

Winter dispersal of rockhopper penguins *Eudyptes chrysocome* from the Falkland Islands and its implications for conservation

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ABSTRACT: In 3 successive years (1998 to 2000), the winter migration of rockhopper penguins *Eudyptes chrysocome* from 3 separate breeding colonies on the Falkland Islands was monitored using satellite transmitters. After their moult, 34 penguins were followed for a mean transmission period of 81 ± 21 d. While there were substantial spatial and temporal variations in migration patterns, we identified several foraging areas where food availability is presumably higher than elsewhere. Coastal areas of the Falkland Islands and South America appeared to provide a sufficient food supply, and many penguins commuted between these 2 areas, which are about 600 km apart. Rockhopper penguins from northern breeding colonies also used areas along the slope of the Patagonian Shelf up to 39°S, about 1400 km northwards. By contrast, only a few birds from the southern breeding colony migrated to the Burdwood Bank, which is situated about 250 km to the south of the Falkland Islands, and adjacent oceanic waters. None of the penguins in this study left the maritime zone of the Falkland Islands in an easterly direction to forage in oceanic waters. The mean distances covered per day by individual birds varied greatly, depending on the phase of the foraging trip. The overall mean travelling speed was 26 km d^{-1} (range: 13 to 45 km d^{-1}). Inter-annual variation was evident both in the use of different foraging areas, and also in the time at which the winter migration began. In 1998 and 2000, penguins from Seal Bay and Sea Lion Island left their breeding colony within 1 wk after being equipped with transmitters and did not return, whereas in 1999 most penguins made short foraging trips and returned repeatedly to their colonies for periods of up to 100 d. Potential threats to the rockhopper penguins during their winter migration, resulting from human activities such as fishing and oil pollution within the Falkland Islands maritime zone and the Argentine Exclusive Economic Zone, are discussed.

KEY WORDS: Rockhopper penguins · Satellite telemetry · Winter migration · Foraging areas · Southwest Atlantic

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INTRODUCTION

Rockhopper penguins *Eudyptes chrysocome* breed on sub-Antarctic and temperate islands throughout the Southern Ocean (Williams 1995). In the Falkland Islands, the rockhopper penguin population was estimated to

comprise about 3 million breeding pairs in the early 1930s (Bennett 1933). However, the population has since declined to about 275 000 breeding pairs (Clausen 2001). A similar trend has been observed on Campbell Island in the South Pacific, where breeding numbers of rockhopper penguins have fallen from 1.6 million breeding pairs in the early 1940s to fewer than 100 000 (Moors 1986). Declines in the rockhopper penguin population have also been noted on the Auckland Islands (Cooper 1992), Marion Island (Cooper et al. 1997), Antipodes Islands

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(Ellis et al. 1998) and Amsterdam Island (Guinard et al. 1998). By comparison, the population of the recently discovered colony on Staten Island seems to have remained stable, as there are no signs of ground erosion indicating a larger colony in former times (Schiavini 2000). Nevertheless, the widespread reduction in population has resulted in the classification of rockhopper penguins as a globally threatened species according to IUCN criteria (BirdLife International 2000).

The reasons for the significant population declines are largely unknown. Starvation prior to moult was thought to be responsible for a mass mortality of rockhopper penguins in the Falkland Islands during the 1985/86 breeding season (Keymer et al. 2001). The decline on Campbell Island has been attributed to a rise in sea temperature, which may have resulted in reduced food availability (Cunningham & Moors 1994). On the other hand, it has been assumed that a drop in sea surface temperature caused a population decline of rockhopper penguins on Amsterdam Island, although populations on Saint Paul Island, 80 km to the south of Amsterdam Island, increased over the same period (Guinard et al. 1998). Given the wide breeding range of rockhopper penguins, from sub-Antarctic to subtropical waters, it seems unlikely that the cited changes in sea surface temperature were solely responsible for the population declines. Other factors must contribute to the global decrease in breeding pair numbers, such as possible changes in the oceanographic features of the Southern Ocean (e.g. Croxall 1992, Fraser et al. 1992). Furthermore, human activities such as commercial fishing (e.g. Montevercchi 2002) and pollution (e.g. Burger & Gochfeld 2002) may contribute locally to the declines.

Human activities in Falkland Island waters have increased greatly over the past 2 decades. Fishing has expanded rapidly since the mid-1970s, eventually threatening fish and squid stocks (Patterson 1987). As a result, maritime conservation zones have been established around the Falkland Islands and the number of fishing vessels within these areas has been strictly regulated (Barton 2002). Exploration for hydrocarbon deposits began north of the Falkland Islands in 1998, and the results of this drilling are fuelling growing interest in further oil exploration and production in Falkland Islands waters (Richards 2002). Ship-based tourism has also grown and more than 30 000 tourists now visit the islands each season (Ingham & Summers 2002). All these activities have the potential to threaten penguin populations breeding in the Falkland Islands, adding to the existing threats.

The breeding success and diet of rockhopper penguins have been monitored on the Falkland Islands for the last 15 yr. The data collected so far have failed to highlight any detrimental influences during the breed-

ing season (Pütz et al. 2001). Rockhopper penguins are probably exposed to potential threats during their winter migration, which can last up to 6 mo, and it is essential to gain insight into their utilisation of the marine habitat during winter. The aim of this study was to monitor the winter dispersal of rockhopper penguins from the Falkland Islands using satellite transmitters. To allow for spatial and inter-annual variation, transmitters were attached to penguins from colonies distributed over the entire archipelago, over 3 successive years. The data may assist in identifying areas that need special attention in order to protect Falkland Islands rockhopper penguins.

MATERIALS AND METHODS

Field work was conducted between 1998 and 2000 at Seal Bay to the northeast of the Falkland Islands (51° 37' S, 58° 02' W), in 1999 and 2000 on Sea Lion Island to the south of the Falkland Islands (52° 45' S, 59° 12' W), and in 2000 on Saunders Island to the northwest of the Falkland Islands (51° 31' S, 60° 23' W). The breeding sites chosen were assumed to be representative of the most important concentrations of rockhopper penguins in the Falkland Islands (see Bingham 1998). A total of 34 rockhopper penguins were equipped with satellite transmitters at their breeding colonies after completion of the moult. At Seal Bay, satellite transmitters were attached to penguins on 24 March 1998 (n = 5), 19 March 1999 (n = 6) and 4 April 2000 (n = 6). On Sea Lion Island, penguins were equipped with satellite transmitters on 26 March 1999 (n = 6) and on 27 March 2000 (n = 6). Satellite transmitters were attached to birds on Saunders Island on 30 March 2000 (n = 5).

Rockhopper penguins were caught at their ankle joint using a 1.5 m length of wire bent into a hook at one end. After covering the head and immobilising the penguin to minimise disturbance, the birds were weighed and bill dimensions measured to determine their gender (following the methodology established by Hull 1996, K. Pütz unpubl. data). The satellite transmitters were attached on the mid-line of the back as far distally as possible without impairing the preen gland, using black tape (Tesa) and 2-component neoprene glue (Deutsche Schlauchbootfabrik) according to Wilson et al. (1997). The devices were then covered with a layer of quick epoxy (Loctite® 3430) to prevent the birds from removing the tape with their beaks. Equipping the penguins took place in the back of a heated vehicle to minimise the hardening times of the glues. The whole process took less than 20 min per bird.

Two types of satellite transmitters were used in this study. In 1998 and 1999, ST-10 satellite transmitters (manufactured by Telonics and modified by Sirtrack)

were attached to the penguins, whereas in 2000 KiwiSat 101 satellite transmitters (Sirtrack) were used. All devices were embedded in epoxy resin and hydrodynamically shaped following the recommendations by Bannasch et al. (1994). From 1999 onwards, the base of all the devices was moulded into a concave

shape to better match the anatomy of the penguin's back. The satellite transmitters were powered by 2 AA lithium cells; they weighed approximately 100 g, equivalent to less than 5% of the mean penguin body mass (Table 1). Maximum dimensions of the ST-10 transmitters were 130 × 40 × 20 mm, whereas the KiwiSat 101

Table 1. *Eudyptes chrysocome*. Data from satellite transmitters deployed on Falkland Island rockhopper penguins. Calculation of the minimum distance covered per day is based on the total transmitting time minus residence time

Penguin name	Body mass (kg)	Sex	No. of locations per hour of transmission	Residence time in colony (d)	Transmission period (d)	Maximum distance to colony (km)	Minimum distance covered (km)	(km d ⁻¹)
Seal Bay								
1998 <i>Hugo</i>	2.6	M	0.36	3	60	572	1095	19
<i>Jule</i>	2.0	F	0.48	3	69	690	1488	23
<i>Marianne</i>	2.5	F	0.63	6	111	158	1333	13
<i>Scouty</i> ^a	3.0	M	0.35	6	54	685	1175	24
<i>Sir Stanley</i>	2.9	M	0.43	3	73	659	2119	30
Means ± SD			0.45 ± 0.11	4.2 ± 1.6	73.4 ± 22.3	553 ± 226	1442 ± 407	21
1999 <i>Paradise</i>	2.3	M	0.48	2	129	654	4526	36
<i>Reinhold</i>	2.9	M	0.60	32	105	300	1727	24
<i>Romana</i>	2.0	F	0.43	52	97	1447	2019	45
<i>Sarah</i> ^a	1.8	F	0.15	45	100	1406	1864	34
<i>Sokrates</i>	2.3	M	0.55	102	111	46	119	13
<i>Vontobel</i> ^a	2.6	M	0.08	1	94	298	1740	19
Means ± SD			0.38 ± 0.22	39.0 ± 37.5	106.0 ± 12.8	692 ± 601	1999 ± 1420	30
2000 <i>Chippys</i>	2.1	F	0.30	3	83	703	1985	25
<i>Friedli</i>	2.2	M	0.35	3	89	194	1348	16
<i>Ocean Speedy</i>	2.4	F	0.20	4	60	646	964	17
<i>Otto</i>	2.3	M	0.28	2	84	985	1913	23
<i>Susanne</i>	2.2	F	0.23	2	56	673	1355	25
<i>Victory</i>	2.4	M	0.32	7	81	1217	2066	28
Means ± SD			0.28 ± 0.06	3.5 ± 1.9	75.5 ± 13.9	736 ± 346	1605 ± 445	22
Sea Lion Island								
1999 <i>Aika</i>	1.8	F	0.42	27	86	501	2419	41
<i>Balou</i>	2.7	M	0.42	21	86	546	2378	37
<i>Hope</i>	1.7	F	0.63	25	107	414	2947	36
<i>Karajan</i>	2.1	M	0.32	39	84	699	1186	26
<i>Leonardo</i>	1.8	M	0.20	46	86	585	1348	34
<i>Summer</i>	2.1	M	0.48	27	73	658	1738	38
Means ± SD			0.41 ± 0.15	30.8 ± 9.6	87.0 ± 11.0	567 ± 104	2003 ± 689	36
2000 <i>Benno</i>	2.2	M	0.32	6	67	304	1083	18
<i>Max</i>	2.1	M	0.33	7	46	65	573	15
<i>Moritz</i> ^b	2.3	M	0.02	2	83			
<i>Petra</i>	1.7	F	0.53	2	64	294	974	16
<i>Stella</i>	2.0	F	0.42	7	90	284	1588	19
<i>Vreni</i>	2.2	F	0.48	6	23	232	401	24
Means ± SD			0.35 ± 0.18	5.0 ± 2.4	62.2 ± 24.6	236 ± 99	924 ± 465	16
Saunders Island								
2000 <i>Benji</i>	2.1	M	0.15	26	86	563	1530	26
<i>Cyrus</i>	2.0	M	0.42	10	69	883	1604	27
<i>Inca</i>	2.1	F	0.38	29	87	844	1765	30
<i>Mapa</i>	2.0	M	0.43	7	87	645	1900	24
<i>Millie</i>	2.4	F	0.38	6	73	1363	2063	31
Means ± SD			0.35 ± 0.12	15.6 ± 11.0	80.4 ± 8.7	860 ± 312	1772 ± 217	27
Total	2.2 ± 0.3		0.37 ± 0.15	16.7 ± 21.2	81.0 ± 20.8	613 ± 365	1646 ± 782	26
Males	2.3 ± 0.3							
Females	2.1 ± 0.3							

^aSatellite transmitters started accidentally in the afternoon; ^bsatellite transmitter defective, only few positions obtained

used in 2000 was slightly slimmer with $130 \times 35 \times 20$ mm. The flexible antenna at the rear of the device was 170 mm long and 3 mm in diameter.

To reduce the energy requirements of the satellite transmitters, devices were programmed to transmit at a duty cycle with a repetition period of 60 s, and a submersion switch prevented transmission while underwater. Duty cycles were 8:64 h on:off in 1998, 6:42 and 6:18 h in 1999 for penguins from Seal Bay and Sea Lion Island, respectively, and 6:18 h on:off for all penguins in 2000. Transmitters were usually switched on at night (but see Table 1), as this time offered the best compromise between low penguin activity and high frequency of satellite overpasses (local time = GMT + 3 h). Positional data obtained from Argos (CLS) were classified according to the quality of the positional fix, with location Classes 0, 1, 2 and 3 representing accuracies of >1 km, <1 km, <350 m and <150 m, respectively (Argos 1996). However, the margin of error may be greater, because of the movement of the penguins between satellite uplinks (cf. Kerry et al. 1995). Positions were processed using the EXCEL program (Microsoft). The most accurate position obtained in each duty cycle for each penguin ($\geq 76\%$ of locations in Class 1) was transferred to MAPINFO Professional 5.0 (MapInfo). Calculation of the maximum distance to the colony and distance between two consecutive fixes was carried out using HOWFAR (Jensen Software Systems).

The submersion switch of the ST-10 transmitters continuously recorded and subsequently transmitted in 16-bit format the time spent underwater by the penguins. The submersion switch could record a maximum of 65 535 units (1 unit = 1.024 s), or 18.6 h overall. Therefore, reliable values for the time spent underwater were obtained only from devices programmed to transmit with a duty cycle of 6:18 h (essentially birds from Sea Lion Island in 1999). Calculation of travelling speed was based on the relationship between time spent underwater and the distance travelled between 2 consecutive locations. Values for travelling speed are minimum values and differ from the actual swim speed of the birds since horizontal and vertical deviations from a straight line course between 2 locations, and drift with water currents, are neglected. All values given are mean \pm standard deviation (SD) unless otherwise indicated in the text. Statistical tests were performed using PRISM 2.01 (GraphPad Software).

RESULTS

The winter migration of rockhopper penguins from the Falkland Islands was monitored for a mean tracking duration of 81 ± 21 d (range 23 to 129 d). Data on the foraging trips are summarised in Table 1. Six rock-

hopper penguins were re-sighted in their colonies in the following breeding season, apparently following the usual breeding routine. They were identified by the absence of the outer part of the feathers in an area corresponding to the base of the devices.

Seal Bay

In 1998, all 5 rockhopper penguins from Seal Bay left their colony within 1 wk after being equipped with a satellite transmitter. Thereafter, their migration was monitored for a mean duration of 73 ± 22 d (Table 1). The area utilised by these birds ranged from the Falkland Islands northwestwards to an area off Puerto Deseado, Argentina, about 600 km from their colony (Fig. 1). They remained in this area for varying periods,

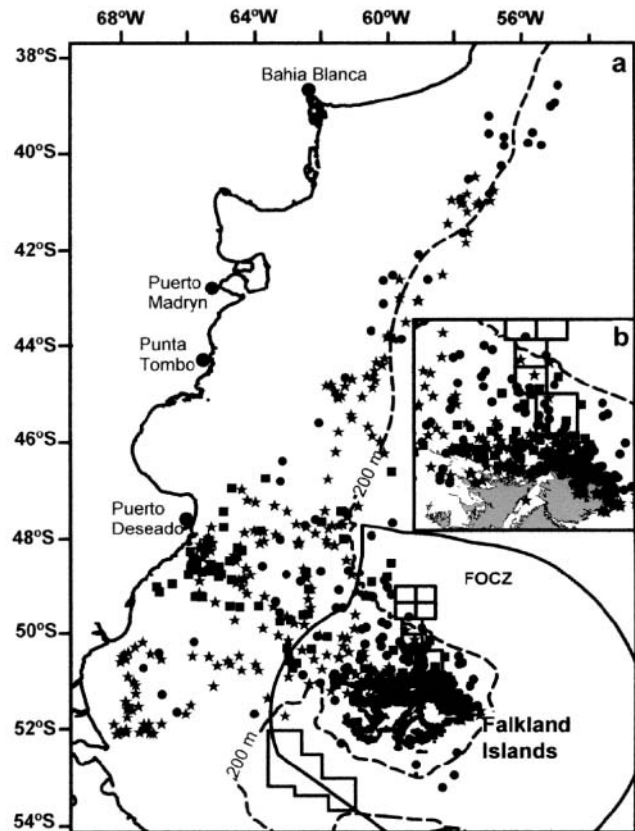


Fig. 1. *Eudyptes chrysocome*. Positions of rockhopper penguins from Seal Bay during winters 1998 to 2000 (■ = 1998, ● = 1999 and ★ = 2000). Data for all 3 study years were combined, due to the lack of significant inter-annual differences in foraging parameters (see Table 2). The squares to the north and to the southwest of the Falkland Islands are prospective areas for oil exploration and exploitation. The solid line indicates the border of the Falklands Outer Conservation Zone (FOCZ), and the dotted line is the 200 m water depth contour. (a) Overview, (b) coastal detail

and transmissions from all penguins ceased before they returned to the Falkland Islands. One of the penguins remained for the whole transmission period within coastal waters of the Falkland Islands, never travelling further than 160 km from the coast (Table 1).

In 1999 the migrations of the rockhopper penguins tracked at Seal Bay were monitored for a mean duration of 106 ± 13 d. During the initial tracking period, 4 of the 6 penguins repeatedly returned to the breeding colony after making brief foraging trips of up to a few days, whereas the 2 other penguins left the colony immediately after being fitted with a transmitter (Table 1). As all of the positions obtained from the penguins during the initial period, during which they returned frequently to the colony, were either at the colony or close to shore, only positions obtained after this period for each individual were plotted (Fig. 1). Of the 6 penguins, 3 remained within the Falklands Outer Conservation Zone (FOCZ) throughout the study period, and 3 left the FOCZ. Of the latter, 1 penguin left the FOCZ repeatedly on westerly courses and the other 2 migrated north until transmission ceased north of 40° S. These differences in the foraging behaviour are reflected in the calculated maximum distances to the colony and minimum distances covered (Table 1).

During the austral winter 2000, contact with rockhopper penguins from the colony at Seal Bay was maintained for a mean period of 76 ± 14 d (Table 1). As had been the case in 1998, most penguins left the moulting site within 1 wk after being equipped with a transmitter (Fig. 1). Of the 6 penguins tracked, 2 individuals again used the area off Puerto Deseado, Argentina, 1 individual also foraged further south between 50° and 52° S, 2 individuals migrated north until transmission ceased at about 39° S, and 1 penguin remained within coastal waters of the Falkland Islands during the entire transmission period of 89 d, never travelling further than 200 km from the coast.

Sea Lion Island

Rockhopper penguins from Sea Lion Island were tracked for a mean period of 87 ± 11 d during the austral winter 1999 (Fig. 2). After finishing their moult, the penguins undertook day trips for a mean duration of 31 ± 10 d, during which time they returned frequently to their colony, thus displaying the same behaviour as their conspecifics from Seal Bay in that year (Table 1). After this period, 5 of the 6 penguins left the FOCZ at

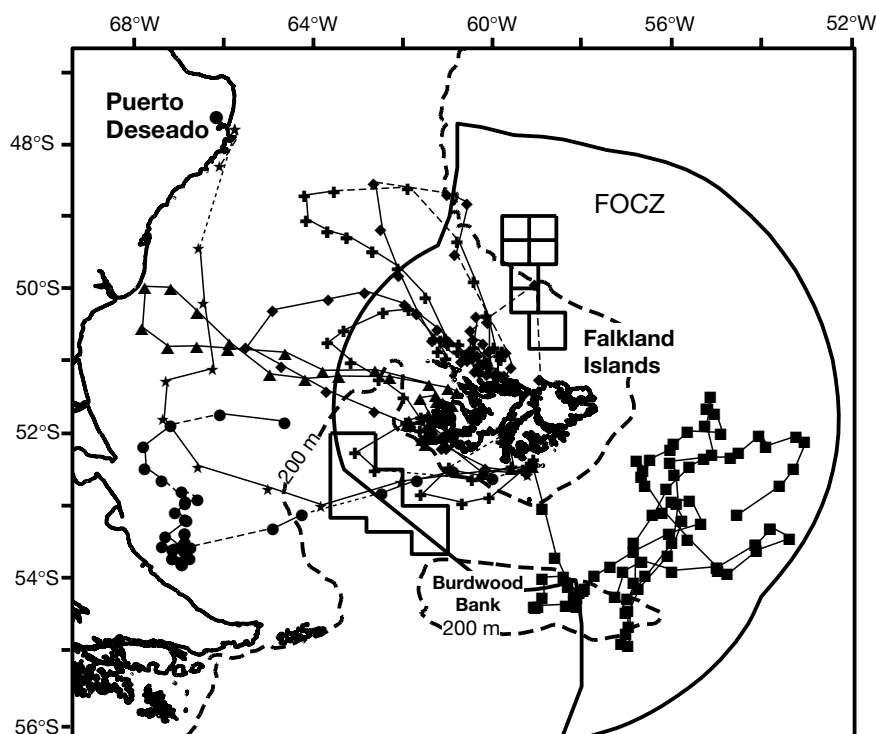


Fig. 2. *Eudyptes chrysocome*. Migration routes of rockhopper penguins from Sea Lion Island during winter 1999 (◆ = Aika, + = Balou, ■ = Hope, ★ = Karajan, ● = Leonardo and ▲ = Summer). Consecutive positions separated by more than 1 duty cycle are connected by a dotted line. For further explanations see Fig. 1

least once in a westerly direction and foraged close to the South American coast at different latitudes and for various periods. The remaining penguin travelled 250 km southwards to Burdwood Bank, an isolated extension of the Patagonian Shelf with a water depth of less than 200 m, and adjacent areas to the northeast.

The submersion switch in the satellite transmitters allowed calculation of the time spent underwater between consecutive locations in penguins from Sea Lion Island, because these devices were programmed to transmit with a duty cycle of 6:18 h on-off. The frequency distribution of the time spent underwater is skewed to the right (Fig. 3). The mean time spent underwater was 9.4 ± 2.5 h d^{-1} (range 4.3 to 17.9, median 8.9). More than 25% of all periods underwater ranged between 8 and 9 h, and about 75% of all periods were within the range of 6 to 10 h. The mean travelling speed for these penguins, based on the time spent underwater and the distance covered between 2 consecutive locations, was 1.1 ± 0.1 m s^{-1} (range 1.0 to 1.3).

In 2000, rockhopper penguins from the colony at Sea Lion Island departed

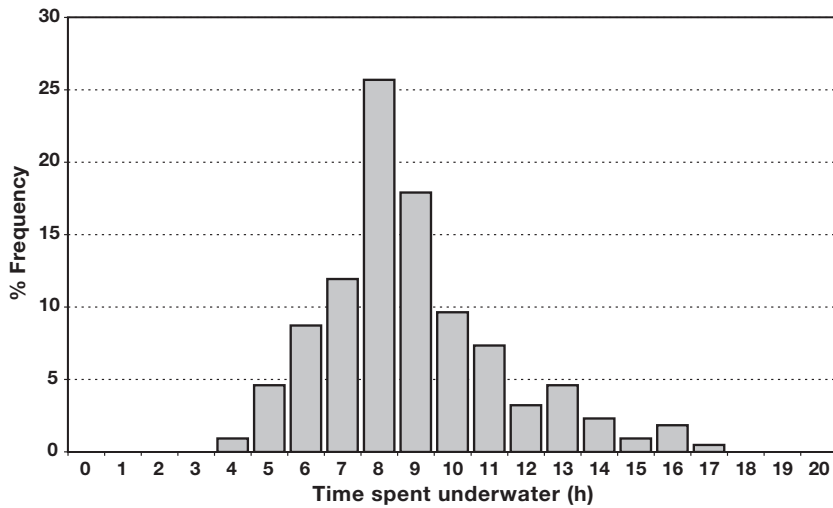


Fig. 3. *Eudyptes chrysocome*. Frequency distribution of the daily amounts of time spent underwater by 5 rockhopper penguins from Sea Lion Island in winter 1999

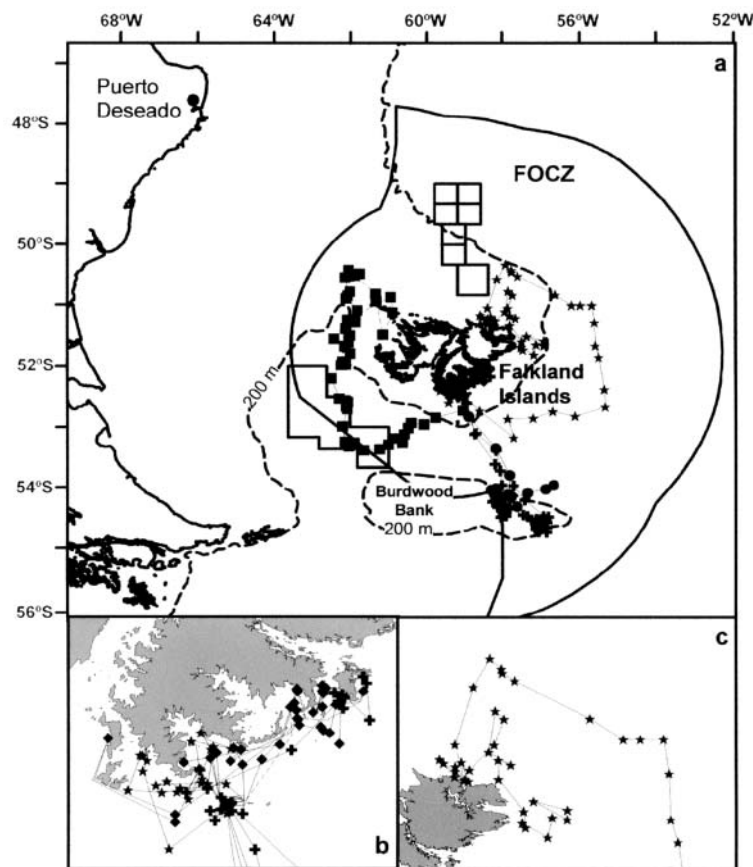


Fig. 4. *Eudyptes chrysocome*. Migration routes of rockhopper penguins from Sea Lion Island during winter 2000 (■ = Benno, ◆ = Max, + = Petra, ★ = Stella and ● = Vreni). Consecutive positions separated by more than 1 duty cycle are connected by a dotted line. For further explanations see Fig. 1. (a) Overview, (b,c) coastal details

within 1 wk after being fitted with transmitters and were subsequently monitored for a mean duration of 62 ± 25 d (Fig. 4). During that time, all of the penguins stayed within the FOCZ or adjacent waters and never travelled further than 300 km from their colony. Of the 6 penguins, 2 individuals migrated about 250 km south and remained close to Burdwood Bank, 2 individuals travelled to the northern coast of the Falkland Islands, and 2 penguins stayed in inshore waters off the SE coast until transmission ceased.

Saunders Island

In 2000, migrations of the rockhopper penguins from the colony on Saunders Island were investigated for the first time; contact was maintained for a mean period of 80 ± 9 d (Table 1). All of the penguins left the FOCZ westwards during the study period (Fig. 5): 2 individuals travelled to the area south-east of Puerto Deseado, Argentina, and 3 penguins migrated northwards. The northernmost point reached by one bird was at about 39° S, 1350 km from the breeding site (Table 1).

Comparison of the foraging trips

Rockhopper penguins migrated various distances from their moulting site, depending on the location of their winter foraging area (Fig. 6). Apart from those penguins that stayed in coastal waters of the Falkland Islands, the shortest distance between a foraging area and the breeding colony was covered by penguins from Sea Lion Island travelling 200 km southwards to Burdwood Bank. Other penguins travelled more than 500 km westwards to the coast of South America. The greatest distances from the colony, nearly 1500 km, were covered by rockhopper penguins from the northern colonies travelling directly or via the South American coast to the north.

Some spatial and temporal differences between the foraging trips were established by statistical comparison of selected foraging parameters (Table 2). Significant inter-annual differences (Mann-Whitney U -test, $p < 0.01$) occurred in residence time in the colony after being fitted with the transmitter, maximum distance from the colony during the period monitored, and minimum dis-

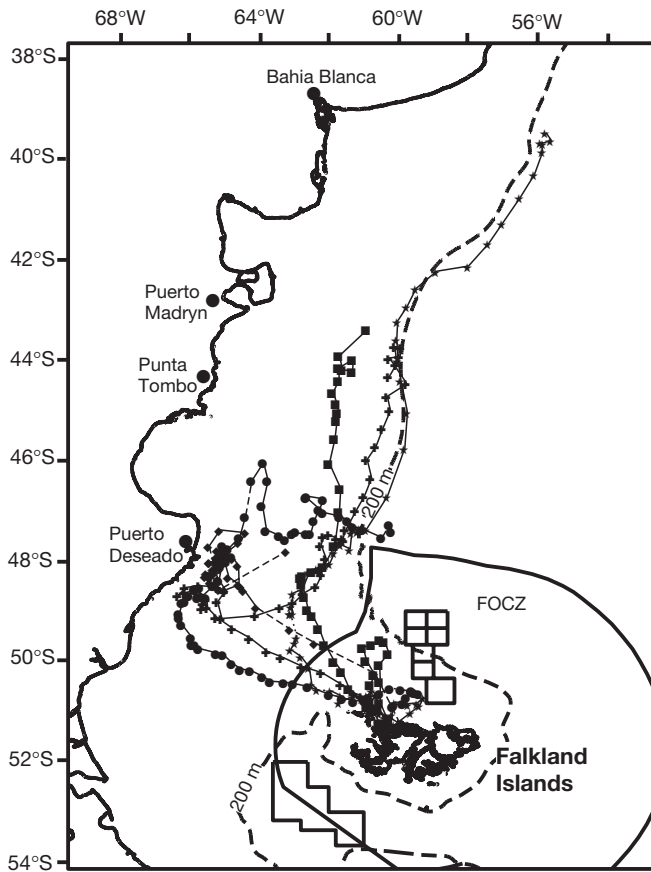


Fig. 5. *Eudyptes chrysocome*. Migration routes of rockhopper penguins from Saunders Island during winter 2000 (\diamond = Benji, \blacksquare = Cyrus, $+$ = Inca, \bullet = Mapa and \star = Millie). Consecutive positions separated by more than 1 duty cycle are connected by a dotted line. For further explanations see Fig. 1

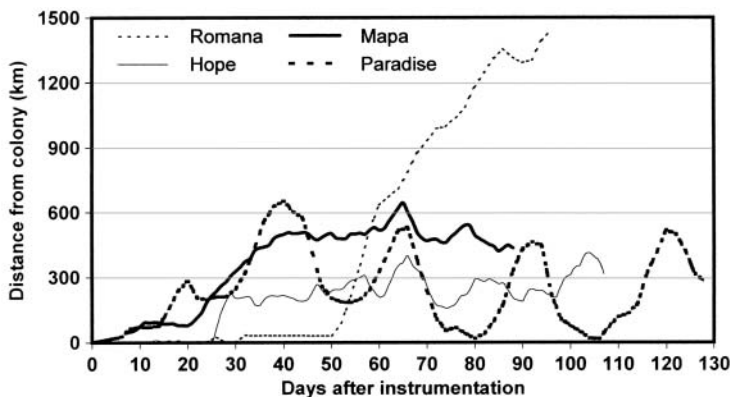


Fig. 6 *Eudyptes chrysocome*. Maximum range of selected rockhopper penguins from the Falkland Islands satellite-tracked during the initial part of their winter migration: Romana (Seal Bay 1998) migrated northwards, Mapa (Saunders Island 2000) migrated westwards, Hope (Sea Lion Island 1999) migrated southwards, and Paradise (Seal Bay 1998) commuted between Falkland Islands waters and foraging areas to the west

tances covered per day in birds from Sea Lion Island in 1999 and 2000 (Table 2). Spatial differences were apparent in 2000 between rockhopper penguins from Sea Lion Island and Saunders Island with respect to maximum distance to the colony and distance covered per day, and between birds from Sea Lion Island and Seal Bay with regard to residence time in the colony after being equipped with a satellite transmitter. The lack of further significant differences in the foraging patterns of rockhopper penguins from the Falkland Islands is probably due to the small sample size per colony and year. For example, in some instances p-values between 0.05 and 0.1 were noted (see Table 2).

DISCUSSION

The winter dispersal of rockhopper penguins breeding on the Falkland Islands has been studied by the use of satellite telemetry for the first time. The amount of data collected over 3 yr makes this study the most comprehensive ever performed with satellite transmitters on any seabird species outside the breeding season. Results not only highlighted the importance of the Patagonian Shelf as a wintering area for rockhopper penguins, but also revealed significant inter-annual and spatial differences in their migration patterns. This, in turn, has major implications for the validity of conclusions drawn from the majority of satellite telemetric studies, which were performed at one locality and during one season only. However, in an attempt to verify whether the winter movements of these birds were typical, it seems appropriate to evaluate first any potentially detrimental effects of the devices on the penguins studied.

Potential impact of the satellite transmitters on the behaviour of the penguins

The attachment of devices to free-ranging animals may influence their foraging behaviour (e.g. Bannasch 1995, Ropert-Coudert et al. 2000). Externally attached units increase the penguins' hydrodynamic resistance (Bannasch et al. 1994), increasing energy expenditure and/or reducing swimming speed (Culik & Wilson 1991). This effect is even more pronounced with satellite transmitters, as the antenna adds substantially to the drag of the backpack. Measures were taken to minimise impacts in this study. The penguins were not marked individually with the commonly used flipper bands, because these may have detrimental effects themselves (cf. Jackson & Wilson 2002) that are likely to add to any

Table 2. *Eudyptes chrysocome*. Mann-Whitney *U*-test of spatial and inter-annual differences in foraging parameters of Falkland Island rockhopper penguins equipped with satellite transmitters over the winter period. Significant *p*-values ($p < 0.05$) are shown in bold, *p*-values in italics are < 0.1

Comparison between colonies and year of study	Residence time in colony (d)	Max. distance to the colony (km)	Min. distance covered (km d ⁻¹)
Seal Bay '99 – Sea Lion Island '99	0.7	0.82	0.24
Seal Bay '00 – Sea Lion Island '00	0.48	<i>0.052</i>	0.25
Seal Bay '00 – Saunders Island '00	0.009	0.93	<i>0.082</i>
Sea Lion Island '00 – Saunders Island '00	<i>0.052</i>	0.008	0.008
Seal Bay '98 – Seal Bay '99	0.43	0.93	0.43
Seal Bay '98 – Seal Bay '00	0.54	0.33	0.79
Seal Bay '99 – Seal Bay '00	0.31	0.82	0.48
Sea Lion Island '99 – Sea Lion Island '00	0.002	0.007	0.004

potential disturbance to the birds caused by the satellite transmitters.

It is generally impossible to assess precisely the potential impact of externally attached devices without establishing a control group (but see Ropert-Coudert et al. 2000). Therefore, only indirect measures may indicate potential impacts, such as, for example, energetic studies (e.g. using doubly labeled water) or time budgets. Also, measurement of survival, physical condition or reproduction rates may give some indication of potential effects of the devices. However, in long-term studies on non-breeding animals that are unlikely to be recaptured, these measures are not applicable. The assessment of any potential disturbance caused by the devices is therefore extremely difficult.

In our study, clues about potential effects of the devices on the birds' behaviour can only be derived from the transmitting times, which ranged between 23 and 129 d. Nearly 50% ($n = 15$) of transmission failures occurred after 80 to 100 d, and more than 85% ($n = 29$) of all transmitters lasted between 60 and 120 d. Penguins bite and break their feathers to remove the devices attached to them (Wilson et al. 1997), which has been confirmed by the re-sighting of birds previously equipped with satellite transmitters (Kerry et al. 1995, Stokes et al. 1998, Pütz et al. 2000, this study). Due to the increased energy demands following starvation during moulting, birds should be most vulnerable to any detrimental effects at the very beginning of their winter migration. Thus, any losses linked to the devices should occur within the first few weeks after the birds are equipped. In our study, only 1 penguin was lost within the first 6 wk after being equipped. The reason for the cessation of transmission signals is unknown and it cannot be ruled out that the transmitter contributed to the death of this individual. However, transmission from all other penguins lasted much longer, and it can therefore be assumed that the loss of contact was caused by the loss of the transmitters. This assumption is further substantiated by the fact that

some consistent migration patterns were apparent in the penguins studied, irrespective of the location of their breeding colony or the study period (see next subsection). Therefore, given the urgent need to collect baseline data on the winter dispersal of penguins from the Falkland Islands to develop adequate measures for species and habitat protection, we felt it was justified to equip penguins with satellite transmitters, although the potential effects on their behaviour remains largely unknown.

Winter foraging areas

Like many other marine top predators breeding in the southern Atlantic Ocean (e.g. Croxall & Wood 2002), rockhopper penguins make extensive use of the Patagonian Shelf waters during winter, utilising an area ranging from 38° to 55° S and 51° to 69° W. Vast parts of this region were used mainly for travelling or commuting, and 4 major winter foraging areas for rockhopper penguins from the Falkland Islands were identified (Fig. 7): (1) inshore waters of the Falkland Islands, mainly to the north and west, (2) in the vicinity of Burdwood Bank to the south of the Falkland Islands, (3) at the slope of the Patagonian Shelf northwards beyond 40° S, and (4) waters along the Argentine coast between 48 and 54° S. The utilisation of these areas sometimes varied significantly (Table 2) between years and breeding colonies, maybe due to fluctuations in the food supply. The winter diet of rockhopper penguins is unknown, but presumably does not differ from that in the breeding season; during the breeding season their diet consists mainly of crustaceans, with varying proportions of fish and squid taken according to locality and season (for a review, see Williams 1995). In the Falkland Islands, rockhopper penguins feed opportunistically on a mixture of lobster krill *Munida gregaria*, fish and squid (Pütz et al. 2001). The Patagonian squid *Loligo gahi* has been found in the diet of rockhopper penguins breeding on Penguin

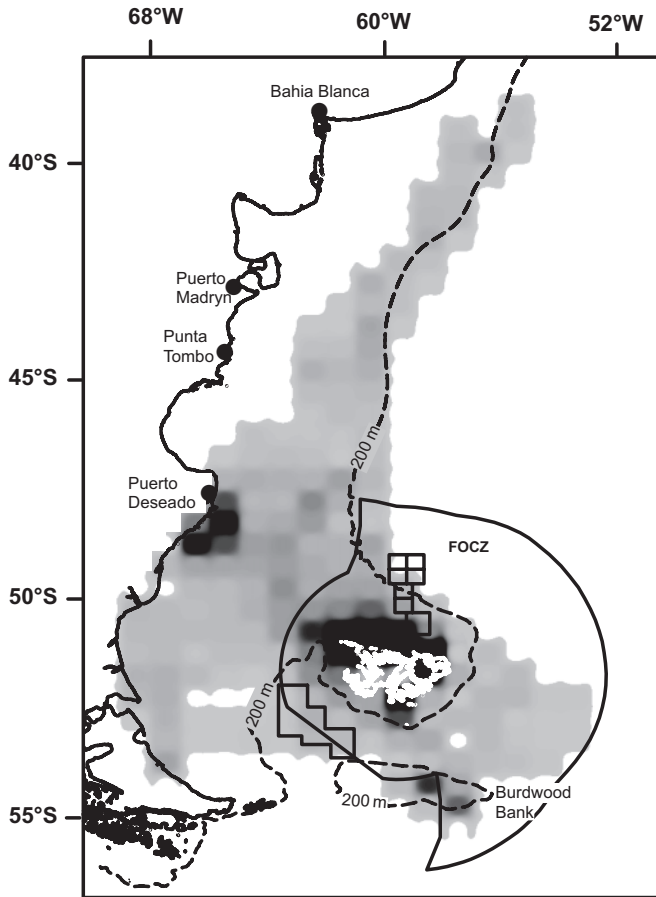


Fig. 7. *Eudyptes chrysocome*. Density distribution of positions received from rockhopper penguins breeding in Falkland Islands waters, satellite-tracked during the initial part of their winter migration. The level of shading is proportional to the number of positions obtained in each grid square (light grey = 1 position (total range), dark grey ≥ 17 positions (1% of all positions), black ≥ 35 positions (2% of all positions)). The density plot was derived using the raster grid procedure in Map-Info 5.0. All raster grids were based on a resolution of 0.5° latitude \times 1° longitude. In order to obtain one locational fix per day and bird, the different duty cycles were standardised by interpolating missing locational fixes in cases where the duty cycle was longer than 1 d. This procedure was based on the assumption that birds travelled on a straight line course and at a constant speed between 2 consecutive fixes. For further explanations see Fig. 1

Island, about 50 km southeast of Puerto Deseado, Argentina (E. Frere & P. Gandini pers. comm.), and this prey species appears to be abundant in the area all year round (Pineda et al. 1996).

Threats from fisheries and oil drilling

Food availability is largely influenced by the productivity of water masses transported to the main foraging

areas. The major oceanographic feature influencing the waters of the Falkland Islands is the Falklands Current (Glorioso & Flather 1995), which has its origin in the Antarctic circumpolar current and transports nutrient-rich sub-Antarctic water masses to the north. It flows in 2 branches around the Falkland Islands and then continues its northward flow along the shelf slope (Glorioso & Flather 1995). Further to the west, along the Argentine coast, the Brazil current acts as a counter-current and transports subtropical waters from north to south. These hydrographic features create a nutrient-rich system over the Patagonian Shelf that supports the development of a rich marine life. As a consequence, these areas are heavily exploited by fisheries, posing potential threats to the rockhopper penguins and/or their prey. A fishing fleet of more than 200 vessels operates in the FOCZ, catching approximately 200 000 t of fish and squid annually (Falkland Island Government 2000). At the beginning of the 1990s exploitation was even higher, but the number of fishing licenses issued has been reduced to conserve fish and squid stocks. Approximately the same number of fishing vessels operate from harbours in Patagonia (Crespo et al. 1997), and foreign vessels also operate within the Argentine EEZ and adjacent waters.

Another potential threat to seabirds and mammals foraging over the Patagonian shelf comes from oil pollution. In the Argentine EEZ oil exploration is taking place at a number of sites, and oil exploration and production in the FOCZ are being promoted by the Falkland Islands Government (2001). Hydrocarbon exploration was conducted in 1998 the north of the Falkland Islands, and a Special Area of Co-operation (SAC) to the southwest is earmarked for future exploration. Oil-related activities within Falkland Islands waters are currently suspended, but hydrocarbon exploration and production may start in the near future (Falkland Islands Government 2001). Both fishing and oil drilling have the potential to threaten the winter foraging areas of rockhopper penguins from the Falkland Islands or may, at least, add to limitations imposed by the fluctuating food supply.

Rockhopper penguins, as all other migratory penguin species, depart from their moulting sites very soon after completing their moult, and remain absent until the next breeding season (Williams 1995). Consistent with this, in 1998 and 2000, all birds investigated at Seal Bay and Sea Lion Island left their moulting site within 1 wk after being equipped with their transmitter, and did not return. In contrast, most penguins investigated in these 2 colonies in 1999, as well as some penguins from Saunders Island in 2000, frequently returned to their moulting/breeding site after making short foraging trips. How can this behaviour be explained? Obviously, the local food supply was suffi-

cient to meet the rockhopper penguins' energy demands following their 1999 moult, as commercial catches of the Patagonian shortfin squid *Illex argentinus* in Falkland Islands waters between April and June were 3 times higher than in 1998 and twice as high as in 2000 (Falkland Islands Government 2000). A high abundance of shortfin squid was associated with a lower proportion of frontal waters, or a higher proportion of favourable waters in the range 16 to 18°C within the inferred hatching area in the year preceding the fishery (Waluda et al. 2001). On the other hand, favourable conditions for shortfin squid were not reflected in the catch of other commercially exploited species, as in April to June 1999 the total catch excluding *I. argentinus* was about 25% lower than in the other 2 years (Falkland Islands Government 2000). Both rockhopper penguins and *I. argentinus* feed mainly on crustaceans, namely hyperiids and euphausiids (Mouat et al. 2001), and rockhopper penguins also take small-sized shortfin-squid (Pütz et al. 2001). Conditions favouring the development of shortfin squid may thus have an effect on the food available to rockhopper penguins. Water temperatures to the northwest of the Falkland Islands waters were unusually high in 1999 compared to 1998 and 2000 (D. Middleton & A. Arkhipkin pers. comm.), but further research is needed to gain more insight into the interactions between oceanographic conditions and food availability for top predators in the SW Atlantic.

Inshore Falkland waters

Apart from the areas directly adjacent to the moulting/breeding colonies, the inshore area most frequented by birds from all 3 colonies was situated in shallow coastal waters to the northwest of the Falkland Islands. At-sea observations also noted locally high densities of rockhopper penguins west of the Falkland Islands (White et al. 2002). Due to the inter-annual variations in residence times of penguins in that area, prey abundance can be assumed to undergo inter-annual fluctuations. This area is neither directly affected by fishing activities (Falkland Islands Government 2000) nor by hydrocarbon exploration (Falkland Islands Government 2001). However, as this area is influenced by the western branch of the Falklands Current, any oil pollution originating from SAC to the southwest of the Falkland Islands will be transported to the western part of the Falkland Islands, with presumably detrimental consequences for all marine life in the area. This study provides baseline data which should be taken into account in the creation and maintenance of an appropriate oil spill response capability.

Burdwood Bank

The foraging area situated furthest south, Burdwood Bank and adjacent oceanic areas to the northeast, was frequented only by birds breeding at Sea Lion Island. This area is directly influenced by the Falklands current (Glorioso & Flather 1995) and is not threatened by oil pollution, because shipping routes and oil rigs are located further north. Fishing in the area is restricted to longlining, either from vessels licensed from the Falkland Islands (Falkland Islands Government 2000) or from Argentine vessels (Crespo et al. 1997). In contrast to flying seabirds, which are in danger of becoming entangled and drowning during the setting or hauling operation of the longlines (e.g. Alexander et al. 1997), this fishing method does not pose any known threat to penguins.

Northern Patagonian shelf

The third major foraging area was situated along the slope of the Patagonian shelf to the north, where only birds from the northern colonies foraged. Fishing operations do occur in the area, but the predominant fishing method is jigging (Crespo et al. 1997). Like longlining, jigging does not pose an immediate threat to rockhopper penguins, which are occasionally caught accidentally on the jigging hooks, but usually released alive (Falkland Islands Fisheries Department unpubl. data). As mentioned earlier, rockhopper penguins and shortfin squid may compete for the same prey, which would explain the importance of this area for wintering rockhopper penguins. The immense light intensity generated by jigging vessels (Rodhouse et al. 2001) may affect seabirds in general and penguins in particular. The Patagonian shelf slope used for jigging is situated to the north of the area where hydrocarbon exploration took place in 1998 (Falkland Islands Government 2000). Any oil pollution generated in these areas will subsequently drift northwards with the Falklands Current and poses an immediate threat to seabirds foraging in that area.

Puerto Deseado area

By far the most important foraging area for wintering rockhopper penguins from the Falkland Islands was situated about 50 km off the coast of Argentina, between Puerto Deseado (48°S) and Rio Gallegos (52°S). Immediately to the north of the area is the southern border of a large fishing area where trawlers target shrimp and hake (Crespo et al. 1997). Apart from the immediate competition between penguins

and fisheries, small numbers of penguins and other top predators may become caught accidentally in the net during fishing operations (e.g. Yorio & Caille 1999, Gandini et al. 1999, K. Pütz pers. obs.). Oil pollution frequently occurs north of this area, killing 40 000 Magellanic penguins *Spheniscus magellanicus* each year along the coast of the Argentine province of Chubut, a coastline of approximately 3000 km to the north of Puerto Deseado (Gandini et al. 1994); breeding pair numbers at some Magellanic penguin colonies have fallen recently (Williams 1995). The main cause of this oil pollution is believed to be bilge water and ballast tank cleaning, and thus may occur further south as well. Rockhopper penguins from the Falkland Islands do not use coastal waters of Chubut province in winter, but they may be exposed to the same threats.

Outlook

Adequate protection of the penguin populations in the Falkland Islands as well as along the Argentine coast can only be achieved by bilateral co-operation in research and legislation, and it is hoped that the recently improved political relations between the Falkland Islands and Argentina (Dodds & Manóvil 2002) will assist in achieving this aim.

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