BEHAVIOR AND NESTING SUCCESS RELATIVE TO NEST LOCATION IN ADÉLIE PENGUINS (*PYGOSCELIS ADELIAE*)

RICHARD TENAZA[1]

Department of Zoology
University of Wisconsin
Madison, Wisconsin

This study is an experimental evaluation of the hypothesis that differences in nest positions within and outside Adélie Penguin colonies influence behavior, egg loss rates, and nest characteristics. "Colony" and "rookery" are used in this report as defined for Adélies by Penney (1968:85): "A colony is a geographically continuous group of breeding birds whose territorial boundaries are contiguous," and a rookery is a "geographical area . . . that contains one or more colonies."

The actions of predators and conspecifics within a dense nesting colony of Adélies or other sea birds are highly predictable. Nests are regularly spaced, just far enough apart to allow owners of adjacent territories to touch bills when reaching toward one another from their nests. This "social pattern" (Hutchinson 1953) minimizes disturbances within the colony. A predator hunting eggs or chicks may have difficulty directing its attention to any single nest because it is always within pecking distance of other nests. For the same reason a conspecific has difficulty approaching a nest to steal nest material (a habit found among many colonial sea birds, e.g., see Fisher and Lockley 1954) or to otherwise disturb its occupant. Colony perimeters furnish less predictable living spaces, and single nest sites entirely separated from colonies are even more unpredictable. Intruders can approach perimeter nests from outside the colony without being attacked by potential victims' neighbors, and isolated nests can be approached from all directions.

Thus, peripheral and isolated nesters might suffer heavier losses of eggs and chicks to predators than do residents within the colony. They might also be expected to lose more nest material (in species where theft occurs) and experience greater stress from the higher frequency of predator contacts and interactions with conspecifics (see Christian 1963: 592, 1964; Barnett 1964).

The Adélie Penguin is particularly well suited for an experimental evaluation of these predictions for three reasons: (1) it is much less disturbed in the presence of man than are most colonial sea birds, (2) it is subject to predation upon eggs and chicks, and (3) theft of nest material from neighbors is conspicuous and frequent. Also, the breeding behavior and ecology of the Adélie is the best known of the Antarctic penguins.

METHODS

The study was conducted at Cape Hallet (72° 18′ 50″ S, 170° 13′ 00″ E), Victoria Land, Antarctica, during the 1967–1968 austral summer. The Cape Hallet Adélie Penguin rookery occupies about 40 ha of a low lying spit ("Seabee Spit"), approximately 1000 m long and 200–650 m wide, projecting into the Moubray Bay inlet of the Ross Sea (fig. 1). Maximum elevation of the spit is about 5 m. This rookery was described and mapped by Reid (1964) who recognized more than 600 colonies at Hallet, ranging in size from less than 10 to more than 1200 nests. Reid (1964:15) censused the breeding population at Cape Hallet and found it to be 62,900 pairs in the 1959–1960 breeding season and 61,955 pairs in the 1960–1961 season. A census made during the present study identified about 43,000 breeding pairs (Brett Turnbull and Thomas Choate, pers. comm.).

The experiments described in this report were conducted 5–11 December 1967 during the late incubation phase of the Adélie breeding cycle. Data collection was confined to this brief period to allow a temporal cross-sectional comparison among birds nesting in different locations. First hatching occurred on 9 December and the peak of hatching was 16–17 December. The Adélie's incubation period averages 35–37 days (Penney 1968:93), so the birds evaluated in this study had already been exposed to approximately 3.5–4.5 weeks of nest predation and intraspecific disturbances.

SUBJECTS

The three experimental groups whose behavior, nests and clutch sizes are compared in this report were 60 inner-colony ("central") and 60 colony-perimeter ("peripheral") nesting Adélies from among 15 different breeding colonies, and 22 isolated nesters (fig. 2). Each "central" nest was surrounded by six other nests and had insufficient adjacent space to support another nesting territory. It was therefore central in relation to its six nearest neighbors rather than central within the colony. Most central nests evaluated were actually near colony edges (to minimize observer disturbance). Isolated nests were located outside of colonies and at least 2 m from the nearest neighboring nest; such nests comprised less than 1

FIGURE 1. A portion of the Cape Hallet Adélie Penguin rookery on "Seabee Spit." Colonies appear as pale (guano-covered) areas on the spit. Mt. Herschel (3335 m elevation) is in the left background.

per cent of the Hallet rookery. All birds evaluated were incubating eggs. Penguins with mates present at their nest were excluded from the study to avoid confounding the results with interactions between birds.

The number of nests in study colonies ranged from 9 to 470 ($\bar{x} = 95$), and the number of incubating birds tested per colony varied from two in the nine-nest colony to 22 in the 470-nest colony. To control for differences among colonies and possible differences due to time of day or weather, equal numbers of central and peripheral birds from the same colony were always tested within a few minutes of each other during the same experimental session.

PROCEDURE

The parameters chosen for measurement were (1) clutch size (the number of eggs in the nest), (2) nest dimensions, (3) nest quality, rated by visual evaluation of compactness and form, (4) relative size of nest stones, (5) responses to the experimenter, and (6) responses to experimentally displaced eggs. The rationale for these parameters is given in a later section. Each experiment was conducted as follows. The incubating study-subject was approached and nudged from its nest (unless it ran away first), and clutch size, nest quality, estimated average nest stone size, and the birds' responses to the experimenter were noted. Then one egg was removed from the nest and placed on the ground next to (and touching) the outside edge of the nest. Nest measurements were then taken to the nearest cm. Nest rim height was measured next to the displaced egg, and nest radius was measured from the nest center to the outer edge

of the nest next to the displaced egg. Nest radius was also a measure of the distance from the nest center to the nearest edge of the displaced egg. All of these measurements were completed in less than 60 sec. I wore the same bulky red parka, black wind trousers, and black boots during all experiments.

Following these manipulations and measurements I started my stopwatch, then backed 10 paces away from the nest to record the bird's responses to the displaced egg. The test was ended when the egg was retrieved or pecked hard enough to cause it to roll away from the nest, or after 6 min had elapsed with neither event occurring. Egg retrieval was considered complete when the egg was back in the nest cup. Duration of the actual retrieval movement was also measured.

Before collecting the quantitative data in this report I conducted 75 preliminary trials to familiarize myself with the birds' responses, work out appropriate data recording procedures, and practice recording the physical and behavioral measures finally adopted.

RESULTS AND DISCUSSION

RESPONSES TO THE EXPERIMENTER

Responses of incubating birds to disturbing stimuli affect the temperature of their eggs (Baerends 1959:364) and can expose eggs or chicks to predation if the bird leaves the nest. These responses are therefore relevant parameters when comparing the relative nesting potentials of birds nesting in different locations.
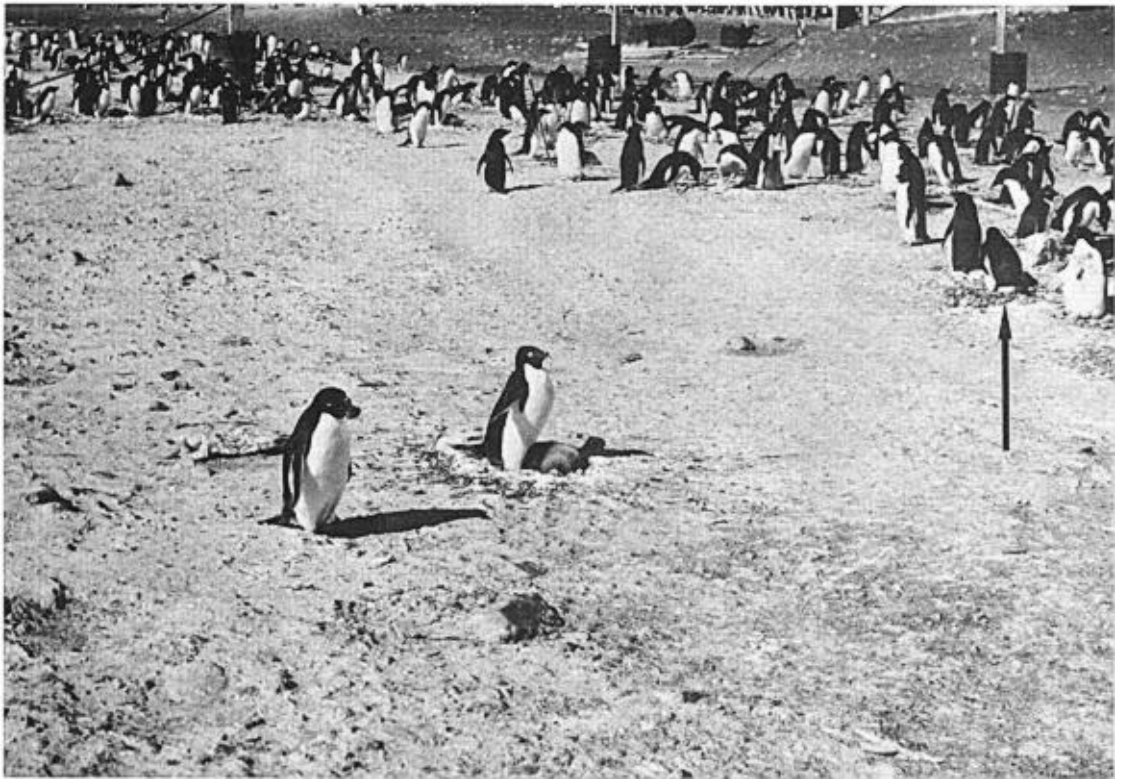
FIGURE 2. A (upper). The arrow points to a central nester, surrounded by its six nearest neighbors (see the hexagonal arrangement of nests in the hypothetical colony of figure 4A). B (lower). The bird brooding a large chick on its nest in the center of the picture is an isolated nester. The arrow at right points to a peripheral nest.

TABLE 1. Comparisons of responses to the experimenter by central, peripheral, and isolated nesting Adélie Penguins.

Response	Central ($n = 60$)	Peripheral ($n = 60$)	Isolated ($n = 22$)	$P < 0.05$[a]
Remained on nest and delivered painful pecks and/or wing blows[b]	42	45	13	None
Ran away	3	12	4	C vs. P
Remained on nest but did not attack, or delivered only mild, painless pecks[c]	15	3	5	C vs. P

[a] Two-tailed binomial test used.
[b] Central birds, which neither attacked nor fled, pecked their experimentally displaced eggs hard enough to cause them to roll away from the nest significantly more often than other central birds (8/15 vs. 9/45, $P < 0.01$).
[c] The Adélie's most intense fighting behavior includes powerful wing blows. Only 3 central, 4 peripheral and 1 isolated nester (6% of all birds) attacked me in this manner.

The higher frequency of running away among peripheral nesters than among central nesters, (table 1) suggests either that central nesters were "trapped" on their nests by their hostile neighbors (J. T. Emlen, Jr., pers. comm.), or that peripheral nesters have stronger escape tendencies than central birds. In any event, central nests were less likely to be left exposed than were peripheral ones. Perhaps one advantage of central nesting is that the tendency to remain on the nest is increased by neighbors' hostility. The tendency to flee activated in Adélies by a man presumably is due to high intensity stimulation produced by man's large size (accentuated by the upright posture) and his unusual appearance and behavior. When a vehicle is driven through a rookery or when a helicopter flies low over it, providing stimuli more intense than a man on foot, birds leave their nests en masse.

CLUTCH SIZE

The smaller mean number of eggs in peripheral nests (fig. 3) agrees with previous reports (Penney 1968:107; Taylor 1962:199–200) that peripheral nesting Adélies produce fewer young than central birds, as Patterson (1965: 438) found in Black-headed Gulls (*Larus ridibundus*). These data have important implications regarding the relevance of colony form and size to reproductive success, discussed in the following section.

RELATION OF COLONY SIZE AND SHAPE TO REPRODUCTIVE SUCCESS

Several observers have reported that small colonies of certain sea birds produced fewer young per breeding adult than larger colonies (Darling 1938, Herring Gulls, *Larus argentatus*; Fisher and Vevers 1944, Gannets, *Morus bassanus*; Fisher and Waterston 1941, Fulmars, *Fulmarus glacialus*; Austin 1945, Common Terns, *Sterna hirunda*; Richdale 1951, Yellow-eyed Penguins, *Megadyptes antipodes*). Darling (1938), who first called attention to this, suggested that social stimulation is its proximate basis. According to Darling's hypothesis, the greater level of social stimulation in larger colonies leads to an earlier, shorter, more synchronous breeding season, the ultimate value of which is shortening the period of egg and chick susceptibility to predation. Although the differences in breeding success that Darling (1938) observed between his small and large study colonies were not statistically significant (Haartman 1945; Coulson and White 1956), his hypothesis (widely known as the "Darling Effect") still is considered an attractive possibility (e.g., Crook 1968:164–165; Klopfer and Hailman 1967:145; Tinbergen 1967:47).

A number of criticisms, contradictions, and alternatives to Darling's hypothesis have appeared in the literature (e.g., Armstrong 1947:
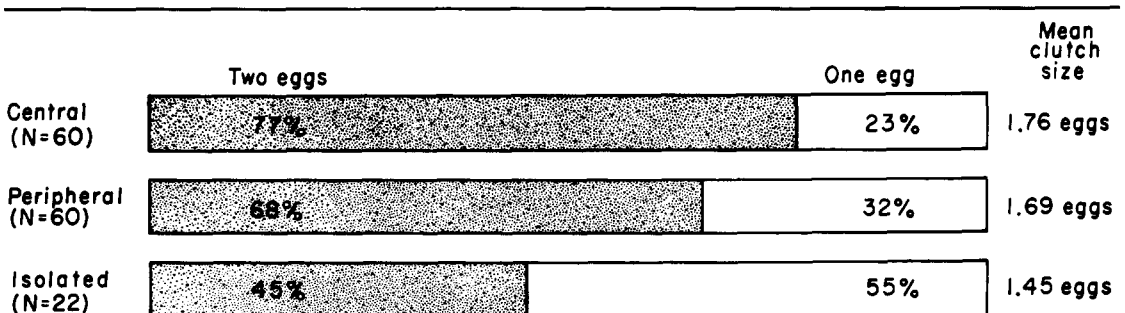

FIGURE 3. Clutch size of Adélie Penguins compared among central, peripheral, and isolated nesters ($P < 0.03$, χ^2 2 × 2 table). Clutch size here refers to the number of eggs observed in nests late in the incubation period, not to numbers originally laid.
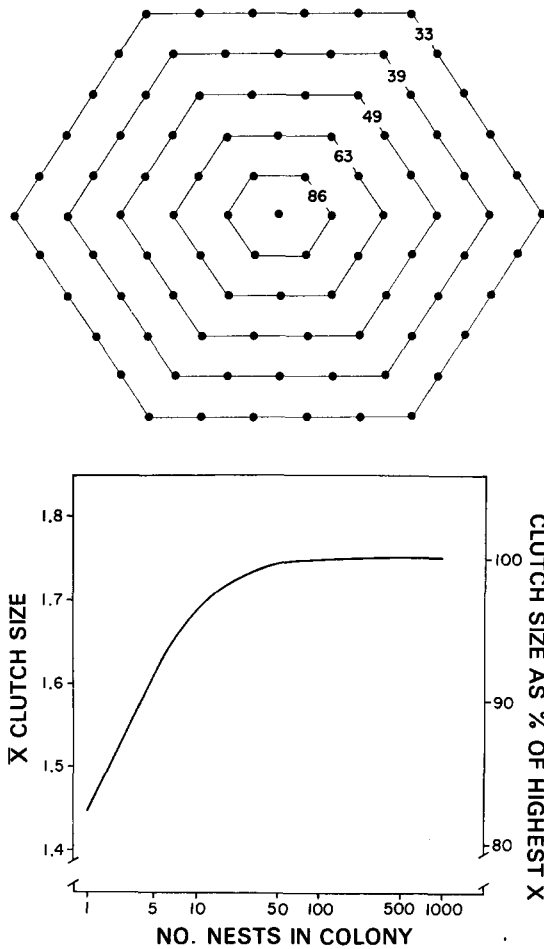
FIGURE 4. A (upper). Each concentric hexagon represents the perimeter of an hypothetical colony having the densest possible arrangement of nests for its size. The numbers represent the percentage of the total numbers of nests in each "colony" that occur on the perimeter, illustrating the increase in proportion of perimeter nests with decrease in colony size. B (lower). An hypothetical curve obtained by applying the clutch size differential observed among central, peripheral, and isolated nests (fig. 3) to hypothetical hexagonal colonies such as those shown above. The curve illustrates expected variation in clutch size with colony size during the sampling period of this study.

183–194; Coulson and White 1956, 1960; Davis 1940:211; Fisher 1952; Haartman 1945; Lack 1943, 1954:257–258; Orians 1961; Richdale 1951; Roberts 1940:234; Tinbergen 1952). The most frequently suggested alternative is that small colonies are often new colonies being founded by young birds, and that the low nesting success of small colonies is therefore due to the youth of the occupants rather than to the "Darling Effect." It is important to note that except for newly-founded colonies (Fisher 1952:349; Richdale 1951:192), and colonies that appear to be declining to ex-

tinction for unknown reasons (Patterson 1965: 436), the status of small colonies that have been reported to be less successful than larger colonies is unknown. However, data collected in this study suggest that even when colonies differ in size alone, fewer young per breeding adult should be produced in smaller colonies than in larger ones. Peripheral nesters appear to lose more eggs (and presumably chicks) than central birds; hence nesting success should decrease with colony size because the ratio of perimeter nests to interior nests increases as the colony gets smaller (fig. 4). Allee et al. (1949: 397–399) discussed similar relationships in several kinds of animals (ranging from protozoans to man) and suggested that "Many of the protective values furnished by animal aggregations depend on the reduced amount of surface in relation to total mass that characterizes aggregated animals as contrasted with a similar number of scattered, isolated individuals." My data support this hypothesis and suggest a simple alternative to the "Darling Effect" to account for lowered breeding success in small colonies as compared with larger ones.

The extent of colony periphery is determined by colony shape as well as by colony size. Linear colonies should therefore be expected to produce fewer young per breeding adult than colonies with shapes having relatively less periphery (fig. 4, 5B).

Penney (1968:106) has proposed that size and shape of Adélie colonies might be limited by the distance a bird will travel through a dense nesting aggregation, enduring attacks by hostile territory holders, to reach its nest. To support this idea, Penney presented a photograph (1968:107, fig. 17) of a large colony devoid of nests in its center. Penney suggested that the colony grew so large that access to the middle was prevented. However, the dense colony shown in figure 5A is larger than the one in Penney's illustration and tends to weaken his hypothesis. Also, close examination of Penney's figure 17 reveals that at one end of the colony birds would have had to travel only the width of two or three territories to reach the colony's central void from outside. Although Penney's hypothesis may be valid in some extreme instances, rookery physiography seems to be a more important factor in determining the size and shape of Adélie colonies; areas which flood during thaws are mostly unoccupied. For example, on Possession Island (71° 48′ S, 171° 30′ E) and at Cape Hallet (72° 18′ 50″ S, 170° 13′ 00″ E), both characterized by uneven topography, nearly
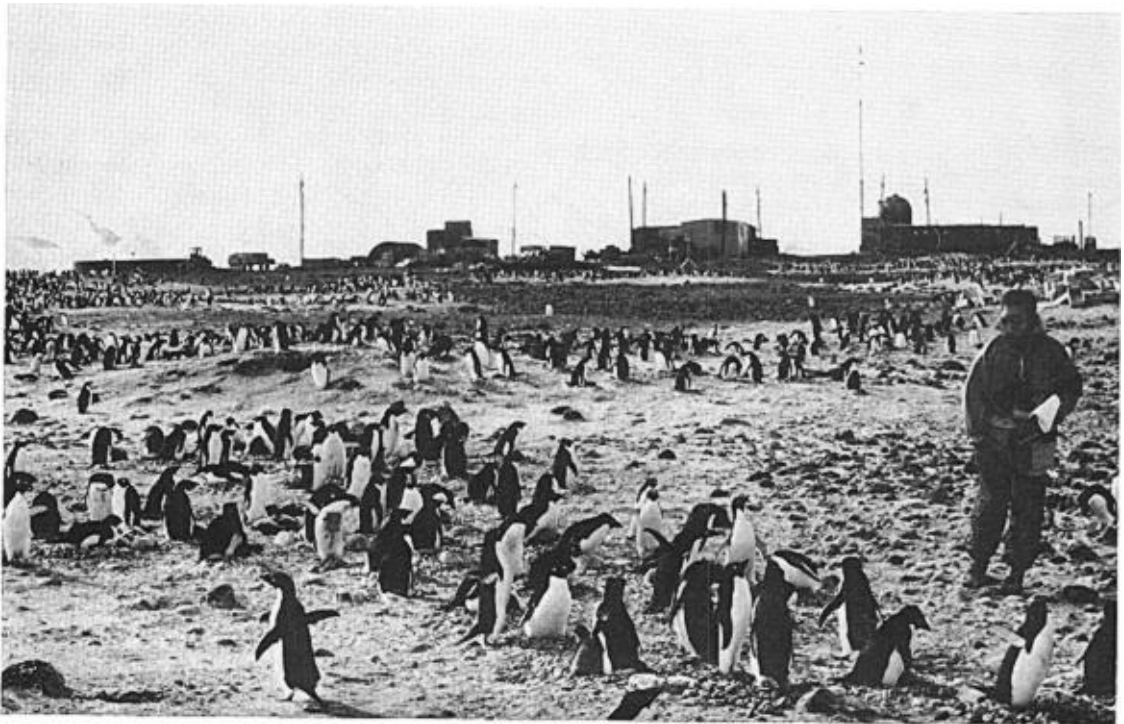
FIGURE 5.   A (upper). A large Adélie Penguin colony with relatively small periphery.   B (lower). A small linear colony with relatively large periphery.
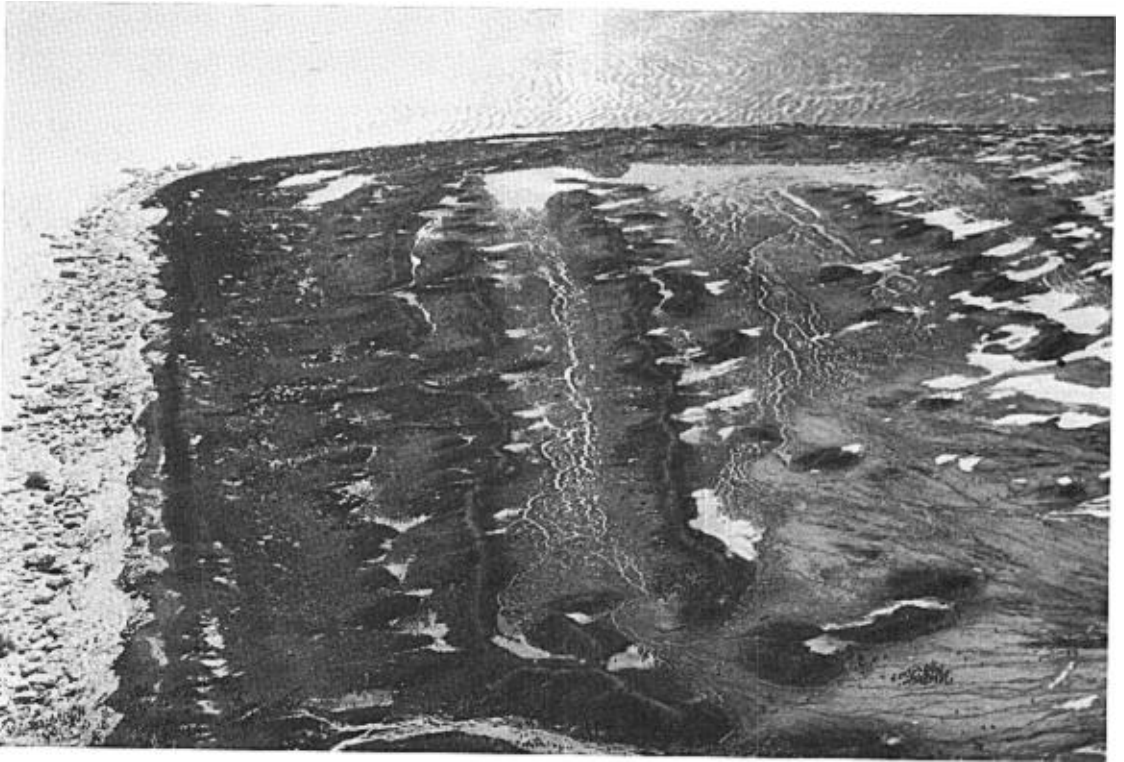
FIGURE 6. Aerial photograph of a portion of the Adélie Penguin rookery on Possession Island. Colonies are restricted to tops of ridges and mounds, while depressed areas, which flood during thaws, are avoided. The dark color of the colony areas is due to the deposit of orange feces by juvenile penguins, which are fed almost entirely on euphausid shrimp ("krill").

all colonies are situated on the tops of ridges and mounds and on well-drained slopes; depressed areas generally do not contain colonies (see fig. 6).

PREDATION AND NESTING SUCCESS

The Antarctic Skua (*Catharacta skua*) is the Adélie's most important natural predator in the breeding colonies, although Sheathbills (*Chionis alba*) and Giant Petrels (*Macronectes giganteus*) also prey on Adélie eggs and chicks, respectively, in some areas (Murphy 1936: 401; Sladen 1958). According to Eklund (1961: 200) Skuas nest at all Adélie rookeries investigated, and Adélie eggs and chicks are an important source of food for both adult and young Skuas. Reid (1964) and especially Maher (1966) have discussed the Skua-Adélie predator-prey relationship at Cape Hallet, and their reports agree with Eklund (1961). Eklund (1961:209), Penney (1968:108), Reid (1964:26), and Taylor (1962:200) have all observed that Skuas attempt to take Adélie eggs and chicks more frequently at colony edges than in colony interiors. Presumably this is because a Skua cannot enter a dense Adélie colony without being attacked by adult penguins. By comparison, it can work colony edges with relative impunity. Levick (1914: 55) saw Skuas snatch eggs from under nesting Adélies, and Taylor (1962:198) reported Skua predation upon Adélie chicks in the same way. Reid (1964:26) recognized the importance of colony size and shape in determining relative vulnerability to Skua predation.

THE NEST

Adélie nests at Cape Hallet are constructed of stones 1–5 cm in diameter (Müller-Schwarze 1968:33) and usually are placed in shallow scrapes on bare ground. Size and quality of a nest presumably affect its temperature regulating efficiency and the ease with which eggs or chicks are accidentally rolled from it. The larger dimensions and better construction of central nests (table 2) therefore suggest that their owners may produce more surviving young than peripheral and isolated nesters.

It is possible that the smaller dimensions and poorer quality of peripheral and isolated nests may be due largely to their greater vulnerability to stone removal. Following nest relief, the relieved bird often makes "short excursions outside the colony to collect stones

TABLE 2. Comparisons of nest parameters of central, peripheral and isolated nesting Adélie Penguins.

Observation	Central (n = 60)	Peripheral (n = 60)	Isolated (n = 22)	P < 0.05[a]
Radius ($\bar{x}$ cm ± 2 s D)	19.7 ± 2.8	17.4 ± 2.2	17.2 ± 1.9	C vs. P, C vs. I
Rim height ($\bar{x}$ cm ± 2 s D)	2.9 ± 1.4	1.3 ± 1.1	1.1 ± 1.1	C vs. P, C vs. I
Quality[b]				
No. "good" ratings	46	12	7	C vs. P, C vs. I
No. "poor" ratings	14	48	15	
Stone size[c]				
Medium to large	57	36	15	C vs. P, C vs. I
Small	3	24	7	

[a] χ^2 (median test) used in comparing radii and rim heights; χ^2 (2×2 table) used in comparing quality and stone size.
[b] Nests were rated 1, 2, 3, or 4, from poorest to best, based upon a visual evaluation of compactness and form. 1 and 2 are considered "poor" ratings, and 3 and 4 are "good" ratings.
[c] The stones in each nest were rated small, medium or large by visual evaluation of their average size as compared to the size ranges of stones in the vicinity of the colony to which the nest belonged.

for the nest, sometimes for several hours" (Penney 1968:93) before leaving for the sea. During these collecting bouts, stones are frequently stolen from other nests. Like a Skua, a stone-stealing penguin can approach a peripheral or isolated nest without being attacked by birds on adjacent nests, but Skuas or penguins moving within a colony must "run the gantlet of aggressive territorial defenders" (Penney 1968:106).

The adaptive significance of stone stealing behavior probably lies in a higher probability for reproductive success among birds with larger, better formed nests and the fact that most suitable stones around colonies are in nests.

Levick (1915:61) noted that within a single colony the size of nest stones can differ noticeably among different nests, as was observed in this study. However, the significance of the fact that central nests are constructed of larger stones than peripheral and isolated nests is unclear. One possibility is that most birds prefer large stones, and these are therefore stolen from peripheral and isolated nests (see above) at a faster rate than smaller stones. The adaptive basis of a preference for large stones could be the time and energy saved by building a nest of large rather than small stones. Stones are gathered one at a time, hence more collecting trips are required to construct nests of small stones.

Taylor (1962:198) observed that early in the incubation period eggs were often knocked out of nests during fights resulting from "territorial competition," and that some eggs were accidentally displaced from nests during routine nest relief ceremonies and even when a parent was simply changing position during incubation. Eggs are presumably more likely to be accidentally rolled out of peripheral nests because of their poorer construction and lower rims. If the poorer quality of peripheral nests is, as I suggest, due largely to stones being stolen by other Adélies, then the reproductive success of peripheral nesters is lowered by intraspecific actions as well as by predation. The advantages of nesting in the colony's interior would then include greater protection from the disruptive influences of neighboring penguins as well as greater protection against predation on eggs and chicks.

RESPONSES TO EXPERIMENTALLY DISPLACED EGGS

The tendency to retrieve eggs from outside the nest occurs in many species of ground nesting birds (Poulsen 1953). It is therefore not surprising that 77 per cent of the birds tested in this study rolled experimentally displaced eggs back into their nests (table 3 and fig. 7). Baerends (1959) studied incubation behavior and egg retrieval in Herring Gulls (*Larus argentatus*) and concluded (p. 362) that "the tendencies to incubate and to retrieve prove to be directly proportional," and that efficiency of nest temperature regulation depends upon the strength of the incubation tendency (p. 364). If this is so, then the responses of birds to eggs outside their nests might indirectly reflect the efficiency of nest temperature regulation. The increase from central to peripheral to isolated nesters in total time taken to retrieve eggs (table 3) suggests that central nesters may have relatively stronger incubation tendencies, and therefore more effective nest temperature regulation, than peripheral and isolated nesters. (This is worth considering even though the differences did not reach statistical significance.)

TABLE 3.   Comparisons of the responses of central, peripheral and isolated nesting Adélie Pengins to experimentally displaced eggs.

Observation	Central (n = 60)	Peripheral (n = 60)	Isolated (n = 22)	P < 0.05[a]
Responses to eggs outside the nest[b]				
No. birds rolling eggs back into the nest[c]	40	51	18	
No. birds aggressively pecking eggs hard enough to cause them to roll away from the nest	17	7	2	C vs. P
No. birds neither retrieving nor pecking away eggs	3	2	2	
Time taken to retrieve eggs				
Total time between observer's displacement of the egg and the bird's completion of its retrieval ($\bar{x} \pm$ s D sec)	21.0 ± 37.6	27.6 ± 39.4	30.6 ± 57.5	None
Duration of egg rolling movement ($\bar{x} \pm$ s D sec)	3.0 ± 2.5	1.9 ± 0.9	2.6 ± 1.5	C vs. P

[a] χ^2 (2 × 2 table) was used in comparing responses to eggs outside nest; the Mann-Whitney U test was used in evaluating the time data.
[b] In a few instances, eggs being retrieved rolled away from the retrieving bird. These were excluded from the study.
[c] Thirty-eight of the 45 birds with 1-egg clutches and 72 of the 97 with 2-egg clutches retrieved their eggs ($P > 0.2$). This shows that the retrieval tendency probably is not influenced by clutch size.

The higher incidence of pecking eggs away from the nest among central nesters (table 3) reflects the higher level of aggressiveness in that group; attacks on eggs are presumed to have represented redirected attack (see Bastock et al. 1954) activated by the experimenter but released on the egg. This assumption is supported by the fact that the central birds which neither attacked the experimenter nor fled pecked their experimentally displaced eggs hard enough to cause them to roll away from the nest significantly more often than other central birds (table 1, footnote b).

The longer time taken to roll the egg back into the nest among central nesters than peripheral nesters (table 1) was due probably

FIGURE 7.   An adult Adélie rolling a displaced egg back into its nest.

to the greater heights of central nests' rims: central birds had greater difficulty rolling an egg back into the nest.

Although Penney (1968:93) and Taylor (1962:198) have reported an absence of egg retrieval behavior in Adélies, the results of the present study show that most Adélies do in fact retrieve eggs (see fig. 7 and table 3). During preliminary observations, eggs were retrieved from distances up to 15 cm away from the outside edges of nests. An egg being retrieved occasionally rolled away from a bird, especially if the nest rim was relatively high and steep; the retrieving bird usually responded by instantly pecking the egg, causing it to roll away (these instances were excluded from the study).

STATUS OF PERIPHERAL AND ISOLATED NESTERS

Young birds of many species raise fewer young than older individuals (Lack 1968:297–298), and it has recently been reported that this is also true of the Adélie (Sladen et al. 1968). This phenomenon and observations that, among colonial sea birds, peripheral nesters are less successful than birds nesting within colonies, has led to the suggestion that peripheral nesters are young birds, and only gradually work their way to the colony's center (Fisher and Lockley 1954:173; Reid 1964: 19; Sladen 1958; Penney 1968:108). As an alternative to this hypothesis, I suggest the following. A bird breeding for the first time may nest peripherally because there are no central vacancies when the bird arrives seeking a territory, or because the bird simply is

not aggressive enough and/or strong enough to obtain a central site for which there is presumably more competition (due to selection for central nesting). For whatever reason a bird first acquires a peripheral territory, returning to the same site in successive years might enhance its procreative potential through the phenomenon of dominance conferred by familiarity with an area (Schjelderup-Ebbe 1935:967–968; Lorenz 1938:212; see also Tinbergen 1957:23) and by providing a place to meet the mate of the previous year. Penney (1968:120) has shown that reunited Adélies have significantly higher reproductive success than ones acquiring new mates in successive years, as Coulson (1966) found in Kittiwake Gulls (*Rissa tridactyla*). Although reproductive success is higher within the colony, the peripheral individual tending to return to the same site and same mate in successive years may produce more offspring than one wasting time and potential reproductive energy competing for a "better" territory. This possibility is enhanced by observations of marked known age Adélies. "After breeding at one site, young males returned to the site for their next breeding nearly 100 per cent of the time . . ." (Sladen et al. 1968:247). Also, I observed several Adélies at Cape Hallet that had been banded as breeding adults as early as 1961–1962 nesting in peripheral sites during the 1967–1968 nesting season. These individuals apparently did not try or were not able to move to central positions.

Penney (1968:107) marked 401 central and 324 peripheral nesting Adélies at Wilkes Station (66° 15' S, 110° 32' E), and the following year 71 per cent of the central and 76 per cent of the peripheral birds had retained their respective central or peripheral positions. (These figures are presented in Penney's table 12, but Penney did not discuss the relative proportions of central and peripheral birds returning to their nest sites of the previous year.) Penney's observations at Wilkes Station and my own at Cape Hallet suggest that peripheral nesters are no more likely than central birds to change their positions, and the assumption that the periphery contains a relatively high proportion of young breeding birds may be incorrect. Although Reid et al. (1967:142) found 13 of 18 young (three- and four-year-old) Adélies occupying peripheral positions, only three of the 18 birds were breeding. Their data can show no significant differences if only the three breeding birds are considered. Sladen et al. (1968) found that the proportion of Adélies producing at least one egg in-creased with age from 4 per cent in three-year olds to 20 per cent in four-year olds to 40 per cent in five-year olds and over 60 per cent in six-year olds.

INFLUENCE OF NEST POSITION ON REPRODUCTIVE SUCCESS

The continual movement of penguins and Skuas through intercolony spaces makes it inevitable that peripheral and isolated nesters should experience disturbing stimuli more frequently than central birds. For example, a Skua or penguin moving 2 m away has quite a different significance for a central nester than for a peripheral or isolated one. In the first case, the nesting bird is buffered from the potential intruder by intervening territories and, in any event, the intruder will probably be induced to move on by attacks from neighboring territory holders. But to a peripheral or isolated bird, a penguin or Skua 2 m away is a more serious threat. There is nothing to prevent it from focusing attention on the potential victim. Through experience and lack of a buffer effect, peripheral and isolated birds may react more strongly to the approach or proximity of predators and conspecifics than a central bird. This susceptibility to disturbance probably has direct and indirect effects that can lower the reproductive success of peripheral and isolated nesters. These include stealing of eggs and chicks by Skuas; stealing of nest stones by other penguins; loss of eggs or chicks accidentally injured or rolled from the nest by a disturbed parent; fluctuations in incubation temperatures during encounters with Skuas and other penguins; the expenditure of time and energy in attacking, fleeing, threat behavior, intention movements and displacement activities; and general disruption of parental behavior tendencies.

SUMMARY

Comparisons were made among Adélie Penguins nesting within colonies, on colony perimeters and at isolated sites entirely separated from colonies at Cape Hallet, Antarctica, in December 1967. The objective was to test the hypothesis that differences in nest location affect behavior and nesting success. Responses to the experimenter, clutch sizes, nest quality and dimensions, and responses to experimentally displaced eggs were measured late in the incubation period, after the birds had been exposed to 3.5–4.5 weeks of intraspecific disturbances and nest predation by Skuas. The following statistically significant

differences were found: peripheral nesters fled from the experimenter more often than central nesters; mean number of eggs per nest decreased from central to peripheral to isolated nests; central nests were larger, better constructed, and made of larger stones than peripheral and isolated nests; central nesters pecked experimentally displaced eggs hard enough to cause them to roll away from their nests (presumably redirected attack) more often than peripheral birds; and it took central nesters a longer time to perform the motion of rolling an egg into the nest from outside (due to higher rims in central nests). It is suggested that the differences are due, at least in part, to higher rates of nest predation and nest stone stealing at peripheral and isolated sites, and to behavioral effects resulting from more frequent disturbances at these locations.

It is further suggested that the average number of young produced per breeding pair should decrease with colony size because of increased proportions of peripheral nesters, which appear to raise fewer young because (at least in part) of detrimental effects of peripheral nesting. This seems to be a simple and readily testable alternative to the "Fraser Darling Effect" to explain the lower breeding success of small colonies of sea birds as compared with larger ones.

The hypothesis is advanced that once a male obtains a breeding territory, it may be advantageous for him to return there in subsequent years, even if the territory is peripheral. This is contrary to the apparently widespread opinion that young birds first nest peripherally and gradually move toward the center of the colony in subsequent years.

ACKNOWLEDGMENTS

LITERATURE CITED

ALLEE, W. C., A. E. EMERSON, O. PARK, T. PARK, AND K. P. SCHMIDT. 1949. Principles of animal ecology. W. B. Saunders, Philadelphia and London.

ARMSTRONG, E. A. 1947. Bird display and behaviour. Reprinted in 1965. Dover, New York.

AUSTIN, O. L. 1945. The role of longevity in successful breeding by the Common Tern (*Sterna hirundo*). Bird-Banding 16:21–28.

BARNETT, S. A. 1964. Social stress. Viewpoints Biol. 3:170–218.

BAERENDS, G. P. 1959. The ethological analysis of incubation behaviour. Ibis 101:357–368.

BASTOCK, M., D. MORRIS, AND M. MOYNIHAN. 1954. Some comments on conflict and thwarting in animals. Behaviour 6:66–84.

CHRISTIAN, J. J. 1963. The pathology of overpopulation. Milit. Med. 128:571–603.

CHRISTIAN, J. J. 1964. Physiological and pathological correlates of population density. Proc. Roy. Soc. Med. 57(3):169–174.

COULSON, J. C. 1966. The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull *Rissa tridactyla*. J. Anim. Ecol. 35:269–279.

COULSON, J. C., AND E. WHITE. 1956. A study of colonies of the Kittiwake *Rissa tridactyla* (L.). Ibis 98:63–79.

COULSON, J. C., AND E. WHITE. 1960. The effect of age and density of breeding birds on the time of breeding of the Kittiwake *Rissa tridactyla*. Ibis 102:71–86.

CROOK, J. H. 1968. The nature and function of territorial aggression. p. 141–178. *In* M. F. A. Montagu [ed.] Man and aggression. Oxford Univ. Press, New York and London.

DAVIS, D. E. 1940. Social nesting habits of the Smooth-billed Ani. Auk 57:179–218.

DARLING, F. F. 1938. Bird flocks and the breeding cycle: a contribution to the study of avian sociality. The University Press, Cambridge, England.

EKLUND, C. R. 1961. Distribution and life history studies of the South-polar Skua. Bird-Banding 32(4):187–223.

FISHER, J. 1952. A history of the Fulmar *Fulmarus* and its population problems. Ibis 94:334–354.

FISHER, J., AND R. M. LOCKLEY. 1954. Sea-birds. Houghton Mifflin, Boston.

FISHER, J., AND H. G. VEVERS. 1944. The breeding distribution, history and population of the North Atlantic Gannet (*Sula bassana*), Part 2. J. Anim. Ecol. 13:49–62.

FISHER, J., AND G. WATERSTON. 1941. The breeding distribution, history and population of the Fulmar (*Fulmarus glacialis*) in the British Isles. J. Anim. Ecol. 10:204–272.

HAARTMAN, L. VON. 1945. Zur Biologie der Wasser- und Ufervögel im Schärenmeer Südwest-Finnlands. Acta Zool. Fennica 44:1–120.

HUTCHINSON, G. E. 1953. The concept of pattern in ecology. Proc. Acad. Nat. Sci. Philadelphia 105:1–12.

KLOPFER, P. H., AND J. P. HAILMAN. 1967. An introduction to animal behavior. Prentice-Hall, Englewood Cliffs, New Jersey.

LACK, D. 1943. Fisher and Waterston on the Fulmar. Ibis 85:115–116.

LACK, D. 1954. The natural regulation of animal numbers. Reprinted in 1967. Oxford Univ. Press, London.

LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

LEVICK, G. M. 1914. Antarctic penguins: a study of their social habits. William Heinemann, London.

LEVICK, G. M. 1915. Natural history of the Adelie Penguin. Brit. Antarctic ("Terra Nova") Exped., 1910. Nat. Hist. Rep. Zool. 1(2):55–84.

LORENZ, K. Z. 1938. A contribution to the comparative sociology of colonial-nesting birds. Proc. Eighth Int. Ornithol. Congr., Oxford. p. 207–218.

MAHER, W. J. 1966. Predation's impact on penguins. Nat. Hist. 75(1):42–51.

MÜLLER-SCHWARZE, D. 1968. Circadian rhythms of activity in the Adélie Penguin (*Pygoscelis adeliae*) during the austral summer. p. 133–149. *In* O. L. Austin [ed.] Antarctic bird studies. Amer. Geophys. U., Washington, D.C.

MURPHY, R. C. 1936. Oceanic birds of South America. Vol. I. Macmillan, New York.

ORIANS, G. H. 1961. Social stimulation within blackbird colonies. Condor 63:330–337.

PATTERSON, I. J. 1965. Timing and spacing of broods in the Black-headed Gull *Larus ridibundus*. Ibis 107(4):433–459.

PENNEY, R. L. 1968. Territorial and social behavior in the Adélie Penguin. p. 83–131. *In* O. L. Austin [ed.] Antarctic bird studies. Amer. Geophys. U., Washington, D.C.

POULSEN, H. 1953. A study of incubation responses and some other behaviour patterns in birds. Videns. Medd. Dansk Naturh. Foren. 115:1–139.

REID, B. E. 1964. The Cape Hallet Adelie Penguin rookery—its size, composition, and structure. Rec. Dominion Mus. 5:11–37.

REID, B. E., F. C. KINSKY, H. J. CRANFIELD, AND R. C. WOOD. 1967. Notes on recoveries and breeding behaviour of Adelie Penguins of known age at Cape Hallet. Notornis 14(3):140–143.

RICHDALE, L. E. 1951. Sexual behavior in penguins. Univ. Kansas Press, Lawrence.

ROBERTS, B. 1940. The breeding behaviour of penguins with special reference to *Pygoscelis papua* (Forster). Sci. Rep. Brit. Graham Land Exped. 1934–1937 (London) 1(3):195–254.

SCHJELDERUP-EBBE, T. 1935. Social behavior of birds. p. 947–972. *In* C. Murchison [ed.] A handbook of social psychology. Clark Univ. Press, Worcester, Mass.

SLADEN, W. J. L. 1958. The pygoscelid penguins. I. Methods of study. II. The Adélie Penguin *Pygoscelis adeliae* (Hombron and Jacquinot). Sci. Rep. Falkland Is. Dependencies Surv. 17:1–97.

SLADEN, W. J. L., R. E. LERESCHE, AND R. C. WOOD. 1968. Antarctic avian population studies, 1967–1968. Antarctic J. U.S. 3:247–249.

TAYLOR, R. H. 1962. The Adelie Penguin *Pygoscelis adeliae* at Cape Royds. Ibis 104:176–204.

TINBERGEN, N. 1952. A review of L. E. Richdale's book *Sexual Behavior in Penguins*. Ibis 94:178–180.

TINBERGEN, N. 1957. Functions of territory. Bird Study 4(1):14–27.

TINBERGEN, N. 1967. Adaptive features of the Black-headed Gull *Larus ridibundus* L. Proc. XIV Int. Ornithol. Congr., Oxford. p. 43–59.