

JACKASS PENGUIN *SPHENISCUS DEMERSUS* MOVEMENTS, INTER-ISLAND VISITS, AND SETTLEMENT

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Abstract.—Between 1952 and 1984 14,500 Jackass Penguins (*Spheniscus demersus*) were banded at breeding localities off the coast of South Africa and Namibia. Of these 185 were recovered alive or dead on the mainland and 184 were resighted alive on islands other than where they were banded. Penguins banded as chicks migrated rapidly away from their natal islands and generally moved clockwise around the southern African coast. They occasionally visited non-natal islands before returning to their natal island. Those from the eastern Cape moved westwards towards the Agulhas Bank and Benguela upwelling areas, whereas those from the southwestern Cape and Namibia remained within the Benguela system. Adults, particularly breeders, appeared to be sedentary and rarely visited other islands. Penguins banded as chicks generally settled and bred at their natal islands; the exceptions emigrated to islands in the general area of the natal island. No breeders were recorded settling or breeding at more than one island. Emigration and immigration are apparently rare in Jackass Penguins and cannot explain recent population trends of the species.

MOVIMIENTOS, VISITAS INTER-ISLAS Y ESTABLECIMIENTO DE RESIDENCIA EN EL PINGÜINO *SPHENISCUS DEMERSUS*

Sinopsis.—Entre 1952 y 1984 un total de 14,500 pingüinos (*Spheniscus demersus*) fueron anillados en sus áreas de anidamiento en los alrededores de las costas de Africa del Sur y Namibia. De estos, 185 se recobraron vivos o muertos en tierra continental y 184 fueron observados en lugares diferentes (islas) a las que fueron anillados. Los polluelos anillados se alejaron rapidamente de las islas en donde nacieron por lo general en dirección destrógira alrededor de la costa sur de Africa. Visitaron de forma ocasional otras islas previo a regresar a su lugar natal. Las aves del este del cabo se movieron al oeste hacia el Banco Agulhas y el área de Benguela, mientras que aquellos del oeste del cabo y Namibia permanecieron en el área de Benguela. Los adultos, particularmente individuos reproductores, parecen ser sedentarios y raras veces visitan a otras islas. La gran mayoría de los polluelos anillados regresaron a su isla natal para reproducirse; muy pocos migraron a islas adyacentes. Ninguna de las aves se reprodujo en más de una isla. Patrones de emigración e inmigración son aparentemente raros en este pingüino y no dan lugar a explicar los cambios poblacionales de esta especie.

This paper presents the first analysis of resightings and recoveries of Jackass Penguins *Spheniscus demersus* banded at breeding islands off the coast of South Africa and Namibia. The primary aim is to provide basic information on movements, particularly long-distance movements, of dif-

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ferent age classes and to establish if any migration pattern could be discerned. A secondary aim was to establish if inter-island movement and settlement occurred, and whether differences in regional population trends could be ascribed to emigration and immigration.

Movement patterns remain one of the least understood aspects of penguin biology. Little is known about Jackass Penguin movements apart from the fact that they occasionally visit islands hundreds of kilometers from their natal islands, and will return to the natal island if artificially displaced (Randall et al. 1981).

STUDY AREA

Jackass Penguins breed on islands and a few mainland localities around the coast of southern Africa from Bird Island (33°51'S, 26°17'E) in Algoa Bay in the east to Sylvia Hill (25°10'S, 14°56'E) in the west (Fig. 1; Shelton et al. 1984). For convenience we have divided breeding localities into three areas: (1) Eastern Cape comprising six islands; (2) South-western Cape comprising 10 islands and the mainland site Stony Point; (3) Namibia comprising seven islands and the mainland site Sylvia Hill.

METHODS

Since 1947 Jackass Penguins have been marked with flipper bands (Cooper and Morant 1981). In 1972 stainless steel bands were introduced that could be read at a distance of up to 15 m with binoculars, whereas penguins banded prior to 1972 had to be caught in order to read the band. Most resightings were obtained from the stainless steel bands.

Recoveries were from banded penguins found dead or alive on mainland beaches and reported to the South African Bird Ringing Unit (SAFRING) by members of the public. Our analysis spanned the period 1952–Jun. 1984.

The types of movements recognized were: (1) inter-island movements based upon resightings; (2) mainland recoveries based upon recoveries on mainland beaches. The distance involved in each movement was taken as the distance between the points of banding and recovery or resighting along a line 10 km offshore running roughly parallel to the coastline. This procedure smoothed out small bays and headlands on the coast. For inter-island movements we have used the terms *visiting*, *settling*, and *breeding* to describe the activity of the penguins when observed. *Visiting* was used if a penguin was recorded on one occasion and was not engaged in any breeding activity. *Settling* was used for a penguin observed on two or more occasions on that island, or when it was observed defending a nest site or paired with another. *Breeding* was used for a penguin incubating eggs or guarding chicks.

At the time of banding, three age classes were recognized: (1) *Chicks*—fledglings ready to go to sea for the first time; (2) *Juveniles*—penguins in juvenile plumage that had already been to sea. Juvenile plumage is acquired prior to fledging and is lost at the post-fledging moult, which occurs at any time between 11 and 23 mo after fledging (Randall 1983);

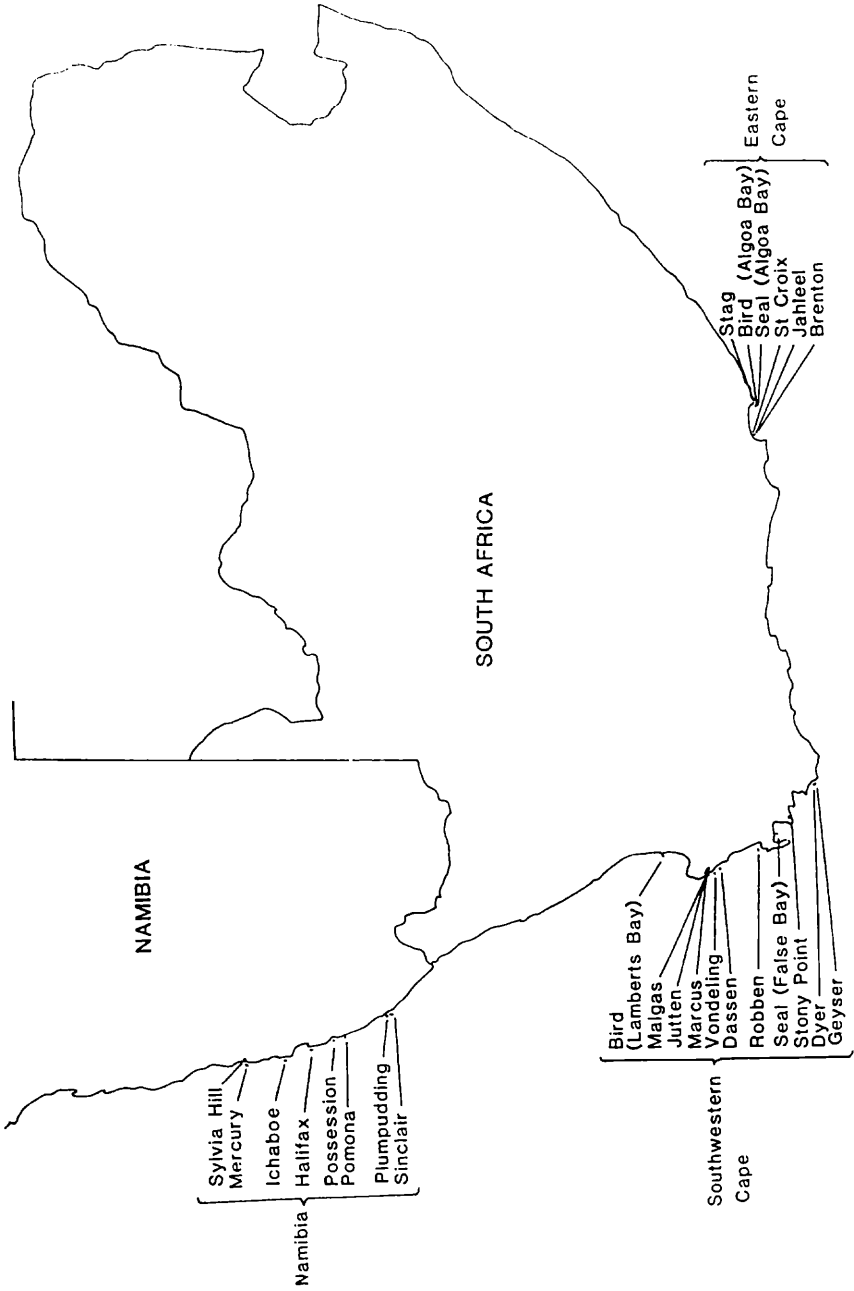


FIGURE 1. Breeding localities of Jackass Penguins showing the three areas referred to in the text.

TABLE 1. Numbers of Jackass Penguins banded and resighted on islands other than where they were banded, 1952-1984.

Age	Banding Area	Number	Resightings		
			Eastern Cape	South-western Cape	Namibia
Chicks	Eastern Cape	1561	10	19	1
	Southwestern Cape	4353	1	26	13
	Namibia	1055	—	1	19
Juveniles	Eastern Cape	227	9	5	—
	Southwestern Cape	623	3	32	1
	Namibia	10	—	—	—
Adults	Eastern Cape	1098	1	—	—
	Southwestern Cape	5516	3	40	—
	Namibia	57	—	—	—

(3) *Adults*—penguins in adult plumage, but not necessarily breeders. Many of those banded were in 'beach groups' or were moulting at the time, so their breeding status was unknown.

The Mann-Whitney *U*-test (Zar 1984) was used to compare distances moved east and west from islands where penguins were banded.

RESULTS

A total of 14,500 Jackass Penguins were banded on islands off southern Africa between 1952 and Jun. 1984 (Table 1). By Jun. 1984 184 individuals had been sighted at islands other than where they were banded, and 185 had been recovered on mainland beaches.

Penguins Banded as Chicks

Inter-island movements.—A total of 90 penguins banded as chicks were resighted on islands other than their natal island. The pattern of resightings differed on the east and west coasts. Penguins from the eastern Cape island were most often (63%) resighted on southwestern Cape islands (Table 1). Resightings on other eastern Cape islands were the next most frequent, and there was one record from a Namibian island. Most (87%) of those banded on the eastern Cape islands were seen on islands west of their natal island.

On the southwestern Cape islands 65% of the resightings were on other southwestern Cape islands (Table 1). Of the remainder all except one, resighted on an eastern Cape island, were resighted on Namibian islands. Overall, 88% of the penguins from the southwestern Cape islands had moved in a northerly direction. The situation on the Namibian islands was similar to that on the southwestern Cape islands, except that an even higher proportion (95%) were resighted on other islands in the area. Most (85%) inter-island movements of penguins from the Namibian islands were in a northerly direction.

TABLE 2. The occurrence and activity of Jackass Penguins at islands other than where they were banded.

Area	Age at banding	Number banded	Activity at other islands		
			Present	Settling	Breeding
Eastern Cape	Chick	1561	30	3	2
	Juvenile	227	14	5	2
	Adult	1098	1	—	—
Southwestern Cape	Chick	4353	40	4	1
	Juvenile	623	36	16	6
	Adult	5516	43	10	3
Namibia	Chick	1055	20	—	—
	Juvenile	10	—	—	—
	Adult	57	—	—	—
Totals	Chick	6969	90	7	3
	Juvenile	860	50	21	8
	Adult	6671	44	10	3

Almost a fifth of those seen on islands other than their natal island are known to have subsequently returned to their natal island. There was a marked regional variation in the proportion that subsequently returned with figures of 50%, 5% and 0% for the eastern Cape, southwestern Cape, and Namibia, respectively.

A small proportion (8%) of those that were seen on islands other than their natal island appeared to be settling (Table 2). These involved three from eastern Cape islands, one of which appears to have settled at another eastern Cape island and two at southwestern Cape islands; and four from southwestern Cape islands, three of which appear to have settled at other southwestern Cape islands and one at an eastern Cape island.

Breeding at islands other than the natal island was rarely recorded (Table 2). One from an eastern Cape island bred at another eastern Cape island, another bred at a southwestern Cape island and one from a southwestern Cape island bred at another southwestern Cape island.

Some individuals appeared very mobile and undertook several inter-island movements. Most of these multiple movements were to islands in the same area. Sightings at other islands were mostly within 3 yrs of banding (Table 3). Five individuals were known to have returned to their natal islands before being seen elsewhere.

Mainland recoveries.—A total of 112 penguins banded as chicks were recovered on the mainland, usually hundreds of kilometers from their natal islands (Table 4). This and the fact that most were recovered soon after fledging, 74% within six months and 84% within one year, showed that fledglings moved rapidly and far from their natal islands. Recoveries after 2 yrs were closer to natal islands, indicating that individuals had probably returned (Table 4). These later recoveries were mostly of penguins that were already adults.

Eastern Cape penguins tended to move in a westerly direction and 83%

TABLE 3. The ages of Jackass Penguins when first sighted on islands other than where they were banded.

Age at banding	Time after banding (yrs)					
	<1	1-2	2-3	3-4	4-5	>5
Chicks	2	48	19	4	7	10
Juveniles	9	4	2	10	7	18
Adults	7	8	5	2	2	20

($n = 72$) of recoveries were from the west of the natal island. The distance-frequency distributions of the westward ($\bar{x} = 469$ km, median = 468 km, range 20–1090 km) and eastward ($\bar{x} = 254$ km, median = 235 km, range 20–630 km) displacements were both markedly skewed. Westward movements were significantly greater than eastward movements ($P < 0.01$). Several eastern Cape penguins were recovered on the west coast of southern Africa within the area of the southwestern Cape islands, between 700 km and 1130 km westwards.

Southwestern Cape penguins tended to move in a northerly direction with 72% ($n = 39$) recovered north of their natal island. The distance-frequency distributions of northward ($\bar{x} = 355$ km, median = 150 km, range 30–1350 km) and southward ($\bar{x} = 345$ km, median = 210 km, range 40–1210 km) displacements were also markedly skewed. There was no significant difference in the north and south displacements ($P < 0.10$). Two southwestern Cape penguins had moved to the east coast, beyond the eastern Cape islands. Four southwestern Cape penguins were recovered farther north than the Namibian islands.

There was a single mainland recovery of a Namibian penguin banded as a chick. It was recovered within a year 510 km north of its natal island.

Penguins Banded as Juveniles

Inter-island movements.—Fifty penguins banded as juveniles were resighted on other islands (Table 1). None of those banded on the Namibian islands was resighted elsewhere. Resightings of penguins banded on the eastern Cape islands were usually on other eastern Cape islands, but they were also seen on the southwestern Cape islands (Table 1). Most (64%) from eastern Cape islands had moved in a westerly direction. Resightings of those banded on southwestern Cape islands were likewise often from other islands in the area (Table 1). Few had moved out of the area and these tended to move towards the east coast. Most (72%) from southwestern Cape islands had moved in a southerly direction.

A small proportion (8%) of those seen at islands other than where they were banded are known to have subsequently returned. They were all originally banded on St Croix Island to which they returned and settled.

Of those penguins seen at islands other than where they were banded, a relatively high proportion (42%) settled (Table 2). The proportions

TABLE 4. Number of mainland recoveries of Jackass Penguins in 100 km distance units from the banding locality.

	Years after banding						Total
	<1	1-2	2-3	3-4	4-5	>5	
Chicks							
0-100	8	1	—	—	2	1	12
100-200	21	1	2	2	—	—	26
200-300	11	—	—	—	1	—	12
300-400	14	1	—	1	1	1	18
400-500	5	1	—	—	—	—	6
500-600	14	—	—	—	—	—	14
600-700	7	—	—	—	—	—	7
700-800	3	2	1	—	—	—	6
800-900	5	—	—	—	—	—	5
900-1000	1	—	—	—	—	—	1
1000+	5	—	—	—	—	—	5
Total	94	6	3	3	4	2	112
Juveniles							
0-100	1	—	—	1	—	1	3
100-200	1	1	—	—	1	—	3
200-300	—	—	—	—	—	—	—
300-400	—	—	—	—	—	—	—
400-500	—	—	—	—	—	—	—
500-600	1	1	—	—	—	—	2
600-700	—	—	—	—	—	—	—
700-800	—	—	—	—	—	—	—
800-900	—	—	—	—	—	—	—
900-1000	—	—	—	—	—	—	—
1000+	—	1	—	—	—	—	1
Total	3	3	—	1	1	1	9
Adults							
0-100	11	6	2	2	1	5	27
100-200	2	1	2	—	1	7	13
200-300	2	2	1	2	1	2	10
300-400	3	2	—	1	—	2	8
400-500	2	—	—	—	—	—	2
500-600	—	—	—	—	—	—	—
600-700	1	—	—	—	—	—	1
700-800	—	—	—	—	—	1	1
800-900	—	—	—	—	—	1	1
900-1000	—	—	—	—	—	—	—
1000+	1	—	—	—	—	—	1
Total	22	11	5	5	3	18	64

were similar for the eastern Cape and southwestern Cape islands, being 36% and 44%, respectively. Breeding was also reported for a relatively high proportion (16%) (Table 2). The proportions for the eastern Cape (14%) and southwestern Cape (17%) were similar.

Mainland recoveries.—Nine penguins banded as juveniles were recovered on the mainland. Most recoveries were within 2 yrs of banding

and varied greatly in distance from the place of banding (Table 4). Later recoveries were all close to the island where the penguins were banded.

Five of the six recoveries of eastern Cape penguins were found west of the island where banded, and, despite the small sample size, westward movements were found to be more extensive than eastward ones. None was recorded as far west as the southwestern Cape islands, although two were within 100 km of Dyer Island. Two of the recoveries were made more than 3 yrs after banding, by which time the penguins would have been of breeding age, and both recoveries were near the island of banding. Two of the three recoveries of southwestern Cape penguins were recovered north of the island where banded. One was recovered farther north than the Namibian islands.

Penguins Banded as Adults

Inter-island movements.—A total of 44 penguins banded as adults were resighted on other islands (Table 1). Only two of these were known breeders and in each case they were present in beach groups. Both records involved short distance movements to islands in the same area; one of the two breeders returned to its breeding island and resumed breeding. The status of the other 42 penguins was unknown at the time of banding and many were caught in beach groups. They had all been banded on southwestern Cape islands and most (69%) had moved in a southerly direction. The great majority (93%) were resighted on other southwestern Cape islands (Table 1). The exceptions were three individuals resighted on eastern Cape islands.

Ten of the 42 penguins appeared to have settled on the islands where they were resighted, and three subsequently bred there (Table 2). Only one of the 42 was seen again on the island where it had been banded.

No complex inter-island movements were noted among adults. Apart from the breeding adult and one other which returned to the island where banded, none of the 44 were known to have visited other islands.

A relatively high proportion of resightings at other islands was first recorded (34%) within 2 yrs of banding. The proportion decreased thereafter, although many were first reported after 5 yrs (Table 3).

Mainland recoveries.—A total of 64 penguins banded as adults were recovered on mainland beaches, usually within 400 km of the banding locality (Table 4).

Eastern Cape adults ($n = 37$) were recovered with a similar frequency both east (46%) and west (54%) of the banding locality. The distance-frequency distributions of westward ($\bar{x} = 304$ km, median = 295 km, range 20–830 km) and eastward ($\bar{x} = 126$ km, median = 120 km, range 5–320 km) displacements had a large variance. The extent of westward movements was significantly greater than eastward movements ($P < 0.01$). Two known breeders were recovered on the southern section of the west coast within the area of the southwestern Cape islands.

Southwestern Cape adults ($n = 27$) were recovered in similar numbers both north (56%) and south (44%) of the island where banded. The

distance-frequency distributions of northward ($\bar{x} = 91$ km, median = 75 km, range 5–285 km) and southward ($\bar{x} = 270$ km, median = 200 km, range 5–1050 km) displacements had a large variance and the southward displacements were markedly skewed. Southward movements were significantly greater than northward movements ($P < 0.05$). Three adult penguins were recovered on the east coast; one had passed beyond the eastern Cape islands, and the other two were recovered on the western part of the east coast. None of these had been recorded breeding. No adult from the southwestern Cape islands was recovered as far north as the Namibian islands.

DISCUSSION

The return of young Jackass Penguins to their natal island after they were resighted at other islands (as high as 50%) shows that these movements can be regarded as a migration. The marked regional difference in the incidence of returns (0% in Namibia to 50% in the eastern Cape) can be ascribed to greater search effort on the eastern Cape islands.

The rapid and extensive movement of Jackass Penguins from their natal area after fledging is a feature common to all penguins for which information is available (e.g., Boersma 1976, Reilly and Cullen 1982, Richdale 1957). This early migratory phase of the Jackass Penguin's life cycle contrasts with the later sedentary adult phase. A non-migratory adult phase is comparatively rare among penguins, except for the genera *Spheniscus*, where only the southern populations of the Magellanic Penguin *S. magellanicus* migrate (Stonehouse 1967), and *Eudyptula* (Reilly and Cullen 1982). The less extreme climate in the lower latitudes where species of these genera occur probably accounts for this phenomenon.

Post-fledging migration of Jackass Penguins from all three island groups showed a strong clockwise movement around the coast. Thus, eastern Cape penguins invariably moved in a westerly direction, whereas both southwestern Cape and Namibian penguins moved northward. Resightings on other islands and recoveries showed that eastern Cape penguins visited the Atlantic Ocean seaboard, whereas west coast (southwestern Cape and Namibian) penguins visited the Indian Ocean seaboard rarely. The result was that most young eastern Cape penguins moved towards the Agulhas Bank and Benguela upwelling areas, whereas young penguins from the southwestern Cape and Namibian islands remained in the Benguela upwelling area of the west coast. Both the Agulhas Bank and the Benguela upwelling areas are regions of high productivity (Shannon et al. 1984, Zoutendyk 1973) and abundant pelagic shoaling fish (Crawford 1981). The apparently contradictory result that most penguins banded as juveniles on the southwestern Cape islands had moved in the opposite direction is thus easier to explain. The natal island of these penguins was unknown at banding and they probably originated from the eastern Cape islands or from other southwestern Cape islands to the south of where they were resighted.

Settling and breeding at islands other than the natal island was rare

and no breeding adults were known to have settled or bred at other islands. Long-distance movements resulting in settling or breeding were extremely rare. A substantially higher proportion of penguins banded as juveniles settled and bred at other islands. This is most likely a consequence of banding juvenile penguins that were visiting the island at the time, and the island where they finally settled was probably their natal island. Some adults settled, including one that bred, at islands other than where they were banded. Since these were caught in beach groups and not breeding colonies we cannot ascertain what their age or breeding status was at banding, and their movements may not represent true adult movements. Whether these were really settlements at islands other than the natal or breeding island is also uncertain as was shown by the presence of a breeding adult in a beach group at another island. The observed movements were most likely those of penguins returning to their breeding island after having been caught in a beach group at another island while visiting.

Overall the numbers of Jackass Penguins have declined since the mid-1950s (Crawford and Shelton 1981). Regionally there have been differences in population trends; on eastern Cape islands there were increases, on southwestern Cape islands (except Dyer Island) decreases, on southern Namibian islands decreases and on northern Namibian islands increases (Crawford and Shelton 1981). Our results indicate that these trends are unlikely to be caused by emigration from some areas and immigration to others (e.g., southwestern Cape to eastern Cape). Movements from one island to another in the same area are more likely and it is probable that the recent establishment of breeding colonies on Robben Island and Stony Point (Shelton *et al.* 1984) was due to immigration from other southwestern Cape islands. Our findings also suggest that the occupation of these sites was by young penguins and not breeding adults.

Large-scale immigration, usually over a short period, has been recorded for more than one penguin species (Budd 1975; Trivelpiece and Volkman 1979). Ainley *et al.* (1983) suggested that these large-scale immigrations could be related to breeding habitat destruction at the previous breeding site. No such immigrations have been noted for Jackass Penguins, and the low incidence of emigration observed in this study is a more typical penguin pattern. The cause of an emigration may have nothing to do with limited resources, since a small portion of a seabird population will disperse regardless of resource availability (Ainley *et al.* 1983). The reoccupation of Robben Island by Jackass Penguins would be difficult to explain by any other hypothesis, since it is near (ca. 50 km) to Dassen Island where there is abundant nesting space and a difference in food abundance is not expected.

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