of band attachment on captive individuals and found that banded Adélie penguins (*Pygoscelis adeliae*) swam at slower speeds than unbanded control birds. There is no study investigating a possible habituation of birds to the presence of a band regarding their diving activity.

Little penguins seem to modify their diving activity in response to, or as consequence of, the presence of an externally attached encumbrance. The relatively slow descent rate of the banded birds compared to that of the unbanded birds is not unlike the response of Adélie penguins impeded by relatively large attached devices that also swam slower in the descent phase (Ropert-Coudert et al. 2007*b*). Similarly, the increase in bottom phase duration by the banded birds is in accordance with the findings by Ropert-Coudert et al. (2007*a*) that little penguins carrying a large device on their backs spent proportionally longer lengths of time in the bottom phase of the dive than birds with a smaller logger. Hydrodynamic drag is the major contributor to energetic cost when swimming (Lovvorn and Liggins 2002), so banded birds may have spent longer in the bottom phase to catch more prey to compensate for their increased energy expenditure. However, the increase in postdive duration and decrease in diving efficiency suggest that these extended bottom times may have been a result of more costly foraging activity (i.e., banded birds had to spend more time to catch the same amount of prey as the unbanded birds). Another study on Adélie penguins showed that in certain years banded birds made foraging trips that were around 8% longer than their unbanded counterparts (Dugger et al. 2006). The treatment group's relatively slow descent rate and extended bottom time contributed to the observed increase in total dive duration in this study, and these may be examples of mechanisms that contribute to the extension of foraging trips. Although the differences before and after banding may have seemed relatively small, an increase in time of only several seconds could make an important difference in terms of aerobic budget. In addition, although we observed little effect of the bands after birds had carried them for several years, we do not know how the behavior of newly banded penguins develops in the short term and whether their performance would continue to deteriorate in subsequent foraging trips. Indeed, it seems that the presence of a flipper band on little penguins reduces survival after banding, particularly in the first year (P. Dann, Phillip Island Nature Park, unpublished data).

Over several years, birds may have become accustomed to changes in their hydrodynamics caused by the band so that their performance became similar to that of unimpaired birds. In this context, it is important to note that the banded birds were older than the unbanded birds and may have been, therefore, more experienced foragers as well as generally fitter individuals. The older banded birds could have represented individuals that were able to overcome the burden of carrying a band. As mortality due to the presence of a band is higher in young individuals (Gauthier-Clerc et al. 2004), birds that could not cope with their bands may have been removed from the population. This implies that any long-term effects of banding may be difficult to detect if only the fitter banded birds survive to an older age. It is also possible that the recording devices used in our experiment may have had a synergistic effect with the flipper bands, possibly exacerbating apparent band effects, but the impossibility of monitoring the diving activity of birds not equipped with data-loggers prevents us from investigating this point any further.

The feather wear results suggest a possible mechanism by which the presence of a band may manifest in changing the hydrodynamic properties of the flippers. The reduction in white pixel area implies a similar reduction in the area and continuity of white feathers in the trailing edge of the flipper (i.e., visible gaps in the line of feathers). Feathers accumulate wear and eventually deteriorate to the point where they fracture, reducing the surface area of the flippers and decreasing the amount of thrust produced in each stroke cycle. It seems reasonable that the presence of a band may directly affect dive performance because a band may also affect maneuverability (Jackson and Wilson 2002). If flipper functional area is reduced, this may produce a need to increase the frequency of flipper strokes, increasing locomotory cost (Williams et al. 2004). We are cautious about inferring too much from our data because the technique has a number of limitations, principally that although it is possible to measure changes in the absolute area of the feathers within a certain color range, it does not measure the functional area of feathers. Differences in the extension of the flipper when photographed will affect the area of feathers subsequently measured and so photos must be taken carefully. Although limitations exist, we think that further refinement of the technique will prove useful.

MANAGEMENT IMPLICATIONS

Our study showed that banding had an immediately negative effect on the diving performance of little penguins. We stress that we detected all these differences just one day after banding. Whether these differences would increase over time is hard to predict and beyond the scope of this study, but deserves further investigation. However, this is the first direct measure of changes on the diving behavior of penguins in relation to banding. There may be important implications of altered diving behavior on the foraging, energy acquisition, and ability of banded animals to reproduce successfully. From a management perspective, we must investigate any practice that potentially decreases the fitness of animals and must seriously consider our findings in any start or review of a penguin flipper-banding program. In addition to the need to refine the design of flipper bands to reduce the encumbrance they cause, we recommend that alternative marking techniques be evaluated wherever possible. These include the use of subcutaneous passive transponders, already used in some penguin colonies such as the one in our study (Chiaradia and Kerry 1999, Daniel et al. 2007, Sidhu et al. 2007).

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