WHERE BREEDING MAGELLANIC PENGUINS *SPHENISCUS MAGELLANICUS* FORAGE: SATELLITE TELEMETRY RESULTS AND THEIR IMPLICATIONS FOR PENGUIN CONSERVATION

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SUMMARY

STOKES, D.L. & BOERSMA, P.D. 1999. Where breeding Magellanic Penguins *Spheniscus magellanicus* forage: satellite telemetry results and their implications for penguin conservation. *Marine Ornithology* 27: 59–65.

We used satellite telemetry to determine foraging locations and behaviours of two male Magellanic Penguins *Spheniscus magellanicus* breeding at Punta Tombo, Argentina during the incubation and early chick-rearing periods of the 1995/96 breeding season. Both birds travelled far from the colony and far from shore, even on foraging trips of short duration. During their longest trips, Males One and Two travelled at least 521 km and 236 km from Punta Tombo and at least 152 km and 139 km from shore, respectively. The farthest points of all but two of the birds' 10 trips were more than 60 km from Punta Tombo. The two birds travelled in significantly different directions to forage and foraged in different locations. Temporal pattern of foraging trips and dive pattern also differed between birds. Male Two took more trips and made proportionally fewer dives of intermediate depth (10–40 m) than did Male One. These results raise the possibility that foraging behaviour may differ among individuals of the same class (e.g. experienced breeding males). Although more study is needed, these results demonstrate that the foraging range of a temperate penguin can be large. This and other recent satellite results for Antarctic and sub-Antarctic species, as well as geolocation results for Magellanic Penguins, indicate that extensive foraging ranges during the breeding season may be more common among penguins than previously recognized. This suggests that coastal marine reserves alone are unlikely to protect Magellanic Penguins and several other penguin species, and that conservation measures that regulate human uses over large areas of the marine environment should also be pursued.

INTRODUCTION

Despite extensive studies of penguin breeding ecology, little is known about some of the most basic elements of penguins' lives at sea. Where penguins forage during the breeding season is one such little-known topic of particular importance. Because the reproductive success of many penguin populations appears to be determined largely by food conditions and foraging success (Boersma 1978, Boersma *et al.* 1990, Whitehead *et al.* 1990, Crawford & Dyer 1995), knowledge of where individuals forage and how they move during foraging trips is essential for a complete understanding of the ecology of penguins. In addition, with the continued decline of many penguin populations, the seriousness of human impacts on penguins at sea and the need to mitigate or prevent those impacts has become evident (Frost *et al.* 1976, Adams 1994, Gandini *et al.* 1994, Boersma & Stokes 1995a). One approach to protection of penguins at sea would follow the traditional terrestrial model for wildlife conservation by establishing protected marine areas around colonies (Weavers 1992). This may be a suitable way to protect penguins because, as swimming birds, they are expected to forage close to their nesting sites during the breeding season (Furness & Monaghan 1987, Wilson & Wilson 1990, Wilson 1995). However, the success of a reserve approach depends on good knowledge of where

penguins forage. Finally, a much-discussed (e.g. Boersma 1978, Croxall & Prince 1979, Croxall *et al.* 1988, Davis & Miller 1990, Trivelpiece *et al.* 1990, Whitehead *et al.* 1990, Ancel *et al.* 1992, Davis & Miller 1992, Handrich *et al.* 1995) potential application of penguin breeding biology data is as an indicator of marine productivity or other environmental conditions. For this application to be credible, the area sampled by foraging penguins must be known.

Initial attempts to track foraging penguins using land-based radio telemetry generally supported the hypothesis that breeding penguins forage close to their colonies (e.g. Trivelpiece *et al.* 1986, Heath & Randall 1989, Sadleir & Lay 1990, Weavers 1992). However, some results suggested that birds foraged outside the limited range of land-based receivers (Davis *et al.* 1988, Sadleir & Lay 1990, D.L. Stokes & P.D. Boersma unpubl. data). With the advent of a practical technique for using satellite telemetry to track penguins, it has recently become possible to obtain a more complete picture of penguin foraging movements. Satellite results indicate that in at least some populations of three Antarctic and sub-Antarctic penguin species, Adélie *Pygoscelis adeliae* (Davis & Miller 1992, Kerry *et al.* 1995), Emperor *Aptenodytes forsteri* (Ancel *et al.* 1992), and King *A. patagonicus* (Jouventin *et al.* 1994), breeding birds forage hundreds of kilometres from the colony, much

farther than previously recognized. These are the largest (Emperor and King) and southernmost (Emperor and Adélie) penguin species. Foraging distance and location in these populations may be in part a function of animal size or sea ice conditions, and therefore these results may not be applicable to the majority of penguin species, which are smaller and/or occur in ice-free waters. Here we add to the scant-but-growing body of satellite-telemetry data on foraging penguins with a report of satellite tracking of a temperate penguin species, the Magellanic Penguin *Spheniscus magellanicus*.

As in other penguin species, male and female Magellanic Penguins share incubation and chick-rearing duties, spelling each other at the nest between foraging trips (see Boersma *et al.* 1990 for description of breeding phenology). Around the time eggs are laid, the male, having fasted for up to five weeks, takes the first foraging trip while the female incubates the eggs. Upon the male's return, typically 1½ to 2½ weeks later, the female makes a foraging trip of similar duration (Yorio & Boersma 1994). Subsequent trips become progressively shorter, until the mates are exchanging nest attendance duties every one-to-two days at hatching (approximately 40 days after eggs are laid). Foraging trips remain short while chicks are small but gradually lengthen, averaging four-to-five days after chicks are left unattended (at approximately 30 days of age) and both adults forage simultaneously (an additional 30–60 days; Boersma *et al.* 1990).

Although the temporal patterns of Magellanic Penguin foraging trips and nest attendance are well known (Boersma *et al.* 1990, Scolaro & Suburo 1995), spatial patterns of foraging are not. In the only published study to address this question, Wilson *et al.* (1995) used miniature global location sensors to determine that Magellanic Penguins breeding at the northern edge of the species' range often foraged approximately 120 km, and as far as 300 km, from the colony during the 1994 incubation period.

Information on the foraging locations of breeding birds is needed to develop an effective strategy to halt the decline of this species, the largest breeding population of which has decreased by 20% in eight years (Boersma 1997). Currently, the primary threats to Magellanic Penguins are oil pollution and commercial fishing (Gandini *et al.* 1994, Boersma & Stokes 1995a), and the major determinant of fledging success is rate of food delivery to chicks (Boersma *et al.* 1990, Boersma & Stokes 1995b). Although some nesting areas along the Argentine coast are protected as (terrestrial) reserves, the penguin's marine environment remains largely unprotected. A recent proposal for protection of the species would designate a 30 km-radius marine reserve around Punta Tombo, Argentina, site of the largest colony of the species. Determining where birds forage during the breeding season is a necessary first step in evaluating whether such marine reserves can effectively protect this species. Results may be applicable to other penguin species as well.

METHODS

We tracked two male penguins nesting near one of our intensively monitored study areas in the colony at Punta Tombo, Argentina (44°02'S, 65°11'W) during the incubation and early chick-rearing stages of the 1995/96 breeding season. Both birds were experienced breeders; each was banded as a breeding adult at least 11 years prior to this study, and each had nested in the same area of the colony since that time. Sex of the birds was determined from morphological measurements (Williams

1995). We attached a transmitter to Male One on 10 October, the day its mate laid the first egg (a complete clutch consists of two eggs, typically laid four days apart) and three days before the male left for its first foraging trip during incubation. We attached a transmitter to Male Two on 14 November, 10 days before it left for its second foraging trip during incubation. Both birds were tracked during all foraging trips from the date of transmitter deployment during incubation through the end of the early chick-rearing period in late December.

We used quarter-watt, microprocessor-controlled, satellite-linked, time-depth recorder/transmitters manufactured by Wildlife Computers Inc. Each TDR/transmitter was packed in a waterproof epoxy housing and weighed a total of *c.* 155 g, or less than 5% of the male's mass at the time of attachment (Male One = 3.75 kg, Male Two = 4.95 kg). The devices had a rounded rectangular shape with sloped front and trailing faces. They were 9.7 cm long and had a cross-sectional area of 13.5 cm², approximately 7–8% of the cross sectional area of a male Magellanic Penguin, as determined by girth measurements. Using fast-setting epoxy (Devcon brand), we fastened the devices to the feathers in the center of the lower back posterior to the line of maximum girth, approximately 9 cm anterior of the oil gland, to minimize drag (Bannasch *et al.* 1994). We programmed the devices to transmit at 45-second intervals when the bird was at sea and 1.5-minute intervals when on land. After 15 hours on land, the devices were programmed to suspend transmission until re-entry in the water. In addition to location, devices reported maximum depths of dives deeper than two metres.

We received transmissions through the Service ARGOS satellite system, which uses National Oceanic and Atmospheric Administration satellites in polar orbit. Fifty-eight percent (n = 59) of locations received (n = 102) were based on at least four messages per satellite pass and were accurate to within 1 km (location class 1 or better; ARGOS 1996). The accuracy of the remainder of locations could not be determined with certainty (ARGOS 1996); however, based on locations received when birds were at a known position (the nest), locations calculated from three messages per pass (class 0 and class A, n = 31) were sufficiently accurate for the purposes of this study (mean difference between calculated and actual position = 2.9 km, sd = 3.6, maximum = 10.2 km, n = 12). We did not use locations based on fewer than three messages (n = 12). For the purposes of calculating travel speed, we used only locations of class 1 or better.

We checked the birds' nests twice daily for attendance patterns and survival of nest contents. We also monitored nests in a nearby study area to check for differences in breeding phenology and duration of initial foraging trip between the birds we were tracking and non-experimental birds. Food conditions for penguins at Punta Tombo were poor at the beginning of the 1995 breeding season, and many chicks starved when very young. To ensure that the instrumented birds would continue to return to the nest and forage to feed offspring, we replaced their chicks that died with second chicks from nearby nests (the smaller of the two chicks in a brood usually fails to fledge). The adults fed these adopted chicks, and a chick eventually fledged from both nests where males carried transmitters.

Both transmitters were still functioning when we removed them in late December. Transmitters were removed by cutting the epoxy and trimming the feathers to which they were still attached. Males One and Two appeared to be in good health and weighed 4.20 and 4.65 kg, respectively, slightly more than
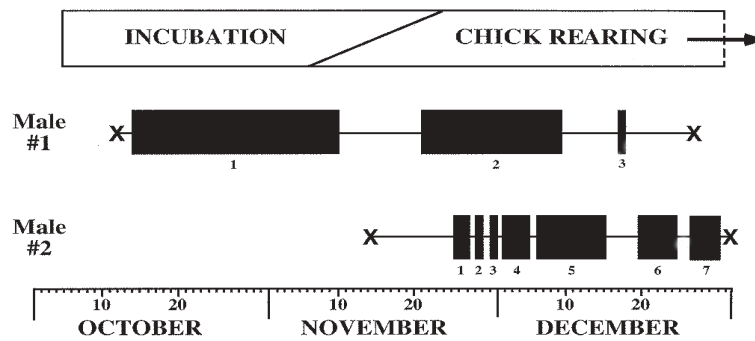
Fig. 1. *Timing of foraging trips of two satellite-tagged male Magellanic Penguins breeding at Punta Tombo, Argentina, during the incubation and early chick-rearing stages of the 1995/1996 breeding season. Solid blocks indicate foraging trips (trip number shown beneath); thin lines indicate presence at the nest. 'X' denotes dates of attachment and removal of devices. Male One's three foraging trips averaged 15.0 days in duration; Male Two's seven trips averaged 3.9 days. Colony breeding phenology is shown at top.*

the typical mean mass of experienced breeding males with chicks in December at Punta Tombo (4.06 ± 0.40 kg, n = 16). Both birds continued to feed chicks through the rest of the breeding season.

RESULTS

Timing and duration of foraging trips

Timing and duration of foraging trips differed between the two instrumented penguins (Fig. 1). From 14 November to 26 December, when both birds were being tracked, Male One made two trips of one and 18 days, while Male Two made six trips averaging 3.9 days, the longest of which was 10 days. This difference was not due to gross differences in breeding phenology. Male One's mate laid the first egg on 10 October and the first chick hatched on 23 November. Corresponding dates for Male Two were 16 October and 27 November. Timing of breeding for the transmitter-carrying birds was similar to that of non-experimental birds in our nearby study area (mean date of first egg 14.7 October, SD = 4.3 days, n = 43; mean date first chick hatched: 24.8 November, SD = 4.9 days, n = 42).

Male One's first foraging trip during incubation lasted a total of 26 days, or 25 days after its mate laid the second egg. Although longer than first foraging trips of breeding males at Punta Tombo in other years (Yorio & Boersma 1994), the duration of Male One's trip was well within the 95% confidence limits for initial trip duration of non-experimental males in 1995/96 (mean 23.9 ± 3.4 d, n = 43). Male One's mate remained at the nest and incubated the eggs for the entire 26 days the male was gone.

Foraging range and location

Both experimental birds foraged far from the breeding colony and far from shore, even on trips of short duration (Table 1 & Fig. 2). During its first trip, Male One travelled at least 521 km from Punta Tombo and at least 152 km from shore. These are minimum values, as the bird could have been farther away when no signals were received. Male Two travelled at least 236 km from the colony and 139 km from shore on its longest trip, and was more than 100 km from the colony and more than 100 km offshore on the last four of its seven trips (Fig. 3). The farthest points of all but two of the 10 trips made by both birds (mean 173.2 ± 41.9 km) were more than 60 km from the colony. For

none of the trips was there any indication that the birds went ashore between departure from and return to the colony.

The foraging locations of the two birds differed, with no overlap in routes farther than 70 km from the colony (Fig. 2). Male One travelled from the colony in a north-easterly direction (mean bearing to farthest point of trip = 53.3°, s [angular deviation] = 1.6°) for all three trips; Male Two foraged in locations east-north-east of the colony (mean 75.4°, s = 8.9°). Mean directions travelled by the two birds differed significantly ($F_{0.05,1,8} = 14.67$, $P < 0.01$; circular statistics after Zar 1984).
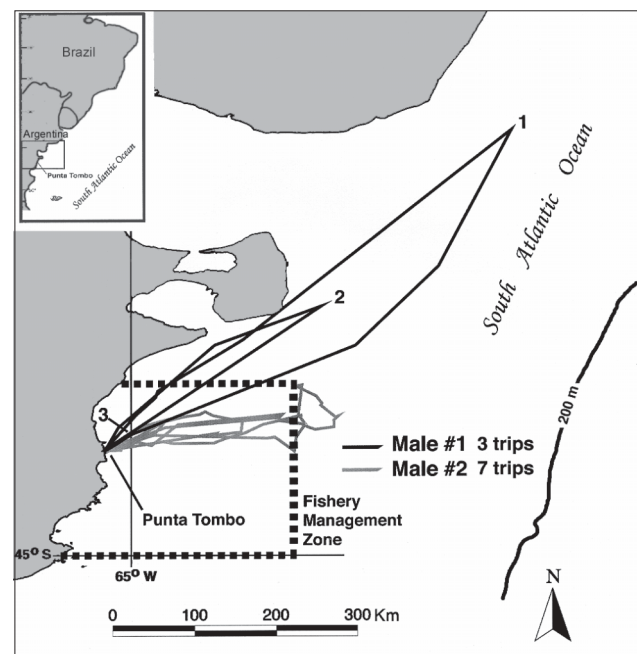

Fig. 2. *Tracks of foraging trips of two male Magellanic Penguins breeding at Punta Tombo, Argentina, during the incubation and early chick-rearing stages of the 1995/1996 season, as determined by satellite telemetry. Male One's three trips (12 Oct–27 Dec) are numbered chronologically at the point in each trip farthest from the colony. The 200-m isobath indicates approximate location of the shelf-break. The dashed line indicates the boundaries of the fishery management zone (see text).*

TABLE 1

Foraging trips of two male Magellanic Penguins breeding at Punta Tombo, Argentina during the incubation and early chick-rearing periods of the 1995 breeding season, as determined by satellite telemetry

Bird	Trip #	Duration (days)	No. of usable locations[1]	Max. distance from colony (km)	Max. distance from shore (km)	Direction (°)	Total distance travelled (km)
Male One							
	1	26	13	521	152	51	1074
	2	18	7	263	53	55	534
	3	1	3	34	28	54	65
Male Two							
	1	2	6	72	60	62	144
	2	1	6	66	58	64	134
	3	1	3	17	12	88	35
	4	4	12	140	104	76	300
	5	10	31	236	139	81	621
	6	5	8	180	105	77	366
	7	4	1	203	113	80	407

All distances are minimum values, because birds could have travelled farther between transmissions. Direction is the compass bearing from the colony to the farthest location of each trip.

[1]Locations based on more than three satellite messages (location class 'A' or better, see text).

Travel speed

On its first trip, Male One swam a minimum of 1074 km at an average of 41 km per day. Because few (13) locations were received during this trip, these figures are likely to be strongly under-estimated. Male Two's fifth trip (Fig. 3) had the highest number of locations per day (31 locations, 24 of class 1 or better, in 10 days) and provides a more complete picture of movement patterns over the course of a foraging trip. On this trip the bird covered a minimum of 621 km, averaging 62 km/day. During the initial period (6–8 December) when the bird was moving in a relatively straight line away from the colony, travel speed averaged 2.3 km/h (for 52.8 h, two trip segments of precise temporal and spatial endpoints). From 9–14 December, the bird followed a wide looping course and averaged 2.0 km/h (104.6 h, 14 trip segments). The bird travelled faster during the day (2.8 km/h, 27.7 h, six daytime trip segments) than during the night (2.2 km/h, 9.7 h, two trip segments). Because of the timing of satellite passes, nearly all trip segments included some hours of significant daylight, probably leading to an overestimate of night travel speed. During the single period (2.4 h) which included no daylight, the bird moved at 0.8 km/h. On the last full day of the trip (15 December), the bird travelled more than 100 km in a relatively direct line toward the colony (Fig. 3), averaging 4.9 km/h over 21.8 h (five trip segments). Speed was greater during the daylight periods (7.0 km/h for 10.5 h, three trip segments) than during mostly nighttime periods (2.9 km/h for 11.3 h, two trip segments). The top speed recorded for the entire trip, 8.9 km/h, occurred in the early evening (17h17–19h36) of the next-to-last day.

Dive patterns

Dive patterns of the two birds differed (Fig. 4). Although both birds dived most frequently to 3–5 m, Male One dived to all depth classes from 6–80 m with similar frequency, whereas Male Two dived more often to 6–10 m and 41–80 m than to intermediate depths. Neither the difference in dive depths between birds nor the high frequency of shallow dives for both birds were a result of foraging in shallow water *per se*, as both birds spent nearly all of their time at sea in areas with depths greater than 40 m.

During the trip with the most complete dive record (Male Two's fifth trip), dives below 10 m were less likely to occur when the bird was moving to and from the colony than during the rest of the trip. From 9–14 December, 39% of the bird's 804 dives were deeper than 10 m, compared to 29% ($\chi^2 = 6.93$, df = 1, $P < 0.01$, n = 241) on the outward leg (6–8 December), and 4% ($\chi^2 = 103.7$, df = 1, $P < 0.001$, n = 235) on the homeward leg (15 December) of the trip.

DISCUSSION

Our results suggest that male Magellanic Penguins breeding at Punta Tombo forage far from the colony during incubation and chick-rearing. Both of the birds we tracked foraged in locations hundreds of kilometres from the colony, and even on some short-duration trips (1–2 days) were more than 60 km from the colony. Preliminary satellite tracking data from a foraging male tagged in 1996, a year of apparently good food conditions, likewise indicated that it was more than 500 km from Punta Tombo on its first foraging trip during incubation (P.D. Boersma & D.L. Stokes unpubl. data). Geolocation data (Wilson *et al.* 1995) also indicates that Magellanic Penguins breeding at the colony at San Lorenzo, approximately 250 km north of Punta Tombo, travelled far (up to 300 km) from the colony during the incubation period.

These results are surprising, given that penguins must return to the nest frequently during the incubation and chick-rearing periods, and are more geographically constrained than are flying birds. Studies of other temperate penguins (African Penguins *S. demersus*, Wilson *et al.* 1988, Heath & Randall 1989; Little Penguins *Eudyptula minor*, Weavers 1992) indicate that breeding adults of these species foraged close to their
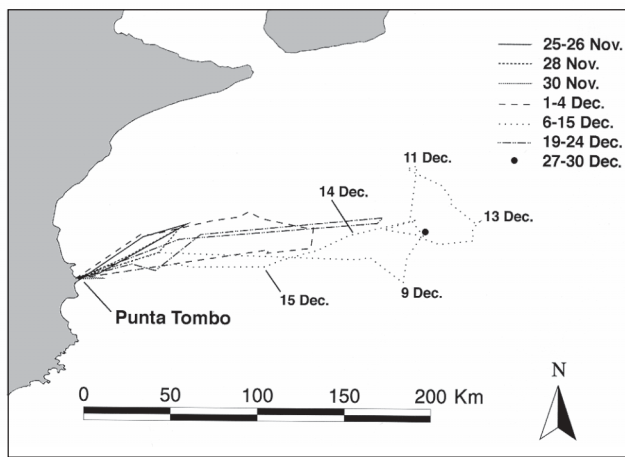
Fig. 3. *Tracks of Male Two's seven foraging trips during the late incubation and early chick-rearing stages (14 Nov–31 Dec) of the 1995/1996 breeding season. Filled circle indicates the single location received for the seventh trip. Location of Male Two on selected dates during the fifth trip is indicated.*

Fig. 4. *Dive depths for Males One and Two during incubation and early chick rearing. Frequency distributions of the two birds' dives differed significantly ($\chi^2 = 284.1$, df = 1, P < 0.001, n = 4706).*

colonies and close to shore. Our results are more similar to recent satellite results obtained for Antarctic and sub-Antarctic species which indicate that breeding birds from two populations of Adélie Penguins forage up to 272 km (Davis & Miller 1992) and 341 km (Kerry *et al.* 1995) from their colonies, breeding Emperor Penguins forage up to 895 km from the colony (Ancel *et al.* 1992), and breeding King Penguins forage up to 690 km from the colony (Jouventin *et al.* 1994). Unlike the Antarctic species, the great distances travelled by foraging Magellanic Penguins are neither facilitated nor required by sea ice conditions. We infer that the penguins swim these distances to reach waters where prey are available due to hydrographic conditions (Jouventin *et al.* 1994, Wilson *et al.* 1995). This region of the Patagonian shelf is characterized by a high degree of tidal mixing and nutrient availability, conditions believed responsible for the spawning activity and high seasonal concentrations of anchovy *Engraulis anchoita* in the area (Bakun & Parrish 1991). Anchovy was found to be an important component of the Magellanic Penguin diet during the breeding season at a colony 100 km south of Punta Tombo (Frere *et al.* 1996).

The difference between the foraging range found by this study and the ranges of other temperate penguin species is not related to differences in swimming speed among species. The travel speeds we obtained are similar to those reported for other similarly-sized penguin species (Wilson 1995). More likely, other studies have tracked populations from colonies with nearby reefs, shelf-break, or other oceanographic features where prey reliably concentrate (e.g. African Penguins breeding on St. Croix Island in Algoa Bay foraged near Cape Recife, Heath & Randall 1989). Such nearby localized foraging areas may not exist around Punta Tombo, where the shelf-break is more than 500 km offshore.

Neither of the birds we tracked appeared to concentrate their foraging efforts in the area most frequented by penguins during the 1994 incubation period at San Lorenzo, as determined by global location sensors (Wilson *et al.* 1995). Male One travelled through, and may have foraged in, the area on its first trip. However, the farthest point of the trip was more than 100 km to the north-east.
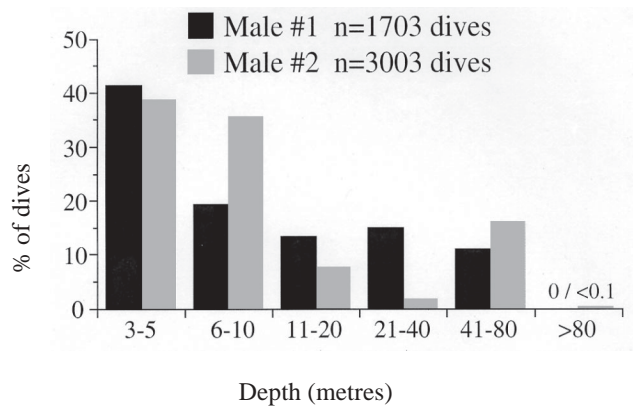
Although the possible effects of the devices must be investigated further, our results give little indication that the long foraging distances we observed were a result of device effects. Neither bird departed from the usual condition or behaviour of breeding birds, with the exception of Male One's second trip, which lasted longer than usual for that stage of the breeding season. Long trips such as this are made by some birds in poor food years, as the early 1995 season appeared to be. Male One's first trip, although of long duration, was not significantly longer than first trips of non-instrumented birds. Preliminary results using devices of the size used in this study and devices with half the cross-sectional area, show no detectable difference in foraging pattern of birds with the two types of devices, and indicate that birds forage far from the colony under more favorable food conditions as well (P.D. Boersma & D.L. Stokes unpubl. data).

An interesting aspect of our results is that the two birds, both old males and experienced breeders, foraged in different locations. This is similar to the results of Davis & Miller (1992), who found that rather than using a common foraging ground as had been earlier hypothesized, Adélie Penguin females foraged in markedly different locations. Not only did the birds we tracked forage in different locations, they seemed to remain faithful to their foraging area or direction of foraging throughout the breeding season. This, along with differences in dive patterns between the two birds, suggests that foraging behaviours may differ among individuals. Such differences have been proposed for different classes of penguins (e.g. partitioning of food resources between males and females as an explanation of sexual dimorphism in penguins, Davis & Speirs 1990), but our results suggest that differences may exist among individuals of the same sex and similar age, breeding experience, and location of nest within a breeding colony.

The results of this study, although awaiting confirmation with larger samples, may have important implications for conservation. A reserve large enough to encompass the foraging range of this species would extend several hundred kilometres from Punta Tombo, making it much larger than all but a few of the world's existing marine reserves (World Resources Institute 1996). At present, establishment of such a reserve is

unlikely, and thus the reserve approach to conservation, by itself, appears to be inappropriate for Magellanic Penguins. A more feasible approach is establishment of marine management zones in which the specific human activities affecting penguins (commercial fishing and oil transport) are regulated. A limited precedent already exists: since 1976 commercial fishing for Argentinian Hake *Merluccius hubbsi* has been regulated in a fishery management zone around Punta Tombo during part of the penguin breeding season (Fig. 2). In 1996 exclusion of large fishing vessels from the zone was extended through the entire penguin breeding season in an effort to maintain fish stocks, as well as populations of penguins and other marine organisms. However, enforcement appears to be ineffective (pers. obs.). Furthermore, the results of this study suggest that the restricted zone probably comprises only a portion of the penguins' foraging area.

To expand the protection zone to include the entire penguin foraging range and to regulate all human activities in the zone that affect penguins are daunting prospects, given the large area involved. However, with detailed knowledge of how penguins use their marine habitat, the size and cost to humans of regulated marine conservation zones could be minimized. For instance, our results give no indication that breeding penguins forage in waters south of Punta Tombo. If further study confirms this and if penguins from other colonies to the south also do not depend on these areas, they could be excluded from the management zone.

Clearly, more study is needed, with larger samples. However, these results show that the foraging range of a medium-sized temperate penguin can be large. In light of this and recent satellite results for other species, penguin conservation strategies cannot be based on an assumption that breeding penguins forage close to their colonies. Where colonies are close to shelf break (e.g. Galapagos Penguins *S. mendiculus*) or productive reefs (e.g. African Penguins at St. Croix Island), small coastal reserves may effectively protect breeding penguins at sea. However, where localized predictable foraging grounds do not exist near colonies, it is likely that penguins forage over a much larger area than was previously recognized, and reserves needed to protect them adequately would be impractical. In such cases, large marine zones where specific threats to penguins are regulated may be a more effective conservation strategy.

ACKNOWLEDGEMENTS

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