

Klemens Pütz · Andrea Raya Rey · Adrián Schiavini
Andrea P. Clausen · Bernhard H. Lüthi

Winter migration of rockhopper penguins (*Eudyptes c. chrysocome*) breeding in the Southwest Atlantic: is utilisation of different foraging areas reflected in opposing population trends?

Received: 27 October 2005 / Revised: 9 January 2006 / Accepted: 9 January 2006 / Published online: 3 February 2006
© Springer-Verlag 2006

Abstract Rockhopper penguins (*Eudyptes chrysocome*) breeding on Staten Island, Argentina, were satellite tracked in 2002 and 2003 during the onset of their winter migration. After their moult, the dispersal of 24 birds was monitored for a mean period of 50.0 ± 40.3 days. Birds travelled at a mean velocity of 3.1 ± 1.1 km/h. The mean minimum distance travelled was $1,640 \pm 1,425$ km; the maximum distance to the colony was generally less than 1,000 km, although one bird travelled more than 2,000 km from the colony. The penguins dispersed over an area totalling about 1.3 million km², ranging from 50 to 62°S and from 49°W in the Atlantic to 92°W in the Pacific, and covering polar, sub-polar and temperate waters in oceanic regions as well as shelf waters. Despite the very wide dispersal, both temporally and spatially, two important wintering grounds for rockhopper penguins from Staten Island could be identified, both located over shelf regions: one extended from Staten Island to the north along the coast of Tierra del Fuego up to the Magellan Strait; the other was located over the Burdwood Bank, an isolated extension of the Patagonian Shelf to the south of the Falkland Islands. The Drake

Passage also appeared to be an important area for wintering penguins, although dispersal was far more widely spread. Comparison with data obtained during winter from rockhopper penguins originating from the Falkland Islands showed that the area off the coast of Tierra del Fuego was used more or less exclusively by birds from Staten Island, whereas the Burdwood Bank was shared with penguins coming from southern colonies in the Falkland Islands. The implications of these findings are discussed with regard to (a) opposing population trends of rockhopper penguins in the Southwest Atlantic, and (b) the urgent need to establish adequate conservation measures for species and habitat protection.

Introduction

Rockhopper penguins (*Eudyptes chrysocome*) breed on sub-Antarctic and temperate islands in the Southern Ocean (Williams 1995). Over the past few decades, dramatic declines in population have been observed throughout their breeding range (Moors 1986; Cooper 1992; Cooper et al. 1997; Ellis et al. 1998; Guinard et al. 1998; Crawford et al. 2003; Pütz et al. 2003a). The reasons for these declines are still unclear, although concurrent changes in sea surface temperatures are assumed to have reduced food availability (Cunningham and Moors 1994; Guinard et al. 1998). Starvation prior to moult was also assumed to be linked to a mass mortality of rockhopper penguins on the Falkland Islands following the 1985/86 breeding season (Keymer et al. 2001). The widespread reduction in the rockhopper penguin population has resulted in its classification as “vulnerable” under IUCN (World Conservation Union) guidelines (BirdLife International 2000).

The rockhopper penguin subspecies population in the Southwest Atlantic and Southeast Pacific Oceans consists essentially of breeding colonies on the Falkland

K. Pütz
Antarctic Research Trust, Stanley FIQQ 1ZZ,
PO Box 685, Falkland Islands, South Atlantic

A. R. Rey · A. Schiavini
Consejo Nacional de Investigaciones Científicas y Técnicas,
Centro Austral de Investigaciones Científicas, Bernardo Houssay
200, V9410BFD Ushuaia, Tierra del Fuego, Argentina

A. P. Clausen
Falklands Conservation, Stanley FIQQ 1ZZ, PO Box 26,
Falkland Islands, South Atlantic

B. H. Lüthi
Antarctic Research Trust (Switzerland), General-Guisanstr. 5,
8127 Forch, Switzerland

Present address: K. Pütz (✉)
Am Oste-Hamme-Kanal 10, 27432 Bremervörde, Germany
E-mail: puetz@antarctic-research.de

Islands, Staten Island, Isla Noir, Diego Ramírez and Ildefonso islands. In the Falkland Islands, the rockhopper penguin population has fallen from an estimated 1.5 million breeding pairs in the early 1930 (Pütz et al. 2003a) to about 287,000 breeding pairs to date (Clausen and Huin 2003), equivalent to an annual decrease of ca. 2.5%. By contrast, the population of a recently discovered breeding colony on Staten Island, Tierra del Fuego, Argentina, numbering about 175,000 pairs, seems to have remained stable, as there are no signs of ground erosion indicating the previous existence of a larger colony (Schiavini 2000). The breeding population in Chile was estimated to consist of about 100,000 breeding pairs on Diego Ramírez, 50,000 breeding pairs on Ildefonso islands (Kirkwood et al., unpublished data), and 70,000 on Isla Noir (Woehler and Croxall 1997), but nothing is known about historical numbers on either island. A few, albeit much smaller, breeding colonies are located on other south Chilean islands and on Penguin Island, Argentina. Thus, it appears that the current population size for this subspecies is around 700,000 breeding pairs.

Mortality rates during the breeding and the non-breeding period of both adults and immature birds have a significant impact on the size of the breeding population. In the Falkland Islands, breeding success and diet of rockhopper penguins have been monitored since the late 1980s, and data collected so far has indicated potential threats from commercial fisheries (Pütz et al. 2001; Clausen and Pütz 2002). In addition, it could be shown that during the breeding season, rockhopper Penguin foraging areas are vulnerable to hydrocarbon

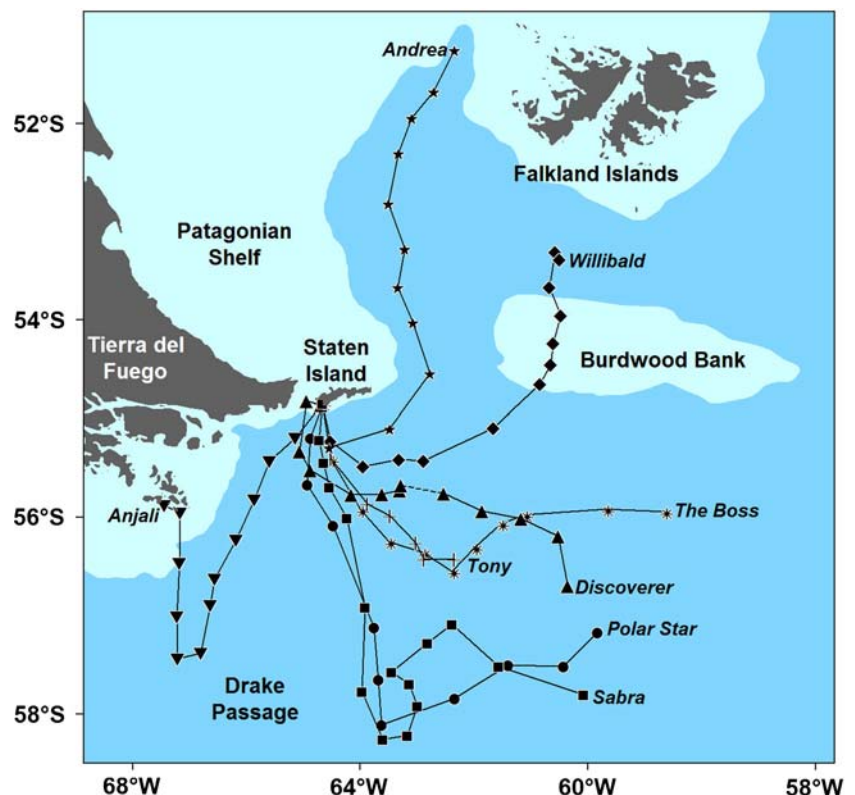
exploration and future exploitation (Boersma et al. 2002; Pütz et al. 2003b). As is the case for most migratory penguin species, data on the dispersal of rockhopper penguins during the non-breeding period, when they can migrate much greater distances and are thus affected by more numerous and diverse threats, are sparse. However, it could be shown that during the non-breeding period rockhopper penguins from the Falkland Islands are under serious threat from oil pollution and fishing activities over the Patagonian Shelf as far north as 38°S, as well as along the Argentine coast (Pütz et al. 2002a). It is thus essential to study penguin ranges and foraging areas during the winter period to gain a more comprehensive understanding of apparent population trends.

The aim of this study was to investigate for the first time the winter dispersal of rockhopper penguins breeding on Staten Island, Argentina, to (a) determine their preferred foraging areas during the non-breeding period; (b) identify potential threats within these foraging areas; and (c) compare their wintering grounds with those used by conspecifics from the Falkland Islands to more fully understand the reasons behind the opposing trends of these two breeding populations.

Materials and methods

Fieldwork was conducted at the rockhopper penguin breeding colony at Bahia Franklin (51°51'S, 64°40'W) on Staten Island, situated about 30 km east of the

Fig. 1 Migration paths of Rockhopper Penguins tracked for shorter periods and without a preferred feeding area (*Andrea*, *Discoverer*, *Polar Star*, *Sabra*, *Anjali*, *The Boss*, *Tony*, *Willibald*). Light blue shading indicates shelf areas with water depths of less than 200 m



southeastern tip of South America (Fig. 1). Rockhopper penguins were equipped on 21 and 22 March 2002 ($n=9$) and 2003 ($n=15$) with satellite transmitters at their breeding colonies after completion of their moult. After their capture, penguins were weighed (mean weight females: 1.8 ± 0.3 kg; mean weight males: 2.1 ± 0.2 kg) and bill dimensions measured (mean bill depth and length females 18.5 ± 0.9 and 38.2 ± 2.6 mm; mean bill depth and length males: 21.7 ± 0.8 and 43.4 ± 1.8 mm) to determine their gender (sensu Hull 1996). 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, Beiersdorf AG, Hamburg, Germany) and 2-component neoprene glue (Deutsche Schlauchbootfabrik, Eschershausen, Germany) according to the method described by Wilson et al. (1997). The devices were then covered with a layer of quick epoxy (Loctite® 3430, Loctite Deutschland GmbH, München, Germany) to prevent the birds from removing the tape with their beaks. The whole process took less than 20 min per bird.

The KiwiSat 101 satellite transmitters (Sirtrack) used had maximum dimensions of $130 \times 35 \times 20$ mm and the epoxy resin in which they were embedded was hydrodynamically shaped following the recommendations by Bannasch et al. (1994). The satellite transmitters were powered by 2 AA lithium cells and weighed approximately 100 g, equivalent to about 5% of the mean penguin body mass of 2.0 ± 0.2 kg. To further reduce hydrodynamic drag (Wilson et al. 2004), the flexible antenna, 170 mm long and 3 mm in diameter, protruded at an angle of 60° from the rear of the device.

To reduce the energy requirements of the satellite transmitters, devices were programmed to transmit with a duty cycle of 6 h on/18 h off with a repetition period of 60 s, and were equipped with a saltwater switch that prevented transmission while under water. All transmitters were switched on at 22:00 local time (= GMT-3 h), thus transmitting at night when penguins usually rest at the surface. The mean number of locations received per duty cycle was 12.3 ± 4.3 . Positional data obtained from Argos (CLS, Toulouse, France) are 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). The most accurate position obtained in each duty cycle for each penguin (97.4% of processed positions were accurate to within 1 km or better) was then transferred to MAPINFO Professional 5.0 (MapInfo Corporation, Troy, NY, USA) for graphical display of the migration routes, the creation of a density distribution map and the calculation of area utilisation.

The transmitters' saltwater switch also continuously recorded and subsequently transmitted the time birds spent at the surface (surface time counter, STC). The STC could record a maximum of 43,200 units (1 unit = 2 s), or 1 day. Surface time values were used to calculate time spent underwater by subtracting the time spent at the surface from the time elapsed between two

positional fixes. Calculation of travelling speed was based on the relationship between time spent underwater and the distance travelled between two consecutive positional fixes. 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 two locations, and drift with water currents, were ignored. All mean values are given \pm standard deviation (SD). Means were compared using MINITAB 14 one way ANOVA and post-hoc Tukey multiple comparison.

Due to the lack of any significant differences between the calculated migration parameters with regard to study year or gender (Mann–Whitney-test), which was at least partly a result of small sample sizes, and to account for the observed differences in migration patterns, rockhopper penguins were grouped into three categories: (a) birds with no pronounced foraging area, mostly because transmission periods were less than 2 weeks; (b) birds that foraged for at least part of their winter migration off the northeastern coast of Tierra del Fuego; and (c) birds that did not forage off the northeastern coast of Tierra del Fuego but travelled extensively. Although this classification is somewhat artificial as it is based on a mixture of transmission periods and foraging areas, it provided the most practical approach to analyse the different migration patterns.

Results

All rockhopper penguins left their moulting site within 4 days of being equipped with a satellite transmitter. They were subsequently tracked for a mean duration of 50.0 ± 40.3 days (range 7–147), providing a total of 1,200 daily at-sea positions. The mean minimum distance covered was $1,640 \pm 1,425$ km (range 251–5,281), and the birds travelled at a mean speed of 3.1 ± 1.1 km/h (range 1.5–4.8 km/h). The mean maximum distance to the colony was 442 ± 390 km (range 143–2,006). The individual values for each bird are summarised in Table 1.

Eight rockhopper penguins from Staten Island showed no preferred foraging area during the period tracked (Fig. 1), which was generally less than 2 weeks (Table 1). Two birds, *Andrea* and *Willibald*, migrated northwards, while five birds first headed south and then turned east (Fig. 1). *Anjali*, the remaining bird, also initially travelled in a southerly direction for 1 week, before turning north again and swimming back onto the shelf, where transmission ceased. Overall, these birds had a mean travelling speed of 4.2 ± 0.5 km/h (range 3.3–4.8; Table 1).

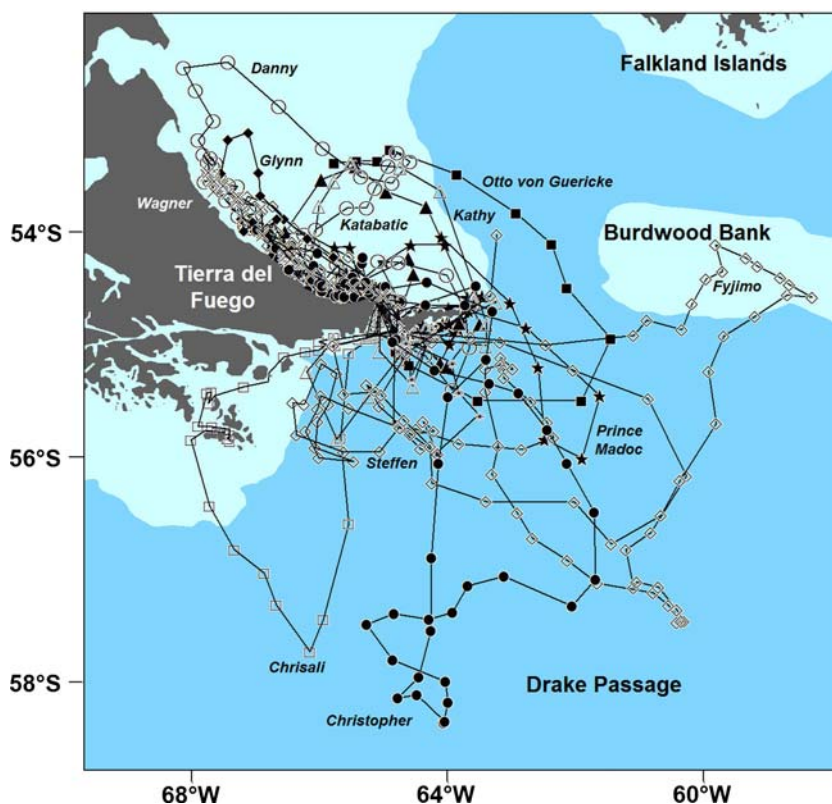
The second group comprised the majority of rockhopper penguins (Fig. 2). The common feature of their migration was that they foraged for at least some time during the transmission period off the northeastern coast of Tierra del Fuego. Some of these birds also spent some time in the Drake Passage. In general, all these penguins

Table 1 Summary of data obtained from satellite transmitters attached to Rockhopper Penguins from Staten Island

Penguin	Sex	Start of migration	Transmission period (days)	Maximum distance to the colony (km)	Minimum distance covered (km)	Mean travelling speed \pm SD (km/h)	Maximum travelling speed (km/h)
<i>Andrea</i>	F	24.03.02	9	429	596	4.0 ± 1.3	6.6
<i>Anjali</i>	F	23.03.03	12	329	531	3.8 ± 1.2	5.4
<i>Discoverer</i>	M	24.03.02	10	339	453	3.3 ± 1.6	7.2
<i>Polar Star</i>	M	25.03.02	9	397	644	4.8 ± 2.1	9.5
<i>Sabra</i>	F	25.03.02	14	434	749	4.3 ± 2.4	10.1
<i>The Boss</i>	M	22.03.03	10	400	511	4.4 ± 1.6	6.7
<i>Toni</i>	M	23.03.03	6	229	251	4.6 ± 2.1	7.4
<i>Willibald</i>	M	23.03.03	12	316	483	4.0 ± 1.9	7.3
Mean \pm SD			10.3 ± 2.4	359 ± 69	527 ± 147	4.2 ± 0.5	
<i>Christopher</i>	M	24.03.02	82	394	2,514	2.3 ± 1.6	6.9
<i>Chrisali</i>	F	23.03.03	59	334	1,342	1.9 ± 1.8	7.5
<i>Danny</i>	F	23.03.03	69	344	1,587	1.9 ± 1.5	6.6
<i>Fyjimo</i>	M	24.03.02	121	411	4,064	2.9 ± 2.0	12.0
<i>Glynn</i>	F	26.03.02	17	260	459	1.9 ± 1.1	4.7
<i>Katabatic</i>	M	22.03.03	91	170	1,662	1.6 ± 1.8	9.6
<i>Kathy</i>	F	23.03.03	61	173	1,731	2.3 ± 1.9	9.6
<i>Otto von Guericke</i>	M	22.03.03	32	206	1,016	2.5 ± 1.9	7.7
<i>Prince Madoc</i>	F	24.03.03	53	218	1,462	2.2 ± 1.7	7.1
<i>Steffen</i>	M	22.03.03	61	143	1,420	2.0 ± 1.5	5.9
<i>Wagner</i>	F	22.03.03	35	253	621	1.5 ± 1.3	6.4
Mean \pm SD			61.9 ± 29.2	264 ± 93	$1,625 \pm 982$	2.1 ± 0.4	
<i>Elisabeth</i>	F	21.03.03	44	1,020	2,304	4.6 ± 2.8	17.3
<i>Norbert</i>	F	23.03.03	68	403	1,399	2.1 ± 1.9	12.2
<i>Paul</i>	M	23.04.02	59	2,006	3,509	3.4 ± 1.7	8.9
<i>Rob</i>	M	24.03.02	120	863	4,764	4.0 ± 2.3	10.3
<i>Werner F.</i>	M	22.03.03	146	537	5,281	3.4 ± 2.1	12.0
Mean \pm SD			87.4 ± 43.5	966 ± 632	$3,451 \pm 1,628$	3.5 ± 0.9	
Total mean \pm SD			50.0 ± 40.3	442 ± 390	$1,640 \pm 1,425$	3.1 ± 1.1	

The minimum distance covered is the sum of all distances between consecutive positions; calculation of travelling speed also takes into account the time spent underwater between two positions

Fig. 2 Migration paths of Rockhopper Penguins that, at least once during their winter migration, spent some time off the northeastern coast of Tierra del Fuego (*Christopher*, *Fyjimo*, *Glynn*, *Chrisali*, *Danny*, *Katabatic*, *Kathy*, *Otto von Guericke*, *Prince Madoc*, *Steffen*, *Wagner*)



remained within a distance of about 400 km from the colony, but the minimum distances travelled were, in some instances, up to ten times greater than the maximum distance to the colony (e.g. *Fyjimo*, *Katabatic*, *Kathy* and *Steffen*; Table 1), which was mainly due to extensive distances covered between the Drake Passage and the Tierra del Fuego coast. Minimum distances covered in this group were generally greater than 1,000 km. The mean travelling speed of 2.1 ± 0.4 km/h (range 1.5–2.9) for these birds was only half that calculated for birds from the first group (Table 1).

The migration paths of the remaining rockhopper penguins were much more diverse, although they had in common that all of them travelled in the Drake Passage, but none of them in the coastal areas of Tierra del Fuego (Fig. 3). During their winter migration, *Rob* and *Elisabeth* both migrated as far south as the South Shetland Islands at 62°S, about 900 km south of the breeding islands. *Rob* subsequently travelled west into the Pacific and then on around Cape Horn, along the slope of the Patagonian Shelf, a total distance of at least 4,750 km. *Elisabeth*, on the other hand, headed eastwards first before travelling to the South Shetland Islands, where transmissions ceased. *Paul* also initially migrated south into the Drake Passage, but then maintained a north-westerly course until transmissions ceased about 2,000 km west of Staten Island. *Norbert* and *Werner F.* both travelled to the Burdwood Bank, an isolated extension of the Patagonian Shelf. However, while *Norbert* stayed in the vicinity of the Burdwood Bank during the tracking period, *Werner F.* also travelled extensively in the Drake Passage, reaching nearly 60°S. Two other birds from the first two groups, *Willibald* and *Fyjimo*, also briefly visited Burdwood Bank during their winter migration. The mean travelling speed of 3.5 ± 0.9 km/h (range 2.1–4.6) recorded for this group of birds was in between those calculated for the other two groups.

The average transmission periods of groups two and three were not significantly different ($F_{(1,14)}=1.94$, $P=0.185$; Table 1) and it is thus appropriate to statis-

tically compare the migration parameters calculated for these two groups. The mean travelling speed for group three birds was significantly faster than that of birds from the second group ($F_{(1,14)}=18.85$, $P=0.001$). Also, the differences in the mean minimum distance covered and mean maximum distance to the colony, being more than three times and more than two times higher in these birds than in birds from the second group, respectively, were also significant ($F_{(1,14)}=7.93$, $P=0.014$ and $F_{(1,14)}=14.07$, $P=0.002$, respectively).

To identify the preferred winter foraging areas of rockhopper penguins breeding on Staten Island, data for 2002 and 2003 were pooled to create a density distribution map (Fig. 4). This analysis suggests the most important wintering ground was northwestwards from Staten Island along the Tierra del Fuego coast up to about 52°S, an area of about 44,000 km². Another important area, of 15,000 km², was situated at the Burdwood Bank. Thus, the vast majority of positions were within a radius of 400 km around the island. However, the overall range of rockhopper penguins from Staten Island was far larger, ranging from 50°S to the west of the Falkland Islands to 62°S north of the South Shetland Islands, and from 92°W in the Pacific to 49°W in the Scotia Arc, comprising a total area of approximately 1.3 million km². However, about 250,000 km² alone were due to the westward migration of a single penguin, *Paul* (c.f. Fig. 3).

Discussion

The winter dispersal of rockhopper penguins breeding on Staten Island was studied over a 2-year period using satellite telemetry. In the following, the potential impact of the satellite transmitters on the birds, and thus the results obtained, are examined; the migration paths of the birds studied are then put into perspective, and finally the implications of the results for conservation measures are discussed.

Fig. 3 Migration paths of Rockhopper Penguins that dispersed widely with no preferred feeding area (*Paul*, *Rob*, *Elisabeth*, *Norbert*, *Werner F.*)

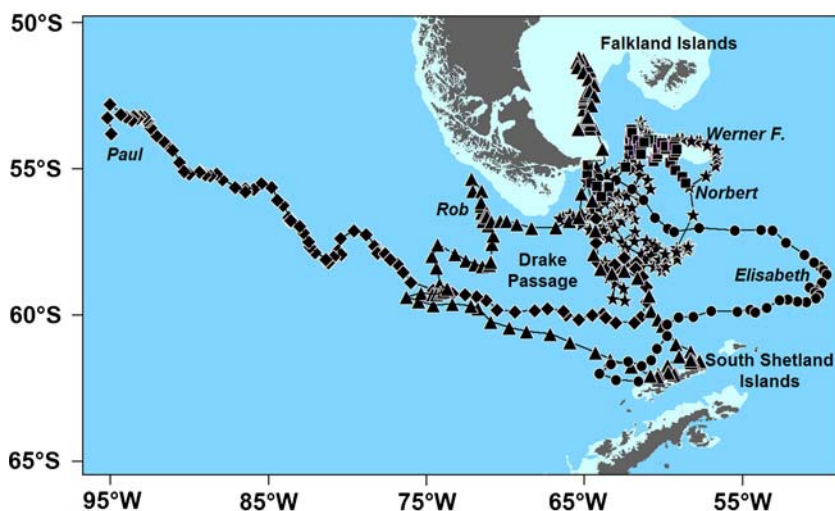
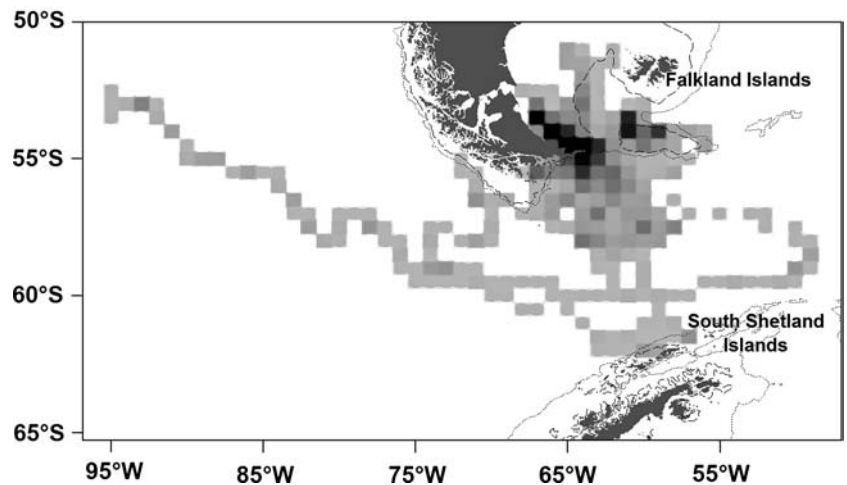


Fig. 4 Density distribution of daily positions received from Rockhopper Penguins during winter 2002 and winter 2003. The level of shading is proportional to the number of positions obtained in each grid square ($0.5 \text{ latitude} \times 1.0 \text{ longitude}$). The dotted lines indicate the 200 and 1,000 m water depth contours



Potential reasons for the satellite transmitter failure and effects on penguin behaviour

Attaching devices to free-ranging animals may influence their foraging behaviour (e.g. Bannasch 1995; Ropert-Coudert et al. 2000). Externally attached units are known to increase the penguins' hydrodynamic resistance (Bannasch et al. 1994), which may result in greater energy expenditure and/or a reduced swim speed (Culik and Wilson 1991). This effect is even more pronounced with satellite transmitters, as these units have an antenna that adds substantially to the drag already caused by the backpack (Wilson et al. 2004). Therefore, in this study, all possible measures were taken to keep any potential impact to a minimum (see **Materials and methods**). These measures had proved successful in a comparable study conducted over a 3-year period in the Falkland Islands, where, based on the recorded transmitting times and the re-sighting of individual birds, no detrimental effects of the transmitters on the birds were found (Pütz et al. 2002a). Two birds equipped with satellite transmitters were also re-sighted in this study (A. Raya Rey, personal observation).

Despite these measures, some transmitters were lost within 2 weeks of being deployed (four PTTs in 2002 and four PTTs in 2003) and, accordingly, the affected birds were grouped together for analysis purposes. How can this failure be explained? Penguins are known to 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, 2002a, this study). Furthermore, due to the increased energy demands during moulting starvation, birds are most vulnerable to any adverse conditions at the very beginning of their winter migration, and losses relating to any negative effect of the devices should occur within the first few weeks after the birds are equipped. Therefore, being fitted with a transmitter may have been one contributory factor leading to the death of birds from the first group. However, other

factors, such as predators or technical failure of the transmitter, may also have caused cessation of transmitter signals. In general, the mean and maximum transmission periods achieved using this method on wintering penguins (Pütz et al. 2000, 2002a, this study) indicate that being fitted with a satellite transmitter was per se not detrimental to the birds. Therefore, we assumed that although the transmitters have had an influence on the birds' energy expenditure, they did not affect their migration behaviour in general.

Winter foraging areas

The distributional range of rockhopper penguins from Staten Island covered over 1 million km² and extended north-south from temperate to polar shelf regions and west-east from temperate oceanic waters in the Pacific to Antarctic deep waters in the Atlantic. Given the breeding range of this penguin species—from temperate to sub-polar regions—the migration of at least three birds (12.5% of the birds studied) into polar waters as far south as the South Shetland Islands is most surprising. However, food availability at the northern ice edge is particularly plentiful (Knox 1994) and may provide a reliable food source for rockhopper penguins in winter. The only other penguin species that is known to travel from sub-polar into Antarctic waters during winter is the far larger king penguin *Aptenodytes patagonicus* (Pütz 2002; Bost et al. 2004). However, the two main foraging areas for the rockhopper penguins, where daily positions were highly concentrated, were situated on the shelf: one off the northeastern coast of Tierra del Fuego and the other at Burdwood Bank, an isolated extension of the Patagonian Shelf. In general, rockhopper penguins appear to be capable of migrating distances of more than 5,000 km during winter, characterising them as a truly migratory species (Croxall and Davis 1999).

Calculation of travelling speeds for satellite-tracked animals may give an indication of prey distribution, because the lower the travelling speed, the longer the

animal remains in a certain area. Accordingly, the first group of penguins, which were tracked for only a limited period, exhibited a high mean travelling speed compared with their conspecifics as the tracking period covered only the initial migration to certain foraging areas. The second group remained for extended periods in the coastal region of Tierra del Fuego, reducing their travelling speeds considerably, whereas the third group of rockhopper penguins appeared to have foraged throughout their migration without stopping in specific areas, resulting in intermediate travelling speeds. This strongly suggests that the Tierra del Fuego coast is an important foraging area for rockhopper penguins from Staten Island.

Overall, the mean travelling speed was highly comparable to that of incubating male rockhopper penguins (3.4 km/h; Pütz et al. 2003b) and breeding magellanic penguins *Spheniscus magellanicus* (4.6 km/h; Pütz et al. 2002b) in the Falkland Islands, whereas during winter rockhopper penguins from Sea Lion Island, Falkland Islands, travelled only at an average speed of 1.1 km/h (Pütz et al. 2002a). The maximum travelling speed calculated for individual birds in some instances exceeded the average swim speed of rockhopper penguins of 7.4 km/h (Brown 1987), indicating that birds were passively transported by water currents, a phenomenon which has also been found in foraging magellanic and rockhopper penguins from the Falkland Islands (Pütz et al. 2002b, 2003b).

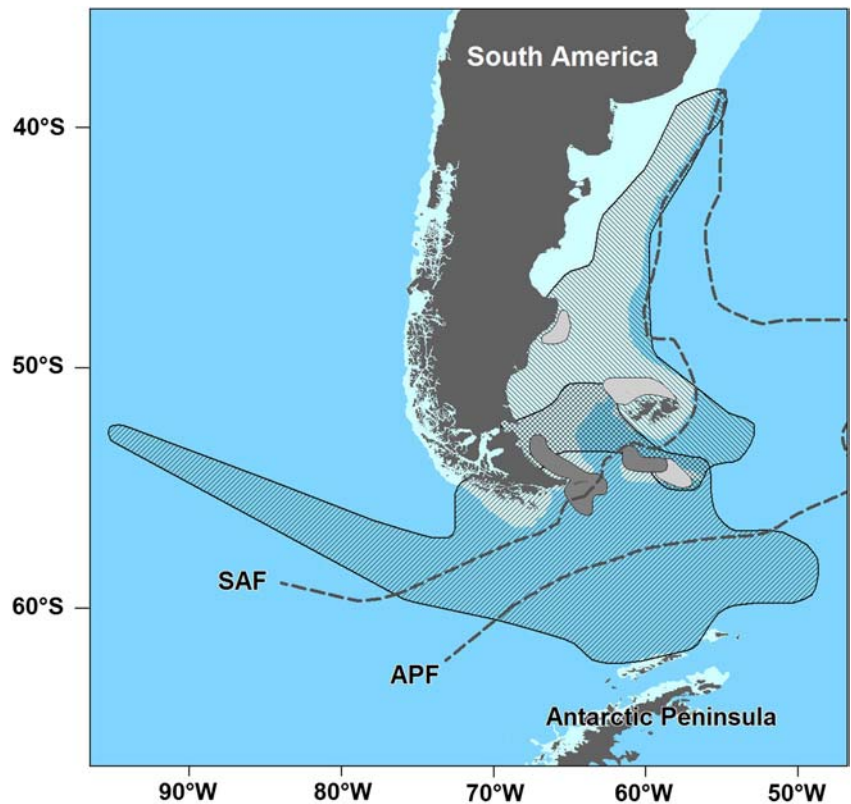
A comparison of the winter distribution of rockhopper penguins from Staten Island with conspecifics from the Falkland Islands is given in Fig. 5. In contrast to rockhopper penguins from Staten Island, birds from the Falkland Islands rarely left the Patagonian Shelf during their winter migration (Pütz et al. 2002a), although their winter distribution covers an area of approximately 0.9 million km². It thus appears that, while rockhopper penguins from the Falkland Islands leave the shelf only briefly to travel to other areas, e.g. Burdwood Bank, penguins from Staten Island are much more likely to migrate significant distances in oceanic waters during winter. Three major winter foraging areas were identified for rockhopper penguins from the Falkland Islands (Pütz et al. 2002a): apart from coastal areas around their breeding sites, by far the most important feeding ground, comprising about 12,000 km², was situated about 50 km off the coast of Puerto Deseado (48°S), Argentina. Rockhopper penguins from Staten Island concentrated their foraging efforts about 400 km further south, between 53 and 56°S, and never travelled as far north as Puerto Deseado. In contrast, only one out of 34 rockhopper penguins from the Falkland Islands used the coastal areas of Tierra del Fuego. This is surprising as both feeding grounds are equidistant from the Falkland Islands and it thus appears that there is a distinct segregation between the two populations. However, there was considerable overlap in another major foraging area, the Burdwood Bank situated to the south of the Falkland Islands, al-

though only rockhopper penguins originating from southern breeding colonies in the Falkland Islands foraged in this area (Pütz et al. 2002a).

If we assume that the migration paths of satellite tracked birds were representative, and ignore spatial and temporal variability, extrapolation of the number of breeding rockhopper penguins on Staten Island and the Falkland Islands may provide an indication of the numbers of birds frequenting these foraging areas in winter. As there were distinct differences in the migration patterns of rockhopper penguins originating from different colonies in the Falkland Islands (Pütz et al. 2002a), population figures were divided into northern colonies (192,000 breeding pairs or 67% of the population), southern colonies (62,000 breeding pairs representing 22% of the population) and southwestern colonies (33,000 breeding pairs or 11% of the population; calculated from Clausen and Huin 2003). The Burdwood Bank was frequented by 4 out of 24 birds from Staten Island, which would represent about 17% of the population of 175,000 breeding pairs. Thus, about 60,000 breeders from Staten Island may use the Burdwood Bank as winter foraging area. In contrast, only 25% of the birds from the southern colonies in the Falkland Islands make use of this area, which translates into 31,000 breeders foraging at Burdwood Bank in winter. Thus, Burdwood Bank nurtures around 90,000 breeding rockhopper penguins over the winter period, two-thirds of which are from Staten Island and the remaining third from the Falkland Islands. The area off the northeastern coast of Tierra del Fuego was used by 8% of the rockhopper penguins from the south of Falkland Islands and 46% of the birds from Staten Island, which translates into 10,000 breeders from the southern colonies in the Falkland Islands and 161,000 breeders from Staten Island using that area, giving a total of 171,000 birds. However, this area was also frequented by rockhopper penguins from New Island to the southwest of the Falkland Islands during the breeding season (Boersma et al. 2002) and it cannot be ruled out that birds from the southwest of the Falkland Islands also forage in the area during winter. Finally, 40% of birds from northern colonies and 17% of birds from southern colonies in the Falkland Islands foraged off the coast of Puerto Deseado, translating into 171,000 breeding birds. To summarise, it appears that at least half of the rockhopper Penguin populations on Staten Island and on the Falkland Islands forage in distinct areas, which together comprise only 85,000 km², or less than 5%, of the combined wintering area of about 2 million km². These calculations, although simple, highlight the importance of distinct foraging grounds for wintering rockhopper penguins in the Southwest Atlantic.

Rockhopper penguins in the Falkland Islands suffered a severe population decline over the past few decades (Pütz et al. 2003a), whereas the colony on Staten Island appears to have slightly increased or at least been stable (Schiavini 2000). Recent events indicate that

Fig. 5 Contour plots of the winter range (*striped areas*) of Rockhopper Penguins from Staten Island (this study) and the Falkland Islands (data from Pütz et al. 2002a), and the main foraging areas within each range (*shaded areas*). The *dotted lines* indicate the approximate positions of the Antarctic Polar Front (APF) and the sub-Antarctic Front (SAF)



rockhopper penguins in the Falkland Islands continue to decline, at least at some colonies. For example, in 2002, a year when sea surface temperature in the area was colder than the long-term average, a considerable number of rockhopper penguins died in the Falkland Islands, presumably from starvation prior to, or immediately after, moult (Huin 2002). The reason for this may have been a food shortage occurring throughout the Southwest Atlantic that affected not only the rockhopper penguins, but the ecosystem in general. For example, commercial catches of the Argentine shortfin squid *Illex argentinus* in Falkland Islands' waters between March and May 2002 yielded only 12,116 t, whereas on average the catch over the last 15 years (1989–2003) had been about 125,000 t, the previous poorest year being 1995 with a catch of 57,275 t during the same period (Falkland Islands Government 2004). In the adjacent Argentine fishery zone, commercial *Illex* catches between March and May were also poor during the study period, reaching only 80% (2002) and 62% (2003) of the mean catch of 144,129 t over the past 12 years. Both rockhopper penguins and *I. argentinus* feed mainly on crustaceans, namely hyperiids and euphausiids (Mouat et al. 2001; Raya Rey and Schiavini 2005), and it thus appears that, apart from other factors contributing to low commercial catches, both species may have suffered from a general food shortage. Additionally, another mass mortality in the Falklands occurred later that year which was proven to be the result of algal poisoning (Ingham and Morris 2004). Accordingly, most recent counts indicate that between 2000 and 2003 the numbers

of rockhopper penguins on Steeple Jason Island in the northwest of the Falklands have diminished from 90,000 to 30,000 breeding pairs (Huin 2004). In contrast to this trend, the population size on Staten Island appears to have remained stable during that period (A. Schiavini and A. Raya Rey, personal observation).

The differences in the winter foraging areas used may be another contributing factor to the contrasting population trends of rockhopper penguins at different breeding colonies. The two distinct major foraging areas of both populations, one situated off the coast of Patagonia for Falkland Islands' rockhopper penguins (Pütz et al. 2002a) and the other located off the coast of Tierra del Fuego for birds breeding on Staten Island (this study) experience different anthropogenic threats and subsequently activities such as shipping, fishing and oil exploration are much greater and their effects, such as exploitation of marine life and pollution, are much more pronounced. For example, the Patagonian area comprises seven coastal cities together with five important oil ports for transport of crude oil from Patagonia, whereas only two coastal cities and three oil ports are found in the area used by birds from Staten Island. Furthermore, fishing to the north of 52°S is much more pronounced than further south (Crespo et al. 1997; Schiavini et al. 1998), and there is also growing interest in further oil exploration and potentially exploitation in various areas of the southern Patagonian Shelf. Variation in the level of human activities and associated threats to the penguins in these foraging grounds may result in different survival rates of rockhopper penguins, and this would be

reflected in the recently observed population trends. However, more research on survival rates of rockhopper penguins originating from different breeding populations, including the rockhopper penguin population on Diego Ramirez and Ildefonso Islands, in conjunction with a more detailed analysis of the extent of potential threats in their respective wintering grounds, is necessary to confirm this hypothesis.

Recently, political discussions on the establishment of marine protected areas (*sensu* Boersma and Parrish 1999) on the southern Patagonian Shelf were initiated and, despite the aforementioned lack of information, the data obtained in this study will be used to support the urgent demand for the immediate establishment of marine protected areas encompassing, for example, coastal waters of Tierra del Fuego and the waters surrounding Staten Island, as well as coastal waters of Patagonia, to prevent further population declines.

Acknowledgements The Antarctic Research Trust gratefully acknowledges the generous financial support of the passengers aboard MV World Discoverer. Special thanks are due to those who sponsored individual penguins, in particular Patricia Anderson, Lesley Baxter, Erika Bodmer, Kirsten and Wolfgang Berg, Maria Diamond, Winford Evans, Kay and Lois Gray Gilmour, Connie Graetz, Werner Jost, Elisabeth and Dieter Krause, Marianne and Greg Moser, Nora Neilson, Willis B. Snell, H. Snyder, Joseph Snyder, Denise and Whitney Solso, Anneliese Stremme, Peter Taylor and Susanne and Axel Wagner, and to those who sponsored satellite transmission times, in particular Sheila & Ed Braun, Ernesta Coray, Zita and Dominique Destrax, Hedi and Rudolf Engel, Stefanie Reischauer, Albert Sicker and Franz Thiele. The authors are very grateful to Lesley Baxter for language editing. This study was approved by the National Council of Scientific Research and the Natural Resources Agency of the province of Tierra del Fuego and complied with the legal requirements in Argentina.

References

- Argos (1996) User's manual. CLS service Argos, Toulouse, p 176
- Bannasch R (1995) Hydrodynamics of penguins—an experimental approach. In: Dann P., Normann I, Reilly P (eds) *The penguins: ecology and management*. Surrey Beatty & Sons, Melbourne, pp 141–176
- Bannasch R, Wilson RP, Culik BM (1994) Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *J Exp Biol* 194:83–96
- BirdLife International (2000) *The threatened birds of the world*. Lynx Editions, Barcelona, Spain
- Boersma PD, Parrish J (1999) Limiting abuse: marine protected areas, a limited solution. *Ecol Econ* 31:287–304
- Boersma PD, Stokes DL, Strange IJ (2002) Applying ecology to conservation: tracking breeding penguins at New Island South reserve, Falkland Islands. *Aquat Conserv Mar Freshw Ecosyst* 12:63–74
- Bost CA, Charrassin J-B, Clerquin Y, Ropert-Coudert Y, Le Maho Y (2004) Exploitation of distant marginal ice zones by king penguins during winter. *Mar Ecol Prog Ser* 283:293–297
- Brown CR (1987) Travelling speed and foraging range of macaroni and rockhopper penguins at Marion Island. *J Field Ornithol* 58:118–125
- Clausen AP, Huin N (2003) Status and numerical trends of King, Gentoo, and Rockhopper penguins breeding in the Falkland Islands. *Waterbirds* 26:389–402
- Clausen A, Pütz K (2002) Recent trends in diet composition and productivity of Gentoo, Magellanic and Rockhopper penguins in the Falkland Islands. *Aquat Conserv Mar Freshw Ecosyst* 12:51–61
- Cooper W (1992) Rockhopper penguins at the Auckland Islands. *Notornis* 39:66–67
- Cooper J, Wolfaardt A, Crawford RJM (1997) Trends in size and success of breeding colonies of Macaroni and Rockhopper penguins at Marion Island, 1979/80–1995/96. *CCAMLR Sci* 4:125–147
- Crespo EA, Pedraza SN, Dans SL, Alonso MK, Reyes LM, García NA, Coscarella M, Schiavini ACM (1997) Direct and indirect effects of the high seas fisheries on the marine mammal populations in the northern and central Patagonian coast. *J Northwest Atl Fish Sci* 22:189–207
- Crawford RJ, Cooper J, Dyers BM, Greyling MD, Klages NTW, Nel DC, Nel JL, Petersen SL, Wolfaardt AC (2003) Decrease in numbers of the Eastern Rockhopper Penguin *Eudyptes chrysocome filholi* at Marion Island, 1994/95–2002/03. *Afr J Mar Sci* 25:487–498
- Croxall JP, Davis LS (1999) Penguins: paradoxes and patterns. *Mar Ornithol* 27:1–12
- Culik BM, Wilson RP (1991) Swimming energetics and performance of instrumented Adelie Penguins (*Pygoscelis adeliae*). *J Exp Biol* 158:355–368
- Cunningham DM, Moors PJ (1994) The decline of Rockhopper Penguins *Eudyptes chrysocome* at Campbell Island, Southern Ocean and the influence of rising sea temperatures. *Emu* 94:27–36
- Ellis S, Croxall JP, Cooper J (1998) Penguin conservation assessment and management plan. IUCN/SSC Conservation Breeding Specialist Group
- Falklands Islands Government (2004) Fisheries Department Fisheries Statistics, vol 8, 2003. Stanley, FIG Fisheries Department, p 72
- Guinard E, Weimerskirch H, Jouventin P (1998) Population changes of the Northern Rockhopper Penguin on Amsterdam and Saint Paul Islands. *Col Waterbirds* 21:222–228
- Huin N (2002) Dead penguins present complicated problem. Falklands Conservation Newsletter, May 2002
- Huin N (2004) Penguin and albatross monitoring 2003–04. In: Brown A (eds) *Wildlife conservation in the Falkland Islands*, Issue 4, Falklands Conservation, pp 15–16
- Hull CL (1996) Morphometric indices for sexing adult Royal *Eudyptes schlegeli* and Rockhopper *E. chrysocome* Penguins at Macquarie Island. *Mar Ornithol* 24:23–27
- Ingham B, Morris A (2004) Cause of penguin deaths proven. Falklands Conservation Newsletter January 2004. Falklands Conservation, Stanley, Falkland Islands
- Kerry KR, Clarke JR, Else GD (1995) The foraging range of Adelie Penguins at Bechervaise Island, Mac Robertson Land, Antarctica as determined by satellite telemetry. In: Dann P, Normann I, Reilly P (eds) *The penguins: ecology and management*. Surrey Beatty & Sons, Melbourne, pp 216–243
- Keymer IF, Malcolm HM, Hunt A, Horsley DT (2001) Health evaluation of penguins (Sphenisciformes) following mortality in the Falklands (South Atlantic). *Dis Aquat Organ* 45:159–169
- Knox GA (1994) *The biology of the Southern Ocean*. Cambridge University Press, Cambridge
- Moors PJ (1986) Decline in numbers of Rockhopper Penguins at Campbell Island. *Polar Rec* 23:69–73
- Mouat B, Collins MA, Pomper J (2001) Patterns in the diet of *Illex argentinus* (Cephalopoda: Ommastrephidae) from the Falkland Islands jigging fishery. *Fish Res* 52:41–49
- Pütz K (2002) Spatial and temporal variability in the foraging areas of breeding King Penguins. *Condor* 104:528–538
- Pütz K, Ingham RJ, Smith JG (2000) Satellite tracking of the winter migration of Magellanic Penguins (*Spheniscus magellanicus*) breeding in the Falkland Islands. *Ibis* 142:614–622

- Pütz K, Ingham RJ, Smith JG, Croxall JP (2001) Population trends, breeding success and diet composition of gentoo *Pygoscelis papua*, magellanic *Spheniscus magellanicus* and rockhopper *Eudyptes chrysocome* penguins in the Falkland Islands. *Polar Biol* 24:793–807
- Pütz K, Smith JG, Ingham RJ, Lüthi BH (2002a) Winter dispersal of Rockhopper Penguins *Eudyptes chrysocome* from the Falkland Islands and its implications for conservation. *Mar Ecol Prog Ser* 240:273–284
- Pütz K, Ingham RJ, Smith JG (2002b) Foraging movements of Magellanic Penguins *Spheniscus magellanicus* during the breeding season in the Falkland Islands. *Aquat Conserv Mar Freshw Ecosyst* 12:75–87
- Pütz K, Clausen AP, Huin N, Croxall JP (2003a) Re-evaluation of historical Rockhopper penguin population data in the Falkland Islands. *Waterbirds* 26:169–175
- Pütz K, Smith JG, Ingham RJ, Lüthi BH (2003b) Satellite tracking of male Rockhopper penguins *Eudyptes chrysocome* during the incubation period at the Falkland Islands. *J Avian Biol* 34:139–144
- Raya Rey R, Schiavini A (2005) Inter-annual variation in the diet of female southern rockhopper penguin (*Eudyptes chrysocome chrysocome*) at Tierra del Fuego. *Polar Biol* 28:132–141
- Ropert-Coudert Y, Bost CA, Handrich Y, Bevan RM, Butler PJ, Woakes AJ, Le Maho Y (2000) Impact of externally attached loggers on the diving behaviour of the King Penguin. *Physiol Biochem Zool* 73:438–445
- Schiavini ACM (2000) Staten Island, Tierra del Fuego: the largest breeding ground for Southern Rockhopper Penguins? *Waterbirds* 23:286–291
- Schiavini A, Frere E, Gandini P, Garcia N, Crespo E (1998) Albatross–fisheries interactions in Patagonian shelf waters. In: Robertson G, Gales R (eds) *Albatross biology and conservation*, Surrey Beatty & Sons PTY Limited, Australia, pp 208–213
- Stokes DL, Boersma PD, Davis LD (1998) Satellite tracking of Magellanic Penguins migration. *Condor* 100:376–381
- Williams TD (1995) *The penguins*. Oxford University Press, Oxford p 295
- Wilson RP, Pütz K, Peters G, Culik B, Scolaro JA, Charrassin J-B, Ropert-Coudert Y (1997) Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildl Soc Bull* 25:101–106
- Wilson RP, Kreye JM, Lucke K, Urquhart H (2004) Antennae on transmitters on penguins: balancing energy budgets on the high wire. *J Exp Biol* 207:2649–2662
- Woehler EJ, Croxall JP (1997) The status and trends of Antarctic and sub-Antarctic seabirds. *Mar Ornithol* 25:43–66