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EFFECTS OF FLIPPER BANDS ON FORAGING BEHAVIOR AND SURVIVAL OF ADÉLIE PENGUINS (*PYGOSCELIS ADELIAE*)

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Abstract.—Since the 1950s, flipper bands have been used widely to mark penguins (Spheniscidae), but not without concerns regarding possible negative effects on survival and fitness. As part of a demographic study of Adélie Penguins (*Pygoscelis adeliae*) in the western Ross Sea, Antarctica, we investigated effects of flipper bands on foraging-trip duration and food loads, as well as apparent survival, during four breeding seasons (2000–2003), using mark–recapture and radio-frequency identification (RFID) technology. Foraging-trip durations were ~8% (3.5 h) longer, on average, for banded compared with unbanded birds, but the effect varied among years. Food loads did not differ between banded and unbanded birds, but males carried heavier food loads than females. Flipper bands decreased apparent annual survival by 11–13% during 2000–2003, but over a longer time period (1996–2003) we observed high annual variability, including years of high survival for banded birds. Males had slightly higher survival than females in both banded and unbanded birds. Mechanisms resulting in band effects on foraging behavior and survival, the variable effect of bands by season, and the potential ameliorating effect of age or experience on the effects of bands need further investigation in Adélie and other penguin species. We recognize a need to understand and balance the negative consequences of flipper bands for penguins against the beneficial gains in information associated with their use. *Received 5 January 2005, accepted 14 October 2005.*

Key words: Adélie Penguin, band effects, foraging behavior, *Pygoscelis adeliae*, survival.

Effets du Baguage à l'Aileron sur le Comportement de Recherche Alimentaire et la Survie de *Pygoscelis adeliae*

Résumé.—Depuis les années 1950, le baguage à l'aileron a été largement utilisé pour marquer les manchots, non sans soulever des inquiétudes concernant d'éventuels effets négatifs des bagues sur la survie et la valeur sélective (« fitness »). C'est pourquoi, dans le cadre d'une étude démographique du manchot Adélie (*Pygoscelis adeliae*) dans l'ouest de la mer de Ross, Antarctique, nous avons souhaité examiner les effets du baguage à l'aileron sur la durée des voyages alimentaires, sur la masse des bols alimentaires et sur la survie apparente, durant 4 saisons de reproduction (2000-2003) en utilisant les techniques de capture-recapture et la technologie RFID (identification par fréquence radio). Les voyages alimentaires sont en moyenne 8% (3,5h) plus longs chez les oiseaux bagués que chez les oiseaux non-bagués, mais l'effet varie selon les années. La masse du bol alimentaire ne diffère pas entre oiseaux bagués et non-bagués, mais les mâles rapportent des bols alimentaires

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plus lourds que les femelles. Durant la période 2002-2003, les bagues à l'aileron diminuent la survie apparente annuelle de 11-13%, mais sur une plus longue période, nous observons une forte variabilité inter-annuelle, incluant des années de survie élevée pour les oiseaux bagués. Les mâles ont une survie légèrement meilleure que les femelles, à la fois chez les oiseaux bagués et non-bagués. Des études supplémentaires sont requises, chez le manchot Adélie comme chez d'autres espèces de manchot, afin de mieux comprendre les mécanismes responsables de l'effet des bagues sur le comportement de recherche alimentaire et la survie, la variabilité de l'effet des bagues selon les années, et le possible effet compensatoire de l'âge ou de l'expérience. Nous reconnaissons la nécessité de comprendre les conséquences négatives des bagues chez les manchots et de les mettre en regard des gains d'informations associés à leur utilisation.

Flipper bands have been used widely for marking penguins (Spheniscidae) since the 1950s (Stonehouse 1999), because they are economical and easy to attach with little disturbance, and because large numbers of individuals can be monitored easily without recapture. Throughout the history of their use, however, concerns have been raised regarding possible negative effects on penguin survival and fitness (for review, see Jackson and Wilson 2002, Petersen et al. 2006). Results of investigations regarding the effects of bands on penguins have been equivocal, varying among studies and among and within species. Lower return rates or survival estimates for banded individuals have been reported for Adélie Penguins (*Pygoscelis adeliae*; Ainley and DeMaster 1980, Ainley et al. 1983) and King Penguins (*Aptenodytes patagonicus*; Froget et al. 1998), but these effects were not apparent in other studies of Adélie (Clarke and Kerry 1998), King (Gauthier-Clerc et al. 2004), and Royal Penguins (*Eudyptes schlegeli*; Hindell et al. 1996). Band-related decreases in reproductive success have been reported for King Penguins (Gauthier-Clerc et al. 2004), but in Royal Penguins such effects were not reported (Hindell et al. 1996). Variable effects of bands between and within species may reflect the true complexity of the issue, different band designs, or different experimental and analytical designs between studies. It is possible that flipper bands have negative effects on penguins only in years with low food availability or large environmental perturbations (e.g., extensive winter ice in the case of polar species), but no effects in years with "normal" environmental conditions (Hindell et al. 1996, Froget et al. 1998).

Perhaps the ultimate issue concerns the need to increase our understanding of the mechanisms by which flipper bands negatively affect penguin well-being. Direct wounding associated with flipper bands likely resulted in decreased survival for banded birds in some studies, but this negative effect has been greatly decreased or eliminated through improvements of earlier band designs (Sallaberry and Valencia 1985). Experimental work has suggested that bands negatively affect swimming energetics (Culik et al. 1993), and several authors have suggested that these effects should negatively affect penguin foraging efficiency, which, in turn, would be expected to decrease survival or reproductive success (Hindell et al. 1996, Froget et al. 1998, Gauthier-Clerc et al. 2004). However, no work has been conducted to detect these energetic constraints on banded, free-swimming, wild birds; in fact, no one has previously studied direct effects of bands on penguin foraging behavior or effort.

Here, we analyze effects of flipper bands on apparent survival and foraging behavior of breeding Adélie Penguins using mark–recapture methodologies and radio-frequency identification (RFID) technology, which allows the "recapture" of known, unbanded individuals. We had four seasons of mark–recapture data on banded birds and unbanded RFID-tagged birds suitable for investigations of direct effects on survival and foraging behavior. We also had an additional four years of mark–recapture data on banded birds, for a total of eight years, to provide insight into interannual variation in survival and recapture–resighting rates of banded birds in our study population. We investigated the hypothesis that Adélie Penguins with flipper bands are affected negatively during at-sea travel compared with unbanded individuals by studying variation in food-load mass brought back to the colony and foraging-trip duration during the chick provisioning period. We predicted that, if flipper bands negatively affect swimming energetics of Adélie Penguins, we would observe lower survival, longer foraging trip durations, lower food loads, or a combination of these effects, in banded birds compared with unbanded birds.

Methods

Study area and data collection.—Our study colony was located at Cape Crozier, Ross Island (77°30′S, 168°E), Antarctica. Total colony size ranged from 118,000 to 137,000 breeding pairs, depending on season. Study of Adélie Penguin foraging and breeding effort was initiated in 1996, when plastic fencing was used to surround a subcolony that grew over the course of the study but ranged from 160 to 259 pairs, depending on the season. One access point to the subcolony was filled with a weighbridge (WB), as described in Ballard et al. (2001). The WB consisted of an electronic scale, a direction indicator, and an RFID reader connected to a data logger (following Kerry et al. 1993; see also Beigel et al. 2004) and was installed between 10 and 15 December—around peak hatching time—in all seasons.

We implanted unique RFID tags in 251 Adélie Penguins between 1996 and 2003. Tags, manufactured by Avid (Norco, California) weighed 0.1–0.3 g and were 1.2–1.8 cm long and 0.2–0.3 cm wide. They were injected subcutaneously between and a little above the scapulas. Until 2000, all birds with RFID tags were also banded on the left flipper with a numbered band, following the "Boersma design" from Porzana (East Sussex, United Kingdom) (P. D. Boersma pers. comm.). These bands are teardrop-shaped and constructed of stainless steel 0.1 cm thick. The dimension at the widest cross-section, which is oriented toward the anterior edge of the flipper, is 2.0 cm, and the inside length is 3.6 cm. Numbers stamped into the bands are 0.8 cm high. The bands close so that the ends of the band butt together on the outside of the flipper. The steel used is strong (it takes two hands to open one of these bands).

Bird identification, time, direction, and body mass for >95% of WB crossings were recorded each season, and analyses of these foraging data have been published elsewhere (Ainley et al. 1998, 2004; Ballard et al. 2001). The ultimate goal of our overall study is to understand Adélie Penguin demography in the context of climate change (materials are available at the "penguinscience" website; see Acknowledgments). In 2000, having determined that our RFID system was at least as accurate as band-resighting by eye, we initiated the present band-effects study within the WB subcolony. We were interested in gathering data to calibrate our band-sighting data (i.e., quantifying such factors as band loss or band-related mortality). The present study covered most of the guard and crèche stages of chick-rearing (21 December to 22 January) for four austral summers, 2000–2001 to 2003–2004 (hereafter, each season is identified by its initial year; e.g., "2000 season" refers to 2000–2001). In 2000, 28 birds (about equally split between the sexes) were RFID-tagged, but left unbanded (RO group) and 22 new individuals were RFID-tagged and banded (RB). In subsequent years, 6 to 28 new individuals were added to each group (RB vs. RO) to maintain equal samples of banded and unbanded pairs in the subcolony. Handling time was generally <2 min per individual, and we attempted in each season to maintain ≥30 active nests at which both adults were tagged. Only birds of known sex were used in these analyses. We determined sex primarily by copulatory position, but we also used behavior, "tread marks" (evidence of female copulatory position), bill- and head-size differences, and body mass (Ainley et al. 1983, Kerry et al. 1992). For the recapture data set, a bird was considered alive and present on the study area if it was recorded by the WB ≥1 time during the season.

Because we did not monitor the nests of all birds, we used a foraging-behavior criterion to establish breeding status of both RB and RO birds: individuals had to make >4 trips, from 6 to 120 h long, between 21 December and 22 January, to be classified as breeders (Ballard et al. 2001). This criterion correctly classified the breeding status of all but one known-status individual (which was given a false negative). Food load, or the size of meals delivered to chicks, was calculated as the difference between an individual parent's out-mass and its most recent in-mass. Mass was calculated using a highly accurate, year-specific algorithm, because each WB installation varied slightly in physical characteristics. In all cases, the scales were calibrated against known standard weights and measured mass 12 times per second, and the bird had to be on the scale ≥0.8 s for a valid estimate to be recorded. For the food-load analysis, only individuals that carried at least three measurable meals during the same period were included. Measurable meals (~80% of WB crossings) excluded individual trips where the WB was subject to error because multiple Adélie Penguins were moving across the scale (Ainley et al. 1998, 2004).

Statistical analyses.—We used generalized linear modeling to investigate effects of breeding season (i.e., year), sex, and bands on mean foraging-trip duration and food load per individual per year. Previous analysis of WB foraging data (Ballard et al. 2001) supported the inclusion of season and sex in the foraging behavior models, so this was our base model, from which we built our *a priori* model set to investigate band effects, as well as the two-way band*season and band*sex interactions. Band effects may vary by season (Hindell et al. 1996, Froget et al. 1998) in relation to energetic constraints associated with resource limitation. In addition, given the energetics associated with body-size differences, any negative effects of bands may be more pronounced in female Adélie Penguins, because they are, on average, smaller than males.

Residual plots and formal statistical tests (e.g., STATA, version 8.0; sktest; Stata, College Station, Texas) suggested that residuals were independent and normally distributed, with homogeneous variances (Zar 1999); thus, we did not transform the foraging data. We used an information-theoretic approach including the corrected version of Akaike's Information Criterion for small sample sizes (AIC_c), the difference in AIC_c between each candidate model and the model with the lowest AIC_c value (ΔAIC_c), and Akaike weights (w_i) to rank and select the best models for foraging-trip duration and food load (Burnham and Anderson 2002). The degree to which 95% confidence intervals for slope coefficients (β_i) overlapped zero was also used to evaluate the strength of evidence for specific effects in competing models (<2 AIC_c values) within the model set. The model with the lowest AIC_c value was generally considered best, unless confidence intervals on slope coefficients suggested more support for a close competitor. All foraging behavior calculations were performed using STATA.

The program MARK (White and Burnham 1999) was used to generate models, model-selection criteria, and estimates of apparent survival and recapture probabilities from capture–recapture data and Cormack-Jolly-Seber (CJS) models (Lebreton et al. 1992) for Adélie Penguins from our WB subcolony. We used an information-theoretic approach (Burnham and Anderson 2002), as detailed above, to select our best models. We were primarily interested in determining what effect flipper bands had on Adélie Penguin survival, but annual variation in survival and sex-related survival differences, particularly in relation to band effects, were also of interest. We collected capture–recapture data for both males and females with RFID tags and flipper bands (RB) and with RFID tags only (RO). Mark–recapture data were coded into four groups (female RB, male RB, female RO, male RO), which allowed us to investigate band effects, as well as sex and time (i.e., year) effects. We collected capture–recapture data for RB birds over eight seasons (1996–2003), but capture data for RO birds only during the last four (2000–2003). Our mark–recapture data set included 83 females and 75 males in both groups (RB vs. RO) during eight breeding seasons (1996–2003). The RO group included 46 females and 47 males during the last four seasons (2000–2003). We used the linear modeling capabilities in MARK (White and Burnham 1999) to code models that accounted for the lack of data on RO birds during the first four years of the study. We only modeled band effects for years 2000–2003, when we had birds in both band groups. To increase precision of other estimates, we fixed parameters for the RO group to zero during the years these birds were not present (1996–1999). This structure, which was maintained throughout the modeling process for capture rates and survival, allowed us to model band ("b"), sex ("s"), and season-specific time effects ("t") with all the mark–recapture data we had available, rather than just the four years when we had both groups represented.

We used RELEASE (Burnham et al. 1987) to test for goodness-of-fit (GOF) of our global model to the general CJS model and to estimate overdispersion ($\hat{c}$); we used the combined chi-square values and degrees of freedom from test 2 and test 3 to estimate overdispersion ($\hat{c} = \chi^2 / \text{df}$; Lebreton et al. 1992, White 2002). With four groups in our initial data set, RELEASE provided chi-square values and degrees of freedom for each group separately; we combined these to create an overall GOF statistic. There was no indication of overdispersion or lack-of-fit for the general CJS model ($\chi^2 = 9.0253$, df = 18, $P = 0.9591$; $\hat{c} < 1.0$), and the four age and sex subgroups also fit the CJS model well.

We used a multistep process to model capture probability and survival, because the potential model set was much too large if we took the approach of modeling every possible combination of the three main effects (i.e., band group, sex, and season) and interactions on survival and capture probability simultaneously. Instead, we modeled capture probabilities first, while maintaining the most general, global model structure on survival (ϕ_{b*s*t}). We then used the best capture probability structure from this first step to model survival. Our *a priori* model set for capture probability included the single-, double-, and triple-factor additive-main-effect models for band effect, sex, and season. Bands may have a differential effect on recapture rates by season or between sexes, so we predicted a band*season and band*sex interaction. However, we did not hypothesize a differential effect of flipper bands on capture rates of females compared with males by season, so band*season interaction models were not included in our *a priori* model set. We also included the global model (p_{b*s*t}) and the constant capture-probability model (no season, group, or sex effects) in our initial model set.

After choosing the best structure for capture probability from the first step (p_{best}), we modeled apparent survival, investigating the additive effects of bands, sex, and season and the interactions of band*season, band*sex, and sex*season. Previous researchers hypothesized a variable band effect by year on survival, so we believed that this was an important *a priori* model, as were any variations in survival by sex over time. In addition, because of body-size differences between the sexes, we believed that there was some potential for band effects on survival to vary by sex, so we included a model with the band*sex interaction. The global model with the most general structure on survival ($\phi_{b*s*t,}\ p_{\text{best}}$) and a model with no time, sex, or band effects was also included in our *a priori* model set (ϕ, p_{best}).

Early work addressing the effects of flipper bands of a slightly different design (less oval-shaped; described in Sladen and LeResche [1970]) suggested that Adélie Penguin survival may only be affected in the first year after banding (Ainley and DeMaster 1980). To test this hypothesis, we also analyzed the eight years of mark–recapture data for RB birds without the RO birds, to simplify the coding. We modeled capture probability for this data set as we did for the larger data set above, but without the band effects. We then investigated survival models that estimated the first year's survival after banding different from all other years for each newly banded cohort. Our global model included time-dependent survival the first year, time-dependent survival for all years after the first year, and the best capture-probability model from the initial step ($\phi^1{}_t\phi^2{}_t$, p_{best}). We also included time-dependent survival (with no first-year-after-banding effects) and constant survival models (both with and without first-year-after-banding effects) in this model set to determine whether survival was lower for banded birds the first year after banding.

Results

Foraging behavior.—Number of individuals and number of foraging trips per individual varied by group (RB vs. RO), sex, and year (Table 1). There was substantial support for a band effect on foraging-trip duration; all models with a band effect (or band-effect interaction) had lower AIC_c than the base model including only sex and season (Table 2). The mean difference in trip duration between banded and unbanded birds from our best model was 3.5 h, or 8% longer trips for banded birds, but the magnitude of the band effect varied by season. Average foraging-trip duration for banded birds was 3.9–9.2 h longer than for unbanded birds during 2000, 2002, and 2003; but in 2001, it was 6 h longer for unbanded birds. Mean trip duration averaged 8.1 h longer for females than for males, and this was a strong main effect ($\hat{\beta} = 7.58$, 95% CI: 3.35 to 11.82). A competitive model (<2 ΔAIC_c) also included the band*sex interaction (Table 2); however, confidence intervals for the band*sex interaction coefficient included zero ($\hat{\beta} = 2.80$, 95% CI: –3.37 to 8.97), indicating a weak effect.

The best model for food load supported a band*season interaction, but two other models were competitive: the model without any band effects, and a model with both band*season and band*sex interactions (Table 3). However, the

Table 1. Number of individuals, number of trips, and trip duration in hours (means ± SE) by sex and season for banded (RB) and unbanded (RO) Adélie Penguins nesting in the weighbridge subcolony at Cape Crozier (2000–2003).

	RB			RO		
Season	Trip duration (h)	Individuals (*n*)	Trips (*n*)	Trip duration (h)	Individuals (*n*)	Trips (*n*)
			Males			
2000	20.3 ± 0.9	21	284	18.2 ± 1.0	13	195
2001	27.0 ± 0.6	7	56	32.4 ± 6.4	6	50
2002	41.7 ± 3.6	16	103	35.5 ± 2.9	13	97
2003	36.7 ± 5.1	5	36	36.6 ± 2.5	18	140
			Females			
2000	25.9 ± 2.2	17	183	19.6 ± 1.2	13	183
2001	36.2 ± 3.6	7	49	41.0 ± 4.9	9	64
2002	55.1 ± 4.6	11	62	40.4 ± 3.0	14	109
2003	60.3 ± 5.2	4	21	51.5 ± 3.7	13	87

Table 2. Model-selection results from an *a priori* generalized linear model set relating foraging-trip duration to the effects of band, sex, and season on Adélie Penguins (n = 187) nesting in the weighbridge subcolony at Cape Crozier (2000–2003). Included for each model are Akaike's Information Criterion adjusted for small sample sizes (AIC_c), difference in AIC_c between each candidate model and the model with the lowest AIC_c value (ΔAIC_c), AIC_c weights (w_i), value of the maximized log-likelihood function ($\text{Log}_e[L]$), and number of parameters (k). Asterisks between covariates indicate interactions.

Model	AIC_c	ΔAIC_c	w_i	$\text{Log}_e(L)$	k
Season, sex, band, band*season	1,427.63	0.00	0.56	–703.19	10
Season, sex, band, band*sex, band*season	1,429.05	1.42	0.28	–702.77	11
Season, sex, band	1,430.87	3.24	0.11	–708.12	7
Season, sex, band, band*sex	1,432.53	4.90	0.05	–707.86	8
Season, sex	1,436.37	8.74	0.01	–711.95	6

Table 3. Model selection results from a generalized linear model set relating food loads to the effects of band, sex, and season for Adélie Penguins (n = 187) nesting in the weighbridge subcolony at Cape Crozier (2000–2003). Included for each model are Akaike's Information Criterion adjusted for small sample sizes (AIC_c), difference in AIC_c between each candidate model and the model with the lowest AIC_c value (ΔAIC_c), AIC_c weights (w_i), value of the maximized log-likelihood function ($\text{Log}_e[L]$), and number of parameters (k). Asterisks between covariates indicate interactions.

Model	AIC_c	ΔAIC_c	w_i	$\text{Log}_e(L)$	k
Sex [a]	–123.60	0.00	0.54	64.87	3
Sex, band [a]	–121.51	2.09	0.19	64.87	4
Season, sex, band, band*season	–120.65	2.95	0.12	70.95	10
Season, sex	–119.43	4.17	0.07	65.95	6
Season, sex, band, band*sex, band*season	–118.84	4.76	0.05	71.17	11
Season, sex, band	–117.41	6.19	0.02	66.02	7
Season, sex, band, band*sex	–115.70	7.90	0.01	66.25	8

[a] *A posteriori* models.

confidence intervals associated with the main effects of season in these top three models all included zero, which suggests that season may not have a significant effect on food loads. We had not included models in our initial model set to directly test the effect of season on food loads, because we expected food loads to reflect the same seasonal variation noted in previous work on trip durations (Ballard et al. 2001). However, *a posteriori*, we added a model with the additive effects of sex and bands, and a model with a sex effect only, to the model set (Table 3). The best model now included only sex and received almost 3× the support of the sex and band-effect model, and >4× the support of the third-best model with season, sex, and band main effects and band*season interactions that were no longer competitive (Table 3). Bands had little effect on food loads but, on average, males carried 55 g more food than females ($\hat{\beta} = -0.055$, 95% CI: –0.11 to –0.005). Food loads for males and females (means ± SE) were 0.64 ± 0.02 kg and 0.59 ± 0.02 kg, respectively.

Apparent survival.—The capture-probability model from our *a priori* model set with the lowest AIC_c included time-dependent effects only (p_t). For two years, capture-probability estimates were close to 1.0. The years for which capture rates were <1.0 (2001, 2003) corresponded to those having either low reproductive success or low reproductive effort (i.e., some birds did not attempt to breed), owing primarily to an immense iceberg (B-15) that grounded nearby and interfered with the Adélie Penguins' access to the colony (Arrigo et al. 2002, Ainley et al. 2004). Therefore, to improve the precision of our capture-probability estimates, we decreased the number of model parameters by creating, *a posteriori*, a model with only two estimates of capture probability. The first included the two years when reproductive success at Cape Crozier differed from the other years and capture rates were <1.0 (2001=2003), and the second included all the other years of the study. We called this the "repro" model (p_{repro}), and we also looked at this model with additive effects of sex and band ($p_{\text{repro+s}}$, $p_{\text{repro+g}}$); these three models with the repro-year effect had 99% of the model weight. The model with the repro effect only (p_{repro}) had the lowest AIC_c, but the $p_{\text{repro+s}}$ model was competitive (within 2 AIC_c). However, the sex effect was weak, with confidence intervals on the slope coefficients that included zero, so we continued our survival modeling using the repro structure on capture probability (p_{repro}). Capture-rate estimates for this model were 1.0 (95% CI: 0.99 to 1.0) in seasons 1997, 1998, 1999, 2000, and 2002; and 0.91 (95% CI: 0.81 to 0.96) in seasons 2001 and 2003.

The two survival models with the lowest AIC_c values and a combined model weight of 0.89 both included a negative band effect independent of either time or time and sex (Table 4). This band effect was strong ($\hat{\beta} = -0.80$, 95% CI = –1.46 to –0.13) and resulted in an 11–13% decrease in apparent survival for RB compared with RO birds. In general, annual variation in survival of RB birds was high (Fig. 1), as evidenced by the inclusion of a time effect in our top models (Table 4). Support for a sex effect on survival was weak ($\hat{\beta} = -0.30$, 95% CI = –0.74 to 0.14), but females may have lower survival than males in both RB and RO birds (Fig. 1).

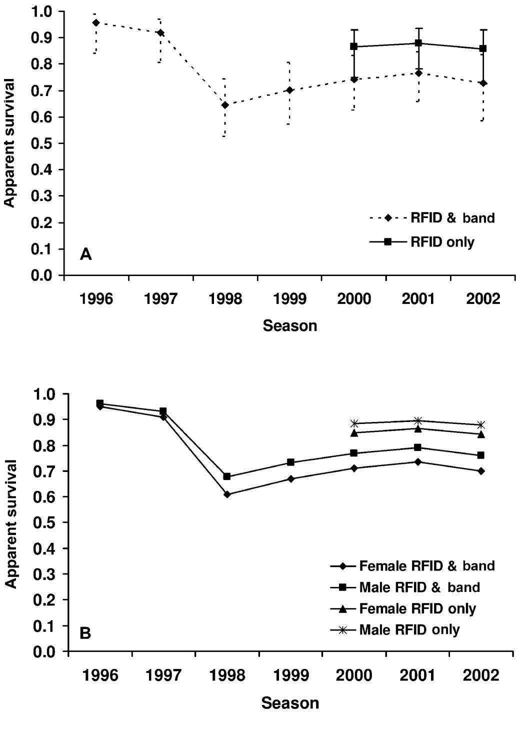

Fig. 1. (A) Apparent-survival estimates (± 95% confidence intervals) from best Adélie Penguin survival model ($\phi_{\text{b+t}}$, p_{repro}). (B) Apparent-survival estimates (± 95% confidence intervals) from the second-best Adélie Penguin survival model ($\phi_{\text{b+s+t}}$, p_{repro}).

Table 4. Model-selection results for *a priori* investigations of band ("b"), sex ("s"), and season-specific time ("t") effects on apparent survival of Adélie Penguins nesting in the weighbridge subcolony at Cape Crozier (1996–2003). Capture probability structure reflects best model (p_{repro}). Included for each model are Akaike's Information Criterion adjusted for small sample sizes (AIC_c), difference in AIC_c between each candidate model and the model with the lowest AIC_c value (ΔAIC_c), AIC_c weights (w_i), model deviance, and number of parameters (k). Asterisks indicate interactions, and a plus sign (+) denotes an additive effect. The global model ($\phi_{b*s*t}\ p_{b*s*t}$) and a model with no effects on survival (ϕ, p_{repro}) are also included.

Model	AIC_c	ΔAIC_c	w_i	Deviance	k
ϕ_{b+t}, p_{repro}	610.04	0.00	0.47	71.24	10
ϕ_{b+s+t}, p_{repro}	610.31	0.27	0.42	69.43	11
ϕ_{t}, p_{repro}	614.13	4.09	0.06	77.41	9
ϕ_{s+t}, p_{repro}	614.66	4.63	0.05	75.87	10
ϕ_{b*t}, p_{repro}	620.24	10.20	0.00	68.83	16
ϕ_{s*t}, p_{repro}	625.11	15.07	0.00	73.69	16
ϕ_{b}, p_{repro}	625.98	15.94	0.00	99.52	4
ϕ_{b+s}, p_{repro}	626.20	16.17	0.00	97.71	5
ϕ_{b*s}, p_{repro}	628.25	18.21	0.00	97.71	6
ϕ, p_{repro}	629.59	19.55	0.00	105.16	3
ϕ_{s}, p_{repro}	630.11	20.07	0.00	103.65	4
ϕ_{b*s*t}, p_{repro}	633.62	23.58	0.00	60.54	26
ϕ_{b*s*t}, p_{b*s*t}	676.39	66.35	0.00	57.36	46

Table 5. Model-selection results for survival models investigating whether the effect of flipper bands was limited to the first year after banding for Adélie Penguins nesting in the weighbridge subcolony at Cape Crozier (1996–2003). Included for each model are Akaike's Information Criterion adjusted for small sample sizes (AIC_c), difference in AIC_c between each candidate model and the model with the lowest AIC_c value (ΔAIC_c), AIC_c weights (w_i), model deviance, and number of parameters (k). Notation indicates effects as follows: ϕ^1 = first-year survival, ϕ^2 = after-first-year survival, and subscript "t" = season-specific annual variation. Capture probability structure reflects the best model (p_{repro}), and $\phi^1_t \phi^2_t\ p_{\text{repro}}$ indicates the global model.

Model	AIC_c	ΔAIC_c	w_i	Deviance	k
$\phi_t p_{\text{repro}}$	483.78	0.00	0.995	51.43	9
$\phi^1_t \phi^2_t\ p_{\text{repro}}$	495.31	11.54	0.003	50.23	15
$\phi^1_t \phi^2\ p_{\text{repro}}$	496.60	12.82	0.002	62.16	10
$\phi\ p_{\text{repro}}$	499.91	16.13	0.000	79.64	3
$\phi^1\ \phi^2_t\ p_{\text{repro}}$	500.10	16.33	0.000	67.76	9
$\phi^1\ \phi^2\ p_{\text{repro}}$	501.63	17.85	0.000	79.63	4

We found no evidence that first-year and after-first-year survival differed for banded birds; thus, differential survival the first year after banding was not responsible for the lower survival we observed in RB birds. The time-dependent survival model with no difference between first-year survival and after-first-year survival had almost all the model weight, and none of the first-year-survival models had substantial support (Table 5).

Discussion

We report here the first direct observations of a band effect on foraging behavior in penguins; foraging-trip durations were slightly longer for banded than for unbanded birds in three of four seasons, which is consistent with hypotheses predicting increased swimming costs for banded penguins (Culik et al. 1993, Jackson and Wilson 2002). However, our WB results regarding trip duration assess only total time away from the nest, and not specifically foraging time. Therefore, one possibility is that banded birds spend more time preening, which Adélie Penguins do extensively after jumping onto ice floes or upon return to the beach. While preening, the leading edge of their upper flipper is important for distributing uropygial oil to the remainder of their plumage (Ainley 1974). The existence of a flipper band may impede this activity, increasing time spent away from the nest and total foraging-trip durations.

There was little support for band effects on food loads, but females generally carried smaller food loads than males, which is consistent with results from other studies (e.g., Clarke et al. 1998, 2002). The amount of food an Adélie Penguin brings back to its chick during each foraging trip may be fairly constant for each individual and primarily related to body size—hence, the sex effect observed here. The length of time it takes to achieve that food-load size can vary from year to year, depending on a variety of annual energetic constraints, including distance to pack ice (Ainley et al. 1998), variation in prey access (Ainley et al. 2004), or, in this case, the wearing of flipper bands. The mechanism responsible for longer foraging trips, whether it be more time spent traveling to foraging areas, more time spent diving, or more time spent preening, must be determined to fully understand the effects of flipper bands on Adélie Penguin foraging energetics and fitness.

Valid estimates of apparent survival of banded birds based on mark–recapture models have been developed for Emperor Penguins (*A. forsteri*; Barbraud and Weimerskirch 2001), Little Penguins (Johannesen et al. 2002, 2003), and King Penguins (Olsson and van der Jeugd 2002), but none of these studies investigated the effects of bands, though information was based on banded individuals. Thus, along with those of Ainley and DeMaster (1980; see below) our results are among the first to document true effects of flipper bands on apparent survival, without the potential negative bias of unknown detection probabilities. The results of survival modeling on unbanded birds from our larger, longer-term data were also noteworthy, because we found that apparent survival can be variable and quite high for banded birds in some years. Although we do not have data from unbanded birds during the 1996 and 1997 seasons, it is not likely that we would have observed a band effect in either year, because apparent survival rates of banded birds were very high (0.96 and 0.92, respectively). Unfortunately, given that we saw no such annual variation in apparent survival during the three years for which we had returning birds in both groups (RB vs. RO), we have yet to obtain support for a model with an interaction between band effects and time. However, we believe that environmental conditions for WB birds during the last four years of the study were much poorer than in previous years, owing to the two very large icebergs grounded nearby, which occupied most of the foraging area for Cape Crozier's Adélie Penguin colony (Arrigo et al. 2002, Ainley et al. 2004). The band effects on apparent survival documented in the present study during 2000–2004 are also associated with overall increased immigration and decreased reproductive success, breeding propensity, and decreased breeding-population size at Cape Crozier and the other colonies in the vicinity, indicating that environmental conditions for these Adélie Penguins during these years have been suboptimal (D. G. Ainley, G. Ballard, and K. M. Dugger unpubl. data).

Also of interest, and contrary to Ainley and DeMaster (1980; also Ainley et al. 1983, Ainley 2002), we found no evidence that band effects are associated only with the first year after banding. It was believed that the earlier band designs, which were oblong rather than broadly teardrop-shaped, constricted blood flow to flippers when they swelled during the first molt after banding. The new design has apparently addressed this issue. Our results, however, indicate that Ainley and DeMaster (1980) underestimated the band effect, which likely occurred during all years following banding.

In general, the range of apparent survival rates of banded (0.73–0.96) and unbanded (0.85–0.88) birds in the present study was comparable to those reported for banded Adélie Penguins at Cape Crozier during 1961–1969, when rates varied annually by age and by sex, ranging from 0.80–0.97 (Ainley and DeMaster 1980; see also Ainley 2002). Rates of both band loss and resighting probability were accounted for in these earlier estimates, so they are the most comparable to our current effort. However, our estimates of survival were also comparable to return rates reported by Clarke and Kerry (1998), who also reported high annual variation during 1992–1997, ranging from 63% to 90% for banded birds and from 78% to 91% for unbanded birds. Recapture rates are unknown in the Clarke and Kerry (1998) study.

Other than early studies on Yellow-eyed Penguins (*Megadyptes antipodes*; Richdale 1957) and Adélie Penguins (Ainley and DeMaster 1980), sex-specific differences in penguin survival have not been well studied. However, Barbraud and Weimerskirch (2001) noted higher survival in female Emperor Penguins compared with males, in contrast to female King Penguins, which exhibited lower survival than males after a year characterized by poor food resources and low reproductive success (Olsson and van der Jeugd 2002). We observed a similar trend in Adélie Penguins (females had lower survival than males) for both banded and unbanded birds, but sex effects on survival in the present study were generally weak.

Age was one potential confounding effect for which we could not account, in either the survival or the foraging-behavior analysis. Age-specific survival differences have been observed for Yellow-eyed (Richdale 1957), Adélie (Ainley and DeMaster 1980), and King penguins (Olsson and van der Jeugd 2002), but we currently have no clear understanding of the complexity of age effects on survival or foraging behavior. On the basis of indirect evidence, Ainley et al. (1983) concluded that Adélie Penguins improve foraging efficiency with age. All birds in the present study were banded or RFID-tagged as breeding adults, thus precluding resolution of age-specific biases. However, the chances of banding or tagging an older bird may have decreased annually as more individuals were added to the study. A possible result was that, over time, a larger percentage of the available unbanded–untagged birds in the subcolony were new recruits, placing them in the four- and five-year-old age groups (Ainley et al. 1983, Ainley 2002). Given that we did not start using RFID tags alone until later in the study, it is possible that a higher percentage of the unbanded birds were younger than the banded birds, some of which must have been ≥12 years old in 2003. The addition of two *a posteriori* models—one that included a "year since tagging" (YST) main effect and one that included the YST*band interaction—to our best foraging-trip-duration model set indicated that age or experience may decrease trip durations for both RB and RO birds, with some support for an interaction between YST and bands as well (Table 6). However, on the basis of model weights, the best YST model (season, sex, band, band*season, YST) had less than twice as much support as the next-best model without YST (Table 6), and the 95% confidence intervals for the YST coefficient included zero ($\hat{\beta}$ = –0.84, 95%CI: –1.8 to 0.14), so support for this effect was generally weak. We found no support for any YST effect on either food load or survival.

Although RFID technology has opened new avenues for less-invasive research on penguins and other wildlife, there are still major limitations associated with the number of individuals that can be monitored and the kinds of information that can be gained. In addition, although we did not note any problems with RFID tag failure, migration, or infection, these problems have been noted by other researchers (Clarke and Kerry 1998), so continued evaluation of this technique is warranted. We should note, however, that our RFID tags were from a different manufacturer and were of a different size than those used by Clarke and Kerry (1998). By design, our WB reader was not sensitive to placement or orientation of the tag in the bird. No technology has yet been invented that allows fast, efficient scanning of large numbers of RFID-tagged birds with minimal disturbance. Measuring dispersal among colonies is an important and (to the penguin-research world) unique aspect of our work that would be impossible to do without bands, because dispersing individuals cannot easily be made to pass near electronic RFID readers in most situations. Age-related questions can be answered only by marking large numbers of fledglings because, banded or not, only a small fraction subsequently survive to at least subadulthood. Therefore, in addition to a continued effort to apply evolving transponder technology to penguin research (e.g., Beigel et al. 2004), it is important to fully understand band effects on penguins, especially regarding any variation

Table 6. Model-selection results after addition of two *a posteriori* generalized linear models relating foraging trip duration of Adélie Penguins (n = 187) nesting in the weighbridge subcolony (1996–2003) to the effects of band, sex, season, and "year since tagging" (YST). Included for each model are Akaike's Information Criterion adjusted for small sample sizes (AIC_c), difference in AIC_c between each candidate model and the model with the lowest AIC_c value (ΔAIC_c), AIC_c weights (w_i), value of the maximized log-likelihood function ($Log_e[L]$), and number of parameters (k). Asterisks between covariates indicate interactions.

Model	AIC_c	ΔAIC_c	w_i	$Log_e(L)$	k
Season, sex, band, band*season, YST	1,426.94	0.00	0.36	–701.71	11
Season, sex, band, band*season	1,427.63	0.70	0.25	–703.19	10
Season, sex, band, band*season, YST, YST*band	1,428.22	1.29	0.19	–701.22	12
Season, sex, band, band*sex, band*season	1,429.05	2.11	0.13	–702.77	11
Season, sex, band	1,430.87	3.93	0.05	–708.12	7
Season, sex, band, band*sex	1,432.53	5.59	0.02	–707.86	8
Season, sex	1,436.37	9.43	0.00	–711.95	6

associated with sex and resource changes. In addition, the negative consequences associated with flipper bands need to be recognized and balanced against the gains in information associated with their use, as recommended by Peterson et al. (2006). Despite the use of newer band designs that decrease direct wounding, we observed decreased survival and increased foraging-trip durations among banded birds in the present study. However, we also provide more evidence that band effects can vary over time and may be associated primarily with years of harsh environmental conditions. This relationship needs to be investigated, because although bands can negatively affect apparent annual survival by ≤13% (present study), declines in lifetime survivorship may be much smaller, depending on environmental conditions.

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