NEST-SITE COMPETITION BETWEEN ADELIE AND CHINSTRAP PENGUINS: AN ECOLOGICAL INTERPRETATION

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ABSTRACT.—A study of nest-site competition between Adelie (*Pygoscelis adeliae*) and Chinstrap (*P. antarctica*) penguins was conducted during the 1977–78 austral summer at Point Thomas, King George Island, Antarctica. Data were collected on the timing of the reproductive cycle, the reproductive success, and the behavioral interactions between Adelie and Chinstrap penguins in areas of competition. Adelie Penguins in mixed sites had their nests usurped by arriving Chinstrap males, and reproductive success was significantly depressed for Adelie pairs nesting in these areas. We suggest that nest-site competition is a relatively recent phenomenon correlated with dramatic population increases among pygoscelids in response to the increased availability of krill in areas of past whaling activities. *Received 2 February 1979, accepted 1 May 1979.*

OBSERVATIONS have been recorded of Chinstrap Penguins (*Pygoscelis antarctica*) usurping nest sites from congeneric Gentoo (*P. papua*) (Downes et al. 1959) and Adelie penguins (*P. adeliae*) (Crawford 1974). These relatively recent observations of interspecific nest-site competition are especially interesting in light of reports of dramatic increases in pygoscelid populations over the last century (Sladen 1964, Conroy 1975, Croxall and Kirkwood 1979, this study). During the 1976–77 austral summer, we observed Chinstrap Penguins invading Adelie colonies and aggressively displacing Adelies from occupied nest sites at Point Thomas, King George Island, Antarctica. In the 1977–78 field season, we returned to Point Thomas to investigate nest-site competition between Chinstraps and Adelies over the course of the breeding season. The specific objectives of the present study were (1) to describe the aggressive interactions between Chinstraps and Adelies in areas of nest-site competition, (2) to document the effect of this competition on the reproductive success of both species, and (3) to interpret these data in light of recent literature pointing to apparent increases in pygoscelid numbers in the Antarctic.

STUDY SITE AND METHODS

Our study was conducted at Point Thomas, King George Island, South Shetland Islands (62°10′S, 58°30′W) from 1 November 1977 to 21 February 1978. The Point Thomas site contained breeding colonies of all three pygoscelid species in both an east and a west rookery separated by a glacial tongue 2-km wide (see definitions). A census of the pygoscelid population at Point Thomas was conducted 1–2 weeks following the peak of egg laying for each species. Chinstrap and Gentoo data are from individual counts of nest sites in each rookery. Adelies were counted in small colonies and estimated in large colonies by determining the colony's area and using a figure of 1.13 pairs/m^2, the mean of 5 small ($n < 150$ pair) Adelie colonies graphed to scale. The population estimates for 1977 are shown in Table 1.

Data were collected on the dates of arrival, egg laying, chick hatching, creche formation, and reoccupation for Adelie and Chinstrap penguins (definitions after Sladen 1958). These observations were made daily from 1–11 November 1977 and at 4-day intervals thereafter. To facilitate data collection, penguins were banded with flipper bands that were color coded to indicate sex. A bird's sex was determined by cloacal examination (Sladen and LeResche 1970, Ainley 1975a), by the bird's position during

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TABLE 1. A 12-yr comparison of pygoscelid population growth in the east and west rookeries at Point Thomas, King George Island, Antarctica.

	Number of breeding pairs		
	1965[a]	1977[b]	Yearly increase
Adelie	10,400	18,000	14%
Gentoo	2,152	2,613	10%
Chinstrap	240	1,015	35%

[a] Data from Conroy 1975.
[b] This study.

an observed copulation, or by tread marks on the back of one member of a breeding pair made by the male's feet during copulation. Nest sites under study were mapped (with reference to coded bamboo poles driven into the ground in the colonies), and inter-nest distances (from nest rim to nearest nest rim) were measured in single- and mixed-species sites (see definitions). Eggs were marked with permanent ink for identification. Nest checks for reproductive-success data were accomplished by slowly approaching the penguins until they assumed an upright posture, allowing the investigators a clear view of the nest contents. Intrusion into the sites under study was kept to a minimum.

The measures of reproductive success used were: the number of eggs laid per pair, the number of chicks hatched per pair that laid eggs, the number of chicks surviving to creche per pair that laid eggs, and the number of chicks creched per chicks hatched. Inter- and intraspecific statistical comparisons for mixed- and single-species sites were performed with the Kruskal-Wallis test for ranked data. Whenever a significant "H" value was obtained, Dunn's test for multiple comparisons of unequal sample sizes was performed to differentiate significant groups.

Aggressive encounters between Adelie and Chinstrap penguins were recorded opportunistically during observations at one of nine mixed-species sites in early November. An observation period began when an arriving Chinstrap Penguin made physical contact with an incubating Adelie Penguin. Data collection continued for 1 h, or until one of the participants left the area.

DEFINITIONS

Rookery.—A geographical area, usually a portion of an island or peninsula, that contains one or more colonies (groups) of breeding birds and a landing beach or beaches that the birds used to reach the nesting areas from the sea (Penney 1968).

Colony.—A geographically continuous group of breeding birds whose territorial boundaries are contiguous (Penney 1968).

Mixed-species sites.—Discrete areas within Adelie Penguin colonies that were later invaded by arriving Chinstrap Penguins. These areas were not all colonies *per se* (according to Penney's definition); some were separated from other such sites by homogeneous groups of Adelies or Chinstraps.

Single-species sites.—Colonies of one species only, or sites within large colonies containing both species that were separated from any mixed areas by at least 50 m.

RESULTS

Reproductive cycle.—Adelies arrived at the west rookery on Point Thomas in large numbers beginning 20 October 1977, the day after ice left Admiralty Bay (P. Presler, pers. comm.). The peak of Adelie egg laying was 3 November, with 97% of all clutches completed by 15 November 1977. Chinstraps began arriving at the rookery on 2 November, and 95% of the breeding pairs were present by 18 November 1977. The Chinstrap egg-laying peak was 27 November, and the Adelie and Chinstrap egg-laying and chick-hatching peaks were 24–25 days apart during the 1977–78 breeding season (Fig. 1). The Chinstrap arrival and subsequent nest-site competition occurred shortly after the peak of Adelie egg laying, at a time when the male of the Adelie pair was incubating the completed clutch, the female having

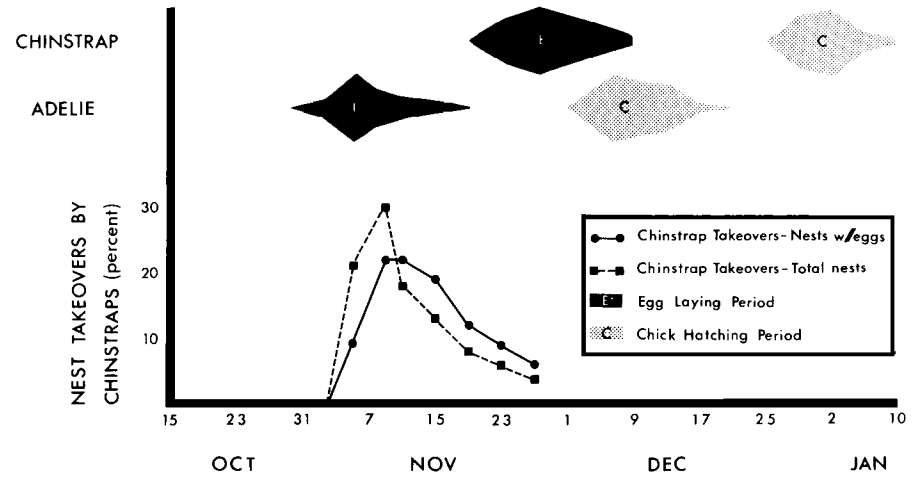

Fig. 1. A comparison of the timing of the nest site competition between Adelie and Chinstrap penguins with respect to their breeding cycles. The peak of Adelie nest losses to Chinstraps occurred between 7–11 November, shortly after the peak of egg laying. The relative numbers of eggs laid and/or chicks hatched per nest-check dates are indicated by the widths of the bars.

returned to the sea to feed. The timing of the Adelie nest-site takeovers by Chinstraps is summarized in Fig. 1.

In nine mixed-species sites, 60% (89/148) of the Adelie nests with eggs were lost to arriving Chinstrap Penguins. An additional 66 nests occupied by Adelie pairs were later claimed by Chinstraps, although the Adelies were not known to have laid eggs before they disappeared. A total of 66% (141/214) of all Adelie nests under study in the mixed sites were used by Chinstrap pairs for their own reproduction during the breeding season. The sites under study in the west rookery represented approximately one-half of all such areas of interaction in that rookery; thus, we estimated that 300 nests used for breeding by Chinstraps were usurped from Adelies. Chinstraps in the east rookery also engaged in nest-site competition with Adelie pairs. It was determined that approximately 40% (110/270) of the Chinstrap pairs nesting in this rookery used nests previously occupied by Adelie pairs. The data from this rookery were collected during weekly visits, and, therefore, an accurate estimate of the number of eggs laid in Adelie nests lost to Chinstraps was not possible.

Conflict description.—In all competitive encounters observed between the two species, a male Chinstrap aggressively contested the incubating Adelie for its nest site (n = 18). Further evidence that males played a major role in such interactions was obtained by banding lone unsexed Chinstraps on newly acquired Adelie nests where the actual conflict was not witnessed. The birds were sexed following pairing, and in 24 cases all of the Chinstraps on newly acquired nests proved to be males.

The duration and intensity of the conflict between the male Chinstrap and incubating Adelie proved to be extremely variable. In 8 of the 18 aggressive encounters, the Adelie lost its nest within 10 min, while 6 other encounters were unsettled at the conclusion of a 1-h observation period. In the encounters that were rapidly decided, the Chinstrap approached the incubating Adelie and began pecking at its head while

Fig. 2. Progressive stages of an aggressive interaction between an incubating Adelie Penguin and an arriving Chinstrap Penguin. (a) Adelie on nest incubating egg is attacked by a male Chinstrap. (b) and (c) Chinstrap aggression continues, and Adelie moves off its former nest until it is outside the nest cup, now defended by the Chinstrap. Note the position of the egg in the center of the nest. (d) Chinstrap, having usurped nest, is shown advertising for a mate with the ecstatic vocalization. Note that the Adelie's egg is still intact following the nest loss to the Chinstrap.

repeatedly striking it with its flippers. The incubating Adelie gradually relinquished its nest under the continued aggression of the Chinstrap, until the Chinstrap possessed the nest. Upon acquiring the nest, the Chinstrap began advertising with the ecstatic vocalization first noted by Wilson (1907) in the Adelie Penguin. This vocalization has been described as a display that is primarily a strong advertisement of self, mostly given by lone unpaired but territorial males; it tells other males to stay away and unpaired females to approach if ready to pair (Ainley 1975b). Photographs depicting the nest-site competition between the two species are shown in Fig. 2. The defeated Adelie made several unsuccessful attempts to regain its nest, approaching its egg(s) in a distinct hunched-back posture, while calling at the nest with the locomotory hesitance vocalization observed between Adelie pairs during nest relief (Ainley 1975b). Each approach elicited an attack from the Chinstrap now in control of the nest, and after several exchanges of bill grabbing and flipper striking, the Adelie left the colony in the direction of the beach.

The Adelie's eggs were intact in nine of the 18 recorded nest-site conflicts following the Chinstrap's acquisition of the nest. The eggs were normally lost or discarded from the nest during the Chinstrap's copulatory and nest-building activities; however, we recorded the hatching and successful rearing of an Adelie chick to creche age by a Chinstrap pair. Displaced Adelie Penguins left for the sea to feed and returned 2–3 weeks later (with other unsuccessful breeders and young inexperienced birds) during the reoccupation phase of the breeding cycle. Reoccupying Adelies were not observed to attack incubating Chinstraps. Of 12 nests with eggs being incubated by Chinstraps on one nest-check date, however, 6 were found to be occupied by a single Adelie and 6 by an Adelie pair on the following nest-check

TABLE 2. Comparison of the mean ($\bar{x}$) and standard error (SE) for the number of eggs laid/pair, chicks hatched/pair, chicks creched/pair, and chicks creched/chicks hatched for Adelie and Chinstrap penguins breeding in single- and mixed-species sites.

		Number of eggs/pair	Chicks hatched/pair[a]	Chicks creched/pair[a]	Chicks creched/chicks hatched
Sites of Adelie only (n = 13)	$\bar{x}$	1.85	1.28	1.07	0.83
	SE	0.02	0.09	0.10	0.04
Sites of Adelie mixed (n = 9)	$\bar{x}$	1.77	0.37[b]	0.30[b]	0.76
	SE	0.04	0.04	0.06	0.11
Sites of Chinstrap only (n = 3)	$\bar{x}$	1.91	1.09	1.00	0.91
	SE	0.05	0.10	0.08	0.02
Sites of Chinstrap mixed (n = 9)	$\bar{x}$	1.85	1.10	1.06	0.95
	SE	0.04	0.05	0.06	0.02

[a] Dunn's multiple comparison test (Hollander and Wolfe 1973: 124–126) was used to determine significant differences between pairs within the categories chicks hatched/pair and chicks creched/pair.
[b] $P < 0.001$; Kruskal-Wallis test for ranked data.

date. In two of these 12 cases, the eggs of the Chinstrap were still intact in the nest. One Adelie continued incubating the eggs for 2 weeks, the other for 1 week; neither acquired a partner during this time, and no eggs were known to have hatched.

Inter-nest distances between Chinstrap nests in mixed-species sites were significantly greater than the inter-nest distances of the original Adelie nests in these same sites (t = 8.98, df = 63, $P < 0.001$). The mean (±SE) inter-nest distances were 370 ± 8 mm for Adelies and 516 ± 15 mm for Chinstraps in these mixed sites. Chinstraps having acquired a nest from an Adelie would shift the position of the new nest site to comply with spacing patterns typical for their species in single-species sites (501 ± 11 mm).

Reproductive success.—Adelies in mixed sites suffered greater egg losses than Chinstraps in mixed sites or either species in homogeneous sites (Table 2). The number of chicks surviving to creche per pair that laid eggs was significantly lower for Adelie pairs nesting in mixed sites when compared to Chinstraps in mixed sites or either penguin in single-species sites (χ^2 = 18.84, $P < 0.001$). The number of chicks hatched per pair was also significantly depressed in Adelie mixed sites (χ^2 = 20.28, $P < 0.001$). There were no differences in egg production or the number of chicks creched per chicks hatched between Adelies and Chinstraps in mixed- or single-species sites. No significant differences were found for any of the reproductive variables measured among homogeneous Adelie sites, homogeneous Chinstrap sites, and Chinstraps nesting in mixed-species sites (Table 2).

DISCUSSION

The Adelie Penguin begins its reproductive cycle in the latitudes of the Antarctic Peninsula in early October, with clutches initiated between late October and early November (Sladen 1958: 84), while the Chinstrap Penguin has a reproductive cycle that begins 3–4 weeks later (Conroy et al. 1975a, b). Perhaps the asynchrony in the pygoscelid reproductive cycles better explains the Chinstrap's advantage in nest-site competition than do any inherent differences in aggression between the two species. The peak of nest-site conflicts occurred shortly after the peak of Adelie egg laying (Fig. 1). At this time, Chinstraps arrived fresh from the sea and were aggressively

competing with broody male Adelies that had been fasting for 3–4 weeks. Although the relative weights for Adelies (4.5 kg) and Chinstraps (4.3 kg) are similar (Volkman et al. in press), the newly arriving Chinstrap may have a slight advantage in body mass towards the end of the male Adelie fasting period.

Because there were no differences in the number of chicks that hatched and survived to creche age in mixed- or single-species sites, and significantly higher egg losses were found only for Adelies in mixed sites, the Adelie-Chinstrap conflict appears to be the major source of the Adelie egg losses. Furthermore, Adelie chicks reared in mixed sites did not differ from Adelie chicks in single-species sites for the growth parameters: body weight gain and culmen, flipper and foot growth (Volkman and Trivelpiece MS). This indicates little effect of the interspecific conflict on the chick phase of the reproductive cycle.

Although quantitative behavioral studies of the Chinstrap have not been conducted to date, there are numerous anecdotal references to its aggressive nature summarized by Murphy (1936). Downes et al. (1959) reported Chinstraps on Heard Island taking over Gentoo nests and incubating their eggs. Crawford (1974) reported a transient Chinstrap at Cape Hallett that was known to have acquired nine different Adelie nests during its brief 15-day visit. It is interesting to note that Sladen (1955) makes no mention of conflict between the two species at Signy Island, though both are present in large numbers and breed in close proximity. White and Conroy (1975) suggested that Chinstraps may be forced to rocky slopes where they breed near Adelies. A quantitative analysis of habitat selection among pygoscelids in a three-species rookery is under way (Volkman and Trivelpiece MS), though the nests we studied for the analysis reported here were on relatively flat, unbroken slopes, habitat typically described for Adelies by earlier authors (Sladen 1955, Conroy et al. 1975a, White and Conroy 1975).

Recent census data indicate that pygoscelid penguin populations are on the increase in Antarctic fringe areas such as the Scotia Arc (Sladen 1964, Conroy 1975, Croxall and Kirkwood 1979). More than any other species, the Chinstrap appears to have extended its range and increased markedly in numbers during the past few decades (Conroy 1975, Croxall and Kirkwood 1979). Although all three pygoscelid species have increased in number over the past 12 yr at Point Thomas, the 35% average annual increase exhibited by Chinstrap Penguins at this location is by far the most dramatic change (Table 1). It has been generally accepted that the major cause of the recent penguin popoulation increases is the decimation of the whale populations of the southern oceans during the latter half of the 19th and the early 20th centuries. Krill (prey of whales and penguins) freed by the decrease in whale numbers has been estimated to be enough to rear $2–3 \times 10^8$ penguins/yr (Sladen 1964, Emison 1968). Although penguins are not the only benefactors of the krill surplus, the rapid increase in their numbers at locations of past whale concentrations in the Antarctic supports the contention that penguins have responded to the increased food supply.

It is interesting that actual possession of a nesting territory does not outweigh, in defense terms, loss of condition by the incubator. We hypothesize that the nest-site competition described in this study is a direct result of the recent expansion of pygoscelid populations. Penguins are long-lived birds, and conditions at these rookeries have been different in the recent past, as evidenced by the substantial increases in Adelie and Chinstrap numbers (Table 1). It is possible that Chinstrap pairs originally selected nesting sites on what was then the Adelie colony's periphery. As populations expand, Adelies, establishing breeding territories before the Chinstraps'

arrival, might be selecting nest sites viewed by the later arriving Chinstraps as their own. The ensuing conflict would clearly give the arriving Chinstrap an advantage over the fasting Adelie and account for the results observed here.

Acknowledgments

Field support for the austral summer 1977–78 was provided by the Polish Academy of Sciences, Arctowski Station, where the authors were visiting scientists. We are deeply indebted to J. Jersak, station leader, and many other personnel at Arctowski for their assistance, allowing us to complete this research. Further logistic support was provided by the U.S. Antarctic Research Program (USARP) and the RV Hero under the command of Captain P. Lenie. We thank R. G. Butler for his helpful criticisms of earlier versions of the manuscript. H. Church provided photographic assistance, and D. S. Miller provided encouragement and financial assistance during the manuscript's preparation. This study was financed by a grant to D. Muller-Schwarze from the Division of Polar Programs, National Science Foundation, Washington.

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