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DIVING BEHAVIOR DURING FORAGING IN BREEDING ADÉLIE PENGUINS[1]

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Abstract. We used electronic time depth recorders to examine diving patterns of Adélie Penguins (*Pygoscelis adeliae*) breeding near Palmer Station, Antarctica. Most hunting dives consisted of a rapid descent to depth, a period of bottom time at near-constant depth, and a rapid ascent to the surface. Most hunting activity occurred in bouts of consecutive dives to similar depths. Adélies foraged at depths between 3 and 98 m, with a mean of 26 m. Descent and ascent rates averaged 1.2 and 1.1 m/s, respectively. Foraging was primarily diurnal, but there was relatively little circadian change in foraging depth. The birds' overall hunting effort (cumulative bottom time) was concentrated between 0500 and 2100 at depths between 10 and 40 m. Bottom time decreased slightly with increasing depth but the correlation was weak. Dive duration was positively correlated with dive depth. Maximum dive duration was 160 s; most hunting dives lasted 60–90 s with a mean of 73 s. Post-dive surface intervals averaged ≈50% of dive duration. Time use efficiency during dive bouts (bottom time/[dive duration + surface interval]) decreased with increasing dive depth. Estimates of oxygen stores and diving metabolic rates indicate that the aerobic dive limit of Adélies is 46–68 s and that most hunting dives require some anaerobic metabolism. Use of anaerobiosis engenders an energy penalty and probably affects both the behavior and energetics of foraging.

Key words: Antarctica; penguin; physiology; Pygoscelis adeliae; *seabird; spheniscid.*

INTRODUCTION

Diving seabirds are important components of many oceanic ecosystems; their abundance, wide distributions, and high metabolic rates place substantial demands on prey populations. However, the underwater foraging behavior of diving seabirds was poorly understood until the recent development of miniaturized microprocessor-based recorders. Use of these devices, which store detailed records of time and depth throughout foraging trips, has greatly increased our knowledge of seabird foraging ecology and revealed some impressive diving capabilities. For example, King and Emperor Penguins (*Aptenodytes patagonicus* and *A. forsteri*) can dive to 240–400 m with dive durations exceeding 5–8 min (Kooyman 1989, 1990, Kooyman et al. 1992*a*). Common and Thick-billed Murres (*Uria aalge* and *U. lomvia*) reach depths of 180 and 200 m, respectively, and the latter species can remain submerged for >5 min (Piatt and Nettleship 1985, Croll et al. 1992*a*). Recorders have also revealed that maximum depths and dive durations may not be representative of typical feeding dives. In Thick-billed Murres and several penguin species, mean foraging depths and dive durations are considerably less than maximum values for these parameters (Kooyman 1989, Croll et al. 1992*a*).

One remarkable aspect of diving seabirds is their ability to sustain repetitive diving for long periods. Most voluntary diving in pinnipeds is accomplished aerobically using oxygen stored in the lungs, muscle, and blood (Kooyman 1989). However, analysis of metabolism and oxygen stores in diving seabirds suggests that foraging dives routinely require substantial anaerobiosis. Kooyman (1989) calculated a maximal aerobic dive duration of 4.1 min for Emperor Penguins, but the birds repeatedly dive for 6–8 min during foraging bouts; for King Penguins the estimated aerobic dive length (ADL) is 2 min, but mean hunting dive duration is 2.5–5 min (Kooyman et al. 1992*a*). Similarly, almost half of the foraging dives of Thick-billed Murres exceed aerobic dive limits (Croll et al. 1992*a*). The physiological basis of this phenomenon is poorly understood (Kooyman 1989, Kooyman et al. 1992*b*), but use of anaerobiosis is likely to affect the time budgeting and efficiency of foraging (Ydenberg and Clark 1989, Croll et al. 1992*a*).

Here we report results from an investigation of diving and foraging behavior in Adélie Penguins (*Pygoscelis adeliae*). This Antarctic species is especially appropriate for such studies because its physiology and breeding ecology have been intensively investigated

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TABLE 1. Summary of recorder deployments for Adélie Penguins at Palmer Station, Antarctica. The total dives category includes dives shallower than 3 m, which were counted but not classified as either hunting or traveling dives.

Season	Nesting stage	Number of deployments	Hunting dives	Traveling dives	Total dives
1990–1991	Guard	13	3044	5945	9032
1990–1991	Creche	13	2516	4733	7745
1991–1992	Incubation	8	5014	11112	16541
1991–1992	Guard	13	2594	7465	10060
1991–1992	Creche	3	880	1322	2202
Both years combined		50	14048	30577	45580

(e.g., Ainley et al. 1983, Lishman 1985, Chappell and Souza 1988, Culik and Wilson 1991). Our analyses focused on temporal patterns of foraging, the depth distribution of hunting effort, and physiological aspects of diving. We were particularly interested in the relationship between hunting dive depths, durations, surface recovery periods, and time use efficiency during foraging bouts. We also examined the potential time and energy costs of anaerobiosis during repetitive diving.

MATERIALS AND METHODS

Study area.—We worked on Torgersen Island, near Palmer Station (64°46′ S, 64°05′ W) on Anvers Island off the west coast of the Antarctic Peninsula. Torgersen supports approximately 8000 breeding pairs of Adélie Penguins distributed among a number of colonies; there were 2700–2800 nests in the seven colonies from which we selected study birds. We obtained dive records during the 1990–1991 and 1991–1992 breeding seasons in the months of December, January, and February.

Study animals.—Penguins selected for recorder deployment were adults marked with numbered aluminum flipper bands. We determined sex by observing mating and incubation behavior (Ainley et al. 1983) and checked nests daily (whenever weather and sea ice conditions permitted access) from the time of pair formation through fledging. Consequently we compiled comprehensive records of nest attendance (daily presence or absence) and the status of eggs or chicks for each study bird. We deployed recorders during late incubation and the period of chick care. Chick rearing in Adélies consists of two more-or-less distinct phases: the "guard" stage, when at least one parent continually broods or guards small chicks, and the "creche" stage, when large chicks are left unattended. The guard stage lasts from hatching until chicks are 18–28 d old, and the subsequent creche stage lasts until chicks are abandoned at 35–40 d. We obtained 8 dive records from incubating birds, 26 records from birds with guard-stage chicks, and 16 records from birds with creche-stage chicks (Table 1). For all stages, the numbers of males and females were approximately equal.

Dive recorders.—We used electronic time–depth recorders (TDRs; Mk. 4.5, Wildlife Computers, Woodinville, Washington) that sampled depth at preset intervals of 1 s or 5 s. The units were 5.7 cm long × 3.4 cm wide × 1.3 cm high and weighed 45 g. TDRs stored up to 131 000 depth records, equivalent to 1.5 d of cumulative diving at 1 s intervals or 7.5 d of diving at 5 s intervals. Depth resolution was ±1 m; accuracy (tested by submerging TDRs to known depths) was within ±1 m. Clock accuracy was within ±5 s/d. TDRs also had an immersion sensor that indicated when birds were in the water.

We selected penguins for TDR deployment after inspecting nest check records and determining that prospective test birds were behaving normally. Penguins were captured by hand and weighed to the nearest 25 g (3.4–4.6 kg) on an Ohaus electronic balance. We attached TDRs by placing a patch of rapid-hardening epoxy glue (Devcon) about 10 cm long × 3.5 cm wide onto the center of the lower back. We worked the glue into the outer 2–4 mm of the feathers and placed the TDR on the anterior portion of the patch. After the glue cured, the TDR was secured with two plastic cable ties threaded through the feathers between the skin and the glue patch. The procedure took 15–20 min. Penguins were released at their nests; in 48 of 50 deployments and recaptures the birds immediately resumed incubation, chick feeding, or guard behavior, and the remaining birds did so within 1 h.

Penguins carried TDRs for periods of 1 d (creche stage) to 8 d (incubation). When they returned to their nests after a foraging trip they were recaptured and weighed within 15 h (most birds were recaptured within 4 h of their return). After weighing the birds, we cut the cable ties and removed the recorders (the glue adhered poorly to the smooth, plastic-covered TDRs). Dive records were downloaded to IBM-compatible computers.

Analysis of dive records.—We examined dive records with software from Wildlife Computers. Dives with maximum depths <3 m were counted but otherwise ignored, since wave action and recorder noise degraded depth accuracy for dives this shallow. Deeper dives were displayed individually and categorized as traveling or hunting dives according to the following criteria: dives with maximum depth ≥20 m or durations ≥1.0 min were called hunting dives; dives with durations shorter than 0.33 min were called traveling dives; the remaining dives were called hunting dives

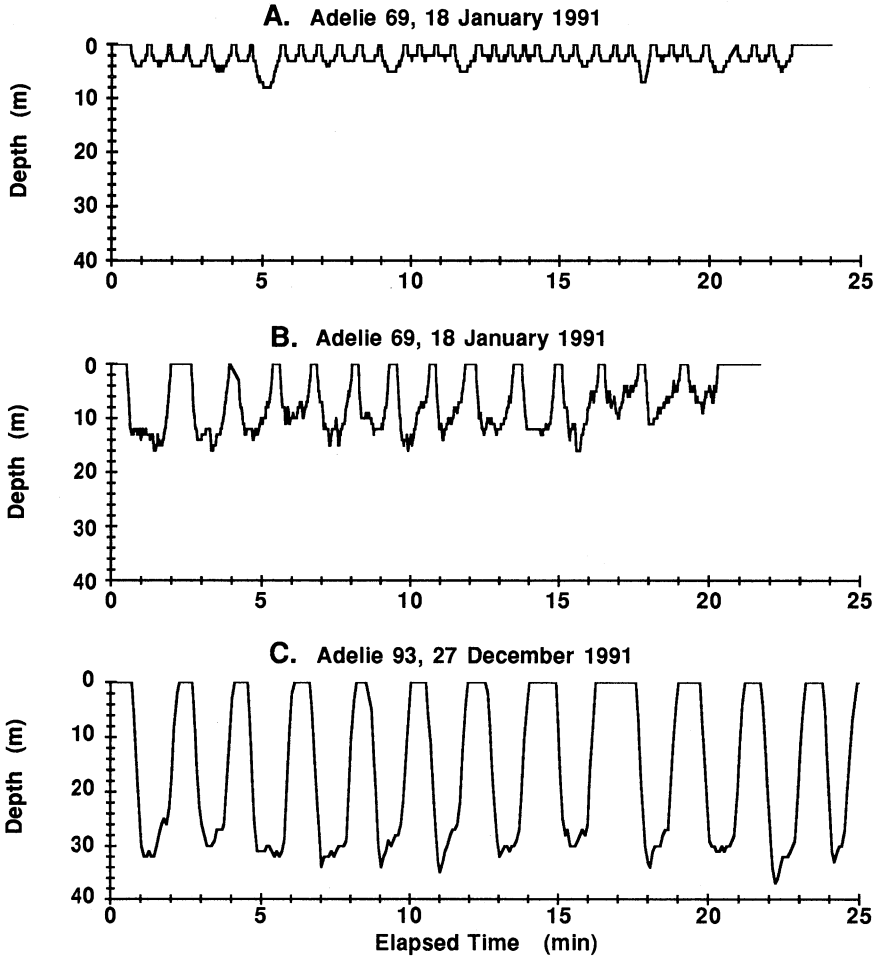

FIG. 1. Typical TDR records of dive patterns of Adélie Penguins near Palmer Station, Antarctica. (A) Traveling dives (sample interval 1 s, mean depth 4–5 m). (B) Shallow hunting dives (sample interval 1 s, mean depth 13–15 m). (C) Moderately deep hunting dives (sample interval 5 s, mean depth 34–36 m).

if they had abrupt inflections in descent and ascent rate and traveling dives if they lacked such inflections. Our rationale was that penguins performing traveling dives would show smoothly changing depth profiles, but birds chasing prey would descend rapidly to the depth of the prey, remain at or near that depth while pursuing them ("bottom time"), and then ascend to the surface. We designated bottom time as the period between the inflection at the end of descent and the inflection at the start of ascent. The software stored the type, date, start time, duration, maximum depth, bottom time (if any), and the descent and ascent rates of each dive. Rates of descent and ascent were calculated only for dives with sample intervals of 1 s and depth change of ≥ 5 m. Examples of dive patterns are shown in Fig. 1.

Dive data were transferred to a Macintosh computer and analyzed with spreadsheets and statistics software (Excel, Statistica). To estimate travel times and temporal patterns of traveling and hunting we used custom software and a laser printer to plot dive records in "stripchart" form.

Physiological data for calculating oxygen stores.— We measured plasma volumes of freshly captured penguins with the Evans Blue dilution method (Linden and Mary 1983). A measured quantity of Evans Blue dye dissolved into normal saline was injected into a flipper vein through a heparinized catheter. Sequential blood samples were taken from an adjacent artery at intervals of 5 min (arterial hematocrits were obtained from pre-injection samples). Absorbance of plasma samples was measured at 630 nm and compared to known dye concentrations in plasma. We obtained venous blood samples from a second group of penguins. These samples were taken from an interdigital vein using Vacutainer tubes and 0.75 mm outside diameter (22-gauge) needles. Hematocrit was measured in heparinized microcapillary tubes. We assumed 30% of plasma is arterial and 70% venous (Croll et al. 1992*a*) and calculated arterial and venous blood volume using the respective hematocrit values.

We used data on myoglobin concentrations for Adélie penguins from Kooyman (1989) and calculated blood

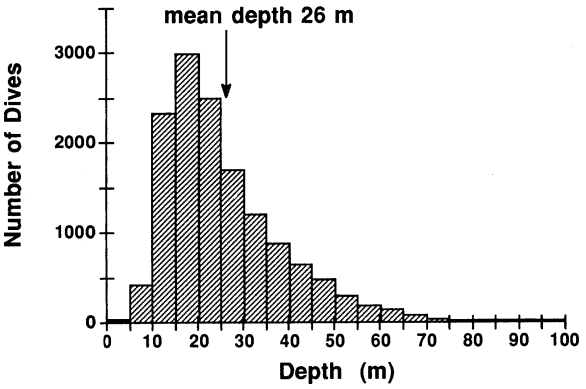

FIG. 2. Depth distribution of hunting dives by Adélie Penguins near Palmer Station, Antarctica. Minimum depth was 3 m; maximum depth was 98 m. Data from 50 deployments in two breeding seasons; $N = 14\,048$ dives.

hemoglobin content by scaling Kooyman's figures of 16.5 g/100 mL blood at a hematocrit of 46.2% to our measured hematocrit values. The volume of the respiratory system (lung + air sacs, in millilitres) was calculated as $160.8M_b^{91}$, where M_b is body mass in kilograms (Lasiewski and Calder 1971). Muscle mass was estimated as 35% of M_b, based on dissection results and literature data (Kooyman 1989).

RESULTS

Swimming activity.—We recorded 45 580 dives, of which 14 048 were hunting dives (Table 1). Typically, penguins departed the colony in the morning and returned a day or more later in the afternoon, but some departures and returns occurred throughout the day. At-sea behavior had a circadian pattern; some swimming took place throughout the day but most was concentrated between 0700 and 1900.

Time budgets were highly variable. When away from their nests, penguins spent from 6 to 70% of their time swimming, averaging ≈50% during incubation and 30–35% during the guard and creche stages. The length of at-sea periods (when penguins were continuously in the water) varied from 20 min to 26 h (mean ± 1 SD = 6.45 ± 4.7 h; $N = 127$); the longest at-sea periods occurred during incubation. Travel time between the colony and foraging sites (the time between the first traveling dive and the first hunting dive when departing the colony, or between the last hunting dive and the last traveling dive when returning) varied from <10 min to 5 h (outbound mean 70 ± 65 min; inbound mean 75 ± 65 min). If Adélies swim at an average of 2 m/s (Culik and Wilson 1991), these travel times correspond to straight-line distances between 1 and 36 km, with a mean of 8.7 km. If they travel by porpoising at 3.7 m/s (Hui 1987), the mean distance is 16 km and the maximum is 67 km. Penguins often emerged from the water (onto floating ice or islands away from the colony) one or more times between leaving the nest and returning to it.

Gender effects.—Hunting dives averaged 0.5 m deeper for males than females ($P = .014$; $N = 6269$ dives by 24 males and 7779 dives by 26 females), but there were no gender differences in dive duration or post-dive surface interval (the time between the end of one dive and the beginning of the next). We used ANCOVA to test for gender differences in the relationships between depth and duration, and between duration and surface interval. Gender did not influence the relationship between duration and surface interval ($P = .34$). However, there was a slight but significant gender effect on the relationship between depth and duration. Durations of dives to a given depth averaged slightly longer (≈0.8%) for females than for males ($P = .006$). Since gender differences were small or insignificant, we pooled data from males and females for other analyses.

Performance during hunting dives.—The depth of hunting dives was 26 ± 13 m (mean ± 1 SD, range 3–98 m; Fig. 2). There was a strong circadian pattern to hunting effort, with a lull between 2200 and 0400 (Fig. 3A, B). Circadian changes in mean dive depth were significant but small (Fig. 3C). All dives deeper than 75 m occurred between 0800 and 2100. Foraging effort (bottom time) was broadly distributed with respect to time and depth (Fig. 4), but was largely concentrated between 0500 and 2000 at depths between 10 and 40 m (Figs. 3B and 4).

About 70% of hunting dives were 55–90 s in duration (mean ± 1 SD = 73.2 ± 18.6 s; maximum 160 s; Fig. 5). Duration was strongly correlated with depth (Fig. 6A) but depth explained less than half the variance in duration ($r^2 = 0.48$, $P < .001$). Bottom time was largely independent of depth (Fig. 6B), averaging 32.4 ± 12.6 s (range 1–93 s); there was a significant tendency for bottom time to decrease as depth increased, but the correlation was weak ($r^2 = 0.02$) and the significance is largely a reflection of high sample size. Rates of descent (ROD) and rates of ascent (ROA) differed slightly ($P < .001$, $N = 4991$). ROD averaged 1.22 ± 0.29 m/s ($N = 5128$) with a maximum of 2.5 m/s; ROA averaged 1.10 ± 0.37 m/s ($N = 5005$) with a maximum of 3.2 m/s. Both ROD and ROA were positively correlated to depth ($r^2 = 0.146$ and 0.231, respectively; $P < .001$). Duration was significantly correlated with ROD and ROA, but the correlations were very weak ($r^2 = 0.003$ and 0.001, respectively). If swim speed is 2 m/s, the mean ROD corresponds to a descent angle of 38° (relative to the surface), and the mean ROA corresponds to an ascent angle of 33°.

Hunting bouts.—Most hunting dives occurred in discrete bouts, defined as periods during which birds dove repeatedly to similar depths with minimal surface interval (<5 min); portions of two such bouts are shown in Fig. 1B and C. A typical foraging trip included several bouts, usually with different mean depths and separated by intervals of rest or shallow traveling dives (Fig. 1A). We reasoned that during bouts the birds would spend as little time as possible on the surface in

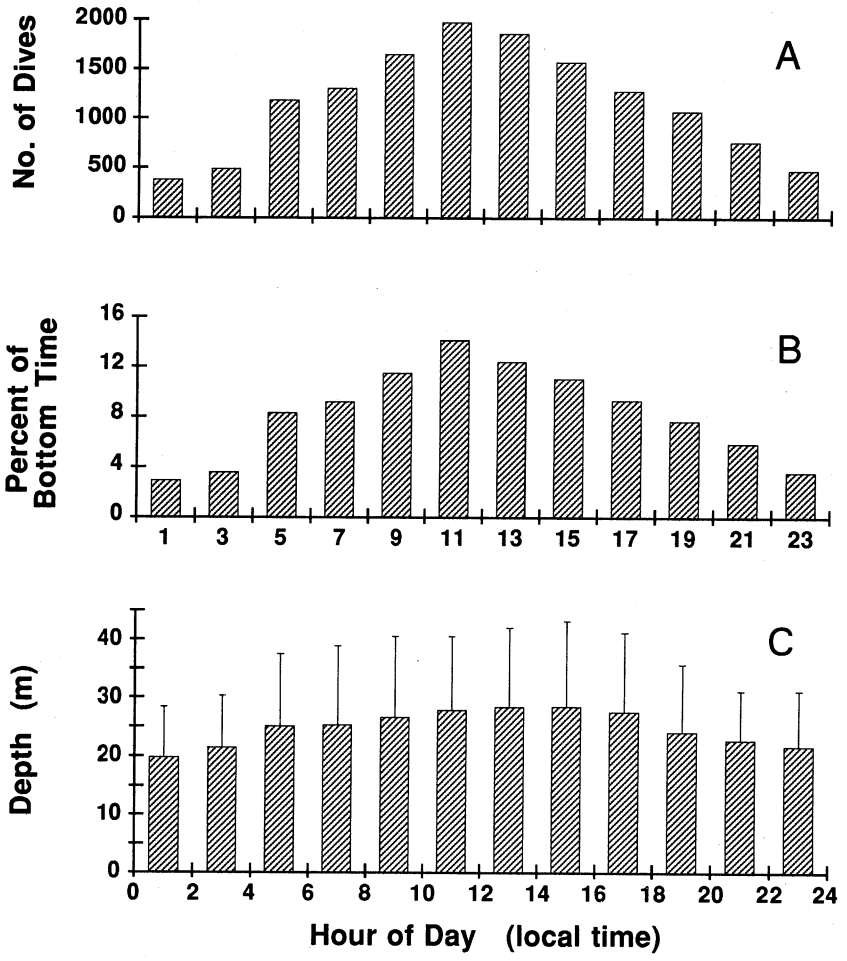

FIG. 3. Circadian changes in foraging by Adélie Penguins near Palmer Station, Antarctica. $N = 14\,048$ dives. (A) Number of hunting dives. (B) Percent of total bottom time. (C), Mean depth (error bars are 1 SD).

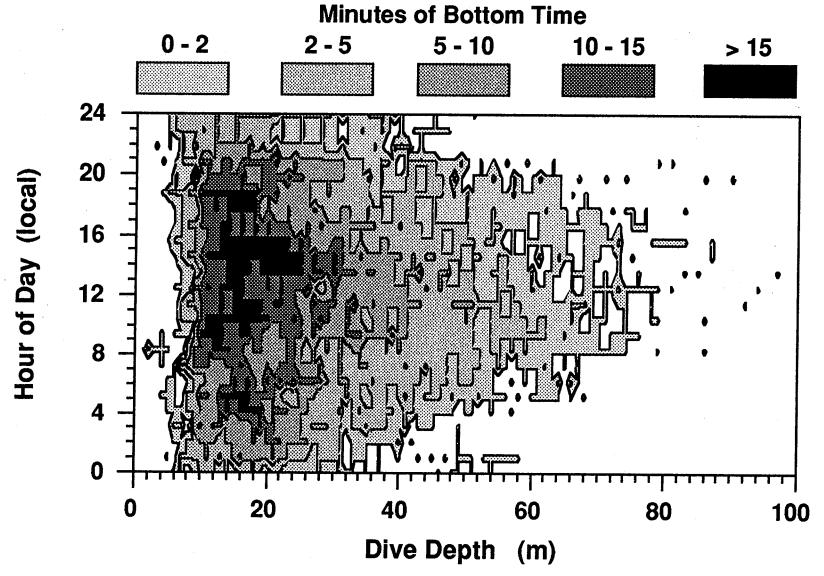

FIG. 4. Distribution of hunting effort as a function of dive depth and time of day for Adélie Penguins near Palmer Station, Antarctica. Shadings indicate cumulative bottom time at each combination (1 h by 1 m) of time of day and depth. $N = 14\,048$ dives.

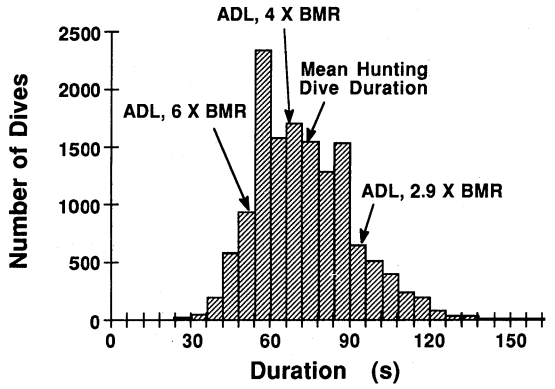

FIG. 5. Durations of hunting dives by Adélie Penguins near Palmer Station, Antarctica. Arrows indicate mean duration (73 s) and the aerobic dive limits (ADL) for diving metabolic rates of 6, 4, and 2.9 times basal metabolic rate (BMR). The latter ADL includes 90% of hunting dives (see *Results*: *Performance during hunting dives*). Minimum duration was 25 s, maximum duration was 160 s. $N = 14\,048$ dives.

order to maximize cumulative bottom time in the prey school. Hence, behavior during dive bouts would be a useful index of the birds' capacity for sustained diving. We compiled mean values of depth, duration, bottom time, surface interval, and dive cycle time (duration + the subsequent surface interval) for 455 bouts of 4 to 52 consecutive hunting dives where coefficients of variation of depth and duration were <15%. Mean bout depths ranged from 3.3 to 91 m, with an overall mean ± 1 SD of 32 ± 16 m.

Dive duration during bouts was positively correlated to depth (Fig. 7A; duration in seconds = 50.2 + 0.9·depth; $r^2 = 0.60$; $N = 455$), and surface intervals were positively correlated with dive duration (Fig. 7B; interval in seconds = 0.512·duration − 2.9; $r^2 = 0.37$). Consequently, dive cycle time was strongly correlated to depth (Fig. 7C; cycle time in seconds = 68.0 + 1.52·depth; $r^2 = 0.64$). Bottom time during bouts decreased with increasing depth, but the correlation was weak (Fig. 7D; bottom time in seconds = 39.6 − 0.18·depth; $r^2 = 0.10$).

Blood volume and hematocrit.—Arterial hematocrit was 0.49 ± 0.05 (mean ± 1 SD; $N = 9$; hemoglobin content 17.5 g/100 mL); venous hematocrit was 0.54 ± 0.05 ($N = 77$; hemoglobin content 19.3 g/100 mL). Plasma volume in nine birds (mean mass 3628 g) was 211 ± 36 mL; accordingly, venous blood volume was 322 mL (8.9% of body mass) and arterial blood volume was 124 mL (3.4% of body mass). Total blood content was 12.3% of body mass.

DISCUSSION

Effect of recorders.—Externally attached devices can affect the behavior and locomotory performance of marine birds (Wilson et al. 1986, 1990, Croll et al. 1992*b*). Some effects, such as increased foraging trip duration, may not be apparent until the device has been in place for several weeks (Wilson et al. 1986). In our study, Adélies showed no obvious behavioral changes associated with TDRs aside from the initial disturbance of capture and handling. We saw no attempts to peck or preen TDRs, and the penguins appeared to take no notice of them. However, removal attempts might have occurred when birds were at sea (Wilson et al. 1990).

TDRs added frontal area and mass to penguins and probably reduced hydrodynamic efficiency. Croll et al. (1992*b*) reported increased foraging trip duration in Chinstrap Penguins (*Pygoscelis antarctica*) carrying instruments. They attributed longer trip times to drag-related decreases in swimming speed; their units increased the birds' frontal cross-sections by 2.3–5.3%. The TDRs we used were 1.5–2% of frontal cross-section. Since the thrust needed to swim at constant velocity is equal to drag (Webb 1975), our TDRs may have slightly reduced velocity or increased the metabolic cost of swimming. Attached TDRs weighed 1.2–1.5% of an Adélie's body mass (range 3.4–4.6 kg), but in water the buoyancy loss was only 18–20 g. This is of minor importance compared to the buoyancy effects of gas volume changes in the feathers and respiratory tract as birds change depth.

Penguins carrying TDRs were able to forage successfully, as indicated by the quantity of food they brought back to their nests. The mean mass increase between departure and return was 352 g for 20 TDR birds recaptured before they fed chicks (Appendix). This is similar to the average stomach contents of unmanipulated returning foragers at Palmer (W. R. Fraser, *personal communication*). Several TDR birds returned with >600 g of food. To summarize, we feel that TDRs may have had some impact on swimming performance or foraging efficiency, but any effects were probably minor.

Diving behavior during foraging.—Adélie hunting dives resemble those reported for other diving birds (e.g., Kooyman et al. 1992*a*, Croll et al. 1992*a*). Adélies usually descended at a rapid, constant rate to a particular depth, remained at or near that depth for a substantial fraction of the dive, and then rapidly and steadily ascended to the surface. After a surface interval the cycle was repeated, with successive dives attaining similar depths for the duration of the bout. We interpret this pattern as repeated diving into a school of prey congregated within a discrete depth range. The pattern is also consistent with feeding on benthic prey, but most of the water in the vicinity of Palmer Station is considerably deeper than typical Adélie foraging dives, and Antarctic krill (*Euphausia superba*), which comprise 95–99% of Adélie diets near the Antarctic Peninsula (Volkman et al. 1980, Lishman 1985), are midwater organisms (Miller and Hampton 1989).

There were several variations to this basic pattern. Some dives were V-shaped, with steady, rapid ROD and ROA but little or no bottom time. We interpreted these as search dives or as hunting dives in which the

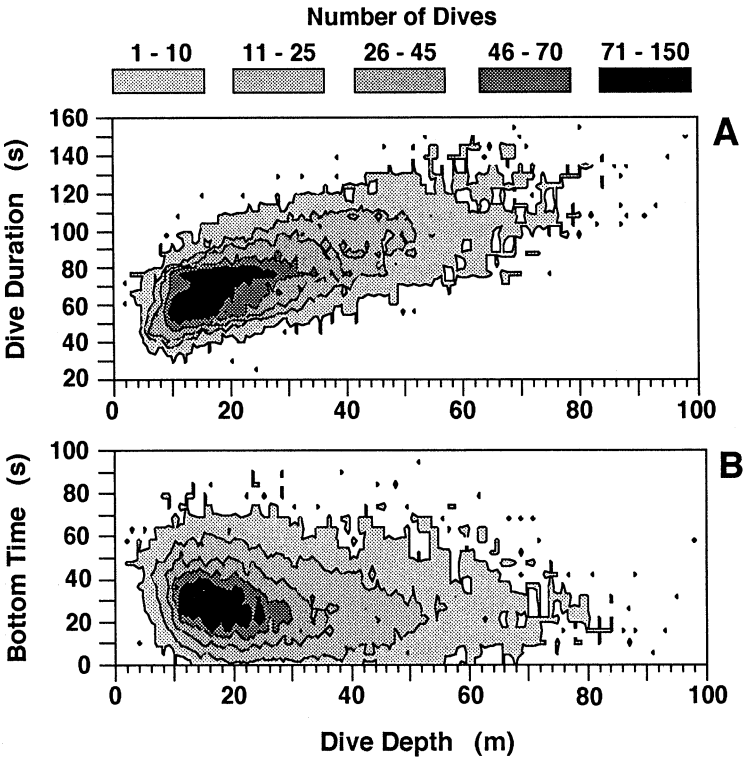

FIG. 6. Influence of depth on dive duration (A) and bottom time (B) for foraging Adélie Penguins near Palmer Station, Antarctica. Shadings indicate number of dives at each combination (1 m by 1 s) of depth and duration or depth and bottom time. $N = 14\,048$ dives.

bird was unable to locate prey. A second variant consisted of a rapid descent to an intermediate depth, a period of bottom time during which the bird descended at a slower and irregular rate to the maximum attained depth, followed by a rapid ascent to the surface at constant rate. A third variant was a rapid descent to the maximum attained depth, a period of bottom time during which the bird ascended at a slow and irregular rate to an intermediate depth, followed by a rapid ascent at constant rate. We interpreted the latter two patterns as hunting dives in which prey were pursued vertically as well as horizontally. All TDR penguins that foraged extensively showed all of these dive profiles.

Time and depth of foraging activities.—The deepest dives we recorded (90–98 m) are less than the depths reached by Chinstrap Penguins (120 m; D. Croll, *personal communication*), Gentoo Penguins (*P. papua*; 135 m; Croxall et al. 1988), and other populations of Adélies (150–175 m; Whitehead 1989). In general, the diving abilities of pygoscelid penguins are comparatively modest. King and Emperor Penguins routinely forage at depths >200 m (Kooyman 1989, Kooyman et al. 1990). These species are considerably larger than pygoscelids, so their ability to attain greater depths is not surprising. However, Thick-billed Murres, which weigh only 25–30% as much as Adélies, can also dive to >200 m (Croll et al. 1992*a*).

Maximum depths may reflect physiological limits, depth distributions of prey, or a depth-related constraint to foraging efficiency. It seems clear that the deepest dives we observed are not the maximum Adélies are capable of, but they may be near the maximum depth permitting sufficient bottom time for efficient foraging. An Adélie diving to 100 m at ROD and ROA of 1.5 m/s would have 27 s of bottom time if it limited dive duration to 160 s (the maximum we observed). Adélies are capable of faster ROD and ROA, but it is unclear if this would permit the birds to reach greater depths because the increased power requirements for faster swimming would reduce dive duration. The time–depth distribution of foraging effort (Figs. 4 and 6) suggests that Adélies catch most of their prey at relatively shallow depths, and the bulk of foraging activity takes place when ambient light intensity is high. Since Adélies can dive considerably deeper than the mean foraging depth of 26 m, the relatively shallow depth of most foraging activity probably reflects the distribution of prey in the water column. In Macaroni (*Eudyptes chrysolophus*) and Gentoo Penguins, foraging depths show a close correspondence to the depth distributions of known prey species (Croxall et al. 1985).

Lack of a strong circadian pattern in foraging depth (Fig. 3C) is surprising. Krill typically remain deep during the day and move toward the surface when light levels fall in the evening (Miller and Hampton 1989).

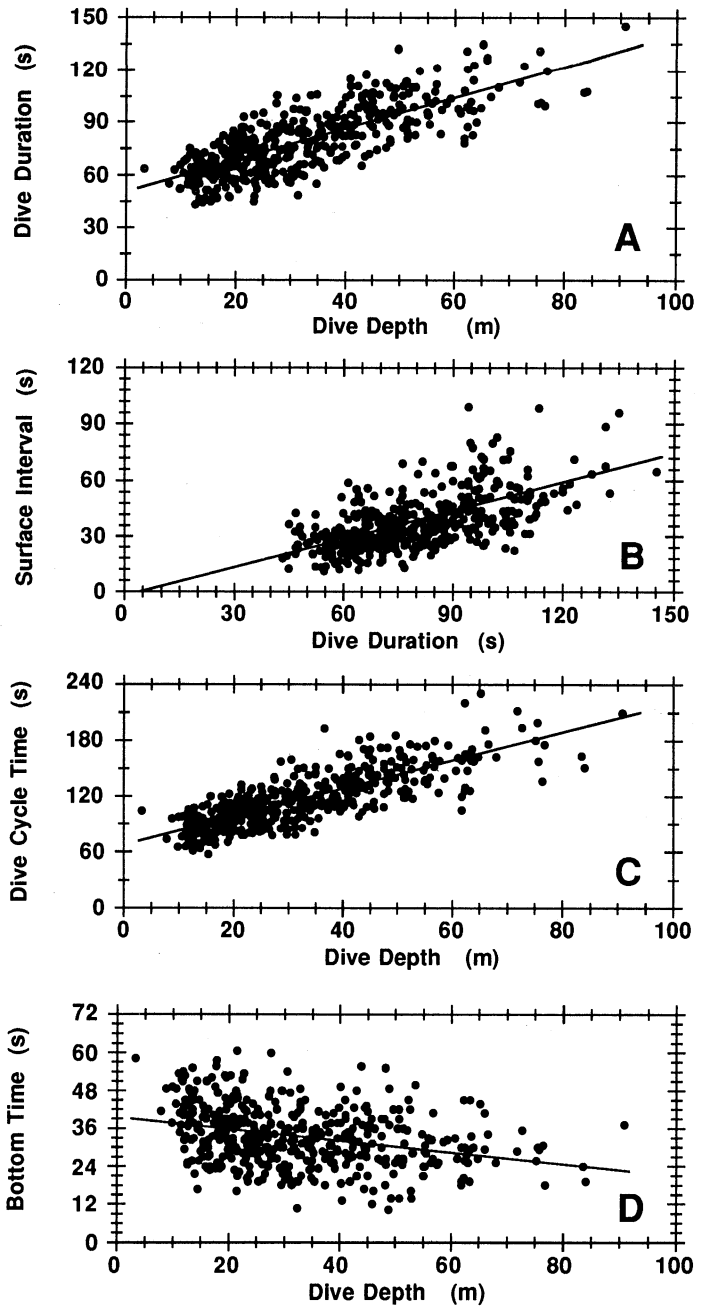

FIG. 7. Depth and duration effects on hunting dive bout parameters for Adélie Penguins near Palmer Station, Antarctica. Each point is the mean value for a bout of 4 to 52 dives; regression equations are given in the text. $N = 455$ bouts. (A) Relationship between depth and duration ($r^2 = 0.60$). (B) Relationship between duration and surface interval ($r^2 = 0.37$). (C) Relationship between depth and dive cycle time ($r^2 = 0.64$). (D) Relationship between depth and bottom time ($r^2 = 0.10$).

Dive depths of krill predators such as Antarctic fur seals (*Arctocephalus gazella*; Croxall et al. 1985) and Chinstrap Penguins (D. Croll, *personal communication*) reflect this movement. Several nonexclusive factors could account for small circadian changes in hunting dive depth in Palmer Adélies. The timing and magnitude of daily vertical migration in krill is geographically variable (Miller and Hampton 1989) and may have been minimal near Palmer during the study period. Alternately, Adélies may depend largely on vision to locate prey (Wilson et al. 1989), which might make foraging most efficient at shallow, well-lighted depths even if prey density is higher at greater depth. Reliance on vision would also explain why hunting effort declined at night, even though krill were presumably nearest the surface then. It is also possible that

the density or behavior of krill swarms is optimal for foraging penguins during the day, independent of visual factors (Everson 1982).

Dive duration, aerobic dive limits, and energy costs of anaerobic diving.—The maximum dive duration we observed (2.7 min) is similar to the longest dive reported for Chinstrap Penguins (3.0 min; D. Croll, *personal communication*). However, it is substantially less than that of many other diving seabirds. Thick-billed Murres can dive for periods >5 min (Croll et al. 1992*a*) and King and Emperor Penguins can dive for >8 min (Kooyman 1989, Kooyman et al. 1992*a*). We presume Adélies are capable of dives >2.7 min; the 175-m dives reported by Whitehead (1989) would have lasted at least 3.9 min at ROD and ROA of 1.5 m/s or 2.9 min at ROD and ROA of 2.0 m/s.

In breath-hold divers, very long dives exhaust stored oxygen reserves and require considerable anaerobic metabolism, with concomitant lactate accumulation and long surface recovery periods. Recovery is more rapid if dives are entirely aerobic; short recovery time increases the proportion of total foraging time that can be spent submerged (Kooyman 1989). Therefore, maximum possible dive duration may be less important than maximum aerobic dive duration, or aerobic dive limit (ADL; Kooyman 1989).

ADL is a function of oxygen stores and rates of oxygen consumption while diving. We calculated oxygen stores following the assumptions of Stephenson et al. (1989) and Croll et al. (1992*a*), using our values of blood volume and hematocrit and published data on myoglobin and hemoglobin concentrations (Kooyman 1989). The mean mass of TDR birds was 3.79 kg, yielding a predicted respiratory tract volume of 541 mL and muscle mass of 1.32 kg. Oxygen stores are 194 mL for a 3.79-kg bird, or 51.2 mL/kg. About 25% of available oxygen is stored in muscle myoglobin, 37% in the respiratory tract, and 38% in blood.

Several methods have been used to calculate diving metabolic rate. Nagy et al. (1984), using doubly labeled water (DLW) and time budgeting, estimated swimming metabolism of African penguins (*Spheniscus demersus*) to be 8–9 × basal metabolic rate (BMR). Our DLW studies of Adélies predict a swimming cost of 8.2 × BMR (M. A. Chappell et al., *unpublished data*). DLW measurements include the energy cost of food utilization (specific dynamic action, or SDA). SDA can account for 25–30% of assimilated energy in a high-protein diet like that of Adélies (Harper 1979). Assuming that SDA does not occur during exercise, the DLW estimates of 8.2 × BMR indicate a swimming cost closer to 6 × BMR, or 67 $mL \cdot min^{-1} \cdot kg^{-1}$. Culik and Wilson (1991) measured oxygen consumption of Adélies swimming in an enclosed canal; their estimate of swimming metabolism was ≈4 × BMR (45 $mL \cdot min^{-1} \cdot kg^{-1}$) at the preferred swimming speed.

Using these values we calculate an ADL of 46 s and 68 s if swimming metabolism is 6 × BMR and 4 × BMR, respectively. The durations of most hunting dives exceed these limits (Fig. 5); mean hunting dive duration (73 s) was 1.07 to 1.6 × ADL. Nevertheless, surface intervals were relatively brief, averaging ≈50% of dive duration during hunting bouts (Fig. 7B). This is similar to the surface interval : dive duration ratio for aerobic dives in Thick-billed Murres (Croll et al. 1992*a*), but somewhat greater than that of Weddell Seals (Kooyman et al. 1980). In both of the latter species the recovery period from long anaerobic dives is longer than dive duration.

It is difficult to understand how Adélies tolerate the prolonged periods of continuous diving typical of foraging bouts (e.g., Fig. 1C) if many dives exceed ADL (Kooyman et al. 1992*a*). Croll et al. (1992*a*) encountered a similar paradox in their study of Thick-billed Murres. They considered several possible explanations which are also germane to Adélies: (1) Oxygen stores are greater than estimated. This is unlikely because unrealistically large increases in some or all of the oxygen storage parameters would be required to produce the necessary increase in ADL. (2) Metabolic rate during diving is considerably lower than estimated. This seems unlikely because our estimates are based on two different and independent measurement techniques. Assuming the ADL is 95 s (which would include ≈90% of hunting dives), metabolic rate during diving would have to be no more than 2.9 × BMR. This is less than the metabolic rate of 3.4 × BMR necessary for swimming at 0.7 m/s (less than the average ROD and ROA) and only slightly larger than the metabolic rate of Adélies resting in cold water (2.2 × BMR; Culik and Wilson 1991). Power requirements may be reduced during bottom time since the birds are not rapidly changing depth. However, Adélies must expend energy to overcome positive buoyancy (especially at shallow depths) and probably need to swim actively to pursue prey. (3) Many dives exceed ADL, but the resulting lactate is metabolized and oxygen stores are replenished during surface intervals. Laboratory studies of recovery times from anaerobic dives in several bird species suggest this is unlikely (Eliassen 1960), but there are no data on lactate recovery rates in penguins. (4) Birds continue to dive with a lactate load; they must eventually stop diving to metabolize accumulated lactate. Croll et al. (1992*a*) considered this to be the most likely explanation for Thick-billed Murres and other divers that feed on patchily distributed and ephemeral prey. Ydenberg and Clark (1989) proposed an optimal foraging model for Western Grebes (*Aechmophorus occidentalis*) based on similar assumptions.

Adélies appear to fit Ydenberg and Clark's assumptions about prey distributions, but many foraging bouts are so long that lactate accumulation per dive would have to be very small. For example, one Adélie foraged continuously for almost 6 h (210 hunting dives to varying depths); during this time the mean dive duration was 76 ± 11 s (range 45–110 s) and the mean surface

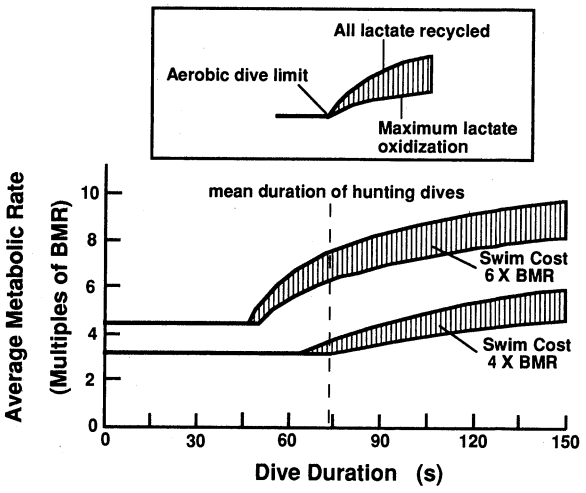

FIG. 8. Predicted energy costs of anaerobic diving at different dive durations for Adélie Penguins. Data are calculated for two metabolic costs of swimming (4 and 6 times BMR). Hatched areas are the range of costs possible between two extremes of lactate recycling: all lactate recycled to glucose (upper lines) or as much lactate as possible oxidized during the aerobic portions of the dive cycle (lower lines). See *Discussion: Dive duration, aerobic dive limits, and energy costs of anaerobic diving* for explanation.

interval was 26 ± 8 s. Most dive durations exceeded even the lower of the two calculated ADL values. This was the longest period of continuous hunting dives we recorded, but many foraging bouts lasted 1–2 h and several exceeded 3 h.

Based on these observations, we tentatively conclude that Adélies are able to eliminate lactate loads during surface intervals and the aerobic portions of dives. Lactate sampling from freely diving birds will be necessary to resolve the question, but it is interesting to estimate the potential energy cost of lactate recycling. Anaerobic glycolysis yields 1 ATP per lactate produced from glucose; 3 ATP per lactate are needed for gluconeogenesis. Therefore anaerobiosis is energetically expensive, as penguins must generate 3 ATP during the aerobic phase for every one used during the anaerobic phase. Moreover, lactate recycling must be performed during the surface interval or the accompanying increase in oxygen consumption will shorten ADL. The energy penalty of gluconeogenesis is reduced if lactate is oxidized as a substrate in the aerobic phase (Kooyman 1989), but this option is limited because for a given rate of ATP utilization the rate of aerobic lactate consumption is only 1/15 the rate of anaerobic lactate production. Moreover, aerobic combustion of lactate will cause a loss of stored carbohydrate (glycogen and blood glucose), and Adélie diets contain little if any carbohydrate.

Working under the assumption that all lactate produced in the anaerobic phase of a dive is eliminated during the aerobic phase, we calculated energy cost of gluconeogenesis at varying dive durations and swimming power requirements under two scenarios: (1) birds preferentially use lactate as a substrate during the aerobic phase, or (2) birds recycle all lactate into glucose. We also calculated mean aerobic metabolic rates averaged across the dive cycle (i.e., the mean of the costs of aerobic swimming, basal metabolism during the surface interval, and gluconeogenesis). Extensive use of anaerobiosis substantially increases energy costs (Fig. 8). For example, using the mean hunting dive duration of 73 s, the regression-derived surface interval of 35 s, and a swimming power requirement of 6 × BMR (67 $mL \cdot min^{-1} \cdot kg^{-1}$), we calculate a mean aerobic metabolic rate of 7.3 × BMR if all lactate is recycled and 6.0 × BMR if as much lactate as possible is oxidized. Metabolic rates during surface intervals will reach 10.6–14.6 × BMR; most of this ATP production is used to

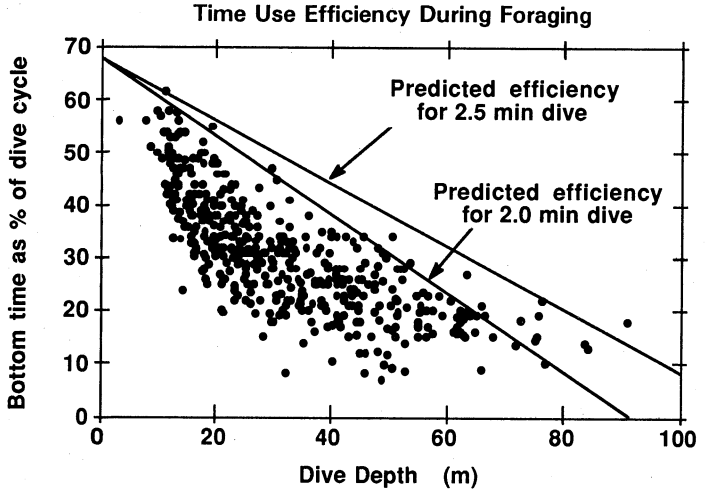

FIG. 9. Efficiency of time use during 455 hunting dive bouts by Adélie Penguins near Palmer Station, Antarctica. See *Discussion: Time-related foraging efficiency* for details.

support lactate recycling. Oxygen uptake rates will be even higher since the birds must simultaneously power gluconeogenesis and replace depleted oxygen stores in myoglobin and hemoglobin. This compares to a mean metabolic rate of 4.4 × BMR if dives are entirely aerobic. The energy penalty of gluconeogenesis will be even larger if dive duration or the metabolic cost of swimming is greater. Costs of anaerobiosis are lower if swimming metabolism is 4 × BMR, but are still substantial for dives exceeding 80–90 s (Fig. 8).

Time-related foraging efficiency.—Foraging efficiency in breath-hold divers has been defined in terms of time budgeting as bottom time over dive cycle time: $T_b/(T_b + T_t + T_s)$, where T_b is bottom time, T_t is transit time (descent and ascent), and T_s is the surface recovery time (Ydenberg and Clark 1989, Croll et al. 1992*a*). In Adélies, T_t is a linear function of depth and T_s is a linear function of dive duration (Fig. 7B). Foraging efficiency declines as depth increases because of the increase in T_t, but at any depth efficiency is highest if bottom time and duration are maximized. Accordingly, durations for shallow and deep hunting dives should be similar. Adélies do not fit this prediction (Figs. 5A, 7A). We calculated the theoretical efficiency of 2.0- and 2.5-min dives to depths from 0–100 m, using ROD and ROA of 1.5 m/s and surface intervals of 0.98 min for 2.0 min dives and 1.23 min for 2.5 min dives (Fig. 7B). These predictions are compared to actual foraging efficiencies for 455 dive bouts in Fig. 9. Actual efficiency was usually considerably less than predicted; agreement between actual and predicted efficiency was greatest for the shallowest and deepest dives.

Several nonexclusive explanations for low time use efficiency include: (1) At shallow and intermediate depths Adélies keep dive duration short in order to reduce lactate buildup. This reduces the energy cost of diving (because it minimizes costly gluconeogenesis), even though time use efficiency is reduced. (2) Bottom time is determined not by depth but by the number of prey captured per dive; the birds must surface for prey handling after a certain number of prey are caught. This is unlikely because Adélies swallow prey underwater. (3) Adélies keep dive duration short in order to minimize surface intervals, thereby reducing the time between leaving the prey school and returning to it. This would increase the probability of relocating mobile prey on successive dives. (4) Although euphausid schools are widely scattered and patchily distributed, they may be extremely dense (>1000 animals/m^3; R. Ross, *personal communication*). Once Adélies locate such patches, the gain rate may be so high that selection to maximize foraging efficiency is weak.

The foraging ecology of Adélie Penguins appears to be quite plastic, particularly the depths used for feeding. Some variability may derive from competition (Trivelpiece et al. 1987) or from different environmental characteristics (e.g., prey species or prey depth distributions) across the species' circumpolar range. Maximum dive depth differed considerably in three studies in different localities, ranging from 26 m (Lutzow-Holm Bay; Naito et al. 1990), to 98 m (this study), to 175 m (Prydz Bay; Whitehead 1989). Adélies apparently find most of their food in large but patchily distributed aggregations. A remarkable ability to sustain repeated diving for long periods, even though most hunting dives seem to require some anaerobiosis, assists Adélies in exploiting such patches once they are located. Reliance on anaerobiosis will increase energy costs during foraging. It may also influence the birds' time budgeting and selection of foraging depths, since the need for anaerobiosis increases with increasing dive duration. Near Palmer Station, most foraging is at depths between 10 and 40 m, considerably shallower than the maximum depths attained by Adélies. The restricted depth range probably reflects both depth-related physiological constraints to foraging efficiency and the depth distribution of the Adélie's euphausid prey.

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APPENDIX

Characteristics of foraging trips for 20 Adélie Penguins recaptured before feeding chicks.

Bird	Sex	Phase*	No. dives ≥3 m	No. hunting dives	Elapsed time (h)	Time in water (h)	Hunt dive time (h)	Bottom time (h)	Mass (kg)	
									Start	End
30	M	Guard	549	427	33.8	10.5	7.3	1.9	3.76	3.99
75	M	Guard	1014	242	45.8	16.3	4.3	3.0	4.24	4.25
87	F	Guard	451	206	42.5	13.0	4.4	2.0	3.94	4.32
144	M	Guard	903	205	33.7	17.5	4.7	2.3	4.14	4.60
145	F	Guard	852	416	37.4	17.5	7.7	3.2	3.18	3.77
154	F	Guard	529	59	28.0	6.0	1.1	1.0	3.56	3.78
232	F	Guard	1972	565	95.8	31.8	10.9	4.4	3.28	3.94
296	F	Guard	1224	360	59.9	19.0	7.7	3.4	3.72	4.18
310	M	Guard	313	163	53.0	7.5	2.8	0.8	4.21	4.32
23	F	Creche	627	333	51.1	20.0	8.4	3.9	3.94	4.71
68	F	Creche	625	153	39.9	10.8	2.8	1.7	3.84	3.75
69	M	Creche	587	260	39.7	12.8	5.6	3.1	3.94	3.95
70	M	Creche	547	170	25.4	9.0	3.6	1.4	3.44	3.96
197	M	Creche	623	160	71.1	14.5	3.0	2.0	3.67	4.50
203	M	Creche	819	390	56.1	21.0	9.3	2.9	3.98	4.50
215	M	Creche	321	94	32.4	7.7	1.4	0.8	3.63	4.14
216	F	Creche	541	236	22.0	14.2	5.8	2.2	3.56	3.99
261	F	Creche	982	300	45.5	12.4	6.4	2.3	4.23	4.28
351	F	Creche	390	176	27.0	8.3	3.3	1.4	3.80	4.22
464	F	Creche	1066	594	46.1	14.0	11.8	2.6	4.10	4.30

* Guard phase: ≥1 parent brooding or guarding small chicks; creche phase: large chicks left unattended.