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EFFECT OF INSTRUMENT ATTACHMENT AND OTHER FACTORS ON FORAGING TRIP DURATION AND NESTING SUCCESS OF ADÉLIE PENGUINS

GRANT BALLARD[1,4], DAVID G. AINLEY[1], CHRISTINE A. RIBIC[2] AND KERRY R. BARTON[3]
[1]*H.T. Harvey & Associates, 3150 Almaden Expressway, Suite 145, San Jose, CA 95118*
[2]*USGS BRD, Department of Wildlife Ecology, University of Wisconsin, Madison, WI 53706*
[3]*Landcare Research New Zealand, Ltd., Private Bag 6, Nelson, New Zealand*

Abstract. We compared foraging-trip duration of Adélie Penguins (*Pygoscelis adeliae*) carrying various combinations of radio-telemetry transmitters, implanted, passively interrogated transponder (PIT) tags, and time-depth recorders at two widely separated colonies of different size on Ross Island, Antarctica, during three austral summers. Trip duration was measured by electronic devices rather than human observation. Instrumentation had no significant effect on foraging trip duration. Most of the variation in foraging trip duration was attributed to individual and year. Males' trips were significantly shorter than females' in a subset of known-sex birds. No effect was evident in nesting success even for birds that wore instruments for >20 days. We recommend use of small, hydrodynamically designed and placed instruments to researchers who wish to collect data unaffected by instrument attachment.

Key words: *foraging, penguin, radio-transmitter, recorder, seabird, sea ice, weighbridge.*

Efectos de la Sujeción de Instrumentos y Otros Factores en la Duración de las Salidas de Forrajeo y el Éxito Reproductivo en *Pygoscelis adeliae*

Resumen. Se comparó la duración de las salidas de búsqueda de alimento de *Pygoscelis adeliae* a los que se les colocaron distintas combinaciones de radiotransmisores, emisores implantados de interrogación pasiva y medidores de tiempo y profundidad de buceo. El estudio fue realizado durante tres veranos australes en dos colonias ampliamente separadas de diferente tamaño en Ross Island, Antártica. La duración de las salidas fue medida por instrumentos electrónicos en lugar de observaciones humanas. Los instrumentos no tuvieron un efecto significativo en la duración de las salidas de búsqueda de alimento. La mayor parte de la variación en la duración de las salidas fue atribuida a individuos y años. Las salidas de los machos fueron significativamente más cortas que las de las hembras en una sub-muestra de aves previamente sexadas. No se detectaron efectos evidentes en éxito de nidificación incluso en individuos que llevaron instrumentos por más de 20 días. Recomendamos el uso de instrumentos pequeños diseñados y colocados hidrodinámicamente a fin de no influenciar los datos colectados.

INTRODUCTION

Adélie Penguins (*Pygoscelis adeliae*) are remarkably sturdy animals, supplying ample opportunities for increasing our knowledge of the Antarctic marine ecosystem (e.g., Croxall and Prince 1979, Wilson et al. 1994, Wilson 1995). Many previous investigators have attached radio-transmitters (Trivelpiece et al. 1986, Davis et al. 1988, Sadleir and Lay 1990) and time-depth recorders (Naito et al. 1990, Watanuki et al. 1993, Wilson et al. 1993) to penguins to learn more about various aspects of their at-sea behavior. Using relatively small samples, several researchers have reported effects of these different instrument packages, as well as effects of the methods and timing of attachment (for review see Wilson and Culik 1992). They have done this either by comparing foraging-trip duration or chick rearing of instrument-wearing birds to unencumbered controls (Croll et al. 1991, Watanuki et al. 1992, 1993, 1997), studying their energetic expenditures (Culik and Wilson 1991, Culik et al. 1994), or examining their hydrodynamic properties at various swim speeds (Bannasch et al. 1994). Results have indicated that many instruments slow penguin swimming speeds significantly (Culik and Wilson 1991, Wilson et al. 1991, Culik et al. 1994); cause ex-

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[4] Present address: Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, CA 94970, e-mail: gballard@prbo.org

TABLE 1. Number of individuals (*n* trips) for weighbridge (WB), transmitter (RT), and time-depth recorder (TDR) groups by season and colony (individuals not repeated among treatments). Each treatment was applied to a separate subcolony at each colony.

Colony	Treatment	1997–1998	1998–1999	1999–2000	All years
Crozier	WB	52 (367)	38 (259)	57 (312)	96 (938)
	RT	21 (187)	17 (135)	17 (127)	55 (449)
	TDR			12 (23)	12 (23)
Royds	WB	65 (571)	52 (375)	64 (495)	120 (1441)
	RT	20 (207)	16 (135)	17 (118)	53 (460)
	TDR			10 (21)	10 (21)

cessive preening, pecking, or other ‘‘psychological’’ hindrance (Wilson et al. 1989, Wilson and Wilson 1989a); generally increase energetic expenditure (Culik and Wilson 1991, Bannasch et al. 1994); and decrease nesting success (Watanuki et al. 1992). It has been proposed that these effects can be minimized by attaching smaller, streamlined instruments on the lower back behind the area of greatest girth, where the thickest boundary layer (area of slowest flow velocity and resulting lowest drag) is found (Bannasch et al. 1994).

Higher energetic costs and associated slower swimming speeds have also been attributed to metal flipper bands on Adélie Penguins in a swim canal (Culik et al. 1993), though such an effect of bands in the wild has not been reported.

Clearly there are many potentially confounding variables involved with interpreting the effects of instrument attachment on trip duration, and these can be difficult to sort out without adequate sample size or other methodological considerations. For example, most works examining factors affecting foraging-trip duration have relied on a relatively small number of birds at a single colony during a single breeding season (but see Watanuki et al. 1992, 1993, 1997 for a previous multi-season study). Few investigators have reported the effect of sex or individual behavior irrespective of instrument attachment, although Clarke et al. (1998) found that male Adélie Penguins made consistently shorter (distance and duration) foraging trips than females. Others have noted differences between the sexes in energetics (Chappell et al. 1993) and timing of colony attendance (Ainley et al. 1983).

We investigated foraging-trip duration and breeding success for Adélie Penguins during the guard and crèche stages of chick rearing at two colonies for three seasons. As a part of this effort we compared banded birds carrying implanted, passively interrogated transponder (PIT) tags and unbanded birds fitted with a streamlined radio-transmitter (RT) or time-depth recorder (TDR) and RT. We tested whether device attachment affected nest success or trip duration for the different colony-season groupings, and whether trip duration was related to colony, season, day within season, individual, sex, or the cumulative number of trips in a season an individual had made at the time of the measured trip.

METHODS

STUDY AREAS

Our study covered most of the guard and crèche stages of chick rearing (21 December to 11 January) for three austral summers, 1997–1998 to 1999–2000. We will refer to the austral summers as seasons. Study colonies were Cape Crozier (120 000 pairs total) and, 77 km away, Cape Royds (4000 pairs) on Ross Island (77°30′S, 168°E) in the southern Ross Sea, Antarctica. At each of these colonies, we selected two subcolonies of approximately 200 pairs for foraging-trip comparisons using two methods of assessment. We will refer to these subcolonies as either RT (radio-transmitter) or WB (weighbridge). RT subcolonies were different each season at Cape Crozier, but were the same at Cape Royds (though individual RT birds were different). WB subcolonies were the same each season and included many of the same individuals among seasons. In the 1999–2000 breeding season we also attached TDRs and RTs to several individuals from an additional subcolony at each site (Table 1).

RADIO-TRANSMITTERS

Each season we attached RTs to approximately 15 adults at each colony, each having chicks in their nests on 20 December. Transmitters pulsed 0.92 times sec^{-1}, were manufactured by Advanced Telemetry Systems (ATS, model PN7, Isanti, Minnesota), weighed 15.7 g, measured 2.0 × 1.1 × 5.3 cm (2.2 cm^2 maximum cross section) and were tapered according to our instructions for better hydrodynamics (Bannasch et al. 1994, Culik et al. 1994). Using published measurements of Adélie Penguin maximum frontal cross-sectional body area of 314 cm^2 and 200 cm^2 (Oehme and Bannasch 1989, Wilson et al. 1989), our RTs measured $\leq$1% of the birds' cross-sectional area. Each RT had a 29 × 0.1 cm whip antenna that angled toward the tail at 42° relative to the bird's back. Birds were caught at their nests by hand and held for approximately 10 min while instruments were attached using black Tesa® tape (Wilson and Wilson 1989b). At Cape Royds in all seasons and at Cape Crozier in the first season, individuals were selected from different nests. At Cape Crozier in 1998–1999 and 1999–2000, we tried to capture both members of pairs as they changed between foraging and brooding duty (i.e., during nest exchanges). We attached most RTs to the lower rump, on the centerline just above the uropygial gland, but in 1998–1999 we attached some (21 of 33) to the area between the scapulas, at approximately the area of maximum girth. RTs were removed on or after 11 January each season.

We used a scanning receiver and an ATS DCCII data logger to record the presence or absence of RT birds in the colonies. The scanner was programmed to ''listen'' for transmitters for 30 sec on each frequency every 90 min. A reference transmitter was also logged, and the scanner was checked throughout the season to verify accuracy. We adjusted sensitivity as necessary. Transmitters that logged fewer than 10 pulses in a 30-sec scan were classified as absent from the subcolony, since background radio interference or other perturbations sometimes caused the scanner to record up to 10 pulses (GB, pers. obs.).

WEIGHBRIDGES

We used plastic fencing to surround subcolonies, leaving one access point, which we filled with a WB. The WB consisted of an electronic scale, direction indicator, and radio-frequency-identification reader connected to a data logger (see Kerry et al. 1993 for a complete description of a similar system). We implanted unique PIT tags in 216 Adélie Penguins between 1996 and 2000. Tags, manufactured by Avid Inc. (Norco, California), weighed 0.1–0.3 g and were 1.4–1.8 cm long and 0.2–0.3 cm wide. Tags were injected subcutaneously in the scruff of the neck, between and a little above the shoulders. Birds with tags were also banded on the left flipper with numbered stainless steel bands (National Museum, Wellington, New Zealand), of the type used on Magellanic Penguins (*Spheniscus magellanicus*) without apparent deleterious results (P. D. Boersma, pers. comm.). Handling time was generally $<$2 min per individual. We attempted to maintain at least 30 active nests at which both adults were tagged at each of the two study subcolonies. WBs were installed between 10 December and 15 December in all seasons. The identification, time, direction, and body mass for $>$95% of crossings were recorded (Table 1). In the WB subcolony at Cape Crozier, sex was determined for 80 individuals (83% of banded birds; 42 males and 38 females) using a combination of copulatory position, behavior, ''tread marks'' (evidence of female copulatory position), bill and head size differences, and body mass (Ainley et al. 1983, Kerry et al. 1992).

TIME-DEPTH RECORDERS

In a third subcolony at each colony, we selected one or two individuals every few days (approximately 2 foraging trips) and attached a TDR (Wildlife Computers, model MK7, Redmond, Washington) and RT in the same way as described for RTs above. TDRs weighed 25.4 g, measured 1.1 × 2.0 × 8.5 cm (2.2 cm^2 maximum cross section, $\leq$1% of the penguins' cross-sectional area), and were streamlined. They were mounted directly behind small, rounded RTs (ATS model PN5, similar but slightly smaller than the PN7 model described earlier), as low on the back as possible without interfering with preening. The two instruments' total length was ca. 13.3 cm. This style RT also had a 29 × 0.1 cm whip antenna pointed toward the tail and parallel with the back. We calculated foraging trip duration using the dive data collected by the TDRs to determine when birds entered and left the water, and adding 0.8 hr for birds at Crozier and 0.5 hr for Royds based on observed walking times from the beaches to the subcolonies. We confirmed these trip durations with data collected by the scanning receiver when available, but due to logistical difficulties we did not always use the receiver for monitoring TDR birds. Once birds had made at least 2 foraging trips, the instruments were removed, downloaded, and moved to new individuals.

NEST CHECKS

All nests (WB, RT, and TDR) were checked on a daily basis, weather permitting. Sample size for the WB subcolonies, totaled for the three field seasons, was 216 individuals among 215 nests (108 at Royds, 97 at Crozier). Sample size for RT birds was 108 individuals and 101 nests (40 at Crozier, 61 at Royds). Transmitters were removed when nests or transmitters failed.

As controls, nests in similar-sized subcolonies were monitored for outcome in each season at each colony. The control subcolonies were within 50 m of WB subcolonies. In both control and study subcolonies, observations were made of eggs and chicks at regular intervals by standing quietly 10 m away and waiting for birds to rise to show nest contents.

STATISTICAL ANALYSIS

We only included trips made by birds that had chicks within at least two days of a trip's completion to ensure that we measured trips of adults that were provisioning chicks. Trip duration data tended to be skewed toward shorter trips and were normalized using log-transformation. Foraging trips as measured by WB or RT were only included if they were between 6 and 120 hr long to help avoid artifacts from the sampling methodologies. For example, the WB often recorded short trips ($<$6 hr), which were primarily made by birds carrying rocks for nests (pers. obs.). Additionally, the RT receiver was susceptible to incorrectly logging a bird as present when radio interference bled onto a penguin's frequency, or as absent when birds were present in the colony for $<$90 min and missed a ‘‘listening’’ session. In general the RT data were less accurate than either WB or TDR, despite the low sample size of the latter. Although we checked the scanner/data logger as often as possible and adjusted the sensitivity and tuning as required, it still missed birds and incorrectly registered their presence. These effects could be mitigated by scanning for a larger range of frequencies around the target to capture drift, and by scanning more frequently (e.g., every 30 min). While these problems are artifacts of our study design, we believe the accuracy is far greater than checking the nests in person once per day or even as often as every 4 hr, protocols used in previous studies.

We tested for differences in trip duration between shoulder-mounted and lower-back attachments for RT animals, controlling for individual and colony, using a 3-way ANOVA. There were no differences in trip duration for the two attachments ($F_{1,236} = 2.5$, $P > 0.1$). Therefore, no differentiation between the attachments was made for any of the following analyses.

Because several individuals in each WB subcolony were present in multiple seasons, we evaluated the effect of season, colony, interaction between season and colony, and individual in the WB subcolonies using a 4-way repeated measures ANOVA. For this model we included only the individuals present as breeders in each year. Because all terms were highly significant, we followed this with a 5-way ANOVA that included treatment (RT versus WB) type and all birds. Wald tests were used to evaluate the significance of differences in trip duration between different colony-season combinations.

Since there was significant variation in trip length with season and season-colony interaction, we tested the effect of two within-season factors: 5-day period and cumulative trip number. Five-day period is the day in the season an individual returned from a foraging trip, binned into 5- or 6-day groups: 1 = 21–25 Dec, 2 = 26–30 Dec, 3 = 31 Dec–4 Jan, 4 = 5–10 Jan). We calculated cumulative trip number of each trip for each individual, and then placed this into one of four categories: 1 = 1–4, 2 = 5–6, 3 = 7–9, 4 = 10–31 trips. Though these variables are usually highly correlated, we treated them separately because RTs were occasionally installed after the beginning of the study (when nests or instruments failed). Because individuals were repeated in period and cumulative-trip-number categories, we used 3-way (treatment, individual, and period or trip number) repeated-measures ANOVAs for each season in order to obtain corrected significance estimates.

For the third season we included the TDR group in the comparison. We used 4-way ANOVA to compare the effects on trip duration of treatment (RT, WB, or TDR), colony, 5-day-period, and individual. Estimates of significance for 5-day-period were biased due to repeated individuals. We left cumulative trip number out of this model because we did not have the data for

TABLE 2. Untransformed foraging trip duration as calculated by weighbridge (WB) and radio-transmitters (RT) compared for Cape Royds and Cape Crozier, December 21 to January 11. Periods are 5-day intervals. All birds had young within at least 2 days of a trip.

		Crozier					Royds				
Season	Period	WB (hr)	*n* (trips)	RT (hr)	*n* (trips)	Difference (hr)	WB (hr)	*n* (trips)	RT (hr)	*n* (trips)	Difference (hr)
1997–1998	all	30.0	367	24.0	187	6.0	16.0	571	23.3	207	–7.3
	1	24.1	61	19.2	43	4.9	17.3	87	19.1	62	–1.8
	2	24.9	103	22.1	51	2.8	15.9	148	25.7	55	–9.8
	3	27.3	99	24.6	46	2.7	15.3	148	24.6	46	–9.3
	4	41.0	104	29.8	47	11.2	14.8	188	25.1	44	–10.3
1998–1999	all	32.6	259	31.6	135	1.0	26.3	375	29.0	135	–2.7
	1	32.0	53	22.8	33	9.2	33.3	57	27.6	33	5.7
	2	30.5	63	31.9	36	–1.4	25.4	97	25.9	39	–0.5
	3	33.7	60	33.5	29	0.2	28.9	84	31.7	26	–2.8
	4	33.8	83	37.8	37	–4.0	22.4	137	31.8	37	–9.4
1999–2000	all	32.5	312	32.9	127	–0.4	23.0	495	23.2	131	–0.2
	1	31.3	61	28.8	30	2.5	31.9	71		no data	
	2	31.9	76	31.6	32	0.3	22.3	94	17.1	21	5.2
	3	29.0	90	29.1	33	–0.1	23.0	142	25.0	46	–2.0
	4	37.4	88	41.9	32	–4.5	20.0	192	24.1	63	–4.1

the TDR birds (which were only measured for two foraging trips each and at different times within the season).

To test the effect of sex on foraging-trip duration, we compared trip lengths among the 80 known-sex birds in the WB group at Cape Crozier using a 5-way ANOVA that included season, 5-day period, cumulative trip number, and individual. Five-day period and cumulative trip number were treated as continuous variables. We then used body mass as a surrogate for sex in order to test for the effect of sex at Cape Royds (as well as at Cape Crozier). To do this, we first included body mass and the interaction between sex and mass in the above model. Finding no significant effect of either term (mass: $F_{1,\ 710} = 6.1$, $P > 0.1$; mass × sex: $F_{1,\ 710} = 0.02$, $P > 0.8$), we compared the mass of males to females using a two-tailed *t*-test and found that males were heavier than females ($P < 0.001$). We then substituted mass for sex in the above ANOVA, and added colony to the model to test if heavier birds (mostly males) made shorter trips than lighter birds (mostly females).

We classified nests (pairs) as successful when they produced at least one crèched chick. We summarized the number of successful and total nests for each study season at each colony for each treatment type (WB, RT, and control). We then used logistic regression to test whether nest success varied among these treatments.

Means are presented ± SE. Significance for all tests was assumed at the 0.05 level and tendencies at the 0.10 level, unless corrections for repeated terms were necessary (see above). Residuals from ANOVAs were normally distributed. All statistical calculations were performed using STATA (Stata Corp. 1999).

RESULTS

TRIP DURATION

Mean trip durations ranged from 16–42 hr (Table 2). Among the 14 WB birds that bred in each season (9 at Royds, 5 at Crozier), chick-provisioning trips varied significantly with individual, season, colony, and the interaction of season and colony (Table 3A). The combined model was surprisingly robust (adjusted $R^2 = 0.89$, $P < 0.001$). WB trips were longer at Cape Crozier than at Cape Royds ($\beta = 0.36$, $P < 0.02$).

WB trips did not differ from RT trips (using all breeders, despite between-season repetition of some) when compared using season, colony, season × colony interaction, and individual (Table 3B). Season, individual, and the interaction of season and colony were all highly significant in this model (all $P < 0.001$, combined adjusted $R^2 = 0.37$). The significance of the season × colony interaction was mostly due to trips being longer at Cape Crozier and shorter at Cape Royds in the first season than in other seasons ($P < 0.001$).

Within-season results were similar (Table 4).

TABLE 3. Factors affecting foraging-trip duration in Adélie Penguins. (A) Weighbridge birds only: results from 4-way repeated-measures ANOVA (using log-transformed data); adjusted $R^2 = 0.89$, residual df = 24. (B) Weighbridge and radio-transmitters compared: results from 5-way ANOVA (using log-transformed data); adjusted $R^2 = 0.37$, residual df = 2957.

Term	df	*F*	*P*
A. Season[1]	2	41.3	<0.001
Colony	1	12.2	<0.002
Season × Colony[1]	2	6.0	0.03
Individual	12	7.8	<0.001
B. Treatment	1	1.5	>0.2
Season[2]	2	69.2	<0.001
Colony	1	2.1	>0.1
Season × Colony[2]	2	20.1	<0.001
Individual	324	3.4	<0.001

[1] *P*-values for these terms adjusted using Box's conservative epsilon.

[2] *P*-values for these terms are possibly inaccurate due to some repeated individuals (see text).

Individual was always the most significant factor affecting trip lengths (Fig. 1). In some seasons there were some significant or marginally significant but irregular effects of 5-day period and cumulative trip number. For example, trip durations grew consistently longer as the 1997–1998 season progressed (i.e., trip duration was significantly correlated with 5-day period, $P < 0.001$, Table 2) and as individuals made more trips ($P < 0.09$). However, cumulative trip numbers tended to be negatively correlated with trip duration in 1999–2000 ($P < 0.07$).

In 1999-2000, trip durations for birds carrying TDRs did not differ from those in WB or RT groups ($F_{2, 980} = 2.3$, $P > 0.1$). Trip durations for all three groups did vary with individual ($F_{179, 980} = 2.8$, $P < 0.001$) and tended to vary with 5-day period ($F_{1, 980} = 3.7$, $P < 0.06$). This was primarily due to trips getting shorter later in the season at Cape Royds.

We next turned our attention to factors affecting trip duration for which we only had data from the WB group: sex and body mass. Males' trips were shorter than females' ($F_{1, 712} = 5.8$, $P < 0.02$) among the known-sex birds at Cape Crozier. Males were also heavier than females (4.0 ± 0.03 kg vs. 3.8 ± 0.03 kg, $P < 0.001$), so we substituted mass for sex and used all WB birds (at both colonies) to see if there was a correlated effect on trip duration. For all birds combined and for Cape Crozier alone, mass did not play an important role. However, when we fit the model for Cape Royds only, heavier birds made shorter trips ($F_{1,1122} = 3.86$, $P = 0.05$), suggesting that males in this colony also made shorter trips than females.

BREEDING SUCCESS

There was no significant difference in nest success between treatments ($P > 0.6$), seasons ($P > 0.3$), or colonies ($P > 0.2$; Table 5). In 1999, we also monitored 22 nests while one adult from each carried a TDR (12 at Crozier, 10 at Royds). None of the TDR nests failed during the study, but these birds were only observed for approximately 2 foraging trips (usually 4–6 days).

DISCUSSION

Differences in trip duration between individuals, seasons, and colonies masked any effects of the instruments measuring the trips in this study. The seasonal and colony-related differences in trip duration were consistent with comparisons of Royds and Crozier birds in the 1996–1997 season using different methods (Ainley et al.

TABLE 4. Within-season trip durations related to treatment, individual, and (A) cumulative trip number or (B) 5-day period using 3-way repeated-measures ANOVA.

	1997–1998			1998–1999			1999–2000		
Term	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
A. Treatment	1	0.3	>0.5	1	4.2	<0.05	1	0.0	>0.8
Trip number[1]	3	2.3	<0.09	3	1.6	>0.1	3	2.5	<0.07
Individual	68	2.9	<0.001	35	3.1	<0.001	51	2.8	<0.001
Residual df	207			147			211		
B. Treatment	1	0.0	>0.9	1	0.1	>0.8	1	2.5	>0.1
5-Day period[1]	3	6.3	<0.001	3	1.5	>0.2	3	1.1	>0.3
Individual	98	4.4	<0.001	87	1.3	<0.05	80	2.3	<0.001
Residual df	399			355			327		

[1] *P*-values for trip number and 5-day period adjusted using Huynh-Feldt epsilon.

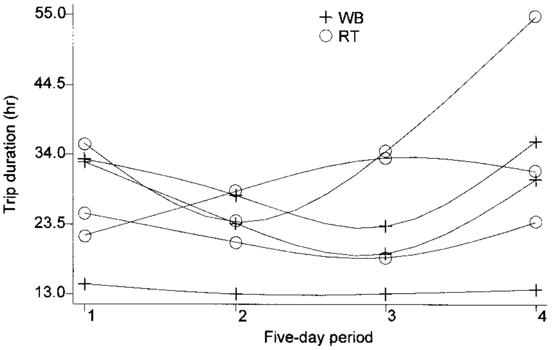

FIGURE 1. Individual variation in foraging-trip duration by 5-day period for six individuals in 1999–2000 at Cape Crozier. Three individuals carried radio-transmitters (RT) and three were in the weighbridge (WB) group.

1998). That study concluded that varying sea-ice conditions near the colonies probably had the greatest effect on foraging-trip duration.

Measuring foraging-trip duration may not be the best way to discern instrument effects on penguins. Kooyman et al. (1992) noted that instrumented Emperor Penguins (*Aptenodytes forsteri*) stayed with the same group of birds during foraging, but dove less often. Similarly, Ropert-Coudert et al. (2000) found that King Penguin (*Aptenodytes patagonicus*) foraging trip durations did not vary with instrumentation, but that there were subtle differences in diving behavior which the authors attributed to drag caused by TDRs (although they were unable to statistically control for individual variation). Watanuki et al. (1992) found stronger effects of instruments on Adélie Penguins by looking at feeding efficiency and chick survival, both of which decreased with instrumentation more obtrusive than used in our study, particularly later in the chick-rearing period. In contrast, Wilson et al. (1997) did not note an effect on breeding success of Adélie Penguins and other penguin species that were carrying relatively large packages. Regardless, some authors have found that instruments lengthened foraging trips of penguins, and that larger packages had bigger effects (Wilson et al. 1989, Hull 1997).

Although we did not see an effect on chick survival, it is possible that birds carrying TDRs and RTs made fewer or shallower dives and carried less food to their chicks, while staying at sea approximately the same amount of time as the WB birds. Also, it is possible that any effects on the chicks' well-being could have been expressed after completion of our study in each season (although we did remove instruments when we finished our measurements). On the other hand, the instruments that we deployed were smaller compared to almost all those used in the various studies we have referenced. Moreover, we applied them with much less obtrusive means than most other studies; we used a single layer of tape instead of surgical implantation or attachment by Velcro® and cable ties to epoxy-glued feathers.

Though trip durations for birds carrying the TDR/RT combinations did not vary from the other treatments, the comparison is not entirely valid because of the relatively short period these instruments were attached. Hull (1997) found

TABLE 5. Proportion of nests from which at least one chick reached crèche for controls, weighbridge (WB), and radio-transmitter (RT) groups in each colony and season. Number of nests monitored for each group shown in parentheses.

	Controls		WB		RT	
Season	Crozier	Royds	Crozier	Royds	Crozier	Royds
1997–1998	0.93 (30)	0.97 (35)	0.93 (30)	0.97 (35)	1.00 (19)	0.95 (21)
1998–1999	0.96 (28)	0.78 (37)	0.91 (23)	0.96 (28)	0.83 (12)	0.83 (18)
1999–2000	0.97 (29)	0.90 (30)	0.93 (44)	0.93 (45)	1.00 (9)	0.91 (22)

that Royal Penguins carrying TDRs made longer foraging trips than controls, and occasionally failed to return from foraging trips at all, especially during the incubation stage when foraging trips were relatively long (20–25 days). However, the TDRs in that study were approximately twice as wide and twice as heavy as ours, and were not tapered for hydrodynamics. Still, a proper comparison of TDRs with RTs and controls would require treatments of equal duration, especially since other researchers have found a cumulative effect, particularly with larger instruments.

Since Wilson et al. (1989) found that effects of instruments were not manifest until later in the season (e.g., after 19 days), we compared later trips to earlier trips. We found no consistent pattern using date or cumulative trip number as the metric. It is possible that this effect is only noticeable in seasons or populations experiencing more difficult conditions (e.g., less food or less access to open water). The positive effect of date on trip duration during the 1997–1998 season may be related to prey-depletion near the colonies, or to late-season movement of pack ice (sea ice not connected to land) farther offshore (Ainley et al. 1998). Adélie Penguins are noted pack-ice obligates when at sea (Ainley et al. 1994) and may make long trips to reach the pack ice when necessary. Prey availability and proximity of pack ice may be highly correlated (Daly and Macaulay 1988). Conversely, fast ice (sea ice connected to land) was more extensive in 1999–2000 than in the other seasons in front of Cape Royds (pers. obs.), meaning that penguins had to walk several kilometers to reach open ocean early in the season. As the season progressed, the ice broke up and walking distances (and foraging trip durations) decreased accordingly.

Some of the differences in trip duration between colonies were no doubt due to different amounts of walking between the water and the study subcolonies. At Cape Crozier, the RT and TDR subcolonies were approximately 500 m from the sea, and Adélie Penguins had to negotiate several other subcolonies and a steep hill to reach their nests. Similarly, the Crozier WB colony was about 300 m from the ocean. At Cape Royds, all study subcolonies were closer to the ocean (approximately 100 m) and there were fewer intervening subcolonies. Adélie Penguins walk at 2.6–3.9 km hr^{-1} (Taylor 1962), but perhaps a little slower when climbing steep hills, so these differences could account for 10 to 30 min of the differences in foraging trips between colonies.

Regardless of instrumentation, some individuals made consistently shorter or longer trips than others (Fig. 1). Birds may revisit the same foraging areas once they find a reliable food supply (Ainley et al., unpubl. data). Most other studies of trip duration have not looked for individual variation, or even sexual variation, though Clarke et al. (1998), using data provided by relatively large satellite transmitters, found that males made shorter trips than females. In that study, the females fed beyond the continental shelf, while the males foraged over the shelf. We found a similar sexual differentiation in trip duration at Cape Crozier, where birds averaged longer trips than at Royds, but both males and females fed only over the continental shelf (unpubl. data). However, sexual differences in trip lengths did not explain all the variation; individual variation remained important.

In the two study seasons that Cape Royds RT birds made their longest trips, RTs were attached to 15 individuals from different nests (rather than to their mates). It is possible that at the time of attachment these individuals were mostly females, since timing of colony attendance can be skewed by sex, particularly during incubation or near peak hatching time (Ainley et al. 1983). It is also possible that attaching a RT to both members of pairs would cause longer trips than if only one member were treated. This would be more of a concern in studies including the incubation period (when trips are longer and one mate must attend the nest). We do not believe that a bird's foraging-trip duration during chick rearing is affected by the presence of a RT on its mate, except under the extreme circumstance that a mate's prolonged absence causes the guarding bird to undergo abnormal food deprivation, requiring more time at sea to recover. If there were such an effect, it should show up in the early part of the study period (while adults are guarding chicks) rather than later (when chicks are crèched and adults do not wait for each other to return). Since foraging trips in this study were relatively short (<6 days) and since we did not see any instrument effect at any time during the study, it does not seem likely that there was such an impact.

We conclude that a careful telemetry or time-depth recorder study, using the latest, smallest possible, streamlined instruments, applied using methods now well worked out (attached using tape to the centerline of the lower back), can result in data not seriously affected by the instruments. All instruments in this study were 1% or less of the cross-sectional area of the study species, which may provide a useful guideline. Antenna angle and length are variables that still need further consideration, and we have yet to properly look for effects of flipper bands on trip durations or foraging effort. The fact that banded birds sometimes made shorter and sometimes longer trips than instrumented birds indicates that no simple result will follow, but with the WB in place we do have the means to pursue this question. We encourage researchers investigating foraging-trip duration to consider a wide range of variables when interpreting their results, particularly those relating to individual variation. Clearly, more effort is still required to understand the factors that cause variation in trip duration among penguins, but it appears that these factors can now be addressed with confidence using the methods described here.

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