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# The effect of chinstrap penguins on the breeding performance of Adèlie penguins

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A b s t r a c t. At Laurie Island, South Orkney Islands, there are some breeding areas where two Pygoscelid species (*Pygoscelis adeliae* and *P. antarctica*) breed at the same sites, competing for the available space. To study the effects of this competition on the breeding performance of the Adèlie penguin, data on breeding chronology, population size and reproductive success were collected from the 1995/96 to 1997/98 breeding seasons in areas of competition (mixed groups) and areas where only Adèlie penguins breed (single groups). The numbers of Adèlie breeding pairs increased by 54% in single groups while they dropped by 14% in mixed groups. The number of chicks in creches followed a similar overall trend in mixed and single groups throughout the study period. However, while the chicks in creches in mixed groups represented 64% of the total number in 1995, they only amounted to 56% in the 1997 season. On average, 32% of the Adèlie nests were usurped by *P. antarctica*. The peak of Adèlie nest losses to chinstraps occurred from 6–20 November in 1995 and 1996, while in 1997 the peak of nest site takeovers took place between 20 November and 6 December due to the later arrival of chinstraps. In areas of competition, the overall breeding success of Adèlie penguins was significantly depressed, this depression being due mainly to egg losses.

We suggest that the presence of chinstraps had not only direct adverse effects on the breeding success of Adèlie penguins in mixed sites, but also a possible long-term effect by negatively impacting on the recruitment of pre-breeding birds.

**Key words**: *Pygoscelis*, Adèlie, chinstrap, South Orkney Islands

## Introduction

Adèlie penguins (*Pygoscelis adeliae* Hombron et Jacquinot, 1841) breed between 60° and 77° S, while chinstrap penguins (*P. antarctica* Forster, 1781) occupy the latitudinal breeding range between 54° and 65° S (T r i v e l p i e c e & F r a s e r 1996). These species share a portion of their breeding range on the Antarctic Peninsula and islands of the Scotia Arc (W a t s o n 1975), a section of the Southern Ocean where Antarctic krill (*Euphausia superba* Dana, 1852) is the single most important prey item for both species (V o l k m a n et al. 1980, L i s h m a n 1985, L y n n e s et al. 2004). Although these congeneric species exhibit broad ecological similarities, they also show differences in their preferred wintering habitats, Adèlies having affinities for pack ice and chinstraps for ice edge or open water habitats (F r a s e r et al. 1992). Current trends in climatic change in the Antarctic Peninsula area, with the reduction in the frequency of cold years, the associated reduction of extensive sea-ice (F r a s e r et al. 1992) and its effects on krill abundance (F r a s e r & H o f m a n n 2003), suggest that conditions could become less favourable to Adèlie penguins than to chinstrap penguins in the main areas where they breed sympatrically (L y n n e s et al. 2002). On land, interspecific

interaction for nesting places resulting in an overall depression of the Adèlie breeding success has been reported at King George Island (Trivelpiece & Volkman 1979). Moreover, competition at sea, in years of low resource availability, resulting in the exclusion of Adèlie penguins from potentially inshore foraging areas by their congener, was observed at Signy Island (Lynnes et al. 2002). As the competition between species in sympatric areas is unlikely to diminish in light of the actual census data in the area (Smith et al. 1999), any quantitative information contributing to a better understanding of the effects of that competition on the breeding performance of Adèlie penguins is valuable. Here, we present a quantitative assessment of the effects of chinstrap penguins on the breeding performance of their congener carried out at Mossman Peninsula, Laurie Island, South Orkney Islands from 1995 to 1997. The main objectives of this paper were: (i) to compare the trends in breeding population sizes and chicks in creches for Adèlie penguins breeding on single species sites and mixed species sites; (ii) to quantify Adèlie nest losses to chinstraps in mixed sites (iii) to document the critical period of inter-specific competition.

## Study Area

The study was carried out at the Mossman Peninsula on Laurie Island, South Orkney Islands (60º46´S, 44º42`W) from the 1995/96 to 1998/99 seasons. Approximately 120,000 pairs of Adèlie penguins and 180,000 pairs of chinstrap penguins breed on Laurie Island, of which 25,000 and 10,000 pairs, respectively, breed on the Mossman peninsula (Woehler 1993, N. Coria unpublished data). In the study area there are breeding places occupied only by Adèlie or chinstrap penguins and areas where both species nest. During 1994/95, six *mixed sites* (areas occupied by Adèlie penguins and later invaded by chinstraps) and two *single sites* (areas where only *P. adeliae* breed) were mapped with reference to poles driven into the ground.

## Materials and Methods

### Breeding population size and breeding success

From 1995/96 to 1997/98 nests of Adèlie penguins with eggs and creches of chicks were counted for the eight breeding groups. Counts were carried out 1 week after the peak egg laying and when two thirds of the chicks were in creches, according to CEMP Standard Methods (CCAMLR 2003).

Additionally, during 1996/97 and 1997/98, when the first egg of Adèlie penguins was observed in the colony, 100 nests were marked in single sites and 50 in mixed sites. Nests were marked along a transect across 10 single breeding groups and 5 mixed breeding groups. Nests were checked every 5 days until Adèlie chicks hatched and every two days until chicks entered a creche. At each sampling date the number of abandoned nests, the number of eggs/chicks and chicks in creches were registered according to CEMP Standard Methods (CCAMLR 2003). For the transect, overall reproductive success was measured using the number of chicks reared to creches per egg laid. Breeding success was also measured as the number of chicks hatched per eggs laid, and the number of chicks in creches per chicks hatched.

### Nest losses due to usurpation

When the first egg of Adèlie penguins was observed in the colony, between 12 and 20 nests were marked on the periphery of each mixed breeding group, totalling between 72 and 120 in each year. Nests were followed daily to quantify losses due to usurpation by chinstraps and abandoned nests which were not occupied by chinstraps. During 1996/97 and 1997/98 31 to 40 nests were marked and checked daily on the periphery of the single groups to determine if the proportion of abandoned nests differed between single and mixed groups. Mixed nest sites under study were mapped every 5 days to see the overall pattern of occupation by chinstraps.

### Survival and site fidelity

To know if chinstraps tended to breed in the same mixed breeding sites, 20 breeding chinstrap pairs were marked each year. Banding dates were 28–29 November, 20 November and 10 December for 1995, 1996 and 1997 respectively. Checks for the presence of marked birds were carried out on three different days during the egg laying period in the 1996/97, 1997/98 and 1998/99 seasons. Moreover, 100 nests were marked in areas where only chinstrap penguins breed to study the breeding chronology of this species.

### Statistical analyses

Comparative analyses of the breeding success of Adèlie penguins between single and mixed groups were done using chi square tests after Yates' correction.

## Results

### Breeding chronology

Adèlie penguins arrived at the rookery in large numbers from 5 October in 1995, 27 September in 1996 and 7 October in 1997, while arrival dates for chinstraps were 11 November, 2

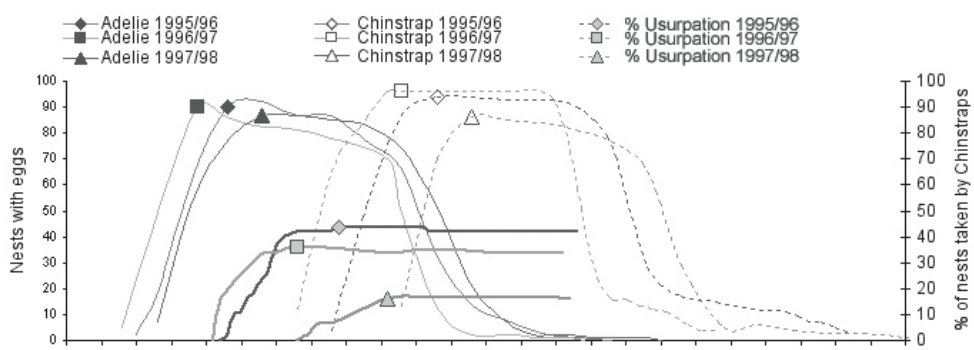


**Fig. 1.** Chronology of egg laying in Adèlie and chinstrap penguins and critical period of Adèlie nest losses to chinstraps at Laurie Island during the 1995/96, 1996/97 and 1997/98 seasons. Egg laying chronology was drawn from 100 marked nests of each species breeding in single sites. Nest take-overs by chinstraps were drawn from Adèlie nests marked on the periphery of mixed groups.

November and 16 November for 1995, 1996 and 1997 respectively. Time of egg laying for both species is shown in Fig. 1. The peak of Adelie egg laying was 12 November in 1995, 7 November and 17 November in 1996 and 1997 respectively. The peak of chinstrap egg laying occurred on 12 December, 5 December and 17 December for the 1995/96, 1996/97 and 1997/98 breeding seasons respectively. Thus arrival date and peak egg laying showed roughly similar displacements among years for both species, with an interspecific delay of 28–30 days.

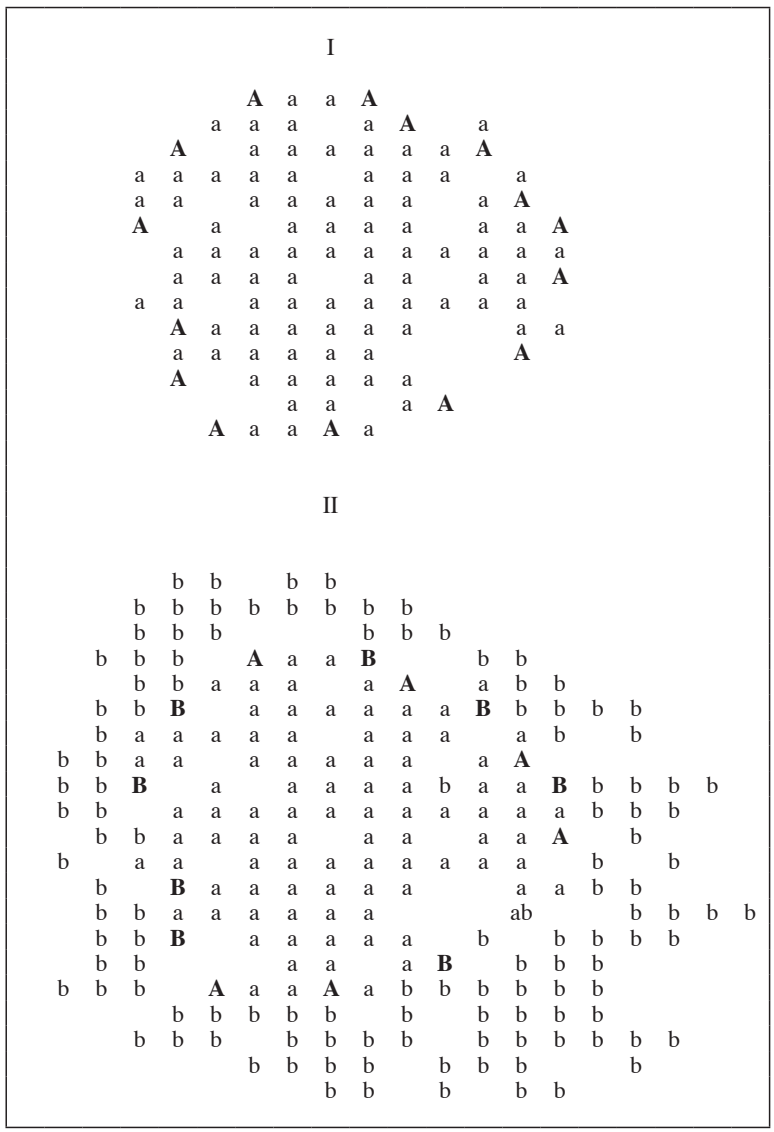


**Fig. 2.** Representation of Adèlie and chinstrap penguin nests in mixed group "C" on two different dates. I: 1/11/1996, II: 5/12/1996. a: Adèlie nests, A: Adèlie nests marked on the periphery of the breeding group, b: chinstrap nests, B: marked Adèlie nests usurped by chinstraps, ab: marked nests abandoned and not usurped by chinstraps. The maximum length for the mixed breeding group "C" was approximately 11m by 5/12/1996.

## Pattern of chinstrap occupation

The aggressive encounters between the species began immediately after chinstrap arrival (Fig 1). The pattern of chinstrap occupation for a mixed site is shown in Fig. 2. Chinstraps began to occupy the periphery of the Adèlie breeding groups (where nest take-over was more frequent) and by the end of their arrival, they had formed a ring inside which Adèlie penguins continued breeding.

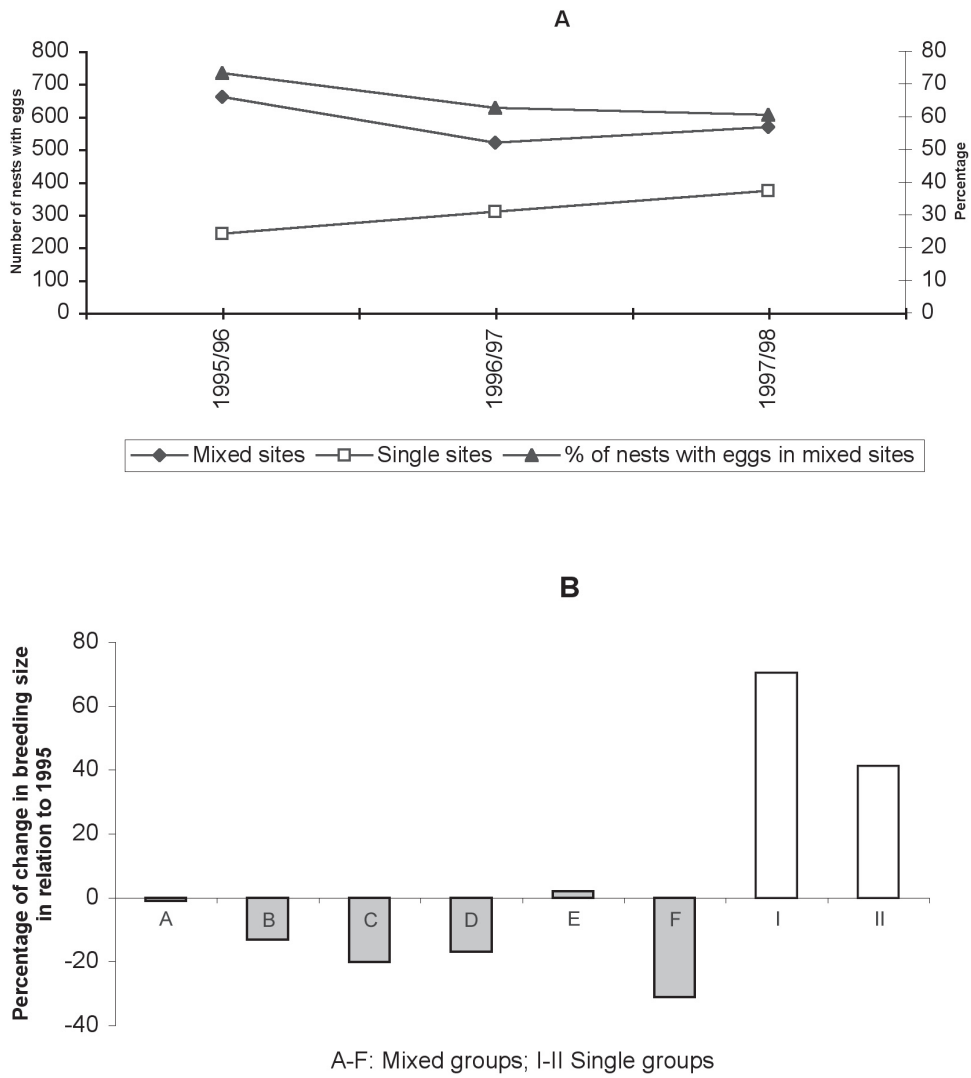


**Fig. 3.** A: Trend in the breeding population size of Adèlie penguins breeding in single sites (n=2) and mixed sites (n=6) and percentage of breeding Adèlie pairs nesting in mixed groups in relation to the total breeding pairs counted in a given year. B: Percentage of increase or decrease of a given breeding group by the 1997/98 season, in relation to its size in 1995/96 season. (a–f): mixed breeding groups; (I–II) single breeding groups.

## Breeding population size and breeding success

Trends in the breeding population size of Adèlie penguins for single and mixed sites are shown in Fig. 3. Overall, breeding population size in single groups increased during the study by 54%. Mixed sites showed a decrease of 21% between 1995/96 and 1996/97, increasing by 9% from 1996/97 to 1997/98. In mixed sites, there was a decrease in the proportion of nests with eggs of Adèlie penguins, which represented 73% of the total nests with eggs counted during 1995/96 and 60% in 1997/98 (Fig. 3). The numbers of chicks in creches followed a similar trend throughout the study period in mixed and single sites (Fig. 4). However, the proportion of chicks counted in mixed groups dropped from about 64 to 56% of the total chicks counted.

An index of breeding success (chicks in creches/nests with eggs) for mixed and single sites is shown in Fig. 5. This index followed a similar overall trend throughout the study, although it was around 10–34% lower in mixed than in single sites.

For the nests which were marked following a transect, there were no significant differences in the clutch size in mixed or single groups for the two seasons for which data were available ( $^2$=0.19, $P$=0.9, $df$=1 and $^2$=0.21, $P$=0.9, $df$=1 for 1996/97 and 1997/98 respectively) (Table 1). Overall reproductive success, taken as the number of chicks surviving to creche per pair that laid eggs, was significantly lower for Adèlie pairs nesting in mixed sites compared to those nesting in single sites ( $^2$=7.5, $P$<0.01, $df$=1 and $^2$=21.4, $P$<0.001, $df$=1 for 1996/97 and 1997/98 respectively). The number of chicks hatched per egg laid was significantly lower for Adèlie pairs nesting in mixed groups when compared to those nesting in single groups for both seasons ( $^2$= 4.1, $P$<0.05, $df$=1 and $^2$= 40.7, $P$<0.001, $df$=1 for 1996/97 and 1997/98 respectively), while no significant differences were found in the number of chicks creched per chicks hatched for Adèlie penguins nesting in single or mixed sites in both seasons.

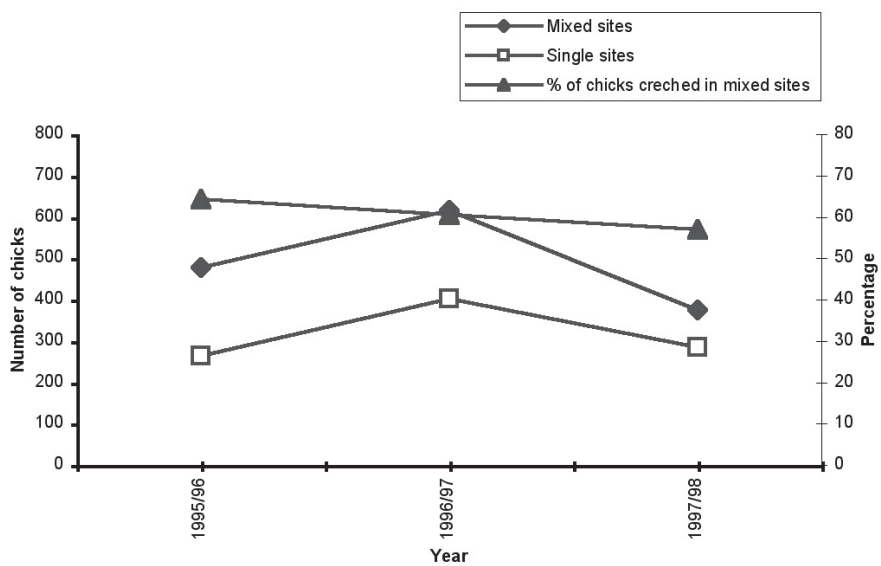


**Fig. 4.** Number of chicks in creches in mixed (n=6) and single (n=2) sites and percentage of chicks in creches in mixed groups in relation to the total number of chicks counted in a given year.

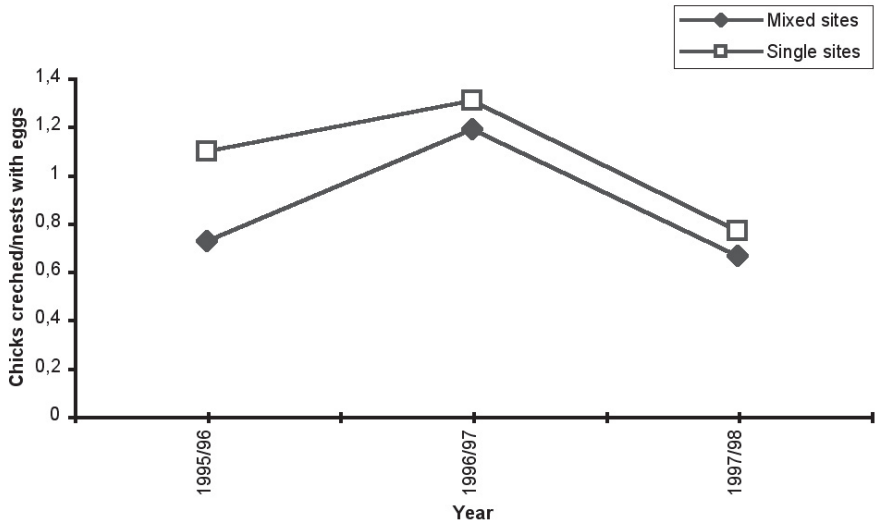


**Fig. 5.** Index of breeding success (chicks creched/nests with eggs) in mixed and single sites.

**Table 1.** Breeding success in Adèlie penguins nesting in single and mixed sites.

| | | Marked nests | Eggs | Chicks hatched | Chicks creched | Chicks creched per nest |
|---|---|---|---|---|---|---|
| 1996/97 | Single sites | 96 | 173 | 124 | 109 | 1.14 |
| | Mixed sites | 50 | 92 | 54 | 41 | 0.82 |
| 1997/98 | Single sites | 100 | 170 | 115 | 86 | 0.86 |
| | Mixed sites | 50 | 83 | 20 | 16 | 0.32 |

## Nest losses by usurpation

On average, 32.0 ±13.9% of the total nests marked on the periphery of mixed groups were usurped by chinstrap penguins over the course of the study. Usurpation began on chinstrap arrival and reached its peak at the beginning of their egg-laying period (Fig.1). The critical period (when more than 90% of nests lost to chinstraps had been occupied in a given season) as well as total Adèlie nests lost varied in relation to chinstrap arrival dates. In those seasons (1995/96–1996/97) when chinstraps arrived during the first week of November, the major part of Adèlie nest losses extended until 20 November. For the 1997/98 season, chinstraps arrived around 20 November and nest site takeovers by this species took place since arrival until 6 December (Fig.1). There were no significant differences in the proportion of Adèlie nest losses to chinstraps between 1995/96 and 1996/97 (44% vs 35.8% respectively; $^2 = 0.9$, $P>0.05$, $df=1$), while losses in 1997/98 (17%) were significantly lower than in 1995/96 ($^2 =16.8$, $P<0.001$, $df=1$) and 1996/97 ($^2 =10.8$, $P<0.001$, $df=1$). The percentage of abandoned nests marked on the periphery of mixed sites not usurped by chinstraps was not significantly different from the proportion of abandoned nests marked in single sites ($^2=2.57$, $P>0.05$, $df=1$ and $^2=1,01$, $P>0.05$, $df=1$ for 1996/97 and 1997/98 seasons, respectively).

### Survival and site fidelity

Information on survival for each banded group is given in Table 2. Chinstrap penguins showed high site fidelity. Some 85% of the chinstrap penguins marked in 1995, 60% of those banded in 1996 and 69% of those banded in 1997 returned to breed in the following seasons (1996/97,1997/98 and 1998/99 respectively) at the same mixed site. No banded birds were observed breeding at sites other than those where they had been marked. At least 57.5% of the birds marked in 1995 survived and returned to breed at the "D" mixed site in the 1998/99 season.

**Table 2.** Survival and site fidelity of banded chinstrap breeding pairs in mixed sites.

| | 1996 | | 1997 | | 1998 | |
|---|---|---|---|---|---|---|
| Banding year and group | Survival (1) | year$^{(i+1)}$/year$^{i}$ (2) | Survival (1) | year$^{(i+1)}$/year$^{i}$ (2) | Survival (1) | year$^{(i+1)}$/year$^{i}$ (2) |
| 1995 | 87.5 | 85.0 | 72.5 | 73.3 | 57.5 | 76.9 |
| 1996 | +++++ | +++++ | 67.5 | 60.0 | 40.0 | 54.2 |
| 1997 | +++++ | +++++ | +++++ | +++++ | 69.2 | 69.2 |

(1) Survival for 1995 includes animals observed during 1996, 1997 and/or 1998. Survival for 1996 comprises animals observed during 1997 and/or 1998, while data reported for 1997 only include birds observed during 1998.
(2) Percentage of birds observed in a given year in relation to their presence in the previous season.

## Discussion

At Laurie Island peak egg laying differed among years for both species with a maximum displacement of about 10–12 days (Fig. 1). The magnitude and direction of the changes observed in the breeding chronology were similar for both species, with the Adèlie penguins breeding about 28 days earlier than chinstraps. It has been suggested that the separation in the breeding habitat, as well as the differences in breeding chronology, between these species were the result of adaptations to differing environmental conditions at the centers of their respective geographical ranges (Trivelpiece & Fraser 1996). While Adèlies would be adapted to early breeding in the short summer of Continental Antarctica, chinstraps breeding in the milder Maritime Antarctic would be selecting for breeding later, increasing in this way the probability of ice free areas near their breeding places (Trivelpiece et al. 1987). In areas where both species compete for nest sites, the asynchrony in the pygoscelid penguin reproductive cycles could give chinstraps an advantage in the competition for nesting places, since the conflicts between species take place upon arrival of chinstraps from the sea, at a time when Adèlie penguins have been fasting for 3–4 weeks (Trivelpiece & Volkman 1979). Results at Laurie Island showed that for the three seasons studied, nest takeovers by chinstrap penguins took place shortly after the peak of Adèlie egg laying, reaching a maximum value at a date when no Adèlie chicks had yet hatched (Fig.1). At that time, chinstraps began to lay eggs, which probably resulted in a decrease in competition for nesting sites, since it is expected that an important proportion of the chinstrap breeding pairs had already been established. It is also possible that nest defence by Adèlie penguins increased after chicks had hatched, thus reducing chinstrap takeovers. Parental investment theory predicts that nest defence should increase as the reproductive value of offpring increases, a fact observed in many studies (i.e. Regelmann & Curio 1983, Andersen 1990, Redondo 1990). Specifically for *Pygoscelid* penguins, Spurr (1974) reported

an increase in nest defence from egg laying to hatching in Adèlie penguins, while offspring age was the main factor influencing nest defence in chinstrap penguins, chicks being more strongly defended than eggs (Viñuela et al. 1995).

### Occupation pattern and nest usurpation

On their arrival, chinstraps began to occupy the periphery of the Adèlie breeding groups where aggressive encounters between species were frequent. As the breeding season progressed, chinstraps occupied zones situated outside the Adèlie breeding groups and in some mixed groups they built a ring inside which Adèlie penguins continued breeding (Fig. 2). The amount of marked nests lost on the periphery of mixed groups due to usurpation differed among years, being greater during 1995 and 1996 than during 1997. Since breeding chronology for both species was displaced in the same direction in the different seasons studied, nest competition probably occurred with Adèlie males during their first incubation shift in most cases. Sea ice break-out around Laurie Island occurred later in the season in 1997/98 (January 1998) than in 1995/96 (November 1995) and 1996/97 (October 1996) (Orcadas Station, National Meteorological Service). When ice covers the sea adjacent to the rookeries during the breeding season, additional reserves are used to walk on ice (Pinshow et al. 1976), probably depleting a portion of the fat reserves available to sustain birds during the 3–4 week fasting period following arrival. It has been shown that sea ice cover near the rookery can adversely affect chinstrap penguins to a greater extent than Adèlie penguins (Trathan et al. 1996, Rombolá et al. 2003). For instance, in spite of the later break-out registered in 1997 at Laurie Island, Adèlie incubating birds were presumably in a better body condition than in 1995 and 1996, since the arrival weight observed in 1997 was significantly higher than that registered in any of the other two seasons (N. Coria, A. Carlini unpublished data). Although data on weight at arrival are not available for chinstraps, the later sea ice break-out might have affected them to a greater extent, this being a possible reason why a smaller proportion of the chinstrap population attempted to breed during this season in relation to 1995 and 1996 (N. Coria, A. Carlini unpublished data). The better body condition of Adèlie penguins, in addition to a smaller number of chinstraps probably arriving in lower body condition, could improve the chances of Adèlie penguins in competition with their congener for nest sites, thereby explaining the lower number of nest site take-overs observed during the 1997/98 season.

As was suggested previously, from the data on the nests marked on the periphery of the breeding groups, it seems that Adèlie nest losses occurred mainly in a period when Adèlie penguins were incubating. This fact was confirmed by the comparison of Adèlie nests marked in single and mixed sites during the 1996/97 and 1997/98 seasons. Since there were no differences in egg production or the number of chicks creched per chicks hatched between mixed and single groups, while significant differences were found in the number of chicks hatched per egg laid, the significant depression in the overall breeding performance of Adèlie penguins in mixed sites seems to be mainly mediated by higher Adèlie egg losses. This is in agreement with previous observations made at King George Island (Trivelpiece & Volkman 1979).

### Breeding population size and chicks fledged

The differences in the breeding population trends observed in mixed and single sites (Fig. 3) suggested that the presence of chinstraps could also operate adversely affecting the

recruitment of pre-breeding Adèlie penguins. It is known that late during the breeding season, pre-breeders are present and prospecting areas on the periphery of the colonies for future reproduction (Sladen 1958). The experience gained by these young pre-breeding birds during the reoccupation phase in a given year influences their subsequent choice of breeding site (Ainley et al. 1983). Human disturbance and short–term changes in environmental conditions have been suggested as possible causes affecting the recruitment pattern of young pre-breeding birds to the colonies (Yeates 1971, Woehler et al. 1994, Trivelpiece & Fraser 1996). The reoccupation phase takes place late during the breeding season, approximately by the time when Adèlie penguins are with the recently hatched chicks and during early creche formation. By that time, chinstrap penguins are present and occupy the adjacent territory to the "original" Adèlie breeding groups (Fig. 2). Chinstrap presence and the consequent interactions between species could cause a disturbance and a negative selection of these mixed breeding groups by young Adèlies, altering the patterns of recruitment to mixed breeding groups in relation to single groups. Additionally, since Adèlie penguins tend to reproduce in their natal colony, and in an important proportion at their natal site (Ainley et al. 1983), the lower breeding success in mixed sites (Fig. 5), will result in a lower number of chicks coming back to breed in the future. These facts could have an adverse effect on the breeding population tendency for Adèlie penguins breeding in mixed sites.

Early census data showed that chinstrap penguins increased in numbers in many colonies and also expanded their range southward along the western side of the Antarctic Peninsula, into areas historically dominated by Adèlie penguins (Laws 1985, Poncet & Poncet 1987). Specifically at Signy Island (South Orkney Islands) a five-fold increase in chinstrap population size was recorded for the period 1958–1978 (Croxall et al. 1981), although further data for the island indicated a relative stability from 1979 to 1991 and a decrease of 15% thereafter (Woehler et al. 2001). Current trends in climatic change with its effects on ice distribution and krill availability seem to create more favourable conditions for chinstrap penguins than for Adèlie penguins in areas where these species co-occur (Lynnes et al. 2002). Trivelpiece & Volkman (1979) suggested that competition between chinstrap and Adèlie penguins is a phenomenon which could have resulted from the expansion of pygoscelid populations during the past decades. From our data it is not possible to judge whether the areas in which competition takes place were areas where only Adèlie penguins bred in the past. Distribution of Adèlie and chinstrap penguins at Laurie Island resembles that observed at King George Island (Trivelpiece & Fraser 1996) with colonies of Adèlie penguins located only on the south coast and major chinstrap colonies situated on the north coast of the Island (N. Coria unpublished data). Moreover, the breeding places where mixed sites are situated are areas with slow slopes, which are characteristic nesting sites for Adèlie penguins (Volkman & Trivelpiece 1981). In this way, it is possible that the mixed groups at Mossmann Peninsula at present are the result of expansions in chinstrap populations. From the data taken on banded chinstrap pairs breeding in mixed groups, it seems that these nest sites are viewed by chinstraps as their own sites, since they returned to breed there in an important proportion. The data in Table 2 show that 60 to 85% of the birds banded in one year came back to breed in the same groups the following season. The value is comparable to that found in single groups of chinstrap penguins at King George, where 77 to 90% of the birds returned to breed at the same site (Williams 1995). Values for the same seasons for Adèlie penguins banded at Laurie Island in single groups, carried out as part of a monitoring program, also prove to be very

similar to those found for chinstrap penguins in mixed sites, ranging between 56 and 85% of the banded birds (N. C o r i a , A. C a r l i n i unpublished data).

In conclusion, the breeding performance of Adèlie penguins breeding in mixed sites was significantly depressed and the decrease observed was mainly mediated through nest losses during the incubation period. The breeding population increases and decreases in single and mixed sites respectively suggest that the disturbance caused by chinstraps could also operate, adversely affecting the recruitment of pre-breeding Adèlie penguins, probably having a long-term effect on Adèlie population size in mixed sites.

A c k n o w l e d g e m e n t s

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## LITERATURE

AINLEY D.G., LERESCHE R.E. & SLADEN W.J.L. 1983: Breeding ecology of the Adèlie penguin. *University of California Press*, *Los Angeles, CA*, *227 pp.*

ANDERSEN D.E 1990: Nest-defence behaviour of red-tailed hawks. *Condor 92:991–997.*

CCAMLR 2003: Standard methods for monitoring parameters of predators species. CCAMLR Ecosystem Monitoring Program. *CCAMLR, Hobart*.

CROXALL J.P., ROOTES D.M & PRICE R.A 1981: Increases in penguin populations at Signy Island, South Orkney Islands. *Br. Antarct. Surv. Bull. 54: 47–56*.

DANA J.D. 1850: Synopsis Generum Crustaceorum Ordinis "Schizopoda". J.D. Dana elaboratus...(Part 1). *Amer J. Sci II 9: 129–132*.

FRASER W.R, TRIVELPIECE W.Z, AINLEY D. & TRIVELPIECE S.G. 1992: Increases in Antarctic penguin populations: reduced competition with whales or a loss of ice due to environmental warming? *Polar Biol. 11:525–531*.

FRASER W. & HOFMANN E. 2003: A predator's perspective on causal links between climate change, physical forcing and ecosystem response. *Mar. Ecol. Prog. Ser. 265:1–15*.

LAWS R.M 1985: The ecology of the Southern Ocean. *Am. Sci. 73: 26–40*.

LISHMANN G.S 1985: The food and feeding ecology of Adélie penguins (*Pygoscelis adeliae*) and chinstrap penguins (*Pygoscelis antarctica*) at Signy Island, South Orkney islands. *J.Zool.Lond. 205:245–263*.

LYNNES A.S, REID K., CROXALL J.P. & TRATHAN P.N. 2002: Conflict or co-existence? Foraging distribution and competition for prey between Adélie and chinstrap penguins. *Marine Biol. 141:1165–1174*.

LYNNES A.S., REID K. & CROXALL J.P. 2004: Diet and reproductive success of Adélie and chinstrap penguins: linking response of predator to prey population dynamics. *Polar Biol. 27: 544–554*.

PINSHOW B., FEDAK M. & SCHMIDT-NIELSEN K. 1976: Terrestrial locomotion in Penguins: It costs more to waddle. *Science 195: 592–594*.

PONCET S. & PONCET J. 1987: Censuses of penguin populations of the Antarctic Peninsula, 1983–87. *Bri. Antarct. Surv. Bull. 76:109–129.*

REDONDO T. 1990: Avian nest defence: theoretical models and evidence. *Behaviour 85:161–193*.

REGELMANN K. & CURIO E 1983: Determinants of brood defence in the Great Tip *Parus major* L. *Behav. Ecol. Sociobiol. 25: 369–378*.

ROMBOLÁ E., MARSCHOFF E. & CORIA N. 2003: Comparative study of the effects of the late pack-ice break-off on chinstrap and Adélie penguins` diet and reproductive success at Laurie Island, South Orkney Islands, Antarctica. *Pol. Biol. 26:41–48*.

SLADEN J.W.L. 1958: The Pygoscelid Penguins. I Methods of study. II The Adèlie penguin. *Falkland Islands Dependencies survey. Scientific reports*, *No 17, 97 pp*.

SMITH R.C., AINLEY D., BAKER K., DOMACK E., EMSLIE S., FRASER W.R., KENNETH J., LEVENTER A., MOSLEY THOMSON E., STAMMERJOHN S. & VERNET M. 1999: Marine ecosystem sensitive to climate change. *Bioscience 49 (5):393–404*.

SPURR E.B. 1974: Individual differences in aggressiveness of Adèlie penguins. *Anim. Behav. 22: 611–616*.

TRATHAN P.N., CROXALL J.P. & MURPHY E.J. 1996: Dynamics of Antarctic penguin populations in relation to inter-annual variability in sea -ice distribution. *Polar Biol. 16: 321–330*.

TRIVELPIECE W.Z. & VOLKMAN N. 1979: Nest-site competition between Adèlie and chinstrap penguins: an ecological interpretation. *The Auk 96:675–681*.

TRIVELPIECE W.Z., TRIVELPIECE S.G. & VOLKMAN N.J. 1987: Ecological segregation of Adèlie, Gentoo and chinstrap penguins at King George Island, Antarctica. *Ecology 68 (2): 351–361*.

TRIVELPIECE W.Z. & FRASER W. 1996: The breeding biology and distribution of Adèlie penguins: adaptations to environmental variability. In: Ross R., Hofmann E. & Quetin L. (eds), Foundations for ecological research west of the Antarctic Peninsula. Antarctic Research Series 70. *American Geophysical Union, Washington DC: 273–285*.

VIÑUELA J., AMAT J.A. & FERRER M. 1995: Nest defence of nesting chinstrap penguins (*Pygoscelis antarctica*) against intruders. *Ethology 99:323–331*

VOLKMAN N.J., PRESLER P. & TRIVELPIECE W.1980: Diets of Pygoscelid penguins at King George Island, Antarctica. *Condor 82: 373–378*.

VOLKMAN N.J. & TRIVELPIECE W. 1981: Nest- site selection among Adèlie, Chinstrap and Gentoo penguins in mixed species rookeries. *Wilson Bull. 93 (2): 243–248*.

WATSON G.E. 1975. Birds of the Antarctic and Subantarctic. *Am. Geophys Union, Washington DC, pp.350*.

WILLIAMS T.D. 1995: The Penguins. *Oxford University Press. Walton Street, Oxford. 295 pp*.

WOEHLER E.J. 1993: The distribution and abundance of Antarctic and sub-Antarctic penguins. *SCAR, Cambridge, pp 76*.

WOEHLER E.J., PENNEY R.L., CREET S.M. & BURTON H.R. 1994: Impacts of human visitors on breeding success and long-term population trends in Adèlie penguins at Casey, Antarctica. *Polar Biology 14: 269–274*.

WOEHLER E.J., COOPER J., CROXALL J.P., FRASER W.R., KOOYMAN G.L., MILLER G.D., NEL D.C., PATTERSON D.L., PETER H-U, RIBIC C.A., SALWICKA K., TRIVELPIECE W.Z. & WEIMERSKIRCH H. 2001: A statistical assessment of the status and trends of Antarctic and subantarctic seabirds. *Cambridge: Scientific Committee on Antarctic Research, pp 44*.

YEATES G.W. 1971: Observation on orientation of penguins to wind and on colonisation in the Adèlie penguin rockery at Cape Royds, Antarctica. *N.Z.J. Sci. 14:901–906*.