

- istry of plurilocular reproductive stages. *Proto-plasma* 77: 1-13.
- BOERSMA, D. 1975. Adaptations of Galapagos penguins for life in two different environments. Pp. 101-114 in *The biology of penguins* (B. Stonehouse, Ed.). London, Macmillan.
- CROLL, D. A., & R. W. HOLMES. 1982. A note on the occurrence of diatoms on the feathers of diving seabirds. *Auk* 99: 765-766.
- RANDALL, R. M. 1983. Biology of the Jackass Penguin *Spheniscus demersus* (L.) at St Croix Island, South Africa. Unpublished Ph.D. dissertation. Port Elizabeth, South Africa, Univ. Port Elizabeth.
- ROUND, F. E. 1981. *The ecology of Algae*. Cambridge, England, Cambridge Univ. Press.

Received 9 February 1984, accepted 14 May 1984.

Further Insights into Nest-site Competition between Adelie and Chinstrap Penguins

WAYNE Z. TRIVELPIECE, SUSAN G. TRIVELPIECE, AND NICHOLAS J. VOLKMAN

Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California 94970

Trivelpiece and Volkman (1979) described male Chinstrap Penguins (*Pygoscelis antarctica*) usurping nest sites of incubating male Adelie Penguins (*P. adeliae*) at Point Thomas, King George Island, Antarctica (62°10'S, 58°39'W). Male Adelie Penguins arrived at the rookery in early to mid-October, established nesting territories, courted females, and took the first incubation shift while females fed at sea. Male Chinstrap Penguins arrived at the rookery in early November, shortly after the peak of Adelie egg laying. They displaced incubating male Adelies in all observed contests, courted female Chinstraps, and bred in the acquired nest sites.

We suggested that Chinstraps were able to displace Adelies partially because of the asynchrony of the breeding cycles of the two species; male Chinstraps, arriving fresh from the sea, competed with incubating Adelie males that had been fasting for 3 weeks. We did not understand however, why actual possession of a nesting territory by the Adelie Penguin did not outweigh, in defensive terms, its loss of condition from fasting. In addition, we were perplexed by this phenomenon because it contradicted the generally held concepts that "established" Adelie Penguins are very faithful to nest sites of previous seasons, and that young Adelies "home in" on their eventual breeding territory during their prebreeding years, an important activity in the establishment process (see Ainley et al. 1983). Therefore, we continued our examination of this phenomenon during the austral summers of 1981-1982 and 1982-1983 to quantify other factors, such as differences in age, breeding experience, and body weight, that might explain the male Chinstrap's superiority in these encounters.

Earlier studies of Adelie Penguins have shown that older, experienced breeders arrive and establish nesting territories earlier than do younger, inexperienced, first-time breeders and that older penguins have greater breeding success and are more nest-site tenacious (LeResche and Sladen 1970, Sladen and LeResche 1970, Ainley et al. 1983). Not having the opportunity to study known-aged birds, we used these criteria for aging our males and compared Adelies

and Chinstraps involved in these agonistic interactions with banded males that had had previous breeding experience outside the areas of conflict.

We banded Adelie and Chinstrap pairs upon their arrival in 1981 and determined their 1982 arrival dates and nest-site tenacity. To quantify differences in body weights between the males of each species at the time of the conflict, we weighed a separate sample of Adelie and Chinstrap males. These penguins, all previously banded, experienced breeders of known sex, were weighed at 3-day intervals beginning on day 3. We calculated arrival weights by regressing the 3-, 6-, 9-, and 12-day weights back to day 0 and thus eliminated the weight of the stomach contents from arrival weights. Finally, we noted the activities of Adelies that lost nests to Chinstraps during their reoccupation period in 1981. At this time (mid-December to mid-January), failed breeders return to reoccupy their nest sites, and younger penguins arrive for their first visit to the rookery (Sladen 1958, Ainley et al. 1983).

The mean arrival dates of male Adelies occupying uncontested nest sites (11 October 1981 and 8 October 1982) were significantly earlier than the mean arrival dates of male Adelies occupying nest sites later claimed by Chinstraps (19 October 1981 and 17 October 1982, Table 1).

Chinstrap males occupying contested nest sites had a mean arrival date of 8 November in both years ($n = 92$ males), not significantly different from the mean arrival dates of the male Chinstrap population (10 November 1981, $n = 64$ and 8 November 1982, $n = 42$).

The 1982 arrival weights (mean \pm SE) of 16 Adelie and 18 Chinstrap males did not differ statistically, although the Adelie males were heavier upon arrival (5.2 ± 0.1 kg and 5.0 ± 0.1 kg, respectively; $t = 1.86$, $df = 32$, $0.05 < P < 0.1$). By the time the Chinstrap males arrived, however, fasting Adelie males weighed only 4.2 ± 0.1 kg, significantly lower than the 5.0 kg Chinstrap arrival weight ($t = 6.32$, $df = 32$, $P < 0.01$).

In 1981, we banded 41 newly arrived Adelie pairs in a mixed colony where Chinstraps were later ex-

TABLE 1. Comparisons of the arrival dates (mean \pm SE) of male Adelie Penguins occupying nests later claimed by Chinstrap Penguins (contested sites) with uncontested Adelie nest sites (controls).^a

Nest sites	Arrival date October 1981	Arrival date October 1982
Adelie males' control site	11.1 \pm 0.3 <i>n</i> = 58	8.4 \pm 0.4 <i>n</i> = 30
Adelie males' contested sites	19.1 \pm 0.9 <i>n</i> = 59	17.2 \pm 1.0 <i>n</i> = 25
<i>t</i> -test	10.44**	8.45**

^a ** = $P < 0.01$.

pected to usurp nest sites. Twenty-three of these males lost their nest-sites to arriving Chinstrap males. We later observed several of these Adelie males during their reoccupation period (mid-December 1981 to mid-January 1982). None was in the area of their former nests, however, even though 11 of the 23 Chinstraps that had evicted them had since failed and these nest sites were vacant.

Twelve banded Adelie males that lost nests to Chinstraps in 1981 returned in 1982. All selected new nest sites in the same colony, but outside of the conflict area, a mean 17 m from their previous season's contested site. The mean arrival date of these 12 males was significantly earlier in 1982 than in the previous year (9 October 1982 vs. 19 October 1981; $t = 7.63$, $df = 22$, $P < 0.01$) and did not differ significantly from the 8 October 1982 mean arrival date of the male Adelie population.

The 18 Adelie males of the originally banded 41 that did not interact with the Chinstraps were also late arrivals (mean arrival 17 October 1981) and, therefore, were young, inexperienced birds by our criteria. Additionally, their reproductive success was 0.47 chicks per pair, significantly below the 1.02 chicks fledged per Adelie pair in 1981 (Volkman et al. 1982) and characteristic of young inexperienced breeders. Seven of these 18 males returned in 1982, however, and all of them occupied their former nest sites.

Thirty-five male Chinstraps were banded in 1981 after acquiring their nest sites by ousting an incubating Adelie. Twenty of these males returned the next breeding season, all to their previous nest sites. Fourteen of these Chinstrap males again found their nest sites occupied by new, unbanded Adelie males, which they displaced; the remaining six male Chinstraps found their nest-sites unoccupied.

Our re-examination of the nest-site competition indicates that the Chinstraps' superiority in these encounters was probably due to differences in the age and past breeding experience of the contestants. Adelies selecting nest sites later claimed by Chinstraps were late arrivals, a characteristic associated with young, inexperienced, first-time breeders

(LeResche and Sladen 1970, Ainley et al. 1983). Adelies losing their nests to Chinstraps the first year selected different nest sites and arrived at the rookery significantly earlier the next breeding season, in time with older established breeders. The following year, a new group of unbanded, late-arriving Adelie males established themselves in the area of conflict.

These conflicts also confirm and further our understanding of territory establishment in these species. Older, experienced penguins are very faithful to their previous season's nest site, whereas younger penguins are less site tenacious (LeResche and Sladen 1970, Ainley et al. 1983). Therefore, our suggestion that differences in age and experience explain the Chinstrap's dominance in these interactions is compatible with the concept of age-dependent philopatry in these species. Furthermore, the idea that young Adelies home in on their eventual breeding territory during their prebreeding years is also compatible with our findings. Adelie males that lost nest sites to Chinstraps chose new sites the following year, but all of them remained in the same colony rather than dispersing.

Adelie and Chinstrap penguin populations have almost doubled over the last 20–30 yr at Point Thomas, a phenomenon documented for both these species throughout the Peninsula and Scotia Sea areas of the Antarctic (Croxall and Kirkwood 1979, Croxall et al. 1981). We hypothesize that Chinstrap males originally selected nest sites on or near the periphery of Adelie colonies. As the Adelie population expanded, some of the young, inexperienced, late-arriving Adelie males selected nest sites on the periphery of the same Adelie colonies, in areas the still-later arriving Chinstrap males considered to be their own. The ensuing conflict pitted an apparently young, inexperienced, fasting Adelie male against an older, established, significantly heavier Chinstrap male, and these factors, we believe, explain the dominance of Chinstraps in these encounters.

We thank Professor S. Rakusa-Suszczewski of the Polish Academy of Sciences for the invitation to live and work at their Antarctic Station, Henryk Arctowski. We also thank the personnel of Arctowski Station, the Chilean Air Force, the *R/V Hero*, and USARP for valuable logistical support and S. H. Ware and K. E. Young for field assistance. D. G. Ainley, D. C. Duffy, and W. J. L. Sladen provided many helpful comments on the manuscript. Funding was provided by NSF Division of Polar Programs grant #8117205 to the authors. This is contribution #273 of the Point Reyes Bird Observatory.

LITERATURE CITED

- AINLEY, D. G., R. E. LERESCHE, & W. J. L. SLADEN. 1982. Breeding biology of the Adelie Penguin. Berkeley, California, Univ. California Press.
- CROXALL, J. P., & E. D. KIRKWOOD. 1979. The distri-

- bution of penguins on the Antarctic Peninsula and islands of the Scotia Sea. Cambridge, England, Brit. Antarctic Surv.
- , D. M. ROOTES, & R. A. PRICE. 1981. Increases in penguin populations at Signy Island, South Orkney Islands. Brit. Antarctic Surv. Bull. 54: 47-56.
- LERESCHE, R. E., & W. J. L. SLADEN. 1970. Establishment of pair and breeding site bounds by young known-age Adelie Penguins. Anim. Behav. 18: 517-526.
- SLADEN, W. J. L. 1958. The pygoscelid penguins. Sci. Rept. Falkland Islands Depend. Surv. 17: 1-97.
- , & R. E. LERESCHE. 1970. New and developing techniques in Antarctic ornithology. Pp. 585-596 in Antarctic ecology (M. Holdgate, Ed.). London, Academic Press.
- TRIVELPIECE, W. Z., & N. J. VOLKMAN. 1979. Nest-site competition between Adelie and Chinstrap penguins: an ecological interpretation. Auk 96: 675-681.
- VOLKMAN, N. J., S. G. TRIVELPIECE, W. Z. TRIVELPIECE, & K. E. YOUNG. 1982. Comparative studies of pygoscelid penguins in Admiralty Bay. Antarctic J. U.S. 17: 180.

Received 13 December 1983, accepted 19 April 1984.

Utilization Efficiency of a Squid Diet by Adult King Penguins (*Aptenodytes patagonicus*)

N. J. ADAMS

Percy FitzPatrick Institute of African Ornithology, University of Cape Town,
Rondebosch 7700, South Africa

Published values for the utilization efficiency of seabirds have come entirely from work on chicks and juveniles fed exclusively on fish (Dunn 1975; Cooper 1977, 1978, 1980). Squid is an important component of the diet of many species, however, comprising up to 90% of prey taken by King Penguins (*Aptenodytes patagonicus*; Stonehouse 1960, Croxall and Prince 1980, Croxall 1984). Because the utilization efficiency of birds is known to vary depending on the food consumed (Uramoto 1961), the applicability of the published data to such species is uncertain. This study presents the first measurements of the assimilation efficiency of a predominately squid-eating adult seabird fed on squid.

The study was conducted at sub-Antarctic Marion Island (46°54'S, 37°55'E) during September 1981 and April 1982. Four nonbreeding adult King Penguins were housed indoors, individually confined to small cages, and fasted for 48 h before commencement of the experiment. Room temperature varied between 5°C and 15°C, within the thermoneutral zone of King Penguins (Groscolas et al. 1981). The penguins were then fed for 5 days on a diet consisting exclusively of the South Atlantic cool-water squid *Loligo reynaudi*. Each bird was weighed daily before being fed a known mass of food sufficient for it to maintain constant mass over the period of the experiment. A pre-weighed plastic sheet underneath a wire mesh floor allowed for the daily collection of excretory products, which were then dried to constant mass at 60°C. Homogenized portions of oven-dried squid and excretory products were analyzed individually for energy content with a Phillips micro-bomb calorimeter. Utilization efficiency was calculated as gross energy intake minus excretory energy expressed as a percentage of gross energy intake.

Gross energy intake, excretory energy, and utili-

zation efficiency were calculated per bird over the 5 days and the averaged results for the four birds are given in Table 1. The wet mass of food consumed daily averaged 6.1% of total body mass. The daily squid intake of 699 g/d was close to the 675 g/d of fish fed to King Penguins maintained at the Montreal Aquarium (Penfold 1979). The energy value of squid was 22.1 ± 0.5 kJ/g dry mass ($n = 8$; 5.23 kJ/g wet mass), a value 14% higher than that obtained by Cooper (1979) for the same species. Excretory output was similar to that measured by Burger et al. (1978), averaging 8.4% higher. The energy value of excretory products was 13.2 ± 0.7 kJ/g dry mass ($n = 23$), a value 8.3% lower than that obtained by Burger et al. (1978). The mean efficiency of utilization of four birds was 81.3%.

The calculated utilization efficiency of captive adult King Penguins fed squid is near the upper limits of the range observed for young piscivorous seabirds fed on fish (Table 2). Estimates of food consumption by squid-eating species based on these data (e.g. Prince et al. 1981, Croxall and Prince 1982a) will therefore be substantially correct. This confirmation has considerable ecological significance for bioenergetics modelling (see Croxall and Prince 1982a), because King Penguins and other squid-eating species comprise a large proportion of the total seabird biomass in the sub-Antarctic region.

Published values for the energy content of squid, mainly from the northern hemisphere, are appreciably lower than those for the energy content of Antarctic krill and fish (Croxall and Prince 1982b). The energy value of squid meals fed to Black-browed (*Diomedea melanophris*) and Grey-headed albatross (*D. chrysoloma*) chicks at South Georgia, however, fall within the range measured for Antarctic fish (Clarke and Prince 1980) and krill (*Euphausia superba*; Clarke