# Variation in Adélie Penguin Foraging Dives Among Breeding Seasons and Colonies

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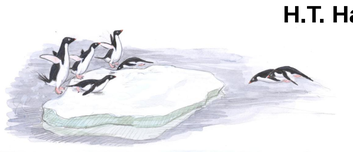


## TDR Methods

At each colony, we selected one or two individuals every few days (approximately 1-2 foraging trips) and attached a time-depth recorder (TDR, Wildlife Computers, model MK7) and radio transmitter (RT).

TDRs weighed 25.4 g, measured 1.1 x 2.0 x 8.5 cm (2.2 $cm^2$ maximum cross section, ≤ 1% the penguins' cross-sectional area), and were streamlined (Fig. 2). They were mounted directly behind small, rounded radio transmitters (RT's, ATS model PN5: 12.4 g, 1.4 x 4.8 cm, 1.54 $cm^2$ maximum cross section, or <1 % of the birds' cross-sectional area), on the centerline and as low on the back as possible without interfering with preening. The two instruments total length was ca. 13.3 cm. The RT had a 29 x 0.1 cm whip antenna pointed towards the tail and parallel with the back (Fig. 1).

Birds were caught at the nest by hand and held for approximately 10 min while instruments were attached using black Tesa® tape (Wilson and Wilson 1989). These instruments and attachment methods have been found to not influence foraging trip length or nest success (Ballard et al. 2001).

TDR's were configured to sample depth, light level, and temperature every 5s in 1999-00 and every 1s in 2000-01, and could store up to 2,031,616 sensor readings, or up to approximately 8 d.

We attempted to determine the sex of all individuals using a combination of copulatory position, behavior, "tread marks" (evidence of female copulatory position), and bill- and head-size differences (Ainley et al. 1983, Kerry et al. 1992).

Figure 1. Adult Adélie penguin with TDR and radio transmitter on lower back feeding its chick upon returning from a foraging trip.

Figure 2. Wildlife Computers MK7 TDR. Less than 1% of the bird's cross-sectional area.

## Abstract

We report results from studies of diving behavior in Adélie Penguins provisioning chicks from 3 breeding seasons at 3 colonies on Ross Island, Antarctica. We attached time-depth recorders with onboard light sensors to 79 individuals, recording 62,166 dives.

• 75% were foraging or exploration dives, and 25% were other types, presumably mostly for traveling.
• Mean foraging dive duration was 104 s, range 30 - 235 s and depth was 44 m, range 6 - 138 m.
• Colony, breeding season, 5-day period within breeding season, sex, individual, and light level all had impacts on duration and depth of foraging dives, though colony was the most important of these factors (Table 2, Fig. 8).
• The number of dives per hour was also affected by colony and sex (Table 4).
• Adélie diving depths in our study area appear to be largely limited by available light level, though the study area has 24 hours of sunlight and Adélies did not exhibit any clear diurnal patterns in foraging activity (Figs. 9-10).

We discuss relationships between these diving variables and sea-ice conditions, diet composition, and chick condition and implications to the metapopulation dynamics of this cluster of colonies.

## Background

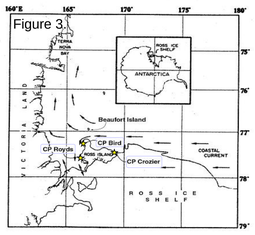
Though Adélie penguins are one of the most studied of all bird species, certain aspects of their diving behavior have not been thoroughly examined.

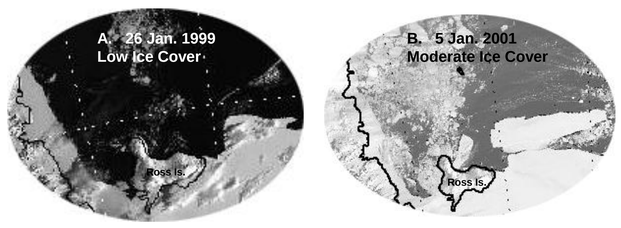
• Only two studies have included more than a single season (Chappell et al. 1993, Watanuki 1993, 1997).
• Only one deals with colony comparisons in the same season with the same methods (Watanuki 1993, 1997).
• Differences between the sexes has not been covered extensively, though at least two authors report on this issue (Whitehead 1989, Chappell et al. 1993) and others have noted sexual differences in foraging durations and distances (Clarke 2001, Ballard et al. 2001).
• Few studies account for the potential impacts of individual variation on diving behavior.
• Only the study by Wilson et al. (1993) considers feeding conditions at the time of diving (in this case, light level). However, the amount of daylight has profound bearing on the foraging behavior and natural history patterns of this species (Chappel et al. 1993, Wilson et al. 1993, Ainley 2002).

Here we are interested in comparing behavior at different colonies within a larger colony cluster, perhaps a metapopulation, with thoughts that results may help elucidate reasons for differences in size and growth rates of the colonies. Further, sea ice conditions vary seasonally (Figs. 4ab) and have been related to population size, colony growth rates, and to prey composition (Wilson et al. 2001). Other aspects of these colonies and their respective population parameters have been reported on previously (eg., Ainley et al. 1983, Ballard et al. 2001).

## Study Area and Timing

This study included most of the chick provisioning stage of the breeding cycle, including both the guard and crèche stages, Dec. 20 – Jan 20, 1999-00, 2000-01, and 2001-02.
Study colonies were distributed around Ross Island in the Southern Ross Sea (Fig. 3):
* Cape Crozier (77° 31´S, 169° 23´E; 140,000 pairs),
* Cape Royds (77° 34´S, 166° 11´E; 3,600 pairs), and
* Cape Bird (77° 13´S , 166° 28´ E; 40,000 pairs).




Figures 4ab. Satellite images showing variable ice conditions among seasons on foraging areas of Adélie Penguins. Open water appears dark, ice and land appear white.

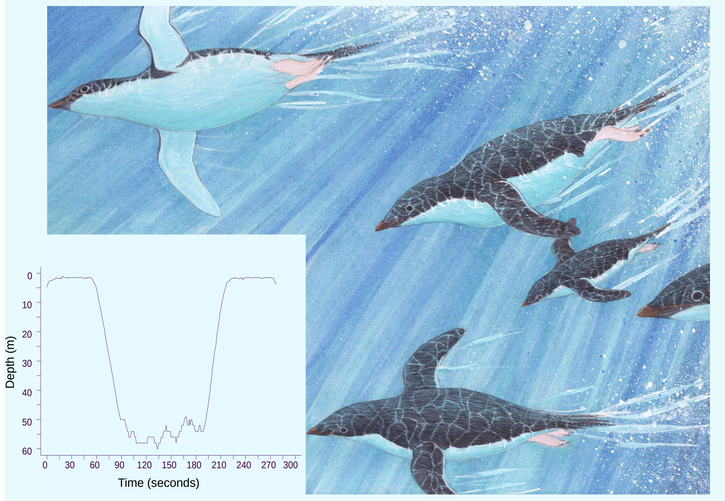



Figure 5. Profile of a typical foraging dive created using 1 second sampling intervals. We used rate of ascent, bottom depth, duration, number of undulations, and other parameters to classify dives as either foraging, exploration, or other.

## Dive Analysis

Diving data were summarized using software written by Ballard. The program summarized 12 parameters on a dive-by-dive basis. We classified dives into three categories based on the time at depth profiles and rates of change between depths largely following other authors (especially Chappell et al. 1993, Wilson et al. 1995, and Ropert-Coudert et al. 2001).

**"Foraging" dives** were ones which spent ≥ 30s within 5m of maximum depth and maximum depth was at least 15m, or that spent ≥ 15s within 5m of maximum depth, total duration was ≥ 30s and spent at least 20% of the dive in a rapid ascent/descent phase and at least 20% in a slower moving "undulatory" phase.

**"Exploratory" dives** were ≥ 15m and spent <30s within 5m of maximum or lacked the distinct transition between ascent/descent and undulatory phases described above.

**"Other" dives** reached at least 5m and lasted at least 10s. Dives <5m and <10s were excluded from these analyses because we doubted the resolution of the TDR's at shallower depths, and because others have documented that most foraging takes place at depths greater than 5m (Chappell et al. 1993, Ropert-Coudert et al. 2001) and during longer dives (Davis et al., 1988). When foraging under fast ice, dive depths can be shallow (eg. 6-11 m), but duration is very long (eg. 84 -114s; Watanuki et al. 1993, 1997).

Residuals from statistical tests were normally distributed, and we assumed statistical significance at $P \leq 0.05$. We used STATA version 6.0 for all statistical procedures.

Table 1. Total sample sizes (individuals and dives) by year and colony.

| | 1999-00 | | 2000-01 | | 2001-02 | |
|---|---|---|---|---|---|---|
| Colony | individuals | dives | individuals | dives | individuals | dives |
| Crozier | 17 | 15,211 | 20 | 12,465 | 10 | 6227 |
| Royds | 11 | 8423 | 25 | 3083 | 0 | 0 |
| Bird | 6 | 6540 | 0 | 0 | 11 | 4455 |

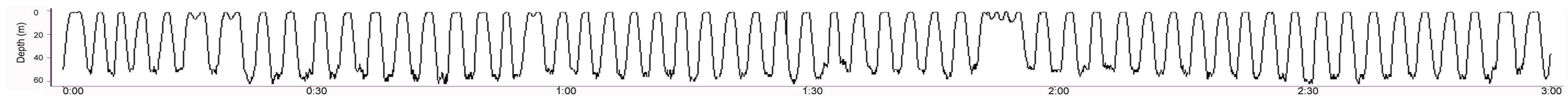



Figure 6. Typical foraging dives during chick provisioning (partial bout, 3 hours).

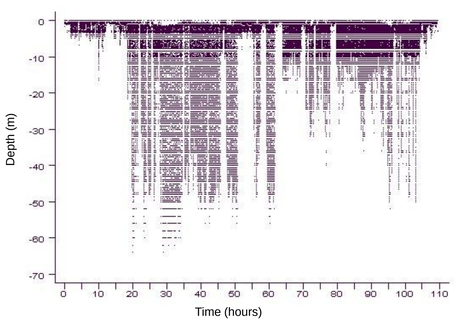



Fig. 7 Example of a 110 hour foraging trip during chick provisioning.

Table 2. Factors affecting Adélie penguin diving depth and duration, results from 6-way ANOVA comparing means derived from 30 randomly selected dives for each individual; 28 individuals at Cape Crozier, 42 at Cape Royds.

**Maximum Depth** ($F_{6,63}$ = 14.86, P<0.001, Adjusted R-squared = 0.55)

| | Df | F | P |
|---|---|---|---|
| Colony | 1 | 10.11 | 0.002 |
| Season | 1 | 0.2 | 0.6 |
| 5-day period | 1 | 17.7 | <0.001 |
| Colony*season | 1 | 1.3 | 0.3 |
| Period*season | 6 | 4.6 | 0.04 |
| Period*colony | 4 | 0.05 | 0.8 |

**Diving Duration** ($F_{6,63}$ = 20.04, P<0.001, Adjusted R-squared = 0.62)

| | Df | F | P |
|---|---|---|---|
| Colony | 1 | 12.4 | <0.001 |
| Season | 1 | 3.7 | 0.06 |
| 5-day period | 1 | 2.5 | 0.1 |
| Colony*season | 1 | 0.0 | 1.0 |
| Period*season | 6 | 2.6 | 0.1 |
| Period*colony | 3 | 0.0 | 0.9 |

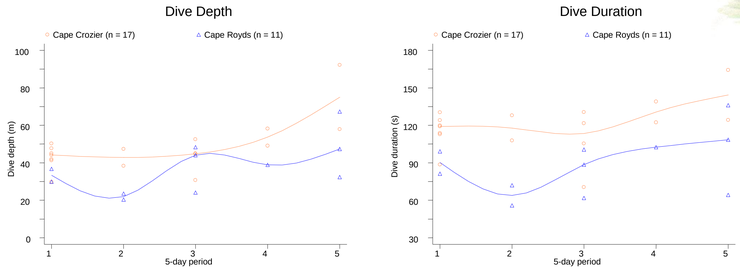



Figure 8. Mean maximum foraging depths (m) and dive durations (s) by Adélie penguins in 1999-2000 at Cape Crozier and Cape Royds compared with 5-day period within season. Curves connect median bands using cubic splines, 30 foraging or exploration dives selected at random from each individual. Sample sizes are number of individuals.

Figure 9. Mean light levels within 5m of maximum depths attained on foraging dives (n = 56,404 dives, 100 individuals, scale is $\log_e$ (watts/$m^2$), 1 lux equivalent is indicated).

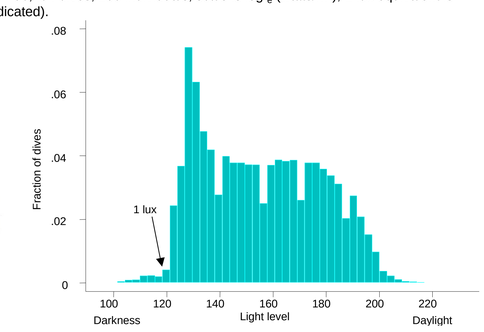



Figure 10. Relationship between numbers of foraging and exploration dives and time of day, Cape Crozier 1999-00 and 2000-01.


Table 3. Mean foraging dive duration, depth, and dives per hour by colony and season. Means calculated for each individual separately.

| | Duration (s) | | | Depth (m) | | | Dives per Hour | | |
|---|---|---|---|---|---|---|---|---|---|
| Colony | 99-00 | 00-01 | 01-02 | 99-00 | 00-01 | 01-02 | 99-00 | 00-01 | 01-02 |
| **Crozier** | 120 | 95 | 110 | 48 | 45 | 48 | 12.3 | 13.5 | 13.5 |
| **Royds** | 89 | 56 | -- | 38 | 23 | -- | 11.5 | 11.0 | -- |
| **Bird** | 114 | -- | 94 | 54 | -- | 41 | 14.7 | -- | 10.6 |

Table 4. Factors affecting number of foraging dives per hour at Cape Royds and Cape Crozier, results from 4-way ANOVA (combined model $F_{10,68}$ = 2.14, P = 0.03, $R^2_a$ = 0.13)

| Variable | F | P | $R^2$ |
|---|---|---|---|
| Sex | 6.33 | 0.01 | 0.07 |
| Colony | 7.20 | 0.01 | 0.08 |
| Season | 0.21 | 0.81 | 0.00 |
| 5-day period | 1.67 | 0.14 | 0.11 |

Table 5a. Mean dive duration(s), depth(m), and dives per hour by sex and colony.

| | Crozier | | | Royds | | | Bird | | |
|---|---|---|---|---|---|---|---|---|---|
| Sex | Dur | Dep | D/hr | Dur | Dep | D/hr | Dur | Dep | D/hr |
| Male | 106 | 43 | 13.5 | 70 | 30 | 14.0 | | | 11.9 |
| Female | 100 | 45 | 13.2 | 65 | 26 | 8.3 | | | 10.4 |

Table 5b. Gender relationship with dive duration, dive depth, and dives per hour, controlling for season, colony, and time within season effects (results of 4-way ANOVA's).

| Variable | F | P | $R^2$ |
|---|---|---|---|
| Dive duration (s) | 5.97 | 0.01 | 0.07 |
| Dive depth (m) | 6.79 | 0.02 | 0.03 |
| Dives per hour | 6.47 | 0.01 | 0.04 |

## Other Relationships to Consider:

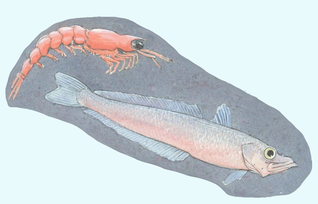


Fig. 11. Mean Adélie chick condition (weight / wing, ± SE), Cape Crozier, 1996-97 to 2001-02.

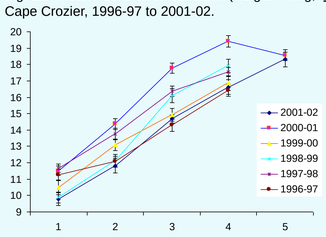



Table 6. Variation in percent fish in diet of Adélie Penguins at Ross Island colonies, 1994-2001.

| | Percent Fish by Season | | | | | | |
|---|---|---|---|---|---|---|---|
| Colony | 1994-95 | 1995-96 | 1996-97 | 1997-98 | 1998-99 | 1999-00 | 2000-01 |
| Crozier | 58 | 47 | 68 | 50 | 38 | 52 | 0 |
| Royds | 26 | 48 | 46 | 42 | 38 | 21 | 0 |
| Bird | 27 | 75 | 78 | 45 | 46 | 36 | 0 |

## Conclusions

Diving effort in terms of duration, depths, and dives per hour all varied significantly and in the same direction: dives at Cape Crozier, a colony 2 orders of magnitude larger than Cape Royds, were deeper, longer, and more frequent. Similarly, distances traveled on foraging trips (unpubl. data) and foraging trip duration (Ballard et al. 2001) were usually much longer at Cape Crozier than at Cape Royds, 1997-2001.

Further, dive duration and depth (but not dives per hour), and trip distances (unpubl. data), increased as the seasons progressed, particularly at Cape Crozier in 1999-2000.

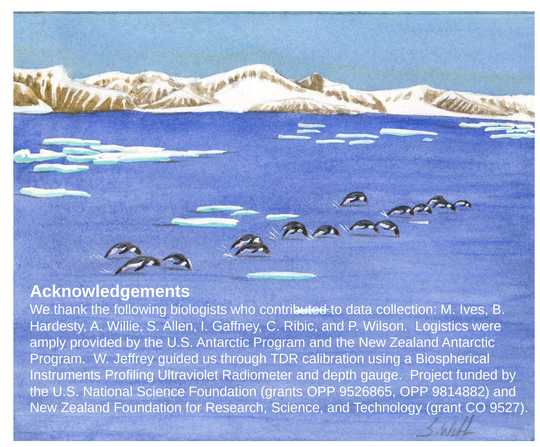
All this points to depletion or reduced availability of prey in the larger colony. The rapid expansion of the Cape Royds colony and coincident stability of the Cape Crozier colony in recent decades (Wilson et al. 2001) may be better understood in this context.

Gender effects, while statistically significant, do not appear biologically meaningful.

Larger sample sizes are required to further measure the impact of individual variation and time of season.

Foraging-dive depths appear to be ultimately limited by light availability, in support of the findings of Wilson et al. (1993). In that study, however, light levels were not measured directly but assumed to vary by time of day in a region where darkness occurred during part of the 24-hour cycle. In our study, with 24 hours of sunlight, light level was related to depth and (presumably) ice cover. These findings have implications for where Adélie penguins can spend the winter (when darkness prevails south of the Antarctic Circle).

***Illustrations by Sophie Webb*** **(swebb@prbo.org)**



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## Selected Literature Cited

Ainley, D. G., L. E. LeResche, and W. J. L. Sladen. 1983. Breeding biology of the Adélie Penguin. Univ. Calif. Press, Berkeley, CA.
Ballard, G., D. G. Ainley, C. A. Ribic, K. R. Barton. 2001. Effect of instrument attachment and other factors on foraging trip duration and nesting success of Adélie Penguins. Condor 103:481-490.
Chappell, M. A., V. H. Shoemaker, D. N. Janes, T. L. Bucher, and S. K. Maloney. 1993. Diving behavior during foraging in breeding Adélie Penguins. Ecology 74:1204-1215.
Wilson, R. P., K. Pütz, C. A. Bost, B. M. Culik, R. Bannasch, T. Reins, D. Adelung. 1993. Diel dive depth in penguins in relation to diel vertical migration of prey: Whose dinner by candlelight? *Mar. Ecol. Progr. Ser.* 94:101-104.
Wilson, P.R., D.G. Ainley, N.Nur, S.S. Jacobs, K.J. Barton, G. Ballard, and J.C. Comiso. 2001. Adélie Penguin population change in the Pacific sector of Antarctica: relation to sea-ice extent and the Antarctic Circumpolar Current. Mar. Ecol. Progr. Ser. 213:301-309.