

- BIRKHEAD, T. R., AND A. P. MØLLER. 1992. Numbers and size of sperm storage tubules and the duration of sperm storage in birds: a comparative study. *Biol. J. Linn. Soc.* 45:363–372.
- BLANCHER, P., A. CYR, S. DROEGE, D. HUSSELL, AND L. THOMAS. 1993. Results of a U.S./Canada workshop on monitoring of landbirds during migration and recommendations towards a North American Migration Monitoring Program (MMP). *Natl. Biol. Survey*, Washington, DC.
- BRISKIE, J. V. 1994. Seasonal patterns of sperm storage in the Yellow-headed Blackbird *Xanthocephalus xanthocephalus*. *Ibis* 136:323–330.
- BRISKIE, J. V. 1996. Lack of sperm storage by female migrants and the significance of copulations en route. *Condor* 98:414–417.
- BROOKS, E. W. 1994. Braddock Bay Bird Observatory: spring 1994 passerine banding report. Rochester, NY.
- DELIUS, J. D. 1965. A population study of Skylarks *Alauda arvensis*. *Ibis* 107:466–492.
- DRENT, R. H., AND S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225–252.
- GUDMUNDSSON, G. A., A. LINDSTROM, AND T. ALERSTAM. 1991. Optimal fat loads and long-distance flights by migrating Knots *Calidris canutus*, Sand-erlings *C. alba*, and Turnstones *Arenaria interpres*. *Ibis* 133:140–152.
- HATCH, S. A. 1983. Mechanism and ecological significance of sperm storage in the Northern Fulmar with reference to its occurrence in other birds. *Auk* 100:593–600.
- KUENZI, A. J., F. R. MOORE, AND T. R. SIMONS. 1991. Stopover of Neotropical landbird migrants on East Ship Island following trans-gulf migration. *Condor* 93:869–883.
- LIGON, J. D. 1974. Green cones of the piñon pine stimulate late summer breeding in the Piñon Jay. *Nature* 250:80–82.
- MOORE, F. R., AND P. KERLINGER. 1987. Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. *Oecologia* 74:47–54.
- MOORE, F. R., AND M. V. McDONALD. 1993. On the possibility that intercontinental landbird migrants copulate en route. *Auk* 110:157–160.
- PROCTOR, N. S., AND P. J. LYNCH. 1993. *Manual of ornithology: avian structure and function*. Yale Univ. Press, New Haven, CT.
- PYLE, P., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. *Identification guide to North American passerines*. Slate Creek Press, Bolinas, CA.
- QUAY, W. B. 1984. Cloacal lavage of sperm: a technique for evaluation of reproductive activity. *N. Am. Bird Bander* 9:2–7.
- QUAY, W. B. 1985a. Cloacal sperm in spring migrants: occurrence and interpretation. *Condor* 87:273–280.
- QUAY, W. B. 1985b. Sperm release in migrating wood-warblers (Parulinae) nesting at higher latitudes. *Wilson Bull.* 97:283–295.
- QUAY, W. B. 1986. Timing and location of spring sperm release in northern thrushes. *Wilson Bull.* 98:526–534.
- QUAY, W. B. 1989. Insemination of Tennessee Warblers during spring migration. *Condor* 91:660–670.
- RICKLEFS, R. E. 1974. Energetics of reproduction in birds, p. 152–292. *In* R. A. Paynter [ed.], *Avian energetics*. Publ. Nuttall Ornithol. Soc. 15., Cambridge, MA.
- WALSBERG, G. E. 1983. Avian ecological energetics, p. 161–220. *In* D. S. Farner, J. R. King, and K. C. Parks [eds.], *Avian biology*. Vol. 7. Academic Press, New York.

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## SATELLITE TRACKING OF MAGELLANIC PENGUIN MIGRATION<sup>1</sup>

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**Abstract.** We tracked four male Magellanic Penguins (*Spheniscus magellanicus*) from the beginning of their winter migration for periods ranging from three to six weeks. Upon leaving the colony at Punta Tombo,

Argentina where they had bred and molted, all four birds traveled northeast along the coast at speeds consistent with sighting and band-return data which suggest a round-trip winter migration in this species of up to several thousand kilometers. Three of the birds followed a similar route, moved at approximately the same rate, and were still moving northeastward at a

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distance of over 800 km from the colony when signals ceased. The fourth bird departed from the northeast route at approximately 300 km into its trip and remained in a large bay for at least 29 days, when the last signal was received. Initially, the birds traveled rapidly and made few deep dives. Later, their rate of travel slowed, their paths became more erratic, and they made more deep dives, all indications of probable foraging. This suggests that location of the penguin migration route and rate of travel along it may be determined by seasonal movement of prey. As all birds were within 250 km of shore for the entire period in which signals were received, our results underscore the importance of controlling pollution associated with petroleum transport along the coast of Argentina, currently a major source of Magellanic Penguin mortality.

*Key words:* Magellanic Penguin, migration, penguins, satellite telemetry, *Spheniscus magellanicus*.

As with other penguins, little is known of Magellanic Penguins' (*Spheniscus magellanicus*) activities during the nonbreeding season. After chicks fledge, breeding adults undergo a synchronous molt in March and April and then leave the breeding colony, not to return until the following September or October. Their whereabouts during this 5-to-6 month period have been inferred from sightings of unmarked birds as well as band returns, mostly from dead birds that have washed ashore. These methods indicate that Magellanic Penguins migrate northward in the winter (Daciuk 1977), in some cases apparently more than 2,000 km (P. D. Boersma, unpubl. data). However, sightings of unmarked birds give no indication of breeding status or colony of origin, and band returns yield imprecise locations of live birds and give little indication of pattern of movement or distance from shore of migrating birds. Such information is important for the protection of this species, which is currently declining (Boersma 1997) primarily due to human activities at sea, chiefly commercial fishing and oil pollution (Gandini et al. 1994, Boersma and Stokes 1995).

The recent development of a practical technique for tracking penguins at sea using satellite telemetry has the potential to improve our understanding of penguin migration by providing precise day-to-day monitoring of live individuals of known breeding site, sex, age, and breeding status. Studies using this technique (Kerry et al. 1995, Davis et al. 1996) have documented long-distance post-breeding migration in Adie Penguins (*Pygoscelis adeliae*) in the Antarctic and have described the routes followed by individuals in the early part of the migration. Here we report on the first use of satellite telemetry to track the migration of a temperate penguin species, the Magellanic Penguin.

## METHODS

From 10–15 April 1996, we attached satellite transmitters to four male Magellanic Penguins (mean wt. of birds = 4.32 kg, range = 4.13–4.53) after they had finished molting at the large penguin colony at Punta Tombo, Argentina (44°02'S, 65°11'W). All four males were experienced breeders, having been banded as breeding adults in the colony prior to the study, and all had bred in the 1995–1996 season. Three of the

devices (attached to males #1–3) were 0.25-watt microprocessor-controlled satellite-linked time-depth recorder/transmitters manufactured by Wildlife Computers Inc. (Redmond, WA) using Telonics ST-10 transmitters. These devices, including waterproof epoxy housing, each weighed approximately 155 g, and had a cross-sectional area of 13.5 cm<sup>2</sup>, approximately 7–8% of the cross-sectional area of a male Magellanic Penguin. The fourth device (attached to male #4) was manufactured by Sirtrack Ltd. (Havelock North, New Zealand) and also used a Telonics ST-10 transmitter packed in an epoxy housing. It weighed 96 g and had a cross-sectional area of 6.5 cm<sup>2</sup>. We used fast-setting epoxy to attach the devices to the feathers in the center of the penguin's lower back. All devices had sloped leading and trailing faces and were positioned posterior to the line of maximum girth to minimize drag (Bannasch et al. 1994).

We programmed the Wildlife Computer devices to transmit at 45-sec intervals every other day, primarily during the night-time hours most likely to coincide with satellite passes. At night, Magellanic Penguins tend to rest at the ocean surface and hence the transmitter signal is less likely to be broken due to submerging of the antenna (P. D. Boersma, unpubl. data). The Sirtrack device was pre-set to transmit at 60-sec intervals for 6 hr every 72 hr. In addition to location, the Wildlife Computer devices recorded frequencies of dives in six depth classes (3–5, 6–10, 11–20, 21–40, 41–60, and 61–80 m) for 6-hr periods (03:00–09:00, 09:00–15:00, etc. local time) each day.

We received transmissions through the Service ARGOS satellite system. Sixty-one percent ( $n = 86$ ) of locations received ( $n = 140$ ) were based upon 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 upon locations received for birds at known positions (Stokes and Boersma, in press), locations calculated from three messages per pass (class 0 and class A,  $n = 45$ ) are sufficiently accurate for the purposes of this study (mean error  $\pm$  SD = 2.9  $\pm$  3.6 km,  $n = 12$ ). We did not use locations based upon fewer than three messages (class B and Z,  $n = 9$ ). For the purposes of calculating travel speed, we used only locations of class 1 or better. Maps of travel routes (Figs. 1 and 2) were made, and distances and swimming speeds calculated, using Arc/Info geographic information software (ESRI 1992). Values presented are means  $\pm$  SD.

## RESULTS

Upon leaving the colony, all birds initially traveled northeast (Fig. 1). After passing Peninsula Valdés, male #1 veered northwest into the Gulf of San Matías and stayed within the Gulf at least until signals stopped, a period of 29 days (Fig. 2). Males #2–4 continued in a northeastward direction, all moving along a similar path at approximately the same rate. None of the birds returned to the colony after leaving, and none were detected on land at any time while they were tracked.

The date of last received signal ranged from 1 to 20

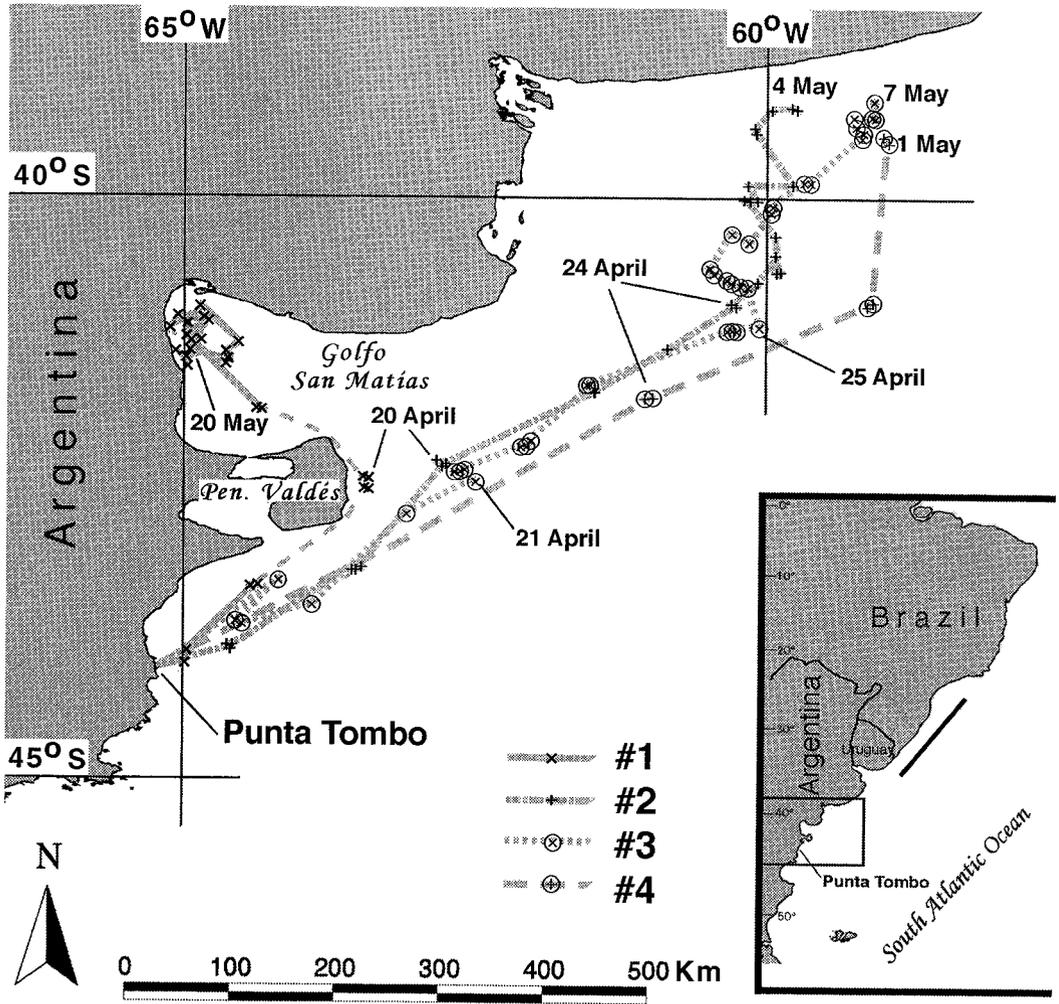


FIGURE 1. Migration routes of four Magellanic Penguins from Punta Tombo, Argentina, April and May 1996. All were males that had bred at Punta Tombo in the 1995–1996 season. Routes of males #1–3 were each based upon an average of 43 locations (range = 30–48). Six locations were received for male #4, two each on 24 and 27 April and 1 May. Dashed line indicates the shortest swimming route between the 18 and 22 April locations for male #1. Black line parallel to coast of South America in inset map indicates the section of coast where most penguins banded during the breeding season at Punta Tombo are found during the nonbreeding season.

May (Table 1). As all birds were seen alive and without transmitters the following season, the devices apparently fell off or failed within 3-to-6 weeks of application. At the time of the last signal from each transmitter, the birds' swimming distance from Punta Tombo averaged  $756 \pm 157$  km. Last locations for males #2–4 were all similar distances from the colony (Table 1). Minimum distance traveled by the tracked birds ranged from 844 to 1,216 km. These are likely to be underestimates of actual distance traveled because birds may have departed from the shorest path between known locations when devices were not transmitting. The location farthest from shore for all birds was 246 km (male #3, 25 April). Maximum distance

from shore was similar for males #2–4 (mean maximum =  $234 \pm 11.3$  km). After passing Peninsula Valdés, these three birds were between 100 and 200 km from shore for most of their routes.

The device with the smaller cross-sectional area (on male #4) undoubtedly caused less drag than the larger devices. Nonetheless, the similar location and rate of movement northward of males #2–4 suggest that although the devices probably affected swimming efficiency, they probably did not affect the pattern of movement.

Travel speed differed by stage of trip. Males #1–3 averaged  $69.4$  km day<sup>-1</sup> in the first week of travel, and  $29.6$  km day<sup>-1</sup> thereafter. Initial travel speed of males

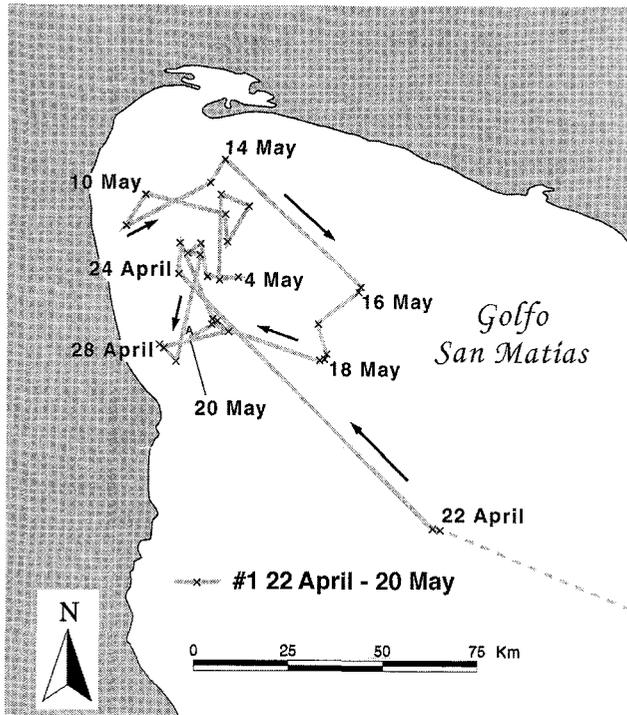


FIGURE 2. Route of male #1, within the Gulf of San Matías, 22 April–20 May 1996. Because of the finer spatial scale, locations of class A (6 of the 39 locations in this time period; see text) were excluded in making this figure. An “A” indicates last location received (20 May).

#1–3 differed very little (Table 1). Males #2 and 3 also had very similar subsequent speeds (37.9 and 37.8 km day<sup>-1</sup>, respectively), whereas male #1 averaged 13.1 km day<sup>-1</sup> during the time it spent in the Gulf of San Matías. Because we received no signals for male #4 before 24 April and were unable to determine its date of departure, its initial and subsequent speeds could not be compared. However, its rate of travel also slowed over the course of its trip, from 72.9 km day<sup>-1</sup> between 24–27 April to 53.1 km day<sup>-1</sup> between 27 April and 1 May.

Dive patterns of the birds also differed markedly between the first days of their trips and the remainder of the tracking period, with a smaller proportion of deep dives in the initial period. This difference was evident for both male #1 (which went to the Gulf of San Matías) and male #2 (which stayed off the coast), the two birds for which we have complete dive records (Fig. 3). For both birds, the distribution of dive depths differed significantly between the first week and thereafter, with more dives to greater depth after the first week (Fig. 4). Dive depth in the initial days of travel was not limited by ocean depth, which is greater than 50 m for most of the area traversed in the initial travel period.

Birds generally did not make deep dives at night. Of the total of 8,510 dives we recorded during 149 6-hr periods, only 45 were made during periods that included no daylight hours (21:00–03:00 local time;  $n$

= 46 6-hr periods), and only one of these was deeper than 5 m.

## DISCUSSION

Returns of bands found during the austral winter suggest that adult Magellanic Penguins breeding at Punta Tombo commonly migrate more than 2,000 miles northeastward along the coast of South America to the waters off the coast of southern Brazil (P. D. Boersma, unpubl. data). The results of the present study are consistent with this conclusion. The birds we tracked moved northeastward along the coast and although signals ceased when the birds were 486–873 km from the colony, the speeds at which they traveled to that point (> 800 km in three weeks for the three birds that continued northward) indicate that the 5-to-6 month migratory period is sufficient for the round-trip migration of up to 5,000 km suggested by band returns and sightings.

The difference between the paths of male #1 and the other three birds also is consistent with winter sightings and band recoveries. Although most bands have been recovered along the coast of southern Brazil (Fig. 1), some have been found along the Argentine coast much closer to Punta Tombo (P. D. Boersma, unpubl. data). Jehl (1974) reported seeing Magellanic Penguins of unknown age and breeding status in the Gulf of San Matías during a ship-transect winter bird survey of the Argentine coastal shelf, and Jehl et al. (1973) sighted

TABLE 1. Summary of movements of four male Magellanic Penguins departing from Punta Tombo, Argentina in April and May 1996, as determined by satellite telemetry. Distance from colony at last location is the minimum swimming distance; actual distance traveled was considerably greater (see text). Initial travel speed covers the first week following departure. Subsequent travel speed covers the remainder of the trip to the date of last signal. Initial and subsequent travel speed could not be determined for male #4 because date of departure from the colony was unknown.

Male	Last date at colony	Date of last location	No. of usable locations	Distance from colony at last location (km)	Greatest distance from shore (km)	Travel speed (km day <sup>-1</sup> )	
						Initial	Subsequent
#1	15 April	20 May	48	487	48	69.0	13.1
#2	14 April	4 May	30	806	219	70.2	37.9
#3	15 April	7 May	47	859	246	69.1	37.8
#4	≥15 April	1 May	6	873	238	—	—

Magellanic Penguins in the Gulf of San José (on the south margin of the Gulf of San Matías) in the winters of 1971 and 1972, estimating that 400 Magellanic Penguins wintered there in 1972. Thus, although it appears that most birds migrate thousands of kilometers, perhaps in a fairly well defined route, some may migrate much shorter distances. Differences among individuals also are observed in foraging location during the breeding season (Stokes and Boersma, in press).

These individual differences and the variable speed of movement by stage of trip suggest that migration pattern may depend upon the rate at which prey is encountered. Penguins may travel until they locate concentrations of anchovy (*Engraulis anchoita*), hake (*Merluccius hubbsi*), or other prey species, and only move when those concentrations move or are depleted. The location and dive data are consistent with this interpretation. In the initial days of their trips, although they probably had not eaten since they began molting several weeks earlier, the tracked penguins traveled in a direct route, at a fast rate, and made few deep dives.

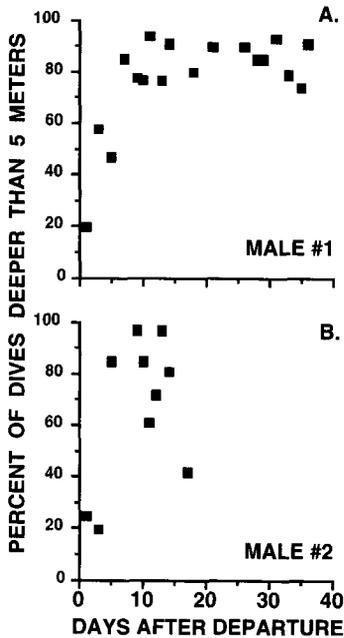


FIGURE 3. Percent of dives deeper than 5 m for (A) male #1 ( $n = 2,535$  dives) and (B) male #2 ( $n = 859$  dives) between 09:00 and 15:00 local time from date of departure from the colony to date of last signal. Only dives in the midday period are included in order to exclude periods of darkness when birds do little or no foraging. Male #3's dive record was incomplete because of device malfunction and therefore was not included.

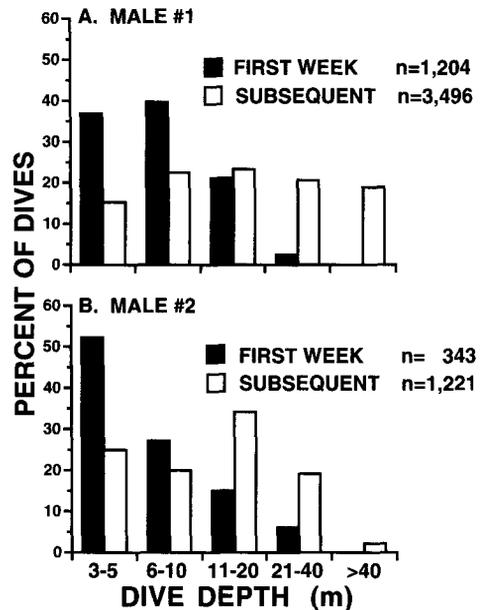


FIGURE 4. Dive depths of males #1 and #2 during 6-hr periods with some daylight (03:00–21:00 local time) in the first week of migration (16–22 April) versus remainder of period tracked. Dive depth frequencies differ significantly by stage of trip. (A) male #1 ( $\chi^2_4 = 705.0$ ,  $P < 0.001$ ). (B) male #2 ( $\chi^2_4 = 129.6$ ,  $P < 0.001$ ).

Later, their paths became more erratic, their travel speeds slower, and their dives deeper, all indications of probable foraging (Wilson 1995). Anchovy, an important component of the Magellanic Penguin diet during the breeding season at a colony approximately 100 km south of Punta Tombo (Frere et al. 1996), are distributed over the continental shelf along the South American coast from approximately 23°S to 47°S, and spawn in high concentrations in the summer between 37°S and 41°S (Lima and Castello 1995). Spawning activity moves northward in fall, and in winter occurs off the coast of southern Brazil, the same section of coast where most banded penguins from Punta Tombo are found between breeding seasons. Thus, the route of Magellanic Penguin migration may follow seasonal movements of anchovy.

The results of this study have implications for conservation. Migrating Magellanic Penguins appear to remain relatively close to shore (within 300 km), and consequently are in the coastal shipping lanes presently used by tankers transporting petroleum from oil terminals south of Punta Tombo to refineries in Buenos Aires. Oil spills and oily ballast discharge associated with this oil transport are estimated to kill 41,000 Magellanic Penguins annually along the coast of southern Argentina (Gandini et al. 1994). Nearly all the lethally oiled penguins observed each year at Punta Tombo and other breeding colonies are seen at the beginning of the breeding season, when birds are returning from winter migration. Taken together, these observations suggest that effective conservation of this species depends upon large-scale approaches that address its extensive marine habitat requirements, and in particular, the problem of chronic oil pollution along its migration route in the coastal waters of Argentina.

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## LITERATURE CITED

- ARGOS. 1996. User's manual. CLS Service Argos, Toulouse, France.
- BANNASCH, R., R. P. WILSON, AND B. CULIK. 1994. Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *J. Exp. Biol.* 194:83-96.
- BOERSMA, P. D. 1997. The decline of Magellanic Penguins. *Penguin Conserv.* 10:2-5.
- BOERSMA, P. D., AND D. L. STOKES. 1995. Conservation: threats to penguin populations, p. 127-139. *In* T. D. Williams [ed.], *The penguins*. Oxford Univ. Press, Oxford.
- DACIUK, J. 1977. Notas faunísticas y bioecológicas de Península Valdés y Patagonia IV. Observaciones sobre áreas de nidificación de la avifauna del litoral marítimo Patagónico (Provincias de Chubut y Santa Cruz, Rep. Argentina). *El Hornero* 11: 361-376.
- DAVIS, L. S., P. D. BOERSMA, AND G. S. COURT. 1996. Satellite telemetry of the winter migration of Adélie Penguins (*Pygoscelis adeliae*). *Polar Biol.* 16: 221-225.
- ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE (ESRI). 1992. ARC/INFO. ESRI, Redlands, CA.
- FRERE, E., P. GANDINI, AND V. LICHTSHEIN. 1996. Variación latitudinal en la dieta del pinguino de Magallanes (*Spheniscus magellanicus*) en la costa Patagónica, Argentina. *Ornithol. Neotropica* 7:35-41.
- GANDINI, P., P. D. BOERSMA, E. FRERE, M. GANDINI, T. HOLIK, AND V. LICHTSHEIN. 1994. Magellanic Penguins are affected by chronic petroleum pollution along the coast of Chubut, Argentina. *Auk* 111:20-27.
- JEHL, J. R., JR. 1974. Distribution and ecology of marine birds over the continental shelf of Argentina in winter. *San Diego Soc. Nat. Hist. Trans.* 17: 217-234.
- JEHL, J. R., JR., M. A. E. RUMBOLL, AND J. P. WINTER. 1973. Winter bird populations of Golfo San Jose, Argentina. *Bull. Br. Ornithologists' Club* 93:56-63.
- KERRY, K. R., J. R. CLARKE, AND G. D. ELSE. 1995. The foraging range of Adélie Penguins at Bechervaise Island, Mac.Robertson Land, Antarctica as determined by satellite telemetry, p. 216-243. *In* P. Dann, I. Norman, and P. Reilly [eds.], *The penguins: ecology and management*. Surrey Beatty, Sydney.
- LIMA, I. D., AND J. P. CASTELLO. 1995. Distribution and abundance of South-west Atlantic anchovy spawners (*Engraulis anchoita*) in relation to oceanographic processes in the southern Brazilian shelf. *Fish. Oceanogr.* 4:1-16.
- STOKES, D. L., AND P. D. BOERSMA. In press. Where breeding Magellanic Penguins forage: satellite telemetry results and their implications for penguin conservation. *Mar. Ornithol.*
- WILSON, R. P. 1995. Foraging ecology, p. 81-106. *In* T. D. Williams [ed.], *The penguins*. Oxford Univ. Press, Oxford.