

# BREEDING DYNAMICS OF A GENTOO PENGUIN *PYGOSCELIS PAPUA* POPULATION AT CIERVA POINT, ANTARCTIC PENINSULA

R.D. QUINTANA & V. CIRELLI

GESER (Grupo de Estudios Sobre Ecología Regional), Universidad de Buenos Aires, Facultad de Cs. Exactas y Naturales, Dpto. de Ciencias Biológicas, Pab. II, C. Universitaria, 1428 Buenos Aires, Argentina  
(rubenq@bg.fcen.uba.ar)

Received 4 October 1996, accepted 24 September 1998

## SUMMARY

QUINTANA, R.D. & CIRELLI, V. 2000. Breeding dynamics of a Gentoo Penguin *Pygoscelis papua* population at Cierva Point, Antarctic Peninsula. *Marine Ornithology* 28: 29–35.

Aspects of the breeding biology of the Gentoo Penguin *Pygoscelis papua* were studied at Cierva Point, Antarctic Peninsula (64°09'S, 60°57'W). From a breeding population of 1044 pairs (85% with two eggs), 83% raised at least one chick to fledging. Survival in different subcolonies was neither correlated with perimeter-area ratio nor with distance to the sea. Chick mortality at the end of January 1993 was 23.9%, whereas for the 1991/92 breeding season it was 14.0%; for 1993/94, 23.9%; for 1994/95, 33.0% and for 1995/96 24.3%. By 17 February 1993, chick mortality was 32.3%. Chick survival was regressed against time for nine selected subcolonies, showing a high correlation between them. Covariance analysis among the regression line slopes showed a non-significant result ( $F = 0.42$ ,  $P > 0.05$ ). No significant differences were also observed when Tuckey's multiple contrasts test was performed on the proportions of surviving chicks in-between weeks ( $P > 0.05$ ), showing a gradual mortality of chicks from egg-laying to créching. These results show that the Gentoo Penguin colony at Cierva Point contains a higher proportion of pairs rearing two chicks and a lower mortality rate than does the species at other maritime Antarctic sites. Average annual growth of the colony increased by 5.7% from 1991 to 1996, in contrast to the period 1954–1958 when the colony decreased by –2.3%. The low impact of the Argentinean station near the study area could account for this fact.

## INTRODUCTION

Penguins represent about 90% of the biomass of birds from the South Atlantic and Indian Oceans and Antarctic Sea, and their colonies are distributed in Antarctic and sub-Antarctic islands as well as on the Antarctic Continent (Williams 1990, Williams & Rothery 1990). Much of this penguin biomass is made up of Gentoo Penguins *Pygoscelis papua*, Adélie Penguins *P. adeliae*, and Chinstrap Penguins *P. antarctica*. Gentoo Penguins have a circumpolar distribution and usually nest in small colonies in sympatry with the other two species on the Antarctic Peninsula.

The total Gentoo Penguin population has been estimated at 298 000 pairs (Woehler 1993). The Malvinas/Falkland, South Georgia, and Kerguelen Islands hold about 75% of the world's population, and only around 13% are found south of the ice pack limit. Most of the world's Gentoo Penguin population is distributed near the Antarctic Polar Front (Bost & Jouventin 1990, Woehler 1993). One third of the population breeds at South Georgia Island, which represents, after the Malvinas/Falkland Islands, the most important locality for this species (Croxall *et al.* 1984a). In contrast to populations of the other two pygoscelid species which have increased since the beginning of this century, it cannot be ascertained whether this is the case for Gentoo Penguin. In addition, the growth rate of Gentoo Penguin chicks is the lowest of all pygoscelid penguins, even at Antarctic localities (Bost & Jouventin 1990).

Although Gentoo Penguins live between 46° and 65°S, most studies have been carried out at sub-Antarctic and Antarctic islands (Williams 1980, Williams 1981, Yáñez *et al.* 1984, Poncet & Poncet 1985, Robertson 1986, Trivelpiece *et al.* 1987, Trivelpiece & Trivelpiece 1990, Trivelpiece *et al.* 1990, Williams 1990, Williams & Croxall 1990, Williams & Rothery 1990, Bost & Jouventin 1991a,b, Bost *et al.* 1992, Williams & Rodwell 1992). Fewer studies have been undertaken on the Antarctic Peninsula (Müller-Schwarze & Müller-Schwarze 1975, Cordier *et al.* 1983, Croxall *et al.* 1984b, Poncet & Poncet 1987).

The objective of the current study was firstly to estimate different parameters of the breeding performance of a Gentoo Penguin colony on the Antarctic Peninsula. Secondly, several reasons might condition chick survival rate: critical mortality periods from hatching to fledging, probable predation differences that might be due to the shape of subcolonies and the difference in energy consumed by parents from nest to feeding sites. Given these reasons, this trend was assessed among subcolonies for time, perimeter/area and distance to the sea parameters.

## STUDY AREA

Cierva Point is located on the Danco Coast, on the west side of the Antarctic Peninsula, at 64°09'S, 60°57'W (Fig.1), where

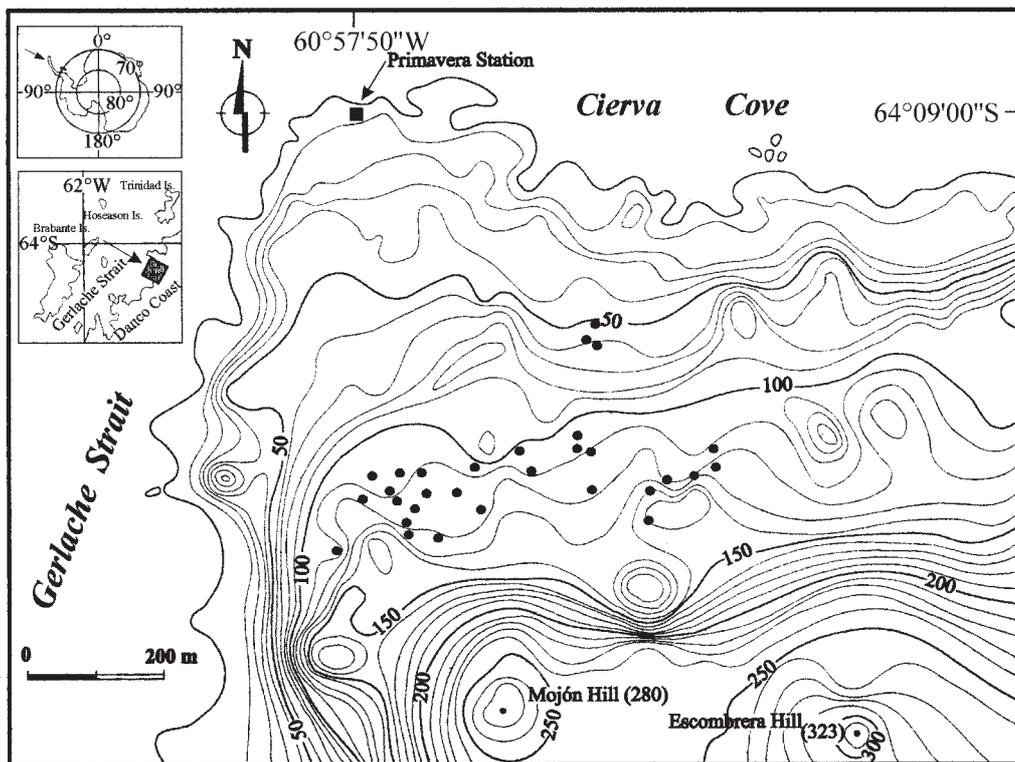


Fig. 1. Location of Gentoo Penguin subcolonies (•) at Cierva Point (SSSI No.15), Antarctic Peninsula.

vegetation is greatly developed, with a continuous cover of mosses, grasses and associated lichens (Agraz *et al.* 1994). Wildlife is very abundant and many species of birds nest at Cierva Point (Quintana *et al.* 1995, 2000). This is probably due to the favourable microhabitats and climatic conditions (GESER 1989) that allow a high diversity of birdlife in this relatively small area (*c.* 3 km<sup>2</sup>). The Gentoo Penguin colony studied at Cierva Point is composed by several subcolonies between 50 and 150 m above sea level (Fig.1).

Weather at Cierva Point is moderate, considering the latitude and compared to more northerly locations on the Antarctic continent. Monthly mean temperature ranged between 1.8 and 2.2°C (range -1° to 6.3°C). Relative humidity averaged 79%; it was cloudy and rainy almost every day, and snowy days were frequent. Mean wind speed was 7.9 km.h<sup>-1</sup> (range 0.0 to 40.6 km.h<sup>-1</sup>).

Human activity is not frequent and limited to summertime (late November to mid-March). Because of its high animal and plant species diversity, the area has been declared as Site of Special Scientific Interest No. 15 in terms of the Antarctic Treaty. Consequently, tourism is not allowed.

## METHODS

The study was carried out between December 1992 and February 1993, during the Gentoo Penguin breeding season. Four counts were performed by direct observation of the nests and the broods in each subcolony from 3 December 1992 to 17 February 1993. Numbers of breeding pairs, nest density and survival rate were estimated for the whole colony and for each of the 29 subcolonies detected. The number of breeding pairs, mortality and survival rates, and occupation pattern of the different subcolonies were compared with data from breeding

seasons between 1991/92 and 1995/96. The total survival rate for all subcolonies was regressed against the perimeter-area rate and distance to the sea, so as to assess their influence on survival.

In order to identify patterns of mortality, a test for multiple comparisons of proportions of weekly surviving chicks with Tuckey's multiple contrasts (Zar 1996) was performed from 3 December to 5 February. This test could not be applied during February because chicks from the subcolonies had formed large crèches and a lack of identity of these subcolonies was produced.

In addition, survival rate of chicks was estimated for nine selected subcolonies on an altitudinal gradient and under different environmental conditions throughout 10 weekly counts. The proportion of surviving chicks at these subcolonies were regressed against time (weeks). In all cases the data were arcsine transformed. These results were analysed with a covariance analysis (Zar 1996), in order to compare the influence of time on chick survival among these nine subcolonies.

Average annual growth rate was calculated using the Yáñez Index, *i* (Yáñez *et al.* 1984).

$$i = \left[ \left( \frac{BP_{pr}}{BP_{ps}} \right)^{1/n} - 1 \right] \times 100$$

*BP<sub>pr</sub>* stands for the number of breeding pairs at present, *BP<sub>ps</sub>* stands for the number of breeding pairs in former surveys and *n* stands for the years that passed by. This was calculated using the population numbers in this study and in Novatti (1978). This rate was compared to data from 1990/91 to 1995/96, and, particularly, with estimates obtained between 1954 and 1958 (Novatti 1978).

## RESULTS

On our arrival on 3 December 1992, the colony had a total number of 1044 nesting pairs distributed in 29 principal subcolonies and five isolated areas (Fig.1, Table 1). Of this total, 85.2% were incubating two eggs. By the end of January 1993, 65% of the pairs were rearing two chicks and 83% of pairs were able to rear at least one chick to fledging. A few nests had three eggs (Tables 1 and 2) presumably with the third egg gathered from a nearby nest. The average nest density was estimated at 0.25 nests/m<sup>2</sup>, ranging from 0.02 to 1.54 nests/m<sup>2</sup> in different subcolonies (Table 1).

The first chicks hatched on 24 December and the first crèches were formed by 20 January. By the beginning of February

chicks from several subcolonies had joined together in bigger groups and some chicks had begun to moult their down. By mid-February chicks from different subcolonies had formed large crèches, the integrity of the subcolonies was lost, and down-free chicks moved to the coast.

By 21 January 1993, the number of surviving chicks was 1450 and mortality rate was 23.9%. By the same date in 1992, mortality was 14.0%; for 1994, 23.9%; 33.0% for 1995 and 24.3% for 1996. By mid-February, when the penguins were more dispersed, the number of surviving chicks was 1291 (Table 2) and mortality rate was 32.3%. Nil survival was observed in isolated nests (Table 1), except for one pair that was able to rear two chicks to the crèche stage.

TABLE 1

**Gentoo Penguin colony characteristics on Cierva Point on 3 December 1992.**

SC: subcolony; A: altitude; S: surface; PAR: perimeter/area ratio; D: density; TN: total nests; TE: total eggs; E: eggs; EM: empty nests (nests without eggs); S: survival chicks at 21 January 1993; las: level above the sea; m: metres; n: nests

SC	A (las)	S (m <sup>2</sup> )	PAR (m <sup>-1</sup> )	D (n/m <sup>2</sup> )	TN	TE	% Nests with				S (%)
							1E	2E	3E	EM	
1	50	444	0.22	0.24	106	201	11.3	87.7	0.9	0.0	83
6	110	66	0.51	0.18	12	23	8.3	91.7	0.0	0.0	95
7	120	1092	0.13	0.13	140	251	16.4	80.7	0.7	2.1	85
8	135	135	0.35	0.22	30	55	10.0	86.7	0.0	3.3	69
9	150	90	0.42	0.12	11	22	0.0	100.0	0.0	0.0	95
10	130	492	0.21	0.25	123	227	8.9	88.6	0.0	2.4	58
11	130	72	0.50	0.34	25	45	4.0	88.0	0.0	8.0	97
12	132	228	0.27	0.16	43	79	7.0	88.4	0.0	4.6	100
13	120	130	0.35	0.28	36	68	11.1	88.9	0.0	0.0	80
14b	110	126	0.43	0.17	22	42	9.1	90.9	0.0	0.0	90
14c	108	28	0.78	1.46	41	78	9.8	90.2	0.0	0.0	78
14d	107	52	0.90	0.32	17	30	11.8	82.3	0.0	5.9	80
14e	110	40	0.70	0.20	8	16	0.0	100.0	0.0	0.0	93
16	110	112	0.41	0.42	47	92	4.2	95.7	0.0	0.0	65
17	100	152	0.35	0.03	5	7	20.0	60.0	0.0	20.0	14
18a	112	162	0.39	0.02	3	3	100.0	0.0	0.0	0.0	0
18b	112	102	0.45	0.04	4	6	50.0	50.0	0.0	0.0	0
19	120	64	0.50	0.33	21	32	38.1	57.1	4.8	0.0	100
20	70	18	1.00	0.72	13	21	30.8	61.5	0.0	7.7	100
21	68	24	0.83	1.54	37	65	27.0	70.3	0.0	2.7	70
22	123	10	1.40	0.10	1	2	0.0	100.0	0.0	0.0	100
23	123	25	1.00	0.48	12	24	0.0	100.0	0.0	0.0	62
24	135	36	0.72	0.83	30	59	3.3	96.7	0.0	0.0	84
25	127	27	0.88	1.40	38	73	2.6	94.7	0.0	2.6	61
26	112	17	0.97	0.74	13	25	7.7	92.3	0.0	0.0	44
27	112	18	0.94	1.00	18	35	5.6	94.4	0.0	0.0	54
28	105	32	0.63	1.13	36	66	13.9	83.3	0.0	2.8	90
29	105	35	0.84	0.49	17	34	0.0	100.0	0.0	0.0	82
30	110	12	0.75	0.58	7	14	0.0	100.0	0.0	0.0	14
31	112	44	0.68	0.68	30	60	0.0	100.0	0.0	0.0	48
32	112	42	0.66	0.45	19	35	15.8	84.2	0.0	0.0	65
33	120	49	0.57	0.37	18	33	5.5	88.9	0.0	5.5	84
34	105	194	0.44	0.29	56	89	19.0	35.0	0.0	2.0	79
37	130	10	1.40	0.20	2	0	2.0	0.0	0.0	0.0	0
41	118	30	0.76	0.10	3	3	33.3	33.3	0.0	33.3	100

TABLE 2

Censuses of Gentoo Penguins at Cierva Point during the 1992/93 breeding season.  
 TN: total nests; TE: total eggs; TC: total chicks; E: eggs; EM: empty nests; C: chicks

Census date	TN	TE	TC	% Nests with				% Nests with		
				1E	2E	3E	EM	1C	E+C	2C
3 Dec 1992	1044	1918	–	12.3	85.2	0.3	2.1	–	–	–
24 Dec 1992	959	1605	116	13.7	75.4	1.1	2.3	1.9	2.6	3.9
20 Jan 1993	906	101	1450	2.6	3.3	0	4.3	27.6	1.0	61.1
5 Feb 1993	–	8	1476	–	–	–	–	–	–	–
17 Feb 1993	–	–	1291	–	–	–	–	–	–	–

There was no correlation between survival rate and both perimeter/area rate and distance to the sea of each subcolony ( $r = 0.06$ ,  $P = 0.73$  and  $r = 0.09$ ,  $P = 0.59$ , respectively). Table 3 shows the number of surviving chicks in each of the nine subcolonies studied during the 10 weekly counts. A high correlation between chick survival and time was found for all nine subcolonies (Table 4). The regression line slopes were not significant (ANCOVA,  $F = 0.42$ ,  $P > 0.05$ ).

Significant differences were observed when the test of multiple comparisons for proportions was used on the proportions of weekly surviving chicks ( $\chi^2_{(0.05, 8)} = 84.42$ ,  $P < 0.05$ ). Tukey's multiple contrasts, however, showed no significant differences in the proportions of surviving chicks between consecutive weeks ( $P > 0.05$ ).

Hatching timing during 1992/93 was similar to that recorded for other breeding seasons (1991/92, 1993/94 and 1994/95), taking place between 15 and 25 December. During the breeding season 1995/96, however, hatching commenced on 10 December. The distribution pattern of the colony was quite constant in the distinct subcolonies during the six breeding seasons. The colony size has increased slightly from 1990/91 to 1995/96 (Table 5). The number of chicks at the end of January increased by 61.3% from 1990/91 to 1995/96. A 31.7%

increase in the number of the breeding pairs was also observed for the same period.

## DISCUSSION

The Gentoo Penguin colony at Cierva Point is small when compared to a number of other colonies located in Maritime Antarctica (Croxall & Kirkwood 1979, Poncet & Poncet 1985, Favero *et al.* 1990, Williams & Rothery 1990, Woehler 1993, Aguirre 1995). This could be related to the latitude and, consequently, to climate, as suggested by Bost & Jouventin (1990a) who showed that population sizes appeared to decrease in the Antarctic Peninsula, where climatic conditions are probably limiting.

A high survival rate of Gentoo Penguin chicks was observed. Bost & Jouventin (1990a) pointed out breeding success should increase from northern localities to southern ones. (Bost & Jouventin 1991b) found 71% breeding success at the sub-Antarctic Crozet Islands whereas Trivelpiece *et al.* (1987) found up to 100% on the Antarctic Shetland Islands. Bost & Jouventin (1990a), on the other hand, pointed out that the higher the latitude, the larger the percentage of pairs that are capable of rearing two chicks, as at Esperanza Bay (63°23'S)

TABLE 3

Number of survivors (eggs and chicks) in each of the Gentoo Penguin subcolonies counted weekly from 3 December 1992 to 5 February 1993

Date	Subcolony									
	1	21	6	7	8	9	24	13	14c	
3 Dec 1992	201	65	23	111	55	22	59	68	78	
10 Dec 1992	203	64	23	95	49	23	59	67	72	
18 Dec 1992	196	54	22	102	46	23	57	66	81	
24 Dec 1992	193	56	22	107	46	22	56	66	69	
31 Dec 1992	201	55	22	102	46	22	56	63	69	
8 Jan 1993	184	59	22	105	44	21	56	62	64	
15 Jan 1993	176	58	22	99	42	21	53	59	65	
20 Jan 1993	172	57	22	75	41	21	50	56	60	
29 Jan 1993	162	51	22	75	41	21	50	56	60	
5 Jan 1993	161	46	21	–	39	19	–	56	–	

TABLE 4

Linear regression analysis between Gentoo Penguin chicks' survival proportion and time in each of nine subcolonies

Subcolony	Regression line	$r$	$P$
1	$y = 1.59 - 0.051 x$	-0.92	<0.0001
21	$y = 1.47 - 0.0 - 43 x$	-0.78	<0.008
6	$y = 1.53 - 0.025 x$	-0.78	<0.007
7	$y = 1.48 - 0.043 x$	-0.71	<0.03
8	$y = 1.35 - 0.040 x$	-0.69	<0.03
9	$y = 1.54 - 0.036 x$	-0.80	<0.005
24	$y = 1.61 - 0.051 x$	-0.95	<0.0001
13	$y = 1.57 - 0.049 x$	-0.97	<0.000001
14c	$y = 1.44 - 0.047 x$	-0.75	<0.02
<b>Total</b>	<b><math>y = 1.52 - 0.047 x</math></b>	<b>-0.93</b>	<b>&lt;0.0002</b>

where siblings represented 31% of the fledging chicks. The high percentage of pairs rearing two chicks to the end of February at Cierva Point supports this statement.

Overall hatching success was similar to that found at other Antarctic localities (Croxall & Prince 1979, Trivelpiece *et al.* 1987, Bost & Jouventin 1990, 1991b). Gentoo Penguins differ from the other pygoscelid penguins because of the degree of breeding asynchrony among the sites where it nests (Williams 1981). Although time elapsed from hatching to cr ching was similar in every subcolony (around 25–30 days), at the Cierva Point colony chicks at fledging stage were younger than at northern localities (50 vs 80–100 days; Despin 1972, Williams 1980, Croxall *et al.* 1988, Bost & Jouventin 1991b).

As regards the correlation between chick survival and time, the non-significant covariance analysis among regression line slopes suggests that mortality shows the same pattern among the different subcolonies during the breeding season. Lack of significant correlation between survival rate and distance to the sea might indicate, on the other hand, that, in the present case, this parameter would not have a strong influence on chick survival, in spite of the presumably different commuting energy costs of parents while feeding chicks.

From the beginning of December until the end of January there were no distinguishable peaks in mortality, showing a gradual effect up to the cr che stage. However, throughout the period surveyed, highest mortality rate was observed between 24 December and 21 January, which coincides with the period from hatching to cr ching. Consequently, this period could be considered as the most critical for chick survival. In contrast, Bost & Jouventin (1991b) found that the main percentage of mortality was 10 days after cr ching at the Crozet Islands.

A large number of fledging penguins was observed leaving the colony during the first weeks of February (R.D. Quintana *et al.* unpubl. data), which could indicate the beginning of migration (see Novatti 1978, Jablonski 1986). More evident signs of migration were seen toward the end of February of the 1992 and 1994 breeding seasons, which matches Novatti's (1978) results.

The main cause of mortality of both eggs and chicks was predation by skuas *Catharacta* spp. Other authors have recognized the importance of skuas as predators of Gentoo Penguins (Novatti 1978, Williams 1980, Bost & Jouventin 1991b). Predators were found to be the main cause of mortality during the cr ching to fledging period at Marion Island (Williams 1980) and at the Crozet Islands (Bost & Jouventin 1991b). Other less important mortality factors we observed were abandonment of eggs and chicks crushed by their parents.

According to Novatti (1978), the colony exhibited a gradual decrease in size between 1954 and 1958, thought due to the construction of the Captain Cobbett Naval Refuge (now Primavera Station). Its construction involved the presence of construction staff and the use of explosives within the penguin breeding areas, some of which have not been reoccupied. Cessation of these activities could be one of the main causes behind the increase of breeding pairs since the 1950s because human disturbance has limited population growth of Gentoo Penguins at other sites (Croxall *et al.* 1984c).

Other species of nesting birds, such as the Pintado or Cape Petrel *Daption capense* and the Antarctic Tern *Sterna vittata*, which decreased in numbers at Cierva Point after 1954, have

TABLE 5

Average annual growth rate (*i*) of the Gentoo Penguin colony at Cierva Point

Time period	Number of pairs	<i>i</i> (%)
1954 – 1956	614 – 599	–1.23
1956 – 1957	599 – 582	–2.84
1957 – 1958	582 – 559	–1.99
1958 – 1991	559 – 800	1.08
1991 – 1992	800 – 890*	11.25
1992 – 1993	890* – 1009*	13.37
1993 – 1994	1009* – 1025*	1.58
1994 – 1995	1025* – 984**	–4.00
1995 – 1996	984* – 1054*	7.11
1954 – 1996	614 – 1054*	1.29
1991 – 1996	800 – 1054*	5.67
1954/58 – 1991/94	589** – 931**	1.24

(\*) Data at hatching date

(\*\*) Average data

begun to increase in recent years (Quintana *et al.* 2000).

The increase of Gentoo Penguin numbers in recent years at Cierva Point has been important, being higher than Novatti's estimation for 1954. This fact is interesting because Gentoo Penguin populations elsewhere appear to have remained stable, in contrast to the other pygoscelid species, which are believed to have increased recently (Bost & Jouventin 1990). For example, whereas Poncet & Poncet (1987) report a small increase (8%) in the Gentoo Penguin population on the Antarctic Peninsula between 1914 and 1920, no evidence of population growth was found at Signy and Malvinas/Falkland Islands by Croxall *et al.* (1981, 1984c).

The shape of subcolonies could influence chick survival since peripheral nests would be under a greater predation risk than central ones (Tenaza 1971, Spurr 1973, Ainley *et al.* 1983, Young 1994). In this study, the results indicate that the border effect, or rather the perimeter/area relationship, did not influence the mortality rate of either eggs or chicks among the different subcolonies. Tenaza (1971) suggested that linear colonies should be expected to produce fewer young per breeding pair than colonies with shapes having relatively less periphery, and that breeding success should decrease as the colony gets smaller. Spurr (1973) found differences in the production of chicks between two-egg clutches from peripheral and central nests in an Ad lie Penguin colony. In our study, however, survival was relatively high in every subcolony.

Nil survival in isolated nests was similar to that reported by Spurr (1973) who observed that of 11 isolated Ad lie Penguin nests, only one chick out of 16 eggs was raised to mid-January. This might be due to skua predation on both eggs and chicks, made easier by isolation. Tenaza (1971) observed that predators attempt to take eggs and chicks of penguins more frequently from colony boundaries and isolated nests than from the middle of the colony.

Results indicate a high breeding performance of this Gentoo Penguin population: high proportion of pairs rearing two

chicks, high hatching success, relatively low mortality rate and a moderate increase in colony size in the last few years. Considering that other bird species are also increasing in the Cierva Point area, we can speculate that both favourable environmental conditions and low human impact contribute to this situation.

## ACKNOWLEDGEMENTS

We thank Dr. Alberto Ripalta Mengual for his cooperation in the field work, Drs. Esteban Frere and Patricia Gandini for their valuable methodological suggestions, the logistic team of the Antarctic summer scientific campaign 1992/3 for cooperating in all we needed, Dr. T. Williams for useful discussion and helpful comments on earlier drafts of this paper, and the anonymous reviewers for constructive criticism. Field work was supported by the Instituto Antártico Argentino. Laboratory work was supported by the University of Buenos Aires.

## REFERENCES

- AGRAZ, J.L., QUINTANA, R.D. & ACERO, J.M. 1994. Ecología de los ambientes terrestres en Punta Cierva, Costa de Danco. *Contrib. Inst. Antártico Argentino* 439: 1–32.
- AGUIRRE, C.A. 1995. Distribution and abundance of birds in the region of Potter Cove and Stranger Point, King George Island, South Shetlands, Antarctica. *Mar. Orn.* 23: 23–31.
- AINLEY, D.G., LERESCHE, R.E. & SLADEN, W.J.L. 1983. Breeding biology of the Adélie Penguin. Berkeley: University of California Press.
- BOST, C.A. & JOUVENTIN, P. 1990. Evolutionary ecology of Gentoo Penguins (*Pygoscelis papua*). In: Davis, L.S. & Darby, J.T. (Eds). Penguin biology. San Diego: Academic Press. pp. 85–112.
- BOST, C.A. & JOUVENTIN, P. 1991a. Relationship between fledging weight and food availability in seabird populations: is the Gentoo Penguin a good model? *Oikos* 60: 113–114.
- BOST, C.A. & JOUVENTIN, P. 1991b. The breeding performance of the Gentoo Penguin *Pygoscelis papua* at the northern edge of its range. *Ibis* 133: 14–25.
- BOST, C.A., JOUVENTIN, P. & PINCSON DU SEL, N. 1992. Morphometric variability on a microgeographical scale in two inshore seabirds. *J. Zool., Lond.* 226: 135–149.
- CORDIER, J.R., MENDEZ, A., MOUGIN, J.-L. & VISBEEK, G. 1983. Les oiseaux de la baie de l'Espérance, Péninsule Antarctique (63°24'S, 56°59'W). *Oiseau* 53: 143–159.
- CROXALL, J.P. & KIRKWOOD, E.D. 1979. The breeding distribution of penguins on the Antarctic Peninsula and islands of Scotia Sea. Cambridge: British Antarctic Survey.
- CROXALL, J.P. & PRINCE, P.A. 1979. Antarctic seabird and seal monitoring studies. *Polar Rec.* 19: 573–595.
- CROXALL, J.P., ROOTES, D. & PRINCE, P.A. 1981. Increases in penguin populations at Signy Island, South Orkney Islands. *Br. Antarct. Surv. Bull.* 54: 47–56.
- CROXALL, J.P., RICKETTS, C. & PRINCE, P.A. 1984a. Impact of seabirds on marine resources, especially krill, at South Georgia. In: Whittow, G.C. & Rhan, H. (Eds). Seabird energetics. New York: Plenum Press. pp. 285–318.
- CROXALL, J.P., PRINCE, P.A., HUNTER, I., McINNES, S.J. & COPESTAKE, P.G. 1984b. The seabirds of the Antarctic Peninsula islands of the Scotia Sea and Antarctic Continent between 80°W and 20°W: their status and conservation. In: Croxall, J.P., Evans, P.G. & Schreiber, R.W. (Eds). Status and conservation of the world's seabirds. Cambridge: International Council for Bird Preservation. pp. 637–666.
- CROXALL, J.P., McINNES, S.J. & PRINCE, P.A. 1984c. The status and conservation of seabirds at the Falkland Islands. In: Croxall, J.P., Evans, P.G. & Schreiber, R.W. (Eds). Status and conservation of the world's seabirds. Cambridge: International Council for Bird Preservation. pp. 271–291.
- CROXALL, J.P., McCANN, T.S., PRINCE, P.A. & ROTHERY, P. 1988. Reproductive performance of seabirds and seals at South Georgia and Signy Island, South Orkney Islands. 1976–1986: implications for Southern Ocean monitoring studies. In: Sahrhage, D. (Ed.). Antarctic Ocean and resource variability. Berlin: Springer-Verlag. pp. 261–285.
- DESPIN, B. 1977. Croissances comparées des poussins chez les manchot du genre *Pygoscelis*. *C.r. Hebd. Séanc Acad. Sci. Paris (Sér. D)* 285: 1135–1137.
- FAVERO, M., BELLAGAMBA, P.J. & FARENGA, M. 1991. Abundancia y distribución espacial de las poblaciones de aves de Punta Armonía y Punta Dedo, Isla Nelson, Shetland del Sur. *Riv. Ital. Orn.* 61: 85–96.
- GESER. 1989. Identificación y caracterización de distintos sistemas ecológicos costeros en el Sector Antártico Argentino. Informe interno de trabajo. Buenos Aires: Instituto Antártico Argentino.
- JABLONSKI, B. 1986. Distribution, abundance and biomass of a summer community of birds in the region of the Admiralty Bay (King George Island, South Shetland Islands, Antarctica) in 1978/1979. *Pol. Polar Res.* 7: 217–260.
- MÜLLER-SCHWARZE, C. & MÜLLER-SCHWARZE, D. 1975. A survey of twenty-four rookeries of pygoscelid penguins in the Antarctic Peninsula region. In: Stonehouse, B. (Ed.). The biology of penguins. London: Macmillan. pp. 309–320.
- NOVATTI, R. 1978. Notas ecológicas y etológicas sobre las aves de Cabo Primavera (Costa de Danco, Península Antártica). *Contrib. Inst. Antártico Argentino* 237: 1–81.
- PONCET, S. & PONCET, J. 1985. Survey of penguin breeding populations at the South Orkney Islands. *Br. Antarct. Surv. Bull.* 68: 71–81.
- PONCET, S. & PONCET, J. 1987. Censuses of penguin populations of the Antarctic Peninsula, 1983–1987. *Br. Antarct. Surv. Bull.* 77: 109–129.
- QUINTANA, R.D., AGRAZ, J.L. & BORGIO, L.C. 1995. Conservación de refugios de alta biodiversidad en ecosistemas terrestres antárticos. *Ciencia Hoy* 32: 37–43.
- QUINTANA, R.D., CIRELLI, V. & ORGEIRA, J.L. 2000. Abundance and spatial distribution of bird populations at Cierva Point, Antarctic Peninsula. *Mar. Orn.* 28: 21–27.
- ROBERTSON, G. 1986. Population size and breeding success of the Gentoo Penguin *Pygoscelis papua* at Macquarie Island. *Aust. Wildl. Res.* 13: 583–587.
- SPURR, E.B. 1973. Breeding of the Adélie Penguin *Pygoscelis adeliae* at Cape Bird. *Ibis* 117: 324–338.
- TENAZA, R. 1971. Behavior and nesting success relative to nest location in Adélie Penguins (*Pygoscelis adeliae*). *Condor* 73: 81–92.
- TRIVELPIECE, W.Z. & TRIVELPIECE, S.G. 1990. Courtship period of Adélie, Gentoo and Chinstrap Penguins. In: Davis, L.S. & Darby, J.T. (Eds). Penguin biology. San Diego: Academic Press. pp. 113–127.
- TRIVELPIECE, W.Z., TRIVELPIECE, S.G. & VOLKMAN, N.J. 1987. Ecological segregation of Adélie, Gentoo and

- Chinstrap Penguins at King George Island, Antarctica. *Ecology* 68: 351–361.
- TRIVELPIECE, W.Z., TRIVELPIECE, S.G., GEUPEL, G., KJELMYR, J. & VOLKMAN, N.J. 1990. Adélie and Chinstrap Penguins: their potential as monitors of the Southern Ocean marine ecosystem. In: Kerry, K. & Hempel, G. (Eds). Antarctic ecosystems ecological change and conservation. Berlin: Springer. pp. 191–202.
- WILLIAMS, A.J. 1980. Aspects of the breeding biology of the Gentoo Penguin *Pygoscelis papua*. *Gerfaut* 70: 283–295.
- WILLIAMS, A.J. 1981. Factors affecting time of breeding of Gentoo Penguins *Pygoscelis papua* at Marion Island. In: Cooper, J. (Ed.). Proceedings of the Symposium on Birds of the Sea and Shore, 1979. Cape Town: African Seabird Group. pp. 451–459.
- WILLIAMS, T.D. 1990. Annual variation in breeding biology of Gentoo Penguin, *Pygoscelis papua*, at Bird Island, South Georgia. *J. Zool., Lond.* 222: 247–258.
- WILLIAMS, T.D. & CROXALL, J.P. 1990. Is chick fledging weight a good index of food availability in seabird populations? *Oikos* 59: 414–416.
- WILLIAMS, T.D. & ROTHERY, P. 1990. Factors affecting variation in foraging and activity patterns of Gentoo Penguins (*Pygoscelis papua*) during the breeding season at Bird Island, South Georgia. *J. Appl. Ecol.* 27: 1042–1054.
- WILLIAMS, T.D. & RODWELL, S. 1992. Annual variation in return rate, mate and nest-site fidelity in breeding Gentoo and Macaroni Penguins. *Condor* 94: 636–645.
- WOEHLER, E.J. 1993. The distribution and abundance of Antarctic and Subantarctic penguins. Cambridge: Scientific Committee on Antarctic Research.
- YAÑEZ, J., NUÑEZ, H., VALENCIA, J. & SCHLATTER, R. 1984. Aumento de las poblaciones de pingüinos pigoscélidos en la isla Ardley, Shetland del Sur. *Ser. Cient. INACH* 31: 97–101.
- YOUNG, E. 1994. Skua and penguin: predator and prey. Cambridge: Cambridge University Press.
- ZAR, J. 1996. Biostatistical analysis. 3rd Edition. New Jersey: Prentice-Hall.
-

