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The movements of gentoo penguins *Pygoscelis papua* from Ardley Island, Antarctica

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Abstract The movements of gentoo penguins (*Pygoscelis papua*) in Antarctica were studied by equipping a total of 37 birds captured at Ardley Island, South Shetlands between December 1991 and May 1996 with position-determining devices. Information on area usage was derived from 20 of these devices and covered the incubation period ($N = 3$ birds), the chick-rearing period ($N = 14$ birds) and the over-wintering period ($N = 3$ birds). During incubation birds only ventured further than 50 km from the colony 20% of the time and no individual ranged further than 200 km from the colony. In contrast, no individuals attending chicks ranged further than 16 km from the colony. During winter the maximum distance ranged from the colony was 268 km. Mean distances between the birds and the colony were 80, 81 and 127 km. Individual birds tended to associate with one spot, making short (10 day) forays away before returning to nodal areas. The ranging capacity of gentoo penguins appears considerably less than that of sympatric congeners and may reflect the ability of gentoo penguins to dive deeper and thus exploit prey not accessible to congeners.

Introduction

The extent to which seabirds can exploit various areas of the marine environment is dependent on a number of

factors. Birds are most limited during breeding when brood constraints necessitate parents to repeatedly associate with the nest site to incubate the eggs or to feed young. Two primary determinants of the marine areas birds can potentially exploit are the length of time that birds can be absent from the breeding site and their travelling speed (e.g. Williams and Siegfried 1980).

Although penguins are the most aquatic of all birds, they are particularly restricted in the areas they can exploit compared to volant species because they only travel slowly (Costa 1991; Wilson 1995). Penguins can be broadly divided into two groups depending on their capacity for movement. Some species, such as the macaroni penguin *Eudyptes chrysolophus*, are migratory during the non-breeding season, while others, such as the African penguin *Spheniscus demersus*, are considered sedentary (Croxall and Davis, in press). Migratory species have a tendency to forage further offshore than sedentary species during the breeding season (Croxall and Davis, in press) and by so doing reduce inter-specific competition for prey with species foraging inshore (e.g. Cooper et al. 1990; Hindell et al. 1995). Why gentoo penguins (*Pygoscelis papua*) are generally thought to be sedentary during the non-breeding season (for summary see Williams 1995) while congeneric Adélie (*Pygoscelis adeliae*) and chinstrap (*Pygoscelis antarctica*) penguins are migratory is unclear (Davis et al. 1996; Wilson et al. 1998), as is why, even during the breeding season, gentoo penguins forage much closer inshore than either congener (cf. Lishman 1985; Trivelpiece et al. 1986, 1987; Wilson 1995). In areas of breeding sympatry the diets of the three species are very similar (Trivelpiece et al. 1987 and references therein; Williams 1995 and references therein).

Despite the general conclusion that gentoo penguins are sedentary for the whole year, the published data considering the movements of these birds are equivocal (see Bost and Jouventin 1990 and references therein) because, to our knowledge, no study has documented in detail distribution at sea in birds from known breeding sites (as has been done, for example, in Adélie penguins

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(see e.g. Sadleir and Lay 1990; Davis and Miller 1992; Davis et al. 1996). To achieve this, foraging individuals must be fitted with some sort of position-determining equipment (see e.g. Trivelpiece et al. 1986). Rather, gentoo penguin area exploitation has been deduced during the breeding season by consideration of foraging trip length and swim speeds (e.g. Adams and Wilson 1987; Trivelpiece et al. 1987; Wilson et al. 1989) or been based on records of the presence or absence of the birds at breeding sites over winter (Bost and Jouventin 1990; Williams 1995).

We determined the movements of gentoo penguins from the South Shetland Islands during three main phases of the year: incubation, chick-rearing and over-wintering using dead reckoning techniques (Wilson et al. 1993) and global location sensors (Wilson et al. 1992, in press; Hill 1994). The aim of the study was to determine the space utilisation by gentoo penguins during different stages of their life-cycle and, where possible, to compare the areas used by gentoo penguins with those used by congeneric Adélie and chinstrap penguins.

Materials and methods

Field work was conducted at Ardley Island (62.22°S, 58.87°W), South Shetlands, Antarctica between December 1991 and November 1996. Adult gentoo penguins were caught and equipped with automatic position-determining devices to elucidate the area utilisation of these birds during incubation, chick rearing and over-wintering. Two types of positioning device were used: global location sensors and vectorial (dead reckoning) loggers.

Global location sensors

The global location sensors were based on the pillbox logger (Driesen and Kern, Bad Bramsted, Germany) and consisted of a light sensor covered by a blue filter (see Wilson et al. in press) set to record light intensity in a 128 kbyte memory once every 128 s. Resolution was 8 bit and the dynamic range to which the unit responded was between approximately 0.1 and 25 lx. The global location sensors were powered by two 3 V lithium cells and all electronics were encased in transparent resin. The fully encapsulated unit was streamlined according to suggestions made by Bannasch et al. (1994), weighed 42 g and had maximum dimensions of 125 × 38 × 25 mm. Recovered data were treated using the programme LOCATE (version 2.0 – Jensen Software Systems, Kiel, Germany), which determines the timing of dawn and dusk (considered to occur when the sun is 4.9° below the horizon) as a function of Greenwich Mean Time and Julian date so that day-length and the timing of local midnight and midday can be used to calculate geographic position (for details see Wilson et al. in press). Dawn and dusk are recognised when the units record that the light intensity has passed a certain threshold, this threshold corresponding to a particular sun angle (nominally -4.9°). The thresholds corresponding to our specified sun elevation angles were determined during calibrations made in Antarctica, Germany and Uruguay. Accuracy of these units is estimated to be better than 40 km for class 1 fixes if no snow covers the sensor (Wilson et al. 1995). Snow can theoretically cover the sensor for short periods, though birds tend to shake it off and, where this occurs over dawn or dusk, it can compromise the quality of fixes so that accuracy may be ±80 km. Numerous other factors compromise the quality of fixes obtained by global location sensors; among these are cloud

cover, extensive diving behaviour around dawn and dusk and sensor orientation with respect to sun angle. These factors are discussed in detail by Wilson et al. (1995) as well as techniques used to minimise such errors. Generally, such errors are non-systematic so that they result in a non-biased scatter around the true position.

All positional information derived from the global location sensors was so treated that data derived from all birds from the incubation period were lumped together as were all data derived from over-wintering birds. A frequency matrix was then produced for each time period. The matrix resolution was 0.25° (latitude by longitude) squared and all data were converted to a percentage time per 0.25° square for graphic representation. In order to examine ice-cover conditions in areas where the penguins were determined to have been, a search was conducted for satellite data on the world wide web with emphasis being placed on comparable timing.

Vectorial loggers

The vectorial loggers were based on the DK101 logger series (Driesen and Kern, Bad Bramsted, Germany), which recorded swim speed (via a paddle wheel), swim heading (using a compass whose orientation was measured using two Hall sensors) and dive depth (8 bit resolution for the range 0–200 m) at intervals of 10 or 15 s. The unit had a memory of 64 bytes and was powered by two DL1/3 N lithium batteries. The electronics were potted in water-proof resin so that the whole unit was hydrodynamically styled (cf. Bannasch et al. 1994; Culik et al. 1994), weighed 200 g (in air) and had maximum dimensions of 140 (length) × 58 (width) × 28 mm (height). More details of this system are given in Wilson et al. (1993).

Devices were programmed and recorded data accessed by a laptop computer linked to the loggers by an interface. Downloaded data were treated by the programme ROUTE (Jensen Software Systems, Kiel, Germany), which integrates all speed, swim direction and depth data together in vectorial calculations so as to reconstruct the swim routes of the equipped birds (Wilson et al. 1993). Errors in vectorial calculations may vary according to drift induced by currents. Overall error in foraging tracks could be assessed by examining the difference in calculated end point with respect to the known start point (since the point of entry into and exit from the water of the birds is known). Maximum differences were never more than 600 m so positional error from vectorial estimates is unlikely ever to have exceeded this value. All derived foraging tracks were combined in a single matrix to derive the percentage total time spent by the birds per square kilometer within the foraging area.

Attachment of devices

Incubation

Between 20 and 21 October 1995, ten gentoo penguins engaged in nest building and courtship activities were equipped with global location sensors. These units were attached to the centre line of the lower back, as recommended by Bannasch et al. (1994), so as to minimise drag, using Tesa tape and special two-component rubber glue (Deutsche Schlauchbootfabrik, Eschershausen, Germany) (for details see method 4 in Wilson et al. 1997). The total time from bird capture to release took between 10 and 20 min. The birds were then released at their nest sites. Between 11 and 20 December 1995, a search was made for the equipped birds. When located, the global location sensors were removed by cutting the ends of the feathers. At this time bird body mass was measured and the status of the nests of the equipped birds noted.

Chick rearing

Between 29 December 1991 and 19 January 1992, 14 gentoo penguins tending small chicks were equipped with vectorial loggers. As

in the case of incubating birds, the units were attached to the centre line of the lower back, but this time were held in place solely by Tesa tape (for details see method 1 in Wilson et al. 1997). After return to the nest, birds were left to undertake a minimum of one foraging trip before the units were removed

Over-wintering

Between 6 and 7 May 1996, 13 post-moult adult gentoo penguins were caught and restrained according to methods described in Wilson et al. (1998) while they were equipped with global location sensors. These units were attached in the same way as the devices used to determine the position of birds at sea during the incubation period. Here, however, the total time from bird capture to release took between 20 and 65 min, the longer times being mainly due to the time it took for the glue to dry at the low temperatures experienced at that time. The birds were then released to allow them to go to sea. During October and November 1996, searches were conducted to recover device-equipped birds that had returned to Ardley Island to breed. Recovered penguins were restrained in the same way as before and the device removed by cutting the ends of the feathers. Devices were then transported to Kiel, Germany pending analysis.

Results

Incubation

All ten device-equipped birds were recovered, the mean mass of recovered birds being 5.69 kg (SD 0.43). All birds appeared in good condition and were breeding successfully: eight nests contained two chicks, one nest contained one chick, and one nest one chick with one egg. Chick ages were determined to be between 1 and 5 days. Only three of the ten global location sensors produced high quality data that could be used for determination of bird position. This was due, in three cases, to data corruption caused by failing batteries or, in four cases, water entering the devices. A total of 622 positional fixes was obtained. Between October and December, during the courtship and incubation period, the monitored gentoo penguins spent most time within 50 km of the colony (Fig. 1a). Only about 20% of the time were birds at distances in excess of 50 km and no individual ever ventured further than 200 km. Excepting the area close to the colony, the sea areas most used by the birds were the Bransfield Strait, between King George Island and the Antarctic Peninsula and the Drake Passage, immediately adjacent to King George Island (Fig. 2a).

Chick rearing

All 14 birds equipped with vectorial loggers foraged successfully and continued feeding their chicks. Units were recovered after a mean of 2.7 days (SD 1.7) and all data could be used for the calculation of bird position. During December and January, no equipped individual foraged further than 16 km from the island (Fig. 1b), with the vast majority of the time being spent within

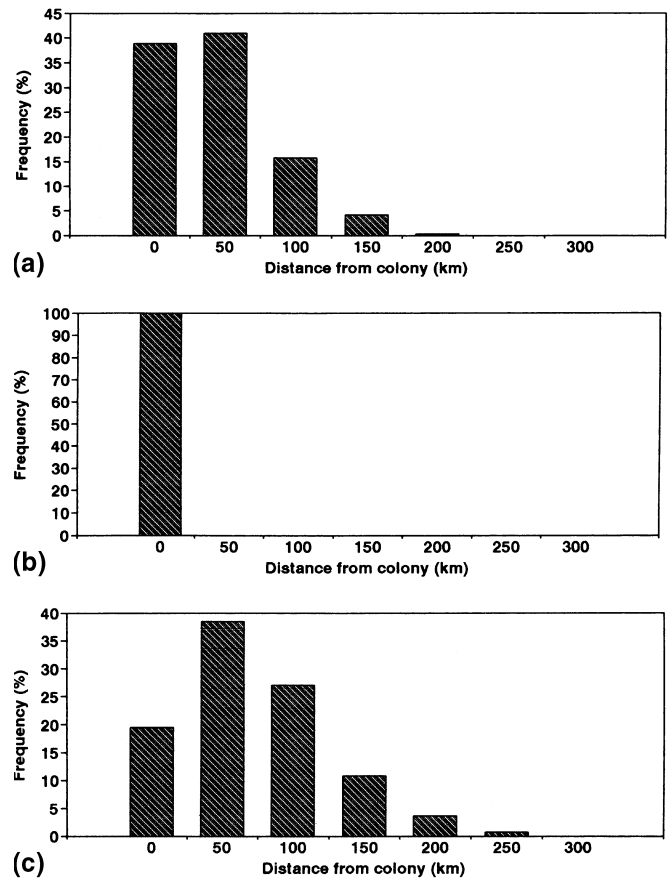


Fig. 1a–c Frequency of occurrence of the direct distance between monitored gentoo penguins and their breeding colony during: **a** the incubation period (derived from 3 birds where fixes were derived twice per 24 h for each individual giving a total of 317 fixes evenly distributed among individuals); **b** the chick-rearing period (derived from 14 birds where fixes were derived once every 15 s that they were at sea); **c** the over-wintering period (derived from 3 birds where fixes were derived twice per 24 h for each individual giving a total of 618 fixes evenly distributed among individuals)

5 km (Fig. 2b). This means that no bird even ranged far enough to move out of Maxwell Bay, either into the Bransfield Strait or into Drake Passage.

Over-wintering

Of the 13 gentoo penguins equipped, 6 were recovered during October and November 1996. All recovered birds appeared in good condition and were engaged in nesting behaviour. Three of the global location sensors had logged data, the other units having suffered unacceptable voltage drops so that the data were corrupt. The three viable global location sensors had all logged data until 17 August 1996 when the memories were full. Between May and August all three gentoo penguins had occupied an area west of the the Antarctic Peninsula (Fig. 2c) and ranged up to a maximum distance of 268 km from Ardley Island (Fig. 1c). Mean distances from Ardley Island for the three birds were 80 km

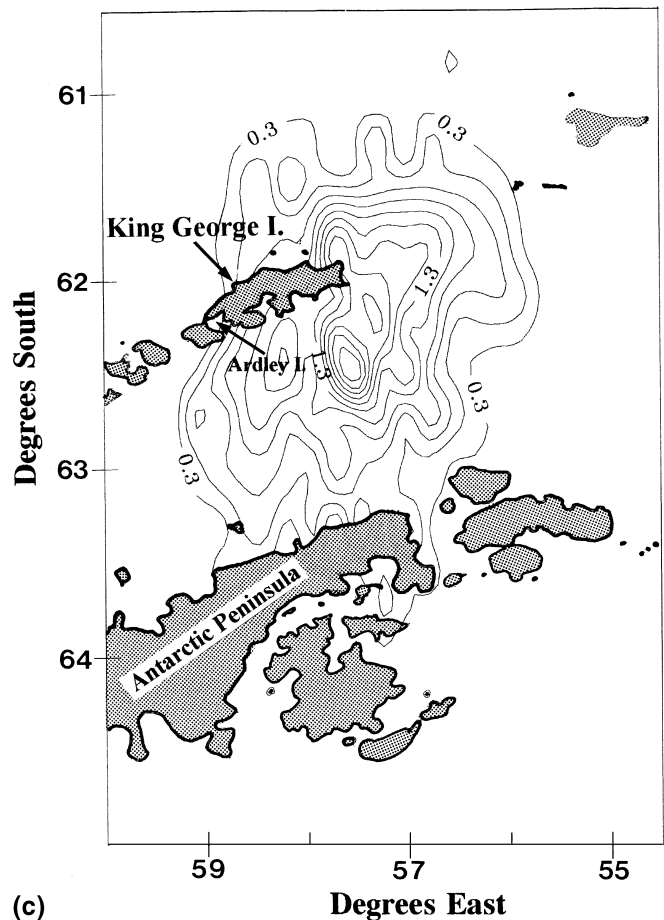
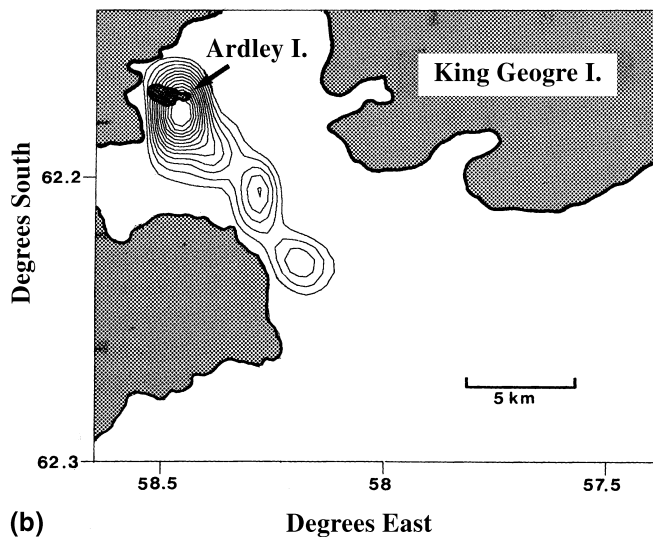
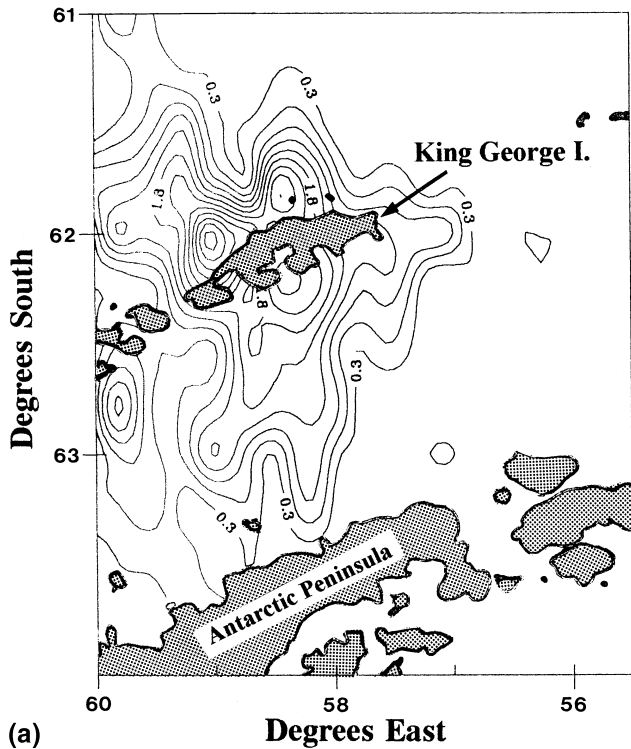


Fig. 2a-c Topographic plot (from SURFER) of the positions of the tracked gentoo penguins: **a** during the incubation period (the *contour lines* refer to the percentage time spent per $0.5^{\circ 2}$ (lat. \times long) summed over the whole of the incubation period; **b** during chick rearing (the *contour lines* refer to the percentage time spent per km^2 summed over the whole of the chick-rearing period where the min. contour is 1 and increments are 1%); **c** during the overwintering period (the *contour lines* refer to the percentage time spent per $0.5^{\circ 2}$ (lat. \times long) summed over the whole of the winter period over which the birds were tracked)

(SD 47, $N = 206$), 81 km (SD 40, $N = 206$) and 127 km (SD 53, $N = 206$). Each bird tended to spend most time within a particular area, apparently engaging in forays away from this area lasting for periods of up to 10 days.

Discussion

The attachment of external devices to penguins has been shown to affect aspects of their behaviour and energetics (see e.g. Wilson and Culik 1992; Culik et al. 1994; Croll

et al. 1996). Device-induced detrimental effects are most likely to make themselves apparent over long time intervals so that the equipment of our gentoo penguins for the winter period for 7 months must be regarded as a severe test of the acceptability of the devices by the birds. That we recovered 6 of the total of 13 equipped birds, all in apparently good condition, and all engaged in nesting behaviour, indicates that our devices are apparently well tolerated by the birds. No equipped bird was sighted in poor condition. The failure to sight the other eight equipped individuals is most likely due to the fact that we equipped some moulting gentoo penguins at Ardley Island that originated from one of the other

numerous colonies round King George Island and that consequently returned to these colonies at the onset of the breeding season. (In support of this, we received reports that at least two gentoo penguins carrying devices had been sighted at the Jubany colony, some 18 km away from Ardley, in November 1996.)

Area exploitation during the breeding season

Earlier calculations of gentoo penguin foraging range based on swim speeds and time absent from the colony ranged between 3 and 35 km (Adams and Wilson 1987; Trivelpiece et al. 1987; Wilson et al. 1989). Studies where birds were equipped with radio transmitters showed that gentoo penguins breeding in colonies bordering Admiralty Bay (62.2°S, 58.8°W) rarely moved outside this area during chick rearing. Our work confirms that gentoo penguins from King George Island during chick rearing do indeed seem to forage almost exclusively close inshore at this time. During incubation, these birds have a more extended foraging range but, even so, apparently spend around 80% of their time within 50 km of the colony. This situation contrasts with that found in Adélie penguins where males take the first shift at incubation, which lasts some 14–17 days (Sladen 1958; Davis and Miller 1982), during which time the females may range up to 186 km from the colony (cf. Davis et al. 1988; Sadleir and Lay 1990; Kerry et al. 1995). Incubation shifts by chinstrap penguins are markedly shorter, generally varying between 6 and 10 days (Williams 1995) so the foraging range is likely less than that of Adélie penguins although to our knowledge no telemetric studies have been done to verify this.

Trivelpiece et al. (1987) calculated that gentoo penguins tending for chicks at King George Island would have a likely foraging range of 17 km (max. 24 km), considerably less than either sympatric Adélie penguins (likely range 43 km, max. 50 km) or chinstrap penguins (likely range 27 km, max. 33 km). Trivelpiece's values for chinstraps are somewhat higher than those calculated by Bengtson et al. (1993) of 3–20 km for Seal Island. Nonetheless, Trivelpiece et al.'s (1987) contention that gentoo penguins at King George Island forage closer inshore than do either Adélies or chinstraps is supported by our results and those presented by Wilson (1995). Sympatrically brooding Adélies and chinstraps from Ardley Island may forage over 30 km away from the colony; this is something that the gentoo penguins never did.

The foraging ranges of pygoscelid penguins in other areas of Antarctica may vary substantially from those determined for King George Island. For example, Lishman (1985) calculated that Adélie and chinstrap penguins during the chick-rearing period from Signy Island (60°43'S, 45°36'W) have foraging ranges of 83–119 km and 66–132 km, respectively. Kerry et al. (1995) determined, using satellite telemetry, that Adélie penguins tending chicks at Bechervaise Island travelled

distances of up to 125 km away from the breeding sites, although the variance was high. Gentoo penguins, almost wherever they occur, are considered to have relatively restricted foraging ranges. Using distance meters, Adams and Wilson (1987) calculated a maximum foraging range of 35 km for gentoo penguins tending chicks at Marion Island (46°54'S, 37°45'E). These data were subsequently re-worked by Wilson et al. (1989), to correct for vertical distance acquired due to diving, to derive a foraging range of only 7 km.

Why should gentoo penguins, in areas of sympatry with Adélie and chinstrap penguins, consistently be able to forage closer inshore than congeners and, in so doing, avoid incurring travelling costs while at the same time exploiting similar prey? Trivelpiece et al. (1987) suggested that gentoo penguins might habitually dive deeper than either Adélie penguins or chinstrap penguins and thus be able to exploit prey closer to their colonies that is not available to either congener. There is a positive correlation between maximum dive depth and body mass in penguins (Wilson 1995). However, the capacity to exploit deeper prey not only depends on the ability of birds to reach the relevant depths, but also to be able to do this consistently and to remain for extended periods at those depths in order to feed. Gentoo penguins do indeed have greater diving capacities than either conspecific (cf. e.g. Lishman and Croxall 1983; Whitehead 1989; Naito et al. 1990; Williams et al. 1991; Wilson et al. 1991a,b; Bengtson et al. 1993). Wilson (1995) suggested that there was little inter-specific difference in the frequency of maximum dive depth of pygoscelids breeding at Ardley Island. Re-evaluation of these data suggests, however, that at depths in excess of 10 m, gentoo penguins dived more often to specific depths than either congener in seven out of nine cases, supporting Trivelpiece et al.'s (1987) hypothesis. This does not mean, however, that the birds necessarily travel overall less far. We analysed the distributions of maximum depth data presented by Wilson (1995) to determine the distance travelled vertically during diving (see Wilson et al. 1989) and found that, over 100 typical dives, Adélie penguins foraging from Ardley cover a vertical distance of 4.1 km, chinstrap penguins 3.3 km while gentoo penguins travel 5.2 km. Thus, in diving deeper, gentoo penguins travel vertically 27% more than Adélie penguins and 58% more than chinstrap penguins, which at least partially compensates for the apparent benefits of the reduced foraging range.

Area exploitation during the non-breeding season

Absences at sea of gentoo penguins during the non-breeding season become longer in the more southerly regions of the range, with birds from the Antarctic Peninsula being absent from colonies for periods in excess of 2 months (cf. Bagshawe 1938; Bost and Jouventin 1990).

Our study demonstrates that gentoo penguins from King George Island apparently do not fit into the classic

scheme as either truly migratory or sedentary birds. The maximum distance between any bird and the breeding site of 268 km is a fraction of that determined for chinstrap penguins from Ardley Island, which may move in excess of 1000 km away from their breeding colonies during the non-breeding season (Wilson et al. 1998). Although there are no data on over-winter movements of Adélie penguins from Ardley Island, birds from other areas may move similar long distances (Davis et al. 1996). Despite this, the mean bird-island distance of around 100 km for gentoo penguins is substantial for a flightless seabird and is certainly well outside the normal foraging radius for breeding birds (see above). The literature on gentoo penguin sightings at sea (cf. Watson et al. 1971; Enticott 1986) indicates that birds are rarely sighted far from breeding colonies although individuals have been seen as far as 2000 km from the nearest potential breeding point (cf. Voisin 1979; Enticott 1986), demonstrating that they are capable of long-distance movements in the same way as their congeners. We conclude from this study that there are grounds for believing that gentoo penguins may undertake appreciable migrations in certain areas of their breeding range and that they certainly cannot be classified as fully sedentary. Bost and Jouventin (1990) indicated that birds in the northerly part of the species range are apparently most sedentary. Gentoo penguins in the southern part of the range have to contend with extensive sea-ice coverage during winter. We would expect, therefore, the longest inter-breeding migrations to be undertaken by the most southerly breeding stocks. Future studies are needed to address this.

Why do gentoo penguins from the South Shetland Islands, which apparently feed principally on krill (*Euphausia superba*) in the same way as do their sympatric congeners, not undertake long migrations like Adélie and chinstrap penguins? One potential explanation is that although the three species feed predominantly on krill during the summer months, they may switch during the austral winter. An indication that this may be the case comes from recent work by Ainley et al. (1992, 1994), who found that Adélie penguins wintering in the marginal ice zone consumed more fish and squid than krill. Equivalent data are not forthcoming for gentoo and chinstrap penguins, except for the case of gentoo penguins overwintering at South Georgia where it is known that the birds consume substantial quantities of krill (Williams 1991). Until more data are forthcoming, however, this hypothesis must be regarded as speculative.

The limited data available on the over-wintering habits of Adélie and chinstrap penguins suggest that the former inhabit the pack-ice zone (Ainley et al. 1984; Enticott 1986 and references therein; Kerry et al. 1995; Davis et al. 1996) whereas chinstraps inhabit both the northern areas of the pack ice and the open sea areas to the north (see Wilson et al. 1998 and references therein). Satellite imagery shows that the area exploited by our equipped gentoo penguins close to the tip of the Antarctic Peninsula was approximately 50% covered by ice

during the austral winter of 1996 (July/August 1996; data from <http://11mullara.met.unimelb.edu.au>). Our few results would indicate that gentoo penguins from Ardley Island during winter exploit an environment that is, with respect to ice coverage at least, somewhat intermediate to that exploited by Adélie and chinstrap penguins. Should this prove to be a general phenomenon, the exact degree to which the different ice-cover conditions selectively favour each of the three pygoscelid penguins will be an exciting, and difficult, topic for future research.

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