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Patterns of immigration to and emigration from breeding colonies by African penguins

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Of over 20 000 African penguins *Spheniscus demersus* that had been flipper-banded as chicks between 1978 and 1999, 2% of those re-sighted after fledging settled to breed at non-natal colonies. This represented 14% of the banded birds that were subsequently recorded breeding. Only one of these immigrants had previously been recorded breeding at its natal colony, the rest presumably being first-time breeders. The largest proportions of banded chicks that emigrated came from Dyer Island on the south coast of South Africa, all of which settled at colonies to the west or north. Penguins emigrating from Namibian breeding colonies either

relocated to the Western Cape of South Africa or settled at colonies farther to the north in Namibia. Emigration and immigration of African penguins are thought to be driven by changes in the distribution and availability of their prey. Eight penguins that were banded in adult plumage were found to have attempted breeding at more than one locality. All were survivors of the *Apollo Sea* oil spill of 1994 and had been cleaned and released by the Southern African Foundation for the Conservation of Coastal Birds. This is thought to be the first documented evidence of attempted breeding by African penguins at more than one locality.

Keywords: African penguin, breeding colonies, emigration, immigration, Spheniscus demersus

Introduction

The African penguin Spheniscus demersus population decreased by at least 90% during the 20th century (Shannon and Crawford 1999, Underhill 2000, Crawford et al. 2001), with present trends differing between colonies (Crawford et al. 2001). The rate of decline or increase of some of these colonies can only be explained by the emigration of birds from and immigration of birds to breeding colonies. The growth in colony size recorded at Dyer Island between 1956 and 1967, and at Robben Island and The Boulders between 1989 and 1995, was attributed mainly to immigration of first-time breeders from other colonies (Shelton et al. 1984, Crawford et al. 1999, Crawford et al. 2000). Randall et al. (1987) stated that settlement and breeding at colonies other than the natal one, by African penguins banded as chicks, was rare and that breeding adults are both colony and site faithful. None

were known to have settled or attempted to breed at any colony other than that at which they were established breeders (Randall *et al.* 1987). These statements are reexamined using the database of African penguin resightings held by the Avian Demography Unit (ADU), University of Cape Town.

Material and Methods

Between 1970 and 1998, 23 400 African penguin chicks were flipper-banded at breeding colonies. Three regions were considered: the Eastern Cape (Algoa Bay colonies) and Western Cape of South Africa, and Namibia (Figure 1). Re-sightings of flipper-banded penguins were made in all three regions up until October 1999 by observing birds through binoculars or a telescope. Re-sightings of banded

birds were made in the Eastern Cape from 1971 until 1986 and resumed again in 1992. Re-sightings in the Western Cape were made at Dassen Island in the early 1970s, at Marcus Island in the early 1980s (La Cock *et al.* 1987, J Cooper, ADU, pers. comm.), and at all colonies from 1989 (e.g. Crawford *et al.* 1995), but were greatly intensified from August 1994, following the *Apollo Sea* oil spill. Regular re-sightings at the Namibian breeding colonies began at Ichaboe Island in 1988, extending to Mercury Island in 1991, Halifax Island in 1995 and Possession Island in 1996 (J Kemper, Ministry of Fisheries and Marine Resources, Namibia, unpublished data).

The database of re-sightings was investigated for evidence of chicks settling at non-natal colonies and of

adults attempting to breed at more than one colony. Birds banded as chicks were considered to have emigrated if they were found incubating eggs or guarding chicks at a colony other than their natal colony. Birds banded as adults were included in the analysis if they were recorded incubating eggs or guarding chicks at more than one colony. In the case of adults, their natal colony was rarely known and their breeding status at the time of banding was seldom recorded on banding schedules. Emigrations between and within regions were investigated, along with the years when most emigration was detected. Data suggesting emigration, particularly those for birds banded as adults, were rigorously checked for the possibility of reading or transcription errors.

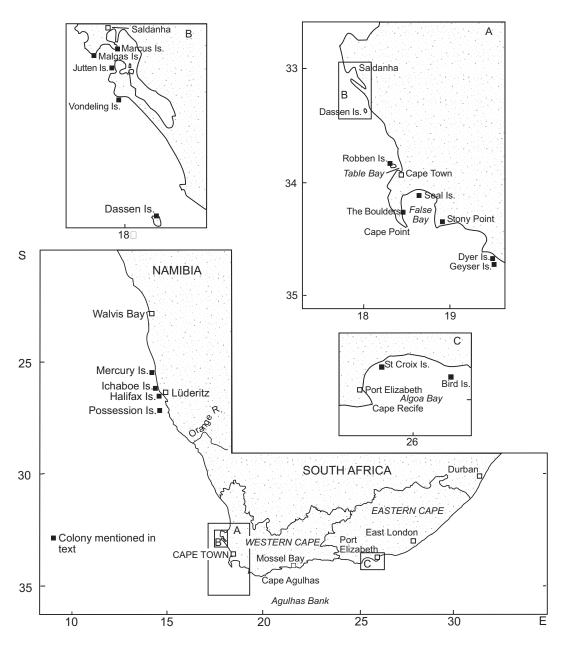


Figure 1: Locations of colonies of African penguins considered in the text (after Crawford et al. 2001)

Results

Penguins banded as chicks

A total of 4 004 chicks was seen alive after banding, 598 of which were recorded breeding. Of the 4 004 chicks resighted, 1 006 (25%) were seen at non-natal colonies. A total of 84 was found to have settled to breed at non-natal colonies, whereas 514 were recorded breeding at natal colonies. Those breeding at non-natal colonies constituted 2% of the total number re-sighted and 14% of those recorded breeding. Only one of the birds breeding at a non-natal colony (banded as S11099) was also recorded breeding at its natal colony. It was recorded incubating one egg, when in its third year, at its natal colony, Robben Island. It was later seen incubating eggs at Dassen Island when in its fourth year. There were 27 pairs of localities recorded among the birds that settled at non-natal colonies (Table 1). In all, 13 of the birds settled in another region (Table 2). Colonies from which penguins banded as chicks emigrated numbered one in the Eastern Cape, six in the Western Cape and four in Namibia. They recruited to one colony in the Eastern Cape, nine in the Western Cape and two in Namibia (Table 1).

Of the five birds emigrating from colonies in the Eastern Cape, four remained within the region (Table 2), moving 48km from St Croix Island to Bird Island (Table 1). The fifth bird (V0685) moved to a colony in the Western Cape. It was in its fourth year after banding on St Croix Island when found incubating an egg at Stony Point, but it disappeared after this sighting.

In the Western Cape, all but two of the 65 birds that emigrated settled at other colonies within the region (Table 2). One bird (V7854) from Jutten Island settled at Bird Island in the Eastern Cape, whereas another (S2202) left Dyer Island for Ichaboe Island in Namibia. The latter bird was only sighted once, when it was incubating eggs, nearly six years after it was banded. The majority of emigrations (29) took place from Dyer Island on the South Coast (Table 1), most (11) settling at Dassen Island on the West Coast. Six and five birds respectively settled at the two South African mainland colonies of Stony Point and The Boulders, and four at the recently re-colonised Robben Island. Twenty-one birds emigrated from Dassen Island, 19 of which settled at nearby Robben Island, 51km to the south. Seven birds emigrated from Robben Island to Dassen Island.

Of the 14 birds recorded emigrating from Namibian colonies, 10 (70%) settled in the Western Cape, the remainder settling at other Namibian colonies (Table 2). All but one of those that settled in the Western Cape did so at Robben or Dassen islands (Table 1). The other bird (V3449) settled at Dyer Island. The four birds that settled within Namibia did so at localities to the north of their natal colonies.

Immigration of birds to Robben and Dassen islands accounted for 63% of the total number of birds banded as chicks that emigrated. These two colonies received the highest intensity of monitoring during the period between 1995 and 1999. The two South African mainland colonies at The Boulders and Stony Point recorded five or more

 Table 2: Emigration and immigration of birds banded as chicks by

 region. Birds were considered to have immigrated to a region if

 they bred there. Numbers making each movement are indicated

Emigrated		Immigrated to	
from	Eastern Cape	Western Cape	Namibia
Eastern Cape	4	1	0
Western Cape	1	63	1
Namibia	0	10	4

Table 1: Localities involved in emigration and immigration by African penguins banded as chicks. Birds were considered to have immigrated to a colony if they bred there. Numbers making each movement are indicated

						Cole	ony re	cruited t	0					
		Eastern Cape				We	stern (Cape					Namit	oia
Colony left from		BI	DYI	SP	SI	BB	RI	DAS	JI	VI	MCI	П	MYI	Total
Eastern Cape	SCI	4		1										5
Western Cape	DYI			6	1	5	4	11		1		1		29
ricetenii eupe	SP		1											1
	RI					1		7	1					9
	DAS					1	19				1			21
	JI	1												1
	MCI		1				1	2						4
Namibia	PSI							1				1		2
	HI						1	3				1		5
	Ш							2					2	4
	MYI		1				1	1						3
	Total	5	3	7	1	7	26	28	1	1	1	3	2	84
BB = The Boulders			= Icha	boe Isla	and			F	RI = R	obben	Island			
BI = Bird Island (Alg	J	I = Jutt	en Islai	nd			SCI = St Croix Island							
DAS = Dassen Islai	N	1CI = N	larcus	sland			SI = Seal Island (False Bay)							
DYI = Dyer Island		N	1YI = N	lercury	Island			5	SP =St	ony Po	bint	,		
HI = Halifax Island				ossessi		nd					g Island			

	Easter	n Cape			W	estern Ca	ре				Namibia	1	
Year banded	BI	SCI	DYI	SP	RI	DAS	JI	MCI	PSI	HI	Ш	MYI	Total
1978								1					1
1979		1											1
1980													0
1981		1											1
1982		1											1
1983		1						1					2
1984		1	2			2							5
1985			1			2							3
1986				1				2			1		4
1987			1									1	2
1988			2				1						3
1989						3					1		4
1990			4			2				4			10
1991			13		2	5			2	1	1		24
1992			5		6	4					1		16
1993					1	3						2	6
1994													0
1995			1										1
Total		5	29	1	9	21	1	4	2	5	4	3	84

Table 3: Years of banding of chicks that subsequently emigrated from their natal colonies to breed at other colonies. See Table 1 for locality abbreviations

immigrations, as did Bird Island in Algoa Bay. These three colonies were also relatively well monitored.

Of the chicks that emigrated from natal colonies, most were banded between 1983 and 1993, with the years 1990–1992 accounting for 60% of recorded emigrations (Table 3). Of the total number of 21 789 chicks that were banded between 1978 and 1995 at the colonies from which at least one bird was known to emigrate, 16 743 (77%) were banded between 1983 and 1993, including 8 256 (38%) in the years 1990–1992 (Table 4). Between 1990 and 1992, most emigrations took place from Dyer Island (44%), with Dassen Island accounting for another 22%. In the 1980s, Dyer and Dassen islands again had the largest numbers of emigrations. Dyer Island had a smaller proportion of the total (24%), but the proportion emigrating from Dassen Island was slightly higher than in the early 1990s (28%). For colonies from which chicks were known to emigrate, the proportion of those banded that emigrated ranged from 0.1% to 8.3% (Table 5). Dyer Island, Stony Point, Jutten Island, Marcus Island, Possession Island and Halifax Island all had proportions of emigrants that exceeded 1% of the total banded in one or more years

 Table 4: Numbers of chicks that were flipper-banded at colonies from which at least one chick was known to emigrate, 1978–1995. See Table 1 for locality abbreviations

	Easter	n Cape			We	estern Ca	ре				Namibia		
Year banded	BI	SCI	DYI	SP	RI	DAS	JI	MCI	PSI	HI	П	MYI	Total
1978	0	173	503	0	0	74	0	12	453	99	314	106	1 734
1979	0	158	0	0	0	0	0	1	0	0	0	0	159
1980	0	192	0	0	0	0	0	179	0	0	0	0	371
1981	0	174	0	0	0	0	0	115	0	0	0	0	289
1982	0	205	0	0	0	69	0	67	24	0	19	18	402
1983	0	104	5	0	0	175	0	315	0	0	0	0	599
1984	0	123	389	0	0	248	5	121	0	0	0	0	886
1985	0	112	661	20	0	484	0	159	0	0	0	0	1 436
1986	0	0	0	25	0	0	24	130	43	0	150	200	572
1987	0	0	35	0	104	266	9	10	45	0	146	152	767
1988	0	0	215	0	29	276	84	33	96	0	0	0	733
1989	0	0	54	1	191	718	1	1	0	0	217	242	1 425
1990	0	0	201	22	464	449	0	0	2	80	374	290	1 882
1991	0	0	901	16	508	963	0	0	40	33	694	41	3 196
1992	1	0	150	5	660	1 062	0	0	104	0	411	785	3 178
1993	1	0	48	6	394	510	0	0	102	37	537	434	2 069
1994	500	0	0	6	81	399	0	0	0	0	112	111	1 209
1995	575	0	50	14	0	0	0	0	0	0	207	36	882
Total	1 077	1 241	3 212	115	2 431	5 693	123	1 143	909	249	3 181	2 415	21 789

	Easterr	n Cape			Weste	ern Cape				Nan	nibia	
Year banded	BI	SCI	DYI	SP	RI	DAS	JI	MCI	PSI	HI	Ш	MYI
1978								8.3				
1979		0.6										
1980												
1981		0.6										
1982		0.5										
1983		1.0						0.3				
1984		0.8	0.5			0.8						
1985			0.2			0.4						
1986				4.0				1.5			0.7	
1987			2.9									0.7
1988			0.9				1.2					
1989						0.4					0.5	
1990			2.0			0.4				5.0		
1991			1.4		0.4	0.5			5.0	3.0	0.1	
1992			3.3		0.9	0.4					0.2	
1993					0.3	0.6						0.4
1994												
1995			2.0									

 Table 5: Numbers of chicks known to have emigrated from natal colonies expressed as a percentage of the number banded, 1978–1995.

 See Table 1 for locality abbreviations

(Table 5). The arrival of most of the immigrants was recorded between 1993 and 1999, with the period 1995–1997 accounting for 57% of the total (Table 6). In the latter period, most of the immigrants were recorded at Robben and Dassen islands (63%). In all, 10 chicks banded between 1991 and 1993 left Dassen Island, recruiting to the Robben Island population between 1994 and 1999. During the same two periods of emigration and immigration, seven chicks left Robben Island to settle at Dassen Island (Table 7). The mean period between banding at the natal

colony and detection at the non-natal colony was 4.3 years for birds moving between Dassen and Robben islands. Only eight immigrants were recorded in the 1980s (Table 6), five of which settled at Robben Island. The remaining three all settled at South Coast colonies.

The period elapsed between banding of chicks and the time when they were first detected breeding at non-natal colonies ranged between two years and 10 months and nine years and six months. To this should be added their age at banding of usually 2–4 months (Randall 1989).

Table 6: Years of arrival at non-natal colonies of birds earlier banded as chicks, 1981-2000. See Table 1 for locality abbreviations

	Eastern												
	Cape			Nam	nibia								
Year arrived	BI	DYI	SP	SI	BB	RI	DAS	JI	VI	MCI	11	MYI	Total
1981	1												1
1982													0
1983													0
1984													0
1985													0
1986			1										1
1987		1											1
1988													0
1989						5							5
1990						1							1
1991	1												1
1992													0
1993	2				2	2							6
1994	1					3	2					1	7
1995		1	2		2	7	7			1	2		22
1996		1	2			4	3				1	1	12
1997			1	1	1	1	8	1	1				14
1998					1	1	4						6
1999			1		1	2	2						6
2000							1						1
Total	5	3	7	1	7	26	27	1	1	1	3	2	84

 Table 7: Years of banding of African penguin chicks that emigrated from Dassen Island to Robben Island and vice versa, and the years in which they were first detected at the recruiting colony

Year banded		
at Dassen or	Year recruited at	Year recruited at
Robben	Robben Island	Dassen Island
islands	(from Dassen Island)	(from Robben Island)
1984	1989 × 2	
1985	1989, 1993	
1986		
1987		
1988		
1989	1989 $ imes$ 2, 1994	
1990	1995 imes 2	
1991	1994, 1995 $ imes$ 2	1995
1992	1995 imes 2, 1996, 1998	1996 $ imes$ 2, 1997, 1998, 1999
1993	1995, 1999 $ imes$ 2	1997
1994		
1995		

 Table 8: Age at first detected breeding (in years) of immigrant

 African penguins banded as chicks, on or after 1 January 1990

	Years of age											
	<1	1–2	2-3	3-4	4-5	5-6	6-7	7–8	>8			
Number of birds	0	0	1	12	11	15	10	7	1			

Table 9: Number of chicks emigrating from and settling at colonies on the south and west coasts of the Western Cape, and emigrating from and settling at colonies in Namibia, south and north of Lüderitz (Halifax Island is included with those colonies south of Lüderitz)

	South	West	South of	North of
	Coast	Coast	Lüderitz	Lüderitz
Emigrating from	30	35	7	7
Recruiting to	18	57	0	5

Breeding attempts by emigrants did not form part of a closely monitored group of nests, so that earlier breeding attempts by some of the birds may have been missed. Most birds were first detected breeding at their new colony when aged between three and seven years old, five to six years being the most frequently recorded age range (Table 8). Birds banded prior to 1990 are excluded from Table 8, because their inclusion led to some unrealistically high ages at first breeding. This was a result of the low observer effort prior to the mid-1990s, causing many first breeding attempts to be missed.

Within the Western Cape, the numbers of chicks emigrating from South Coast and from West Coast colonies were approximately equal (Table 9). However, 57 of the 75 immigrations (76%) were recorded at West Coast colonies. In Namibia, there were equal numbers of chicks recorded emigrating from colonies north and south of Lüderitz, but all recorded immigrants settled at colonies to the north of Lüderitz (Table 9).

Penguins banded as adults

There were 17 apparent instances of African penguins that were banded as adults attempting to breed at more than one colony. Of these, nine were strongly suspected to relate to mistakes in reading or transcribing the band number and these records were rejected. The possibility of further such mistakes having occurred cannot be ruled out, but there was no strong evidence to suggest that the remaining eight records did not consist of genuine observations. All of the records that were treated as genuine related to survivors of the Apollo Sea oil spill of June 1994. Following this incident, which caused 10 000 African penguins to be oiled (Dehrmann 1994), over 4 000 cleaned, flipper-banded penguins were released back into the wild (Underhill et al. 1999). Most of the oiled penguins were from Dassen Island; about 2 500 came to the Southern African Foundation for the Conservation of Coastal Birds (SANCCOB) from Robben Island (Erasmus 1995).

All of the eight birds concerned attempted to breed at two colonies, one of the attempts being at Dassen Island. Of the other breeding attempts, five were made at Robben Island, one at Jutten Island and two at Vondeling Island. All four colonies are situated on the west coast of the Western Cape Province, South Africa, and at all four the number of occupied nest sites increased during the 1990s (Crawford et al. 2001). Two birds (S21661 and S23183) made single breeding attempts at Robben Island and Dassen Island respectively, before settling to become regular breeders at Dassen Island (S21661) and Vondeling Island (S23183). Another two birds (S20953 and S23110) bred at Robben Island and were then recorded breeding at Dassen Island the next year. Both returned to Robben Island within two months of their breeding attempt at Dassen Island, and S23110 was recorded breeding again at Robben Island the following year. S22044 appeared to make two breeding attempts at Dassen Island in 1995, the first of which probably failed. It then moved to Robben Island where it was found to be breeding in 1997. The other records related to single breeding attempts at each of two localities. None of the breeding attempts by any of these eight birds was closely monitored and only S20953 was known to have successfully reared chicks to fledging age.

Discussion

Birds banded as chicks that were subsequently recorded breeding were six times more likely to have been found breeding at natal colonies than at non-natal ones. Randall *et al.* (1987) found that three out of 90 sightings (3.3%) at non-natal colonies of birds that were banded as chicks were of breeding birds. In this study, 84 of 1 006 sightings (8%) at non-natal colonies were breeding records. The proportion is greater than that reported by Randall *et al.* (1987), but it is still a rare event.

The largest numbers of immigrants were recorded at the two colonies with the highest intensities of observer effort (Robben and Dassen islands). After Dyer Island, these two colonies also had the largest number of emigrants. This, to some degree, is a reflection of the re-sighting effort. The best monitored colonies are likely to record the largest numbers of immigrants, whereas birds emigrating from well-monitored to poorly monitored colonies have less chance of being detected. The relatively high number of emigrants recorded from the well-monitored colonies of Robben and Dassen islands is largely owing to birds emigrating from one to the other (Table 1).

In most of the cases where 1% or more of the total number of chicks banded were shown to have emigrated, the number banded was <100 birds (Tables 4, 5). The proportion of penguins emigrating was therefore exaggerated by the small totals of birds banded. However, for the years 1990–1992, the proportion of emigrants from Dyer Island ranged from 1.4% to 3.3% of those banded (Table 5), whereas the total numbers of birds banded in those years ranged from 150 to 901 per year (Table 4). This suggests that relatively large numbers of young penguins were leaving Dyer Island to settle at other breeding colonies. The mean percentage of emigrants from Dyer Island recorded for the years 1984-1995 was 1.65% of those banded, whereas for both Robben and Dassen islands it was 0.5%. Therefore, over three times as many birds were emigrating from Dyer Island than were leaving from Dassen and Robben islands, the colonies with the second and third largest numbers of emigrants respectively. Marcus Island also recorded proportions of emigrants exceeding 1% of the total numbers banded (Table 5). The number of penguins banded at this colony in 1978 was only 12, but the proportion of 1.5% of birds banded in 1986 that emigrated was based on a sample of 130 (Tables 4, This colony was known to be decreasing in size during the mid-1980s (Shelton et al. 1984, La Cock et al. 1987).

Most birds emigrating from Eastern Cape and Western Cape colonies settled at other colonies within the region. This was not the case with birds emigrating from Namibian colonies, most of which settled in the Western Cape.

The data available suggest a movement of some young African penguins away from the south coast of the Western Cape Province, where Dyer Island is situated, towards the western side of the Western Cape, centred on Robben and Dassen islands. Re-settlement of birds from Algoa Bay in the Eastern Cape seemed to be mostly on a local scale, from St Croix Island to Bird Island. There is also evidence for some relocation of birds from southern Namibia to the Western Cape of South Africa, and to colonies farther north off the Namibian coast. This pattern of emigration and immigration of young African penguins may relate to changing patterns of dominance among the main prey species. Sardine Sardinops sagax and anchovy Engraulis encrasicolus are subject to long-term, large changes in abundance, termed regimes (Lluch-Belda et al. 1992). Sardine was the dominant species in the Benguela system up to the mid-1960s off South Africa and until the early 1970s off Namibia. Anchovy then became dominant until the early 1980s off Namibia and the late 1980s off South Africa. Sardine have again become abundant off South Africa and had partially recovered by the early 1990s off Namibia (Crawford 1998). However, the Namibian stock decreased again, exacerbated by continued fishing and poor environmental conditions, resulting in the lowest recorded catch in the history of the fishery in 1996 (Boyer *et al.* 2001).

During the period when anchovy was dominant, food was probably more consistently available to African penguins on the western Agulhas Bank than at other times. Older anchovy remain there throughout the year and sardine are available in the region in the early part of the year (Crawford 1980). For African penguins, colonies closest to the Agulhas Bank would benefit most in periods of anchovy dominance. Those between Lüderitz and Table Bay would have been faced with a diminished food supply, as the sardine distribution contracted to the north off Namibia and to the south off South Africa (Lluch-Belda et al. 1989, Crawford 1998). This distribution of prey resources probably explains the decreasing sizes of African penguin colonies between Lüderitz and Table Bay, and the increasing sizes of those between Table Bay and Cape Agulhas between the 1950s and the 1980s (Crawford 1998). By the end of the 1970s, Dyer Island, which is close to the Agulhas Bank, had become the largest African penguin colony with over 22 000 breeding pairs (Crawford et al. 1995). In contrast, the colony at Possession Island, off the Namibian coast south of Lüderitz, had decreased by 96% between 1956 and 1995 (Cordes et al. 1999). That at Dassen Island decreased from an estimated 145 000 African penguins in 1956 (Rand 1963) to 27 000 in the early to mid-1980s (Crawford et al. 1995).

A return to a system dominated by sardine would benefit African penguin colonies between Lüderitz and Cape Town. The pattern of emigration of birds banded as chicks at Dyer Island to settle at colonies on the west coast of South Africa, and those closer to Cape Town, is in keeping with the change from a system where anchovy are dominant to one where sardine are dominant. Counts of active nests at The Boulders, Robben Island, Dassen Island, Vondeling Island and Jutten Island all increased during the 1990s. In contrast, that at Dyer Island decreased by 90% to just under 2 000 active nests in 1998 (Crawford *et al.* 2001).

However, the pattern is complicated by emigration of some birds from expanding colonies to other expanding colonies. The shift in prey dominance does not explain why 19 chicks from Dassen Island settled at nearby Robben Island, whereas seven chicks from Robben Island settled at Dassen Island. In all, 10 of the Dassen Island birds left the island during the same time period as those that left Robben Island (1991–1993). They all recruited to Robben and Dassen islands respectively between 1994 and 1999 (Table 7). It appears that there is movement of first-time breeders to colonies in the vicinity of their natal colony that are unrelated to shifts in the distribution of prey.

Birds settling at non-natal colonies within Namibia all travelled northwards (Tables 1, 9), presumably as a result of the northerly contraction of the sardine resource off the Namibian coast. Pelagic goby *Sufflogobius bibarbatus* were also readily available to penguins in the vicinity of Ichaboe and Mercury islands (Figure 1) and provided an alternative food source to birds settling at these two localities (Crawford *et al.* 2001). In 1980, pelagic goby constituted 73% of the items found in stomachs of penguins at Mercury Island, whereas penguins at Halifax and Possession islands, farther to the south, were found to be feeding

principally on cephalopods (Crawford et al. 1985).

As only one bird banded as a chick was recorded breeding at its natal colony prior to emigration, it is assumed that the immigrants are almost exclusively first-time breeders. Most were between the ages of three and seven years old when recorded breeding for the first time (Table 8). Crawford *et al.* (1999) found that most birds in a study population at Robben Island bred for the first time between the ages of three and five years. Randall (1983) found ages of first breeding for nine birds at St Croix Island to vary between three and five years old. It is thought that first time breeders may take advantage of the distribution of food resources at the time of commencement of breeding, and that they have the capacity to settle at breeding colonies that are situated close to the best food resources (Crawford 1998).

Randall et al. (1987) stated that no breeding adults were known to have settled or bred at other islands. In this study, there is evidence to suggest that eight birds banded in adult plumage did attempt to breed at more than one locality. The possibility that some of these records relate to misread or incorrectly transposed band numbers cannot be completely excluded, but it was considered unlikely that all such occurrences were the result of human error. All eight birds were victims of the Apollo Sea oil spill of June 1994. Five of them made their first, and probably unsuccessful, breeding attempt within a year of being released after cleaning. The ages and breeding status of these eight birds, none of which were banded prior to being oiled, were unknown. It is possible that the trauma and stress of the oiling, petro-chemical poisoning and rehabilitation experience cause disorientation of some birds, particularly perhaps of first-time breeders, leading them to attempt breeding at a colony other than the one at which they finally chose to settle. It is also possible that some birds lost their mate and formed a new partnership with a bird from a different colony. Breeding at more than one colony by African penguins is still an extremely rare event. It is anticipated that fieldwork following the release of over 16 000 penguins that were cleaned after the Treasure oil spill of June 2000 (Crawford et al. 2000) may reveal further instances of birds attempting to breed at more than one locality.

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References

- BOYER, D. C., BOYER, H. J., FOSSEN, I. and A. KREINER 2001 — Changes in abundance of the northern Benguela sardine stock during the decade 1990–2000, with comments on the relative importance of fishing and the environment. S. Afr. J. mar. Sci. 23: 67–84.
- CORDES, I., CRAWFORD, R. J. M., WILLIAMS, A. J. and B. M. DYER 1999 — Decrease of African penguins at the Possession Island group, 1956–1995: contrasting trends for colonial and solitary breeders. *Mar. Ornithol.* 27: 129–138.
- CRAWFORD, R. J. M. 1980 Seasonal patterns in South Africa's Western Cape purse-seine fishery. J. Fish Biol. 16(6): 649–664.
- CRAWFORD, R. J. M. 1998 Responses of African penguins to regime changes of sardine and anchovy in the Benguela system. S. Afr. J. mar. Sci. 19: 355–364.
- CRAWFORD, R. J. M., CRUICKSHANK, R. A., SHELTON, P. A. and I. KRUGER 1985 — Partitioning of a goby resource amongst four avian predators and evidence for altered trophic flow in the pelagic community of an intense, perennial upwelling system. S. Afr. J. mar. Sci. 3: 215–228.
- CRÄWFORD, R. J. M., DAVID, J. H. M., SHANNON, L. J., KEMPER, J., KLAGES, N. T. W., ROUX, J-P., UNDERHILL, L. G., WARD, V. L., WILLIAMS, A. J. and A. C. WOLFAARDT 2001 — African penguins as predators and prey – coping (or not) with change. In *A Decade of Namibian Fisheries Science*. Payne, A. I. L., Pillar, S. C. and R. J. M. Crawford (Eds). *S. Afr. J. mar. Sci.* 23: 435–447.
- CRAWFORD, R. J. M., DAVIS, S. A., HARDING, R. T., JACKSON, L. F., LESHORO, T. M., MEŸER, M. A., RANDALL, R. M., UNDERHILL, L. G., UPFOLD, L., VAN DALSEN, A. P., VAN DER MERWE, E., WHITTINGTON, P. A., WILLIAMS, A. J. and A. C. WOLFAARDT 2000 — Initial impact of the *Treasure* oil spill on seabirds off western South Africa. *S. Afr. J. mar. Sci.* 22: 157–176.
- CRAWFORD R. J. M., SHANNON L. J. and P. A. WHITTINGTON 1999 — Population dynamics of the African penguin at Robben Island. *Mar. Ornithol.* 27: 135–143.
- CRAWFORD, R. J. M., SHANNON, L. J., WHITTINGTON, P. A. and G. MURISON 2000 — Factors influencing growth of the African penguin colony at Boulders, South Africa, 1985–1999. S. Afr. J. mar. Sci. 22: 111–119.
- CRAWFORD, R. J. M., WILLIAMS, A. J., HOFMEYR, J. H., KLAGES, N. T. W., RANDALL, R. M., COOPER, J., DYER, B. M. and Y. CHESSELET 1995 — Trends of African penguin *Spheniscus demersus* populations in the 20th century. S. Afr. J. mar. Sci. 16: 101–118.
- DEHRMANN, A. 1994 Penguins affected by oil spill in South African waters. *Penguin Conserv.* 7(2): 8–12.
- ERASMUS, Z. 1995 A brief overview of the Apollo Sea incident. In Proceedings Coastal Oil Spills: Effect on Penguin Communities and Rehabilitation Procedures. Barrett, J., Erasmus, Z. and A. J. Williams (Eds). Cape Town; Cape Nature Conservation: 5–7.
- LA COCK, G. D., DUFFY, D. C. and J. COOPER 1987 Population dynamics of the African penguin *Spheniscus demersus* at Marcus Island in the Benguela upwelling ecosystem: 1979–85. *Biol. Conserv.* **40**: 117–126.
- LLUCH-BELDA, D., CRAWFORD, R. J. M., KAWASAKI, T., MacCALL, A. D., PARRISH, R. H., SCHWARTZLOSE, R. A. and P. E. SMITH 1989 — World-wide fluctuations of sardine and anchovy stocks: the regime problem. *S. Afr. J. mar. Sci.* 8: 195–205.
- LLUCH-BELDA, D., SCHWARTZLOSE, R. A., SERRA, R., PARRISH,

R. [H.], KAWASAKI, T., HEDGECOCK, D. and R. J. M. CRAWFORD 1992 — Sardine and anchovy regime fluctuations of abundance in four regions of the world oceans: a workshop report. *Fish. Oceanogr.* **1**(4): 339–347.

- RAND, R. W. 1963 The biology of guano-producing sea-birds.
 4. Composition of colonies on the Cape islands. *Investl Rep. Div. Sea Fish. S. Afr.* 43: 32 pp.
- RANDALL, R. M. 1983 Biology of the jackass penguin Spheniscus demersus (L.) at St Croix Island, South Africa. Ph.D. thesis, University of Port Elizabeth: 262 pp.
- RANDALL, R. M. 1989 Jackass penguins. In Oceans of Life off Southern Africa. Payne, A. I. L. and R. J. M. Crawford (Eds). Cape Town; Vlaeberg: 244–256.
- RANDALL, R. M., RANDALL, B. M., COOPER, J., LA COCK, G. D. and G. J. B. ROSS 1987 — Jackass penguin Spheniscus demersus movements, inter-island visits, and settlement. J. Fld Orn. 58(4): 445–455.

- SHANNON, L. J. and R. J. M. CRAWFORD 1999 Management of the African penguin *Spheniscus demersus* – insights from modeling. *Mar. Ornithol.* 27: 119–128.
- SHELTON, P. A., CRAWFORD, R. J. M., COOPER, J. and R. K. BROOKE 1984 — Distribution, population size and conservation of the jackass penguin *Spheniscus demersus*. S. Afr. J. mar. Sci. 2: 217–257.
- UNDERHILL, L. G. 2000 The *Treasure* saga. *Bird Numbers* **9**(2): 10–13.
- UNDERHILL, L. G., BARTLETT, P. A., BAUMANN, L., CRAWFORD,
 R. J. M., DYER, B. M., GILDENHUYS, A., NEL, D. C., OATLEY,
 T. B., THORNTON, M., UPFOLD, L., WILLIAMS, A. J.,
 WHITTINGTON, P. A. and A. C. WOLFAARDT 1999 Mortality
 and survival of African Penguins *Spheniscus demersus* involved
 in the *Apollo Sea* oil spill: an evaluation of rehabilitation efforts. *Ibis* 141: 29–37.