FORAGING GROUP SIZE AND DIVE DURATION OF ADÉLIE PENGUINS *PYGOSCELIS ADELIAE*AT SEA OFF HOP ISLAND, RAUER GROUP, EAST ANTARCTICA

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SUMMARY

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Adélie Penguins Pygoscelis adeliae were observed off Hop Island, Rauer Group, East Antarctica, during the 1990/91 summer. Group sizes were established, and birds classified into those showing feeding or travelling behaviours. Most (71.3%) of the 797 groups recorded were of one to three birds (38.7%) of the 2460 recorded) and only 2.8% of the groups exceeded 10 penguins. Group sizes of those feeding (x = 2.0) were significantly smaller than those not foraging (x = 5.5). There were significant differences between group sizes throughout the day, and throughout the study period which extended from late incubation into late guard stages. Some 69.4% of the groups (45.6%) of the birds were considered to be foraging, but the proportion feeding showed significant variation with date rather than time of day. Recorded dive durations varied considerably, with some birds apparently foraging underwater for over 350 s, although most dives (90%) were for 230 s or less. There were differences in dive duration with time of day, those near midnight being longer, but the recorded duration of a first dive was not correlated with that of the subsequent one. Data are compared with information on group size and dive duration in other penguins. There appears to be no current evidence of cooperative feeding in large groups, indeed foraging singly or in small numbers is routine and may reduce exposure to predators. Dive durations recorded here are extensive, but within predicted anaerobic capabilities.

INTRODUCTION

Adélie Penguins Pygoscelis adeliae are a dominant component of the avian biomass in Prydz Bay, East Antarctica (Montague 1988), and some 325 000 pairs breed in and around it (Whitehead & Johnstone 1990). In this area, Adélie Penguins feed predominantly on pelagic shoaling krill (both neritic Euphausia crystallorophias and the more oceanic E. superba) and the schooling fish Pleuragramma antarcticum. Although relative proportions may vary from season to season, the fish and E. superba

become more important as food later in chick-rearing (Green & Johnstone 1988, Puddicombe & Johnstone 1988). In Prydz Bay, egg-laying starts in early to mid-November, hatching occurs in mid-December and crèches begin forming in early January. Fledgling departure from natal colonies starts in early February (Puddicombe & Johnstone 1988). Whereas Adélie Penguins may forage widely during incubation, such movement in the chick-rearing stage is more restricted (Davis et al. 1988, Sadlier & Lay 1990) and foraging trips last <1 day (Wilson et al. 1989).

Despite the abundance of Adélie Penguins in Prydz Bay, and the attention paid to aspects of their feeding ecology there, little is known of their activities at sea. Here we provide some details of foraging in the species obtained during the 1990/91 austral summer off Hop Island (68 49S, 77 44E), in the Rauer Group, Princess Elizabeth Land, East Antarctica.

METHODS

During visits to Hop Island made between 23 December 1990 and 31 January 1991, counts of groups of Adélie Penguins were made off the northern coast. in an area $(c. 0.48 \text{ km}^2)$ encompassed by local (unnamed) islets and the island's coast. These counts, made at some distance from breeding colonies, were taken from observation sites some 20-30 m above the sea, and for 15 min every hour for five separate 24-h periods except when abandoned because of inclement weather or the invasion of pack-ice into the survey area. In total, 102 such 15-min observations were made and penguins recorded in 98. Once group size (scored on first sighting, as individual birds or as a number of penguins acting cohesively, and usually showing similar behaviours, Wilson & Wilson 1990) was established, each group was classified as feeding (diving within a localized area) or travelling (moving through the observation area, generally by rapid porpoising, but also associated with occasional bouts of swimming, in a constant direction). Water clarity, and the height of count sites above the sea surface, materially aided observers in maintaining visual separation of the relatively small numbers of individual groups in the study area at any one time. Penguins which moved onto or off the often numerous pack-ice floes were not included in the summaries below. The study area was continuously scanned (using binoculars) for the occurrence of newly-arriving penguins. Whenever individual penguins were observed well isolated from other penguins, attempts were made to establish dive durations for birds considered to be foraging. Dive times were recorded when practicable using stopwatches (to 0.1 s) and occasionally (almost invariably for an individual, isolated from other penguins) it was possible to determine the duration of the subsequent dive, although this was frequently confounded by the loss of the bird into pack-ice or its incorporation into other groups moving about the study area. Timing of dives for such birds was abandoned. In consequence, there may be an unknown bias against longer dive durations. Water depths off Hop Island are unknown, but are likely to exceed 100 m as the result of previous periglacial activity.

Breeding colonies of Adélie Penguins nearest to the study area were about 0.6 km away, on Hop Island (where some 43 000 pairs nest, Whitehead & Johnstone 1990) or 2.9 km, at Filla Island (68 50S, 77 50E; 15 000 pairs) to the east. observed in the study area were considered to be moving to or from breeding sites, or foraging there, and were not influenced by activities associated with leaving or entering colonies. It was not possible to determine the eventual destination of travelling groups. During this study, Adélie Penguin eggs on Hop Island hatched from mid-December onwards. No first-year birds were seen at sea and, although the crèche stage was reached by mid-January, no fledglings had left natal colonies at Hop Island by the end of observations. Whereas daylight was continuous for much of the study, variation in light flux is extensive for colonies at latitudes similar to that studied here (Müller-Schwarze 1968). For the purpose of examining group size and number in relation to time of day, local solar midnight was calculated as 01h48 local time (local times are used in summaries below).

RESULTS

Adélie Penguins primarily used the study area for foraging or for travel between breeding colonies and more distant feeding areas. Bathing, preening and moving onto or off ice floes used as rest sites were also observed, but infrequently. Porpoising was the main method of travel through the study area although some groups moved extensively by shallow, subsurface swimming interspersed by

periods at the surface. Few birds swam on the surface for extended periods except undertaking comfort activities or moving near ice floes. Porpoising was directed and purposeful, and obviously not only restricted to movement near breeding areas (cf. Trivelpiece et al. 1986). In this study, as in others, independence of group size data in consecutive observation periods has been assumed. We believe that this is justified since the study area was close to (but not adjacent to) breeding colonies, and foraging trip durations and ranges are extensive in Adélie Penguins during breeding (e.g. Sadlier & Lay 1990). Since most birds observed would have been involved in local breeding activities, they were probably moving to more distant feeding grounds, or feeding and returning to colonies. Furthermore, the study area on occasion held no birds, and at other times, groups moved directly through the area.

Group size

In this study 797 groups of penguins were counted in 98 (of 102), 15-min observation periods. Mean group size was 3.09 (\pm 3.01 s.d., range 1-26) and the median was two for the 2 460 penguins involved. More than 37% of the groups were of solitary penguins (i.e. 12.1% of the total birds) and 38.7% of penguins were recorded in groups of less than four birds (Fig. 1). Fitting a non-linear regression to group size data (following Wilson et al. 1986) gave $y = 462.54 e^{-0.476 x}$, where y = numbers of groups and x = group size ($r^2 = 0.993$).

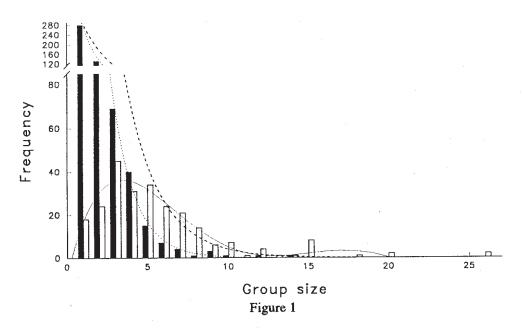
Of the groups categorized during the study, 553 (69.4%; including 45.6% of the penguins) were considered to be actively seeking food. The mean group size for those foraging, 2.02 (\pm 1.5, 1-14, median 1) was significantly smaller (Kruskal - Wallis test, X^2 , df 1, = 264.4, P = 0.0001) than those groups considered to be travelling through the area (5.5 \pm 4.0, 1-26, median 5). Non-linear regressions applied to feeding ($y = 565.90 \ e^{-0.709 \ x}$) and travelling ($y = 39.581 \ e^{-0.128x}$) groups described the relationship between group size and

numbers of groups well $(r^2 = 0.999 \text{ and } 0.817,$ respectively); a multiple linear regression (y = -8.14 $+ 31.6x - 7.4x^2 + 0.65x^3 - 0.025x^4 + 0.00035x^5$ improved the relationship for travelling groups $(r^2 = 0.939)$. The proportion of birds considered foraging decreased with increased group size (Fig. 1). An analysis was performed to estimate the probability (p) of a group of size x being a travelling, rather than a foraging, group. logistic regression, where logit p (the estimated logit of the probability of birds belonging to a travelling, rather than a foraging, group) = -2.8755 + 0.6527x(where the estimated probability $p = e^{-\log it(p)}/(1+e^{-\log it(p)})$ $\log_{\log(p)}$) was highly significant (X^2 tests of parameter estimates, P = 0.0001) and had a concordance value of 80%, further emphasizing the increased group size in travelling birds. Of the 109 groups including >5 penguins, 92 (84.4%) were considered to be moving through the study area rather than foraging there. Occasionally, large (>10 birds) groups of penguins were observed (2.8% of those recorded); many of these dispersed into smaller foraging groups.

Group sizes tended to increase with numbers of birds in the study area. Thus for the 98 sessions when penguins were present, group size was significantly related to the total counted (r = 0.687, P = <0.0001); this relationship was similar for groups travelling (r = 0.739) or foraging (r = 0.735, both P = <0.0001).

Seasonal and diel cycles

Mean group size showed significant differences between each observation period (Kolmogorov-Smirnov, P << 0.01), whether considered for all groups (KS = 0.1347, n = 797 groups), or as foraging (KS = 0.1642, n = 553) or travelling (KS = 0.21227, n = 244) groups. Further, group sizes (and indeed numbers of groups and penguins), recorded prior to the crèche stage (i.e. up to 10 January) were significantly larger whether feeding (Wilcoxon's 2-sample test, Z = 6.0879, n = 383 and 170, P = 0.0001) or travelling (Z = -5.3221, n = 176, 68, Z = 0.0001), or as combined totals (Z = 0.0001)



Numbers of Adélie Penguins recorded in groups of various sizes off Hop Island, Rauer Group, East Antarctica. Solid bars indicate feeding groups; open bars, travelling groups. Regression lines are for all birds (- - -), for feeding groups (...), and for travelling groups (---).

= -6.6241, n = 559, 238, P = 0.0001) than those recorded subsequently. For all groups, mean size was 3.51 (\pm 3.35, n = 559) before, and 2.08 (\pm 1.57, n = 238) during, the crèche stage. For feeding groups, mean size decreased from 2.27 (\pm 1.73, n = 383) to 1.47 (\pm 0.81, n = 170), and in the non-foraging groups, sizes decreased from 6.21 (\pm 4.31, n = 176) to 3.60 (\pm 1.95, n = 68).

There were also diel cycles apparent in the numbers of penguins and the sizes of groups recorded in the study area (Table 1, Fig. 2). Fewer penguins were active around local midnight and early morning, and three (of four) observation periods in which no penguins were seen were between 00h00 and 04h47. Generally, groups (and numbers of penguins) observed 3 h before or after local midnight were smaller than those seen during the remainder of the day (Table 1, Fig. 2). Foraging and travelling groups were larger in late afternoon and evening, and there were significant differences (P < 0.01) in both sets of group sizes (Kolmogorov-Smirnov, KS = 0.1775, all groups; KS = 0.1972, feeding groups; KS = 0.2808, travelling groups) with time.

Separation of groups, and of group sizes, into hourly counts for the study period further emphasized the decrease in numbers of groups and their average size from around 23h00 to 06h00 (Table 1, Fig. 2).

Whereas the proportion of groups considered to be feeding showed no significant difference between 6-h totals based around midnight (X^2 , df 3, = 6.332, P > 0.05), there was a significant variation with date of observation (X^2 , df 13, = 42.726, P < 0.0001), with increased feeding in late December observations.

Dive duration

During this study 130 dives, with a mean duration of 120.8 ± 85.3 s (range 5.7-354.0 s) and a median of 100.7 s, were recorded (Table 2). However, recorded durations were not normally distributed (Shapiro-Wilk test, W = 0.9131, P = 0.0001). Of the dives, 20% were up to 40 s long, 50% were less than 100 s, and 90% were for 230 s or less. Removal of those dives <60 s long (i.e. 41, 31.5% of total dives; considered as travelling dives by some

TABLE 1

SUMMARIES OF NUMBERS OF FEEDING AND TRAVELLING GROUPS AND GROUP SIZES OF ADÉLIE PENGUINS, FOR HOURLY AND 6-H PERIODS (BASED AROUND LOCAL MIDNIGHT, 01H48), HOP ISLAND, RAUER GROUP, DECEMBER 1990 - JANUARY 1991

| Time | No. of observa- | | Foraging groups | | | Travelling groups | | | | All groups | | |
|-----------|-----------------|------------|-----------------|----------|-------|-------------------|------|----------|--------|------------|--------------|-------|
| | vatio | ons n | mean | (± s.d.) | range | n | mean | (± s.d.) | range | n | mean(± s.d.) | range |
| 2248-2347 | 2 | 20 | 1.5 | (0.69) | 1 - 3 | 4 | 5.0 | (3.56) | 2 - 10 | 24 | 2.08 (1.95) | 1 -10 |
| 2348-0047 | 3 | 23 | 1.3 | (0.54) | 1 - 3 | 5 | 3.0 | (1.87) | 1 - 6 | 28 | 1.57 (1.10) | 1 - 6 |
| 0048-0147 | 3 | 4 | 1.0 | | 1 | 1 | 2.0 | , , | 2 | 5 | 1.20 (0.45) | 1 - 2 |
| 0148-0247 | 2 | 7 | 1.1 | (0.38) | 1 - 2 | 2 | 3.5 | (0.71) | 3 - 4 | 9 | 1.67 (1.12) | 1 - 4 |
| 0248-0347 | 2 | 6 | 1.0 | | 1 | 1 | 3.0 | | 3 | 7 | 1.28 (0.75) | 1 - 3 |
| 0348-0447 | 2 | 9 | 1.1 | (0.33) | 1 - 2 | 5 | 4.2 | (1.64) | 3 - 7 | 14 | 2.21 (1.80) | 1 - 7 |
| 2248-0447 | 7 14 | 69 | 1.3 | (0.53) | 1 - 3 | 18 | 3.7 | (2.13) | 1 -10 | 87 | 1.78 (1.47) | 1 -10 |
| 0448-0547 | | | | | | | | | | | | |
| 0548-0647 | 4 | 8 | 1.2 | (0.46) | 1 - 2 | 1 | 2.0 | | 2 | 9 | 1.33 (0.50) | 1 - 2 |
| 0648-0747 | 3 | 15 | 1.6 | (0.98) | 1 - 4 | 4 | 2.7 | (0.50) | 2 - 3 | 19 | 1.84 (1.55) | 1 - 7 |
| 0748-0847 | 6 | 31 | 1.8 | (0.98) | 1 - 4 | 8 | 4.1 | (2.03) | 1 - 7 | 39 | 2.28 (1.55) | 1 - 7 |
| 0848-0947 | 5 | 10 | 1.9 | (0.99) | 1 - 4 | 6 | 3.0 | (1.09) | 2 - 5 | . 16 | 2.31 (1.14) | 1 - 5 |
| 0948-1047 | 4 | 14 | 1.7 | (0.85) | 1 - 3 | 9 | 3.1 | (1.27) | 1 - 5 | 23 | 2.17 (1.27) | 1 - 5 |
| 0448-1047 | 7 22 | 78 | 1.7 | (0.91) | 1 - 4 | 28 | 3.3 | (1.46) | 1 - 7 | 106 | 2.10 (1.29) | 1 - 7 |
| 1048-1147 | | 26 | 2.5 | (1.45) | 1 - 5 | 10 | 3.5 | (1.18) | 2 - 5 | 36 | 2.80 (1.43) | 1 - 5 |
| 1148-1247 | 5 | 31 | 2.6 | (1.96) | 1 - 9 | 17 | 4.8 | (3.33) | 1 -12 | 48 | 3.37 (2.70) | 1 -12 |
| 1248-1347 | 8 | 50 | 2.2 | (1.70) | 1 - 9 | 11 | 5.8 | (1.78) | 3 - 8 | 61 | 2.85 (2.20) | 1 - 9 |
| 1348-1447 | _ | 5 9 | 2.5 | (2.42) | 1 -14 | 19 | 4.7 | (3.16) | 1 -15 | 78 | 3.01 (2.77) | 1 -15 |
| 1448-1547 | 5 | 23 | 2.1 | (1.69) | 1 - 8 | 30 | 5.5 | (3.80) | 1 -10 | 53 | 4.01 (3.47) | 1 -18 |
| 1548-1647 | 4 | 21 | 2.2 | (2.19) | 1 -10 | 13 | 5.5 | (4.54) | 1 -15 | 34 | 3.47 (3.59) | 1 -15 |
| 1048-1647 | 7 34 | 210 | 2.4 | (1.97) | 1 -14 | 100 | 5.0 | (3.35) | 1 -18 | 310 | 3.23 (2.79) | 1 -18 |
| 1648-1747 | 3 | 19 | 2.5 | (1.71) | 1 - 7 | 13 | 7.7 | (4.38) | 2 -20 | 32 | 4.59 (4.00) | 1 -20 |
| 1748-1847 | 7 | 45 | 2.0 | (1.13) | 1 - 5 | 27 | 6.7 | (4.59) | 1 -20 | 72 | 3.75 (3.70) | 1 -20 |
| 1848-1947 | 7 | 48 | 2.4 | (1.74) | 1 - 9 | 26 | 7.2 | (3.02) | 2 -14 | 74 | 4.08 (3.25) | 1 -14 |
| 1948-2047 | 8 | 54 | 2.0 | (1.11) | 1 - 5 | 19 | 8.4 | (7.14) | 3 -26 | 73 | 3.64 (4.65) | 1 -26 |
| 2048-2147 | 3 | 19 | 1.4 | (0.77) | 1 - 3 | 10 | 3.5 | (2.88) | 1 - 9 | 29 | 2.14 (2.01) | 1 - 9 |
| 2148-2247 | 4 | 11 | 1.9 | (1.44) | 1 - 5 | 3 | 3.7 | (1.15) | 3 - 5 | 14 | 2.28 (1.54) | 1 - 5 |
| 1648-2247 | 7 32 | 196 | 2.1 | (1.37) | 1 - 9 | 98 | 6.9 | (4.77) | 1 - 2 | 294 | 3.67 (3.73) | 1 -26 |

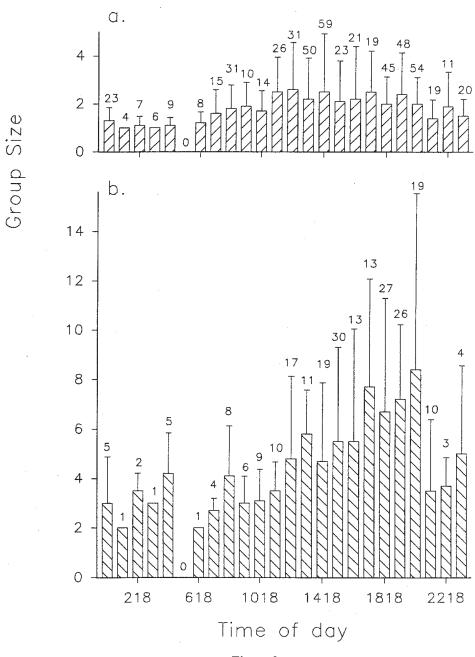


Figure 2

Mean group size in foraging (a) and travelling (b) Adélie Penguins off Hop Island, in relation to time of day.

Numbers of observations are indicated, as are standard deviations.

TABLE 2

DIVE DURATIONS RECORDED FOR ADELIE PENGUINS OFF HOP ISLAND, RAUER GROUP,
DECEMBER 1990-FEBRUARY 1991

| Duration | Frequency | Cumulative frequency (%) | | |
|------------|-----------|--------------------------|--|--|
| (s) | | | | |
| < 10 | 6 | 4.6 | | |
| 10+ - 20 | 5 | 8.5 | | |
| 20+ - 30 | 6 | 13.1 | | |
| 30+ - 40 | 10 | 20.8 | | |
| 40+ - 50 | 4 | 23.8 | | |
| 50+ - 60 | 12 | 33.1 | | |
| 60+ - 70 | 7 | 38.5 | | |
| 70+ - 80 | 7 | 43.8 | | |
| 80+ - 90 | 6 | 48.5 | | |
| 90+ -100 | 3 | 50.8 | | |
| 100+ -110 | 3 | 53.1 | | |
| 110+ -120 | 6 | 57.7 | | |
| 120 + -130 | 6 | 62.3 | | |
| 130+ -140 | 3 | 64.6 | | |
| 140+ -150 | 2 | 66.2 | | |
| 150+ -160 | 3 | 68.5 | | |
| 160+ -170 | 4 | 71.5 | | |
| 170+ -180 | 4 | 74.6 | | |
| 180+ -190 | 4 | 77.7 | | |
| 190+ | 29 | 100.0 | | |

authors, e.g. Davis *et al.* 1988, Wilson *et al.* 1991) increases mean duration (to 160.3 ± 74.5 s (range 60-354 s, n=89) and median score (151.6 s) substantially.

Dive duration, when grouped into four periods of 6 h centred around local midnight, showed a significant variation with time of day (Kruskal - Wallis, $X^2 = 9.682$, df 3, P = 0.0231) and those between 22h48 and 04h47 were longer (173.5 \pm 89.4 s, n = 15) than others; those recorded from 16h48 to 22h47 (109.8 \pm 86.8 s, n = 68) being shorter. There was no apparent change in dive duration in relation to date (Kruskall -

Wallis), although dives recorded after the crèche stage tended to be longer than those before $(112.2 \pm 86.1 \text{ s}, n = 89 \text{ compared with } 139.4 \pm 81.6 \text{ s}, n = 41).$

On 18 occasions, consecutive dive durations were recorded; however, the correlation between first and second dives was very weak $(r_s = -0.009)$ and insignificant.

DISCUSSION

Although Adélie Penguins travelled together in the study area, in groups of up to 26 birds, they

generally foraged in significantly smaller groups, usually of one to three birds. Similar-sized foraging groups have been reported in Jackass Spheniscus demersus (Broni 1985, Wilson et al. 1986, Wilson et al. 1988), Humboldt S. humboldti (Duffy 1983, Wilson & Wilson 1990) and Little Eudyptula minor Penguins (during both breeding and non-breeding periods, Norman 1992). In Spheniscus penguins, such as the Jackass Penguin, individuals in these small foraging groups show synchrony in both diving and emergence, and it is suggested that this synchrony enhances foraging success (Siegfried et al. 1975, Wilson et al. 1986, Wilson & Wilson Synchrony is also evident in Adélie 1990). Penguins, and Ainley (1972) showed that this is facilitated by both visual and auditory signals; group cohesion and visual cues themselves may also enhance foraging success in Adélie Penguins.

Groups of Adélie Penguins in this study were small, whether foraging or travelling, and changed both with time of day (decreasing around midnight) and as the breeding period progressed. Social aspects of foraging, involving large groups, appear to have been overemphasized since most reported foraging group sizes involve small numbers of penguins. Small groups of penguins may be better able to dive synchronously and maintain flock cohesion (Wilson et al. 1986). Members of small groups of penguins may operate more successfully than those in larger groups if prey occurs in small patches, but birds are unlikely to achieve increased success when preying on large prey patches unless they scatter them into smaller aggregations, as do Blackheaded Gulls Larus ridibundus (Götmark et al. 1986). There is. however, no current evidence of cooperative feeding in penguins (Croxall & Lishman 1987, but see Ryan et al. 1987) and Wilson & Wilson (1990) suggested that the small flock size in foraging Spheniscus species may be determined by 'invariant phenomena' (such as improved swimming hydrodynamics) rather than enhanced communal feeding success. In this regard, foraging Adélie Penguins, operating alone or in small groups, are less likely to attract their major predator, Leopard Seals Hydrurga leptonyx, than those foraging in large groups. This may also be the case for other penguins whose predators, like Leopard Seals (Penney & Lowry 1967), may concentrate around breeding colonies where birds move continually into and out of the water. Single penguins, or penguins in small groups, operating away from colonies may be advantaged in the absence of alternative predators (cf. Hamilton 1971).

Group sizes varied both during the day and throughout the study period, which encompassed late incubation and chick-rearing stages: they were also influenced by numbers of birds in the study Activity, as reflected in group sizes (and numbers of Adélie Penguins), showed decreases around local midnight. Whereas Penney & Lowry (1967) found no obvious diurnal rhythm during the guard and crèche stages, others (Müller-Schwarze 1968, Naito et al. 1990) have noted peaks of activity around breeding colonies and, although variable, there is an apparent underlying rhythm (Cockrem 1990) with numbers of birds at sea being related to light intensity (Wilson et al. 1989). Indeed, Davis & Miller (1992) considered that (instrumented) penguins were most likely to be on ice floes during the evening, and showed that the study birds were "nearly always" in the water between 06h30 and 14h30. Off Hop Island the proportion of foraging penguins varied during the study, apparently influenced by the stage of the breeding cycle. Group sizes recorded early in the study were larger than those recorded later, perhaps reflecting both the increase in numbers of birds foraging and the increased foraging trip frequency (and decreased range) which follow hatching (Trivelpiece et al. 1986, Davis et al. 1988, Sadlier & Lay 1990).

Foraging dives are deeper, and last longer, than those associated with travelling (Wilson et al. 1991). Dive duration times reported here, for individual (and non-instrumented) birds, are extensive, and mean values (c. 121 s) are higher than previously reported. Using radio-telemetry or time-depth recorders, Davis et al. (1988) found a mean of 92.5 s for all dives (\pm 45.1 s, maximum 182), and 114.9 \pm 29.7 s for feeding dives; Naito et al. (1990) considered that most dives were 1 - 2 min

long, and those exceeding 3 min were rare (although they noted one of 4.5 min). Such data, from birds carrying attached devices, may be seriously compromised (e.g. Wilson 1989). Differences between species in dive duration, frequency and depth have been related to prey types, with fisheating species diving deeper and for longer than those taking krill (e.g. Davis et al. 1988, Bost & Jouventin 1990). However, Whitehead (1989) and Wilson et al. (1991) showed that Adélie Penguins (which eat both fish and krill, e.g. Puddicombe & Johnstone 1988) can dive deeper than depths recorded for either Chinstrap P. antarctica or Gentoo Penguins P. papua. **Baldwin** (1988) considered that, physiologically, Adélie Penguins could exceed the diving capacity of Gentoo Penguins, and Kooyman (1975) reported survival of Adélie Penguins following enforced dives of up to 6 min.

But prey characteristics must influence foraging behaviour, including dive depth and duration. Whitehead (1989), in measuring mean maximum diving depths in Adélie Penguins (over 150 m), showed a decrease during the crèche stage, coincident with a change in major food types (from mainly amphipods and Euphausia crystallorophias, to an increased importance of E. superba and Pleuragramma antarcticum; Whitehead 1991). Why the change in food type may be associated with decreases in depth of diving is unclear. superba shows diel migration, or dispersal at night, and forms dense swarms during the day (Everson 1982, Croxall & Davis 1990), then this may promote increased dive depth (and duration) during the day and reduced depths at 'night' (Croxall & Davis 1990), contrary to the pattern found in this study. Further, Ainley et al. (1984) considered that Adélie Penguins fed more during early morning, with numbers in the water decreasing from late morning to late afternoon, again the reverse of that found off Hop Island. However, Miller & Hampton (1989) have indicated the irregular distribution of krill, and the increased spacings of aggregations at night: such parameters vary regionally and may materially influence the local penguins' foraging activities.

Although unable to distinguish between searching and successful feeding dives, we found no relationship between the durations of successive dives, suggesting that, in this area and for the study period, penguins were not revisiting the same food aggregation. Searching and success were, therefore, presumably variable and extended diving at night may indicate dispersed prey (Everson 1982). Whereas dives may be shallower in later crèche stages (Whitehead 1989), the scattered krill or fish may require extended foraging. But perhaps short dives (recorded here for isolated, foraging birds) are themselves searching and exploratory in nature (rather than travelling, cf. Wilson & Wilson 1990), indicating prey patches at varying depth, requiring a subsequent dive of variable duration. Indeed the depth available to prey (and predator) must have some influence on dive duration and extent (e.g.Wilson 1985).

Adélie Penguins, like other penguins, forage individually or in small groups. It is difficult to see any social facilitation or benefit related to foraging in such numbers and it is suggested that antipredator behaviour may be involved. Dive duration (which may equate with depth of prey) was longer in this study compared with results obtained elsewhere. That Adélie Penguins may sustain long periods underwater was predicted by Baldwin et al. (1984) and Baldwin (1988). It remains necessary to determine what foods are available in such areas, and how individual penguins are obtaining them.

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