SOCIAL ORGANISATION OF THE ADELIE PENGUIN,
Pygoscelis adeliae.

A thesis presented for the degree of
Doctor of Philosophy in Zoology
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University of Canterbury,
Christchurch, New Zealand.

by

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1.0 INTRODUCTION

1.1 AIMS OF THE STUDY

This study forms part of a comprehensive programme, under the supervision of Dr E.C. Young, of the University of Canterbury*, investigating the relation between the skua, *Catharacta maccormicki*, and the Adelie penguin, *Pygoscelis adeliae*, (Young 1970).

Within this framework, the purpose of the present study was to investigate intra-specific relationships within a population of Adelie penguins at their breeding area (Young op. cit.:583).

Adelie penguins breed in dense colonies on the ice-free shores of the Antarctic continent and off-shore islands during the brief austral summer. In the space of four months, these penguins may establish a territory and nest site, claim a mate, produce a clutch of one or two eggs, take turns at incubation, and provide food and protection for the rapidly developing chicks.

The colonies are not simply groupings of breeding penguins, but are organised into over-dispersed nesting territories. This study investigates mechanisms of dispersion and patterns of organisation within the breeding colonies. For this purpose, it was necessary to describe behavioural interactions in more detail than in previous studies (e.g. Sladen 1958, Sapin-Jaloustre 1960, Penney 1968).

1.2 STUDY AREA

This study was undertaken at the University of Canterbury field station, situated in the Northern Rookery, Cape Bird, Ross Island, Antarctica (77°13'10"S, 166°28'30"E) during four austral summers (1967-68, 1968-69, 1969-70, 1970-71). At Cape Bird there are three breeding rookeries of Adelie penguins. The Northern and Southern Rookeries, separated by about 7 kilometres, are both middle-sized

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rookeries, but the Middle Rookery is only small (Taylor 1964). The rookeries are situated on raised beaches and deposited moraines on the north-western side of Mt Bird. The Northern Rookery is about 5 kilometres south of the cape.

Throughout the winter, the rookeries are closed in by the annual McMurdo Sound sea-ice. The breakup of this sea-ice in spring is vitally important for the survival of the penguins (Stonehouse 1967a). The rookeries are mostly free of snow before (or very soon after) the penguins first arrive in mid-October. Throughout the summer the area is characterised by comparatively mild temperatures and little wind. Weather records (kept as part of the daily routine of the station) are being summarised by Young (pers. comm.).

1.3 METHODS OF STUDY

The study has involved many hours of direct observation. Most observations were made from a hide or from a three-metre step-ladder. Hides were situated on slopes overlooking the study colonies. The step-ladder was necessary where study colonies occurred on flat ground with no nearby slopes. Observations were aided by the use of 10 x 50 binoculars.

The numbers of adults, nests, eggs, and chicks in the study colonies were recorded on colony maps. The positions of nests and topographic features (such as rocks) were mapped by a series of tape measure transects, and also from photographs taken two metres above the colonies. Individual nests were identified from the maps.

Methods used in specific sections of the study are included in the appropriate sections.

1.4 BANDING

Methods of marking penguins are summarised in the literature (e.g. Sladen et al. 1968, Sladen & LeResche 1970). In this study, penguins were fitted with aluminium alloy flipper bands. The bands were issued by the U.S. Fish and Wildlife Service, and kindly supplied by Dr W.J.L. Sladen of the USARP Bird Banding Program. In four seasons, 752 adult penguins were banded.

No attempt was made to band all penguins in the study colonies. Only penguins that could be captured without undue disturbance were banded. Penguins at nests without eggs were caught by the leg with a crook, and pulled out of the colony for banding. Incubating penguins could be banded on the nest site by lifting the tail, causing the penguin to dig its bill into the ground and spread the flippers. The methods used were considered to cause the minimum of disturbance.

1.5 SEX DETERMINATION

Adelie penguins are monomorphic, and cannot readily be sexed by external morphological features. No dissections were made in this study. The sexes of the study penguins were determined by individual marking and detailed observation of their behaviour.

Sladen (1958:23) and Penney (1968:88) discuss several behavioural criteria for sexing penguins. The most reliable appears to be the copulatory position (where the male is uppermost). No instances of reversed copulatory position were observed in the present study. In reported instances of reversed copulatory position in several species of penguins (Roberts 1940:208, Richdale 1941:49, Taylor 1962:182) coition was not achieved and the copulatory behaviour was erratic. At Cape Bird, males were observed attempting to mount other males, but they were never successful.

The sex of most study penguins was determined either by observed copulation, or by their pairing with another penguin of known sex. Some penguins were observed in copulation many times. Where copulation was not witnessed, combinations of other criteria were used to provide a tentative indication of sex. Males generally returned first and established the territory; they persistently performed the Ecstatic display (described in section 3.4) in the absence of females in the occupation period; and they usually took the first incubation watch. These criteria are not infallible, because they may occasionally be true for females. However, when such criteria are combined with an intimate knowledge of the birds concerned, their reliability can usually be judged.

Sex could not be inferred from tread marks because these did not show on the backs of females at Cape Bird, owing to the generally dry ground.

Females usually had a dilated cloaca after laying an egg. The weights of males and females over-lapped, but when a pair was weighed immediately after egg-laying the female was always the lighter of the two. Females were usually, but not always, lighter at other stages in the breeding season.

A "cloacascope" (Sladen & LeResche 1970:587) was not used successfully in this study. The design tried was unsatisfactory, and the technique was not pursued because of the disturbance caused by handling the penguins.

1.6 THE STUDY BIRDS

It was not possible to work with penguins of known age. Penguins cannot be aged by morphological criteria after the first year of life, and none were available that had been banded as chicks.

Sladen (1958:25) suggested a classification of age groups based on both behavioural and morphological data, as follows:

i. Established (experienced) breeders, three to five years old and over; mostly four years old and over.

ii. Unestablished (inexperienced) breeders, two to four years old; mostly three years old.

iii. Non-breeders ("Wanderers") in adult plumage, two to three years old; mostly two years old.

iv. Non-breeders ("Wanderers") in immature plumage (Yearlings); from leaving the rookery until they moult into adult plumage when about fifteen months old.

v. Nestlings (Chicks); up to the time when they leave the rookery, nearly two months after hatching.

In the present study, adult penguins in any one season were classified as follows:

i. mated penguins, that produced eggs; these were sub-divided into
    (a) successful breeders, when they raised chicks to independence,
    (b) unsuccessful breeders, when they lost all their eggs or chicks.

ii. unmated penguins, that occupied territories but did not produce eggs; these unmated penguins may be alone or keeping company with another penguin.

The term non-breeder is reserved for penguins that remain at sea away from the rookeries throughout the breeding season, or only visit the rookeries as "wanderers". In the transition from non-breeder to breeder, penguins become attached to a particular territory and nest site for at least part of the breeding season. However, the division between the two categories is not sharply defined.

Successful and unsuccessful breeders are more or less synonymous with established and unestablished breeders respectively. The observations of LeResche & Sladen (1970:526) would indicate the extension of unestablished breeders to six or even seven years of age.

1.7 SPECIES MENTIONED IN TEXT

Except for the first time mentioned in the text, species are given common names only. A full list of common and scientific names is given below.

Penguins

Adelie penguin	*Pygoscelis adeliae*
Gentoo penguin	*Pygoscelis papua*
Chinstrap penguin	*Pygoscelis antarctica*
Emperor penguin	*Aptenodytes forsteri*
King penguin	*Aptenodytes patagonica*
Yellow-eyed penguin	*Megadyptes antipodes*
Erect-crested penguin	*Eudyptes sclateri*
Macaroni penguin	*Eudyptes chrysolophus chrysolophus*
Royal penguin	*Eudyptes chrysolophus schlegeli*
Rockhopper penguin	*Eudyptes chrysocome*
African penguin	*Spheniscus demersus*
Magellanic penguin	*Spheniscus magellanicus*
Little Blue penguin	*Eudyptula minor*

Other Birds

Skua	*Catharacta maccormicki*
Abbott's Booby	*Sula abbotti*
Ring dove	*Streptopelia risoria*
Chaffinch	*Fringilla coelebs*

Mammals

Leopard seal	*Hydrurga leptonyx*

1.8 GLOSSARY OF TERMS

Definitions or explanations of the following terms may be found in the sections indicated below:

Age and Breeding Status	Section
successful breeder	1.6
unsuccessful breeder	1.6
mated penguin	1.6
unmated penguin	1.6
non-breeder	1.6
"wanderer"	1.6
Territory	
central territory	2.2
peripheral territory	2.2
isolated territory	2.2
nest	2.1
inter-nest distance	2.3
individual distance	10.2
colony	2.1
rookery	2.1
Breeding cycle	
occupation period	4.1
incubation period	4.1
chick period	4.1
reoccupation period	4.1
guard stage	8.2
creche or post-guard stage	8.2
Behaviour	
display	3.1
elementary act	3.1
intention movement	9.9
motivation	9.9
ritualisation	9.9
neighbour	9.2
stranger	9.2

1.9 ORGANISATION OF THE THESIS

The thesis is divided into a number of sections, each of which is a complete entity. Each section has an introduction, and where appropriate, a discussion at the close. A final discussion is presented at the end of the thesis, followed by collective section summaries.

2.0 TERRITORY

2.1 INTRODUCTION

The territory of the Adelie penguin conforms to the "defended area" type (Etkin 1964:23) where, as in some other marine birds (e.g. gulls, guillemots, terns, and gannets), the small nesting territory is vigorously and constantly defended against intruders. A penguin's nest consists of a small hollow scraped in the ground and lined with stones. The territory consists of the nest together with a small area around about that is defended by the owner.

Most Adelie penguins breed in colonies, which consist of groups of nesting territories with contiguous boundaries. Very few penguins breed at isolated territories. All the colonies (and isolated penguins) within a defined geographical area form a rookery. Colonies vary in size and shape, and contain anything from a few territories to several thousand. Some territories occur on flat ground, with few obstructions. Others are built on slopes, ridges, or rocky areas.

Penney (1968:95) has already provided some data on the physical dimensions of Adelie penguin territories. In this section, a further examination is made.

2.2 CLASSIFICATION OF TERRITORIES

Territories may be classified as either

i. central, if at all times through the season there is at least one territory between them and the outside of the colony.
ii. peripheral, if at any stage of the season they are exposed at the colony edge.
iii. isolated, if they occur outside a colony and have no boundary contiguous with other territories.

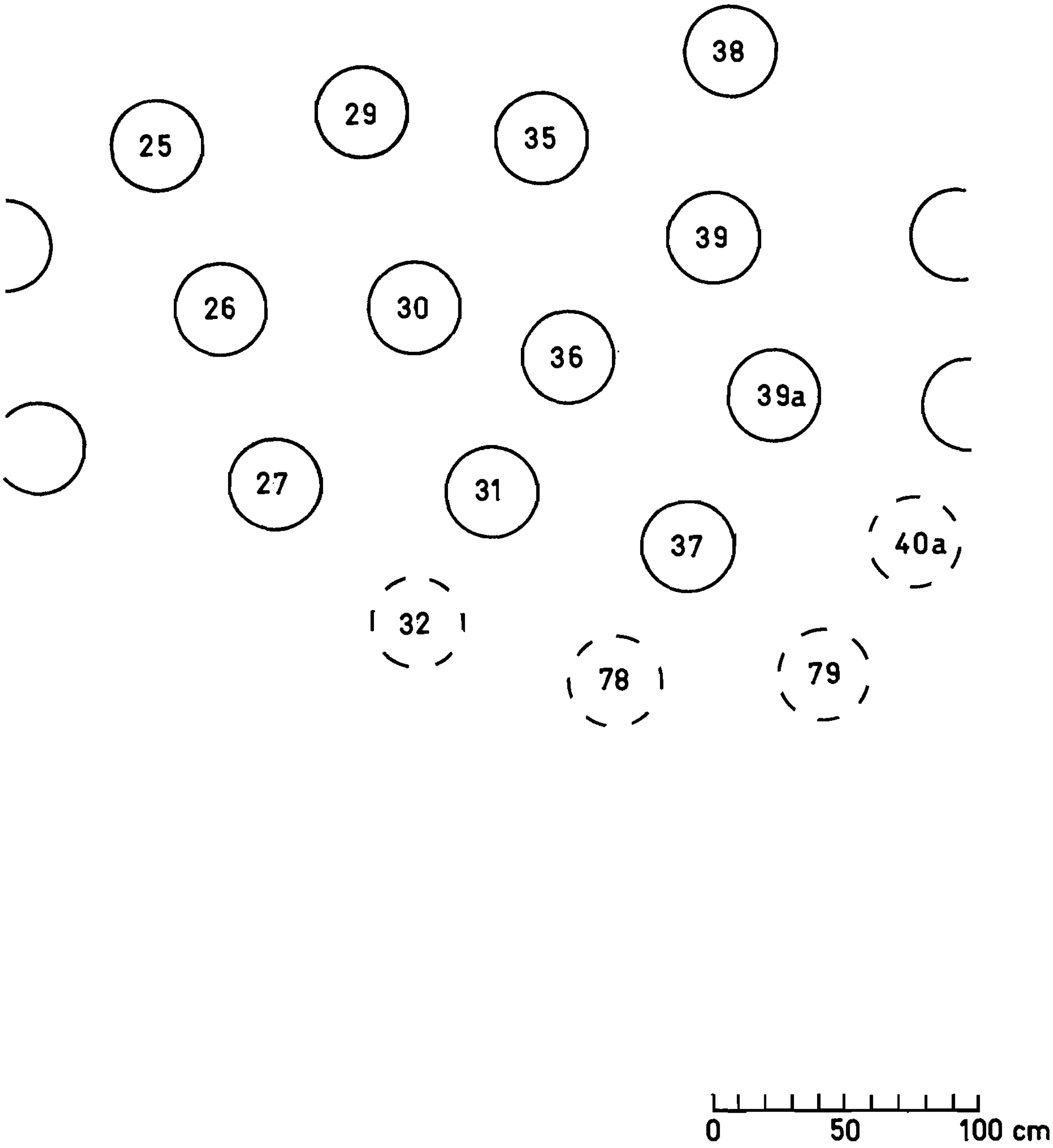
This classification is similar to but slightly more specific than that used by Penney (1968:96). Thus, in figure 1, nests 30 and 36 are central, whereas nests 31 and 37 are peripheral.

The size and shape of a colony influence the number of peripheral territories (see also Tenaza 1971:85). Small and

FIGURE 1. Neighbours of penguins at nests 30, 31, 36, 37.

Complete circles represent nests occupied throughout the season.

Incomplete circles represent nests occupied for chick period only.


38
29
25
35
39
26
30
36
39a
27
31
37
40a
32
78
79
0
50
100 cm

linear colonies have proportionately more peripheral territories than large circular colonies.

2.3 DIMENSIONS AND ARRANGEMENT OF TERRITORIES

Territory boundaries could be determined only from behavioural observations. However, the distance between nest centres (inter-nest distances) could be measured from scaled photographs (see section 1.3). The accuracy of measurements was determined by comparison with fixed objects. Wherever possible natural objects (such as rocks) were used. However, small wooden markers (2 cm square) that protruded no more than 2 cm, were inserted in some areas where the ground was uniform.

The minimum distances between nest centres in one study colony averaged 70 cm, and ranged from 52 cm upwards. Most nest centres were spaced between 65 and 75 cm apart, with very few more than 80 cm apart. It was estimated that a penguin with its feet in the centre of its territory, could reach out to 40 - 44 cm from the centre. Thus, most penguins were within the pecking range of at least one other penguin.

On the average, peripheral nests were spaced no further apart than nests in the centre of a colony. The mean distance to the two nearest neighbours was 75.5 cm for peripheral nests and 70.5 cm for central nests, but the difference is not significant ($p > 0.05$, t-test).

Differences in terrain influenced the size and spacing of territories to some extent. In colonies situated on uneven terrain or among large rocks, the distance between nest centres may be greater than in colonies on uniform, flat ground (see also Penney 1968:95).

Nests on flat ground in the densest parts of colonies tended to be arranged in a hexagonal pattern, so that each penguin had six neighbours within pecking distance (see figure 1, nests 30 and 36). Such an arrangement often resulted in the formation of rows of nests, with lanes between the rows. This orderly pattern tended to break down when nests were not densely packed, either because of the presence of rocks, or because of gaps created by unoccupied nest sites. Thus, some central nests may have only four neighbours.

Peripheral nests usually have between one and three neighbours, depending on the degree of exposure to the outside.

The number of neighbours also depends on the time of season. A penguin that has three neighbours while it is exposed to the periphery during late incubation, may have four or five neighbours during the chick period. Thus, nest 37 (in figure 1) had three neighbours on 7 December 1968, but six neighbours on 8 January 1969.

2.4 STABILITY OF TERRITORY LOCATION THROUGH THE SEASON

Individual nest sites (and their surrounding territories) did not always remain in exactly the same location throughout the season. Many changes were small and without obvious cause. They were possibly an incidental result of the continual rearranging of nest stones which occurred right throughout the summer. The location of a nest could be altered simply by taking stones away from one side of the nest, placing them more to the other side, and re-scraping the hollow.

Major changes of nest location usually resulted when a new territory was established between two or more already existing territories, as in the example shown in figure 2. Nest 61 was originally occupied by a pair of successful breeders. On 25 December, it was taken over by a penguin that had not produced eggs that summer. The previous occupants did not build another nest, but guarded their chicks at location 61a. This caused 55 and 47, both guarding chicks, to shift their nests. These shifts were of comparatively large distances (table 1).

Several instances were observed in which exposed peripheral penguins moved closer to other penguins after egg laying. These penguins originally had only one neighbour, but by moving in and along the periphery obtained two or three neighbours. This behaviour increased the colony density and decreased the peripheral area. It also gave more protection to the penguins concerned, by exposing less of their periphery to the outside of the colony.

Changes of nest location occurred most frequently on uniform, flat ground (as in figure 2). Where a colony was scattered with prominent rocks (as in figure 3), nests tended to remain in much the same position through the season. New penguins could not squeeze in between established territories because the existing nest locations could not readily be shifted. Any changes of nest location that did occur were only minor.

FIGURE 2. Location of nests through the season on uniform terrain.

Complete circles represent nest sites 31 December 1970.

Incomplete circles represent nest sites 16 December 1970.

Small black squares represent wooden nest markers.

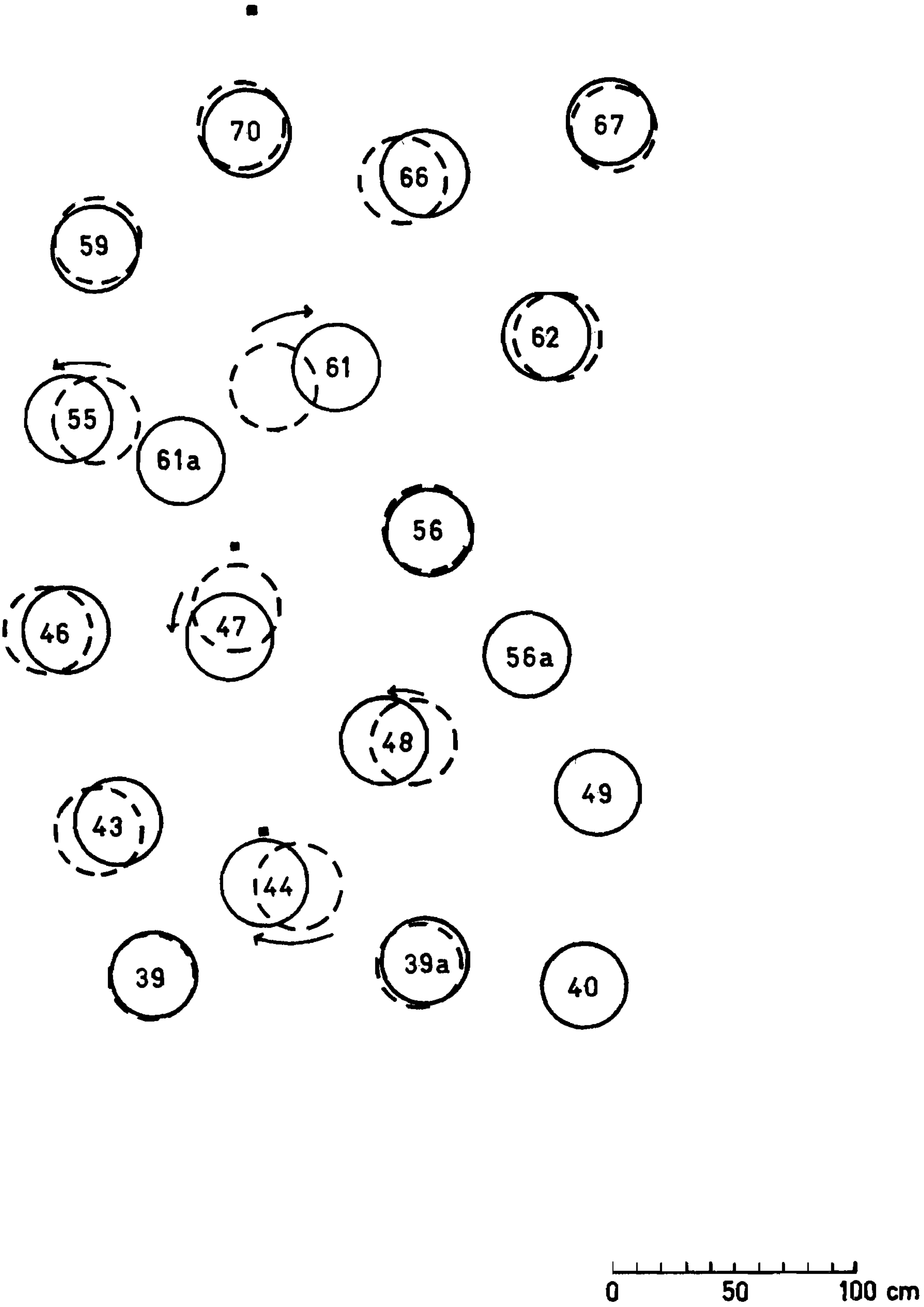

70
66
67
59
62
61
55
61a
56
46
47
56a
48
49
43
144
39
39a
40
0
50
100 cm

FIGURE 3. Location of nests through the season on rocky terrain.

Complete circles represent nest sites 31 December 1970.

Incomplete circles represent nest sites 16 December 1970.

Black patches represent rocks scattered in colony.

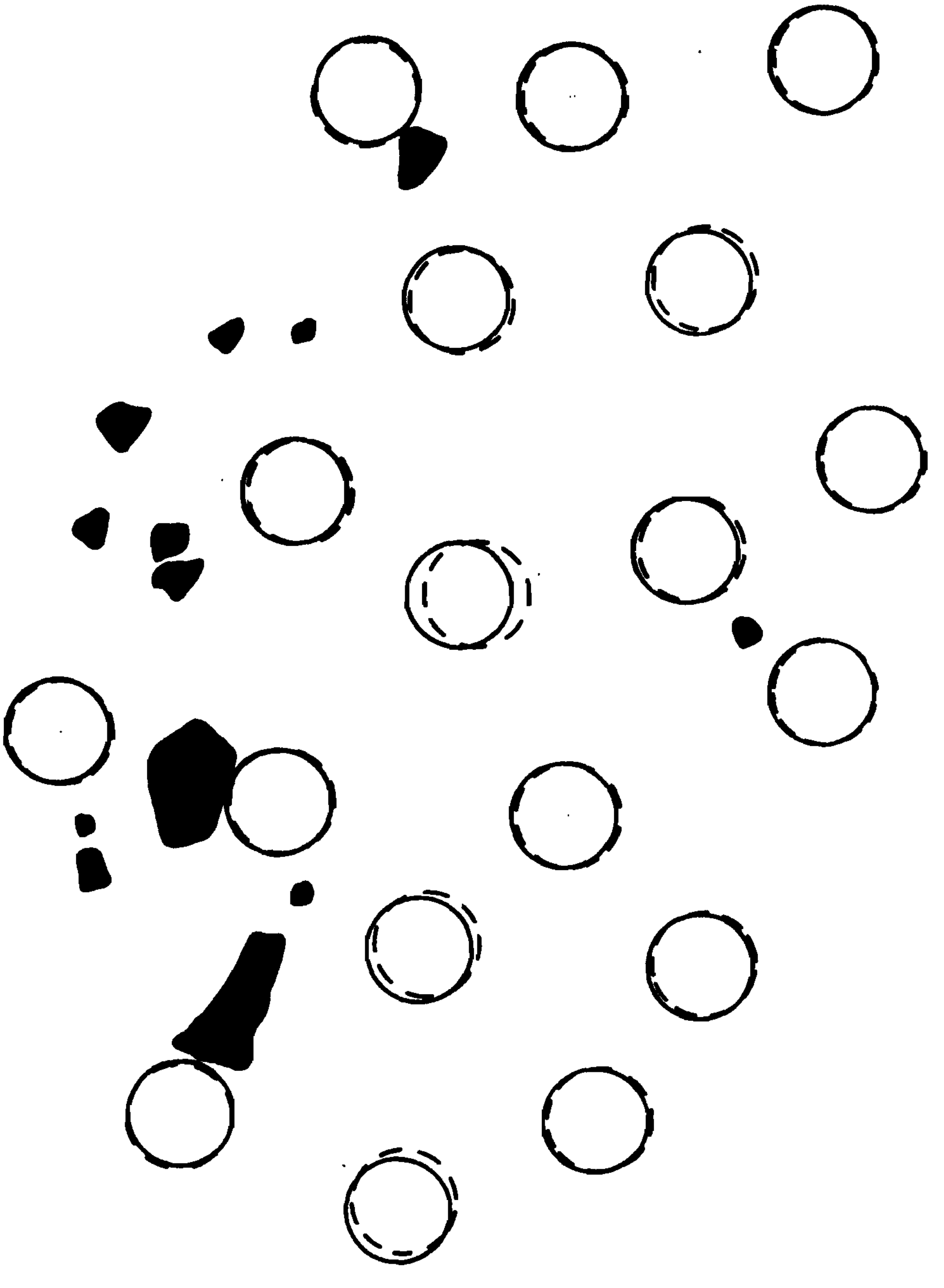

0
50
100 cm

TABLE 1. Seasonal Change of Nest Location on Uniform Terrain

Nest Number	Distance shifted (in cm) 16 - 31 December
39	1.0
40	3.0
43	9.0
44	14.0
46	7.5
47	12.0
48	12.0
55	11.0
56	2.0
59	3.5
61	27.0
62	5.0
67	9.0
68	3.0
70	4.0

2.5 LOCATION OF TERRITORIES IN DIFFERENT SEASONS

At the end of each breeding season, the nests become flattened, the hollows partly filled in, and the stones scattered. At the beginning of the next season there may still be small depressions in the guano indicating where previous nest sites have been, but sometimes it is difficult to distinguish between them and the hollows of former inter-nest spaces.

The actual location of nest sites established by the same pairs in different seasons often depends on the terrain. Where a colony was scattered with prominent rocks, nests beside these usually remained in the same scrape (figure 4). Where there was an unbroken flat surface, however, nest locations sometimes varied considerably (figure 5), though the pattern of nests may have appeared similar.

2.6 AVAILABILITY OF TERRITORIES

There are many areas apparently suitable for nesting that are not used. The penguins are thus not being forced to nest close together because of a shortage of nesting sites. It seems that they "choose" to nest close together.

While there is not a shortage in the total nesting area, there is a limited number of sites available for nesting in the centre of colonies. Thus, unless there is a vacant central site, newcomers can establish themselves only at the colony periphery, or at isolated sites.

2.7 SUITABILITY OF TERRITORIES

Not all territories are equally suitable for reproduction. Isolated territories can be approached from all directions without the intruder coming within the pecking range of neighbours. Peripheral territories can usually be approached from one side, but central territories cannot be approached from any direction without the intruder coming within the pecking range of penguins on neighbouring territories. Thus, nests in the centre of a colony are less disturbed than those at the periphery.

In a series of 10 minute observations on individual

FIGURE 4. Location of nests in consecutive seasons on rocky terrain.

Complete circles represent nest sites 1970-71.

Incomplete circles represent nest sites 1969-70.

Black patches represent rocks scattered in colony.

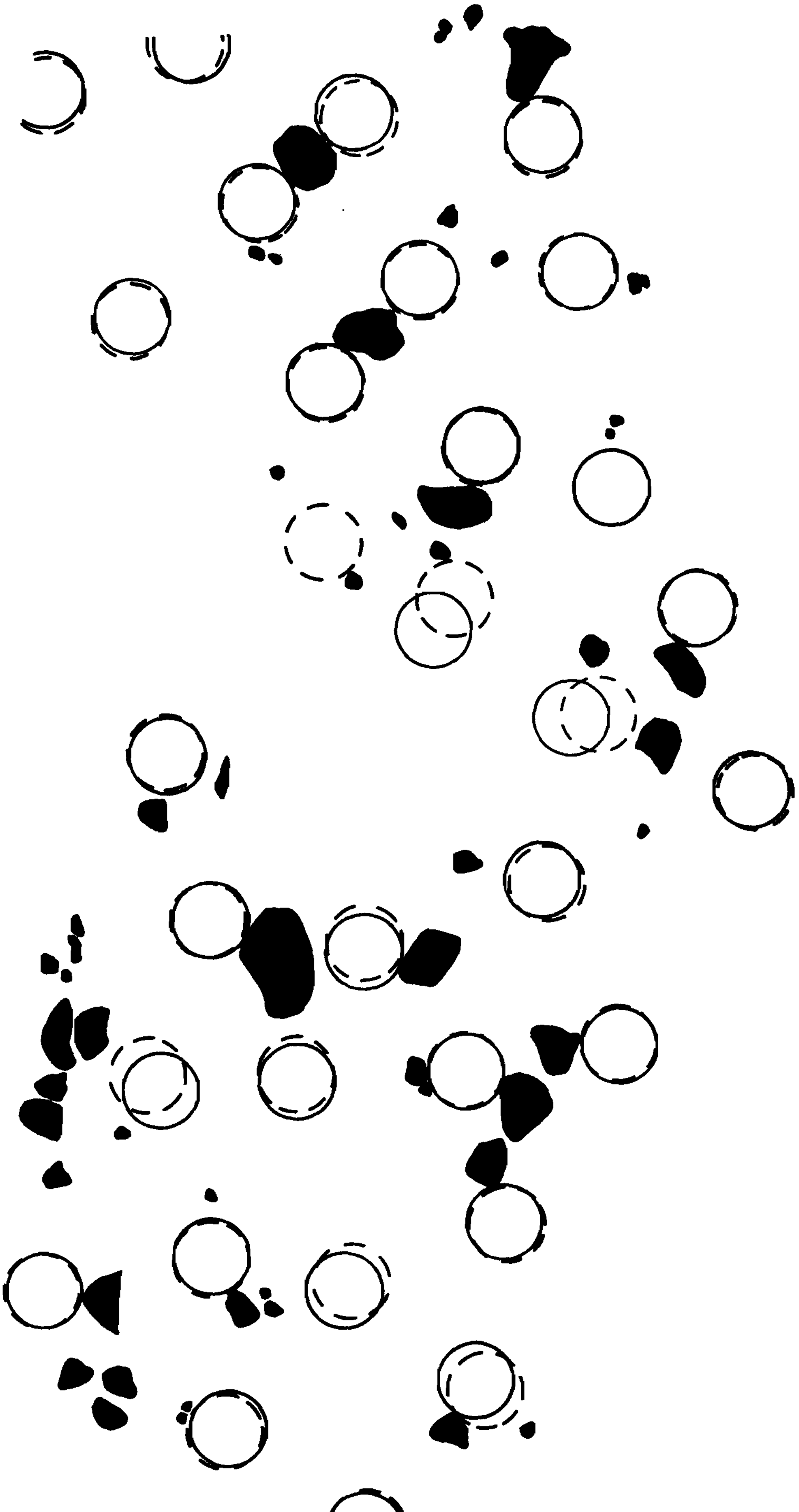
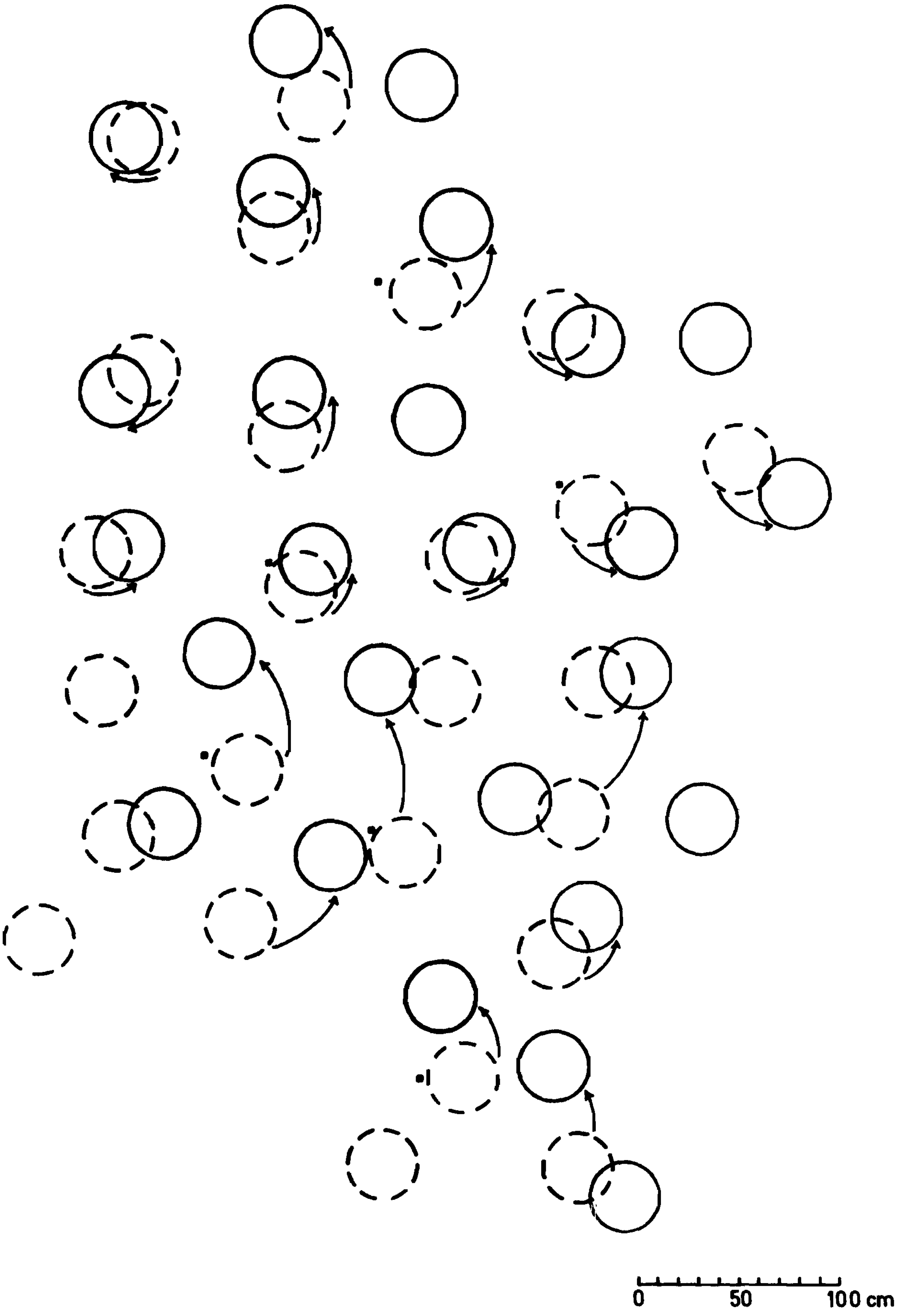

0
50
100 cm

FIGURE 5. Location of nests in consecutive seasons on uniform terrain.

Complete circles represent nest sites 1970-71.
Incomplete circles represent nest sites 1969-70.
Small black squares represent wooden nest markers.


0
50
100 cm

nests, a larger number of intruders passed by the boundary of peripheral territories than central territories (table 2). Some of these peripheral passers-by were resident further in towards the centre of the colony, others were attempting to steal nest stones, while others were complete strangers passing to and from other colonies.

Territories in the centre of a colony were also subject to a lower incidence of skua predation (see section 7.8iv) because skuas could approach them less readily than peripheral or isolated territories.

Thus, of the five specific functions of Adelie penguin territories recognised by Penney (1968:125), only the second and third would appear to differ for territories at the periphery and centre of a colony. That is, peripheral territories appear to provide less protection for undisturbed reproductive behaviour, and less protection for the eggs and chicks.

Access to central territories was more difficult for residents as well as for intruders and predators. Of penguins returning to relieve their mates from nest duty at nests more than six places in from the periphery, only 18 percent were able to return directly to the nest at the first attempt (table 3). Penguins returning to peripheral nests were able to reach them directly on the first attempt 70 percent of the time. The effort required to find a nest in the centre of a colony has been reduced by the evolution of behaviour that quickly identifies individual penguins (see also section 3.4iii). Most penguins quickly recognise their mistakes, and move away from wrong nests.

2.8 DISCUSSION

The structure of Adelie penguin colonies is influenced by topography and population density. In high density colonies, on uniform terrain where topography is unimportant, territory boundaries are determined by behavioural phenomena alone (see also Grant 1968). In this situation, individual territories tend to be arranged in a hexagonal pattern, which represents maximum use of the nesting area. Territory size corresponds to the area that can be defended while a penguin is confined to its nest, as it is during incubation. Territories are

TABLE 2. Number of Intruders Passing by Central and Peripheral Sites

	Centre	Periphery
Number of 10 minute observations	70	181
Number of penguins passing by	25	269
Average passers-by per observation	0.36	1.49

2 x 2 chi square, p = < 0.001

TABLE 3. Number of Penguins Returning Directly to Nests

Nest distance from periphery	Total observed	Penguins reaching nest directly number	Penguins reaching nest directly percent
at periphery	10	7	70
< 3 nests in	69	47	64
3-6 nests in	61	20	33
> 6 nests in	28	5	18

established, however, prior to egg-laying, when penguins could defend a larger area. There is no shortage of area apparently suitable for nesting, so that penguins could establish themselves away from one another, yet most set up a territory within pecking range of other penguins. Thus, territory size is quite constant, so that the density of colonies is much less variable than size or shape.

Topographical landmarks (such as rocks) sometimes dictate the location of territories, causing them to remain in much the same position from season to season, even when occupied by different penguins. In the absence of landmarks, territories may be located in different positions in subsequent seasons, but behavioural factors maintain the relative uniformity of colony spacing. Site tenacity (or the retention of sites by the same penguins in different seasons) is considered more fully elsewhere (section 6.2) but it also is markedly affected by landmarks.

From a physical viewpoint, colonial breeding has the advantage of providing protection from intruders and predators of nest contents. Territories in the centre of a colony are more protected than those at the periphery, but any colonial territory is more protected than an isolated one. This protection affects the breeding success at the different localities (see section 7.8iv).

Each territory is just large enough to accommodate two adults and their chicks, and to allow them to perform various activities. Any encroachment of this minimum area is strongly resisted. Nevertheless, penguins fight strongly to obtain (and retain) a site close to others. Having obtained a site, a penguin has the advantage of dominance over intruders (see section 9.4). Dominance behaviour, and the isolation of aggressive individuals on separate territories, reduces the amount of fighting. Nevertheless, colonial breeding in the Adelie penguin is associated with a high level of aggression. This topic is further discussed elsewhere (section 11.0).

3.0 BEHAVIOUR ASSOCIATED WITH TERRITORY

3.1 INTRODUCTION

The behaviour of an animal may be divided conveniently into two groups (Marler 1956a:3). The first group consists of elementary acts, such as walking, feeding, copulating, and fighting. Elementary acts apparently have no special signal function, but may "communicate" in the sense of showing what an animal is doing. The second group consists of displays. These are postures, movements, and vocalisations that have acquired a special signal function in social communication.

Adelie penguin behaviour has been described several times (e.g. Sladen 1958, Sapin-Jaloustre 1960, Penney 1968), but is described again to bring out the salient features emphasised in this study.

When making the original descriptions of behaviour, no presumptions were made concerning the signal content of the different acts. This was determined later by analysis. An act may be called a display only if it conveys a signal to another animal, and if it seems to be specially adapted for that function (see section 9.0).

3.2 ELEMENTARY ACTS

Only some of the more common elementary acts are described in this section.

i. Rest

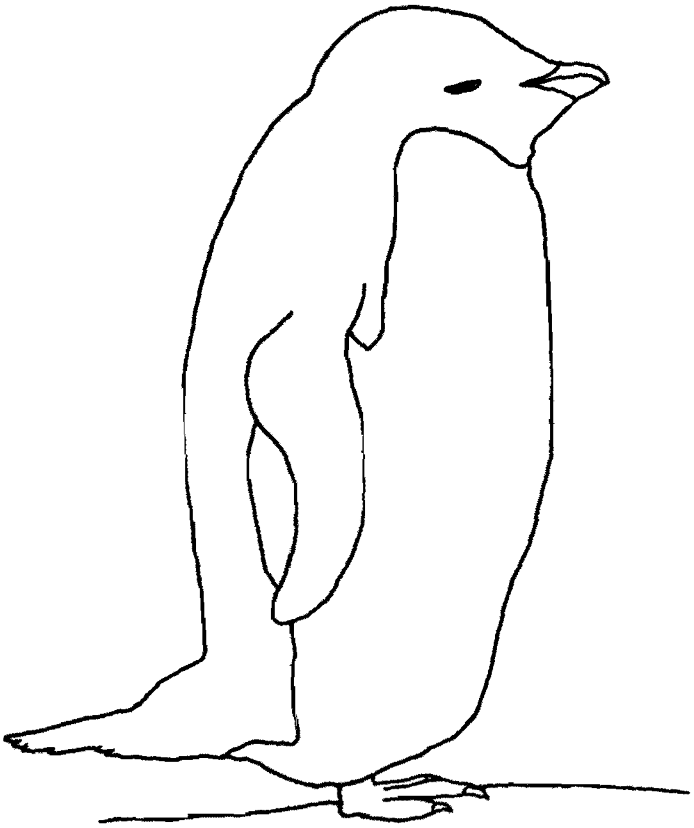
Penguins rest standing or lying down (figure 6). The neck is withdrawn, the head usually faces directly to the front, and the bill is held approximately horizontal. The feathers are relaxed and the flippers usually remain by the side of the body (see also section 9.4). The eyes are closed only when sleeping. Penguins sometimes sleep (standing or lying) with the head turned sideways over one shoulder and the bill tucked under or near one flipper.

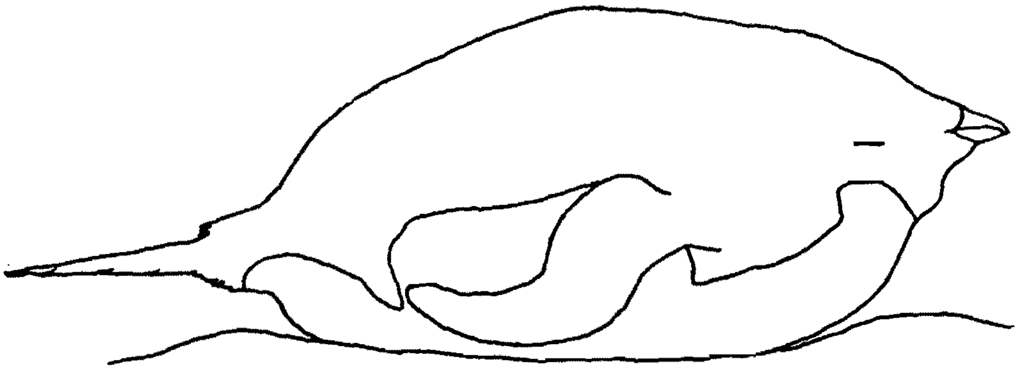
ii. Comfort Activities

Comfort activities are not described in detail. These

FIGURE 6. Resting postures,

(a, upper) standing up.
(b, lower) lying down.





activities include preening, stretching, yawning, scratching, and shaking (all or part of the body, such as head shaking or tail shaking). These activities occur both on and away from the territories (see also Sladen 1958:44).

iii. Walking

Penguins walk in an upright posture. When walking over relatively flat ground,as from the shore to the colonies, or between colonies, the neck is withdrawn, the bill held approximately horizontal, and the feathers relaxed. The flippers are usually held away from the body (figure 7).

The posture is more slender when penguins walk through a colony and encounter the boundaries of occupied territories (figure 8). This is because the neck is extended, the bill held above horizontal, and the feathers, especially of the head and neck, are sleeked. The flippers are usually held out from the body, and may be raised above the back. The degree of feather sleeking and the extension of the neck varies with the situation. Where there are large inter-nest spaces, the posture may be little different from walking outside the colonies. When a penguin is walking between tightly spaced nests, however, the feathers may be strongly sleeked and the head held high in the air. Warham (1963:251) used the term "slender walk" to describe the behaviour of Rockhopper penguins (Eudyptes chrysocome) walking through their colonies. The posture is slightly different in the two species (of different genera) but the function is the same (see also section 9.5).

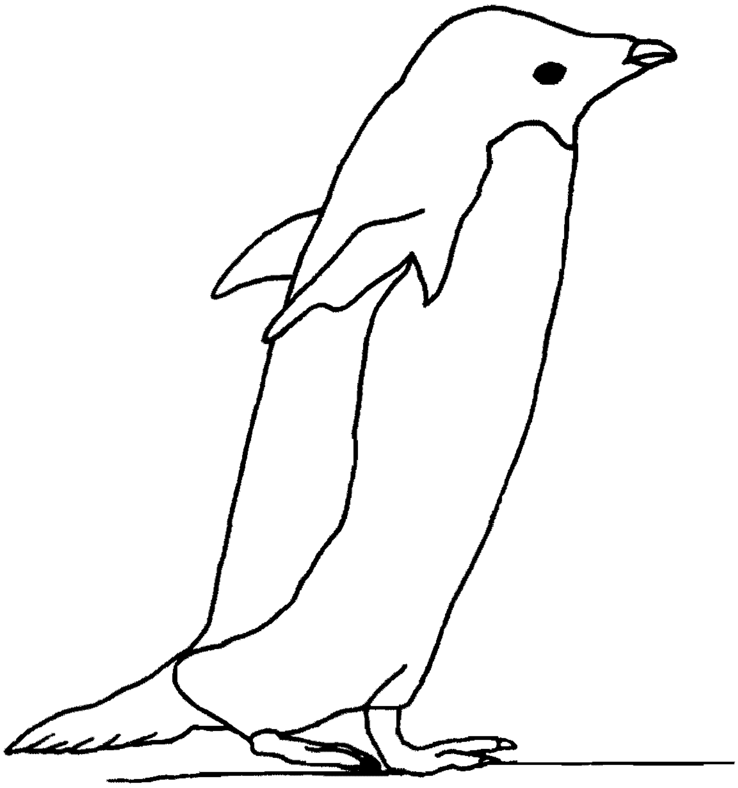
iv. Looking Around

Penguins walking either within or outside a colony often pause to look around (figure 9a). The feathers remain slightly sleeked, the neck is extended, and the head turned to look at the surroundings.

A penguin on a territory may also look around when disturbed by mild activities nearby. This behaviour may be accompanied by erection or partial erection of the feathers of the occipital crest (figure 9b). The feathers may be erected only temporarily, or may remain erected for some time. The eyes are rolled (see section 9.7) only when a penguin is looking around after displaying (to mate or intruder). When a penguin is startled, the crest feathers may be sleeked rather than

FIGURE 7. Walking.

FIGURE 8. Slender walk.



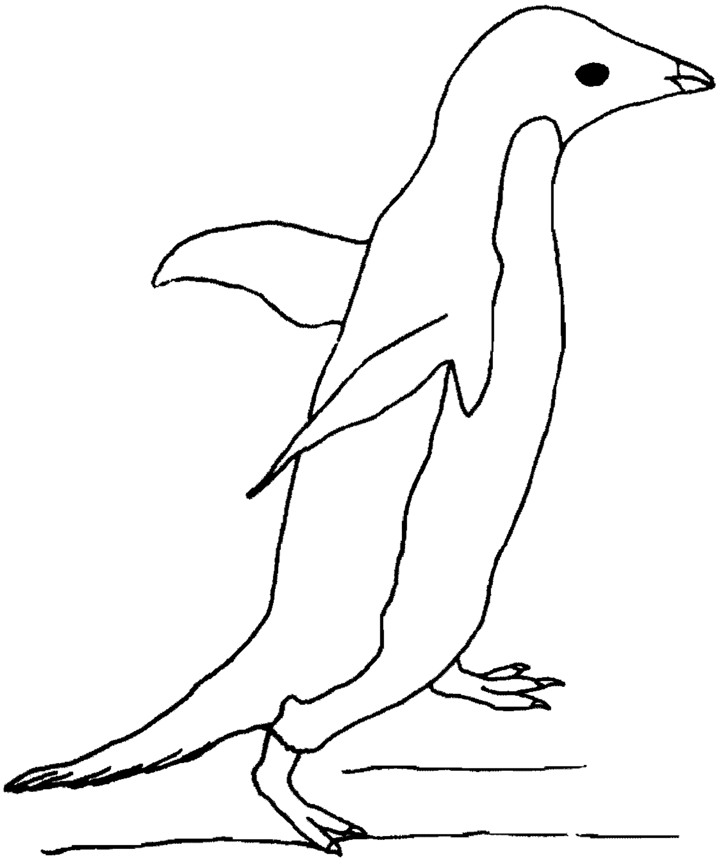
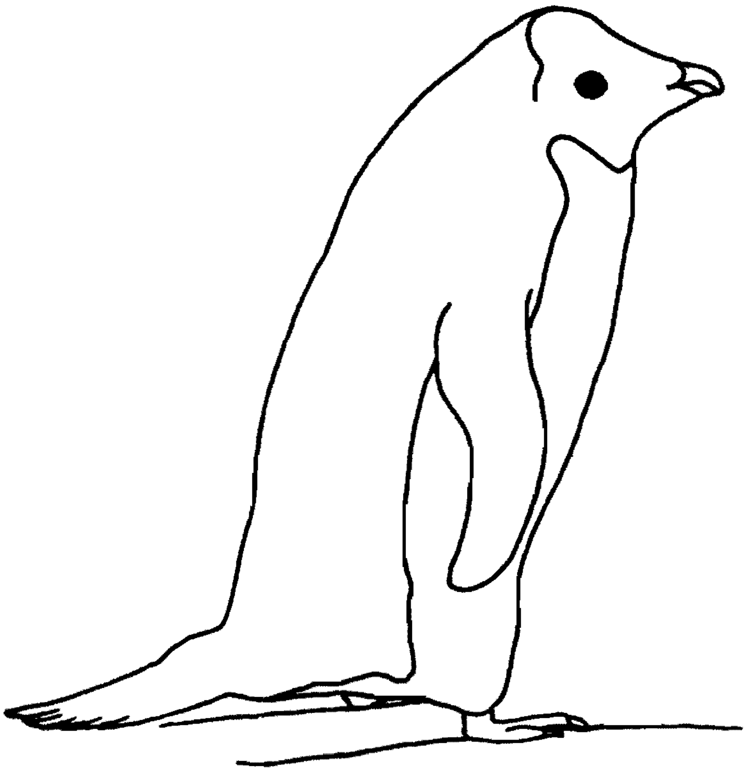
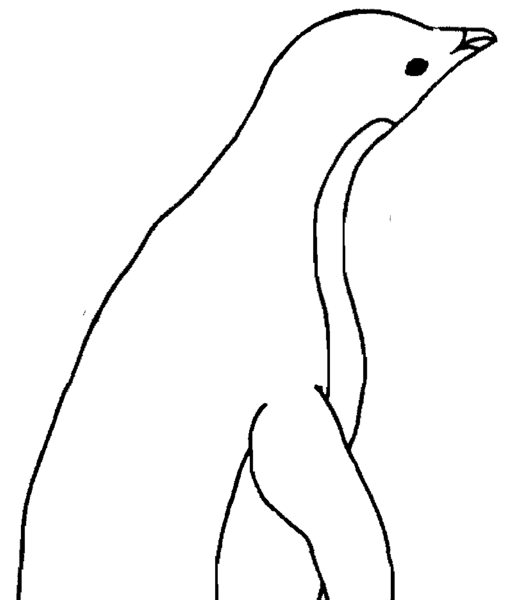


FIGURE 9. Looking around.

(a, upper) on territory.
(b, lower) off territory.





erected.

v. Nest Building Activities

Nest building is performed by both males and females. It may be divided conveniently into five activities.

(a) Stone searching.

Penguins search for nest stones both within and outside the colonies. When searching within a colony, the feathers are usually sleeked. Stealing of stones is common, but usually occurs only from nests where the resident is lying (or standing) with its back to the searcher.

(b) Stone reaching.

A penguin reaching to pick up a stone lowers its body from the shoulders and pelvis, and reaches forward with outstretched neck. The head is held very low to the ground and the feathers are sleeked when attempting to steal stones from another penguin's nest. The flippers may or may not be held beside the body.

(c) Stone carrying.

Stones are carried to the nest in the bill. The feathers are relaxed, partially erect, or sleeked, and the flippers are usually held out from the body. The posture is usually not as slender as when searching for stones among nesting birds.

(d) Nest scraping.

To scrape the nest hollow, a penguin lies down in the nest and scrapes with one foot so that the stones are pushed backwards to the rim of the nest. The feathers on the back of the neck are usually relaxed. Because penguins face different directions at different times, they tend to maintain a circular, cup-shaped nest. Nest scraping may be interspersed with bouts of stone collecting and stone rearranging (see below). Nest scraping also occurs during pair formation (section 9.6), and as a reaction to a disturbance outside the territory, such as a fight nearby, nest scraping or stone rearranging by neighbouring penguins (section 9.2).

(e) Stone rearranging.

Penguins may rearrange stones with the bill while either standing or lying in the nest. Stones along the outer periphery of the nest are dragged in towards the main rim of the nest. Stones in front may be placed to one side of the penguin. Stone rearranging occurs as part of the normal nest construction process, between bouts of nest scraping. When there is a pair of penguins at the nest, one may carry stones to the nest while the other stays in the nest rearranging stones. Contrary to previous reports, the penguin in the nest did not usually pick up the same stone as offered by the collecting penguin. Rearranging of stones and nest scraping by one penguin (or pair) sometimes stimulates neighbouring penguins to do likewise. Stone rearranging also occurs during boundary conflicts (section 9.2) or during pair formation and courtship (section 9.6).

vi. Copulation

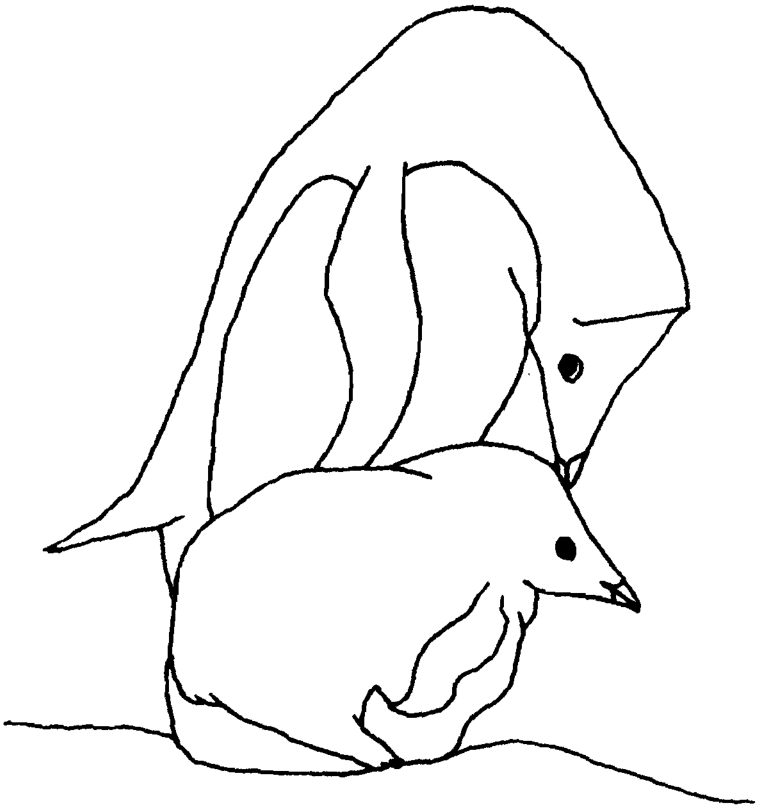
Copulation is used here as a general term to describe the behaviour associated with coition. Coition is defined as cloacal contact (and associated sperm transfer) between male and female. Mounting is a more inclusive term, and refers to the male standing on the female's back, whether or not coition occurs. The arms act is a term that refers to pre-mounting behaviour of the male (Richdale 1951:26). In the arms act, the male sidles up to the female who is lying in the nest. The male keeps his head lowered, and vibrates the flippers while holding them forwards and downwards (figure 10). As the male mounts, his head remains bowed and the flippers continue vibrating. The female raises her bill to meet that of the male, and the tip of each penguin's bill is vibrated against the base of the other's bill. Both birds continue vibrating their bills, and the male continues vibrating his flippers as he treads backwards on the female's back. The male wags his tail from side to side and the female raises her tail upwards. At the climax of the act, the male lowers his tail and brings his protruding cloaca into brief contact with the cloaca of the female (figure 11). The male then jumps off and stands beside the female, who usually remains lying down. The whole act usually takes about one minute.

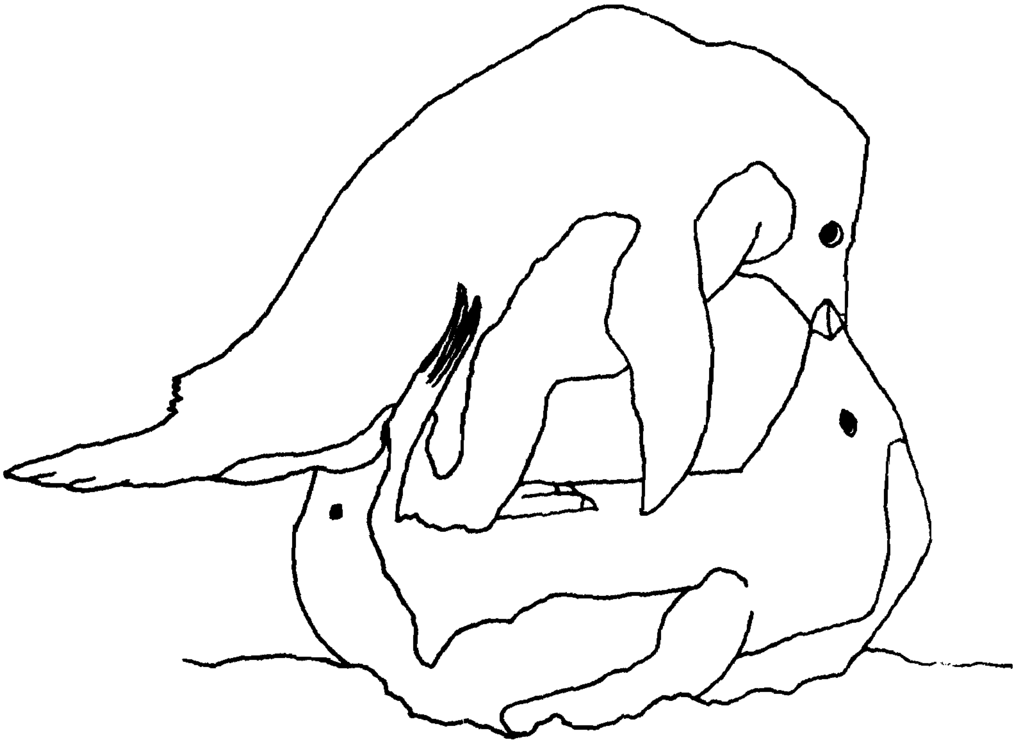
vii. Incubation

Penguins incubate by positioning the eggs between the feet, and lying down in the nest so that the eggs are covered by the brood patch. Very young chicks are brooded in the same way. Partial incubation occurs when a penguin does not fully lie down, but stoops over the eggs. This occurs most commonly when only the first of the two eggs have been laid, and perhaps

FIGURE 10. Arms Act.

FIGURE 11. Coition, just prior to cloacal contact.





helps to slow the development of the first egg during this period.

viii. Withdrawn crouch

Penguins on nests incubating eggs or chicks may go into a withdrawn crouch when attacked by a strange penguin, usually as the result of misidentification of nest sites. When this happens the incubating penguin remains lying down, with its body flattened to the ground, the head feathers sleeked, and the neck withdrawn. Occasionally, the head is turned around and the bill tucked firmly against the side of the body. The incubating penguin keeps very still while in this posture. This seems to reduce the intensity of attack. The attitude also facilitates the protection of eggs or chicks, because penguins that retaliate usually become involved in prolonged fights, which endanger the nest contents.

Females chased out of the colony and attacked by males, sometimes stop running and lie down. The male then stands beside her, while the female keeps very still. The posture here is not so withdrawn as above, and seems to occur mainly at the end of long exhausting chases. However, any movement by the female usually elicits further attack from the male.

ix. Attack

The term attack is generally used to refer to aggressive body contact between individuals, which includes fighting. In this study the following distinction is made. An attack occurs when only one penguin makes aggressive body contact with another, or when it moves to the other penguin's position and supplants it. A fight occurs when the other penguin retaliates; i.e. both penguins attack.

A simple attack, from a stationary position, consists of a peck with the bill (figure 12). The bill may be closed or open, and may jab or grip the opponent. If the other penguin returns the attack, the two opponents may spar with their bills, gripping, twisting and pulling.

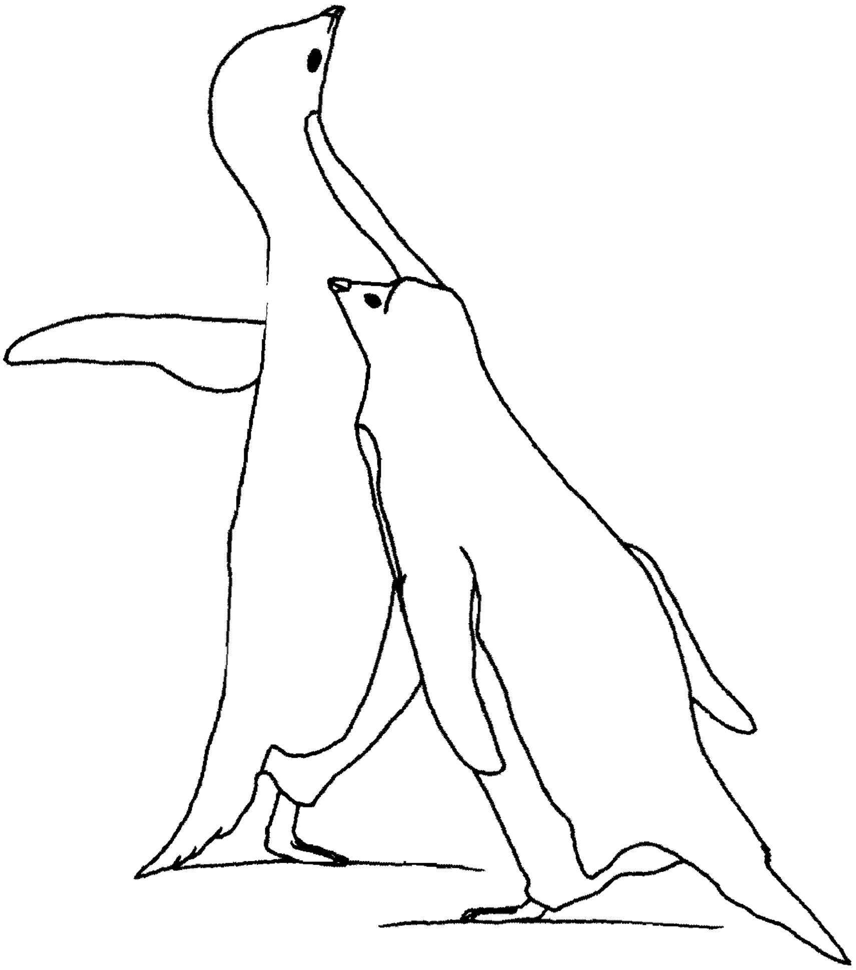
In severe attacks (and in fights) penguins employ their flippers and chests as well as their bills. The bill may be used to grip hold of the opponent while it is beaten with the flippers (figure 14). The chest is used to push the other penguin off balance (figure 15).

FIGURE 12. Peck from stationary position.

Note slender posture of penguin on left.

FIGURE 13. Pre-attack situation.

Penguin at left is about to attack, penguin at right is about to escape.



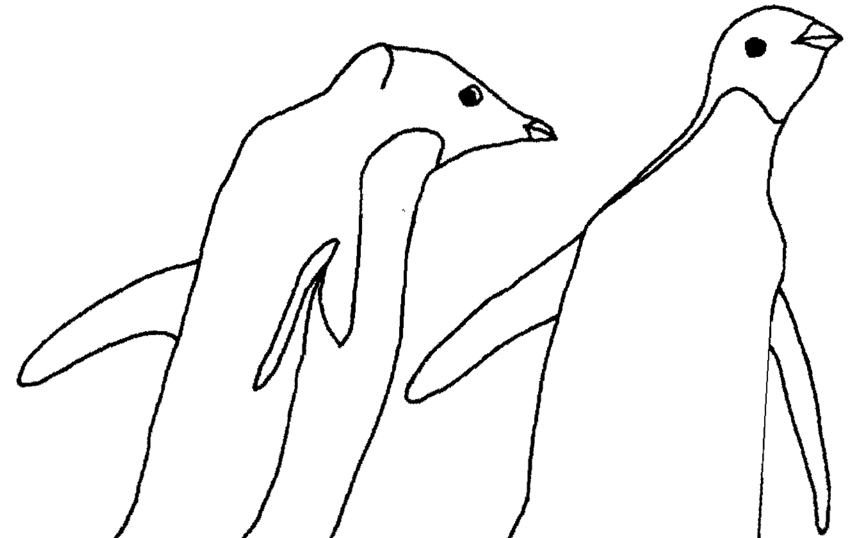
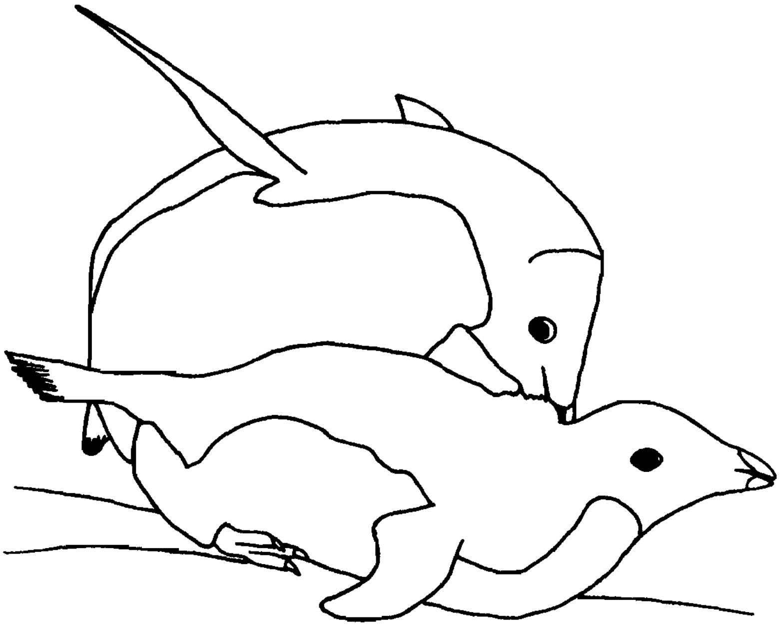


FIGURE 14. Attacking with flippers, while holding with bill.

FIGURE 15. Attack using chest for pushing.



A chase occurs when an escaping opponent is pursued, sometimes for only 2 or 3 metres, but sometimes for as long as 50 metres (figure 16). The feathers on the back of the neck and occipital crest of the chaser are usually erect and the chest is thrust out. This contrasts with the features of an escaping penguin (see below).

The feathers of the occipital crest of fighting birds may be sleeked or erect, and the eyes may or may not be rolled, depending on the circumstances. In an intense fight, there is usually little difference between the attitudes of the two fighters, making it very difficult to predict the outcome.

x. Escape

Escape occurs when a penguin is supplanted, or withdraws from its position by turning and moving away from its opponent (involving movement of the entire body). Withdrawal of part of the body, turning side on, or inching slightly back are not regarded as escape, but only as intention movements of escape (see also section 9.9). During escape, the feathers, especially of the head and neck, are sleeked. The neck is stretched up, and the bill held above the horizontal. The eyes are not rolled. The flippers are held out from the body. These features are well illustrated when a penguin is being chased (figure 16). The attitude of the chased penguin differs markedly from that of the chaser.

3.3 THREAT DISPLAYS

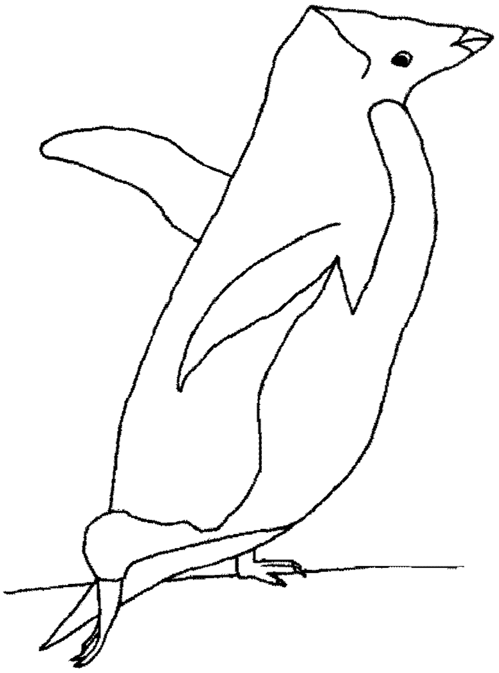
In this study, I have recognised six threat displays, which is a greater number than previously recognised. Three newly recognised displays (Point, Gape, and Charge) taken together correspond to the single display (the Direct Stare) of Penney (1968:98) and the second (unnamed) display of Sladen (1958:37). The fourth new display, the Sideways Stare, perhaps corresponds with the vaguely described "aposematic display" of Roberts (1940:figure 24). The other two displays described here, the Bill-to-Axilla and Alternate Stare, have been recognised previously (see below).

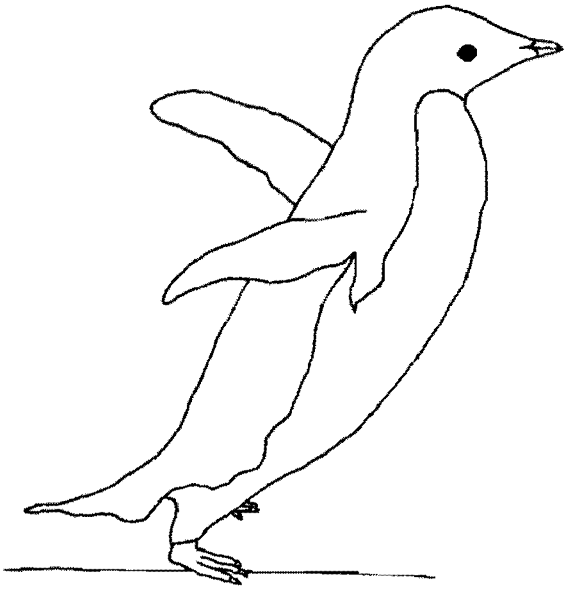
The displays are described fully in the following pages and are summarised in table 4 (page 31).

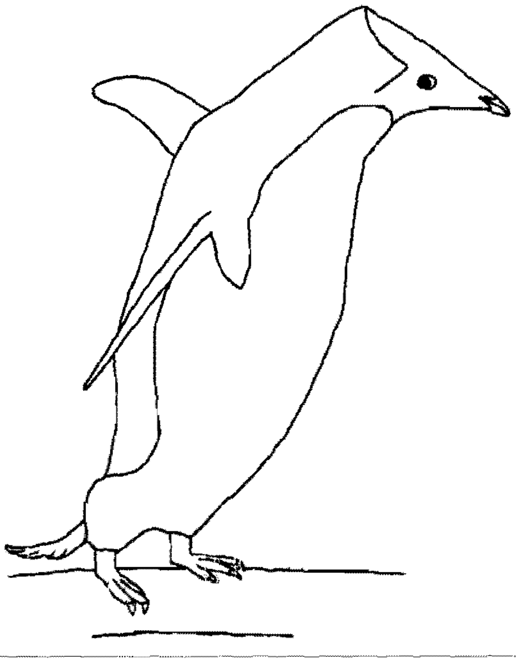
FIGURE 16. Chase,

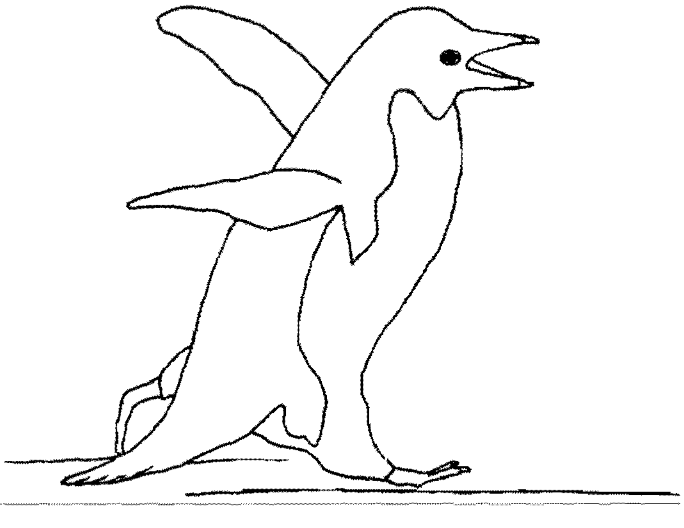
(upper) and (lower) different stages.

Note that bill of escaping penguin is open in (lower).









i. Bill-to-Axilla Display

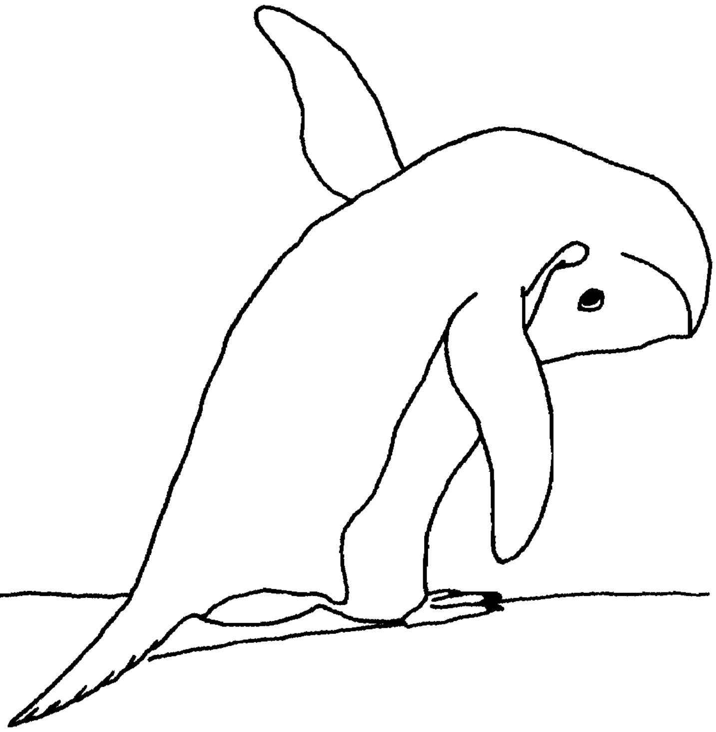
The Bill-to-Axilla display was first described by Sladen (1953:955) as a subsidiary to the Ecstatic display (see section 3.4i). Later, Sladen (1958:33) correctly recognised it as a separate display.

In the Bill-to-Axilla display, a penguin usually stoops forward at an angle of about 45 degrees, though it may remain standing upright or lying down. The head is not extended forwards, but is usually turned to one side of the body so that the bill points to the axilla of one flipper (figure 17). The head is then rolled up and down several times in this position. It may then be rolled on the other side of the body or directly in front of the body. At full intensity, the display is accompanied by a repetitive growl (in time with the rolling) and the flippers beat rhythmically (about 1.5 beats per second). The feathers of the occipital crest are erect and the eyes are rolled to expose the white sclerae.

There is much variability in this display. The head may be rolled on one side of the body, then on the other, then back again, or even directly in front. It may be rolled either above or below the flippers, and on the side of the body facing or opposing the offending penguin. Penney (1968:99,100) has illustrated the considerable variability in the accompanying sound. Much of the variability seems to be explicable from knowledge of the preceding behaviour, and of the intensity of stimulation. At low intensity, the display may involve no more than rolling the head on one side of the body, and a penguin already lying down may not stand up nor beat the flippers. The flippers are usually waved when the display is given following the Ecstatic, or in other high intensity situations.

The Bill-to-Axilla display is most frequently given by penguins (of either sex) alone at the nest site, though it is also given when a mate is alongside. It occurs most frequently in males, after an Ecstatic display, probably as a response to surrounding penguins that might also be performing the Ecstatic. Ecstatic displays occur most frequently in males (see page 27). It is sometimes given to neighbours rearranging stones or nest scraping within their own territories. It is also given after a boundary dispute with a neighbour, or upon the approach of a stranger near the territory. Unlike other threat displays, the

FIGURE 17. Bill-to-Axilla,
(upper) and (lower) different stages.



Bill-to-Axilla often does not seem to be directed at any particular penguin, but appears as a response to the general situation; for example, after a bout of Ecstatics or the disturbance of a fight nearby.

ii. Sideways Stare

The term Sideways Stare has not been used before, although the display may correspond to the "aposematic display" of Roberts (1940:figure 24). It was not specifically named by Sladen (1958:37) and not separated from the Alternate Stare (see below) by Penney (1968:97).

The essential feature of the Sideways Stare is the sideways orientation of the head (figure 18). Instead of the head being moved from side to side, as in the Alternate Stare, or rolled as in the Bill-to-Axilla, it is held to one side, so that only one eye stares directly at the intruder. The flippers usually remain at the side of the body. The exact form of the display depends on the situation. When a penguin is standing upright, the head is usually not lowered more than a third of the way to the ground. The bill may be pointed directly downwards, or it may be pointed obliquely towards the other penguin. However, at no stage is the bill in an inconvenient position for attack.

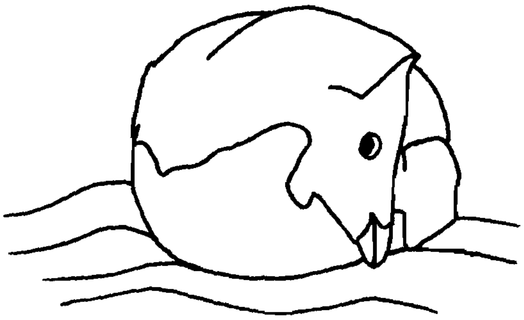
The Sideways Stare is given by territorial penguins in response to other penguins pausing near the territory boundary, or in response to movement by neighbours (figure 19). In these situations the feathers of the occipital crest are erect and the eyes rolled. The Sideways Stare is also given by unattached females as they approach the territory of a bachelor male (perhaps attracted by his Ecstatic display, see section 9.6). In these females, the head feathers are usually sleeked and the eyes not rolled. They often turn their whole body side on and shuffle sideways as they approach closer. The body is usually more hunched and the head lower than in the usual territorial Sideways Stare.

iii. Alternate Stare

The Alternate Stare was named by Penney (1968:97). It was first described (but not named) by Sladen (1958:37).

In the Alternate Stare, the head is moved from side to side so that alternate eyes are presented to the intruder. The

FIGURE 18.   Sideways Stare,
(upper) lying down.
(lower) standing up.



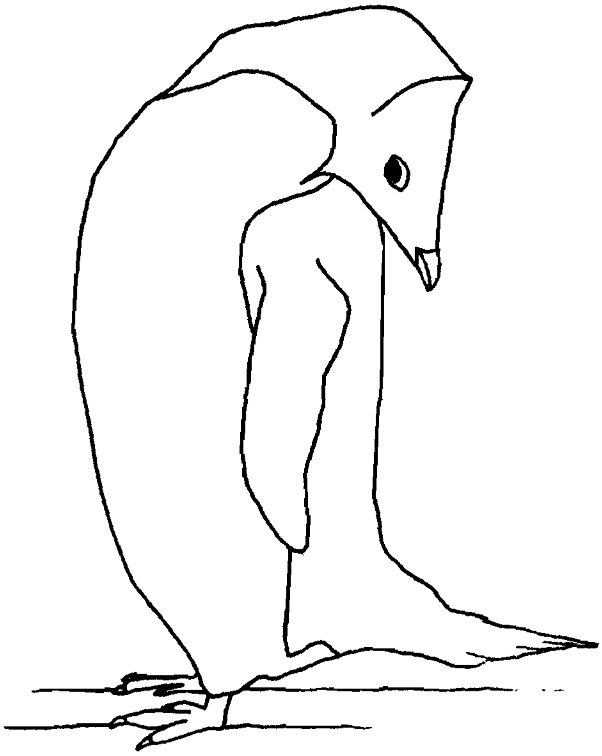
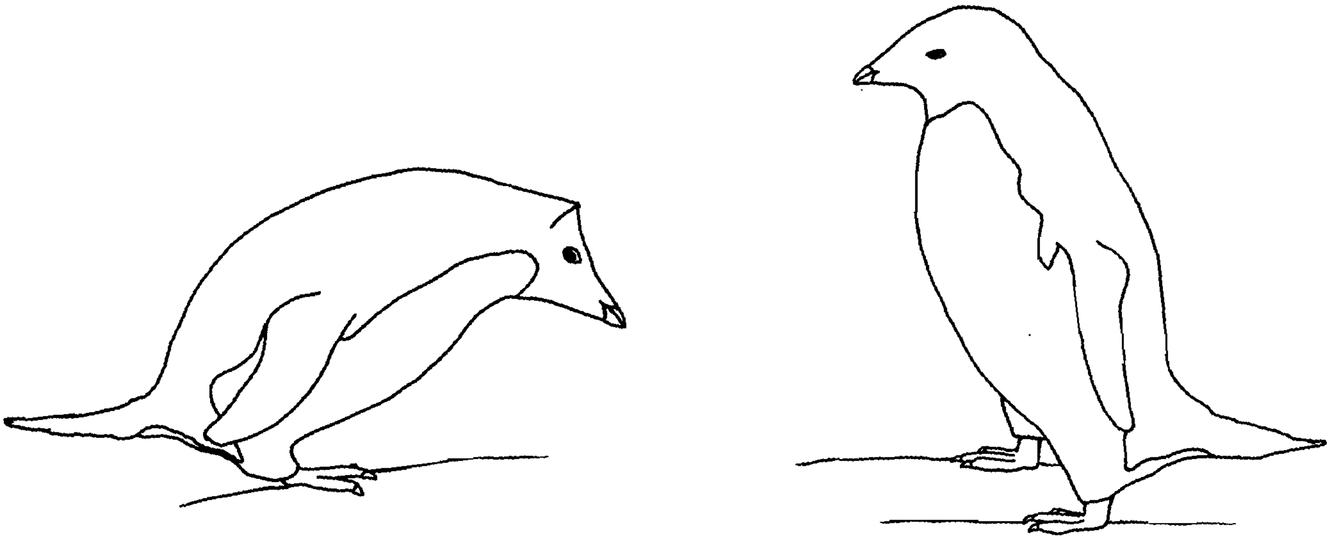
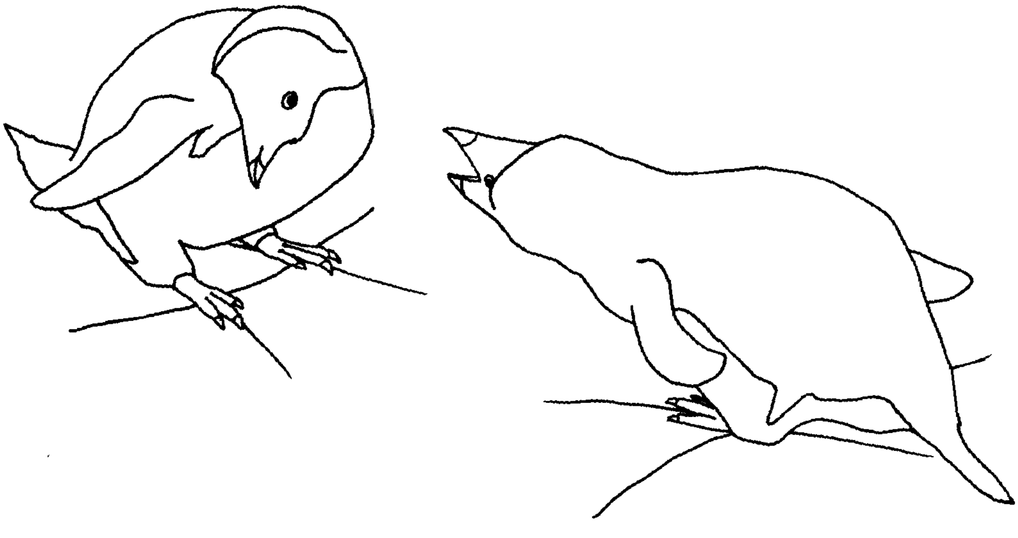


FIGURE 19. Sideways Stare by penguin on left,
(upper) given to Stranger,
(lower) given to neighbour's Gape.





exact form varies with the situation. Thus, the bill is strongly depressed when the display is given in an upright posture, but little depressed when the penguin is crouched. The number of waves from side to side ranged from 3 to 18 in recorded displays. The feathers of the occipital crest are erect, and the eyes are rolled to expose the white sclerae. The flippers are usually waved slowly up and down. The display may be accompanied by a low growl (as illustrated by Penney 1968:figure 12a).

The Alternate Stare is usually given to penguins intruding closer than occurred for either the Sideways Stare or Bill-to-Axilla. It is a response to a persistent intrusion, such as strangers continuing to linger near the territory boundary, repeated attempts at stealing nest stones, prolonged movement by neighbours, and persistent attention from skuas.

iv. Point

The Point is recognised here as a separate display. It was previously included as part of a more general display, the Direct Stare of Penney (1968:98), and the second (unnamed) display of Sladen (1958:37).

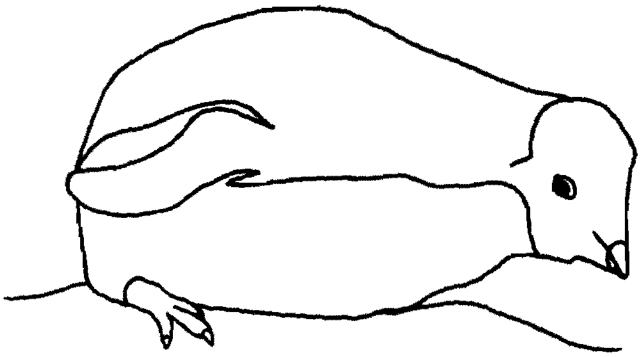
In the Point display (figure 20) the closed bill is pointed directly at the stimulus object. Penguins remain stationary, and display while standing or lying down. The body is usually inclined forward from the pelvis, and the neck extended forwards. The flippers are usually held by the side of the body, but may be spread out (for balance) if the penguin suddenly lunges forward. The feathers of the occipital crest are usually erect, and the eyes rolled to expose the white sclerae. The bill is kept closed and the display is usually silent, although it may be accompanied by a growl (as illustrated by Penney 1968:figure 12b).

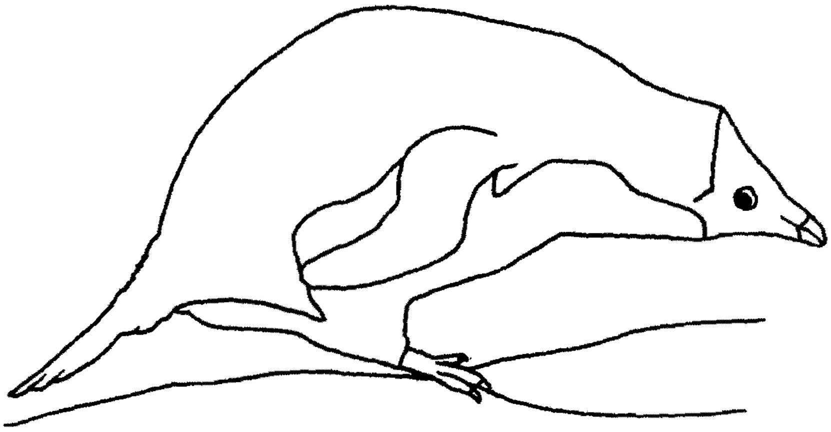
In less intense situations, the body may be more upright (when standing), and the neck little extended. The head and bill were sometimes pointed strongly downwards.

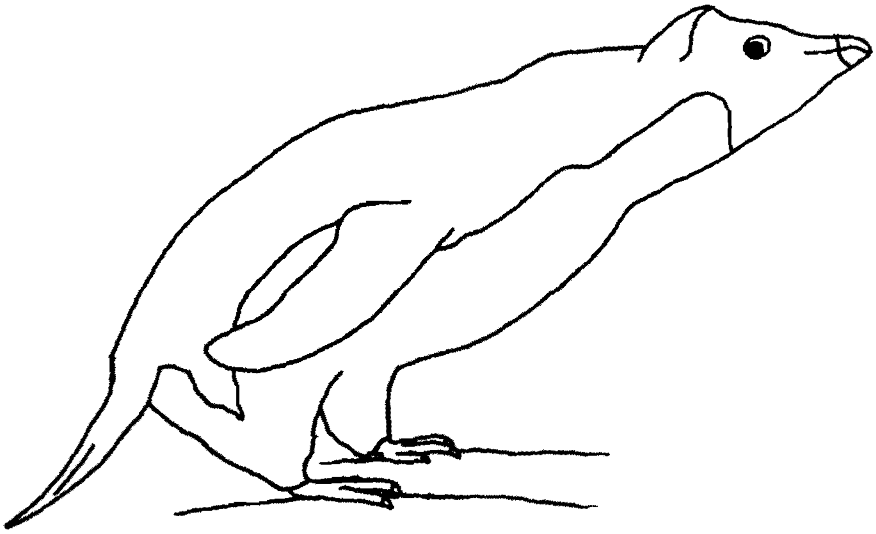
Pointing is mostly used by penguins on their territories. It is directed at strangers moving past the territory or at neighbours moving about in adjacent territories. It is also directed at inter-specific intruders, such as skuas and man. Pointing occasionally occurs outside the territories; e.g. when a penguin is approached too closely while resting on the shore

FIGURE 20. Point,

three different aspects.







before going to sea.

v. Gape

The Gape is recognised here as a separate display. It was previously considered part of the Direct Stare of Penney (1968:98). It is a more aggressive display than the Point.

The body posture is very similar to that of the Point, except that the bill is held wide open (figure 21). The penguin may be standing or lying down with the body extended forward and the neck stretched toward the intruder. The feathers of the occipital crest are erect, and the eyes rolled. The display is usually accompanied by a harsh call made through the opened bill.

A low intensity form of Gaping occurs when the bill is only slightly opened and then snapped shut.

Gaping is initiated by any movement close to the territory boundary (e.g. by a neighbour rearranging nest stones near the boundary). Mutual Gaping between neighbours is very common. One penguin often takes the offensive while the other is defensive. In offensive Gaping, the penguin leans well forward with most weight on its phalanges. It might inch forward in small jumps. The neck is well extended (figure 21a). In defensive Gaping, the body is hunched back and the neck withdrawn. Most weight tends to be on the tibio-tarsus (figure 21b), and the penguin may inch backwards or turn side on. In mutual Gaping, the head is sometimes twisted (or rotated) so that one bird Gapes at right angles to the other (figure 22).

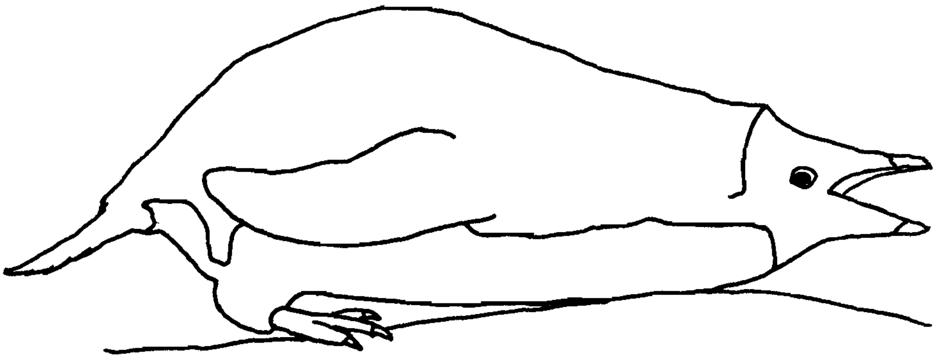
vi. Charge

The Charge is recognised here as a separate display. It was previously included in the Direct Stare of Penney (1968:98). It is a more aggressive display than either Gape or Point.

The most conspicuous feature of the Charge (figure 23) is the forward movement. In this display, the penguin moves toward the stimulus object with a few steps or a short run. The body is held upright, the head is held forward from the shoulders, and the bill is pointed horizontally or slightly downwards. The feathers of the occipital crest are erect, and the eyes rolled. The flippers are usually held out from the body. The bill may be closed or opened, and the display may

FIGURE 21. Gape,

(upper) offensive posture,
(lower) defensive posture.



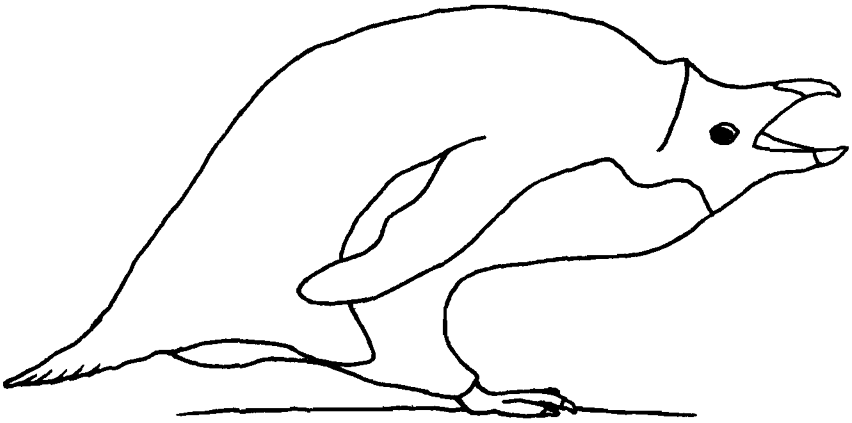
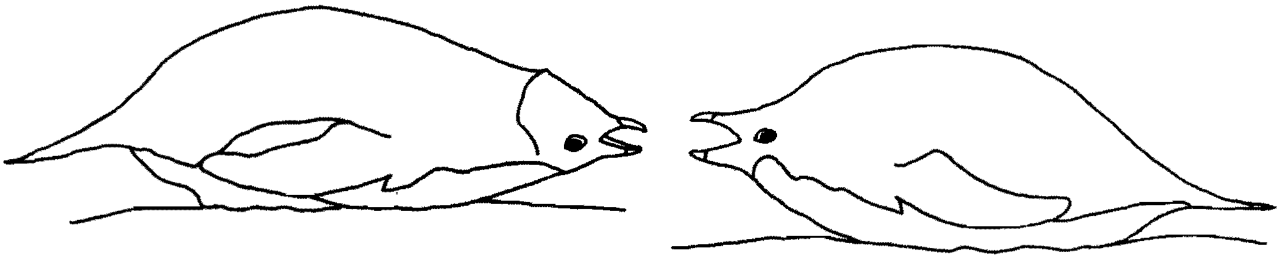


FIGURE 22. Gaping between neighbours.



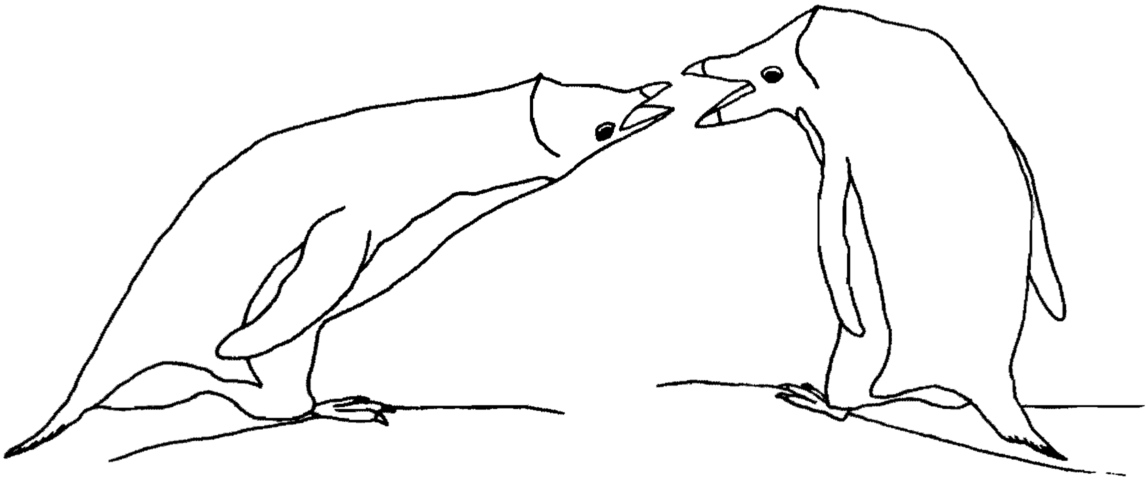
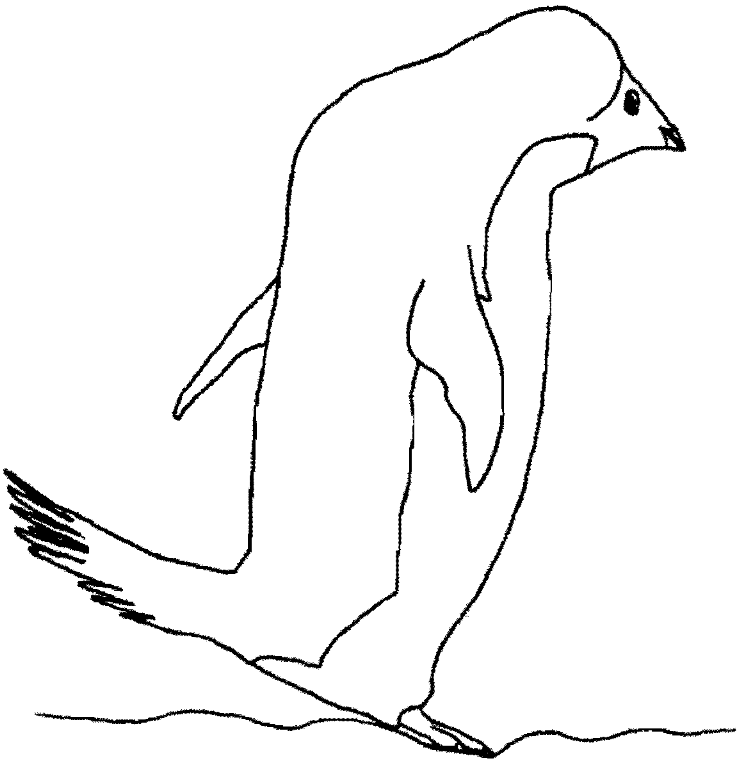
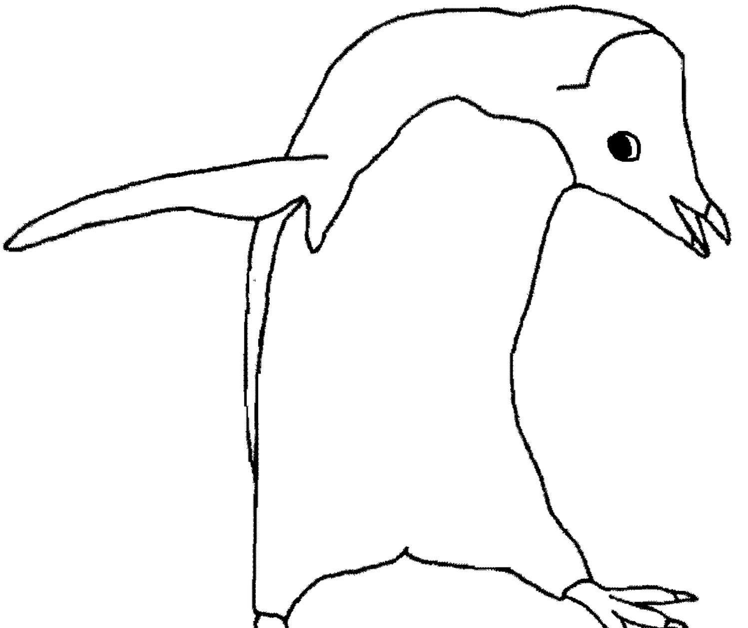


FIGURE 23. Charge,

(upper) bill closed,
(lower) bill open.





be silent or accompanied by a squawk (as illustrated by Penney 1968:figure 12c).

The Charge is more than just incipient attack, though it most strongly gives the impression of attack. In figure 13, the penguin at left has approached the other penguin in a Charge, and this Charge is about to be followed by attack. One reason for distinguishing the Charge from incipient attack is that by itself it is an effective signal to other penguins (see section 9.4). It also contains display components, such as erect crest feathers and rolled eyes.

The Charge is not used by penguins directly involved in incubating eggs or brooding small chicks, because they cannot leave the nest without endangering the nest contents. It may be used by the mate not involved with these activities, or by penguins without eggs or chicks.

The Charge is most frequently used against strangers lingering near the territory boundary. It is also used against inter-specific intruders (e.g. skuas and man).

3.4 SEXUAL DISPLAYS

The following displays are used specifically for communication between penguins of opposite sex, and so are called sexual displays.

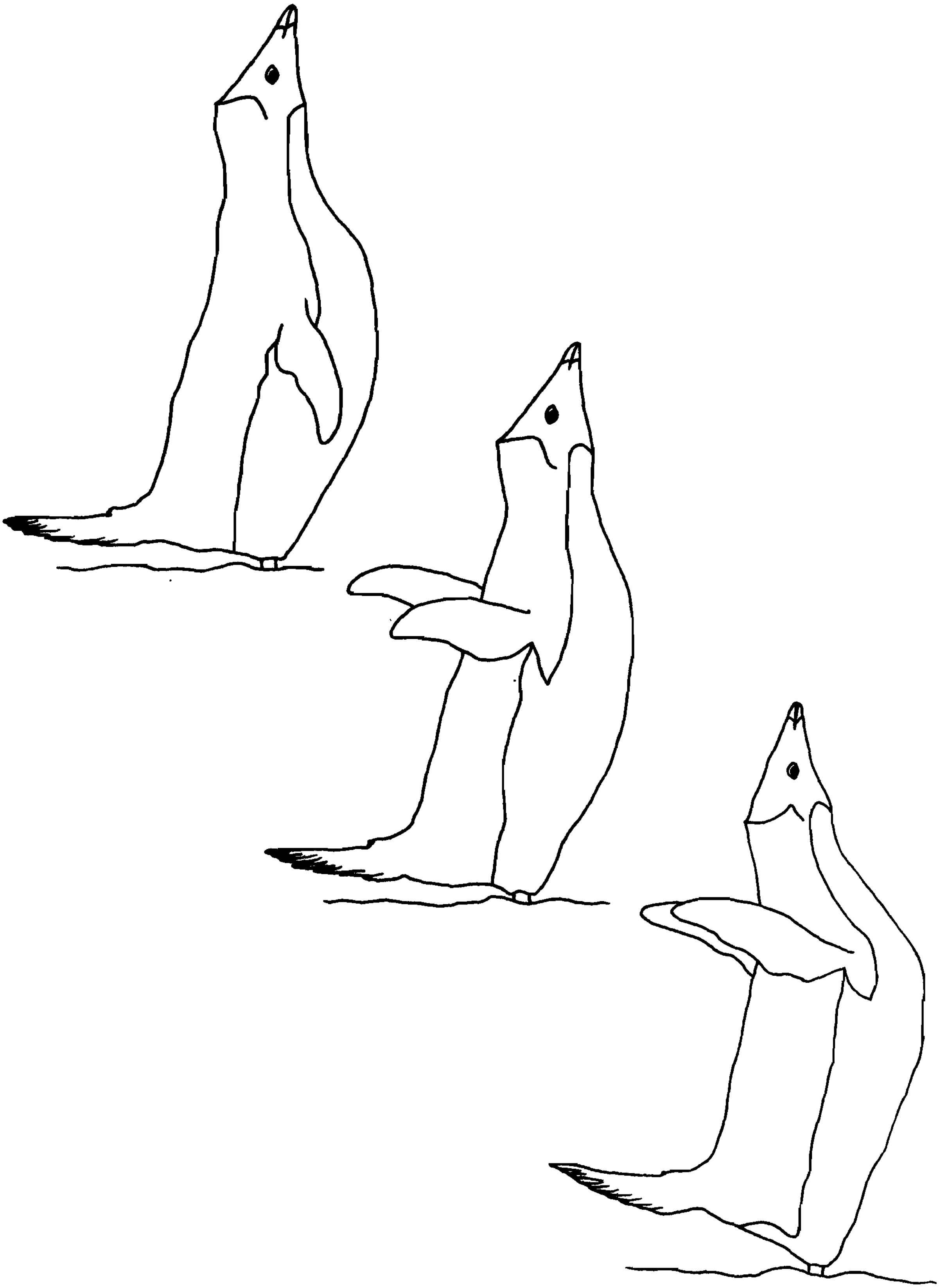
i. Ecstatic Display

The Ecstatic display was first described and named by Wilson (1907:56). As noted by Sladen (1958:32) the name "Ecstatic" is unfortunate because of its emotional overtones. However, as it is in widespread use it is retained here.

In the typical Ecstatic display, a penguin stands upright, with the feet slightly apart, the head and bill raised vertically, and the neck fully stretched (figure 24). The chest is thrust outwards, and vibrates as the bird emits a repetitive sound building up to a climax. The initial soft pumping sound, followed by the harsh climax, is illustrated by Penney (1968:figure 22). At the climax, the bill is slightly opened. The flippers beat diagonally backward and forward in a steady rhythm. The feathers of the occipital crest are usually erect, and the eyes rolled to expose the white sclerae.

Incomplete, low intensity displays (Intention Ecstatic)

FIGURE 24. Ecstatic display,
three different stages.



occur when the head is raised only briefly, the neck not fully stretched, and the flippers lifted but not waved backward and forward. If vocalisation occurs it is only faint. In high intensity displays ("Imploring Ecstatic", Sladen 1958:30) the head is held vertically and the neck fully stretched. The flippers are held out and may beat rapidly, slowly, or not at all. The head may wave slightly from side to side. The display is prolonged, and the vocalisation is given through wide opened bill. The sound is harsher than the typical climax call, and resembles the call of the Loud Mutual display (page 28). A male may repeat the Ecstatic display several times. Between performances he may perform the Bill-to-Axilla display (possibly in response to surrounding males) or may stare intently with the head only slightly raised.

The Ecstatic display is given mostly by unpaired males alone at the nest site. Its main function is to attract unattached females to the nesting territories of bachelor males (see section 9.6). The display sometimes begins without any apparent external stimulation. At other times, disturbances such as the approach of other penguins, fighting, nest relief, or the approach of humans may also cause penguins to give the Ecstatic display. The display is very contagious, so that an Ecstatic by one penguin will often cause neighbours to display. Such outbursts last from a few minutes to over an hour, and may spread widely through a colony. The Ecstatic display is not confined to unpaired males, but may be given by paired males or females, and occurs even in parents incubating or guarding chicks. The various situations in which the Ecstatic display occurs are also discussed by Sladen (1958:32) and Penney (1968:111). The Ecstatic display may attract females in any of the above situations, but seems to have major significance when given by bachelor males.

ii. Bowing

Bowing was first named and described as a display of the Adelie penguin by Roberts (1940:218). It was named Oblique Stare Bow by Penney (1968:114), "to distinguish it from bowing related to the species' upright stance". However, the original term is regarded as satisfactory and is retained here.

The Bow display is typically given between penguins of opposite sex standing at the nest. The head is usually lowered approximately half way to the ground, in front of the body (figure 25). The flippers remain by the side. The display is silent, with the bill closed.

The form of Bowing varies with the situation. In very intense Bowing (e.g. by a male after the approach of a female) the head is often lowered almost to the ground. The crest feathers are strongly erected and the eyes rolled. In less intense situations (e.g. when responding to the mate moving slightly after resting) the head may be lowered only slightly, the crest feathers not erected and the eyes not rolled. After approaching a male on his territory in the Sideways Stare, a female may Bow with crest feathers only partially erect or even sleeked, and the eyes not rolled. Bowing may also be accompanied by feather sleeking when a returning penguin has just passed between surrounding territories to get to the nest.

The lowered head is sometimes turned obliquely to the body so that one side faces the other bird. Head rotation is especially evident during pair formation, when Sideways Stare and Bow displays alternate as male and female overcome their reticence to approach one another. At other times the use of head rotation depends on whether the two birds are displaying side by side, directly in front, or at an angle to one another.

Penguins may walk around the territory while Bowing. The head is held very low, and the walking is very stilted. The flippers are held firmly by the side of the body in contrast to normal walking.

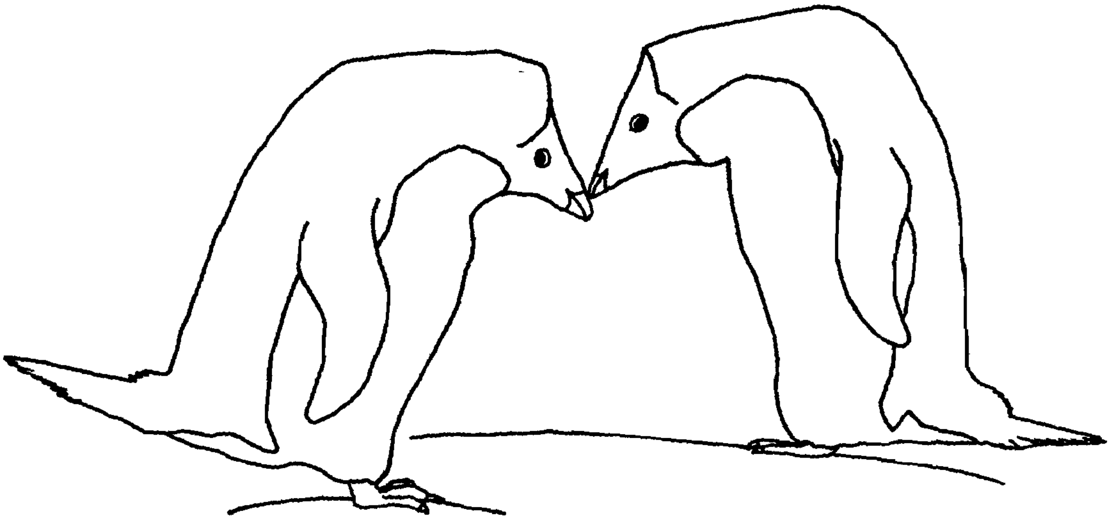
Bowing is a form of appeasement used in maintenance as well as establishment of pairs. It frequently occurs when a pair is disturbed at the nest site; for example, by one of the pair changing its resting position, or by the return of one bird after a short absence. Sometimes only the returning bird Bows, and the other shows no response. Bowing is also given alone by the male, either before or after copulation. It presumably contributes to acceptance of the male by the female. Bowing before copulation seems less common in established pairs than during pair formation.

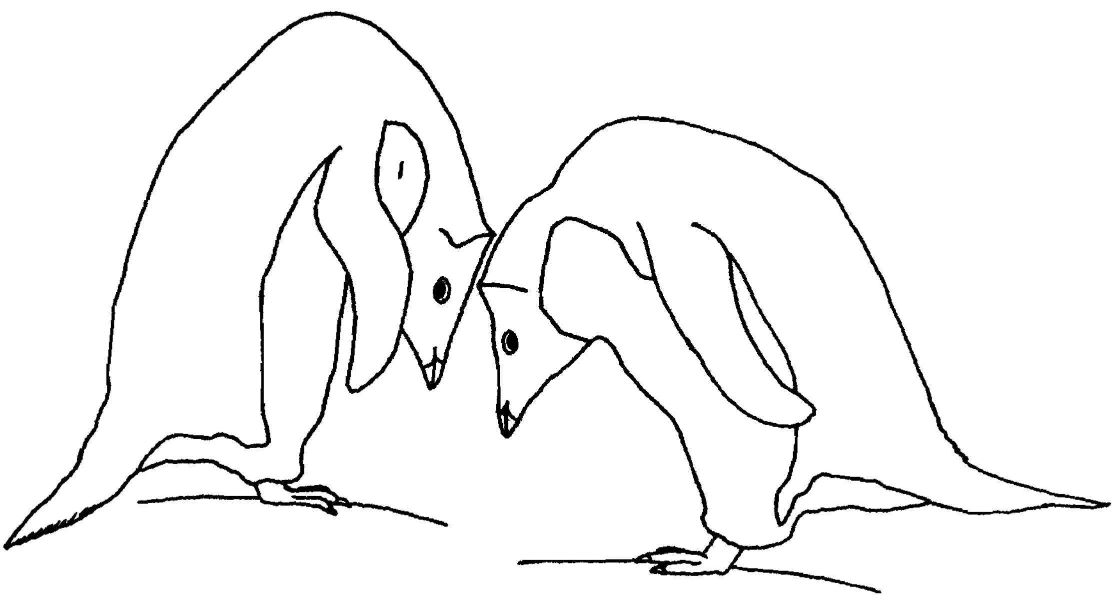
iii. Loud Mutual Display

The Loud Mutual and Quiet Mutual displays (Sladen 1958:34) together correspond to the "mutual epigamic display" of Roberts (1940:218) and the "parade mutuelle" of Sapin-Jaloustre and Bourlière (1952:44).

FIGURE 25. Bow,

(upper) shallow,
(lower) deep.





As the name implies, the mutual displays usually occur between a pair of penguins. The Loud Mutual display may be initiated, for example, when one of a pair arrives at the colony for nest relief. The returning penguin calls loudly through wide opened bill. The individuality of this calling was demonstrated by Penney (1968:125). The initial calling may occur with body inclined forward from the pelvis and head held forward on an extended neck (figure 26). The head may be waved slightly from side to side, or even up and down. The feathers of the occipital crest are erect, and the eyes rolled. The flippers are usually held by the side of the body.

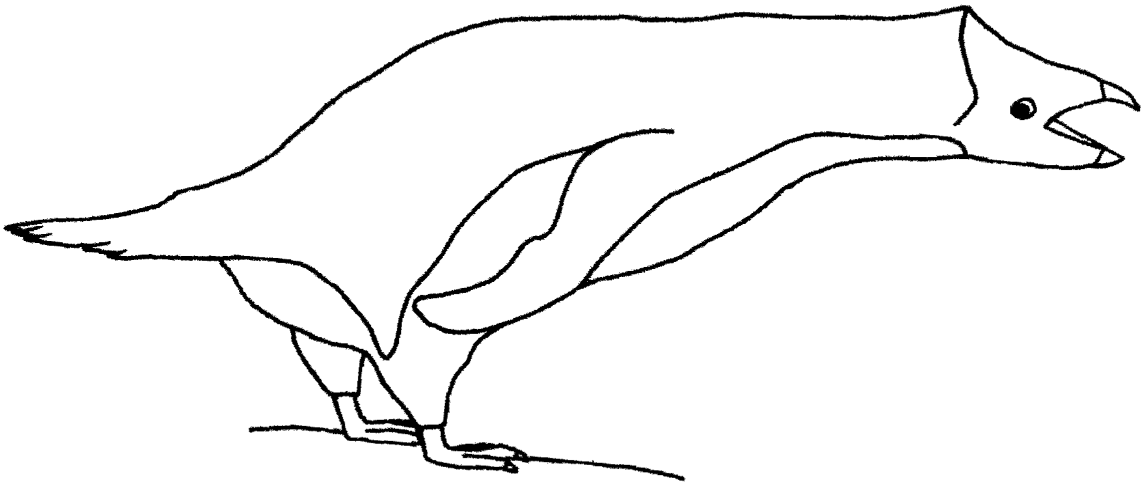
If the penguin has called at the wrong nest, the resident bird usually attempts to peck it. The returning penguin may then turn away and display towards another bird.

If it has called at the correct nest, its mate will respond by calling in an upright posture. The two birds face each other and raise their heads high in the air on extended necks (figure 27). The heads are waved from side to side, one bird often out of phase with the other. The calling continues in time with the waving.

Several bursts of displaying may follow one another. The birds may stop displaying to bend over and investigate nest stones, eggs or chicks, then straighten up and continue displaying. Sometimes the calling is continued while the penguins bend over. Intervening pauses between outbursts of the display gradually lengthen.

Situations in which the Loud Mutual display occurs are also discussed by Sapin-Jaloustre and Bourlière (1952:45), Sladen (1958:34) and Penney (1968:115). In some of these the display is upright, in others it is forward. Loud Mutual displays between parents and chicks are upright displays. Though the parent may appear to lean forward, the bill is directed over the head of the chick. Loud Mutuals between fighting penguins are usually forward displays. They are more often followed by attack than withdrawal. The penguins may pause from fighting, call mutually forward at one another, then continue fighting. The essential difference between this and published descriptions of the Loud Mutual is the recognition of forward and upright components of the display.

FIGURE 26. Loud Mutual display,
given in forward posture by lone penguin.



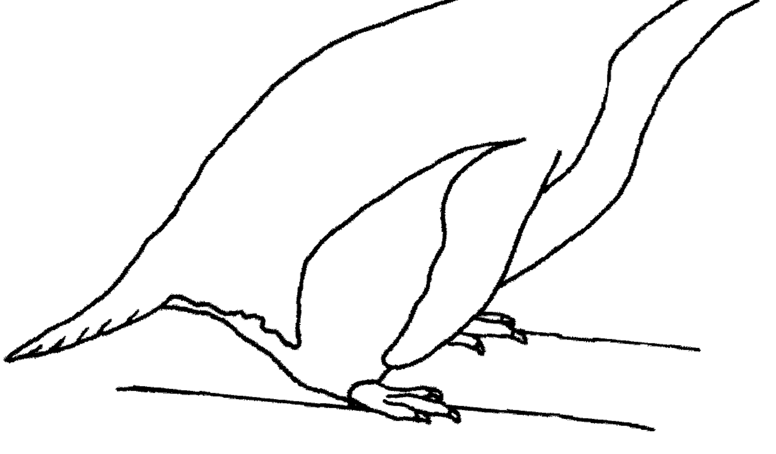
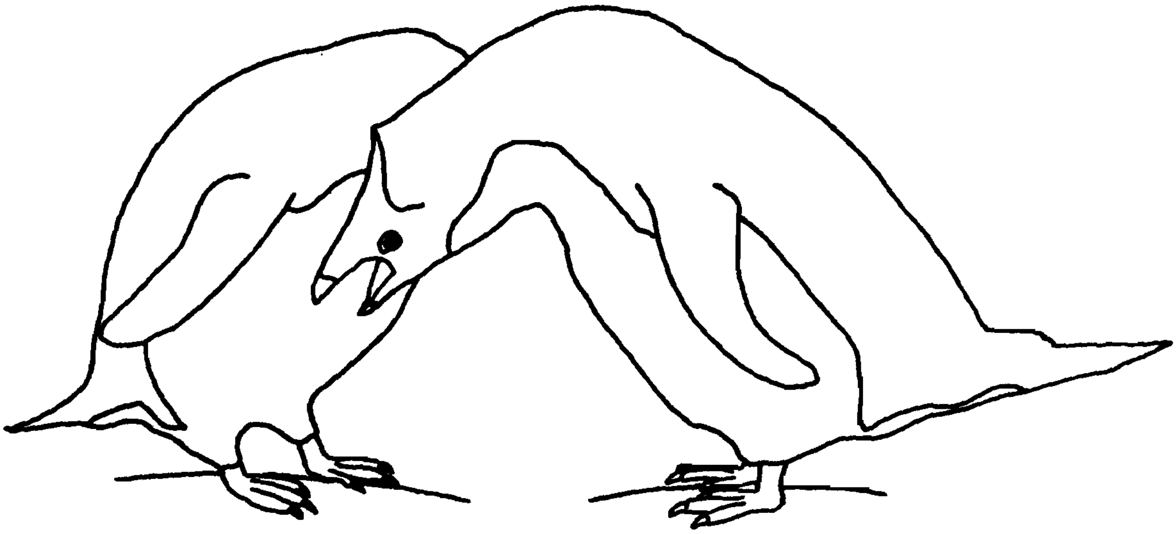
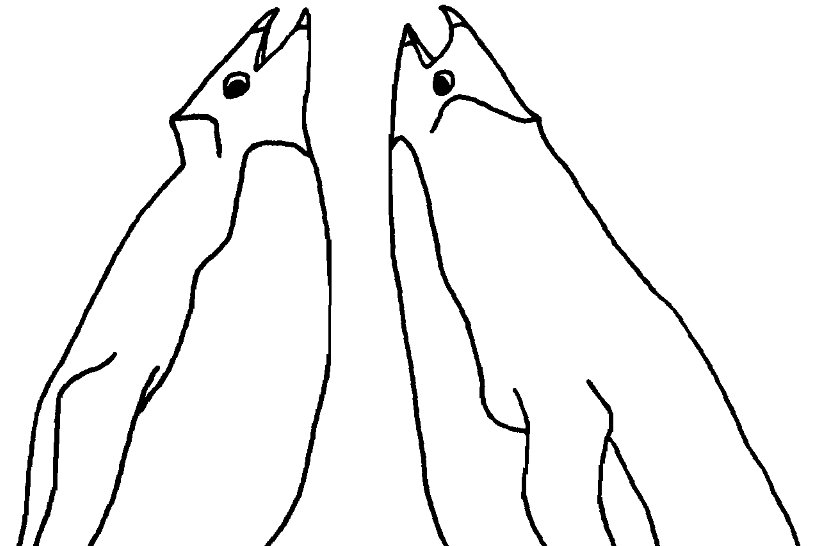


FIGURE 27. Loud Mutual display,
by a pair of penguins.

(upper) initial bending,
(lower) final waving.





iv. Quiet Mutual Display

The Quiet Mutual display is usually given by a pair of penguins standing face to face at the nest site. In the typical display, the head is first lowered sideways (figure 28a), and the bill pointed to the tip of the partner's bill. The head is then raised vertically, bill pointed upwards, and waved from side to side (figure 28b). The pair usually wave their heads out of phase with one another. The full display involves several waves, accompanied by a soft call (as illustrated by Penney 1958:figure 28). The bill is kept closed, and the flippers remain by the side of the body. The feathers of the occipital crest are erect, and the eyes rolled.

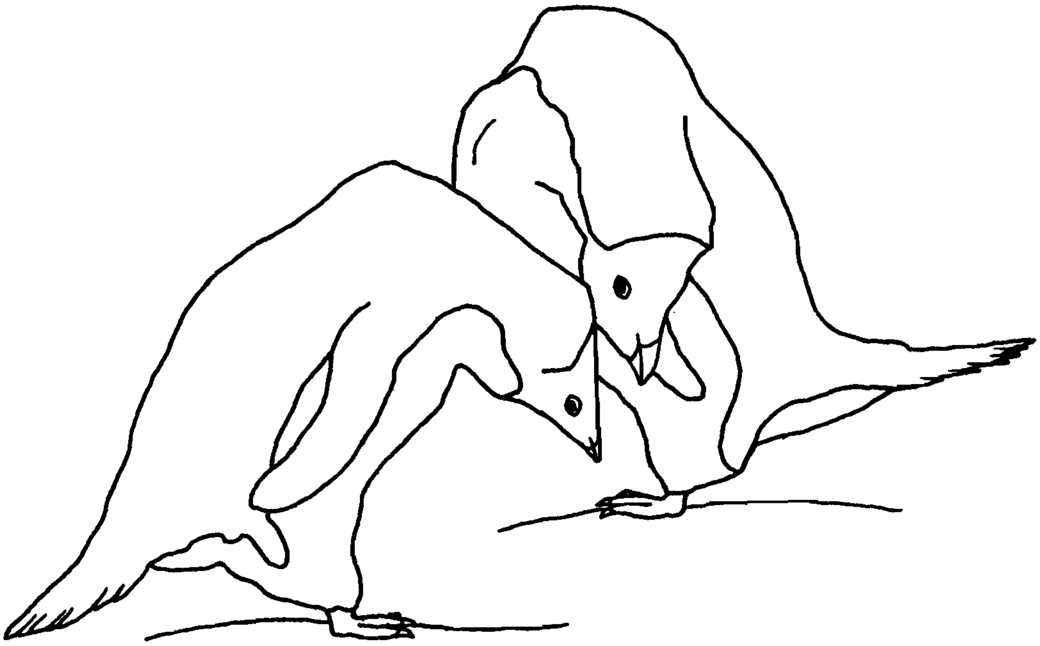
In less intense displays, the head rises slowly to the vertical. There is either no waving or only slight waving (once each way), and no accompanying sound. A penguin may give the display while lying down in its nest, by simply waving its head in the air. The display is sometimes given by only one of a pair, in response to movement by the mate.

In some circumstances, the display consists of no more than the initial sideways bending, in which the bill tip points towards the partner's bill tip. At other times (e.g. when only one of the pair displays) the sideways bending component may be omitted, and the vertical head-waving stressed. In newly-formed pairs, the male occasionally pecks the female after the sideways bending, but not after the vertical head-waving.

FIGURE 28. Quiet Mutual display,

by a pair of penguins.

(upper) initial bending,
(lower) final waving.



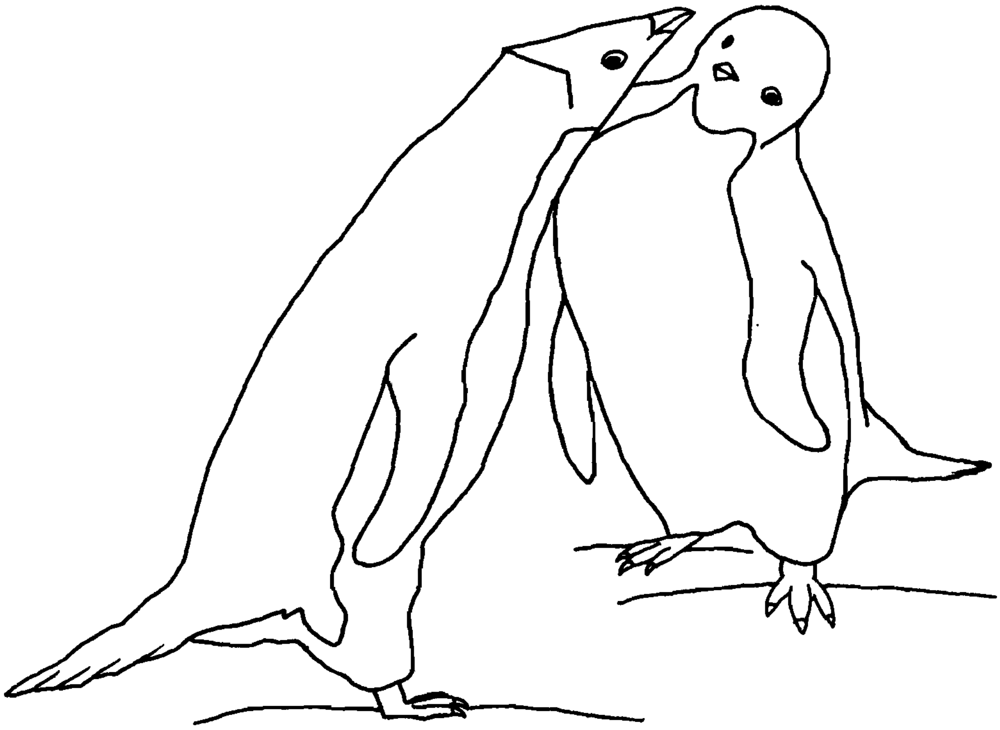


TABLE 4 : Summary of Adelie Penguin Displays

Display	Description
Charge*	Move forward, bill forward, open or closed, ± squawk.
Gape*	Reach forward, bill wide open, silent or harsh call.
Point*	Reach forward with closed bill, silent or low growl.
Alternate Stare	Wave head from side to side, silent or growl.
Sideways Stare*	Hold head to one side, silent.
Bill-to-Axilla	Roll head at side of body, wave flippers, growl.
Ecstatic	Stand upright, bill raised, flippers waved, call.
Bow	Stand, bill lowered, silent.
Quiet Mutual	Stand, bill raised, head waved side to side, ± growl.
Loud Mutual	
- forward*	Stand, bill forward, head waved side to side, loud call.
- upright	Stand, bill raised, head waved side to side, loud call.

* These displays are recognised for the first time (see page 21).

4.0 SEASONAL CYCLE OF BEHAVIOUR

4.1 INTRODUCTION

The cycle of events in the breeding season of Adelie penguins has been described by several authors (Sladen 1958, Sapin-Jaloustre 1960, Taylor 1962, Penney 1968). For penguins that breed successfully, the period at the breeding rookeries is divided into three partly overlapping periods:

(i) occupation period, from arrival to egg-laying,
(ii) incubation period, from egg-laying to chick hatching,
(iii) chick period, from hatching to departure.

The term reoccupation period is used to describe the period when penguins return to the colonies after losing eggs or chicks. It coincides with the chick period of successful breeders. Penguins without eggs or chicks may be found in the colonies all through the season, but their numbers fluctuate, with fewest ashore during mid-incubation.

Quantitative observations of seasonal changes in the frequency of various types of behaviour have been carried out by Sapin-Jaloustre & Bourlière (1952) and Sapin-Jaloustre (1955, 1960). Their observations show two peaks in the incidence of courtship activities (the Ecstatic advertising display, the Mutual display, and copulation) corresponding to the peaks in the numbers of penguins ashore. Penney (1968:111) has also shown the seasonal variation of the Ecstatic display.

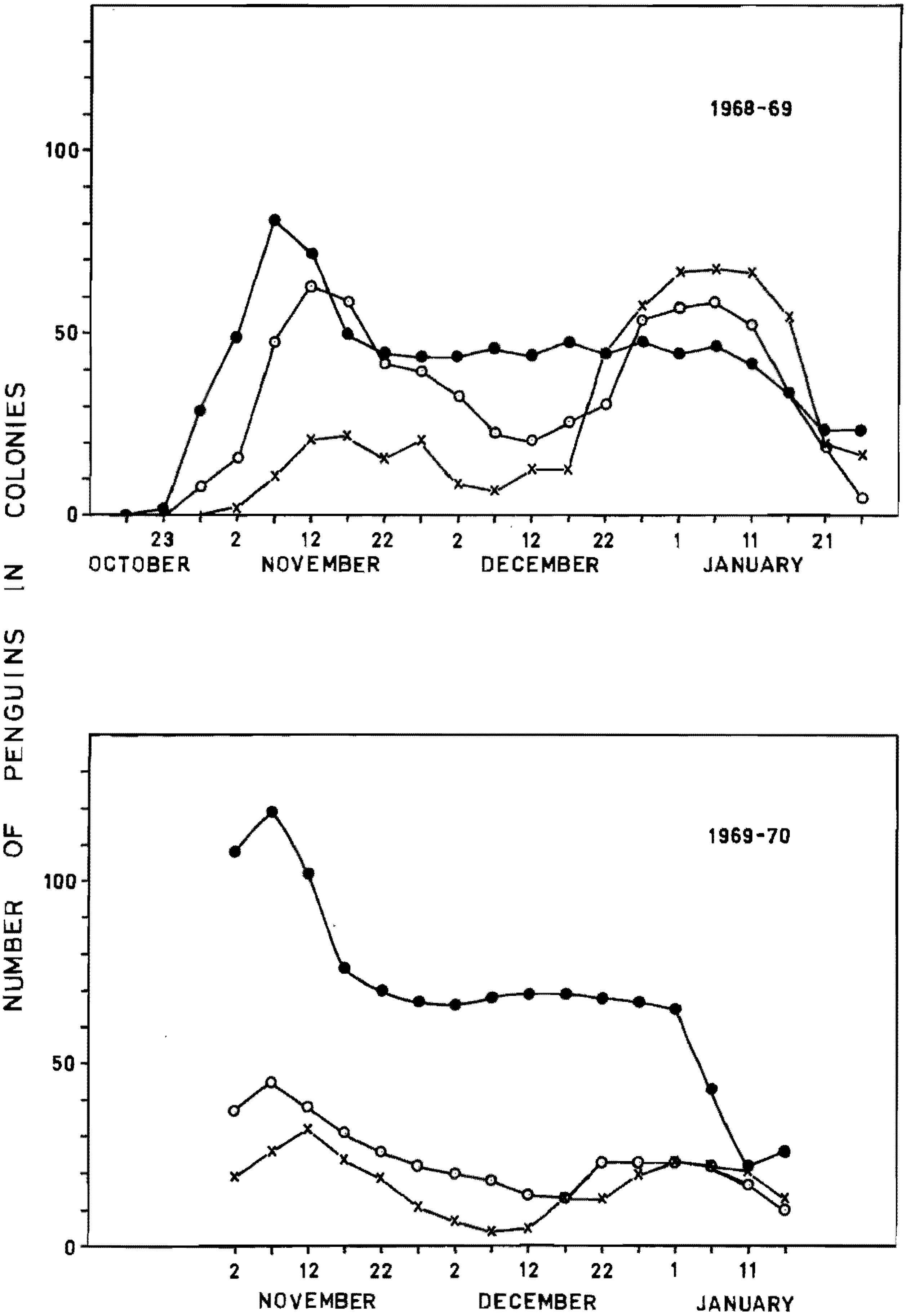
In the present study, seasonal changes in the behaviour of Adelie penguins at Cape Bird are described for penguins of different breeding status: i.e. successful breeders, unsuccessful breeders, and unmated penguins.

4.2 NUMBER OF PENGUINS ASHORE DURING THE SEASON

The numbers of penguins ashore were recorded at five day intervals (figure 29). The numbers reached a first peak in early November, during the occupation period. Mated and unmated penguins both contributed to this peak. A sharp decline in numbers occurred towards the end of November. After egg-laying, one of each mated pair departed to sea (see below). Most

FIGURE 29. Number of penguins ashore through the season.

●—● successful breeders.
o—o unsuccessful breeders.
x—x unmated penguins.


NUMBER OF PENGUINS IN COLONIES
1968-69
0
50
100
23
2
12
22
2
12
22
1
11
21
OCTOBER
NOVEMBER
DECEMBER
JANUARY
1969-70
0
50
100
2
12
22
2
12
22
1
11
NOVEMBER
DECEMBER
JANUARY

unmated penguins also departed about this time. The total number of penguins ashore reached a second peak toward the end of December, during the reoccupation period. This peak consisted mainly of unmated penguins and unsuccessful breeders.

The relationship between the two peaks of population numbers varied from season to season. Thus, in 1968-69 when there was a very low return of penguins to breed, and a high percentage of unsuccessful breeding, the second peak of numbers was larger than the first peak. However, in each of the other three seasons the numbers of penguins ashore in the occupation period was greater than in the reoccupation period.

The number of days that individual penguins spent ashore was determined from observations made at about the same time (2100 hours) each day. Ten examples each of successful breeders, unsuccessful breeders, and unmated penguins are shown in figures 30, 31, and 32. (See also Sladen 1958:figure 16, Taylor 1962:figure 11, Penney 1968:figures 7 & 16).

Successful pairs (figure 30) spent some time ashore together in the occupation period prior to egg-laying (see also section 7.6). Thereafter, only one member of each pair remained at the nest, either incubating eggs or guarding chicks. This meant that after egg-laying only about half the successful breeders were ashore at any one time (see also figure 29). Individual nest watches were at first long (see also section 7.7), but after the chicks hatched parents usually changed nest duty every day or twice every three days.

Unsuccessful breeders (figure 31) followed a routine similar to that of successful breeders until they lost the eggs or chicks. Following this, their behaviour was similar to that of unmated penguins (see below).

Unmated penguins that returned in the occupation period arrived later than breeding penguins. After a period ashore, they then departed for sea again to break their fast (figure 32). However, because of individual variability in departure and arrival there were usually some unmated penguins present in the colonies at all times. Some (banded) unmated penguins, especially females, did not arrive until the reoccupation period. Reoccupying penguins (unmated and unsuccessful breeders) made only infrequent visits to sea. They did not make daily excursions for food as did successful breeders. Females made more frequent visits to sea than males (figure 31 & 32).

FIGURE 30. Nest attendance through the season by ten pairs of successful breeders.

O represents egg-laying.
X represents chick hatching.

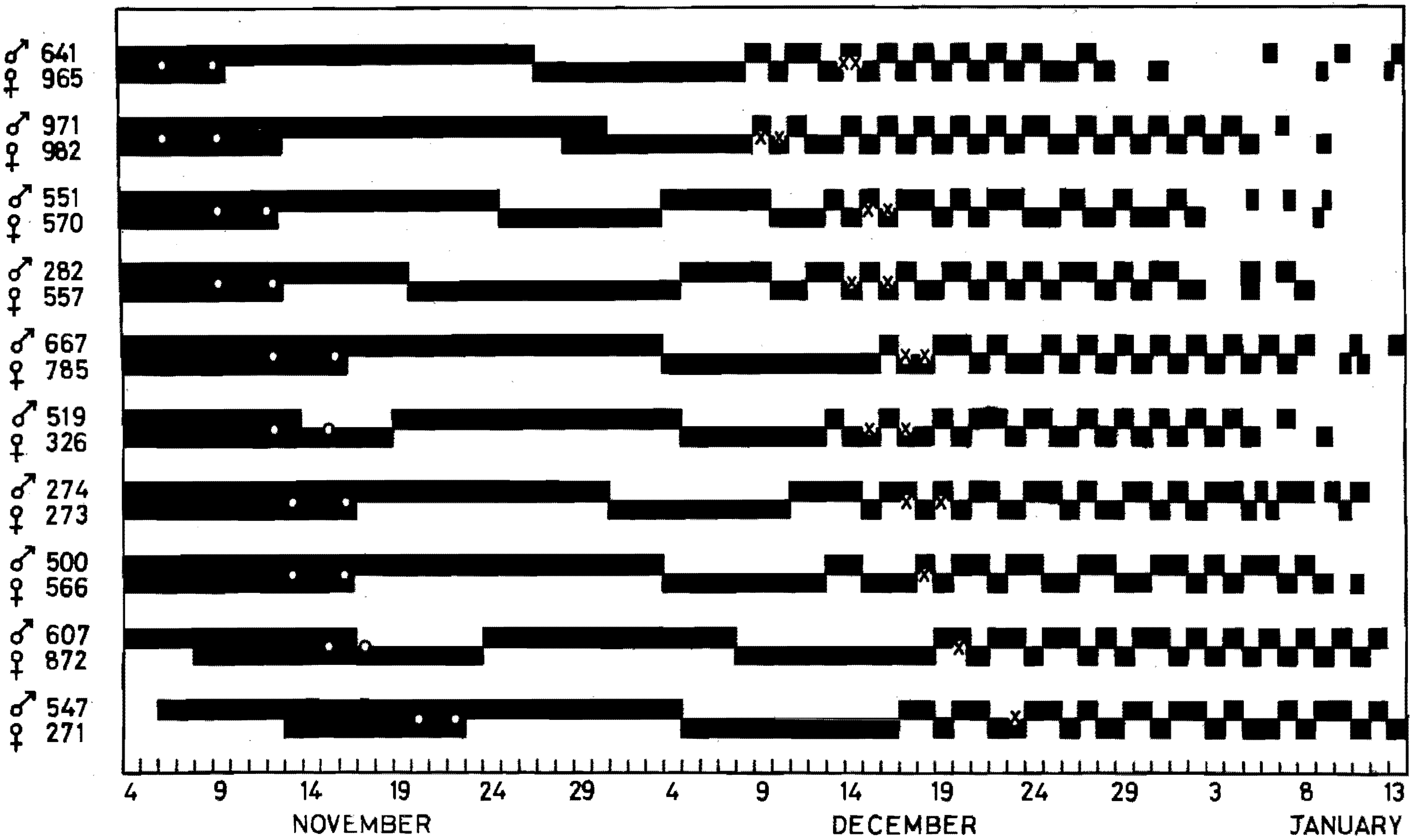

♂ 641
♀ 965
♂ 971
♀ 982
♂ 551
♀ 570
♂ 282
♀ 557
♂ 667
♀ 785
♂ 519
♀ 326
♂ 274
♀ 273
♂ 500
♀ 566
♂ 607
♀ 872
♂ 547
♀ 271
4
9
14
19
24
29
4
9
14
19
24
29
3
8
13
NOVEMBER
DECEMBER
JANUARY

FIGURE 31. Nest attendance through the season by ten pairs of unsuccessful breeders.

O represents egg-laying.
X represents chick hatching.
Arrow represents loss of nest contents.

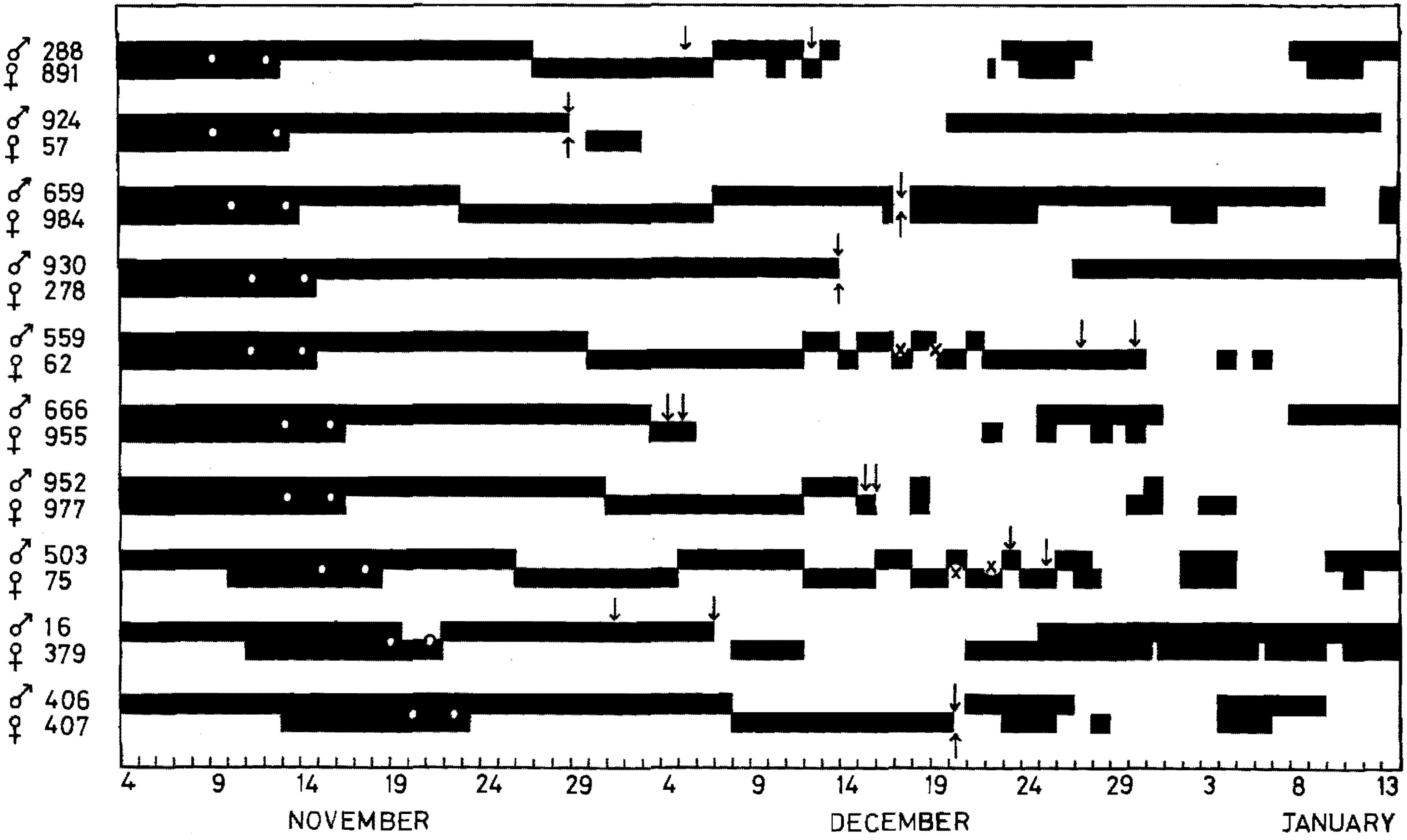
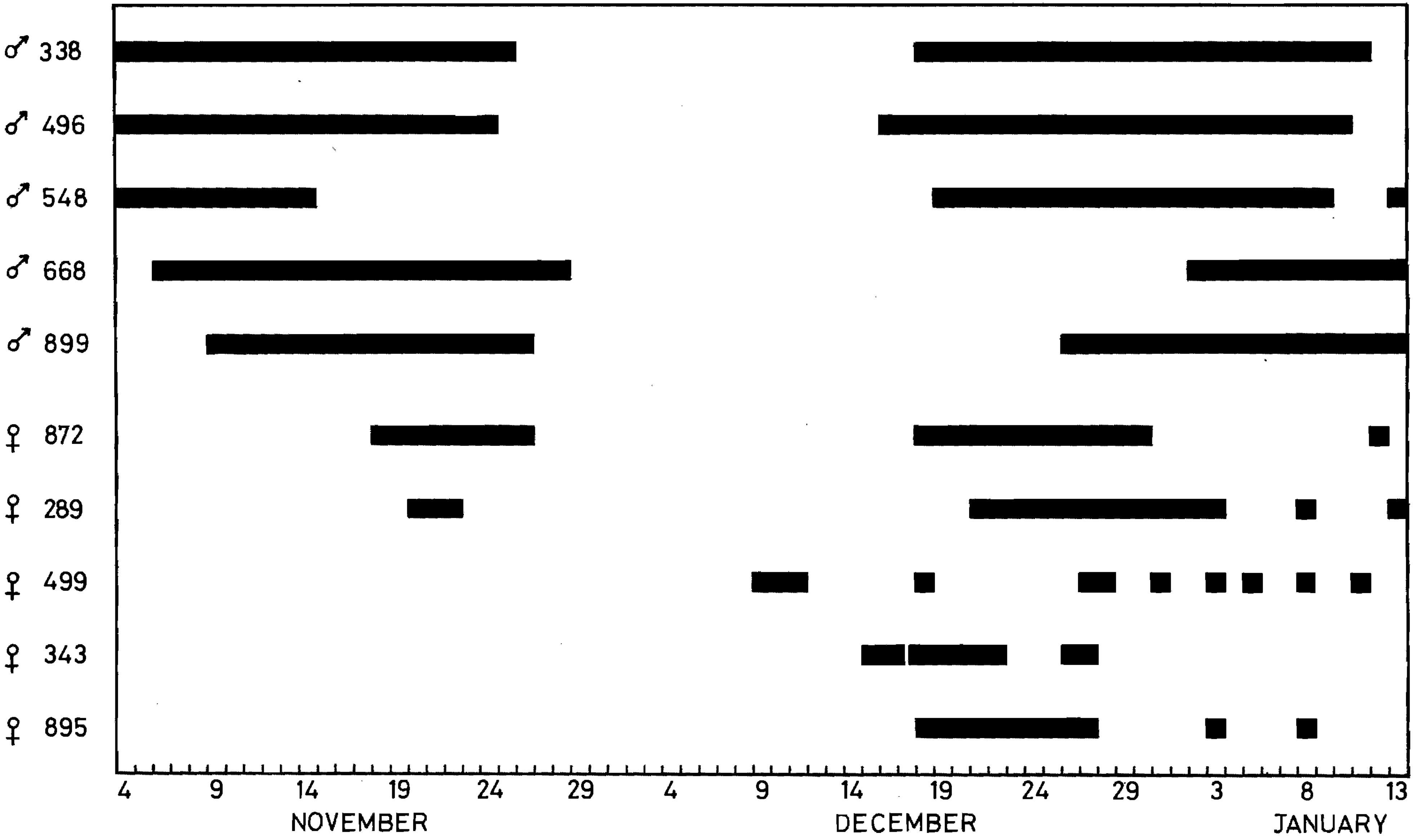

♂ 288
♀ 891
♂ 924
♀ 57
♂ 659
♀ 984
♂ 930
♀ 278
♂ 559
♀ 62
♂ 666
♀ 955
♂ 952
♀ 977
♂ 503
♀ 75
♂ 16
♀ 379
♂ 406
♀ 407
4
9
14
19
24
29
4
9
14
19
24
29
3
8
13
NOVEMBER
DECEMBER
JANUARY

FIGURE 32. Nest attendance through the season by ten unmated penguins.


♂ 338
♂ 496
♂ 548
♂ 668
♂ 899
♀ 872
♀ 289
♀ 499
♀ 343
♀ 895
4
9
14
19
24
29
4
9
14
19
24
29
3
8
13
NOVEMBER
DECEMBER
JANUARY

4.3 FREQUENCY OF DIFFERENT TYPES OF BEHAVIOUR THROUGH THE SEASON

The incidence of different types of behaviour was determined from observations on a group of penguins at about 500 nests in H Block. This group was ideal for such work because it was isolated from the main part of the rookery, and the colonies were linear, a factor which simplified location of individual penguins. The observation hide was sited on a 50 metre ridge directly overlooking the penguins. Observations were made for periods of up to six hours every five days.

Figure 33 shows the incidence of attacks or fights involving flipper beating during the season. They occurred, for example, between rival males disputing territory ownership, between females claiming the same male, and when penguins of either sex were caught stealing nest stones, or otherwise trespassing on the territory. Of 130 fights observed, 75 percent involved penguins without eggs or chicks. A further 18 percent involved one penguin without eggs or chicks and one parent, 4 percent involved parents only, and 3 percent involved penguins of unknown status. The incidence of attacks through the season was closely related to the numbers of penguins ashore without eggs or chicks (compare figures 29 & 33). In the occupation period, both penguins which eventually became mated and those that remained unmated were involved in major attacks. However, in the chick period (or reoccupation period) most attacks and fights occurred among the unsuccessful breeders and unmated penguins.

The change in number of penguins ashore had a marked effect on the incidence of several activities through the season. Figures 34 and 35 show the incidence of activities concerned with pair formation, nest building, and territory defence. In the middle of the season (from about 29 November to 14 December) all activities decline to a low level, in total number as well as incidence per bird. During this time, the total number of penguins present in the colonies is at its lowest, and most of those present are incubating, one penguin per nest.

Successful breeders, unsuccessful breeders, and unmated penguins made different contributions to the seasonal peaks of behaviour. Figures 36, 37, and 38 show the frequency of various

FIGURE 33. Incidence of attacks involving flipper beating.

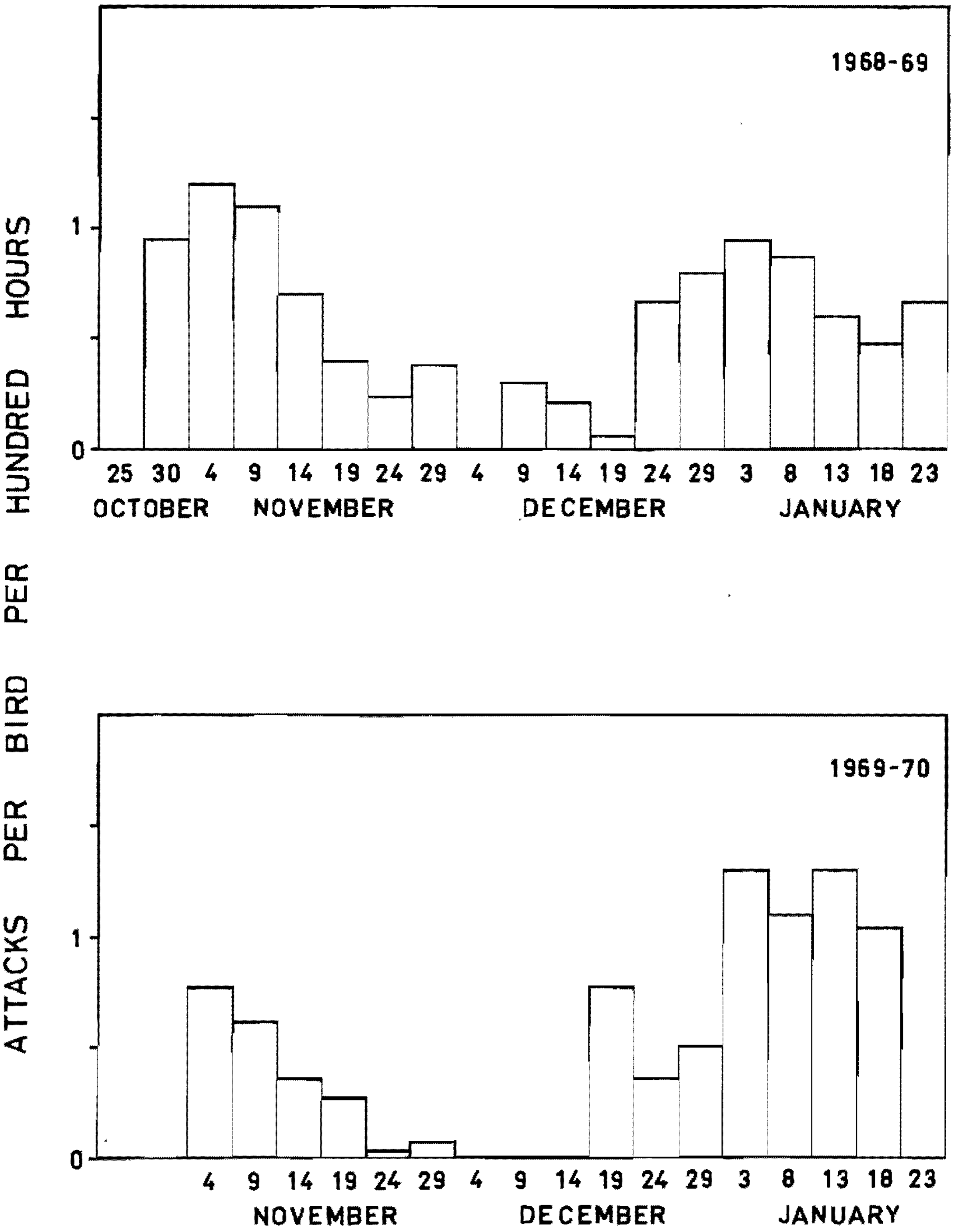

ATTACKS PER BIRD PER HUNDRED HOURS
1968-69
1
0
25 30 4 9 14 19 24 29 4 9 14 19 24 29 3 8 13 18 23
OCTOBER NOVEMBER DECEMBER JANUARY
1969-70
1
0
4 9 14 19 24 29 4 9 14 19 24 29 3 8 13 18 23
NOVEMBER DECEMBER JANUARY

FIGURE 34. Incidence of several activities in 1968-69.

a. Nest Build.
b. Ecstatic display.
c. Bow.
d. Copulation.
e. Quiet Mutual.
f. Loud Mutual.

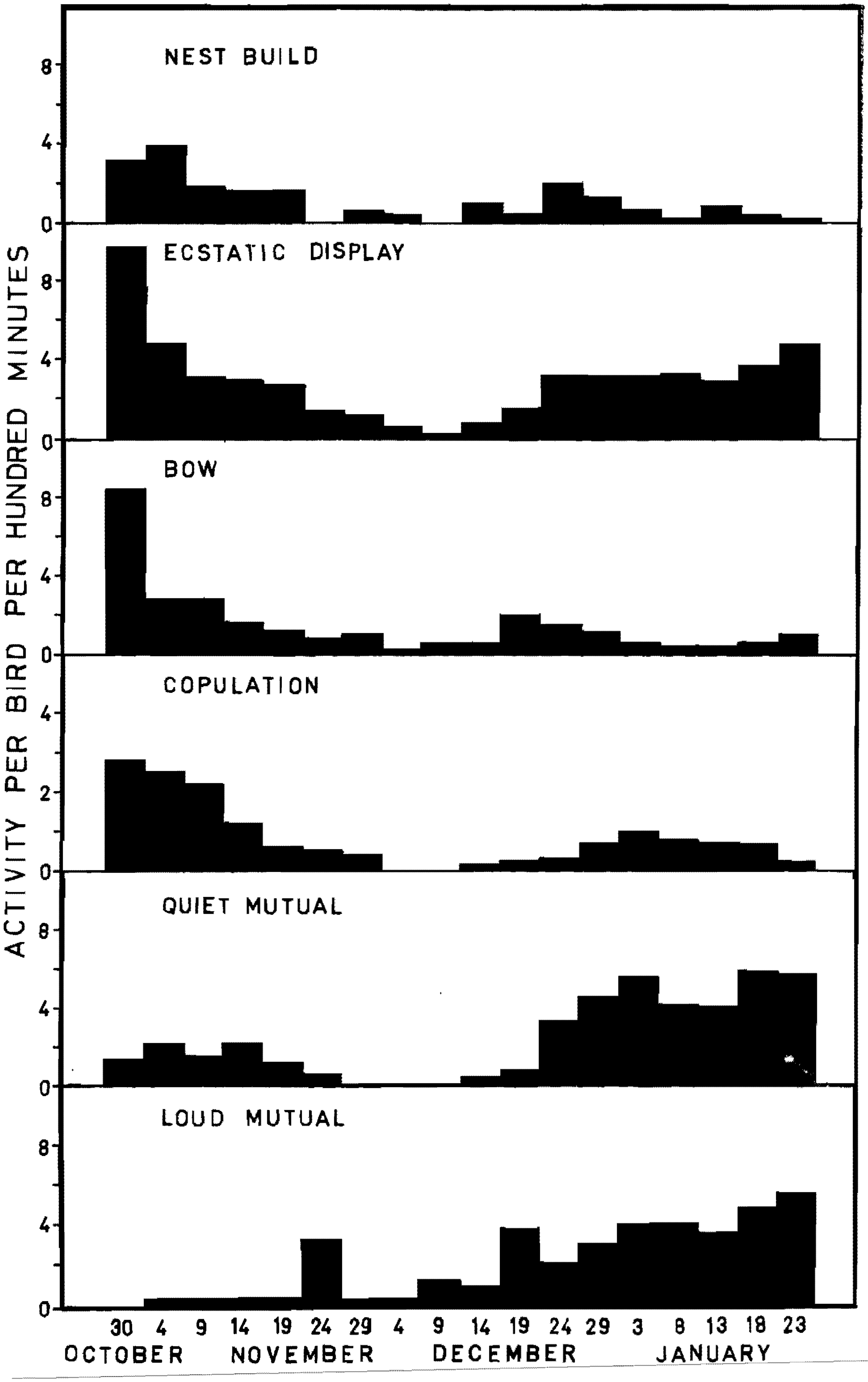
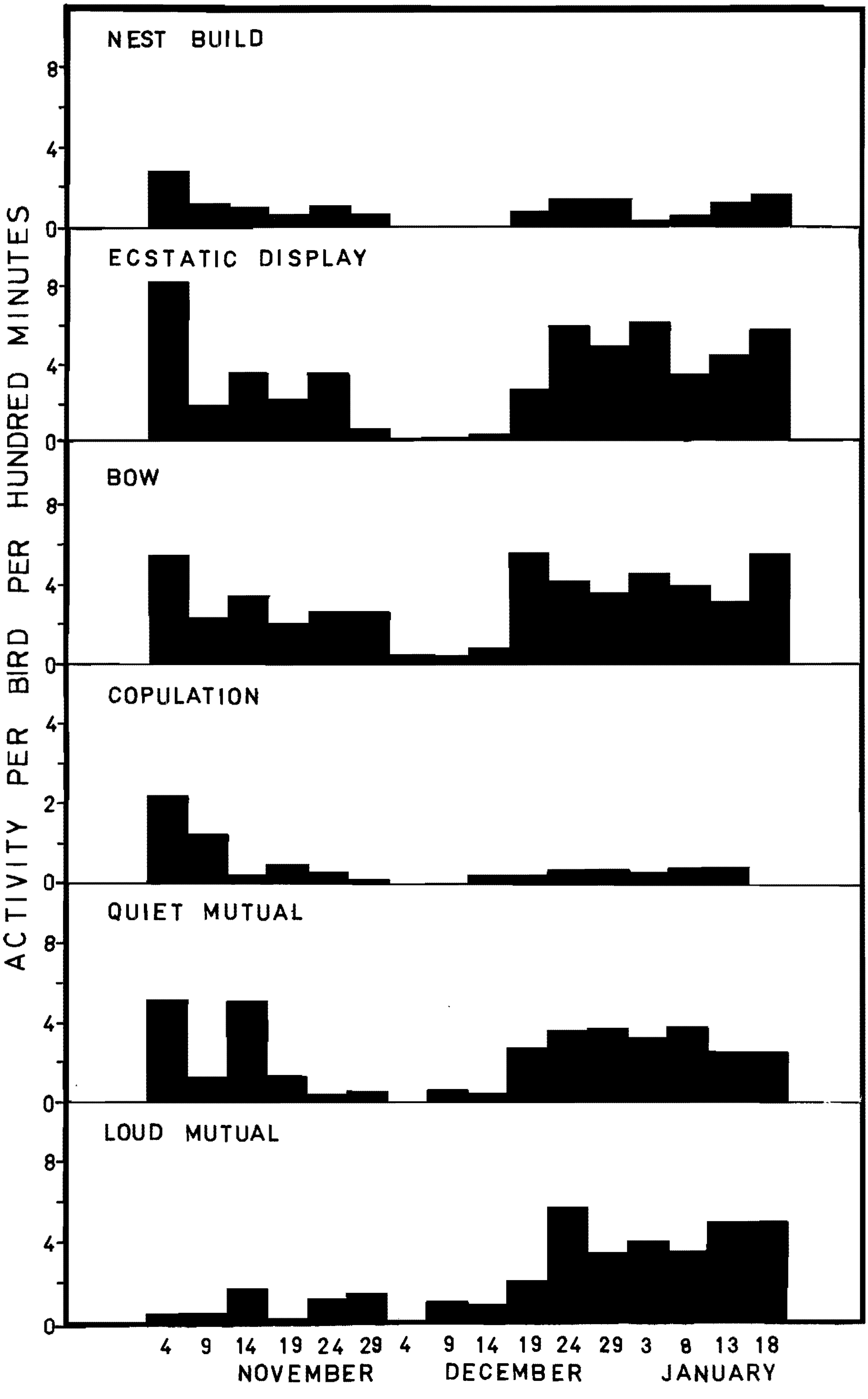

NEST BUILD
ECSTATIC DISPLAY
BOW
COPULATION
QUIET MUTUAL
LOUD MUTUAL
ACTIVITY PER BIRD PER HUNDRED MINUTES
0
2
4
8
30
4
9
14
19
24
29
4
9
14
19
24
29
3
8
13
18
23
OCTOBER
NOVEMBER
DECEMBER
JANUARY

FIGURE 35. Incidence of several activities in 1969-70.

a. Nest Build.
b. Ecstatic display.
c. Bow.
d. Copulation.
e. Quiet Mutual.
f. Loud Mutual.


NEST BUILD
ECSTATIC DISPLAY
BOW
COPULATION
QUIET MUTUAL
LOUD MUTUAL
ACTIVITY PER BIRD PER HUNDRED MINUTES
0
2
4
8
4 9 14 19 24 29 4 9 14 19 24 29 3 8 13 18
NOVEMBER
DECEMBER
JANUARY

activities recorded from 10 minute observations on known individuals throughout the season.

i. Successful breeders (figure 36).

Nest building was usually initiated by the male, who also selected the territory. After pairing up, both male and female continued nest building. Once the eggs were laid the incidence of nest building decreased, though maintenance occurred throughout the season (figure 36a). When a pair changed nest duty, either the arriving or departing penguin may replenish stones lost from the nest.

Prior to pairing, males frequently performed the Ecstatic display advertising their presence in the colony. Among successful breeders, this display was restricted almost entirely to the occupation period (figure 36b). Isolated outbursts of Ecstatic display by parents with eggs or chicks were probably stimulated either by being alone (as before egg-laying) or by other penguins displaying nearby.

Bowing occurred during pair formation, and between members of established pairs (see section 3.4ii). It occurred most frequently before egg-laying (figure 36c) when the pair spent considerable time together at the nest.

Mutual displays, including both the Loud and Quiet Mutual (see section 3.4iii) were performed when members of a pair reunited after a long absence, and at other times when they were together on the territory. These displays were most frequent prior to egg-laying, and again after chick hatching (in mid-December) when parents changed nest duty almost every day (figure 36e).

Copulations were frequent before egg-laying, but sometimes occurred after the female had laid one or two eggs. Soon after the clutch was complete, however, one of the pair (usually the female) departed for sea, and copulation did not occur again (figure 36d).

The incidence of threat displays and simple pecking closely followed the number of penguins ashore. When there were more penguins present in the colonies, there were more to threaten. Thus, in the occupation period, and again in the chick period (when unsuccessful breeders and unmated penguins reoccupied the colonies) successful breeders spent more time defending their territories than during the incubation period.

FIGURE 36. Seasonal variation in behaviour of successful breeders.

a. Nest Build.
b. Ecstatic display.
c. Bow.
d. Copulation.
e. Mutual display.
f. Threat.

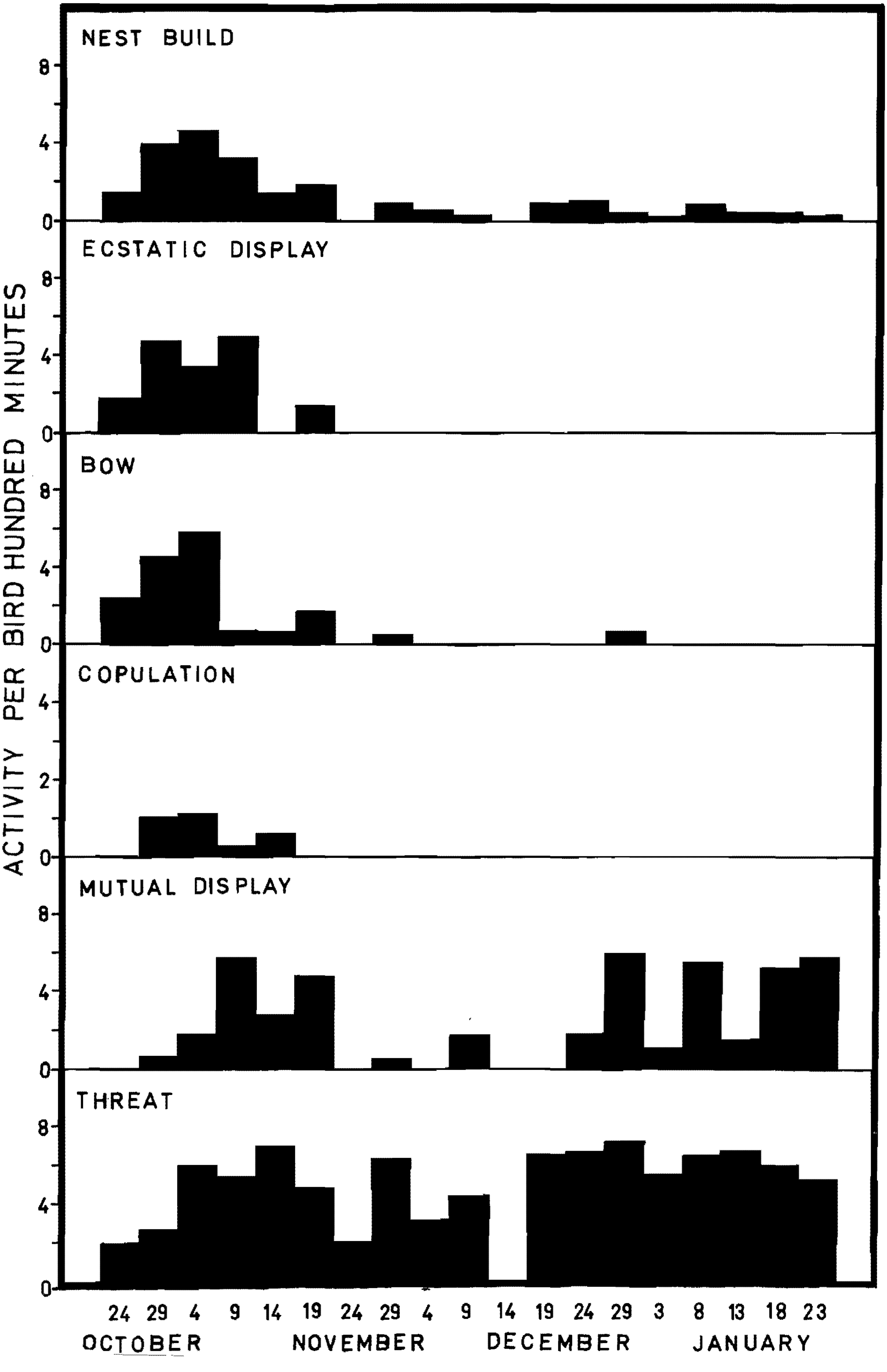

NEST BUILD
ECSTATIC DISPLAY
BOW
COPULATION
MUTUAL DISPLAY
THREAT
ACTIVITY PER BIRD HUNDRED MINUTES
0
4
8
2
24
29
4
9
14
19
24
29
4
9
14
19
24
29
3
8
13
18
23
OCTOBER
NOVEMBER
DECEMBER
JANUARY

FIGURE 37. Seasonal variation in behaviour of unsuccessful breeders.

a. Nest Build.
b. Ecstatic display.
c. Bow.
d. Copulation.
e. Mutual display.
f. Threat.

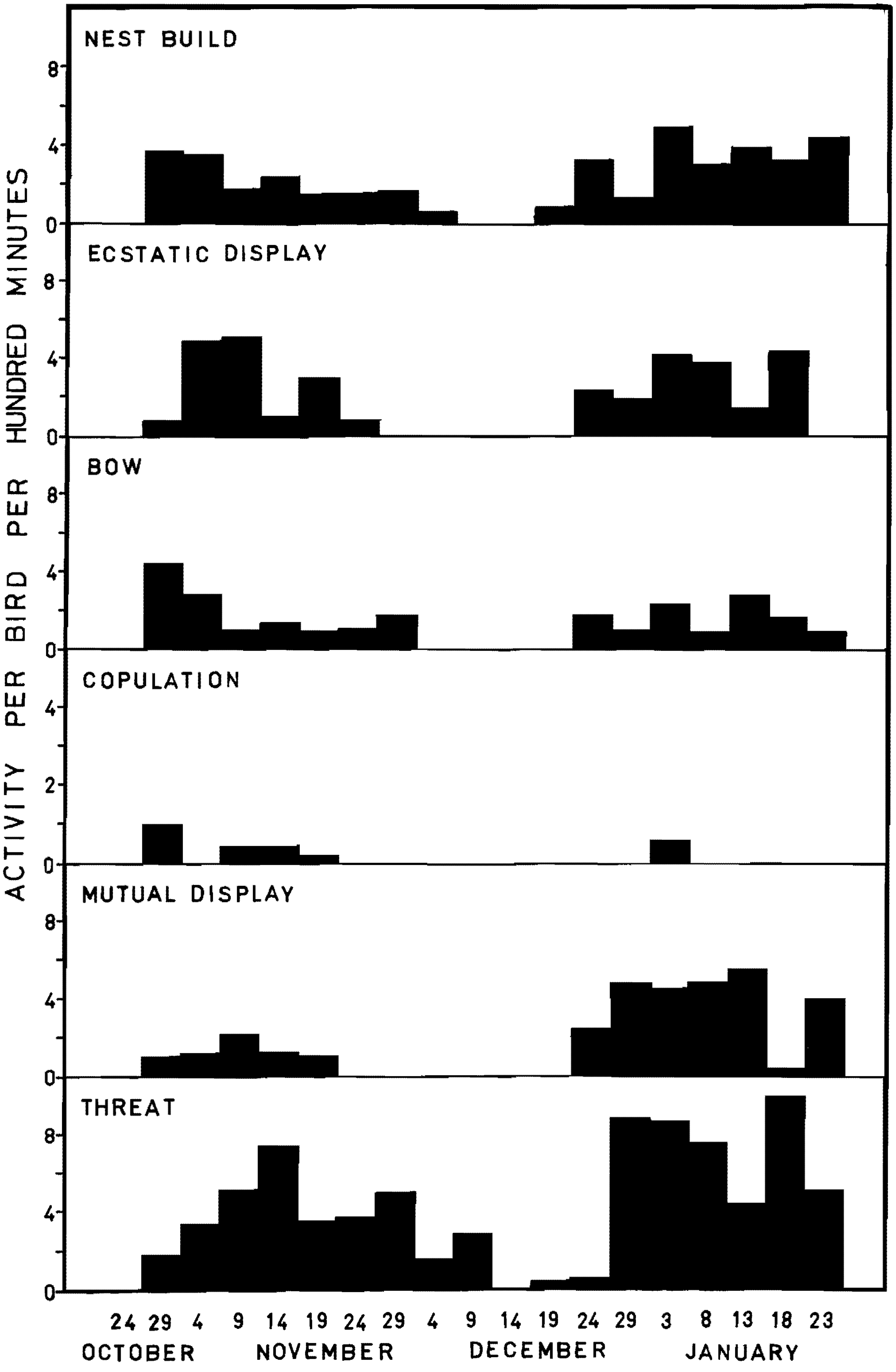
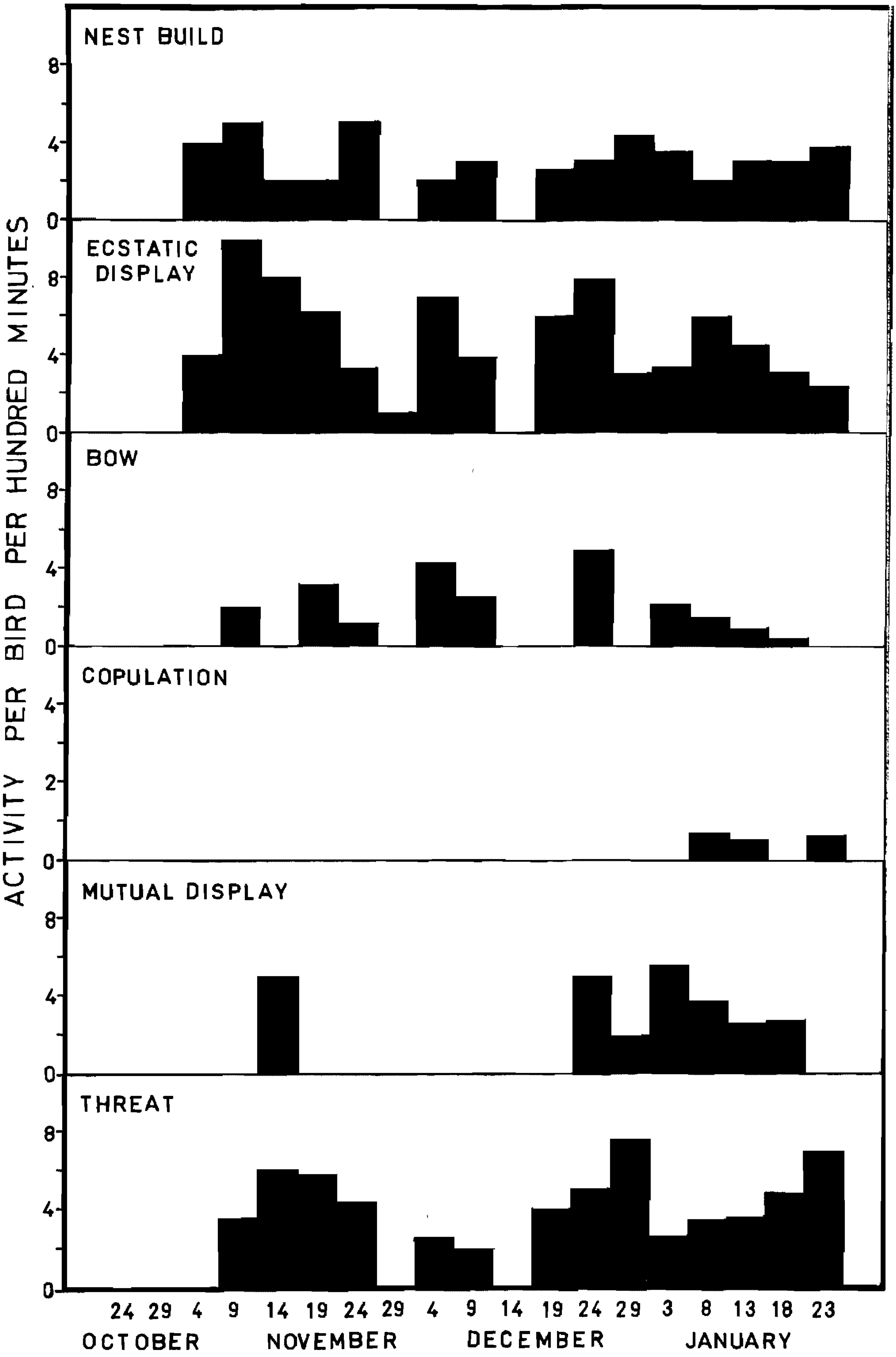

NEST BUILD
ECSTATIC DISPLAY
BOW
COPULATION
MUTUAL DISPLAY
THREAT
ACTIVITY PER BIRD PER HUNDRED MINUTES
0
4
8
2
24
29
4
9
14
19
24
29
4
9
14
19
24
29
3
8
13
18
23
OCTOBER
NOVEMBER
DECEMBER
JANUARY

FIGURE 38. Seasonal variation in behaviour of unmated penguins.

a. Nest Build.
b. Ecstatic display.
c. Bow.
d. Copulation.
e. Mutual display.
f. Threat.


ACTIVITY PER BIRD PER HUNDRED MINUTES
NEST BUILD
ECSTATIC DISPLAY
BOW
COPULATION
MUTUAL DISPLAY
THREAT
0
2
4
8
24 29 4 9 14 19 24 29 4 9 14 19 24 29 3 8 13 18 23
OCTOBER
NOVEMBER
DECEMBER
JANUARY

The increased number of threat displays on November 29 and December 9, 1968, was also noted in the incidence of fighting, and reflects the increased number of unmated penguins present on those days (compare figure 29 and 36).

ii. Unsuccessful breeders (figure 37).

The behaviour of unsuccessful breeders (figure 37) was at first similar to that of successful breeders, but after losing eggs or chicks, their behaviour was more like that of unmated penguins (see below).

iii. Unmated penguins (figure 38)

In the occupation period, unmated penguins performed many of the activities of successful breeders. Males established and defended a territory, built a nest, and advertised for females. However, most unmated males were unable to obtain a mate. This was partly due to the shortage of females (section 7.3). The few associations that did form were usually brief, and did not produce eggs. After a period ashore, unmated penguins departed for sea to break their fast.

The return of penguins (unmated penguins and unsuccessful breeders) in the reoccupation period resulted in a resurgence of threat displays, fighting, nest building, and pair formation activities (figures 37 & 38). Much behaviour that occurred in the occupation period, occurred again in the reoccupation period. Copulation also occurred frequently, especially among pairs together for some length of time, but no eggs were ever produced.

4.4 RELATIONSHIP BETWEEN FIGHTING AND CHICK MORTALITY

The resurgence of fighting in the reoccupation period occurred just after the time of chick hatching, and at a time when chick losses were high (see section 7.8i, and figure 50). Chick losses, however, were not related to fighting. Where the cause of mortality could be established, only about 5 percent of all losses were caused by fighting (see section 7.8ii). Furthermore, in a total of 130 fights, only six (or less than 5 percent) resulted in loss of eggs or chicks. The losses occurred only in fights in which breeding penguins became directly involved (which comprised only about 20 percent of all fights).

It will be noted that in 1968-69, when there was a large number of unmated penguins and unsuccessful breeders present in the reoccupation period, the number of fights per penguin was no greater than in other seasons. Also, the chick mortality was not significantly greater (see section 7.8).

4.5 DISCUSSION; SEASONAL CYCLE IN OTHER SPECIES

In many species of birds there are two peaks of sexual activity, one in spring and one in autumn (e.g. see Morley 1943). That is, many birds which have bred successfully in spring also show a peak of sexual activity in autumn. The autumn resurgence of sexual activity occurs at the end of the moult in both multiple and single brooded species, and corresponds with a reactivation of the gonads (Marshall 1960:56).

Adelie penguins that successfully raise chicks have only one peak of sexual activity, correlated with maximum development of the gonads before the eggs are laid in early November (see Sladen 1958:28). This is also true of the related Gentoo penguin, Pygoscelis papua (Roberts 1940:227).

Adelie penguins that reoccupy the colonies after breeding unsuccessfully may have slightly enlarged gonads (Sladen 1958:57). However, the midsummer reoccupation of Adelie penguin rookeries can be only superficially likened to an autumn resurgence of sexual activity. It most closely resembles an attempt to start a second clutch, because it occurs only in unsuccessful breeders and unmated penguins, and precedes moulting.

The persistence of sexual activity after the time when eggs can be laid and chicks successfully raised suggests that it may confer some advantages upon the individuals concerned. It has been postulated (e.g. Morley 1943:152, Marshall 1960:56) for species with an autumn resurgence, that reoccupation serves as a reservation of the breeding site for the following season. For the Adelie penguin, Sladen (1958:59) suggested that the reoccupation period was important for "the establishment of future territorial rights and pair-bonds among the unsuccessful, unestablished breeders or non-breeders". However, until now quantitative evidence has been lacking.

In another section (section 6) it will be shown that penguins (more especially males) which reoccupy the colonies with a stable partner have a greater chance of pairing up the following season than penguins that do not acquire a stable reoccupation site or partner. Territorial and pair formation behaviour observed at this time is valuable for establishing and stabilising site and pair bonds among unsuccessful breeders and unmated penguins.

5.0 ACTIVITY CYCLES IN CONTINUOUS LIGHT

5.1 INTRODUCTION

Animals in temperate and tropical regions have sharply defined day and night cycles of activity. In polar latitudes, where there is continuous light throughout the summer, animals may be active throughout both day and "night". Even in continuous light, however, there is still a regular fluctuation of light intensity and temperature, and many animals maintain a regular cycle of rest and activity (Armstrong 1954, Cullen 1954, Brown 1963).

There have been two studies published on diurnal rhythms in Adelie penguins. The results of these two studies appear conflicting. Müller-Schwarze (1968) found diurnal variations in several activities at Cape Hallett (72° 19'S), whereas Yeates (1971) did not find any consistent variation in activities at Cape Royds (77° 33'S). The more even light regime of Cape Royds (which is further south than Cape Hallett) was suggested as a possible reason for this difference (Yeates 1971:110).

The present study was made at Cape Bird (77° 13'S) which is at a similar latitude to Cape Royds. The behaviour of selected individuals was compared with fluctuations of incident radiation and temperature. Wind was known to affect the behaviour of penguins (see section 10.4), and observations were not made when the wind speed was stronger than about 3 metres per second.

5.2 CLIMATIC FACTORS

Incident radiation was recorded continuously on an actinograph. On a clear sunny day near the summer solstice (December 22) the diurnal variation in incident radiation ranged from a minimum of 10 $cal/cm^2/hour$ to a maximum of 43 $cal/cm^2/hour$. Bursts of up to 59 $cal/cm^2/hour$ were recorded when the sun penetrated breaks in the cloud cover on partly cloudy days. Maximum radiation on the rookery occurred at midday (LST), but because of shadows cast by Mt Bird minimum radiation did not occur at midnight. The whole rookery was shaded for about three hours (between 0030 and 0330) at midsummer, increasing to about six hours (between 2300 and 0500) in early (and late) summer. On a uniformly cloudy day the variation in incident radiation was less than half that on a uniformly sunny day (figure 39).

Air temperatures were recorded at 150 cm above ground level by a thermograph in a standard meteorological screen. Maximum temperatures occurred at about 1500 hours (LST) and minimum temperatures between 0300 and 0600 hours (figure 40). Temperatures lagged somewhat behind incident radiation. The average daily range (during the period of study) was $5.3^{\circ}C$. The maximum daily range recorded was $10.0^{\circ}C$ and the minimum daily range was $2.7^{\circ}C$. The highest temperature recorded was $5.6^{\circ}C$ (on 5 January 1971) and the lowest was $-13.5^{\circ}C$ (on 21 November 1970).

5.3 NUMBERS AND MOVEMENTS OF PENGUINS AT THE ROOKERY

The number of penguins present in the colonies at any one time fluctuated with the arrival and dispersal of penguins to sea. Throughout the occupation period (October to early November) penguins were arriving to prepare for breeding. After arriving, they spent a considerable period of time continuously in the colonies (section 4.2). In the reoccupation period (December to January) penguins that had lost their nest contents or never laid also spent considerable time ashore. It was only during the chick period (late December to early January) that successful breeders made daily excursions to sea to collect food for chicks. The numbers returning to nests appeared to reach a peak in the early morning (0600 to 0900 hours; see figure 41) but the difference is not significant (Chi square, $p > 0.05$). Nest arrivals continued steadily throughout the 24 hour day.

Müller-Schwarze (1968) found morning peaks for both returning and departing penguins walking over the shore, but only a departing peak for penguins swimming in the water. Yeates (1971) found no significant diurnal variation in outward or inward movements.

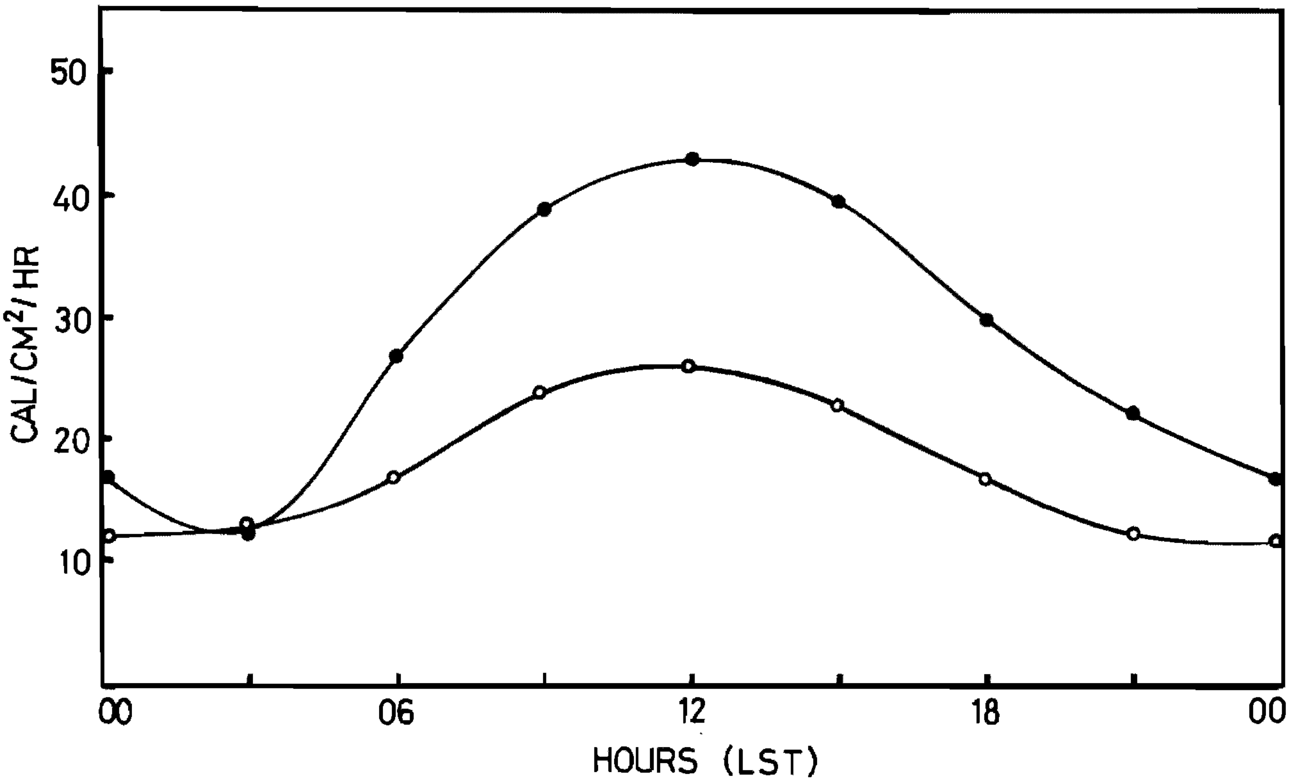
Fluctuations in the numbers of penguins within a colony did not appear to show any diurnal variation (figure 42). The

FIGURE 39. Diurnal variation in incident radiation.

●—● uniformly sunny day.
o—o uniformly cloudy day.

FIGURE 40. Diurnal variation in screen temperatures during two periods of the study.

●—● mid-summer (20 December 1970).
o—o early summer (26 November 1970).


CAL/CM²/HR
50
40
30
20
10
00
06
12
18
00
HOURS (LST)

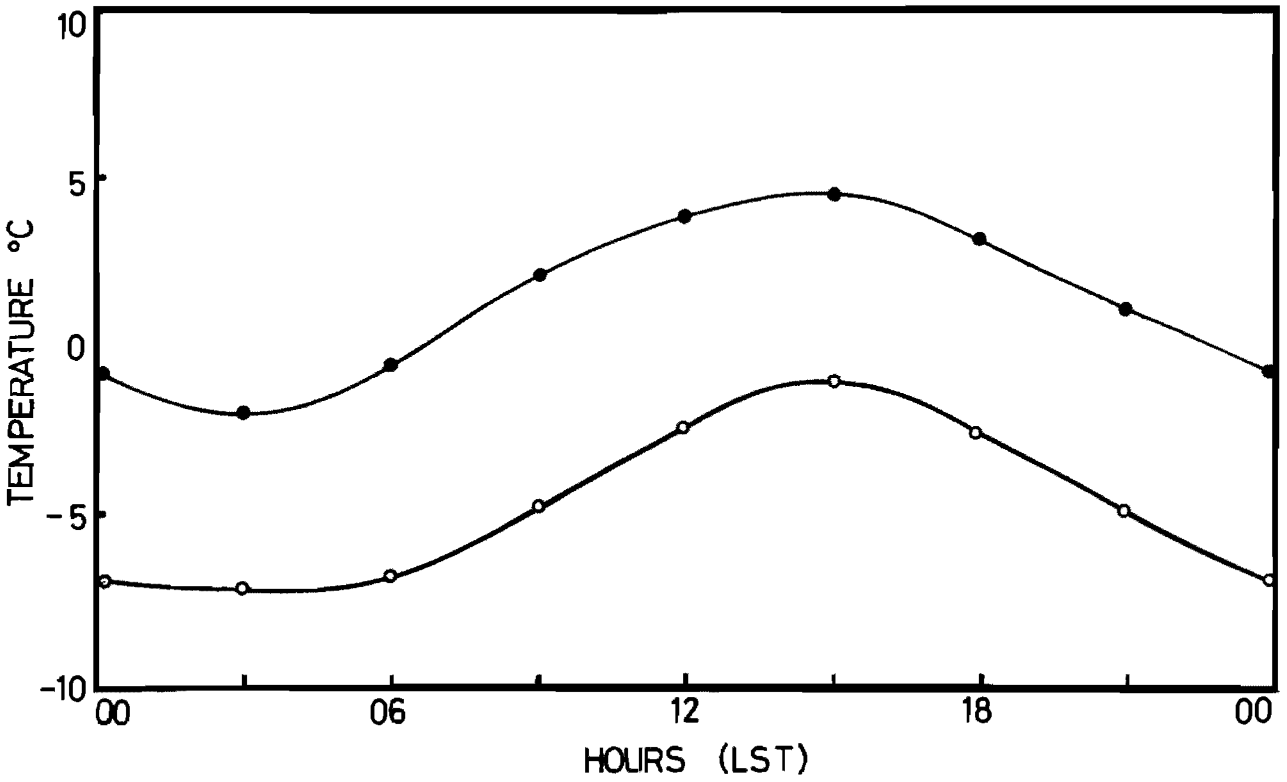
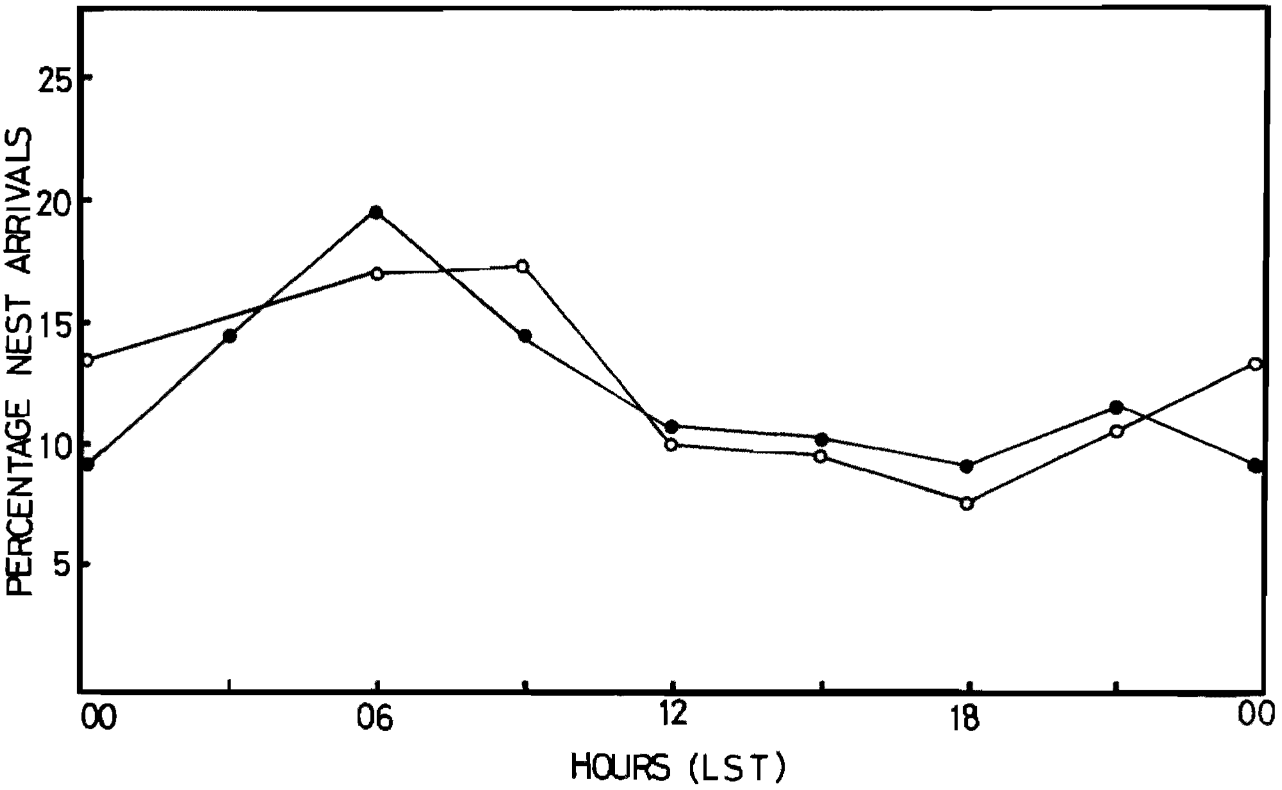
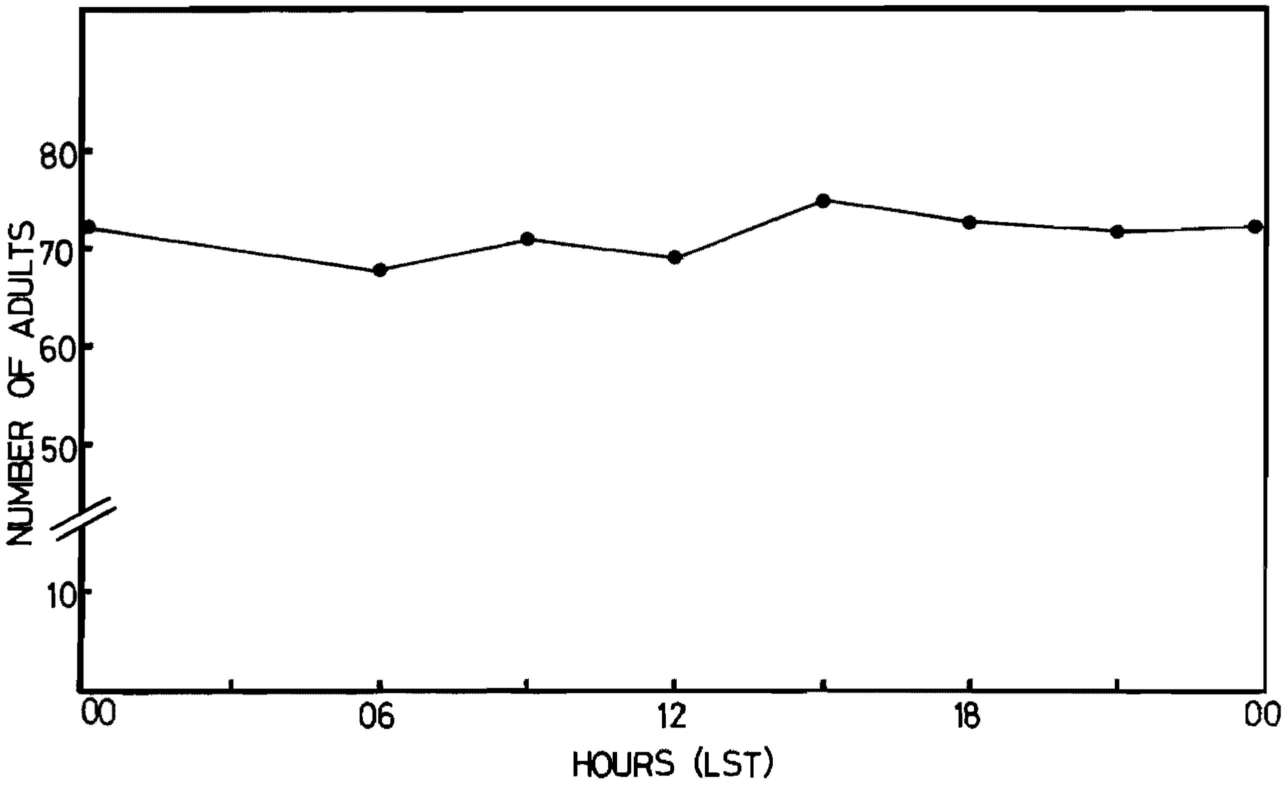

TEMPERATURE °C
10
5
0
-5
-10
00
06
12
18
00
HOURS (LST)

FIGURE 41. Fluctuations in the number of nest arrivals.

●—● 30 December - 14 January 1971.
o—o 29 December - 30 December 1969.

FIGURE 42. Fluctuations in the number of penguins within a colony.


PERCENTAGE NEST ARRIVALS
25
20
15
10
5
00
06
12
18
00
HOURS (LST)


NUMBER OF ADULTS
80
70
60
50
10
00
06
12
18
00
HOURS (LST)

colony population is not likely to be markedly affected by daily nest changes, because the relieved parent departs for sea almost immediately. Irregularities may be caused by parents with only one chick, where the relieved parent might not leave for sea immediately (see also section 8.2). The greatest fluctuations in the colony population, however, were probably caused when groups of unestablished penguins, ranging in size from about three to more than a dozen individuals, "invaded" a colony for a short time during the reoccupation period. Some of these unestablished penguins held territories or remained within the vicinity of a colony, taking part in its activities, for various lengths of time (maybe a whole day) before moving on again.

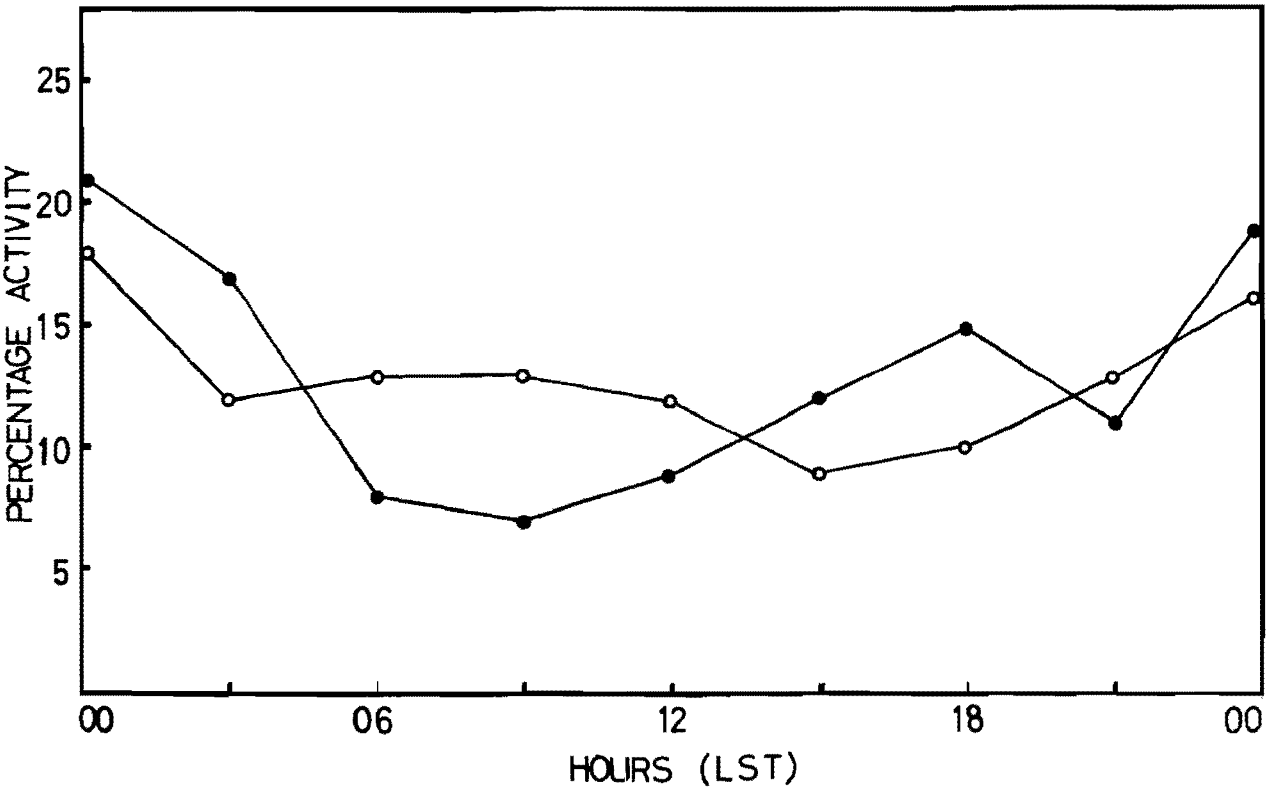
5.4 ACTIVITIES WITHIN THE COLONIES

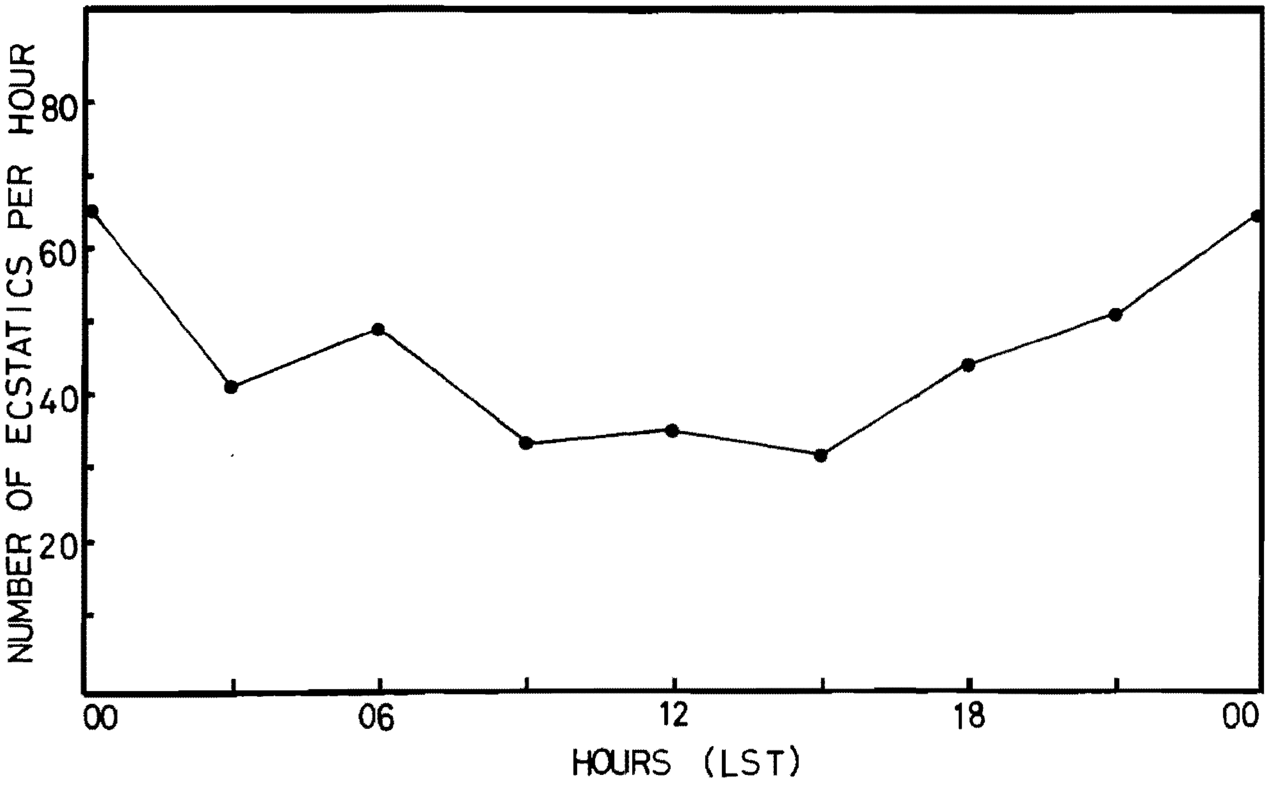
The activities of a known number of penguins were recorded during two periods (November 18 to 29, and December 29 to January 14) at the seasonal peaks of activities (see section 4.3). Observations were made for periods of one hour at various times throughout the 24 hour cycle. All activities were recorded. The penguins selected for observation were all males, and were unmated or unsuccessful breeders. Thus, they remained ashore for long periods of time during the study.

The incidence of activities of any type (nest building, territory defence, courtship, and comfort activities) showed significant day-time minima and "night-time" maxima (figure 43); i.e. an inverse relation to the light and temperature cycles (chi square, $p < 0.01$). As light and temperature increased, activity decreased, and as they decreased activity increased. Müller-Schwarze (1968:139) found a similar relationship between the two measures at Cape Hallett.

The incidence of the Ecstatic (male advertising) display at Cape Bird showed day-time minima and "night-time" maxima in the same way as other activities (figure 44). However, Müller-Schwarze (op. cit.) found two peaks of Ecstatic displays, in the morning and evening, corresponding with times of increasing or decreasing light intensities. Such peaks were not found in this study. Penney (1968:113) and Yeates (1971:108) found no particular rhythm in the frequency of the Ecstatic display.

The previous graphs of activities are averages, obtained by lumping together observation periods for individual days and


PERCENTAGE ACTIVITY
25
20
15
10
5
00
06
12
18
00
HOURS (LST)


NUMBER OF ECSTATICS PER HOUR
80
60
40
20
00
06
12
18
00
HOURS (LST)

individual penguins. In figure 45, the frequency of the Ecstatic display is plotted individually for 14 males, recorded over a period of three days. The males were all within about fifteen metres of each other, so that there may have been some social synchronisation. Nevertheless, individual rhythms of Ecstatic display frequency differed quite markedly, with peaks of activity occurring at various times. Peaks of activities for individual males pooled over three days occurred at midnight, 0300, 0600, 1800, or 2100 hours. For a particular day, however, peaks of activity may occur at any time, including midday. Some males had one marked peak, others had two or three minor peaks a day.

5.5 SHORT TERM CYCLES OF ACTIVITY

The behaviour of an individual penguin showed many short term cycles of activity. Detailed observations were made on a bachelor male (594) in early November. All activities were recorded in a minute by minute analysis continuously for 24 hours. The activities often occurred in bouts, or groups of similar activities (figure 46).

Courtship activities (mainly the Ecstatic display) occurred in bursts of varying length. Some bursts of Ecstatic displays consisted of only one or two displays, and lasted less than two minutes; others contained up to 15 displays and lasted ten minutes or more. The three hour period containing most Ecstatic displays occurred around midday (from 1030 to 1330), but the single most active hour was at midnight (2330 to 0030). On this particular day, there were three peaks of Ecstatic display activity, at about 0000, 1200, and 1800 hours (figure 46).

Periods of nest building activities (stone collecting, rearranging, and nest scraping) occurred both in conjunction with and independently of courtship activities. Some nest building activities were brief, others continued for periods of ten minutes or more.

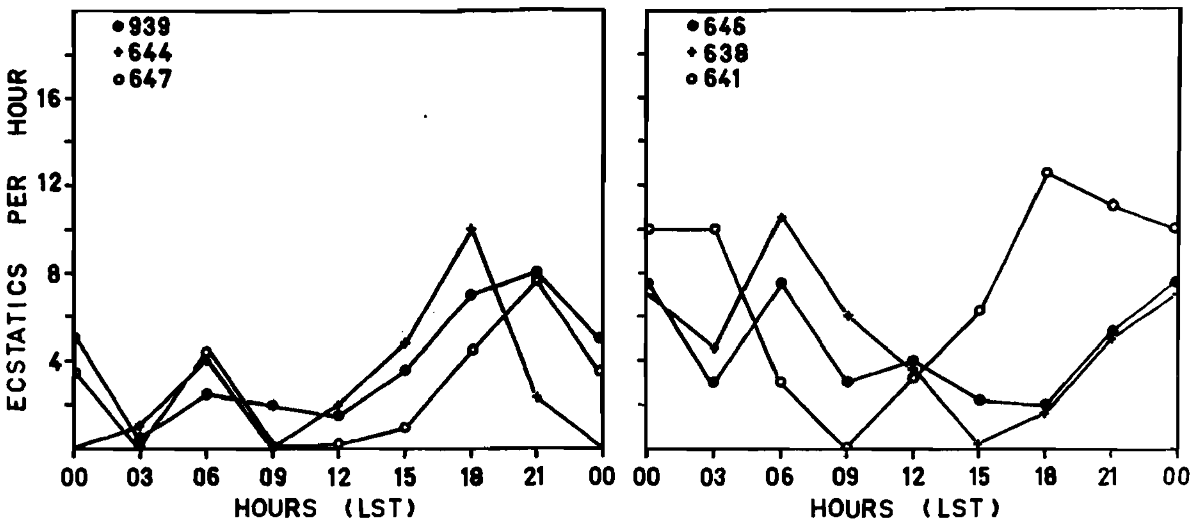
Comfort movements occurred frequently throughout the day. Many activities were followed by shaking (either all or part of the body) and/or swallowing movements. Periods of concentrated comfort movements (e.g. bouts of preening) occurred at irregular intervals. In 24 hours, male 594 performed two major bouts of

FIGURE 43. Diurnal variation in incidence of activities within the colonies.

●—● 26 November - 28 November 1970.
o—o 30 December - 2 January 1971.

FIGURE 44. Diurnal variation in incidence of Ecstatic displays.

FIGURE 45. Diurnal variation in Ecstatic displays of 14 unmated males.


● 939
+ 644
○ 647
● 646
+ 638
○ 641
ECSTATICS PER HOUR
4
8
12
16
00
03
06
09
12
15
18
21
00
HOURS (LST)

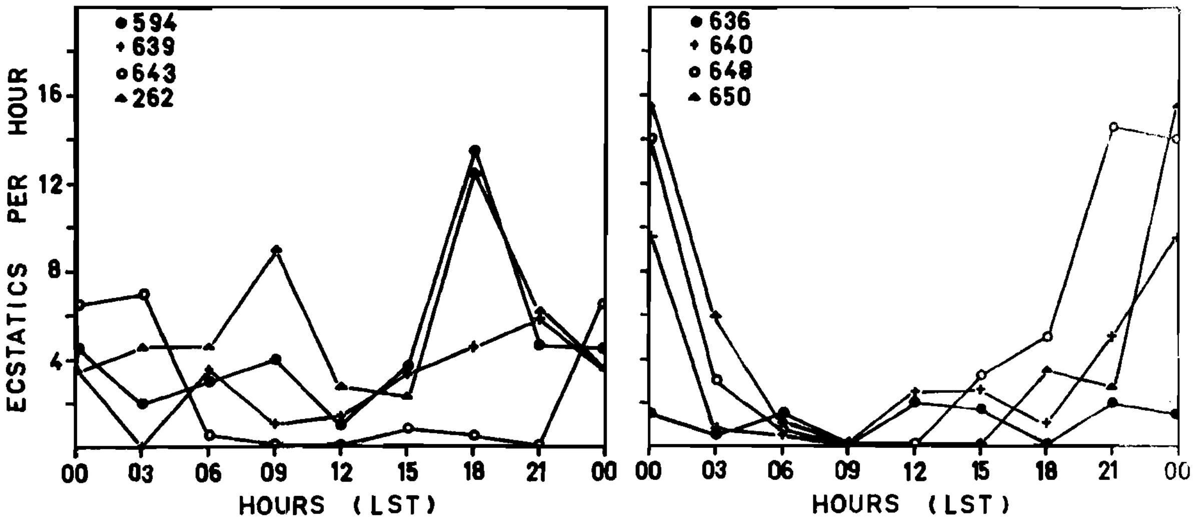
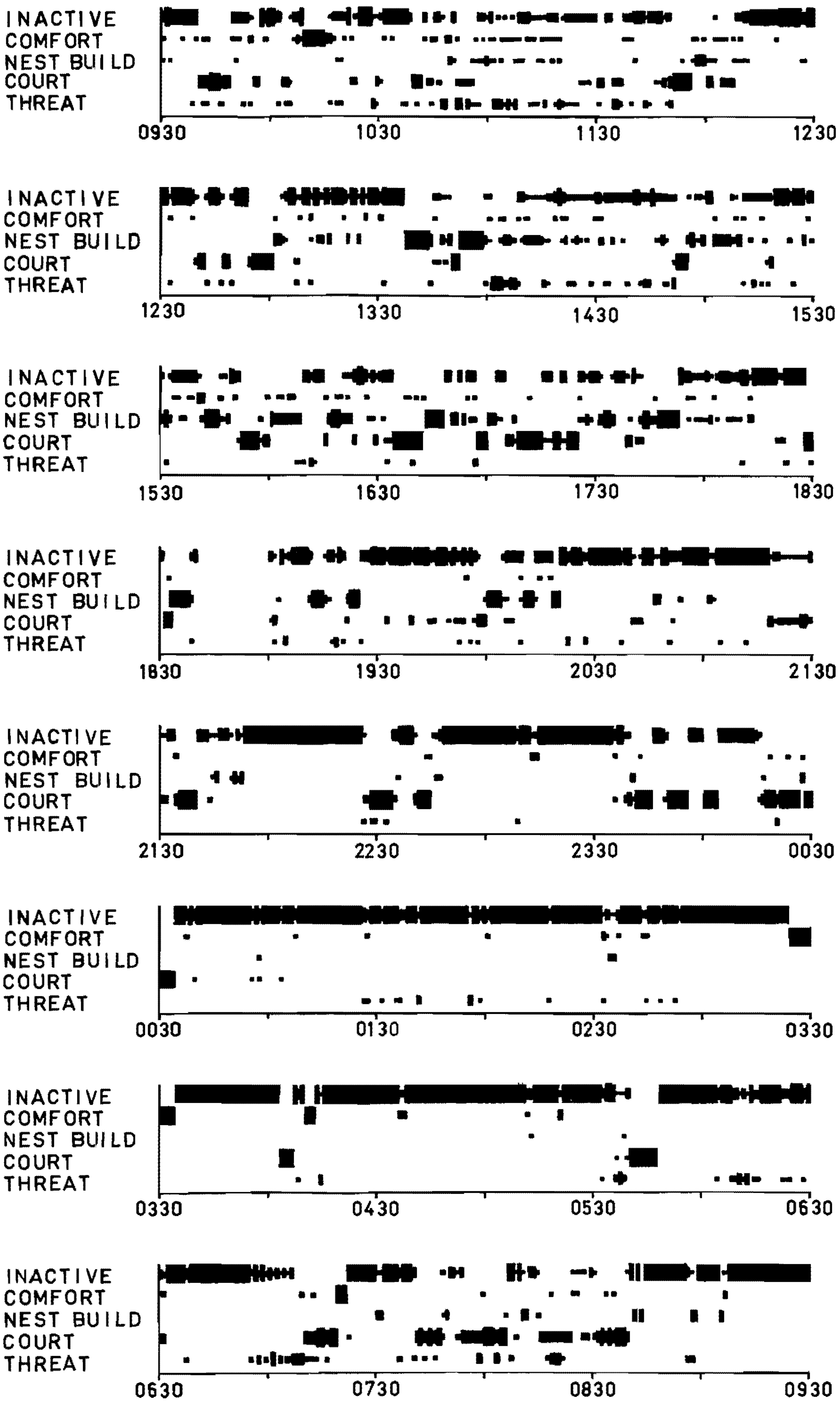

● 594
+ 639
○ 643
▲ 262
● 636
+ 640
○ 648
▲ 650
ECSTATICS PER HOUR
4
8
12
16
00
03
06
09
12
15
18
21
00
HOURS (LST)

FIGURE 46. Incidence of activities performed by male 594 over a period of 24 hours (18 - 19 November 1970).


INACTIVE
COMFORT
NEST BUILD
COURT
THREAT
0930
1030
1130
1230
1330
1430
1530
1630
1730
1830
1930
2030
2130
2230
2330
0030
0130
0230
0330
0430
0530
0630
0730
0830
0930

preening, one for 8 minutes and the other for 10 minutes. During these bouts, preening continued almost uninterrupted, except for a few head shakes, and once to briefly threaten an intruder.

Aggressive reactions occurred frequently throughout the day. No matter what the penguin was doing, its behaviour could be interrupted by the intrusion of either neighbours or strangers. Sometimes, threats and attacks were very brief, and consisted of only one or two acts. At other times, aggressive reactions occurred in quick succession; e.g. when a stranger approached while the male was performing the Ecstatic display, or when a neighbour reacted to nest building activities, or when an intruder attempted to steal a nest stone.

Resting occurred whenever a penguin was inactive (see also section 3.2i). In 24 hours, male 594 spent 9.1 hours resting (for periods of one minute or longer). The rest did not occur all at once. About half was obtained from rest periods of approximately one minute, and the longest period of uninterrupted rest was 32 minutes. The many short periods of rest were frequently interrupted by other activities. This behaviour was typical of other penguins.

On this particular day, however, male 594 was most active during the 12 hours from 0900 to 2100 hours, which corresponds approximately to the normal day-time. Thus, this penguin behaved in the opposite way to the average pattern of diurnal activity, as determined from the activities of a larger number of penguins.

5.6 DISCUSSION

In the continuous light of the breeding season, Adelie penguins are active at all times throughout the 24 hours. There is no single period of rest, but individuals have many short rest periods. Some species of birds do maintain regular rest periods in continuous light (Armstrong 1954, Cullen 1954, Brown 1963). Armstrong (1954:5) also noted, however, that "species which roost in exposed situations, e.g. on open ground, tend to sleep lightly or intermittently". Adelie penguins are open colonial nesters, and cannot retire for a period of time to a cryptic nest or roost. They must be constantly alert for predators, and other penguins intruding or stealing nest stones.

The results of this study and those of Müller-Schwarze (1968) indicate that Adelie penguins, though active throughout the 24 hours, tend to have a reduced level of activity in the middle of the day. This reduced activity is most pronounced on warm midsummer afternoons, and may be associated with the low heat tolerance of Adelie penguins. These penguins are highly adapted to their cold environment (Stonehouse 1967b:189, 1970:533) and may suffer heat stress during prolonged activities. The day-time temperatures in midsummer often cause panting, even when the penguins are inactive.

The apparent lack of a diurnal rhythm observed by Yeates (1971) at Cape Royds, conflicts with these results. Because of individual variation in the timing of activity peaks, it is possible that the colony as a whole may show no particular pattern of activity (see also Cullen 1954:40). Müller-Schwarze (1968:145) demonstrated that under constant illumination, Adelie penguins maintain a free running activity rhythm, but that the peaks of activity shift regularly from day to day (see also Aschoff 1967). If the penguins at Cape Royds were unable to perceive differences in light intensity at different times of the day, they may respond as if subjected to constant light conditions. The individual peaks of activity may occur out of phase, so that the average activity appears uniform throughout the day. However, it is unlikely that the penguins cannot perceive the differences. The apparently contradictory results can only be resolved by making a series of continuous observations on individual birds, rather than pooling observations gathered at different times during the day.

6.0 PAIR AND BREEDING SITE TENACITY

6.1 INTRODUCTION

Several studies have indicated that Adelie penguins have strong pair and breeding site bonds. At Hope Bay, Andrew & Roberts (1952:541) found 88 percent of the breeding penguins that returned had retained the same territory, and 75 percent of the returning pairs were reunited. At Wilkes Station, Penney (1968:106) found 93 percent of breeding males, and 62 percent of breeding females that returned had retained the same territory. Of the pairs that returned, 84 percent were reunited (Penney 1968:119).

Recent work on young known-age penguins at Cape Crozier (LeResche & Sladen 1970:520) has shown that only 50 percent of young breeders (less than 7 years of age) returned to within one metre of their former site, and only 56 percent of returning pairs were reunited. It was suggested (op. cit.:525) that this site and pair-bond lability was advantageous to young penguins.

In this study, it was not possible to work with known-age penguins. Instead, age classifications were based on those suggested by Sladen (1958:25). In this way it was possible to compare the behaviour of established breeders with that of unestablished (presumably young) breeders.

6.2 RETENTION OF BREEDING SITES

Successful breeders occupy the same site throughout the breeding season. However, unsuccessful breeders may occupy more than one site in a season. In 1969-70, unsuccessful males occupied an average of 1.7 different sites, while unsuccessful females occupied an average of 2.0 different sites. Unmated males occupied 2.7, and unmated females 3.3 different sites. The figures for unmated penguins are minimal because some were observed once and never again. They presumably moved on to another site in another colony. Thus, unmated penguins are less attached to any one particular site than either unsuccessful or successful breeders.

Of 752 penguins banded in the Northern Rookery, only 6

(0.8 percent) were found in the Southern Rookery, some 7 km further south, in following seasons. Of these 6 penguins, none were known to have produced eggs at the Northern Rookery, and all may be assumed to be young penguins. Of the penguins that bred in the Northern Rookery and returned the following season, only 1 (0.6 percent) of 154 males, and 1 (0.9 percent) of 109 females returned to a different colony. Thus, breeding penguins show a marked tendency to return to the same colony in successive seasons. In contrast, many unmated penguins changed colony from one season to the next.

Of 154 breeding males that returned the following season, 71 percent retained the same territory (table 5). After four seasons, 54 percent (of 13 males that returned) were still present at the same site. Breeding females showed a lower site tenacity than males, with only 51 percent (of 109 that returned) retaining the same territory.

Unsuccessful breeders change territory more readily than successful breeders. On the average for three seasons, 79 percent of successful males and 62 percent of successful females that returned the following season bred at the same territory (table 6). This contrasts with 54 percent of unsuccessful males and 23 percent of unsuccessful females (table 7).

Successful breeders that change territory the following season must select the new territory during the occupation period before the eggs are laid. However, unsuccessful breeders and unmated penguins may change territories either in the reoccupation period or the following occupation period (or both).

Unsuccessful breeders that maintain a territory for some length of time (here taken as a minimum of 10 days) during the reoccupation period, have a greater chance of retaining the same territory the following season than those that do not maintain a stable reoccupation territory (table 8). Thus, 76 percent of previously unsuccessful males that returned, retained the same territory that they had maintained during the reoccupation period the previous season. Previously unsuccessful females are much less likely to keep the same territory because they frequently change to a new partner on a new territory. Unmated males, as with unsuccessful males, that reoccupy a stable territory also have a greater chance of retaining the same territory as the previous season (table 9).

TABLE 5 : Retention of Individual Nesting Territories by Penguins that Produced Eggs in Consecutive Seasons

Males

Consecutive Breeding Seasons	Number Bred Previously	Return and Breed		Breed Same Territory		
		Number	Percent	Number	Percent	Percent of Returns
2	220	154	70.0	109	49.6	70.8
3	106	61	57.5	39	36.8	64.0
4	32	13	40.7	7	21.9	53.9

Females

Consecutive Breeding Seasons	Number Bred Previously	Return and Breed		Breed Same Territory		
		Number	Percent	Number	Percent	Percent of Returns
2	171	109	63.8	56	32.8	51.3
3	77	45	58.4	12	15.6	26.7
4	26	8	30.8	1	3.9	12.5

TABLE 6 : Retention of Individual Territories by Previously Successful Breeders

Males

Season	Number Bred Previously	Return and Breed	Breed Same Territory	Percent Same Territory	
				c.f. Previous	c.f. Return
1968-69	26	11	8	30.8	72.7
1969-70	36	31	25	69.5	80.7
1970-71	74	63	50	67.6	79.4
Total	136	105	83	61.0	79.1

Females

Season	Number Bred Previously	Return and Breed	Breed Same Territory	Percent Same Territory	
				c.f. Previous	c.f. Return
1968-69	18	8	5	27.8	62.5
1969-70	29	22	15	51.8	68.2
1970-71	69	49	29	42.1	59.2
Total	116	79	49	42.2	62.1

TABLE 7 : Retention of Individual Territories by Previously Unsuccessful Breeders

Males

Season	Number Bred Previously	Return and Breed	Breed Same Territory	Percent same Territory c.f. Previous	Percent same Territory c.f. Return
1968-69	6	0	0	0.0	-
1969-70	38	24	12	31.6	50.0
1970-71	40	24	14	35.0	58.3
Total	84	48	26	31.0	54.2

Females

Season	Number Bred Previously	Return and Breed	Breed Same Territory	Percent same Territory c.f. Previous	Percent same Territory c.f. Return
1968-69	8	2	0	0.0	0.0
1969-70	22	11	4	18.2	36.4
1970-71	25	17	3	12.0	17.6
Total	55	30	7	12.7	23.4

TABLE 8 : Retention of Reoccupation Territories*
by Unsuccessful Breeders

Sex	Number Previously Reoccupied	Number Return	Return Same Territory	Percent Same Territory	
				c.f. Previous	c.f. Return
Male	68	54	41	60.3	75.9
Female	33	26	9	27.3	34.6

TABLE 9 : Retention of Reoccupation Territories*
by Unmated Penguins

Sex	Number Previously Reoccupied	Number Return	Return Same Territory	Percent Same Territory	
				c.f. Previous	c.f. Return
Male	85	77	51	60.0	66.2
Female	41	31	10	24.4	32.3

* Note : Territories occupied for at least 10 days.

Penguins at sites in the centre of a colony retain the same territory more often that penguins at peripheral sites (table 10). Thus, of males from central sites that returned the following season, 84 percent retained the same territory, compared to 64 percent of peripheral males.

Penguins are also more likely to retain the same territory from season to season if the territory is adjacent to a prominent landmark, such as a rock (table 11). Of the males that returned, 97 percent with territories beside a rock retained the same territory, compared to 56 percent of males in more open situations. Nests beside rocks were evenly divided among peripheral and central sites in this sample.

Changes in the position of individual territories within a colony from season to season occurred for a variety of reasons. Females frequently changed territories when their previous mate did not return, or when they returned asychronously. Males usually changed sites only when another site became vacant. The changes were usually of a short distance, often to an adjacent site. Most were parallel changes, from peripheral to peripheral site, or central to central site (table 12). Parallel changes were not accompanied by a significant change in breeding success. Changes from periphery to centre resulted in an increased success, whereas changes from centre to periphery resulted in a decreased breeding success (see section 7.8iv).

In table 12, almost as many penguins changed from centre to periphery as in the reverse direction. It might be expected that young penguins will start breeding at the periphery and move inwards in subsequent seasons, but not many would be detected in the present study. The penguins moving out shifted only a short distance, usually to an adjacent site. Most males became exposed only because of the absence of a few peripheral nests from the previous season. The females moving out were usually from split pairs.

Not all penguins changed territory locality, even when the opportunity occurred. Thus, some penguins remained at the colony periphery in all four seasons of the study.

6.3 RETENTION OF PAIR BONDS

The length of most individual pair bonds could not be

TABLE 10 : Retention of Territories by Males at Different Locations within the Colony

Location	Number Bred Previously	Return and Breed	Breed Same Territory	Percent same Territory	
				c.f. Previous	c.f. Return
Centre	68	51	43	63.3	84.3
Periphery	152	103	66	43.4	64.1
Total	220	154	109	49.6	70.8

TABLE 11 : Effect of Landmarks on Territory Retention of Males

Location	Number Bred Previously	Return and Breed	Breed Same Territory	Percent Same Territory	
				c.f. Previous	c.f. Return
By rock	80	57	55	68.8	96.5
In open	140	97	54	38.6	55.7
Total	220	154	109	49.6	70.8

TABLE 12 : Direction of Changes in Territory Tenure

Direction	Males	Females	Total
Centre no change	43	23	66
Centre to centre	3	6	9
Centre to periphery	5	9	14
Periphery to centre	11	11	22
Periphery to periphery	26	27	53
Periphery no change	66	33	99

determined in this study because of its short duration. Many pair bonds were initiated before the study commenced, and many would continue after it ended.

Unlike successful breeders, unsuccessful breeders may form more than one pair bond in a season. For example, a male that loses eggs shortly after the female has left for sea to break her first fast, may acquire a new mate that produces more eggs. Also, unsuccessful breeders returning in the reoccupation period may keep company (see Richdale 1957:6) with more than one partner. In 1969-70, unsuccessful males were accompanied by an average of 1.8 different females. Females kept company with 2.5 different males (including some previously unmated males). One female kept company with seven different males in one season.

Successful breeders tend to retain the same partner from season to season (table 13). On the average for three seasons, 83.6 percent of pairs that returned were reunited. In 1968-69, only 54.6 percent of returning pairs were reunited. In the two subsequent seasons, however, the figure was closer to 90 percent.

Unsuccessful breeders tend to breed with a different partner in the following season (table 14). On the average for three seasons, 32 percent of pairs that returned were reunited. This contrasts with the high percentage of successful breeders reunited.

When unsuccessful breeders reoccupy the colonies with the same partner for more than 10 days they are more likely to reunite the following season than those that do not reoccupy together (table 15). Thus, 58.3 percent of returning pairs that reoccupied together were reunited. Penguins that had not mated together before, but associated together for more than 10 days in the reoccupation period, also showed a similar trend (table 16). Of those returning, 52.2 percent reunited with their reoccupation partner. Some of these were previous unmated penguins, others had previously bred unsuccessfully with another partner.

The most frequent cause of changing partners among successful breeders was the failure of one partner to return the following season. In this study, there was an unusually high number of changes caused by a high incidence of adult mortality in 1968-69 (see section 7.5). When both partners returned, most changes occurred because of asynchronous return

TABLE 13 : Retention of Partners by Previously Successful Breeders

Season	1968-69	1969-70	1970-71	Total	Percent Total
Pairs Bred Previously	16	27	66	109	100.0
Both return and reunite	6	18	42	66	60.6
Both return but split	5	2	6	13	11.9
One partner not return	5	6	18	29	26.6
Neither partner return	0	1	0	1	0.9
Percent Returning Reunited	54.6	90.0	87.5	83.6	

TABLE 14 : Retention of Partners by Previously Unsuccessful Breeders

Season	1968-69	1969-70	1970-71	Total	Percent Total
Pairs Bred Previously	7	18	21	46	100.0
Both return and reunite	0	5	3	8	17.4
Both return but split	1	6	10	17	37.0
One partner not return	3	6	6	15	32.6
Neither partner return	3	1	2	6	13.0
Percent Returning Reunited	0.0	45.4	23.1	32.0	

TABLE 15 : Retention of Reoccupation Partner* by Penguins Unsuccessful at Breeding Together

Number Previously Associated*	20
Both return and reunite	7
Both return but split	5
One partner not return	8
Neither partner return	0
Percent returning reunited	58.3

TABLE 16 : Retention of Reoccupation Partner* by Penguins that had not Produced Eggs Together

Number Previously Associated*	42
Both return and reunite	12
Both return but split	11
One partner not return	18
Neither partner return	1
Percent returning reunited	52.2

* Note : Association in reoccupation period for at least 10 days together.

of the two partners. Some members did not return until the reoccupation period. Others returned after their former partner had paired up with another penguin and produced eggs. The number of pairs that split when both members returned was greater for unmated and unsuccessful breeders than for successful breeders. It has also been shown (section 4.2) that for unmated and unsuccessful breeders arrival at the rookeries is later and more spread out than for successful breeders.

Penney (1968:118) and LeResche & Sladen (1970:519) consider that pair bonds formed during the reoccupation period do not influence mate choice in subsequent seasons. The data in table 16 do not support this contention. Twelve pairs formed in the reoccupation period reunited the following occupation period. These twelve comprised 29 percent of 41 new pairs that produced eggs; the remaining 71 percent (29 pairs) were formed in the occupation period prior to egg-laying. The examples below illustrate typical situations of two pairs formed in the reoccupation period, and two pairs formed in the occupation period.

Male 930 and female 499 were first observed together late in the reoccupation period of 1969-70. Previously in the same reoccupation period, female 499 had kept company with three other males. However, on each occasion that she was observed toward the end of the season, she was with male 930. Male 930 had earlier bred unsuccessfully, having deserted the eggs when his previous mate failed to return. The following season (1970-71), male 930 and female 499 were again together. The female laid two eggs, and they successfully raised two chicks. This was the first time in four seasons of study that female 499 had laid, but male 930 had bred for at least two summers previously.

Male 905 and female 845 were both unsuccessful breeders in 1969-70, at nests some 2.5 metres apart. Female 845 joined male 905 at his nest on 26 December, and the two were together on each of the nine occasions that they were observed during the remainder of the reoccupation period. The following season (1970-71) they mated at 905's nest and successfully raised two chicks.

These pairs developed a bond the previous season which undoubtedly influenced their pairing the following season. However, if either member of these pairs had not returned within a short time of one another the following season, they may not have mated.

Other successful pairings are initiated in the occupation period prior to egg-laying. Male 338 bred for the first time in the spring of 1970-71. He had occupied the same site but not paired for the three previous seasons. In 1969-70, he was accompanied by various females on only 4 of the 48 days on which he was observed at the nest. In 1970-71, he paired with an unbanded female and they raised two chicks.

Male 899 also bred for the first time in 1970-71. For the previous two seasons he had occupied several sites in the colony, but not mated. In 1969-70, he was accompanied by a female on only one day of the 35 days that he was observed. In 1970-71, he bred successfully with female 982, a successful breeder the previous season, whose mate had not returned. Male 899 and female 982 had not associated in any way prior to the season in which they successfully bred.

6.4 DISCUSSION

It has been shown that previously successful breeders tend to retain the same breeding site and partner from season to season. It is advantageous for individuals to retain a site proven favourable for successful breeding. Likewise, it is advantageous to retain an experienced and successful partner. It is also favourable to the population that previously successful breeders (those likely to leave the most progeny) should have the most favourable breeding sites and mates. Thus, site and pair stability are advantageous to successful individuals and to the population.

It has also been shown that unsuccessful breeders change sites and partners more readily than successful breeders. When a site change is from colony periphery to centre, and a mate change is to a more experienced and/or more synchronous partner, then breeding success may be increased (see also section 7.8iv). Thus, site and pair lability are advantageous to a certain section of the population, as also indicated by LeResche & Sladen (1970:525).

Successful breeders tend to arrive earlier and more synchronously than other members of the population. They also tend to nest at sites in the centre of colonies. They are the most established and presumably most mature members of the population.

Unsuccessful breeders and unmated penguins return later than successful breeders. Their arrival is also more spread out, which does not increase their chances of returning synchronously with a previous partner. Nor does it increase their chances of obtaining a central site. Most unmated and unsuccessful breeders occur at the colony periphery. They are the least established and presumably younger members of the population.

LeResche & Sladen (1970:526) indicated that young penguins had less stable site and pair bonds, and were less successful at breeding, than the population as a whole. Richdale (1957:127) working on known-age Yellow-eyed penguins (Megadyptes antipodes) has shown that young breeders have a lower breeding potential, and are also less successful, than older members of the population. Thus, the age of penguins strongly influences their behaviour. Within a population of Adelie penguins there is a gradient of site and pair stability, ranging from the established and successful breeders, through unestablished and unsuccessful breeders, to unmated penguins.

Not all site or pair bonds formed in the reoccupation period are maintained in the following spring. This is especially true if a penguin returns late, if a more suitable site becomes available, or if the previous partner returns late. It is not essential for successful breeding that a penguin has previously occupied the same site or associated with the same partner. The choice of site and partner ultimately depends on what is available in a particular season. However, the fact that most site and pair bonds are formed in the occupation period does not detract from the importance of the reoccupation period.

A risk in occupying an unclaimed site in the spring is that the claimant may arrive late and precipitate a fight, resulting in loss of eggs. Thus, returning to a site claimed the previous season normally ensures an undisputed tenure. If there were a shortage of breeding sites, a penguin with a previous claim would be more likely to obtain a site than a newcomer. Though it would seem that there is no shortage of breeding sites, there is a limit to the number of central sites available (see section 2.6). If there was a shortage of penguins of one sex, a member of the opposite sex which had a previous association would be more likely to obtain a partner than a stranger that returned at the same time. It appears that there was in fact a shortage of breeding females in these colonies (see section 7.3), and some males were unable to breed because they returned late, by which time all available females were paired.

Not all those that returned earlier had "reserved" a partner, and were able to breed only because of the chance availability of a female. Penguins that had "reserved" a partner were not completely assured of breeding, but had a greater chance than if they had not made a reservation. The phenomenon of keeping company usually ensures that they do not remain unmated if their partner does not return.

7.0 BREEDING BIOLOGY

7.1 INTRODUCTION

Aspects of the breeding biology of Adelie penguins have been recorded at various localities. These include;

Signy Island,	Lat. 60° 43'S,	and
Hope Bay,	Lat. 63° 24'S,	(Sladen 1958)
Wilkes Station,	Lat. 66° 15'S,	(Penney 1968)
Port Martin,	Lat. 66° 49'S,	(Sapin-Jaloustre 1960)
Cape Hallett,	Lat. 72° 19'S,	(Reid 1964, 1965)
Cape Crozier,	Lat. 77° 27'S,	(Sladen et al. 1968, LeResche & Sladen 1970)
Cape Royds,	Lat. 77° 33'S,	(Taylor 1962, Stonehouse 1963, Yeates 1968).

The Cape Bird rookeries (77° 13'S) are among the southernmost Adelie penguin rookeries, and are comparable to Crozier and Royds on Ross Island. Observations were made there during four summers, from 1967-68 to 1970-71 inclusive.

Climatic conditions during the breeding season did not appear to differ significantly in any of the four seasons. Sea-ice conditions, however, were markedly different. In 1967-68, 1969-70, and 1970-71, the sea-ice had broken out south of Cape Bird by early November. In 1968-69, it did not break out until mid December. This late ice breakout was associated, either directly or indirectly, with drastic changes in the breeding biology of the penguins.

7.2 RETURN TO THE BREEDING ROOKERIES

In only one of four summers (1968-69) was it possible to make complete observations on the return of penguins to the rookeries. Unfortunately, it was in this summer that a very low number of penguins returned to breed (table 17). Only 30.4 percent of banded males, and 23.5 percent of banded females that laid the previous season returned and bred in 1968-69. Many returned but did not lay; others did not return and presumably had died (see section 7.5). The proportion returning increased in the two succeeding seasons, so that about 79 percent of males, and 72 percent of females that bred the previous season returned and bred in 1970-71.

i. Arrival of Penguins that Produce Eggs

Penguins that produce eggs start arriving at these rookeries in October. On 23 October 1968 (the earliest visit to the study rookery) approximately 200 penguins were present, which was less than one percent of the total breeding population. The first breeding penguin in the study colonies arrived on 24 October 1968.

Males tended to arrive at the breeding grounds before females. In 1968-69, only 3 percent (4 of 133) females returned before their mates. The mean date of arrival for breeding males was 3 November, and for breeding females was 7 November, giving a mean interval of 4 days. This difference between the arrival date of males and females is significant ($p < 0.01$). In 1969-70, penguins arrived much earlier than in 1968-69, so that by 4 November 1969 about 85 percent of males and 69 percent of females had arrived (table 18).

Unsuccessful breeders tended to arrive later than successful breeders (see figure 29).

ii. Arrival of Penguins that Remain Unmated

The first penguins that remained unmated did not arrive until much later than the first penguins that became mated. Thus, in 1968-69, the first unmated male returned on November 3, by which date 50 percent of mated males had returned. Unmated penguins continued to arrive throughout the season.

There were two main periods for new arrivals (figure 47). Most arrived in November, during the initial occupation of the colonies. Only a few unmated penguins returned during early December (when most of those that had arrived earlier had departed to sea again). The second period for new arrivals occurred in late December, at a time when many previous unmated and unsuccessful breeders reoccupied the colonies.

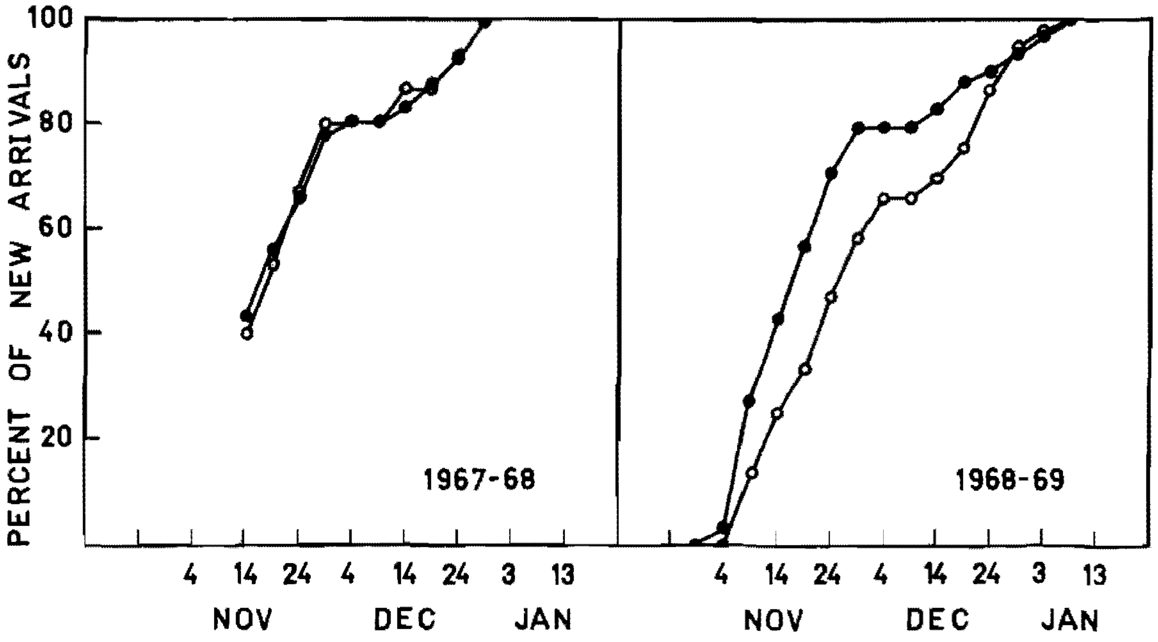
7.3 SEX RATIO

The sex ratio of adult penguins resident in a colony is shown in table 19. The penguins recorded in this table were not all banded, but include all the penguins observed in three colonies. The sex of banded penguins was determined either by

FIGURE 47. Arrival of unmated penguins.

●—● males.

o—o females.


PERCENT OF NEW ARRIVALS
100
80
60
40
20
1967-68
1968-69
4
14
24
4
14
24
3
13
NOV
DEC
JAN

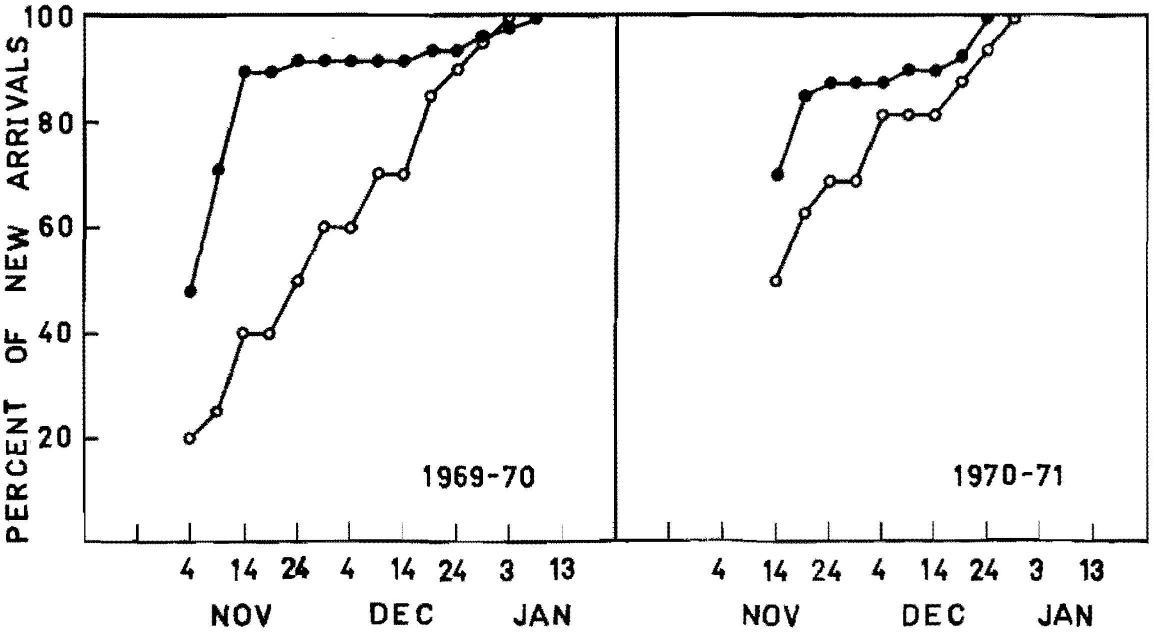

PERCENT OF NEW ARRIVALS
100
80
60
40
20
1969-70
1970-71
4
14
24
4
14
24
3
13
NOV
DEC
JAN

TABLE 17 : Return of Previous Layers

Males

Season	Number Bred Previously	First Return During Occupation	First Return During Reoccupation	Total Percent Return	Total Percent Breed	Percent Returning Breed
1968-69	23	13	2	65.2	30.4	46.7
1969-70	67	54	0	80.6	71.7	88.9
1970-71	104	86	0	82.7	78.9	95.3

Females

Season	Number Bred Previously	First Return During Occupation	First Return During Reoccupation	Total Percent Return	Total Percent Breed	Percent Returning Breed
1968-69	17	7	4	64.7	23.5	36.4
1969-70	43	28	3	74.4	62.8	84.4
1970-71	89	66	1	75.3	71.9	95.5

TABLE 18 : Arrival of Breeding Penguins (percentages)

Males

Date	1967-68	1968-69	1969-70	1970-71
Oct. 25	-	4.5	-	-
30	-	35.4	-	-
Nov. 4	-	54.9	85.3	-
9	-	87.2	89.9	-
14	95.6	95.5	100.0	97.8
19	100.0	99.2		100.0
24		100.0		
Total	179	133	144	135

Females

Date	1967-68	1968-69	1969-70	1970-71
Oct. 25	-	0.0	-	-
30	-	15.8	-	-
Nov. 4	-	33.1	68.6	-
9	-	70.0	86.0	-
14	93.3	91.8	96.5	90.4
19	98.9	98.5	98.6	99.3
24	100.0	100.0	100.0	100.0
Total	179	133	144	135

observed copulation or by association with another penguin of known sex (see section 1.5). The sex of unbanded penguins observed with partners was regarded as opposite to the sex of the partner. Unmated penguins without bands and alone at a well established territory for more than three days were regarded as males, because unmated females did not normally remain alone on a territory for this length of time. This analysis does not record the sex ratio in the whole population, but only the ratio of adults resident in a colony. Because females usually do not initiate nest building and are less attached to a site, their numbers are probably harder to estimate than for males. However, some males (probably young) wander from site to site, and from colony to colony, staying no longer than a few hours at some sites. These penguins are not included in this analysis.

Males outnumbered females on these colonies. In all, 706 males and 603 females were identified. This included 518 mated pairs, 188 unmated males, and 85 unmated females. This gave an average sex ratio of 1.00 to 0.85, in favour of males (table 19). The sex ratio was remarkably constant in each of the four seasons.

7.4 INCIDENCE OF UNMATED PENGUINS

The incidence of unmated penguins is very difficult to determine in a population that does not contain a high proportion of banded birds. However, it has been attempted in this study following the criteria laid down in the preceding section (section 7.3).

For three seasons (1967-68, 1969-70, 1970-71) the average incidence of unmated adults resident at some stage in a colony was 18.0 percent. However, in 1968-69, some 30 percent of the resident population were unmated; i.e. did not produce eggs (table 20).

The unmated population consists of two groups of penguins; those that have yet to produce eggs for the first time (pre-layers), and those that have produced eggs in a previous season (previous layers). Pre-layers fall somewhere into the category of "wanderers" in the classification of Sladen (1958:25). Many previous layers fit into the category of inexperienced breeders. However, some experienced breeders

TABLE 19 : Sex Ratio

Season	Number		Sex Ratio	
	Males	Females	Males	Females
1967-68	169	143	1.00	0.85
1968-69	171	145	1.00	0.85
1969-70	192	164	1.00	0.85
1970-71	174	151	1.00	0.87
Total	706	603	1.00	0.85

The total number of males (706) is significantly greater than the total number of females (603) when tested by Chi square ($p = < 0.01$).

TABLE 20 : Incidence of Unmated Penguins

Season	Mated Penguins	Unmated Penguins		Percentage Unmated
		Male	Female	
1967-68	256	41	15	17.9
1968-69	222	60	34	30.4
1969-70	288	48	20	19.2
1970-71	270	39	16	16.8

may also miss laying for one or more seasons.

Information on pre-laying years can come only from observation of penguins marked as chicks. Several males established territories and built nest sites, but did not produce eggs for four consecutive seasons of the study. However, their previous history is unknown. No females were known to have been unmated for four consecutive seasons. LeResche & Sladen (1970:519) found that the first eggs were produced most often at 4 years of age in females, and 5 years of age in males.

The incidence of unmated penguins among previous layers is shown in table 21. In 1968-69, a high proportion of previous layers were unmated (69.6 percent of males, and 76.5 percent of females). Both the number not returning and the frequency of unmated penguins amongst those returning is higher than for either of the two following seasons. Most instances in which previous layers returned but were unmated occurred when they returned late the following season (see also section 6.3).

7.5 BAND LOSS, ADULT MORTALITY, AND EMIGRATION

None of the penguins which failed to return after breeding the previous season were subsequently observed again. Three possible causes of disappearance are band loss, mortality, and emigration. Emigration of breeding penguins from one colony to another was estimated to be less than one percent (see section 6.2), and because the colonies were regularly checked the number of changes unaccounted for is probably negligible.

The extent of band loss was very difficult to determine without a control such as web punching. Very few penguins were observed with bands partly opened. Most of the partly opened bands were found in the third season after first banding, indicating that losses were probably highest after about this time (table 22). The relationship between partly opened and lost bands is unknown. One partly opened band was known to remain in place for at least three seasons, while a few others remained in place for at least two seasons. Thus, band loss was probably lower than the incidence of partly opened bands. Only two penguins were ever observed with worn feathers on the flippers indicating where a band had been. It is possible, however, that most band losses occurred during the moult or

TABLE 21 : Incidence of Unmated Penguins among Previous Layers

Males

Season	Number Mated Previously	Percent Return & Unmated		Percent Not Return	Total Percent Unmated
		Occupation*	Reoccupation*		
1968-69	23	26.1	8.7	34.8	69.6
1969-70	67	8.9	0.0	19.4	28.3
1970-71	104	3.8	0.0	17.3	21.1

Females

Season	Number Mated Previously	Percent Return & Unmated		Percent Not Return	Total Percent Unmated
		Occupation*	Reoccupation*		
1968-69	17	17.7	23.5	35.3	76.5
1969-70	43	4.6	7.0	25.6	37.2
1970-71	89	2.3	1.1	24.7	28.1

---

* First return in either occupation or reoccupation period.

TABLE 22 : Incidence of Partly Opened Bands

	Seasons after First Banding[1]				
	1st[2]	2nd	3rd	4th	5th[3]
Bands intact	752	462	264	79	6
Bands first split	0	8	12	1	0
Percent first split	0	1.7	4.4	1.3	0

Notes : 1. Not all bands were on for the same length of time.

2. Total number of bands put on over a period of four years.

3. Banded in 1966-67 (the year before this study commenced) by A.J. Peterson.

very soon afterwards. Bands lost at such a time would leave no indication of being lost. Nevertheless, the extent of band loss in the first four seasons (the length of this study) was probably very small, and the average annual loss of bands was probably not in excess of 2 percent (see also Penney 1968:88, LeResche et al. 1970:47).

Band loss can be expected to be similar for males and females, and from season to season. If this is true, and emigration is negligible, it is evident that mortality was higher in females than males, and that mortality was exceptionally high after the winter of 1968 (table 21). In 1968-69, mortality of mated penguins was estimated to be 33 percent for males and females (i.e. 35 percent that did not return minus 2 percent band loss). In the two subsequent seasons, the average mortality of penguins known to have laid previously was 16 percent for males and 23 percent for females.

Most mortality appears to have occurred during the winter. Of the penguins that laid in one season but did not return the next season, 82 percent disappeared during the winter, compared to 18 percent during the summer. Those that disappeared during the summer caused either eggs or chicks to be lost (see section 7.8ii). During the breeding season, parents were exposed to higher risks than penguins without eggs or chicks. Their daily trips to sea to collect food for chicks not only taxed their energy reserves but also exposed them more frequently to encounters with leopard seals (Hydrurga leptonyx).

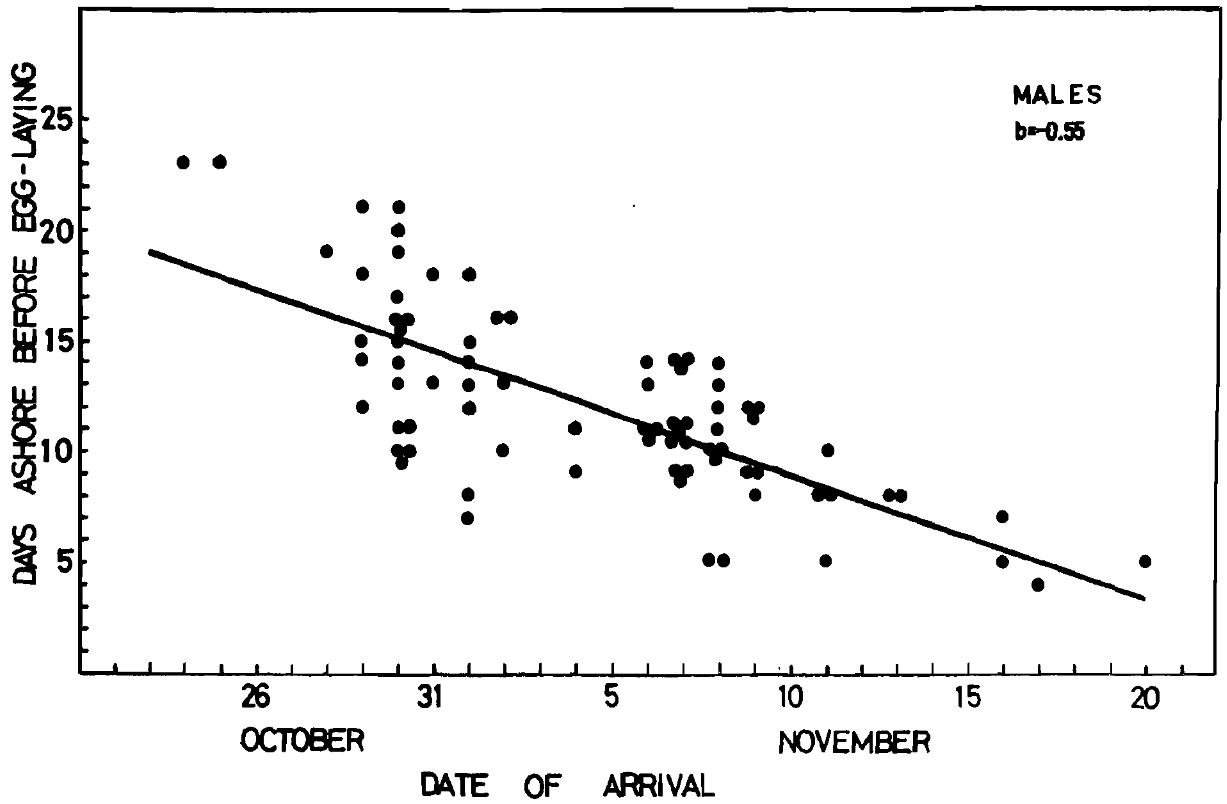
7.6 EGG-LAYING

Egg-laying commences in early November, and continues until the end of the month. The first egg recorded in this study was laid on 4 November.

Penguins that arrived early in the season spent longer ashore before laying than penguins that arrived late (figure 48). However, early arrivals also laid before late arrivals (figure 49). That is, there was a wider spread of arrival dates than laying dates, so that there was a synchronisation of egg-laying. Some early arrivals did not lay until quite late, but this may be accounted for by the mate returning late, or failing to return at all.

Penguins normally lay two eggs. If one or even both

FIGURE 48. Days ashore before egg-laying related to arrival date.


MALES
b=-0.55
DAYS ASHORE BEFORE EGG-LAYING
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20
15
10
5
26
31
5
10
15
20
OCTOBER
NOVEMBER
DATE OF ARRIVAL

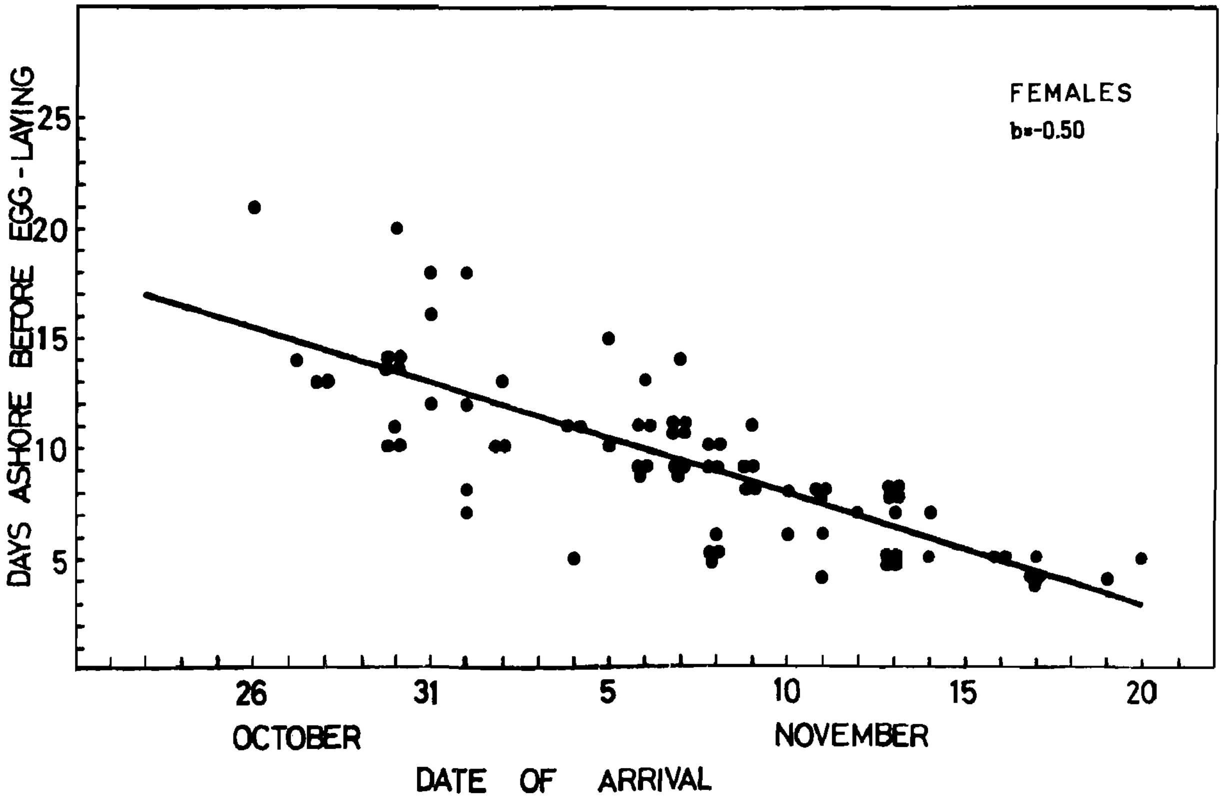
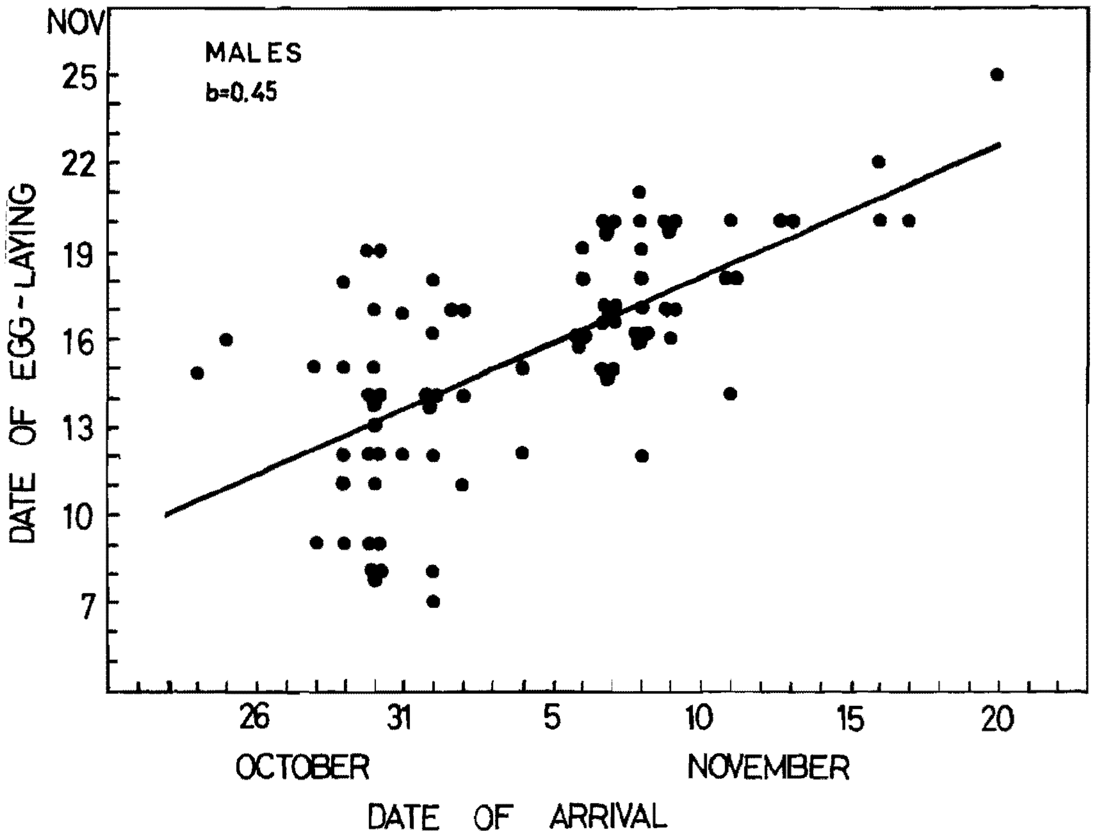
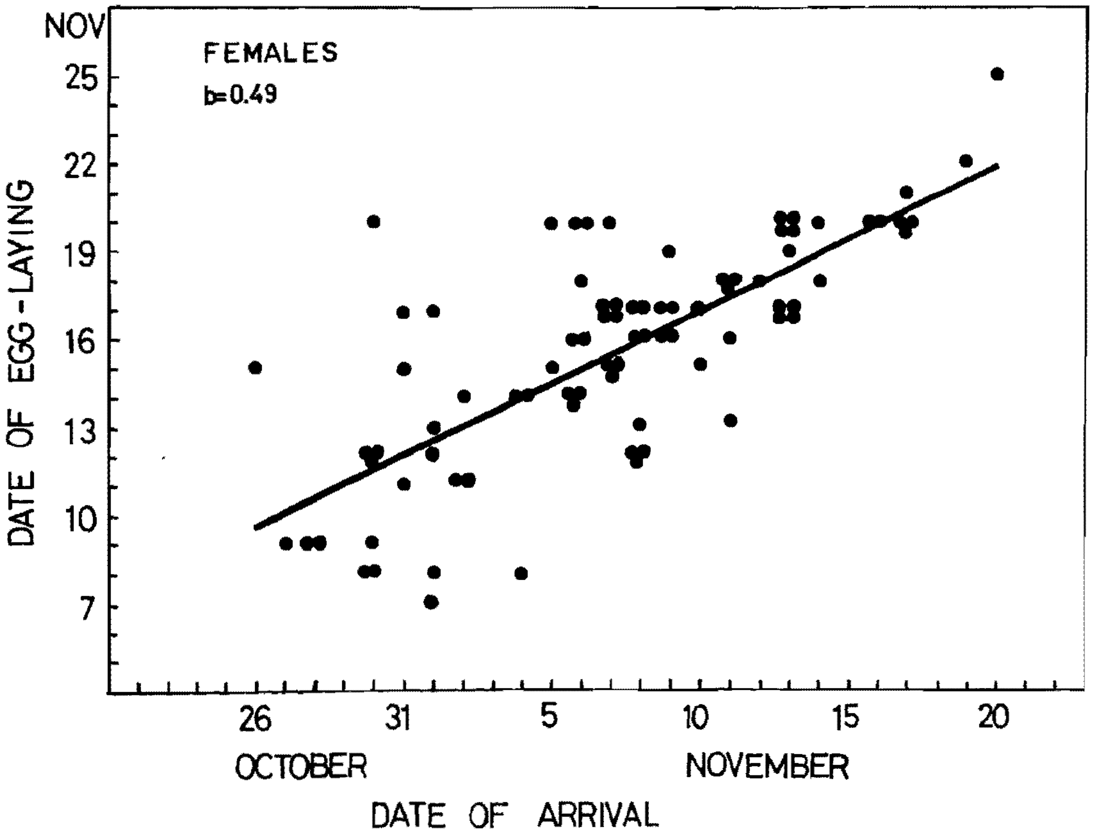

FEMALES
b=-0.50
DAYS ASHORE BEFORE EGG-LAYING
25
20
15
10
5
26
31
5
10
15
20
OCTOBER
NOVEMBER
DATE OF ARRIVAL

FIGURE 49. Date of egg-laying related to arrival date.


MALES
b=0.45
NOV
25
22
19
16
13
10
7
DATE OF EGG-LAYING
26
31
5
10
15
20
OCTOBER
NOVEMBER
DATE OF ARRIVAL


FEMALES
b=0.49
NOV
25
22
19
16
13
10
7
DATE OF EGG-LAYING
26
31
5
10
15
20
OCTOBER
NOVEMBER
DATE OF ARRIVAL

eggs are lost early in the season before the female leaves for sea, a third (replacement) egg may be laid. No natural clutches of three eggs were found in this study. In the three seasons (1967-68, 1969-70, 1970-71) when breeding conditions were typical for the area, about 14 percent of all clutches consisted of only a single egg, and the mean clutch size of penguins that laid was 1.86 eggs per nest (table 23). In 1968-69, when conditions were adverse (see section 7.1), about 39 percent of the clutches consisted of single eggs, and the mean clutch size was 1.61.

Nests in the centre of a colony have a larger mean clutch size than those at the periphery. Thus, the mean clutch size was 1.89 eggs for central nests, and 1.78 eggs for peripheral nests (table 24). At eleven isolated nests, the mean clutch size was 1.45 eggs per nest.

Clutches laid late in the season (after 19 November) were smaller than those laid earlier (i.e. contained more single eggs) (table 24). Clutches laid late in the season also tended to be laid in peripheral nests (table 25). Thus, small clutches, late laying, and peripheral nesting appear to have a common causal basis (see section 7.9).

The mean laying date for first eggs was 12 November, and for second eggs 15 November (table 28). The mean date of laying for single-egg clutches was 18 November, which is later than for two-egg clutches. The adverse conditions of 1968-69 seem to have had little effect on laying dates. Mean date and rate of laying were fairly constant from season to season.

Deviations from the mean laying date of forty females are shown in table 27. This table includes all females for which records are available for at least three seasons. The range of individual laying dates was much greater than the variation in mean laying date from season to season. Nevertheless, some females were consistently late layers, and others were consistently early layers. Richdale (1957:22) also found that individual Yellow-eyed penguins had consistent laying dates.

The interval between the laying of the first and second egg averaged 3.0 days, and ranged from 2 to 4 days, at 61 nests in 1969-70. This compares with observations by other workers (Sapin Jaloustre & Bourliére 1951:67, Sladen 1958:51, Taylor 1962:188, Stonehouse 1963:776, Reid 1965:504, Penney 1968:92).

TABLE 23 : Clutch Size in Different Seasons

Locality	Season	No. Clutches in sample	Percent Single-egg	Mean Clutch size
Cape Bird	1967-68	221	13.6	1.86
Cape Bird	1968-69	224	39.3	1.61
Cape Bird	1969-70	200	12.5	1.88
Cape Bird	1970-71	181	17.1	1.83
Cape Royds[1]	1959-60	100	19.0	1.81
Cape Hallett[2]	1959-62	213	13.6	1.86

1 Taylor (1962:185)
2 Reid (1965:503)

TABLE 24 : Clutch Size in Relation to Nest Location and Laying Date

Nest Location	Laying Date				
	≤ 9 Nov	≤ 14 Nov	≤ 19 Nov	> 19 Nov	Average
Centre	1.7[1]	1.96	1.94	1.68	1.89
Periphery	1.4[2]	1.87	1.78	1.67	1.78

1, sample = 6 2, sample = 5 (see also table 25)

Nest Location, F = 9.20 (1,548 D.F.) p = < 0.01 **
Laying Date, F = 9.87 (3,548 D.F.) p = < 0.01 **
Interaction, F = 0.91 (3,548 D.F.) p = > 0.25 NS

TABLE 25 : Number of Clutches Laid with respect to Nest Location and Laying Date

Nest Location	Laying Date			
	9 Nov	14 Nov	19 Nov	19 Nov
Centre	6	89	64	38
Periphery	5	144	127	114

Chi square, 2 x 4 table, $p = < 0.05$

TABLE 26 : Mean Date of Laying

Season	Two-egg Clutches 1st	Two-egg Clutches 2nd	Single-egg Clutches
1967-68	-	16 Nov	20 Nov
1968-69	13 Nov	16 Nov	17 Nov
1969-70	11 Nov	14 Nov	17 Nov
1970-71	-	15 Nov	18 Nov
Average	12 Nov	15 Nov	18 Nov

TABLE 27 : Deviation in Laying Dates of Individual Penguins

Female	Deviation in days from mean laying date 1967-68	1968-69	1969-70	1970-71	Average deviation in days
379	+13	+ 7	+ 6	+ 4	+7.7
400	+ 5	+12		+ 5	+7.3
774		+ 6	+11	+ 1	+6.0
407		+ 1	+ 7	+ 6	+4.7
431	+ 7	+ 3	+ 4	+ 3	+4.2
343	+ 7	+ 4		+ 1	+4.0
271	0		+ 7	+ 5	+4.0
819		+ 1	+ 5	+ 1	+2.3
813		+ 2	+ 5	0	+2.3
461		+ 6	0	+ 1	+2.3
781		+10	- 3	0	+2.3
273	0		+ 1	+ 4	+1.7
919		+ 1	+ 2	+ 1	+1.3
721		- 2	+ 5	+ 1	+1.3
814		0	+ 2	+ 1	+1.0
788		+ 1	+ 2	- 1	+0.7
396		+ 3	- 3	+ 1	+0.3
364	0	+ 2	0	- 1	+0.3
657		- 4	+ 5	- 1	0
630		- 5	+ 5	- 1	-0.3
785		- 3	+ 1	+ 1	-0.3
900		+ 2	- 2	- 2	-0.7
794		- 2	0	0	-0.7
795		- 6	+ 2	+ 1	-1.0
446		+ 1	- 3	- 3	-1.7
632		- 3	- 1	- 1	-1.7
821		- 3	- 1	- 1	-1.7
708		- 3	- 3	0	-2.0
680		- 1	- 2	- 3	-2.0
845		- 1	- 3	- 2	-2.0
719		- 2	- 3	- 2	-2.3
793		- 2	- 3	- 2	-2.3
787		- 1	- 3	- 4	-2.7
817		+ 1	- 9	0	-2.7
646		- 3	- 3	- 2	-2.7
704		- 8	- 2	- 1	-3.7
520		- 6	- 3	- 3	-4.0
912		- 6	- 4	- 5	-5.0
789		- 7	- 5	- 3	-5.0
662		- 9	- 2	- 5	-5.3

7.7 INCUBATION

The female usually departs for sea (to feed) within a day of laying the last egg in the clutch, leaving the male to take the first incubation watch. However, several authors have already indicated that on occasions females may take the first incubation, and that this is not an infallible method of sexing penguins.

The length of individual incubation watches vary greatly, but the first two watches are usually the longest. In fifty-four nests where incubation watches were completed in 1969-70, first watches by males ranged from 7 to 23 days, and averaged 14.8 days. Males that deserted eggs before being relieved by the female were not included in this analysis. One male incubated the eggs for 30 days before deserting. Another male deserted 37 days after the second egg had been laid, by which time the chicks had hatched and died of starvation.

Fifty second watches by females averaged 11.1 days (range 9 to 15 days). One female deserted the eggs after 21 days.

In five instances the first watches were taken by females, and averaged only 6.4 days, with a range from 3 to 11 days. Some females deserted during the first incubation (in one case, after only two days). Five second watches by males averaged 14.6 days (range 13 to 17 days).

The total incubation time for forty-two first eggs in 1969-70 averaged 34.7 days (range 32 to 38 days), and for second eggs averaged 33.2 days (range 31 to 35 days). In seven single-egg clutches, the average incubation time was 33.8 days (range 32 to 35 days).

In 1970-71, most nests had at least one egg before observations commenced. However, in nine nests, the incubation time for the first egg averaged 35.1 days, and for the second egg averaged 33.1 days. The average time for six single-egg clutches was 33.3 days. When the figures from the two seasons were combined (table 28) the average time for first eggs was 34.8 days, for second eggs was 33.2 days, and for single eggs was 33.6 days. Observations were made at about the same time each day, so that incubation times are accurate to ± 1 day.

The mean interval between the hatching of the first and second eggs at 61 nests was 1.43 days (range 0 to 3 days).

TABLE 28 : Incubation Periods

Incubation Period (Days)	Single-Egg Clutches	Two-egg Clutches	
		1st egg	2nd egg
31			2
32	1	1	9
33	5	4	22
34	5	17	12
35	2	18	6
36		7	
37		2	
38		2	
Totals	13 eggs	51 eggs	51 eggs
Mean	33.6 days	34.8 days	33.2 days

This is comparable with the interval obtained by Taylor (1962:188). On average, the two eggs of a clutch were laid 3 days apart but hatched less than 2 days apart. The slightly longer incubation time for the first egg indicates that incubation of the first egg is incomplete until the second is laid.

7.8 BREEDING SUCCESS

Breeding success is estimated as the percentage of eggs laid surviving as chicks in mid January. By this time, chicks are independent of parental protection from adverse weather and predators, though they are still dependent upon their parents for food. Few chicks are lost after this date before departing for sea in early February. It is expected that many losses would occur shortly after departure for sea, but is not possible to account for these in this study (see also LeResche et al. 1970:46).

i. Seasonal Differences

The breeding success was markedly different in different seasons, being lowest in 1968-69 (table 29). In this summer, only 42.8 percent of the eggs laid survived as chicks in mid January. The average for the other three summers was 62.7 percent.

Mortality was fairly evenly divided between the egg period and chick period, except in 1968-69 when there was a high egg mortality. In this summer, many eggs were lost when parents deserted during incubation (see below). This caused a peak of egg losses in late November and early December (figure 50). In the other three seasons (1967-68, 1969-70, 1970-71) most egg and chick losses occurred in late December and early January.

ii. Causes of Mortality

The main causes of egg mortality were infertile or addled eggs, skua predation, and desertion, of which desertion was probably the most important.

Of the 378 eggs lost (in all four seasons) between laying and hatching, 91 were either addled or infertile. This represented 6.7 percent of the eggs laid, or 24.1 percent of the total egg mortality (table 30).

FIGURE 50. Incidence of egg and chick mortality through the season.

White bars represent egg losses.

Black bars represent chick losses.

Note, this does not include addled or infertile eggs.

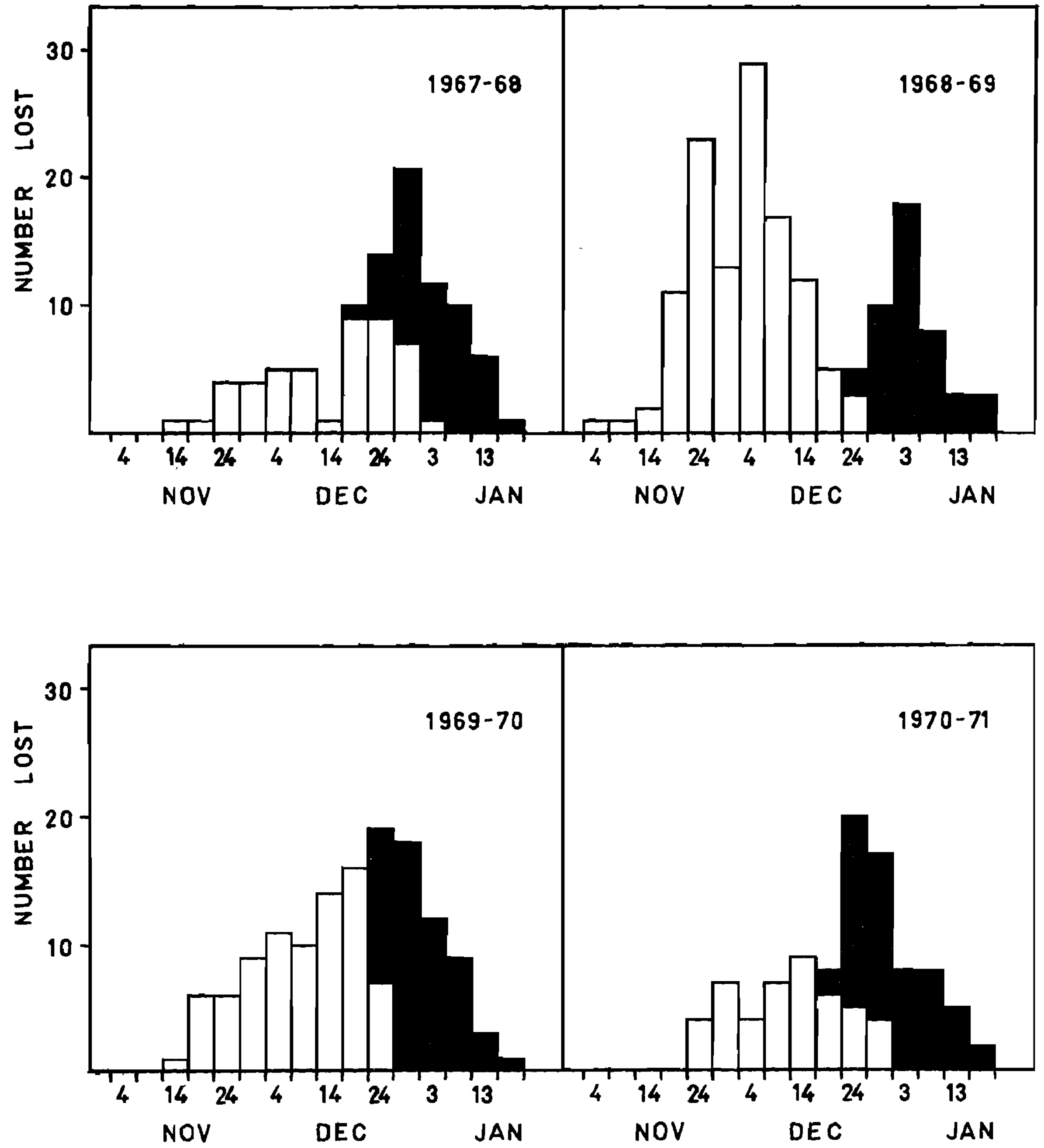

NUMBER LOST
30
20
10
1967-68
1968-69
1969-70
1970-71
4
14
24
4
14
24
3
13
NOV
DEC
JAN

TABLE 29 : Breeding Success

Season	Clutch Size	Eggs Laid	Eggs Hatch	Percent Hatch	Chicks Survive *		
					Number	Percent of Eggs Hatched	Percent of Eggs Laid
	1	29	14	48.3	12	85.7	41.3
1967-68	2	344	283	82.3	235	83.1	68.3
	Total	373	297	79.7	247	83.2	65.9
	1	78	28	35.9	19	67.9	24.4
1968-69	2	240	152	63.4	117	77.0	48.8
	Total	318	180	56.6	136	75.6	42.8
	1	22	10	45.4	7	70.0	31.8
1969-70	2	328	243	74.1	185	76.1	56.4
	Total	350	253	72.3	192	75.9	54.9
	1	31	20	64.6	17	85.0	54.9
1970-71	2	296	240	81.1	191	79.6	64.6
	Total	327	260	79.6	208	80.0	63.7
	1	160	72	45.0	55	76.4	34.4
Total	2	1208	918	76.0	728	79.3	60.3
	Total	1368	990	71.7	783	79.1	57.3

* Chick survival till mid January.

Some of the losses from unknown causes were probably desertion of eggs by parents, so that the percentage of deserted eggs would probably be higher than shown in table 30. Most eggs were deserted in mid-incubation, when one partner (usually the male) deserted the eggs before the other returned from sea. The reasons for desertion were not always clear. Some desertions occurred after a longer than average spell at the nest, but a few occurred after a shorter than average spell. Many of the desertions during early incubation were by females that were left to take the first incubation watch.

Some desertions were caused by the death (or disappearance) of the partner at sea. These are included in table 30 under the heading of adult mortality, and accounted for only 3.7 percent of egg losses. In a few (rare) cases, the male (who took the first incubation watch) remained throughout the whole incubation, and deserted only after the chicks had hatched and died of starvation (see also section 7.7).

Skuas took any deserted eggs, but also took some eggs by active predation. Most eggs taken by active predation were from two-egg clutches. This was probably because two eggs were harder to keep under the cover of the brood pouch than one egg. The figure in table 30 should be regarded as a minimum, because some of the losses from unknown causes were probably by skua predation.

Fighting for nest sites during the occupation period only occasionally resulted in loss of eggs (see also section 4.4). Such losses were quite evident when the egg was crushed or knocked out of the nest. However, the effect of shocks or chills to the embryo caused by being bumped or exposed during attacks was unknown.

Some eggs, especially in 1968-69, were lost by poor incubation. Some were scraped out of the nest, and others were only partly covered or left uncovered while the parents stood at the edge of the nest. The eggs were most likely inviable before being taken by skuas. All these eggs were from single-egg clutches that were laid late in the season, suggesting that the parents were inexperienced birds.

For a large number of eggs the cause of mortality was unknown. The majority of unknown losses occurred either in the 10 days after egg-laying or at about the time of hatching

TABLE 30 : Egg Mortality

Cause	Number	Percent	Percent Known Causes	Age of Egg (in days) 1-10	11-20	21-30	31-40
Addled	91	24.1	24.1				
Deserted	90	23.8	44.4	13	67	10	0
Skua predation	35	9.2	17.4	13	13	9	0
Adult mortality	14	3.7	6.9	0	1	6	7
Poor incubation	9	2.4	4.3	9	0	0	0
Fighting	6	1.6	2.7	6	0	0	0
Unknown	133	35.2	-	55	8	18	52
Total	378	100.0	100.0	96	89	43	59

TABLE 31 : Chick Mortality

Cause	Number	Percent	Age of Chick (in days) 1-5	6-10	11-15	16-20	21-25	26-30
Skua predation	27	45.0	7	7	3	6	4	0
Adult mortality	18	30.0	6	4	4	4	0	0
Fighting	3	5.0	3	0	0	0	0	0
Unknown	12	20.0	6	3	2	1	0	0
Total	60	100.0	22	14	9	11	4	0

These figures for the number of chicks produced at the different nest locations do not take into account the age and experience of the penguins in these areas. It could be argued that the lower productivity of peripheral nests (compared to central nests) is not so much a consequence of nest location as of the age of the occupying penguins, but this can only be resolved from studies of known age birds. In this study it was only possible to compare the breeding success of known individual penguins that either remained at the periphery or the centre in subsequent seasons, or changed from periphery to centre (or vice versa).

There was no significant change in breeding success of individuals that remained at the periphery or centre in subsequent seasons (table 35). Also, on average, change of nest location did not affect subsequent breeding success (table 34). However, penguins that changed from the periphery to the centre had a higher breeding success than those that remained at the periphery. Furthermore, penguins that changed from centre to periphery had a lower breeding success than those that remained at the centre.

Much of the difference in breeding success between periphery and centre can be attributed to the higher incidence of skua predation at the colony periphery.

v. Influence of Laying Date on Breeding Success

Two-egg clutches completed after 19 November (i.e. more than four days after the mean laying date) produced fewer chicks than clutches completed earlier. The difference in table 33 was not significant, but these figures accounted for mortality only until mid January. At this stage, some late chicks were only about three weeks old, and still had about three weeks ashore prior to departure for sea, when they would certainly suffer further mortality.

vi. Influence of Experience of Mate on Breeding Success

On the average, change of mate did not affect subsequent breeding success of either males or females (table 34). It might be expected, however, that a change to a "more experienced" mate might help improve breeding success, whereas a change to a "less experienced" mate might decrease breeding success.

In this study, knowledge of the previous experience of individual penguins was limited to a maximum of three seasons,

TABLE 32 : Influence of Clutch Size and Laying Date on Chick Survival (percentage of eggs laid)

A. Central Nests

Clutch Size	Laying Date		
	$\leq$14 Nov	$\leq$19 Nov	>19 Nov
1	33	40	39
2	84	74	66

Clutch size, F = 14.31 (1,190 D.F.) $p < 0.01$ **

Laying date, F = 1.91 (2,190 D.F.) $p > 0.10$ NS

Interaction, F = 0.60 (2,190 D.F.) $p > 0.10$ NS

B. Peripheral Nests

Clutch Size	Laying Date		
	$\leq$14 Nov	$\leq$19 Nov	>19 Nov
1	24	43	36
2	49	55	41

Clutch size, F = 5.73 (1,363 D.F.) $p < 0.025$ *

Laying date, F = 2.09 (2,363 D.F.) $p > 0.10$ NS

Interaction, F = 1.13 (2,363 D.F.) $p > 0.10$ NS

(30-40 days after egg laying) (table 30).

Chick mortality has been determined from a much smaller sample than used to analyse egg losses, for which mortality was better known (table 31). The two main causes of chick losses (until mid January) were skua predation and adult mortality. The table clearly indicates that skua predation of chicks was more important than predation of eggs. Losses also occur after the disappearance of one parent during the guard stage because the other parent has to remain guarding the chicks, and so cannot provide them with food. The chicks consequently die of starvation. Fighting by unmated penguins and unsuccessful breeders returning during the chick period was not an important cause of chick mortality. Most of the unknown cases of chick mortality could probably be attributed to skuas.

Chick mortality was highest in the colonies in the first 10 days after hatching (table 31), but as noted earlier (page 76) a high mortality would also occur after the chicks left for sea.

iii. Influence of Clutch Size on Breeding Success

The survival of single-egg clutches was significantly lower than two-egg clutches (table 32). The greater losses from single-egg clutches were independent of nest location and laying date. Most of these losses occurred during the egg period (table 29), and were due to parental failure (desertion and improper incubation behaviour). After hatching, chicks from single-egg clutches suffered similar mortality to chicks from two-egg clutches.

iv. Influence of Nest Location on Breeding Success

For two-egg clutches, nests at the colony periphery produced significantly fewer chicks than nests in the centre of a colony (table 33). This was independent of laying date. For single-egg clutches, there was no apparent difference in breeding success between nests at the periphery or centre. Most single-egg clutches were laid at the periphery (see section 7.6), but losses from single-egg clutches were high at all locations.

From 16 eggs laid at eleven isolated nests, only one chick (6.3 percent of the eggs laid) was raised up to mid January.

TABLE 33 : Influence of Nest Location and Laying Date on Chick Survival (mean chicks per nest)

A. Two-egg Clutches

Nest Location	Laying Date $\leq$ 9 Nov	 $\leq$ 14 Nov	 $\leq$ 19 Nov	 $>$ 19 Nov
Centre	1.50	1.68	1.47	1.32
Periphery	0.50*	0.99	1.10	0.82

* Note : From a sample of two clutches only.

Nest Position, F = 46.63 (1,448 D.F.) $p < 0.01$ **

Laying Date, F = 1.99 (3,448 D.F.) $p > 0.10$ NS

Interaction F = 1.19 (3,448 D.F.) $p > 0.25$ NS

B. Single-egg Clutches

Nest Location	Laying Date $\leq$ 14 Nov	 $\leq$ 19 Nov	 $>$ 19 Nov
Centre	0.33	0.40	0.40
Periphery	0.16	0.43	0.36

Note: Clutches laid before 9 Nov insufficient to be analysed separately.

Nest Position, F = 0.10 (1,105 D.F.) $p > 0.10$ NS

Laying Date, F = 0.98 (2,105 D.F.) $p > 0.10$ NS

Interaction, F = 0.08 (2,105 D.F.) $p > 0.10$ NS

TABLE 34 : Chicks per Clutch of Banded Penguins
Related to Change of Partner and Nest Location

Breeding Partner	Nest Location: Same	Nest Location: Different
Same	1.2	1.1
Different	1.3	1.2

TABLE 35 : Breeding Success of Banded Penguins
Related to Nest Location in Subsequent Seasons

Change in Nest Location (independent of laying date)		Change in Breeding Success (%)			
		Male		Female	
Season 1	Season 2	Season 1	Season 2	Season 1	Season 2
Periphery	to same periphery	55	53	58	52
Periphery	to different periphery	52	52	58	51
Periphery	to centre *	28	90	29	72
Centre	to periphery *	75	55	73	53
Centre	to different centre	75	80	75	79
Centre	to same centre	72	80	76	78

* Sample size too small to test for significance.

and for most penguins only one or two seasons. Thus, observations made here must be regarded as only tentative.

The behaviour of male 406 and female 407 led me to believe that they were "young" penguins. The first season they kept company without producing eggs. The second season they produced one egg at a peripheral site, but the chick was lost to skuas. The third season, at a central site, they produced two eggs which were both lost when the nest was taken over in a fight by another penguin. The fourth season they split, the male remaining unmated, while the female paired at a peripheral site with a previously successful male whose mate had not returned. The female laid two eggs, and one chick was raised. However, this increase in breeding success may be attributed to maturation and experience of the female, as much as to the experience of the newly acquired mate. There was no reason to suppose that the pair 406 and 407 would not have passed from a stage of unsuccessful breeding to successful breeding had they not separated.

It was easier to distinguish drastic reduction in breeding success when an apparently established and successful penguin paired with an unestablished penguin. Such an example occurred in the case of male 348. In the first season male 348 bred successfully with an unbanded penguin, raising two chicks. The following season, male 348 paired with female 400 (who, late the previous season, had laid only one egg which had been lost). With male 348, female 400 again produced one late egg, that was also lost. Female 400 did not lay the third season, and laid one late egg (that was lost) the fourth season. Thus, female 400 (a late breeder) bred unsuccessfully with three different males. Male 348 bred successfully, raising two chicks, in each of the two seasons after breeding with female 400. Thus, he produced the maximum of two chicks in each of three seasons, but in the one season that he was paired with female 400 he produced none.

Differences in the experience of mates did not always (or even normally) result in drastic reduction of breeding success. Male 930 had experienced at least two seasons attempting to raise chicks before he paired with female 499, who for at least three seasons had been unmated (see also page 56). The new pair (one experienced, one probably laying for the first time) successfully raised two chicks.

7.9 DISCUSSION

The return of penguins, incidence of unmated penguins, adult mortality, clutch size, and breeding success at Cape Bird were all markedly affected by the persistence of sea-ice along the western shores of Ross Island in 1968-69. In this summer, the date of arrival at the rookeries was slightly delayed, especially for the early arriving penguins. However, the mean date of egg-laying was not markedly different to other seasons. Fewer penguins returned, those that did return laid fewer eggs, and many that laid deserted, so that breeding success was lower than in other seasons. Many previous layers did not lay. Thus, the number of chicks raised was influenced not only by a higher egg and chick mortality, but also by a lower reproductive potential (i.e. fewer laying and smaller average clutch size).

It is not known exactly how the sea-ice conditions were related to the breeding biology. It may have delayed some and prevented others from returning to the rookeries. It may have been associated in some way with poor winter conditions and poor spring food supply. Unfortunately, no arrival weights were taken. However, the high incidence of nest desertion by incubating penguins indicates that many were in poor physical condition. This contention is further supported by the high incidence of single-egg clutches.

Males outnumbered females on the colonies in all seasons. There were always some unmated females but there were many more males in this condition. Females that returned in the occupation period but did not lay were presumably physiologically unable to lay. There was certainly no shortage of male partners. However, some males were unable to find partners. Except in 1968-69, when some previously successful breeders did not lay, all unmated males were either previously unmated or unsuccessful breeders. They did not have a previous partner to pair with (see also section 6.4). The unequal sex ratio of mature adults seems to result from a higher mortality of females. A possible reason for the higher female mortality of the Yellow-eyed penguin has been proposed by Richdale (1957:142), who suggested that females may suffer a greater strain while breeding.

The two main causes of egg and chick losses were predation and parental failure. Losses were highest in single (compared to two) egg clutches, at peripheral (compared to central) nests, and probably among late and unestablished breeders. Age was an unknown factor in this study.

Richdale (1957:117) has shown that age has a marked effect on clutch size in the Yellow-eyed penguin, and it quite possibly has a similar effect in Adelie penguins. It is also possible that young birds tend to establish territories at peripheral sites. Thus, the higher losses in single-egg clutches and at peripheral nests may be partly the result of the age of penguins in these categories. It is known that young birds of many species raise fewer young than older individuals (Lack 1968:297). Regardless of age, however, penguins at peripheral territories are more exposed and are subject to a higher incidence of skua predation than penguins at territories in the centre of a colony.

The laying dates of individual females tended to be similar from season to season. Thus, age seems to have little or no effect on laying date in Adelie penguins. Richdale (1957:21) suggested that the differences in individual laying dates may have a genetic basis. It seems certain that there is selection against late laying. Females that consistently laid late would supply a lower recruitment to the population than females that laid earlier. Late arriving males would also leave fewer progeny, either because they were unable to find a partner, or because they paired with a late arriving female. There may also be selection against penguins laying very early in the season, because early eggs and chicks are very susceptible to skua predation. Early chicks, especially, are conspicuous targets for skuas, and are also susceptible if left unguarded before the formation of creches.

Some synchronisation of breeding is provided by seasonal changes in the environment. Close synchronisation, however, probably results from social stimulation rather than from a response to the physical environment. Penguins returning later (when there are large numbers already ashore) are subjected to a higher degree of social stimulation than those returning earlier. This stimulation may have helped induce laying, leading to a general synchronisation of laying within the colonies. Synchronisation of breeding probably has many advantages. If all eggs are laid about the same time then the predation risk is lowered, complementing the clustering of nest sites. The chicks also grow up at the peak of food abundance, and depart for sea before the deterioration of the weather at the end of summer.

8.0 CHICK BEHAVIOUR

8.1 INTRODUCTION

In this study Adelie penguin chicks were observed at marked nests from the time of hatching. In the first summer (1967-68), chicks were observed until they departed for sea, but in subsequent summers observations had to be terminated just before chick departure. In the summer of 1968-69, individual chicks were observed for periods of ten minutes each, at intervals of approximately five days. In 1969-70 and 1970-71, nests were checked daily, but with no set observation period.

Adelie penguin chicks are semi-altricial at hatching (see also Nice 1962:20 & 25, Reid 1965, Reid & Bailey 1966). They are at first unable to leave the nest, and require a great deal of parental care. The chicks are covered in down at hatching, but their body temperature is not completely regulated until about the age of 15 days (Sapin-Jaloustre & Bourlière 1951:76, Goldsmith & Sladen 1961:257).

The growth rate of Adelie penguin chicks approximates a truncated normal curve (Sladen 1958:55, Taylor & Roberts 1962:194). For the first few days there may be little or no gain in weight. Some chicks are not fed until 3 days old. With regular feeding, however, chicks show a rapid and steady increase in weight from about 90 grams to nearly 4000 grams in about 6 weeks. In the week prior to departure, the average weight decreases slightly, though there may be marked fluctuations in weight due to the infrequency of large feeds.

8.2 PARENTAL CARE

The period for which parents care for their chicks is divided into the guard stage and the creche or post-guard stage.

In the guard stage, one of the parents guards and feeds the chicks while the other goes to sea to collect more food. The parents usually change duty every day or twice every three days (see also section 4.2). For about the first five days, chicks spend most of their time completely under the cover of the parent's brood pouch. The parent lies down over the chicks in a manner similar to the egg incubation posture (see section 3.2vii). As the chicks grow larger they become more exposed and can be only partly brooded by their parents. Thus, until they are at least 10 days old, chicks usually have their heads in the brood pouch, with only the hind quarters sticking out. Between 11 and 15 days, the chicks may simply huddle against the parent (who may lean against the chicks). After about 15 days, by which time chicks are completely homeothermic (see section 8.1), most parents stand to one side of the nest, leaving the chicks lying or standing in the nest.

In the creche or post-guard stage, the chicks are left unguarded by their parents for many hours of the day. Parents continue feeding their own chicks, but neither parent remains with the chicks for long after feeding. In the absence of their parents, the chicks may remain at the parental nest site, or may cluster with other unguarded chicks to form creches. (The term creche is meant to imply simply a collection of young. There are no "guardians" of the creches - see also Sladen 1958:61).

The age at which chicks are first left unguarded varies slightly from colony to colony, and year to year. Thus in 1969-70 the average age was 19.2 days at one colony and 21.6 days at another colony. In 1970-71, the respective ages were 20.6 and 20.1 days. The youngest chick left unguarded was 14 days, and the oldest chick was 30 days before being left unguarded. At Cape Royds, Taylor (1962:191) recorded an average of 22.4 (range 17-32) days. Sladen (1958:59) recorded an average of 30 (range 28-32) days in six chicks at Hope Bay, and 19 (range 17-28) days in 10 chicks at Signy Island. However, he considered that the Signy Island dates were atypical, and that the average age of creching was "about one month". At Cape Bird, the average age at which the chicks in the study colonies were first left unguarded was about three weeks.

Taylor (1962:191) established that chicks hatched early in the season tend to be guarded for longer than those hatched later. Also, parents at the colony peripheries tend to guard their chicks longer than parents in the centre of a colony. These same relationships were observed at Cape Bird. In addition, parents that hatched only one chick tended to guard their chicks longest of all. These parents do not have to supply as much food as parents with two chicks. Consequently, parents of single chicks may not feed their chick immediately upon arrival, and the relieved parent may not leave for sea immediately.

Chicks are fed throughout the creche stage, and probably do not go long without food before they depart for sea. However, for about two weeks before departure, they receive progressively fewer feeds from their parents, and their weight decreases slightly (see also Taylor & Roberts 1962:192)

8.3 BEHAVIOUR OF CHICKS

The behaviour of chicks is described in its approximate order of appearance (see also table 36). References are made to adult behaviour described earlier (see section 3).

i. Food Begging

Food begging occurs on the day of hatching, but is not at first essential to initiate feeding. A parent will bend over and place its bill beneath the bill of a newly hatched chick without any prior begging. Subsequent begging by the chick then stimulates the parent to regurgitate food into the chick's now open bill. As the chicks grow older, they help initiate more feedings by begging from passive parents.

When begging for food, the chick reaches up, with wobbly head movements, and vibrates the bill at the base or tip of the parent's bill (figure 51). The mandibles of the bill may be rubbed slightly against one another. Begging is usually accompanied by a single syllable call (termed "peep" by Sladen 1958:46). The white sclerae of the eyes may show slightly, apparently as a consequence of raising the head. The flippers may be held out for balance.

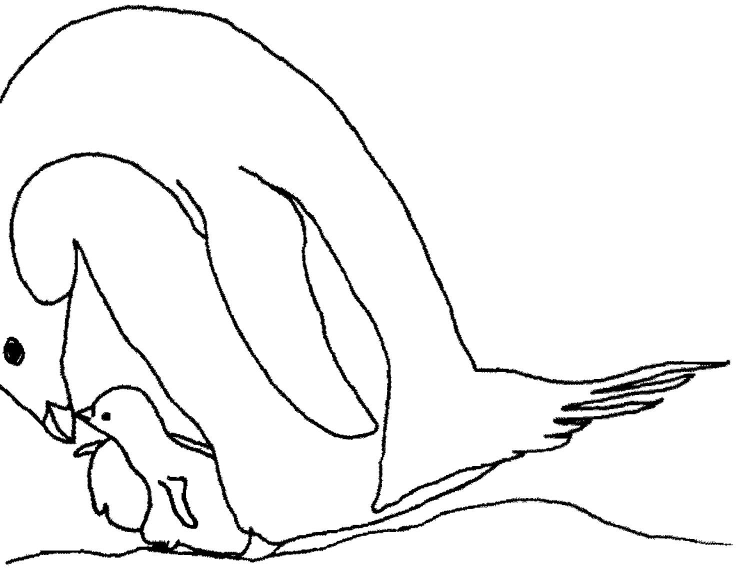
Chicks may beg from parents at any time, but especially when a parent has just returned from sea. Older chicks may beg immediately following the Loud Mutual display movements and vocalisations (see section 8.3v), but begging and Mutual display should not be confused.

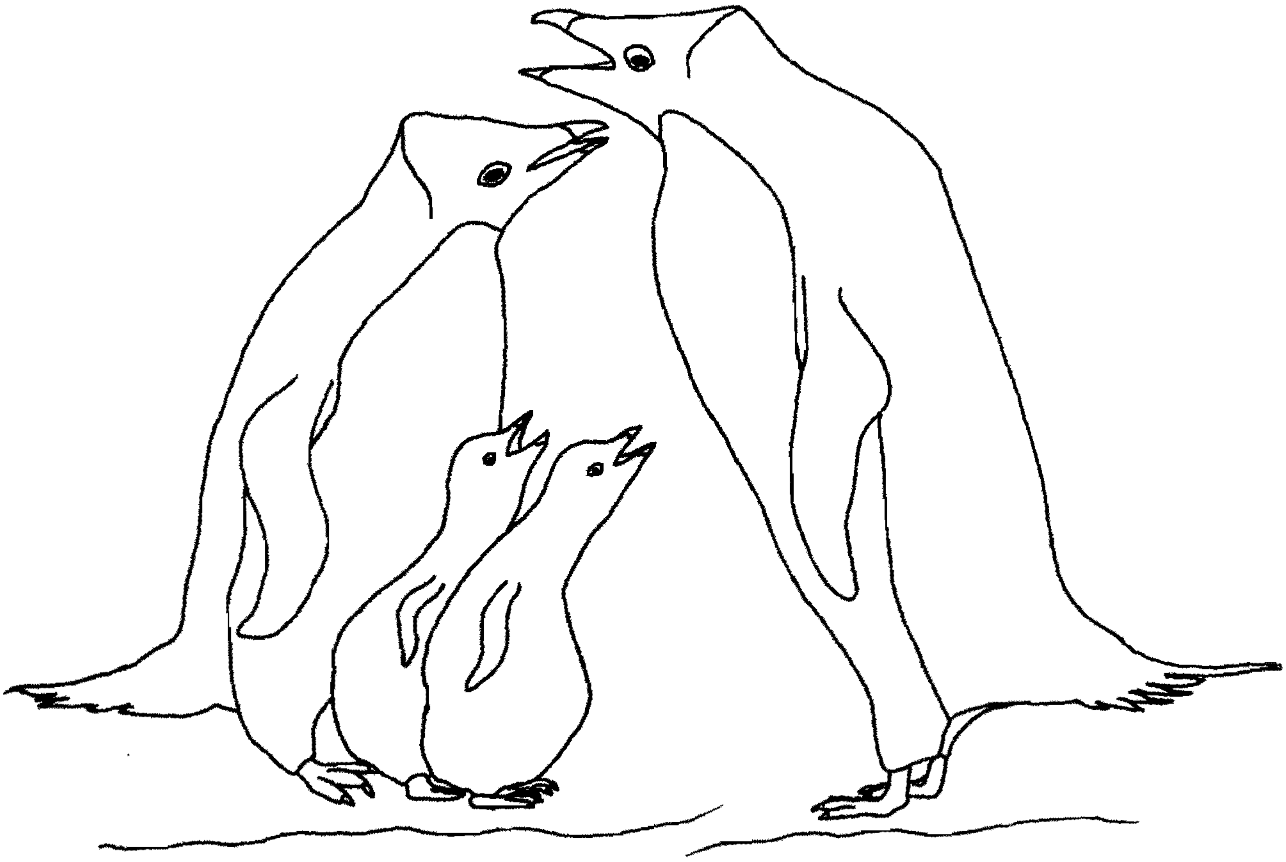
ii. Comfort Activities

Comfort activities are among the first types of behaviour

FIGURE 51. Chick begging for food from parent.

FIGURE 52. Chick Loud Mutual display with parent.





recorded (table 36). Yawning, shaking (the whole body, head, or flippers), stretching (including stretching the flippers upwards), swallowing, scratching (with foot over flipper), and preening are all similar to adult activities. All occur in chicks less than 10 days old. Panting occurs from 7 or 8 days of age, although chicks are not completely homeothermic until about 15 days old (see section 8.1). Chicks commonly sleep while lying flat on the ground, but as they grow older they may also sleep while standing. After about 15 days, chicks may sleep with the bill tucked under the flipper, as in adults.

Chicks sometimes preen the breast feathers of their parents or the breast of siblings. Such allo-preening does not occur in adult Adelie penguins.

iii. Gripping at Nest Stones

Chicks less than 5 days old may grip at nest stones with the bill. Between 6 and 10 days, chicks start reaching out and dragging in nest stones from the periphery of the nest (similar to the stone rearranging of adults during nest building). Small stones are sometimes swallowed.

iv. Locomotion

Newly hatched Adelie penguin chicks are unable to move out of the nest. However, within 6 to 10 days they may stand up at the edge of the nest. Between 11 and 15 days, chicks start moving freely around the nesting territory. However, they seldom venture far from the nest until about 21 days. After this, chicks left unguarded by parents may move away from the nest to join with others in a creche.

v. Loud Mutual Display

At about 11 days, chicks start performing an immature version of the adult Loud Mutual display. This displaying occurs at re-union with parents, usually at the nest site (figure 52). It is clearly distinguished from begging. The raised head is waved from side to side in a much more exaggerated manner than for begging, the bill is opened wide, and the accompanying call consists of several syllables (termed a tremulous call, by Sladen 1958:36). At first, the eyes may not be actively rolled downwards, but after about 16 days of age the eyes are usually strongly rolled, exposing much white of the sclerae. It is often difficult to determine whether or not feathers are erected owing to the covering of down. However, after they become visible, the crest feathers are certainly erect. Loud Mutual display, begging, and feeding may follow in quick succession, but the three stages are quite separate.

vi. Quiet Mutual Display

Chicks perform the Quiet Mutual display with parents after both have been disturbed, for example, by an intruder. The head is raised and waved from side to side, but there is no accompanying call.

vii. Escape Behaviour

Chicks show obvious escape reactions from about the time they become mobile. Stimuli that elicit escape reactions include intruding adults, skuas, and humans. When disturbed at the nest, a young guard stage chick will crouch low to the ground and huddle against its parent or sibling. When a parent has been drawn into a fight, so that the chicks are exposed at the nest site, young chicks usually remain crouched in the nest, keeping very still. Older chicks, however, often run away from these disturbances (see section 8.5).

Creche chicks actively huddle together when disturbed. Chicks in these huddles characteristically face towards the source of disturbance. This is in contrast to facing inwards as in undisturbed huddles, which may or may not be a response to temperature conditions.

viii. Aggressive Behaviour

Adelie penguin chicks actively seek contact with others. Sibling chicks frequently huddle together, side by side or one on top of the other. As they get older, chicks from adjacent nests often huddle together into creches, without any signs of aggression.

The first indications of aggressive behaviour occurred after about 11 days, when sibling chicks would occasionally gape and bill-grip with one another. From about 16 days of age, a chick may grip its sibling by the feathers of the back, and beat it with the flippers. Creche chicks also gape and peck with the bill, and beat one another with the flippers. However, these "aggressive" reactions are probably best termed play behaviour, because they lack any quality of "seriousness" (see also Marler & Hamilton 1966:193). In these situations, the chicks do not compete with a rival for a possession.

Serious aggressive behaviour was only observed in chicks older than about 21 days. This behaviour was directed toward strange adult penguins or other chicks passing by the parental territory or coming too close to a creche. Older creche chicks also react aggressively to skuas. The change in response to skuas seems to occur at a time when the chicks are large enough to defend themselves.

The aggressive reactions of chicks are all similar to those of adults. Physical attack (with bill or flippers) is the commonest form of aggression. However, charging forward, gaping, pointing the bill, waving the head from side to side, holding the head to one side, and rolling the head at the side of the body also occur. Until the down feathers start to moult it is difficult to determine whether or not the feathers are erected. However, the eyes are rolled to expose the white sclerae during threatening.

ix. Feeding Chase

Feeding chases become frequent when chicks are older than about 21 days, and have joined a creche. A parent that gives the Loud Mutual call on approaching the vicinity of its territory usually attracts only its own chick(s), though other chicks sometimes come out of the creche. The parent then runs away from the area, often right out of the colony, and is pursued by the chicks. The chicks run along with flippers held up over the back, and open and close the bill to utter the peep call. Strange chicks usually give up the chase very quickly. When there are two sibling chicks, one also gives up the chase, and walks back to the colony (usually to the vicinity of the parental territory). The other chick may be fed several times before it also loses contact with the parent. Contact is re-established when both parent and chicks return to the parental territory.

Sibling chicks do not fight one another for food. However, when the two chicks are together they constantly reach up for food, and this interferes with feeding and spills food. The feeding chase separates siblings, so that interference is reduced. Parents ensure that both chicks are fed by periodically returning to the nesting area. There are, however, marked differences in the ability of parents to feed their chicks.

x. Aark Call

An immature aark call (Sladen 1958:39) is first heard among creche chicks. It occurs when chicks are alerted, for example by the presence of skuas or humans. It becomes more frequent when the creches start to disperse and the chicks move about outside the colonies. Aark calling is strongest when the chicks enter the water on departure for sea.

xi. Ecstatic Display

An immature version of the adult Ecstatic (advertising) display occurs in creche chicks older than about 35 days. The head is raised vertically, eyes rolled, and the flippers beat up and down. The bill is opened, and a shrill multiple syllable call is uttered. The call resembles that of the Loud Mutual display. Such an Ecstatic display was given by a chick after losing its parent in a feeding chase. Another display was performed by a creche chick standing at the colony periphery. The stimulus for these chick Ecstatic displays may be separation from parents (e.g. away at sea), but may also be precocious sexual development. In adults, the Ecstatic display seems to be stimulated by being alone and sexually receptive.

8.4 PARENT-CHICK RECOGNITION

Sladen (1958:60) was the first to show that Adelie penguins feed only their own creche chicks. This behaviour implies that parents and chicks are able to recognise one another as individuals. Some aspects of this recognition can be determined from responses in both natural and experimental situations.

Creche chicks clearly recognise their own parents. Many adults return with food to the vicinity of the creche, but individual chicks usually respond only to the Loud Mutual call of their own parents. Occasionally, strange chicks will initially respond to an adults call, but they do not persist. Most creche chicks ignore the call of adults other than their parents. Penney (1968:124) provides experimental evidence of the importance of the parents' vocalisations in bringing parent and chick(s) together.

TABLE 36 : Age of Chick at Which Behaviour Patterns were First Recorded

Age in days	Behaviour Recorded
0-5	Completely brooded by parent. Begging with peeping call. Some comfort movements; e.g. yawning. Gripping at nest stones.
6-10	Head in brood pouch of stooping parent. May stand up at edge of nest. Comfort movements common; yawn, shake, stretch, scratch, preen. Panting. Reach out and pull in stones; swallow small stones.
11-15	Head in brood pouch, or lie in front of parent (who leans against chick). Move around nest freely when parent gets off, as at nest change. Loud Mutual display with parents, especially at nest relief. Avoidance reactions to disturbance by intruding adults, skuas etc. Gape at one another, and peck at one anothers bill.
16-20	Chicks lie in nest while parents stand beside. Some chicks left unguarded by parents. Chicks now completely homeothermic. Free movement around territory. Quiet Mutual display with parents when disturbed. Peck and grip feathers on back of sibling and beat with flippers.
21-25	Most chicks left unguarded by parents. May venture alone outside colonies. React aggressively to adults or other chicks passing too close. Feeding chases before and after feeding.

Parents also recognise their own chicks. This was demonstrated when, during a disturbance in the colony, a 14 day old chick was displaced several metres from the nest. The parent was apparently unaware of its disappearance, and remained guarding the sibling. The chick scrambled around between nearby nests, occasionally squawking loudly. Suddenly, the parent heard the squawking, became restless and started looking around. The parent then gave a Loud Mutual call. The chick recognised this call and ran a little closer, before pausing and squawking again. The parent again replied with a Loud Mutual call. The chick soon found its way to the nest, where it joined in a Loud Mutual display with the parent. From cross fostering experiments, Thompson & Emlen (1968:132) reported that parents begin to identify their own young between the 8th and 17th days. This is also the period in which chicks start performing immature versions of the Loud Mutual display (see section 8.3v).

Apart from auditory recognition, adults and chicks also probably recognise one another visually, by various characteristics of appearance and behaviour. However, rapid growth in size, and changes in appearance of chicks, require constant learning of visual recognition. Vocalisations also change slightly as the chicks grow, but not so markedly as external appearances. The importance of auditory recognition is illustrated by its early appearance in the development of chicks. By the time chicks are first left unguarded, parents are able to recognise their own chicks, and chicks are able to recognise their own parents. This has also been reported for Yellow-eyed penguins and Little Blue penguins, Eudyptula minor (Richdale 1951:276), Rockhopper penguins (Pettingill 1960, Warham 1963:240), and Royal penguins, Eudyptes chrysolophus schlegeli (Warham 1971:100).

8.5 ADULT AGGRESSION TO CHICKS

Chicks of any age wandering away from their natal territory are attacked by other territorial penguins as strongly as are intruding adults. This is especially evident before the breakdown of the territorial structure of colonies and the formation of creches. Chicks of between 16 and 20 days, with some degree of mobility, but not yet creched, taking a few steps from the edge of the nest, may be pecked by neighbours. Sometimes, instead of turning back to the parental nest, they may run further away, drawing threats and pecks from all territorial penguins in their path, and creating chaos in the colony. These wandering chicks usually run with the body almost horizontal and the head held low to the ground. Younger chicks with little locomotory ability can be seriously injured and even killed by the vicious pecks of adults, which are usually directed at the head. The chick's avoidance behaviour clearly has survival value in that the chick is withdrawn as far as possible from adult attacks. However, it appears to have little appeasement value, as the adults continue to attack wandering chicks as long as they remain within range. Wandering chicks often attempt to bury their head into the brood pouches of territorial adults. If they are successful, pecking may stop, at least for a short while, especially when the adult has one or two chicks of its own.

Adult aggression to wandering chicks has marked survival value for their own chicks. Parents normally cannot raise more than two chicks. A few instances in which adults adopted a strange third chick all resulted in death by starvation of the smallest chick. This was usually the parents' own smallest chick, because the adopted chick, already old enough to move about freely, was usually larger than the parents' own chicks.

Creched chicks are sometimes molested by strange adults. These adults are usually unsuccessful (probably young) breeders. They may approach a creche chick and attempt to mount it. When the chick tries to escape it may be chased, severely pecked, and beaten with the flippers.

Parents show mild aggression towards their own chicks older than about 16 days, when they persistently beg for food. Such aggression usually consists of mild snapping and jabbing the bill at the chicks bill, sometimes while backing away. This frequently occurs when the chicks approach a parent prior to, and during, feeding chases.

8.6 CHICK RECOGNITION OF NATAL TERRITORY

Even before the age at which they are left unguarded, chicks that are displaced or wander from the nest, usually find their way back again. However, they may be vigorously pecked by other adults and wander aimlessly for some time before returning. Return to the nest may in fact be aided by parental vocalisations (see section 8.4).

Chicks that have entered creches, however, are easily able to find their natal territory again. Before the return of the parent with food, chicks may leave the creche and return of their own accord to the vacant natal territory. (The timing of this response is undoubtedly based on the regularity of feeding and the amount of food in the chick's stomach). Chicks that lose contact with a parent during a feeding chase may also return to the natal territory (a response that facilitates re-establishment of contact with the parent - see section 8.3ix). Playbacks of parent Loud Mutual vocalisations from outside the colony by Penney (1968:124) also caused chicks to return to their natal territory.

The ability of chicks to return to their natal territory is thus very important for establishing contact with parents in a crowded colony. Nelson (1966:412) has suggested that this ability may lead to philopatry, "the tendency for young adults to acquire nesting sites in the precise area of their birth". LeResche & Sladen (1970:518) have now demonstrated that philopatry exists in the Adelie penguin.

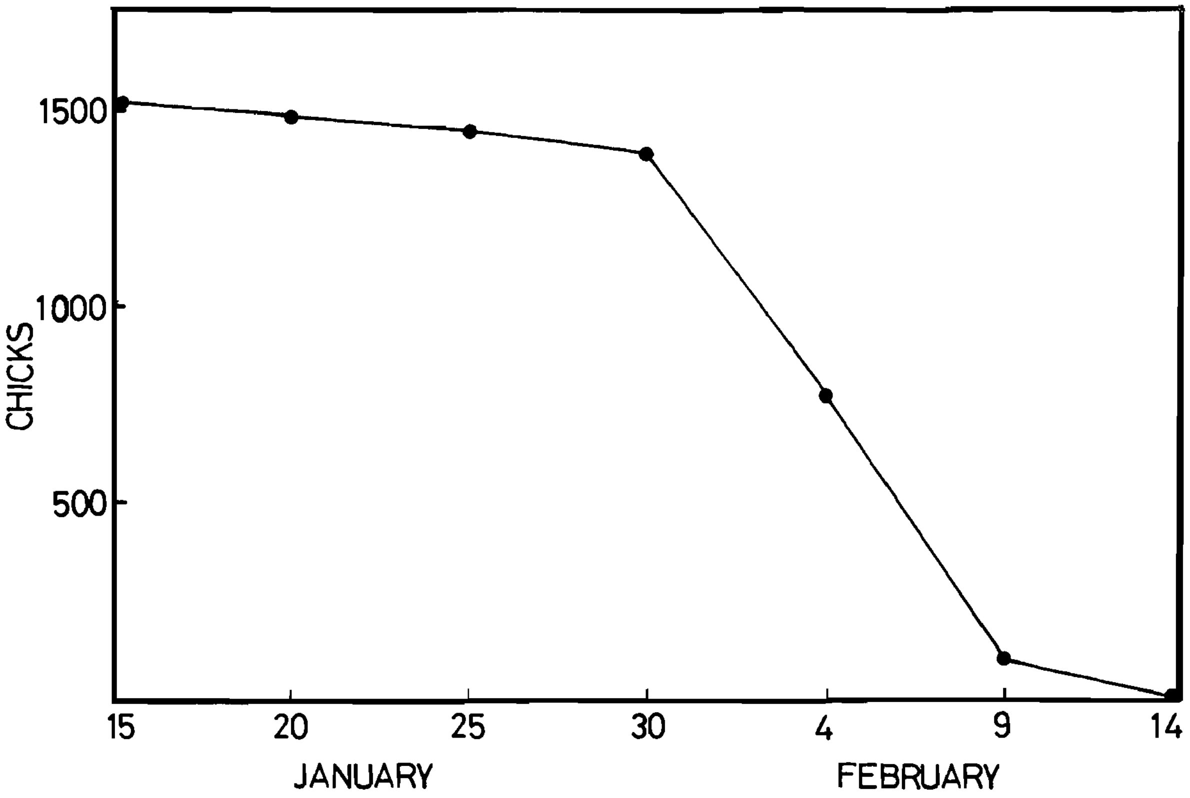
8.7 CHICK DEPARTURE FOR SEA

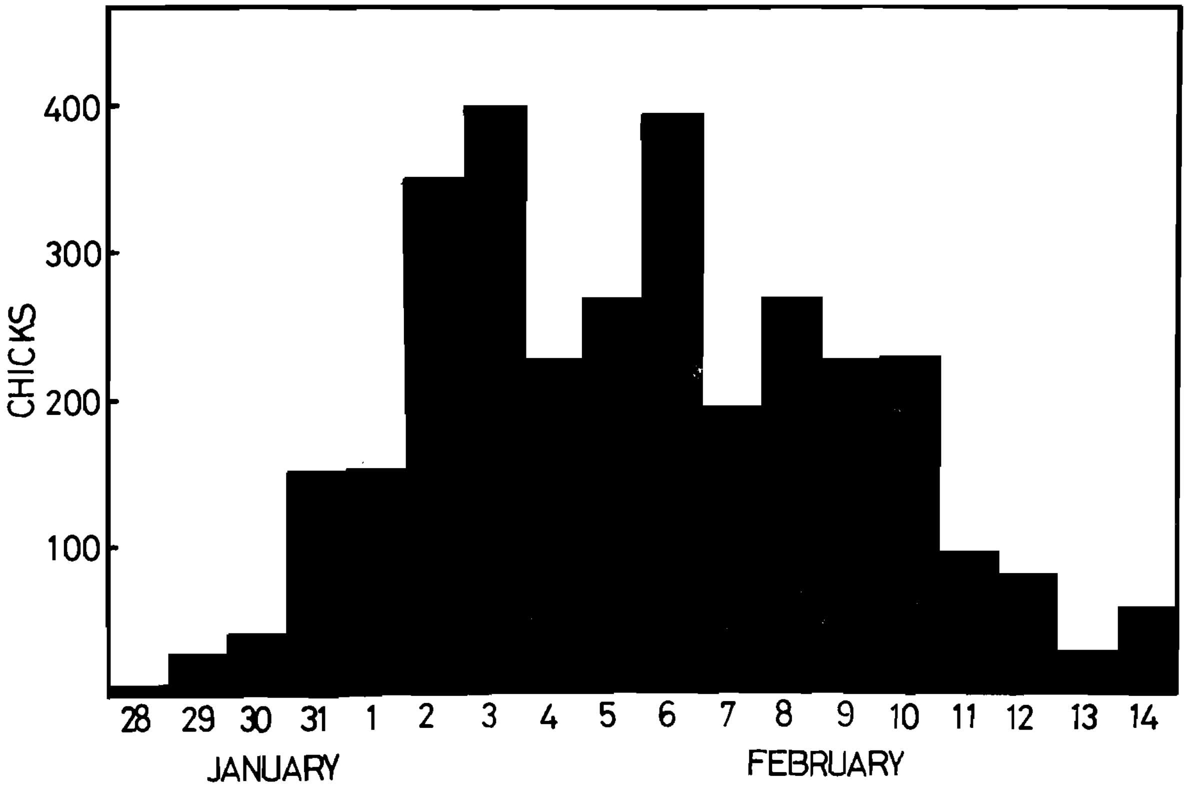
Taylor (1962:194) documented the departure of chicks at Cape Royds. He recorded the first departure on 30 January, but it was not until 3 February that large numbers left. The mean age at departure was 50.6 (range 41-56) days. Chicks that hatched later in the season tended to leave at a younger age than those that hatched earlier.

At Cape Bird, in the summer of 1967-68, chicks began gathering on the beaches at the water's edge on 28 January. The same day, a few were observed to swim out to sea, some alone, some in pairs. Unfortunately, no chicks were marked the first summer, and it was not possible to make observations in subsequent summers. However, the maximum possible age of the chicks seen leaving in 1967-68 was 54 days. Most chicks had left their colonies by the second week in February of that

FIGURE 53. Number of chicks remaining in a sample of colonies, January - February 1968.

FIGURE 54. Number of chicks gathered on a section of the shore, January - February 1968.


1500
1000
CHICKS
500
15
20
25
30
4
9
14
JANUARY
FEBRUARY


400
300
CHICKS
200
100
28
29
30
31
1
2
3
4
5
6
7
8
9
10
11
12
13
14
JANUARY
FEBRUARY

summer (figure 53). Once they had reached the beach, chicks usually did not remain ashore long. The numbers gathered on the shore each day probably reflect the rate of departure quite closely (figure 54).

The chicks usually departed for sea in groups. The average size of these groups was 13, but the range was from 1 to 100. At Cape Royds, the departing groups never contained more than 12 chicks (Taylor 1962:195). However, the long sandy beaches at Cape Bird provide a much wider access than the small rocky beach at Cape Royds.

Chicks often left for sea when there were no adults present. Nevertheless, departure of adults certainly encouraged chicks into the water. Once in the water, the adults soon left the chicks behind. Chicks sometimes return to the shore after entering the water (see also Taylor, op. cit.), and may climb up onto ice floes in the water.

When there was a large surf, the chicks had trouble getting through the breakers. A group of chicks would rush towards the breakers, but only a few might get through. The rest would be swept back up the beach. After re-grouping, they would rush toward the breakers and repeat the sequence over again.

Once in the water, past the narrow line of breakers, the chicks would splash around on the surface, with much loud calling (see section 8.3x). They could swim under the water, but none were observed to "porpoise" as the adults do. After swimming several metres under water, the chicks would stop and come to the surface. After splashing around on the surface for several seconds (sometimes minutes) they would then dive under the water again. By this slow alternation of swimming and surfacing the chicks gradually headed out into the middle of McMurdo Sound in a northerly direction.

8.8 STAGES IN DEVELOPMENT OF BEHAVIOUR: DISCUSSION

Nice (1962:28) recognised five stages in the development of behaviour, and compared these in a number of species. Adelie penguin chicks appear to follow much the same pattern of development as the young of other birds. The first three stages of Nice (op. cit.) are passed in about 10 days (table 36). During this period activities are mostly concerned with feeding and comfort behaviour. After about 10 days, mutual recognition develops between chicks and parents. Locomotion also becomes more evident, along with escape reactions (from strange adults and predators). After about 21 days, serious aggressive behaviour occurs. Isolated occurrences of the Ecstatic display in chicks older than about 35 days may represent precocious sexual behaviour. However, sexual behaviour does not develop fully until the young penguins are more than two years old. First breeding does not occur until at least the age of three years in females and four years in males (LeResche & Sladen 1970:518).

The development of complete independence from the parents does not occur until the chicks depart for sea. Swimming movements at first are not as efficient as those of adults, and probably take some time to perfect. Observations are lacking on the development of self-feeding.

The limited breeding season means that chicks hatched early in the season receive more care before being left unguarded and before departing than chicks hatched late in the season. This means that they will be in a better condition to face the northward migration to the wintering quarters.

9.0 SOCIAL COMMUNICATION

9.1 INTRODUCTION

Communication may occur at various levels of interaction (Tavolga1970:286), but most referred to in this section is at the signal level. Signals are necessary both for the formation and maintenance of breeding pairs, and for the defence of the nesting territory. The displays described earlier (in section 3.0) are used as signals in communication. Communication, however, involves more than just the sending and receiving of signals. It also involves concepts such as the context in which the signals occur, the message "intended" by the sender, and the meaning of the signal for the recipient (Smith 1965:405). Displays are the structural units of signals, but the timing of displays also affects signal content. Thus, the message or meaning of a signal may differ in different contexts.

Communication is necessary both for the formation and maintenance of breeding pairs, and for the defence of the nesting territory. Pair formation only occurs after the acquisition of a territory, and so communications involved with territory defence are described first. The descriptions of defence behaviour are amplified by detailed quantitative analyses. The data for these analyses were collected in set observation periods, during which individual penguins (or pairs) were watched for ten minutes at randomly selected, numbered nest sites. A total of 300 hours observation was made throughout one entire season.

Four types of analyses are presented.

1. Situations in which the displays occur.
2. Sequences in which the displays occur.
3. Component structure of displays.
4. Effectiveness of displays.

The first three of these analyses are more usually applied to studies of display causation or motivation (Tinbergen 1959:30, Ficken & Ficken 1966:644). However, they are really observational analyses valuable for investigating objectively the function of displays, though they can also be used to make inferences about causation.

9.2 SITUATIONS ASSOCIATED WITH TERRITORY DEFENCE

Three types of intra-specific encounters can be distinguished.

i. Disputes over territory ownership.
ii. Encounters with neighbours across a common boundary.
iii. Encounters with strangers approaching the territory boundary.

Disputes over territory ownership mainly occurred when penguins were setting up territories, and mainly involved fighting. Encounters with neighbours and strangers occurred even after penguins had established their territories, and involved many displays. These are analysed in the following sections (sections 9.3 to 9.8).

i. Territory Ownership

Disputes over territory ownership may be brief or prolonged. Brief encounters occurred when a penguin returned to the wrong territory, for example, after collecting a stone for its nest. Such encounters usually consisted of only a few blows from the flippers. Prolonged encounters (lasting longer than about 30 seconds, and sometimes more than 15 minutes) occurred only when two penguins had strong claims to the same mate or territory. Levick (1914) gives vivid descriptions of typical fight scenes. These prolonged fights usually occurred only between penguins of the same sex. Such encounters occurred when males returning late in the season found the previous season's territory occupied. For females, fighting was more often for the possession of a former mate than for a former territory. In prolonged fights, the opposing penguins bump one another with their chests, grip with their bills, and strike with their flippers. Fighting may be interspersed with bursts of Loud Mutual calling, given in the forward posture (see also section 3.4iii). The fights often continued until the penguins were very exhausted. Sometimes bleeding occurred (from the flippers and bill) but serious damage seldom resulted. Some fights were clearly one sided, but others appeared so even that it was difficult to decide why one penguin suddenly stopped fighting and escaped. When the loser tried to escape it was sometimes chased by the winner (see figure 16). Winners of fights were usually penguins that had the longest association with the territory (or mate).

ii. Neighbour Encounters

When resting, penguins avoided facing directly towards the head of a neighbouring penguin (see also section 10.4). However, when disturbed by activities in a neighbouring territory, penguins turned and faced the source of disturbance. Penguins crouched on their nests in the centre of their territory could reach just far enough to exchange pecks with their neighbours.

Many activities in adjacent territories elicited no obvious response in resting penguins. Sometimes neighbouring activities elicited a mild response. For example, when a neighbour rearranged nest stones, or started nest scraping, a penguin on an adjacent territory might do likewise. Alternatively, a pair of penguins moving around on a neighbouring territory may elicit a response, such as the Bill-to-Axilla, Sideways Stare, or Alternate Stare. The most intense reactions occurred when the neighbour's activities were performed near the common boundary; for example, when a neighbour started rearranging nest stones near the boundary. The two penguins may then Gape at one another and exchange pecks. After such an exchange, the penguins may remain facing one another for a short while before continuing the encounter or turning away again.

Some encounters were initiated when a neighbour accidentally crossed the boundary with its tail or foot. This would elicit a Point, Gape, or peck. The neighbour usually withdrew immediately from such an encounter. Most encounters, however, were initiated before the neighbour had actually crossed the boundary.

iii. Encounters with Strangers

Strangers included penguins without any territory or penguins well away from their territory. Many of these encounters occurred at greater distances than neighbour encounters. Strangers wandering about a colony looking for nest stones, for example, often attempted to steal from territories on which the occupant was resting and facing in the other direction. Approach could be inhibited simply by the occupant opening an eye and turning its head to look around. When strangers paused in inter-nest spaces they might elicit a Bill-to-Axilla or Sideways Stare while still some distance away from the nest. If the stranger were to come closer it might elicit an Alternate Stare, Point, or Gape. Charging was used against strangers outside the territory only by penguins not involved with incubation duties.

A stranger reaching towards the boundary of an incubating penguin, attempting to steal a nest stone, may elicit a sequence of responses. The incubating penguin may reach forward and Point at the stranger, causing it to withdraw its head. If the stranger does not withdraw completely, but remains poised to reach forward again, the incubating penguin may then give the Alternate Stare, by retracting the neck slightly from the Point and waving the head from side to side (see also figure 56d). The incubating penguin gradually retracts its head and neck more and more, and this entices the stranger to reach forward again. The incubating penguin then immediately lunges forward with another Point or Gape. The sequence may be repeated several times before the stranger either obtains a stone or withdraws entirely from the encounter.

9.3 SEQUENCES IN DEFENCE OF TERRITORY

The behaviour of an individual penguin consisted of both isolated acts and sequences of acts. In this study, time intervals between successive acts were not recorded. The sequences recognised consist of acts which the observer considered related at the time of recording.

Any of the seven acts listed in table 37 may occur as an initial response in an encounter with another penguin. The most frequent initial responses were Sideways Stare, Point and Gape. The probability of the occurrence of these responses is increased when the conditions of an encounter are specified (table 38). Thus, Sideways Stare was the most frequent initial response to strangers pausing near the territory (i.e. within about two inter-nest distances). It was also the commonest response to "distant" disturbances (at the centre or far side) of a neighbouring territory. Point was the most frequent response to strangers passing directly close-by the territory (within about one inter-nest distance). Gape was the commonest response to a neighbour disturbance close to the boundary. Other responses occurred less frequently. The Bill-to-Axilla was given mostly by males (table 37) to more "distant" stimuli (e.g. neighbours well within their territories, or strangers about two or three inter-nest distances away). The Alternate Stare was most frequently given to strangers pausing close to the territory (usually within one to two inter-nest distances). The Charge was also used by some penguins against strangers lingering near the territory (see also section 3.3vi).

The effect of proximity of a stimulus was further examined in an experiment in which a model was presented at different distances from the nests of incubating penguins (see also section 10.3). The initial responses of incubating penguins to the model are shown in figure 55. Responses occurred in the order Sideways Stare, Alternate Stare, Point, Gape, peck attack, as the model was moved closer. Thus, at 150 centimetres the Sideways Stare comprised about 70 percent of the responses, but at 60 centimetres the Gape comprised 70 percent of the responses. Neither the Charge nor the Bill-to-Axilla appear in these results, because the appropriate situations for these responses were not established. Charge did not occur because incubating penguins did not leave their nests. Bill-to-Axilla occurred (but rarely) in preliminary trials at the greatest distances (usually in excess of 150 centimetres). At the time the experiment was performed (during late incubation) it was difficult to attract the penguins' attention to the model beyond this distance.

Proximity of the stimulus clearly influenced the initial response of these penguins. However, other characteristics of the stimulus, particularly movement, were also important. Thus, whereas slow approach of an intruder may elicit a Sideways Stare (figure 56b), a sudden approach to the same distance would normally elicit a Point or Gape (figure 56a). Sometimes the same type of approach would elicit different reactions. This could mostly be attributed to the previous stimulation of the defending penguin. Thus, a male that had been undisturbed for some time might only open an eye at the approach of another penguin. However, a male that had just repelled one penguin (that had tried to steal nest stones, for example), would react more aggressively to the approach of another penguin.

FIGURE 55. Initial responses to a model.

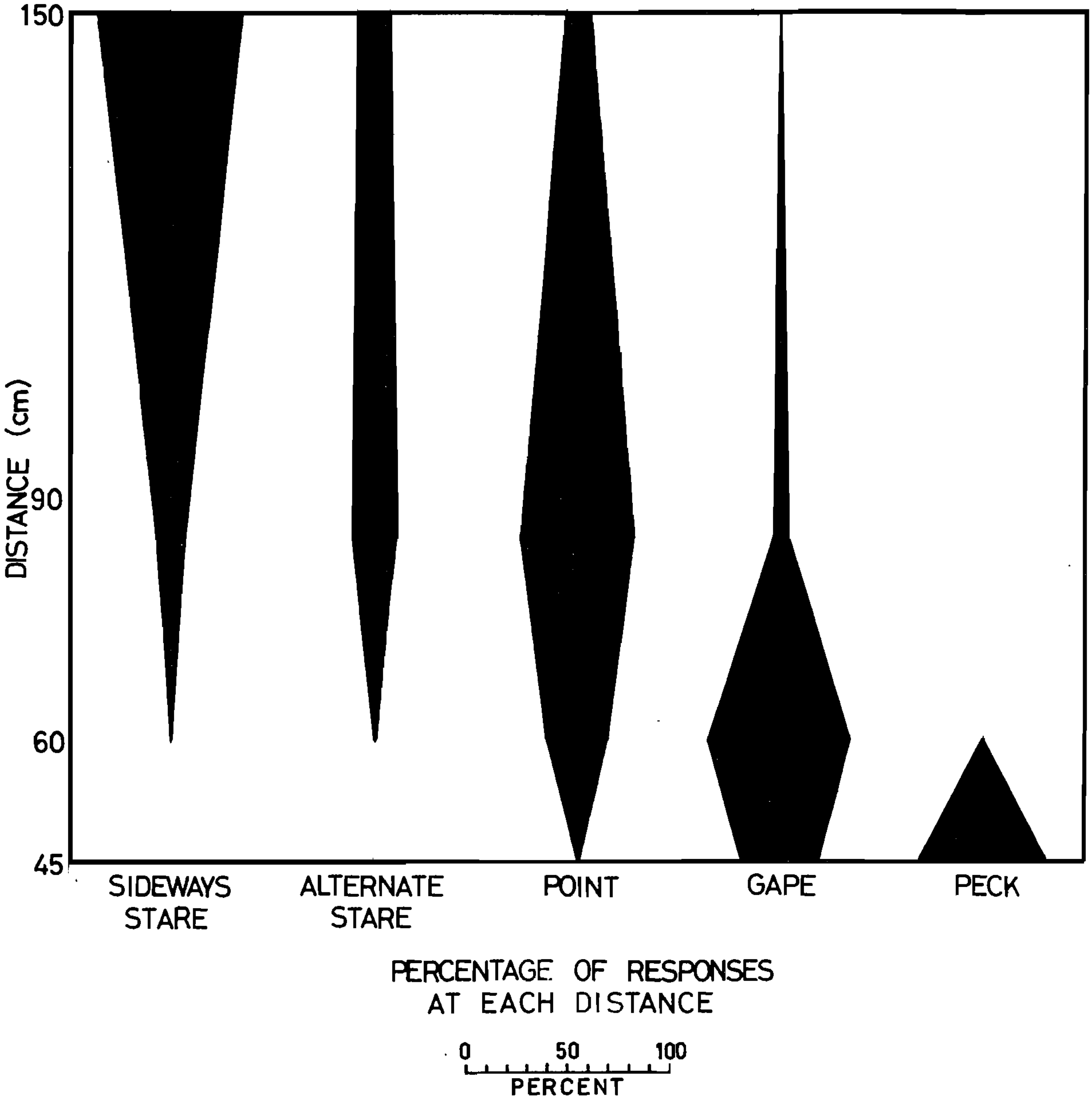

150
90
60
45
DISTANCE (cm)
SIDEWAYS STARE
ALTERNATE STARE
POINT
GAPE
PECK
PERCENTAGE OF RESPONSES AT EACH DISTANCE
0
50
100
PERCENT

TABLE 37: Incidence of Initial Acts from Total Encounters

	Probabilities from Total Encounters			
	Initial Acts*	Single Acts	Male	Female
Bill-to-Axilla	.06	.07	.14	.02
Sideways Stare	.30	.34	.32	.33
Alternate Stare	.04	.05	.06	.03
Point	.29	.27	.24	.31
Gape	.23	.16	.15	.20
Charge	.03	.04	.04	.02
Attack	.05	.07	.05	.09
Total Probability	1.00	1.00	1.00	1.00
Total Acts	1200	813	351	179

* Includes both single acts and first acts in sequence.

TABLE 38 : Incidence of Single Acts from Different Types of Encounters

	Probabilities from Separate Encounters			
	"Close" Neighbour	"Distant" Neighbour	Strangers Pass Directly	Strangers Pause
Bill-to-Axilla	.00	.22	.00	.03
Sideways Stare	.07	.43	.06	.52
Alternate Stare	.01	.03	.01	.08
Point	.30	.23	.43	.22
Gape	.57	.08	.29	.05
Charge	.00	.01	.01	.08
Attack	.05	.00	.20	.02
Total Probability	1.00	1.00	1.00	1.00
Total Acts	74	158	211	370

(a)

Territorial Penguin	.... Point
Stranger	approach directly ..... withdraw

(b)

Territorial Penguin	.... Sideways Stare (hold) .. relax
Stranger	approach slowly .... pause .... leave

(c)

Territorial Penguin	.... Point .... Sideways Stare ... relax
Stranger	approach directly .... withdraw slightly .... stay .... leave

(d)

Territorial Penguin	.... Point .... Alternate Stare ... relax partially ... etc.
Stranger	approach and reach forward ...withdraw head ..... stay .... reach forward ...

(e)

Territorial Penguin	.... Sideways Stare ....Point
Stranger	approach slowly ......continue approach ......withdraw

(f)

Territorial Penguin	...........Gape....peck...Gape...peck...Gape...peck...
Neighbour	rearrange nest stones...Gape...peck...Gape...peck...Gape...peck...

FIGURE 56. Models of interactions between penguins.

Initial responses may be followed by subsequent acts. Most sequences consisted of only two acts, and these have been listed in table 39. Levels of significance were determined from separate 2 x 2 chi-square tables for each sequence. Sequences with expected values lower than 5 were not tested (following Cochran 1954).

Some sequences occurred at significantly higher than expected values. Others occurred significantly less often than expected by chance alone. (That is, some sequences were directive, others inhibitive; see Hazlett and Bossert 1965:363). Sequences occurring at higher than expected frequencies included Sideways Stare—Point, Point—Sideways Stare, Point—Alternate Stare, Gape—attack, and Charge—attack.

Sideways Stare was most frequently followed by Point when the offending penguin moved closer (figure 56e). Point was followed by Sideways Stare when the offending penguin moved away only slightly or slowly (figure 56c). However, Point was followed by Alternate Stare when a penguin offending at close range withdrew only partially from an encounter; e.g. when a penguin attempting to steal nest stones withdrew only its head in response to the Point (figure 56d, and page 105). Gape was frequently followed by attack when the intruder approached to within pecking range. This occurred most commonly in encounters with neighbours, who retaliated in response to the initial challenge (figure 56f, and page 104). Charge was not often followed by a physical attack, but frequently resulted in a supplanting attack. This occurred when the offending penguin moved away before it could be attacked. The Charging penguin advanced at least to the former position of the offending penguin, where attack was assumed to have occurred had the offending penguin remained there.

Bill-to-Axilla, Sideways Stare, and Alternate Stare tended to occur at the ends of sequences rather than at the beginning (table 40). They tended to occur at the ends of sequences in which attack had not been stimulated, and so did not precede attack. Point, Gape, and Charge tended to occur at the beginning of sequences rather than at the end. Charge and Gape were usually followed by attack. Point, however, was seldom used within the stationary attacking range, and so was seldom followed by attack (table 41).

The lengths of encounters between penguins depended on

TABLE 39 : Incidence of Two-Act Sequences

First Act	Second Act	Observed	Expected	Significance	Direction
Bill-to-Axilla	Bill-to-Axilla	18	1.9		
	Sideways Stare	4	7.7	NS	
	Alternate Stare	0	2.1		
	Point	1	2.0		
	Gape	0	1.3		
	Charge	0	0.2		
	Attack	0	7.7	NS	
Sideways Stare	Bill-to-Axilla	17	10.2	NS	
	Sideways Stare	56	39.4	NS	
	Alternate Stare	3	10.7	NS	
	Point	33	10.4	**	Directive
	Gape	6	7.0	NS	
	Charge	2	1.0		
	Attack	1	39.4	**	Inhibitive
Alternate Stare	Bill-to-Axilla	1	1.2		
	Sideways Stare	7	4.7		
	Alternate Stare	0	1.3		
	Point	2	1.2		
	Gape	4	0.8		
	Charge	0	0.1		
	Attack	0	4.7		
Point	Bill-to-Axilla	3	12.8	NS	
	Sideways Stare	79	49.5	**	Directive
	Alternate Stare	38	13.4	**	Directive
	Point	6	13.1	NS	
	Gape	7	8.7	NS	
	Charge	1	1.2		
	Attack	14	49.5	**	Inhibitive
Gape	Bill-to-Axilla	2	13.6	*	Inhibitive
	Sideways Stare	12	52.8	**	Inhibitive
	Alternate Stare	2	14.3	*	Inhibitive
	Point	0	13.9	*	Inhibitive
	Gape	11	9.3	NS	
	Charge	1	1.3		
	Attack	130	52.8	**	Directive
Charge	Bill-to-Axilla	0	1.3		
	Sideways Stare	1	5.0	NS	
	Alternate Stare	0	1.4		
	Point	0	1.3		
	Gape	0	0.9		
	Charge	0	0.1		
	Attack	14	5.0	**	Directive

Significance levels : NS = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$

Chi-square (2 x 2 table)

TABLE 40 : Initial and Terminal Responses in Two-Act Sequences

Response	Position in sequence Begin %	 End %	Total No.
Bill-to-Axilla	37	63	38
Sideways Stare	36	64	143
Alternate Stare	15	85	39
Point	84	16	138
Gape	85	15	85
Charge	93	7	14
Attack	0	100	89

TABLE 41 : Probability of Attack Following an Initial Response

	Probability of attack by same penguin on		
Initial Response	Close Neighbour	Distant Neighbour	Lingering Stranger
Point	.44	.00	.08
Gape	.96	.90	.50
Charge	-	1.00	1.00

the situation. Most encounters were brief and consisted of only one or two acts. Thus, a stranger passing directly by a territory boundary usually elicited only a single response or no response at all. Sequences of three or more acts occurred mainly in encounters with neighbours across the boundary or strangers attempting to steal nest stones (figure 56d & f). However, these may really consist of no more than a series of single acts (response and counter-response) because most sequences were caused by a change in the external stimulus situation presented by another penguin (e.g. a penguin moving closer, or a stationary penguin suddenly moving). In this respect the acts should be regarded not as occurring in sequence, but as separate acts in response to separate stimuli. Thus, an initial act may be followed by another if the stimulus becomes weaker, or by yet another if the stimulus becomes stronger. In the analysis of behaviour, account should be taken of such variables as distance of encounter, speed of approach, further movement towards or away, retaliation by neighbours and so on, to allow much greater precision in the prediction of responses.

Sequences of events can readily be analysed in terms of information theory. The method measures how much information is gained by basing predictions on i rather than i-1 preceding events. Chatfield and Lemon (1970) advise that the method is best applied only to sequences of the same length and by the same individual. A major analysis cannot be attempted here because there are insufficient observations on individual penguins. The method also has very restricted use when analysing the behaviour of interacting animals.

There were only a few occasions (for example, when the offending penguin was standing with its back towards the challenging penguin) when the external stimulus situation remained unchanged following an initial response. In these circumstances, Bill-to-Axilla, Sideways Stare, and Alternate Stare usually follow themselves or one another. Point is followed by another Point, Gape, Charge, or attack. Gape is followed by another Gape, Charge or attack, and Charge is followed by physical attack.

The different responses, Bill-to-Axilla, Sideways Stare, Alternate Stare, Point, Gape and Charge thus appear to represent increasing levels of aggressiveness, in that order.

They are responses to different intensities of stimulation, and may occur individually or in sequences, depending on the situation.

9.4 EFFECTIVENESS OF AGGRESSIVE SIGNALS

The effectiveness of behaviour signals has often been investigated with the aid of models (e.g. Tinbergen 1948, Dilger 1956, Lack 1965, Stout and Brass 1969). This approach could not be used in the present study, however, because penguins did not distinguish between models in resting and aggressive postures. Any object approximately penguin size was attacked when presented within a certain distance of a penguin on its territory (see section 10.3).

An alternative approach, used in this study, is to measure the response of one animal to the actions of another (see also Stokes 1962, Grant 1963, Hazlett and Bossert 1965, Allin and Banks 1968). The signal content of the responses of territorial penguins was determined from their ability to elicit withdrawal of intruders. Most encounters were initiated not because intruders trespassed onto the territory, but because of movement near the boundary (e.g. a neighbour rearranging nest stones, or the approach of a stranger). Whereas strangers usually withdrew from such close range encounters, neighbours usually returned the response across the shared boundary. Thus, most attacks (90 percent) elicited return attack from neighbours (table 42), usually resulting in mutual bill-gripping. Gape also frequently elicited retaliation, usually a return Gape followed by bill-gripping and more Gaping. These encounters presumably served to reinforce the definition of the territory boundary. The encounters often ended as abruptly as they began, and it was difficult to determine which penguin was the winner.

Responses such as the Bill-to-Axilla, given to movements in the centre of a neighbour's territory, generally seemed to have no observable effect, though it was often very difficult to decide whether such responses had in fact been perceived. Also, a Bill-to-Axilla given to a neighbour nest scraping may have had no observable effect, but it may have deterred the neighbour from reaching over for a nest stone. Neighbours obviously withdrew from encounters only when they accidently crossed the boundary with the tail or foot, in which situation Point, Gape, Charge or attack were elicited.

The number of withdrawals by strangers provided a more useful measure of the signal content of the different responses of territorial penguins. Three responses (Point, Gape, and Charge) were highly effective in eliciting the withdrawal of strangers (table 43). The most effective response was the Charge, which was almost fully effective in driving away intruders. The Gape (90 percent) and Point (80 percent) were also very effective.

The other three responses (Alternate Stare, Sideways Stare, and Bill-to-Axilla) were less effective in eliciting withdrawal (table 43). Reactions of intruders to these responses were very difficult to measure because they were often delayed. For example, a penguin pausing near a territory boundary may not leave immediately after a Sideways Stare by the owner (figure 56b). In this case, the response may be recorded as having "no effect". While not effecting immediate withdrawal, however, it may have prevented further approach of intruders. Intruders were often inhibited simply by the opening of an eye of a territorial penguin. The Sideways Stare clearly indicated that the occupying penguin was alert, without provoking or engaging contact.

Each of the responses (Bill-to-Axilla, Sideways Stare, Alternate Stare, Point, Gape, and Charge) has been shown to be a signal, affecting the behaviour of other penguins. That is, they function in communication. The opening of an eye communicates in that it may prevent the approach of an intruder, but it cannot be said to be a display. The above responses, however, seem to be used specifically for communication, and therefore are termed displays. The forward displays (Point, Gape, and Charge) may be termed repellent threat displays; they repel or drive away the intruder. The sideways displays (Bill-to-Axilla, Sideways Stare, and Alternate Stare) may be termed deterrent threat displays; they deter intruders from approaching closer.

9.5 AVOIDANCE REACTIONS OF STRANGERS

Strangers moving about within a colony, either toward their own territory, toward an advertising male, or out collect-

TABLE 42 : Effectiveness of Responses to Neighbours

Initial Response of Territorial Penguin	Subsequent Response of Neighbour Withdraw %	No Effect %	Retaliation %	Total No.
Bill-to-Axilla	0	100	0	41
Sideways Stare	3	97	0	67
Alternate Stare	14	86	0	14
Point	24	76	0	58
Gape	2	5	93	1
Charge	100	0	0	1
Attack	10	0	90	83

TABLE 43 : Effectiveness of Responses to Strangers

Initial Response of Territorial Penguin	Subsequent Response of Stranger Withdraw %	No Effect %	Total No.
Bill-to-Axilla	6	94	35
Sideways Stare	51	49	156
Alternate Stare	52	48	23
Point	80	20	141
Gape	90	10	129
Charge	97	3	72
Attack	100	0	125

The difference between the effectiveness of Alternate Stare and Point is highly significant, $p < 0.01$, 2 x 2 Chi square.

ing nest stones, frequently encounter penguins on territories. They usually adopt the slender walk whether or not territory occupiers threaten them. When threatened, they may do one of three things: return the aggression, withdraw, or continue without further obvious response. Only the last two of these usually occur. Extreme sleeking of the feathers and raising of the head occurs when escape is temporarily prevented, or when a penguin hesitates before passing between closely spaced nests. These acts are best termed avoidance reactions rather than displays. They do not appear to alter or modify the behaviour of territorial penguins. Encroachment to within the range of attack elicits attack no matter what posture (other than sexual appeasement) is adopted. The sleeked feathers, raised head and flippers are suited for squeezing between closely spaced nesting territories. The components are also directly opposite to those of threat.

Penguins reaching across occupied territory boundaries in an attempt to steal nest stones, frequently exhibit incomplete escape behaviour (section 3.2v). The head and body are held very low to the ground and the feathers are strongly sleeked. Again, these are avoidance reactions, and they do not appease the territorial penguins.

9.6 PAIR FORMATION AND MAINTENANCE

Prior to pair formation, unmated (bachelor) males claim territories within a colony, begin nest construction, and frequently perform the Ecstatic attitude. Unmated females "prospect" by walking between, around, and through the colonies. The Ecstatic is performed by males many times without any apparent response from other penguins, but receptive females are definitely attracted by it, occasionally from some distance. Other penguins (including males) may go past while a bachelor male is performing the Ecstatic, but there is no indication that they are attracted by it, The Ecstatic thus functions as an advertising display that attracts receptive females to the displaying male's position within a colony.

On the approach of a stranger (male or female), bachelor males usually respond with the Sideways Stare. This is a typical response of territorial penguins to strangers pausing near the territory (section 9.3). It is usually sufficient to deter males and some (presumably unreceptive) females from approaching any further. However, other (presumably receptive) females do not withdraw, and may continue to advance. Thus, bachelor males usually do not distinguish between male and female on first approach, but depend on the subsequent response of the approaching penguin.

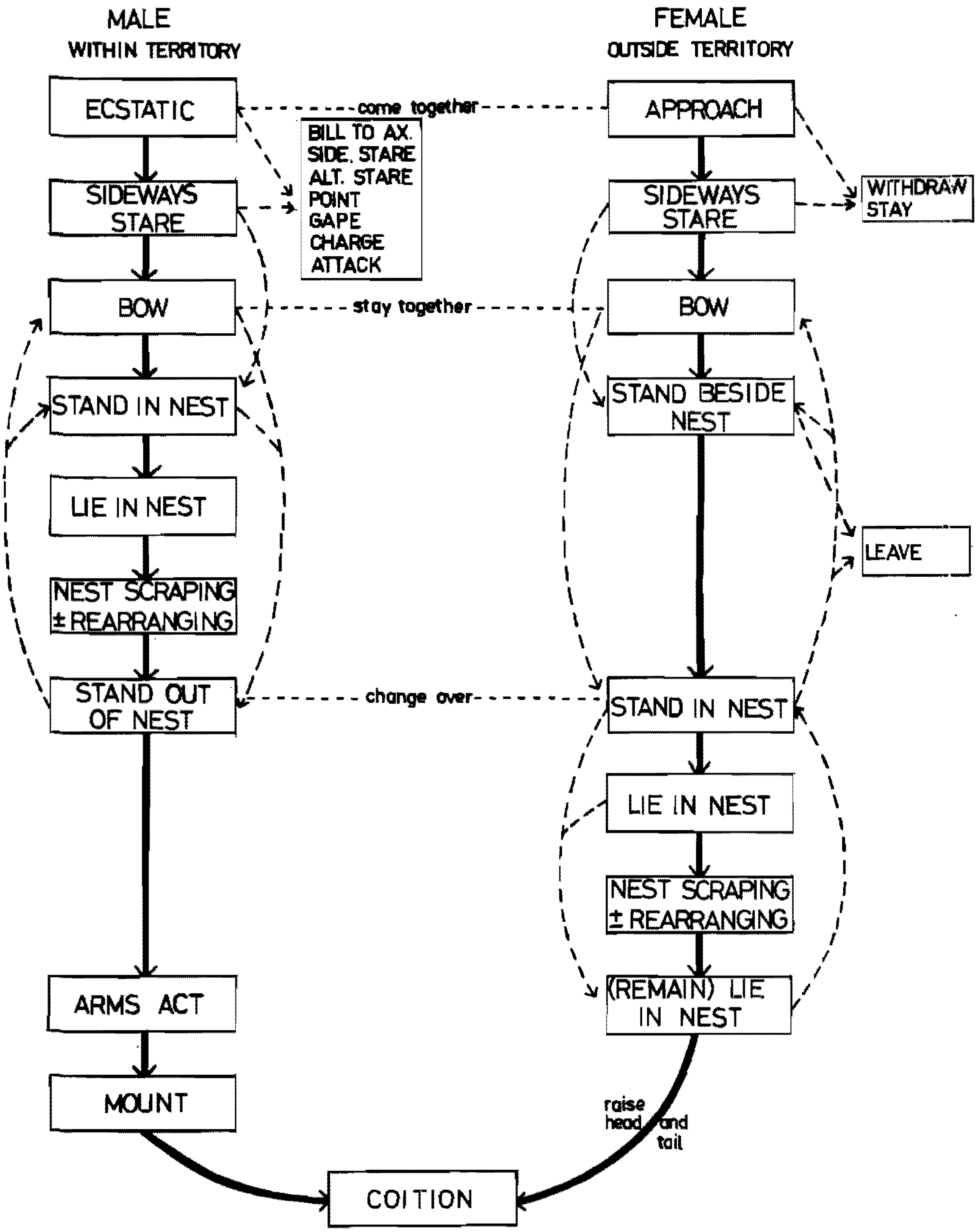
A receptive female often advances towards a male by shuffling sideways, and turning the head as in a Sideways Stare. The head is held very low, as in a Bow, and the feathers are very sleeked. The bill may be pointed slightly towards the male. In this situation, the female is highly stimulated to approach, and at the same time highly stimulated to withdraw.

On close approach of the female, the male's Sideways Stare is usually followed by a deep Bow. The female may also Bow, but with sleeked feathers. The male may then lie in the nest, rearrange stones with the bill, and scrape the nest with the feet, while the female stands beside the nest. Sometimes, however, close approach of the female elicits either a threat or an attack from the male. Attacks by males on prospective mates are much more common in the early stages of pair formation than in later stages. Thus, attacks and threats occur most commonly after the Ecstatic display or the Sideways Stare than after any other "steps" in the sequence of events leading to coition (figure 57).

Closer approach of the female is successful only when the male assumes a Bowing attitude. The essential difference between the Sideways Stare and Bowing is in the position of the bill. In the Bow, the head is often lowered almost to the ground, so that the bill is well out of line of attack. In the Sideways Stare, however, though the bill is often inclined sharply downwards, it is still in a position where it can be directed into attack. Thus, Bowing seems to signify a reduction of aggression that facilitates a reduction in distance between penguins, and so may be termed a display. Bowing by the male probably helps prevent the female from withdrawing, whereas Bowing by the female helps prevent the male from attacking. Nest scraping by the male may also entice the female, and prevent her from withdrawing, by directing her attention to the nest site.

The sequence of events leading to coition may stop or start almost anywhere. The full sequence can be completed in

FIGURE 57. Sequence of events leading to coition.


MALE
WITHIN TERRITORY
FEMALE
OUTSIDE TERRITORY
ECSTATIC
come together
APPROACH
BILL TO AX.
SIDE. STARE
ALT. STARE
POINT
GAPE
CHARGE
ATTACK
SIDEWAYS STARE
SIDEWAYS STARE
WITHDRAW
STAY
BOW
stay together
BOW
STAND IN NEST
STAND BESIDE NEST
LIE IN NEST
LEAVE
NEST SCRAPING ± REARRANGING
STAND OUT OF NEST
change over
STAND IN NEST
LIE IN NEST
NEST SCRAPING ± REARRANGING
(REMAIN) LIE IN NEST
ARMS ACT
MOUNT
raise head and tail
COITION

less than three minutes, and coition is sometimes achieved immediately on meeting for the first time. Often, however, a male is successful only at keeping a female on his territory, and not immediately successful at achieving coition. When coition is attempted again later the initial steps involved in bringing the two sexes together are omitted. Sometimes, a male is unsuccessful at keeping a female after having attracted her to his territory. Some (presumably inexperienced) males attempt to mount the female before she lies down in the nest, so that she leaves almost immediately. At other times, the female may leave while the male is scraping the nest, or she may even leave after actually getting in the nest herself.

Established pairs already on a territory also omit the initial steps of the sequence, and begin after a period of rest, frequently when the female is lying in the nest, with the male standing beside. The male approaches the female in the arms act, and if she remains lying in the nest, he may mount and complete coition.

The Quiet Mutual and Loud Mutual do not occur in early pair formation, but develop as the pair bond strengthens. Territorial penguins, responsive to any movement near the territory, are at first very responsive to movements by the mate (such as suddenly standing after lying down, or changing position on the nest). Many movements by the mate elicit a Sideways Stare, in which the head is turned sideways and the bill pointed slightly towards the mate. Subsequent recognition, and raising or lowering the bill, as in the Quiet Mutual or Bowing, then reduce the probability of attack, and help reinforce the pair bond. Thus, the Quiet Mutual may be termed a display, that, like Bowing, functions in sexual appeasement. It may indicate more complete appeasement (or acceptance) than does Bowing, because it does not occur in early pair formation and occurs more frequently after a shallow Bow than vice versa.

The Loud Mutual is usually performed by mates meeting at the territory after an absence exceeding several hours. Mate reunion consists of two stages, the first of which is identification. Sometimes this occurs without any prior display. However, when a penguin does not at first recognise its mate, it gives the Loud Mutual call in a forward posture (section 3.4iii). This call is individually recognisable, and identifies the calling bird to others nearby. The forward posture of the Loud

Mutual very much resembles aggressive Gaping, and challenges the identity of the bird at which it is directed. The second stage of re-union occurs after recognition has occurred. The displaying birds then raise their bills high in the air and wave their heads from side to side. This undoubtedly reinforces recognition and at the same time reduces the probability of attack. The Loud Mutual is thus a display that helps maintain a reduced distance between mates.

The Mutual and Bowing displays are not submissive displays, in which one bird becomes subordinate to the other (see also Schenkel 1967). Rather, they serve as sexual appeasement displays in that they facilitate the maintenance of reduced distance between mates or potential mates. They occur in conjunction with individual recognition, which itself facilitates reduction of aggression.

9.7 COMPONENT STRUCTURE OF DISPLAYS

Each display consists of a combination of different components, of which the following are recognised in this study.

i. Feather Postures

Feathers can be relaxed, sleeked, or erected. The major area of feather erection occurs on the back of the neck, extending from the shoulders to the top of the head where it may form a crest (the occipital crest). Minor feather erection may also occur between the eyes (orbital crest) and at the base of the bill (nasal crest). Feather sleeking may occur on the face (or forehead) simultaneously with erection of feathers on the back of the head and neck. Alternatively, feathers over the whole head and neck may be sleeked.

All displays concerned with territory defence and reproductive behaviour are characterised by erection of the occipital crest and sleeking of the face feathers. These components do not occur when penguins are resting on their territories (figure 6), though they sometimes occur while penguins are looking around after being disturbed by activities nearby (figure 9a). Erection of the feathers is a sympathetic reaction facilitating insulation (McFarland and Baher 1968:174) that at the same time increases apparent body size. Large size would seem important in an animal in which body weight can be a deciding factor in fighting (see also section 10.4). The fact that the feathers are usually not erect during actual fighting correlates with the increased activity.

Major feather sleeking (of the head and neck) occurs only when the penguins are escaping, or show intention movements of escape (such as in the slender walk (described in section 3.2iii) given when walking through a colony between other penguins' territories).

After walking through a colony a penguin usually erects the crest feathers on arrival at the nest. However, in some instances, for example if the passage through the colony has been difficult, the feathers may remain sleeked while the penguin performs displays such as the Sideways Stare, Bowing, or the Quiet Mutual. During pair formation, females have sleeked feathers when approaching a male's territory, while the male on the territory has erect feathers. When a penguin is stimulated suddenly (e.g. suddenly approached from behind), the feathers may be sleeked while it gives a hasty threat display (such as a Point), and may be erected only after the stimulus has passed. Thus, on occasions, both threat displays and sexual displays may occur with sleeked feathers.

ii. Eye Postures

When penguins are relaxed, the white sclerae of the eyes are barely visible. In threat and sexual displays, however, the eyes are rolled down and backwards, so that the white sclerae are prominent. The increase in area of white caused by rolling the eyes is further increased by sleeking the face feathers around the eyes, exposing the white fleshy eyelids. The area of white contrasts markedly with the black feathers of the head and dark pupils in the centre of the eyes. In escape movements, the white eyelids are exposed but the sclerae are not rolled to increase the area of white. The significance of eyes and eye-like patterns has been noted in various animals both for intra- and inter-specific signalling (Hingston 1933:54 & 142, Baerends 1950:357, Cott 1940:193 & 387, Blest 1957:209).

iii. Head Orientation

When resting, the head is usually held directly in front of the body, in a horizontal position. The neck is withdrawn. In the various displays, the head may be raised, lowered, turned sideways, or stretched forward. In the threat displays, the head is either stretched forward (as in the Charge, Gape, and Point) or turned sideways (as in the Sideways Stare, Alternate Stare, and Bill-to-Axilla). In some threat displays the bill may point downwards, but the head is not lowered. In sexual displays, the head is either markedly raised (as in the Loud Mutual, Quiet Mutual, and Ecstatic) or lowered (as in the Bow). In escape, or intention movements of escape, the head is held up, and the bill tends to be held above horizontal.

In some displays the bill is opened wide. This may be purely for vocalising, as in the upright Loud Mutual display, or as an intention movement of pecking, as in the Gape and Charge displays.

iv. Body Orientation and Movement

Penguins may rest either while standing upright or lying down (figure 6). Some displays are given from either standing or lying positions, whichever the penguin happens to be in at the time the stimulus is presented. In some displays (e.g. the Point and Gape) the body is extended forward by leaning over from an upright position, or stretching the neck when lying down. In other displays (e.g. the Mutual displays) the body is extended upwards, by raising the head and stretching the neck.

Some displays involve very little movement of the body, but in the Charge the whole body is moved forward by walking or running.

v. Flipper Position

When penguins are resting, the flippers are usually held beside the body (figure 6). When penguins are walking, however, the flippers are held out from the body (figure 7). The flippers are also held out when penguins are moving forward in a Charge and when running away in escape. Thus, the component "flippers held out" is associated with movement, whether towards or away from another individual, and possibly has a balancing function.

The flippers may be waved backwards and forwards in a steady rhythm, as in the Ecstatic, Bill-to-Axilla, and Alternate Stare displays, and in copulation. This waving makes the displays more conspicuous. A more erratic flicking of the flippers occurs when penguins have been startled or disturbed suddenly, often preceding escape.

9.8 COMPONENT STRUCTURE OF THREAT DISPLAYS

The six threat displays recognised in this study each have a different component structure. Most of the components occur together either more or less frequently than expected by chance alone (table 44). Thus, moving forward (as in a Charge) is significantly associated with body held upright and flippers held out from the body. It does not occur when the head is held to the side of the body, the crest feathers sleeked, or the eyes not rolled. Only three of the twenty-eight combinations appear to be not significant, and two of these concern the flippers.

When components of responses to strangers are considered singly, only four permit confident prediction of subsequent action by the same penguin (table 45). Moving forward (as in a Charge) has a 91 percent chance of being followed by (physical or supplanting) attack. Flippers held out (which is significantly associated with moving forward) has an 87 percent chance of being followed by attack. Head held to the side and remaining stationary both indicate high probabilities of staying, or not attacking. Feathers sleeked and eyes not rolled usually do not occur in territorial penguins. Of all components considered alone, only those associated with Charge and the sideways threat displays permit any prediction of outcome (attacking and staying, respectively).

When components of responses to neighbours are considered singly, a different pattern emerges (table 46). All attacks in this sample were made from a stationary posture. Consequently, flippers held in is followed by attack more often than flippers held out. Head held to the side of the body again indicates a high probability of staying (or not attacking).

Prediction of outcome of encounters is increased by combining components into pairs (table 47). All components associated with moving forward have a greater chance of being followed by attack than components associated with a stationary penguin. Components of stationary penguins are more likely to be followed by attack when directed at neighbours than at strangers.

Combining components into triplets (table 48) or still

TABLE 44 : Simultaneous Occurrence of Components of Behaviour given by Territorial Penguins to Strangers

	Crest erect	Crest sleeked	Eyes rolled	Eyes not rolled	Head side	Head front	Bill open	Bill closed	Body forward	Body upright	Flipper out	Flippers in	Move forward	Stationary
Crest erect	516	-	509	7	61	455	212	304	238	278	119	397	259	257
			***		***		***		***		***		***	
Crest sleeked	-	0	0	0	0	0	0	0	0	0	0	0	0	0
Eyes rolled			509	-	61	448	207	302	234	275	119	390	259	250
					***		***		***		***		***	
Eyes not rolled			-	7	0	7	5	2	4	3	0	7	0	7
Head side					61	-	0	61	0	61	14	47	0	61
							**		**		NS		**	
Head front					-	455	212	243	238	217	105	350	259	196
Bill open							212	-	139	73	52	160	115	97
									**		NS		NS	
Bill closed							-	304	99	205	67	237	144	160
Body forward									238	-	2	236	61	177
											**		**	
Body upright									-	278	117	161	198	80
Flippers out											119	-	105	14
													**	
Flippers in											-	397	154	243
Move forward													259	-
Stationary													-	257

Chi-square (2 x 2 table) levels of significance
NS = $p < 0.05$, ** = $p < 0.01$,
*** = expected values less than 5 and therefore not tested.

TABLE 45 : Probability of Subsequent Action from One Component of Territorial Penguins' Response to Strangers

Component of Behaviour	Subsequent Action by Same Penguin		
	Attack*	Stay	Total
Feathers sleeked	.00	.00	0
Feathers erect	.51	.49	516
Eyes not rolled	.00	.00	0
Eyes rolled	.51	.49	516
Head forward	.57	.43	455
Head sideways	.03	.97	61
Bill closed	.45	.55	304
Bill open	.59	.41	212
Body upright	.71	.29	278
Body forward	.28	.72	238
Flippers in	.40	.60	397
Flippers out	.87	.13	119
Move forward	.91	.09	259
Stationary	.10	.90	257

* Includes supplanting attack

TABLE 46 : Probability of Subsequent Action from one Component of Territorial Penguins' Response to Neighbours

Component of Behaviour	Subsequent Action by Same Penguin		
	Attack	Stay	Total
Feathers sleeked	.17	.83	6
Feathers erect	.73	.27	765
Eyes not rolled	.00	.00	0
Eyes rolled	.72	.28	771
Head forward	.74	.26	754
Head sideways	.00	1.00	17
Bill closed	.11	.89	28
Bill open	.75	.25	743
Body upright	.59	.41	58
Body forward	.74	.26	713
Move forward	.00	.00	0
Stationary	.72	.28	771
Flippers in	.73	.27	764
Flippers out	.29	.71	7

TABLE 47 : Probability of Subsequent Action of Territorial Penguins from Combinations of Two Components

		Subsequent Action by Same Penguin		
Components of Behaviour		Attack	Stay	Total
Move forward	+ Body upright	.97	.03	198
(vs. stranger)	+ Body forward	.71	.29	61
	+ Bill closed	.94	.06	144
	+ Bill open	.88	.12	115
	+ Flippers in	.86	.14	154
	+ Flippers out	.99	.01	105
	+ Head forward	.91	.09	259
	+ Head sideways	.00	.00	0
Stationary	+ Body upright	.04	.96	80
(vs. stranger)	+ Body forward	.13	.87	177
	+ Bill closed	.02	.98	160
	+ Bill open	.24	.76	97
	+ Flippers in	.11	.89	243
	+ Flippers out	.07	.93	14
	+ Head forward	.12	.88	196
	+ Head sideways	.03	.97	61
Stationary	+ Body upright	.09	.91	11
(vs. neighbour)	+ Body forward	.74	.26	427
	+ Bill closed	.05	.95	19
	+ Bill open	.75	.25	419
	+ Flippers in	.73	.27	432
	+ Flippers out	.17	.83	6
	+ Head forward	.75	.25	421
	+ Head sideways	.00	1.00	17

TABLE 48 : Probability of Subsequent Action of Territorial Penguins encountering Strangers from Combinations of Three Components.

Components of Behaviour			Subsequent action by same penguin Attack	Stay	Total
Move forward	+ Body upright	+ Bill closed	.96	.04	133
		+ Bill open	1.00	.00	65
		+ Flippers in	.95	.05	95
		+ Flippers out	1.00	.00	103
Move forward	+ Body forward	+ Bill closed	.62	.38	11
		+ Bill open	.72	.28	50
		+ Flippers in	.71	.29	59
		+ Flippers out	.50	.50	2
Stationary	+ Body upright	+ Bill closed	.03	.97	72
		+ Bill open	.13	.87	8
		+ Flippers in	.05	.95	66
		+ Flippers out	.07	.93	14
Stationary	+ Body forward	+ Bill closed	.01	.99	88
		+ Bill open	.25	.75	89
		+ Flippers in	.13	.87	177
		+ Flippers out	.00	.00	0

larger groups improves the prediction of the outcome of an encounter, especially for some components.

When considering component options, one component usually has a higher probability of being followed by attack than the other. Thus, moving forward is more aggressive than remaining stationary. Bill open is more aggressive than bill closed, especially when the penguin is stationary. Body upright is more aggressive than body forward only when the penguin is moving forward. When the penguin is stationary, body forward is more aggressive than body upright. Head pointed forwards is more aggressive than head held to the side. Flippers held out is more aggressive than flippers held in by the body only when the penguin is moving forward. Feathers erect and eyes rolled were associated with all territorial displays.

Most components considered alone do not permit confident prediction of subsequent action by the same penguin. However, some are more likely to be followed by attack than others. Moving forward is the most aggressive component. Components associated with moving forward cannot be considered aggressive themselves unless they are also aggressive when associated with a stationary posture. This is not so for flippers out and body upright. The second most aggressive component would seem to be bill open. This is the most aggressive component of a stationary penguin. Body forward and head forward are the next most aggressive components. All these aggressive components assist in presentation of the bill, the main weapon of attack.

The component structure of the different displays is shown in table 49. Charge has more aggressive components than Gape, which has more than Point. Charge also contains the most aggressive component, moving forward. Here the bill is advanced towards the intruder. In the Gape, the opened bill is less aggressive than that of the Charge, but more aggressive than the closed bill of the Point. These three displays are characterised by forward presentation of the fighting weapon, and all may be termed forward threat displays.

The Alternate Stare, Sideways Stare, and Bill-to-Axilla do not contain any highly aggressive components. All have the bill turned away to the side; Alternate Stare less so than the Sideways Stare, and Sideways Stare less than the Bill-to-Axilla. However, in none of these displays is the bill strongly removed from an attacking position. All may be termed sideways (or

TABLE 49 : Component Structure of Threat Displays

Display	Component												
	Crest erect*	Crest sleeked	Eyes rolled*	Eyes not rolled	Head front*	Head side	Body forward*	Body not forward	Bill open*	Bill closed	Move forward*	Stationary	Number of most aggressive components
Bill-to-Axilla	+		+			+		+		+		+	2
Sideways Stare	+		+			+		+		+		+	2
Alternate Stare	+		+			+		+		+		+	2
Point	+		+		+		+			+		+	4
Gape	+		+		+		+		+			+	5
Charge	+		+		+		±		±		+		6

* Denotes the most aggressive component of each pair option.

lateral) threat displays.

9.9 DISCUSSION

Motivation

Motivation may be defined as "that which induces an animal to act" (Marler 1956a:5) and includes both internal and external factors that stimulate a response. In this study, no attempt is made to evaluate the exact contributions of these factors, because behavioural observations can show only general patterns of motivation.

There remains considerable controversy concerning causal mechanisms and methods used for analysis of motivation (e.g. Brown and Hunsperger 1963, Rowell 1964, Orians and Christman 1968). Much behavioural evidence indicates that displays occur when a particular behavioural response is simultaneously stimulated and inhibited (e.g. Tinbergen 1959, Marler and Hamilton 1966). In the Adelie penguin, threat displays are associated with defence of the nesting territory. It has been shown that the closer the intruder, the more aggressive the display. These threat displays are "intention" movements of attack (see below), and would seem to represent a conflict between attacking and not attacking. To attack, a penguin would often have to advance out of the territory. As well as being stimulated to attack, however, a penguin is also stimulated to remain within the territory (i.e. not to leave the territory). It may be the conflict to advance and to remain that results in threat display. Conflict may also occur in sexual displays. Sexual attraction leads to closer proximity, and this in turn stimulates attack and escape reactions. During pair formation, escape reactions are more evident in females (approaching the male's territory) than in males (section 9.6).

Derivation

In the Adelie penguin, there appear to be two main trends in the evolution of displays. The first is similar to that described by Darwin (1872:28) under the heading of the principle of serviceable associated habits. According to this principle, movements used in communication derive from preparatory or incomplete movements ("intention movements") of elementary acts, such as attack or escape. Thus, forward orientation of the head, stretching the body forward, opening the bill, and moving forward are all movements preparatory to pecking. The second evolutionary trend is similar to that described by Darwin (op. cit.) as the principle of antithesis. According to this principle, some movements and postures are the opposite of intention movements of elementary acts, and signify the absence of such a movement. This means that instead of the fighting weapons being presented, they are withdrawn from a position of attack. This occurs during appeasement movements between members of opposite sexes, and between parents and chicks.

Displays are more than just incomplete behavioural reactions. During evolution, movements and postures have been changed or ritualised, making them more conspicuous. The changes involved in ritualisation are summarised by Bastock (1967:111). In the territorial displays of the Adelie penguin, the head is made conspicuous by erection of the crest feathers, sleeking of the face feathers, and rolling of the eyes (see section 9.7). These features are characteristic of both threat and appeasement displays, and probably represent ritualised autonomic reactions (see also Morris 1956). Raising and bending the body are often regarded as intention movements of locomotion (in this case, walking), based on the work of Daanje (1950). Whether or not this interpretation is correct, appeasement displays are the antithesis of threat displays. Appeasement displays in no way indicate, however, that the penguins are preparing to withdraw. In Mutual displays, the bill is certainly held up as in locomotory and escape reactions, but this is combined with erect crest feathers, rolled eyes, and flippers held in beside the body. This last component is an indication of remaining stationary (see sections 9.7 and 9.8). The raised bill is a non-aggressive component, and is accentuated by exaggerated waving from side to side.

In the threat displays, the bill is made conspicuous in various ways (e.g. moved forward, opened wide, pointed forward, and turned sideways). These and other features of ritualisation help make the signals more effective for communication.

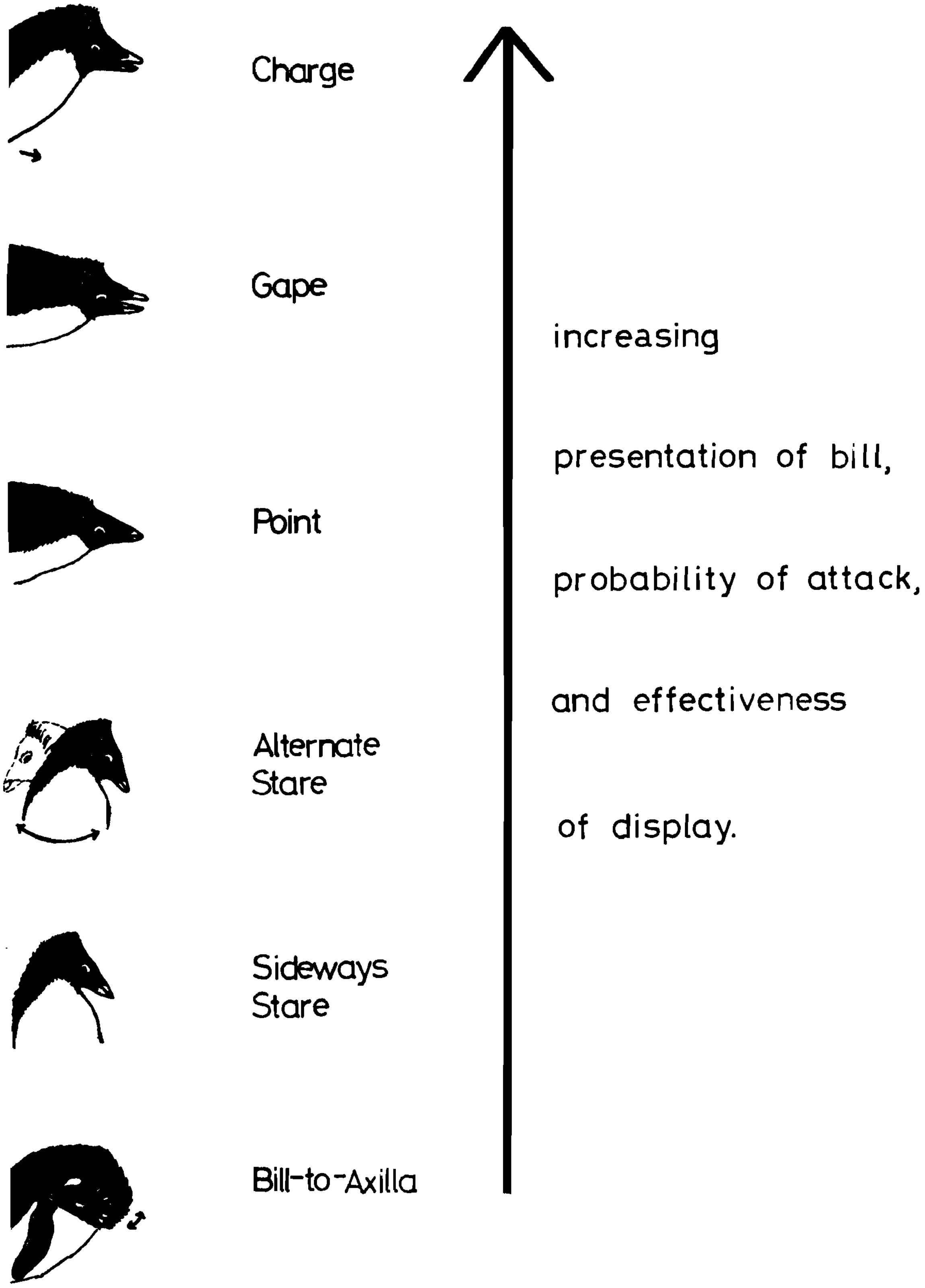
Communication.

In the displays of the Adelie penguin, most ritualisation has occurred in connection with the head and bill. The bill is the most frequently used weapon of attack. The flippers are used only in major attacks, when penguins come into close body contact. There is considerable flexibility in the use of the bill, which can be presented forwards simply by stretching the neck. The flippers are more rigid, and tend to be used only as an elaboration of a basic posture, often as a balance mechanism.

In the evolution of displays for clear communication, it seems that selection has acted to maximise or minimise the presentation of the bill. In the forward threat displays, the bill is clearly presented forwards as a weapon. In the sexual appeasement displays, the bill is clearly raised or lowered out of line of direct contact with the other penguin. These two sets of displays are sufficiently conspicuous and distinct to exclude ambiguity of meaning.

There is, however, a gradient in the degree of bill presentation, linking the least and most aggressive displays (figure 58). The bill may be turned sideways even when the head is still extended forwards. It may be then gradually withdrawn, first from side to side as in the Alternate Stare, then to one side as in the Sideways Stare. While the bill is held to one side, the head may then be rolled about its axis, as in the Bill-to-Axilla. In the sequence from Charge to Bill-to-Axilla there is a decrease in the presentation of the bill. The Bill-to-Axilla, however, appears to be too elaborate to be a basic display. The exaggeration components of ritualisation (rolling the head, waving the flippers, and the vocalisation) make it conspicuous from a distance. Thus, it seems to function as a general, "long" distance display, given at low intensity of stimulation. The relationship of the Bill-to-Axilla to the Ecstatic display agrees with these findings. After performing an Ecstatic (advertising) display, a male may be slightly stimulated to react aggressively to other males advertising nearby, or to penguins moving about in the general vicinity. In all the sideways threat displays, the bill is turned to one side of the body, but is neither hidden nor in an inconvenient position for attack. Turning the head to one side may improve monocular fixation, but also fully presents the striking eye pattern to intruders. The Sideways Stare seems to represent a very basic display, and it is probable that the Bill-to-Axilla, though less aggressive, is a derivation

FIGURE 58. Gradation of threat displays.


Charge
Gape
Point
Alternate Stare
Sideways Stare
Bill-to-Axilla
increasing
presentation of bill,
probability of attack,
and effectiveness
of display.

especially elaborated for long distance communication. In the Alternate Stare the bill is shown more effectively than in the Sideways Stare, but not as effectively as in the forward displays. Each of the threat displays functions in different situations, related to the intensity of stimulation (see also section 9.3).

There is also a gradient in the degree of bill presentation between sideways threat displays and sexual appeasement. After the head has been turned sideways, as in the Sideways Stare, it may gradually be lowered into a Bow, or raised into a Quiet Mutual display. As explained earlier (section 9.6), this gradation is important in pair formation and maintenance. The use of the same display in pair formation as well as in threat occurs commonly in monomorphic species as a means of sex identification (Huxley 1938, Collias 1944).

Penguins are thus able to present clear and unambiguous signals, to indicate either threat or sexual appeasement, but can also present graded signals for different levels of stimulation, and when both aggressive and sexual responses are stimulated.

It is interesting to note the absence of allo-preening in adult Adelie penguins (although it occurs in Adelie penguin chicks). Allo-preening occurs in adults of several species of penguins (e.g. the Yellow-eyed penguin, Richdale 1951:28, the Little Blue penguin, Eudyptula minor, Warham 1958:613, the Erect-crested penguin, Eudyptes sclateri, Richdale op. cit., the Macaroni penguin, Eudyptes chrysolophus chrysolophus, Downes et al. 1959:54, the Rockhopper penguin, Warham 1963:244, the Royal penguin, Eudyptes chrysolophus schlegeli, Warham 1971:106, the Magellanic penguin, Spheniscus magellanicus (Conway 1965:122), and the African penguin, Spheniscus demersus (Kearton 1930). Nelson (1971:458) attributed the absence of allo-preening in Abbott's Booby, Sula abbotti, to the apparently high degree of internal inhibition of aggression in that species. The Adelie penguin, however, is a highly aggressive species nesting in dense colonies. Perhaps frequent appeasement displays between mates are an alternative to allo-preening, as suggested by Harrison (1965:201 & 203). Other aggressive, densely nesting penguins (such as the Rockhopper and Royal penguins) which perform allo-preening may not perform appeasement displays as frequently as Adelie penguins, but more comparitive data are needed.

There do not appear to be any special displays for appeasing the aggressiveness of territorial penguins toward intruders. Most intruders terminate encounters by withdrawing, and are able to move away without being chased. This indicates that withdrawal is an acceptable method of appeasement. Penguins moving about outside their territories show avoidance behaviour which indicates a certain probability of escape, but these avoidance reactions do not appear to have a major appeasing or inhibiting effect on the reactions of territorial penguins. At close proximity any movements, including "intention" movements of escape, are effective in eliciting aggression. Thus, appeasement of aggression is achieved either by an appeasement display (of mate or potential mate) or by withdrawal (of intruders). In both situations, the aggressive weapon is removed from an offending position; in appeasement displays it is raised or lowered, and in escape it is completely withdrawn.

The importance of bill presentation may be correlated with the dense nesting situation, and displays that minimise contact will have a high selective advantage. Additional elaborations to displays (such as erection of the feathers, rolling the eyes, waving the flippers, and vocalisations) seem secondary to bill presentation, and only occur in displays at full intensity of performance. There are many subtleties of presentation, and the division between ritualised and non-ritualised behaviour is not always sharply defined. Together with contextual information, the gradient of responses reflects quite closely the degree of stimulation of the displaying bird, and provides quite precise communication.

10.0 DIFFERENCES IN AGGRESSIVENESS OF INDIVIDUAL PENGUINS

10.1 INTRODUCTION

An Adelie penguin colony is not simply an amorphous mass of penguins, but an ordered and patterned community. The individuals comprising the community may appear morphologically similar, but are behaviourally quite distinct. Reference has previously been made to differences in arrival date (section 7.2), pair and site stability (section 6.0), breeding success (section 7.8), and frequency of behaviour patterns (section 4.0) among different groups of the community. This section is concerned with differences in the aggressiveness of individual penguins.

10.2 SPATIAL ORGANISATION

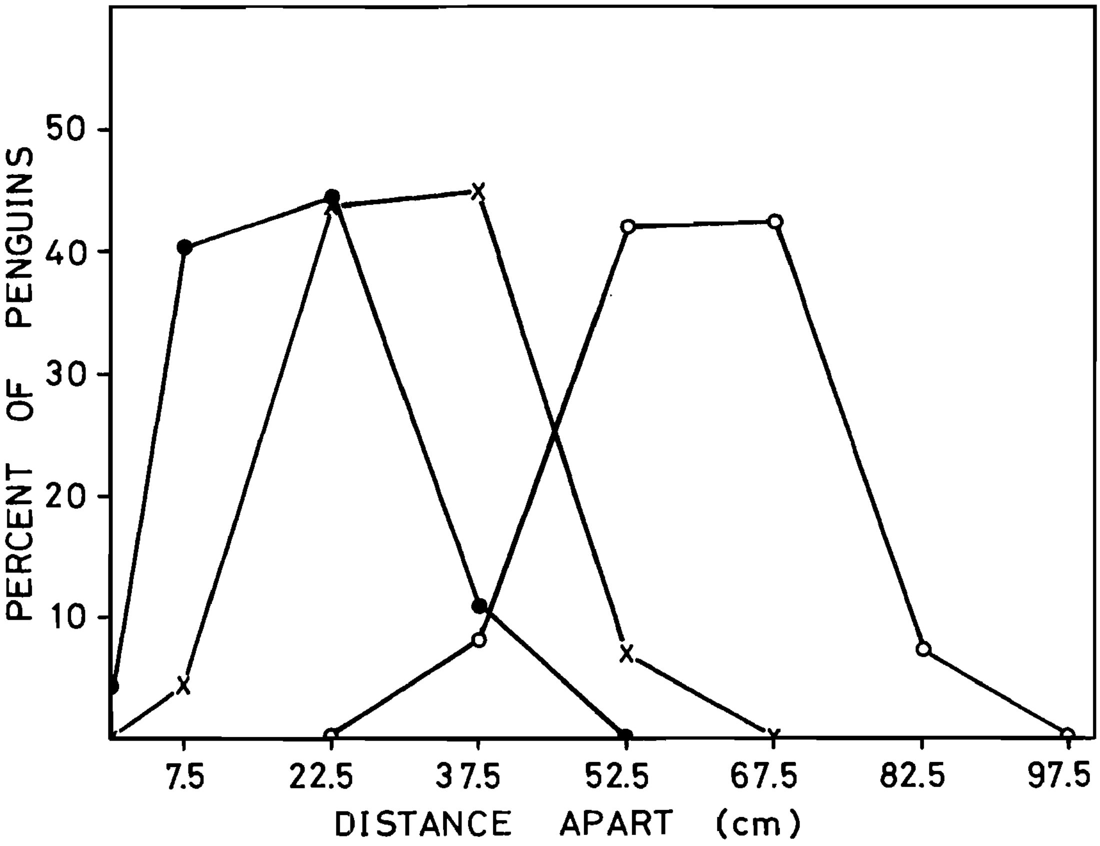
The spacing of individual Adelie penguins varies with different activities. Flocks of penguins resting on the sea ice or on the shore are normally spaced about 30 cm apart (figure 59). When disturbed, for example by man or leopard seal, or when entering the sea, they cluster more tightly and may even permit body contact.

In the breeding colonies, penguins on adjacent territories are usually spaced about 60 cm apart (figure 59). This is slightly less than the inter-nest distance recorded in section 2.3, because inter-nest distances were measured from the nest centres, whereas the distances between individuals (individual distances) were measured from the outside of the body. Penguins are aggressive to one another while on their territories, but are more tolerant while clustered on the shore away from the breeding colonies. This increase of individual distance on the territories (territorial distance) also occurs during the breeding season in other bird species (e.g. the Chaffinch, <u>Fringilla coelebs</u>, Marler 1956a:68).

On an individual territory, a pair of penguins usually stand about 15 cm apart (figure 59), although body contact frequently occurs. Two chicks in a nest, even when too large to be completely brooded, often huddle together or huddle

FIGURE 59. Spatial distribution of penguins in different situations.

●—● penguins within territories.
x—x penguins resting on shore.
o—o penguins on adjacent territories.


PERCENT OF PENGUINS
50
40
30
20
10
7.5
22.5
37.5
52.5
67.5
82.5
97.5
DISTANCE APART (cm)

against the parent (section 8.2). Chicks from adjacent nests also huddle together in creches. Huddling is common in the young of many species even when the adults maintain wide individual distances (Crook 1961:147 & 149).

10.3 DIFFERENCES IN AGGRESSIVENESS OF MALES AND FEMALES

Differences in aggressiveness of males and females is related to their roles in territory selection and pair formation. The territory on which a pair of Adelie penguins breed is invariably selected by the male before pair formation (see section 9.6). A female must appease the male's aggressiveness to be able to enter his territory. Throughout early pair formation males frequently attack and chase females. This behaviour is described in an earlier section (section 9.6).

Females that reunite with previous mates are not so strongly dominated as in new pairs, largely because individual recognition apparently reduces aggression. In addition, the pair perform various forms of mutual behaviour at reunion (see section 9.6), so that very little aggression ever occurs between mates of a stable pair.

Once accepted into the territory, a female shares in its defence. Males normally participate in more encounters when both are on the territory together, although there appears to be no difference in the quality of response. After the eggs are laid, when only either the male or female is present, the female appears to defend the territory as strongly as the male.

In order to investigate further the differences between males and females in territory defence, a series of model experiments were carried out at selected nests (see also section 10.6). Different types of models were tried. No difference could be detected in the responses of the test penguins to a stuffed penguin and an artificial model approximately penguin-sized. The stuffed penguin would have been ideal for this experiment except that the penguins soon tore through the skin when pecking. A sack-cloth model was also easily torn. A plastic detergent bottle (approximately penguin-sized) was quite strong enough but could not be gripped by the penguins, and caused undesirable noise effects. The final model tested was approximately penguin size, and was made from a tough finely woven fabric. The penguins were able to grip it with their bills, but the material was strong enough to resist tearing. The model was attached to a 3 metre pole mounted on wheels, so that it could be pushed up to the outside edge of the nest. The number of pecks delivered in one minute, and notes on behaviour, such as raising or sleeking of the occipital crest, and reaching forward or turning away, were all recorded. It was difficult to present this model to the penguins prior to egg-laying because they either moved away from it or attacked it with their flippers. Flipper attacks were dangerous because the penguins could injure their flippers on the wooden back-supports of the model. For this reason, the model had to be withdrawn when attacked in this way.

The few results obtained for males alone at the nest before egg-laying average 16 pecks per minute (figure 60). Females were not normally found alone at nests without eggs or chicks. When a pair were together at the nest prior to egg-laying, males averaged 19 pecks per minute, and females 5 pecks per minute. This difference was due mainly to the males being dominant at this stage of pair formation.

Pairs together at the nest after the first egg was laid, each averaged 23 pecks per minute. After the second egg was laid, males alone during the first incubation averaged 52 pecks per minute. Females alone during the second incubation watch averaged 58 pecks per minute. These results indicate that the early difference in the responses of males and females to the model had disappeared after egg-laying (by which time the pairs were truly mated).

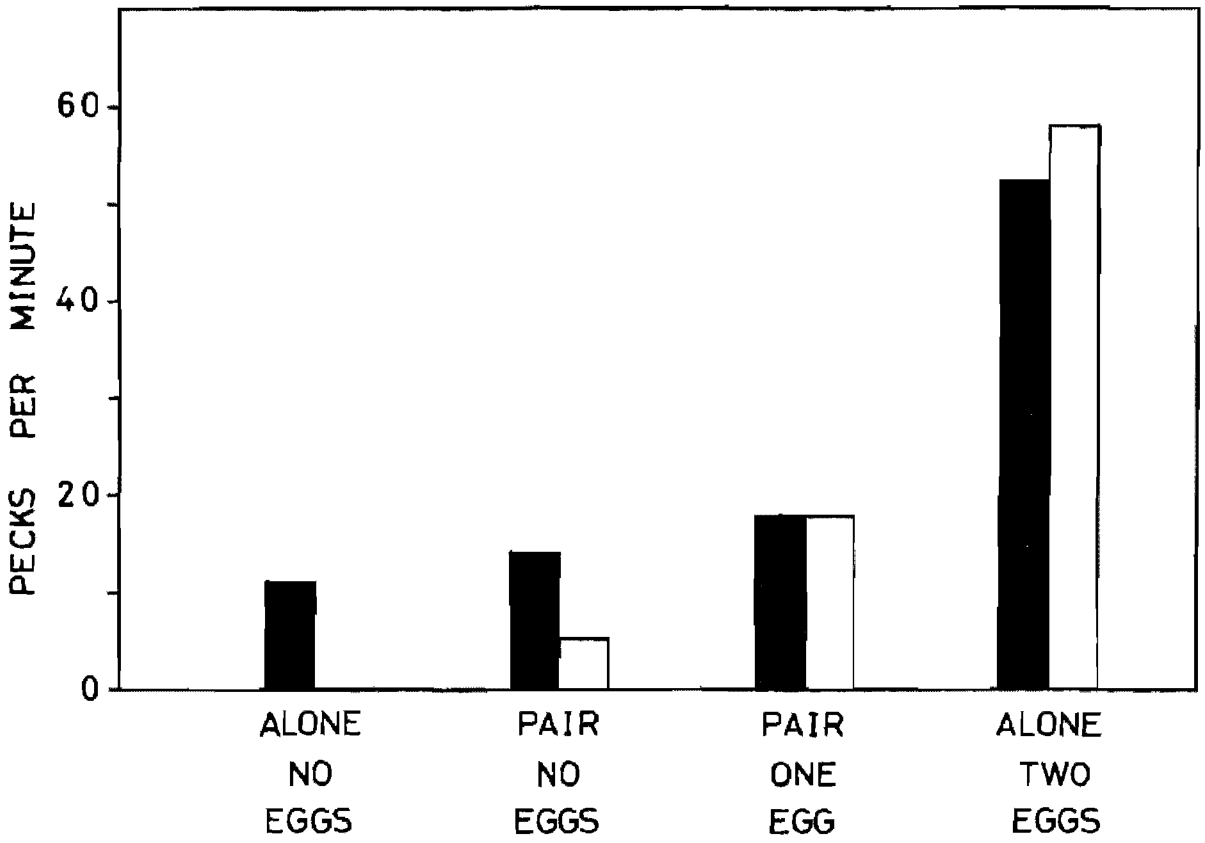
10.4 TERRITORIAL DOMINANCE

Territory boundaries are fairly sharply defined where they are shared with other penguins (see section 9.2ii). However, the area within which a penguin responds to intrusion extends beyond the boundaries. Thus, responses are sometimes given to strangers approaching within about one metre of the boundary, or to neighbours moving in an adjacent territory. Differences in responses to neighbours and strangers are mentioned in an earlier section (section 9.2).

Responses of penguins to intrusions or near intrusions of their territories vary from outright attack and fighting to subtle threat displays and mutual avoidance. Most fights occur

FIGURE 60. Responses to a model by the same penguins before and after egg-laying.

White bars represent females.
Black bars represent males.


PECKS PER MINUTE
60
40
20
0
ALONE NO EGGS
PAIR NO EGGS
PAIR ONE EGG
ALONE TWO EGGS

for possession of either territory or mate, during the occupation or reoccupation periods. Major fights do not normally occur between members of the opposite sex (see section 9.2i). Winners of fights tended to be penguins that had prior ownership rights, where these could be determined. Thus, a male usually won a fight for a territory that he had previously occupied, provided the other penguin had not occupied it for too long.

In the few records made, winners of fights also tended to be the heavier of the two fighters, especially where the differences in weight were large (table 50). However, more records need to be made, and more needs to be known of the circumstances of the fight. It would not be surprising if weight were an important factor in an animal that uses barging as a form of attack.

Penguins at central sites in Colony A8 engaged in encounters with neighbours more frequently than penguins at peripheral sites (table 51), probably because they had boundaries with more neighbours than peripheral penguins (see section 2.3). On the other hand, peripheral penguins engaged in more encounters with strangers moving past their boundaries because more passed by peripheral territories than central ones. Overall, peripheral penguins in table 51 appeared to participate in more encounters than central penguins, but in the sample available the difference is not significant.

Strangers were normally repelled without resistance. However, in encounters with neighbours across a mutual boundary, it was difficult to determine a winner (see section 9.4). On its own territory, each penguin was dominant.

During the incubation period, there is usually only one penguin (incubating eggs) on each territory. The direction in which these penguins face is strongly influenced by wind speed (table 52). In strong winds, incubating penguins tend to face into the wind, so that the feathers are not ruffled (see also Yeates 1971b:903).

In calm, or light winds, orientation is predominantly influenced by neighbouring penguins. There tend to be fewer nests located directly in front of a penguin (0 degrees in table 53) compared to other locations (e.g. 45 degrees from the front of a penguin). This means that penguins tend to face

TABLE 50 : Weights of Fighting Penguins

Date	Winner	Weight (kg)	Loser	Weight (kg)
27.11.69	544	5.00	581	3.60
15.12.69	315	4.65	586	4.65
22.12.69	16	4.37	569	3.96
24.12.69	592	4.30	591	4.41
5. 1 .70	772	4.27	708	3.72

TABLE 51 : Number of Encounters at Central and Peripheral Sites

	Centre	Periphery
Number of 10 minute observations	70	181
Number of penguins passing by	25	269
Average passers-by per observation	0.36	1.49
Encounters with passers-by/observation	0.24	0.97
Encounters with neighbours/observation	1.06	0.86
Total encounters per observation	1.30	1.83

Note : An encounter occurred when a penguin reacted to a disturbance by a neighbour or stranger.

Chi square (2 x 2 table) $p = 0.06$

into inter-nest spaces, rather than directly towards another nest. When they do face toward a neighbouring nest, the orientation of the neighbour is significantly different from that of other neighbours (table 53). The neighbour directly in front never rested facing directly towards the central penguin, though penguins on other surrounding nests may face toward the central nest (figure 61), or in the opposite direction (180 degrees) to the central penguin (figure 62). It is evident that when penguins are undisturbed they show a significant tendency to avoid facing another penguin's head.

Penguins did not directly face one another when resting, but when a neighbour started rearranging nest stones near its boundary, a penguin would turn to face (and maybe threaten) that neighbour. When the neighbour stopped rearranging stones, the other penguin would then turn and face into the wind (or face some other direction away from its neighbour) again.

The orientation of a penguin crouched on a nest is thus determined by several factors, including

(i) the strength of the prevailing wind,
(ii) the behaviour of the penguin itself, and
(iii) the behaviour of neighbouring penguins.

10.5 CAGE EXPERIMENTS

In order to further investigate dominance relationships between individuals, groups of five penguins were placed in cages approximately two square metres in area. Each penguin was banded, and the band marked with coloured tape for ready identification. It was hoped that the cages would both restrict the movements of the penguins to a limited area and would provide a neutral ground for contacts, free from the influence of territorial rights. Within a few days, however, territories were established in the cages, and this tended to defeat the original purpose of the experiment. Nevertheless, some valuable results were obtained.

Some penguins clearly dominated others, sometimes to the extent of chasing them around the cage. Mostly however, dominance was shown by exclusion of other penguins from the individual territories.

The dominant bird in each cage usually occupied the centre of the cage, and also maintained the largest territory.

TABLE 52 : Orientation of Penguins in Relation to Windspeed

Wind speed (metres/sec)	Number of Penguins Facing				Percent
	into wind	with wind	other	total	face into wind
8.5	48	8	5	61	79
1.6	2	2	56	60	3

TABLE 53 : Orientation of Penguins in relation to One Another at Low Wind speeds (see text for further explanation)

Location of Surrounding Nests (w.r.t. central penguin)	Number of Surrounding Nests	Number (and percent) of Penguins		
		Face toward central penguin	Face 180° to central penguin	Face other directions
0 degrees	90	0 (0.0)	0 (0.0)	90 (100.0)
45 degrees	136	17 (12.5)	17 (12.5)	102 (75.0)
90 degrees	108	11 (10.2)	8 (7.4)	89 (82.4)
135 degrees	96	16 (14.7)	10 (9.2)	83 (76.1)
180 degrees	96	16 (16.7)	15 (15.6)	65 (66.7)
225 degrees	112	14 (12.5)	11 (9.8)	87 (77.7)
270 degrees	106	9 (8.5)	7 (6.6)	90 (84.9)
315 degrees	136	12 (8.8)	15 (11.0)	109 (81.2)
Total	893	95	83	715
X^2 probability	< 0.05	< 0.03	< 0.01	> 0.05

FIGURE 61. Frequency of neighbours facing towards a central nest.

Broken arrow represents direction of central penguin.

Solid arrow represents direction of surrounding penguins.

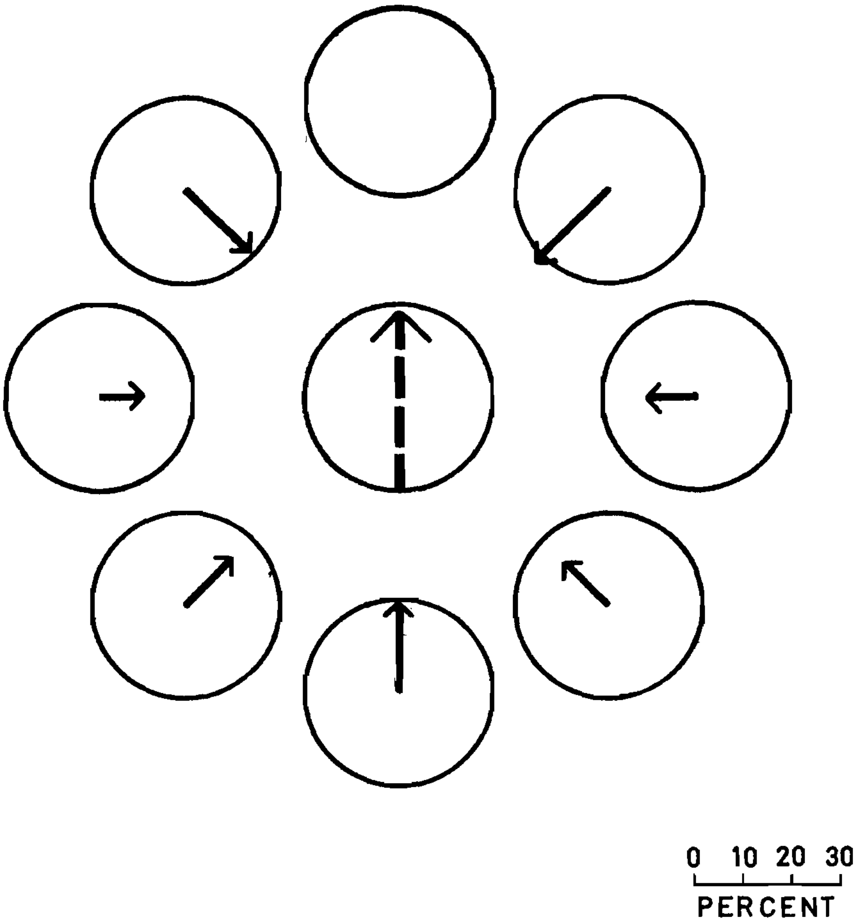
Length of solid arrow represents frequency.

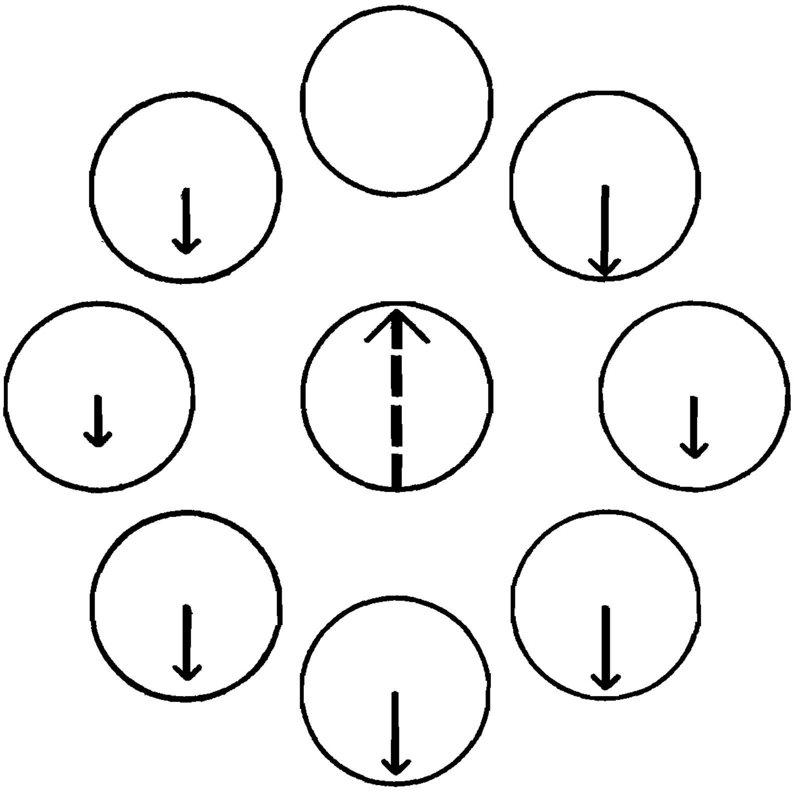
FIGURE 62. Frequency of neighbours facing in the opposite direction to a central penguin.

Broken arrow represents direction of central penguin.

Solid arrow represents direction of surrounding penguins.

Length of solid arrow represents frequency.


0 10 20 30
PERCENT



The other four penguins usually occupied the four corners of the cage. They often faced out of the cage, increasing their apparent individual areas. At different times, the penguins occupied different positions within the cage, so that these territories were not as fixed as a natural territory. The bottom ranked penguin usually moved around more than the others, it was more often pecked than the others (see below). When ice was added to the cage the lower ranked penguins seldom fed from it. The dominant penguin kept others away from the ice while it was feeding. When it had finished feeding, it lay down beside or even on the ice, and continued to keep the others away.

The contacts observed between penguins in cages were obviously affected by "territorial rights" within the cages. Nevertheless, the contacts observed did allow the penguins to be ranked (table 54 & 55).

Individual ranks determined on the first day remained similar throughout the experiment. Top and bottom rankings were most easily determined, both from the percentage of encounters won and from observation of the general behaviour (see above).

In all except one trial (out of nine) the bottom ranked penguin was the lightest weight. However, the top ranked penguins were not always, or even usually, the heaviest. There was a much closer relationship between weight and ranks of lighter penguins than heavier penguins. Because no fighting occurred, ranks within the cages were not likely to have been directly influenced by the weight of the penguins. However, it is possible that the light weight penguins were younger than the heavier penguins.

In another series of experiments, new penguins were introduced from a holding cage into established cages. This invariably resulted in a general upset, because the newly introduced penguin moved around a lot, and was pecked or threatened by the established penguins. The new penguin immediately assumed bottom rank, but may increase in rank after a few days. Initially, the new penguin is introduced into a strange environment, where other penguins have established ownership rights. After an initial period, however, the new penguin becomes established, and may become more established than lower ranked residents. Thus, the existence of ownership

TABLE 54 : Rank Order of Male Penguins in Cage C3

Encounters Between	Number of Wins from Encounters			
	Initial	4 days	5 days	6 days
W : Y	0:36	0:12	0:20	0:23
W : R	1:25	0: 6	0:11	0:10
W : BU	6: 8	5: 0	1:10	0:15
W : BK	2: 3	0: 0	0: 4	0: 0
Y : R	1:34	5: 7	0:20	2:17
Y : BU	19: 1	10: 0	14: 0	18: 0
Y : BK	33: 1	0: 0	8: 0	9: 0
R : BU	12: 0	11: 0	11: 2	5: 0
R : BK	17: 0	4: 0	10: 0	7: 0
BU : BK	0: 0	1: 5	7: 0	0: 0
Rank	R	R	R	R
Order	Y	Y	Y	Y
from	BU	BK	BU	BU
top to	BK	W	BK	BK
bottom	W	BU	W	W

TABLE 55 : Rank Order of Male Penguins in Cage E2

Encounters Between	Number of Wins from Encounters			
	Initial	4 days	5 days	6 days
W : Y	0: 2	0: 8	0:11	1: 5
W : R	0:21	0:16	0:24	0:21
W : G	0:11	0:24	0:28	0: 9
W : B	0: 2	0: 0	1:18	0: 1
Y : R	0: 7	1: 9	0:31	0: 7
Y : G	0: 2	8: 1	3:18	0:12
Y : B	4: 0	8: 0	13: 9	8: 0
R : G	13: 0	9: 0	11:21	15: 0
R : B	5: 0	12: 0	20: 1	10: 0
G : B	3: 0	14: 0	21: 0	3: 0
Rank	R	R	G	R
Order	G	Y	R	G
from	Y	G	Y	Y
top to	B	B	B	B
bottom	W	W	W	W

TABLE 56 : Rank Order of Penguins in Mixed Cage

Rank Score	Penguin	Sex	Previous Rank
1.0	R_2	M	top of cage E_2
0.8	R_3	M	top of cage C_3
	Y_3	M	2nd in cage C_3
0.7	G_2	M	2nd in cage E_2
0.5	Y_2	M	3rd in cage E_2
0.4	B_1	F	top in cage 1
0.3	BU_3	M	3rd in cage C_3
0.2	B_2	M	4th in cage E_2
	W_3	M	5th in cage C_3
0.0	Y_1	F	4th in cage 1
	W_2	M	5th in cage E_2

rights (to territory, for example) modifies the aggressiveness of individuals.

Observations were also made on 9 males and 2 females that had broken out of separate cages into an unused cage. It was not possible to keep trace of all wins and losses, so individuals were scored according to the number of other individuals that they decisively defeated or were defeated by. The new rankings established in the new cage (table 56) closely reflected the previous rankings obtained in individual cages. The two females were well down in the rankings (6th, and equal bottom) in this mixed group.

10.6 MODEL EXPERIMENTS

Differences in the responses of individual penguins were also shown by the response to a model (see also section 10.3).

Unmated penguins and unsuccessful breeders without eggs or chicks scored many fewer pecks per minute than penguins with eggs or chicks (figure 63). Thus, 106 males without eggs or chicks scored an average of 14.8 pecks per minute; 26 females without eggs or chicks scored an average of 7.2 pecks per minute. The difference in the responses of males and females was noted earlier (section 10.3). The average score was fairly constant throughout the season.

The scores of breeding penguins prior to egg-laying were very similar to those of unmated and unsuccessful breeders without eggs or chicks (see section 10.3, and figure 60). Their scores increased, however, after egg-laying in early November, and continued to increase until about chick hatching in mid December (figure 64a). The highest average scores were obtained between 30 and 44 days after egg-laying (figure 64b). This means that the penguins showed most aggression toward the model at about chick hatching, which occurs between 31 and 38 days after egg-laying (section 7.7). Thereafter, the average scores decreased.

The scores of breeding penguins followed a normal distribution (figure 65). Individuals were classified according to their average score for the season. They were considered average if the score fell within one standard deviation of the population mean. Scores lower than one standard deviation below the population mean were classified as below average. Scores

FIGURE 63. Comparative distribution of model scores.

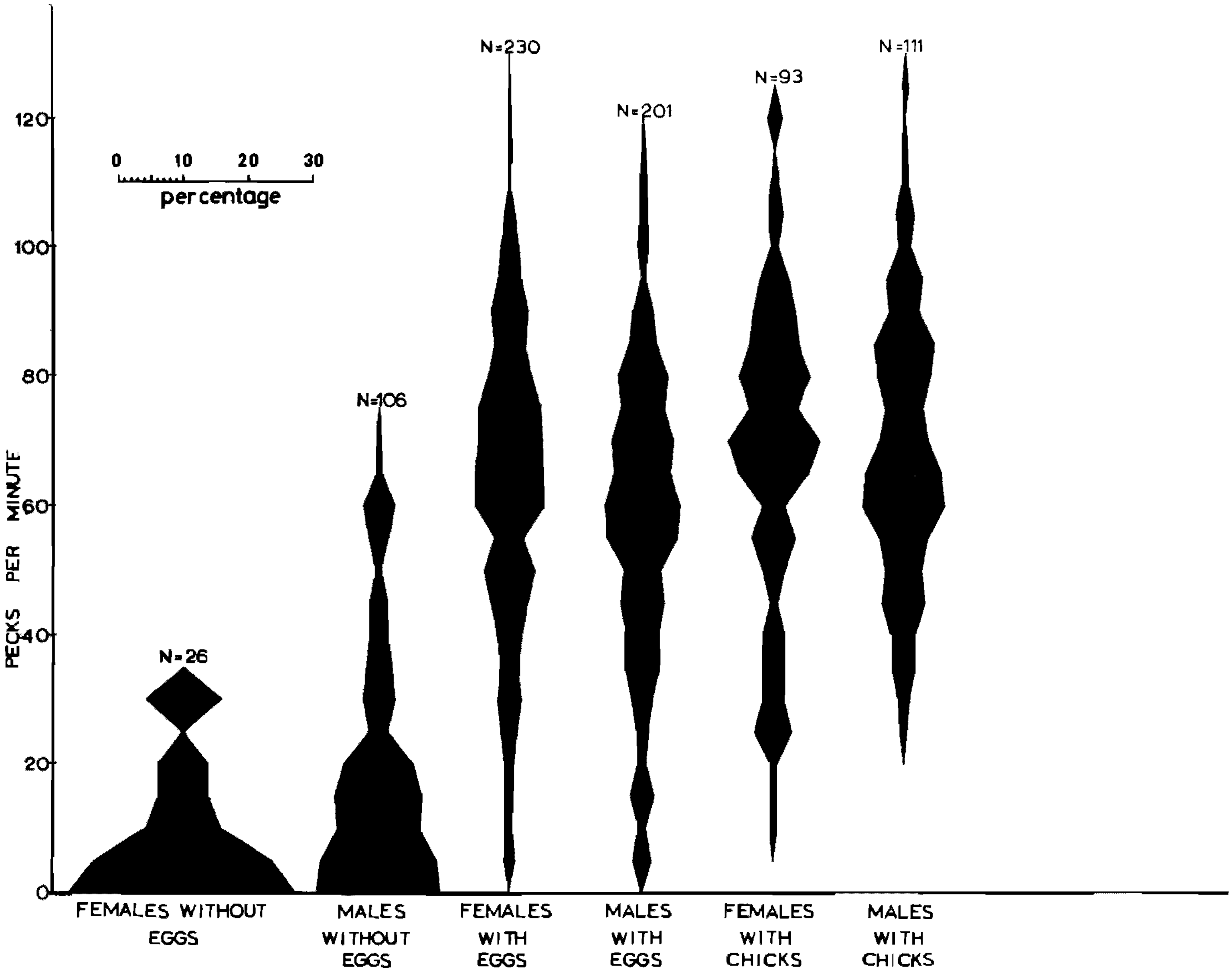

PECKS PER MINUTE
0
20
40
60
80
100
120
0
10
20
30
percentage
N=26
N=106
N=230
N=201
N=93
N=111
FEMALES WITHOUT EGGS
MALES WITHOUT EGGS
FEMALES WITH EGGS
MALES WITH EGGS
FEMALES WITH CHICKS
MALES WITH CHICKS

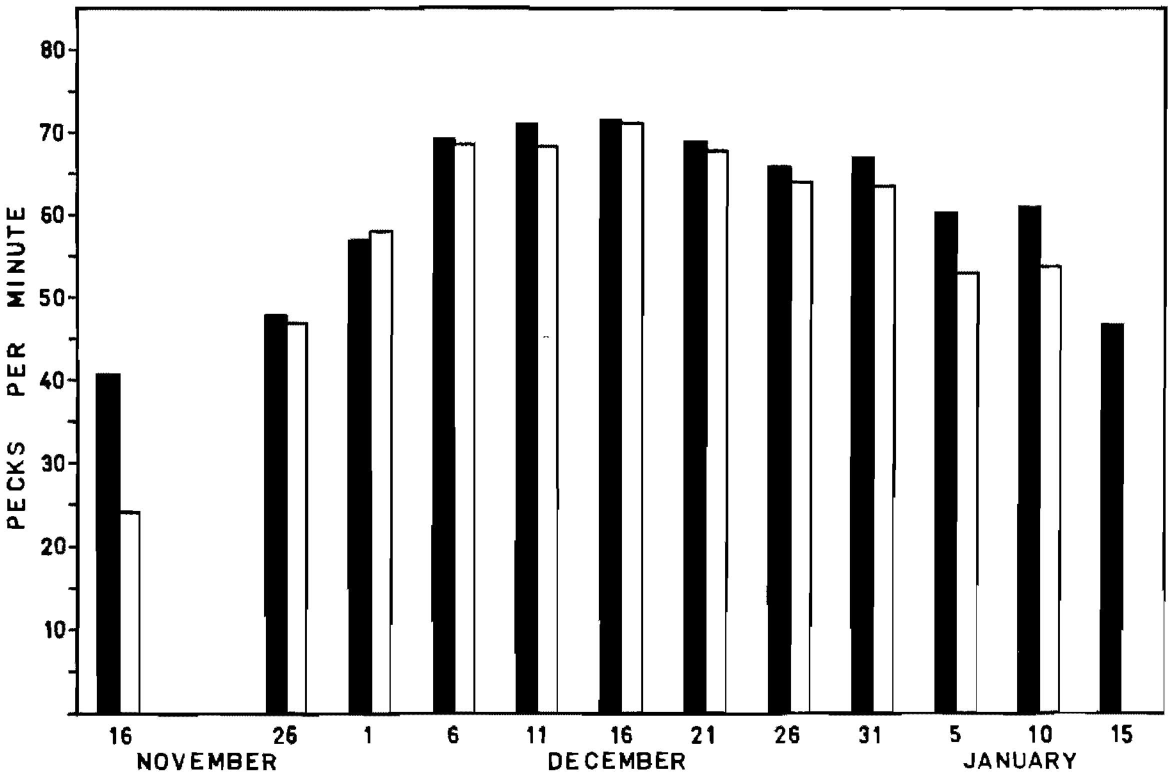
FIGURE 64. Response of penguins to model presented at different times after laying of first egg.

a. (upper) monthly time base

b. (lower) time corrected to date of laying first egg.

White bars represent females.

Black bars represent males.


PECKS PER MINUTE
80
70
60
50
40
30
20
10
16
26
1
6
11
16
21
26
31
5
10
15
NOVEMBER
DECEMBER
JANUARY

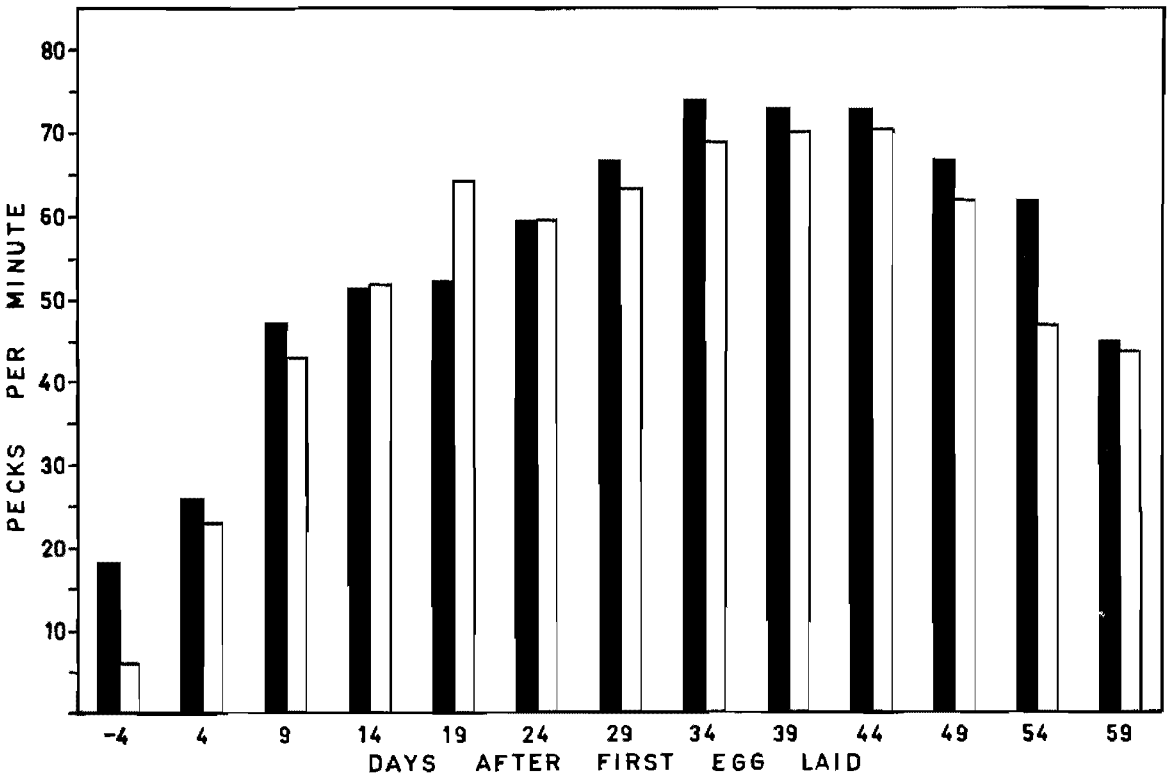
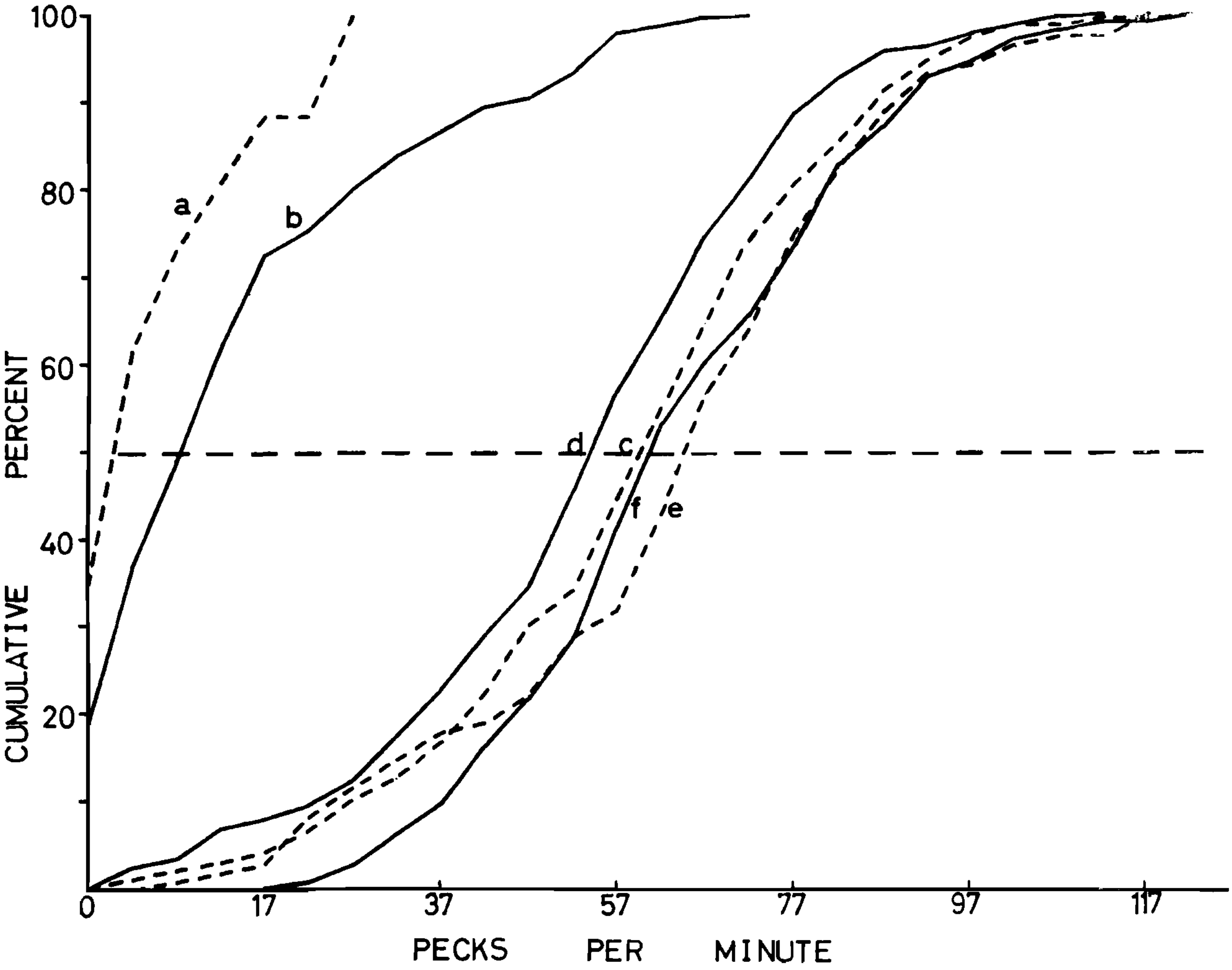

PECKS PER MINUTE
80
70
60
50
40
30
20
10
-4
4
9
14
19
24
29
34
39
44
49
54
59
DAYS AFTER FIRST EGG LAID

FIGURE 65. Distribution of model scores (pecks per minute) over total range.

a. Females without eggs.
b. Males without eggs.
c. Females with eggs.
d. Males with eggs.
e. Females with chicks.
f. Males with chicks.


100
80
60
40
20
CUMULATIVE PERCENT
0
17
37
57
77
97
117
PECKS PER MINUTE
a
b
c
d
e
f

greater than one standard deviation above the mean were classified as above average.

The distribution of scores within a colony is shown in figure 66. Most penguins (males and females) with above average scores were located at territories in the centre of the colony. Penguins with below average scores tended to occur at the periphery of the colony.

Penguins with high model scores also had a significantly higher breeding success than penguins with low model scores (table 57). The significance should perhaps be tempered by the small sample size, and because factors known to affect breeding success (clutch size, territory locality, and time of laying) were not considered. Nevertheless, penguins that were aggressive toward the model clearly had a high breeding success.

10.7 DISCUSSION

Hediger (1964:111) divided flocks of animals into two types:

(i) "contact" animals, which maintain touch contact with one another, especially when resting, and

(ii) "distance" animals, which maintain an "individual distance" and seldom come into contact, even when resting. This binary division is really a simplification of more complex classifications of spacing behaviour, in which it is considered that contact and distance types form the two extremities of a spectrum of spatial distribution in animals (Lill 1968:287). The actual distribution is known to be activity dependent in several species. Furthermore, the distance between animals has a zone boundary, rather than a sharp line (section 10.2, and see Marler 1956b:23).

In the Adelie penguin, both the most distant and the closest spacing occur in the breeding colonies. Penguins on their territories are highly aggressive to penguins on adjacent territories and to penguins approaching from outside the colonies. The level of aggressiveness increases as the intruder approaches closer to the boundary. Neighbours avoid crouching face to face when resting, and increase their apparent individual areas by facing into inter-nest spaces. This probably reduces stress in the crowded conditions of the colony. Within the territory, aggressiveness is reduced

FIGURE 66. Distribution of model scores of penguins at different positions in a colony.

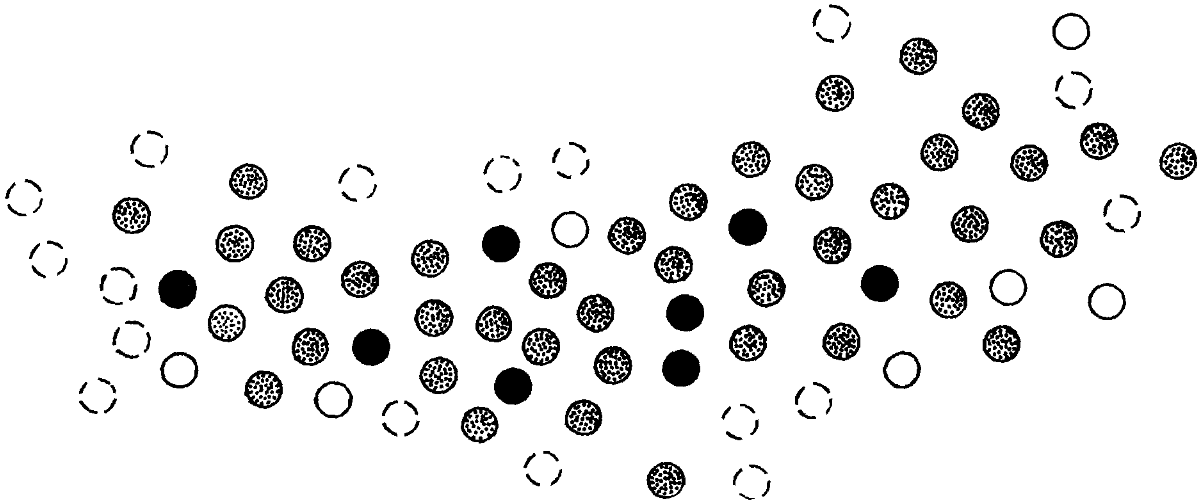
(upper colony males, lower colony females)

Black circle represents above average score.

Dotted circle represents average score.

White circle represents below average score.

Incomplete circle represents unmated male present for part of season only, no female.



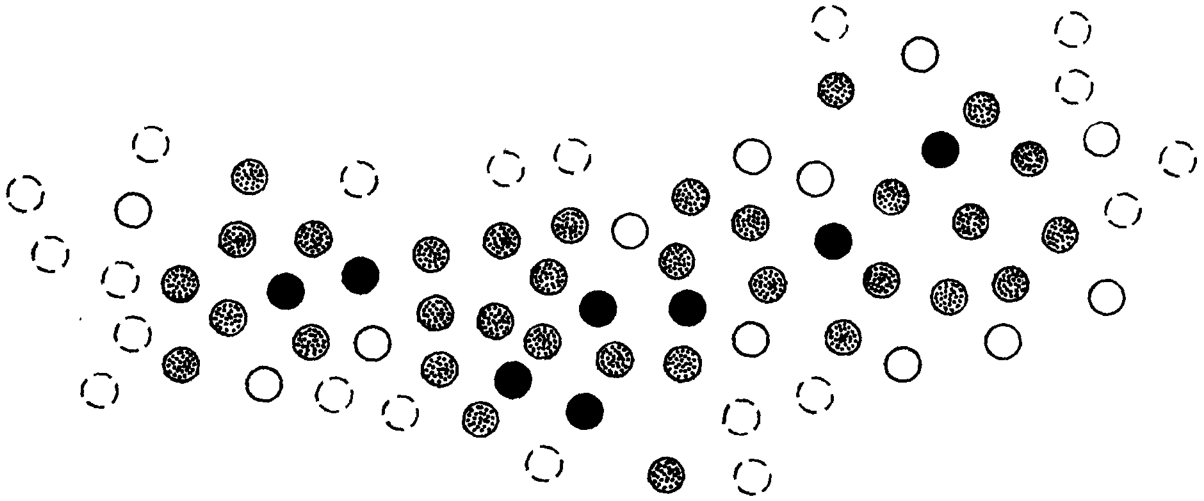


TABLE 57 : Breeding Success of Males Related to Model Score

Average Model Score	Number in Sample	Breeding Success (percent)
10	1	0.0
20	0	–
30	1	0.0
40	2	16.5
50	8	54.0
60	9	77.3
70	11	72.7
80	6	80.7
90	3	78.3
100	2	93.0

$F = 18.7$, (1, 42 DF), $p < 0.01$

towards the mate or young by individual recognition and appeasement displays (section 9.6).

Each penguin is dominant on its own territory, and there is no peck order. Encounters between neighbours are peck dominance, not peck right. That is, in each encounter, the winner is determined according to the circumstances of that encounter, not according to any previous encounter. Encounters with strangers tend to be peck right because the strangers rarely return the attack of a territorial penguin. This is not based on individual recognition, however, but is associated with the possession of a territory. Groups of penguins moving away from the colonies (e.g. feeding at sea) are only transitory groups with no fixed composition, and so have no opportunity to develop a true hierarchy.

Although the territorial system precludes the formation of a definite peck order, it can be readily established that some penguins are more aggressive than others (see below).

The difference between the number of pecks per minute delivered to the model by mated compared to unmated penguins must not be taken as a direct measure of the difference in aggressiveness of the two groups. Before egg-laying (and after losing eggs or chicks) mated penguins had a similar score to unmated penguins. The increase in aggressive responses to the model by parents after egg-laying is associated with increased attachment to the nest site provided by the presence of eggs or chicks. The increase in aggressiveness of parents from egg-laying to chick hatching may be controlled by secretions of progesterine and prolactin, as indicated by Vowles and Harwood (1966:47) for ring doves, Streptopelia risoria.

Differences in the responses of individual breeding penguins at the same point in the breeding cycle probably do reflect differences in inherent aggressiveness. The lower number of pecks per minute delivered towards the model by penguins at the colony periphery indicates that they are less aggressive than penguins in the colony centre. There is no suggestion that either group of penguins became habituated to the model. Peripheral penguins did not seem to be habituated in any way to the larger number of strange intruders they encountered (compared to central penguins). Apart from genetic differences, it is possible that the peripheral (less aggressive) penguins are younger than the central (more aggressive) penguins.

It has been shown previously (section 7.8iv) that penguins in the colony centre tend to be more successful breeders as well as more aggressive than penguins at the colony periphery. Furthermore, the most aggressive penguins had the highest breeding success. This means that aggressiveness will tend to be maintained within the population. Aggressiveness is advantageous for maintaining a prime breeding site. There will, however, also be selection pressures against over-aggressiveness. It is essential that penguins remain within an aggregated group, and do not prevent others from grouping around them. They must not spend all their time defending the territory, or be too aggressive to mate. Breeding in groups provides some protection against skua predation, while travelling in groups at sea provides some safety in numbers against leopard seal attack. Feeding in groups probably aids greatly in location of food (see also section 11.0).

11.0 FINAL DISCUSSION

The commonly observed aggressiveness of densely nesting colonial bird species has interested many authors (e.g. Wynne-Edwards 1962, Patterson 1965, Lack 1968, Nelson 1970) because on the one hand the birds are grouping together very closely, yet on the other hand they seem to be doing so in the face of intense individual competition. The present study of the Adelie penguin, a typical colonial species, has provided some insight into the origin and requirement for this.

The large rookeries of Adelie penguins probably originated primarily as an adaptation to a strongly clustered food supply. When Adelie penguins became adapted to exploit the vast supplies of plankton in the Antarctic waters, breeding sites were selected along the coast and off-lying islands of the Antarctic continent. These sites were in an area devoid of land predators, so that it was possible for large numbers of penguins to breed together on open ground. The rookeries were restricted to certain areas by the limited availability of suitable beaches and conditions for nesting. However, within these areas the available space is still by no means fully utilised. This suggests that population numbers are not limited by this factor.

The characteristic density of the colonies is higher than might be expected from a mere aggregation for feeding purposes, and it is inferred that penguins "choose" to nest within pecking distance of neighbours. The advantages and disadvantages of colonial breeding have been investigated in several studies (see references above). Some possible advantages are noted below.

1. Facilitation of pairing, by bringing together large numbers of potential mates.

2. Proved safety of the general locality, where others have bred successfully before.

3. Protection from predation of nest contents, by distraction through numbers and by buffering effects.

4. Social stimulation, from close contact with neighbouring penguins, which may stimulate reproductive physiology.

In considering the last of these first, it will be noted that some effects of social stimulation in the Adelie penguin have already been discussed in section 7.9. These include synchronisation of laying dates, with consequent reduction of predation pressure by exposing nest contents for the shortest possible time; ensuring that most young grow up when food is plentiful; and ensuring that the young depart for sea in good condition before the onset of the harsh Antarctic winter. In some circumstances, a certain level of social stimulation may be necessary before laying will occur at all. The evidence is purely behavioural, so that there is still plenty of scope for physiological studies to analyse hormone levels, and the ways in which they are affected by various factors, such as age, weight, colony density, and time of season. Much behaviour is socially facilitating, some by sight (e.g. nest building activities), and some also by sound (e.g. sexual advertisement). The impact of these stimuli is greatest in dense conditions (i.e. within colonies rather than at isolated nests).

The density of nesting territories remains relatively constant throughout the season, but the numbers of penguins on these territories show two marked seasonal peaks (see section 4.2). The incidence (per bird) of various activities (such as the advertising display, nest building, copulation, mutual display, and aggressive behaviour) also show seasonal peaks (see section 4.3) which coincide with peak numbers of penguins ashore; that is, at times of maximum inter-bird stimulation. The possible effects of such stimulation on reproductive physiology have been reviewed by Lehrman (1959).

As well as the advantages of social stimulation, the physical clustering of nests in colonies also provides greater protection against predation of nest contents (section 2.7) with consequent increased breeding success (see section 7.8iv). However, suitable locations for breeding and facilitation of pairing are not exclusively associated with dense colonial nesting, but occur even in loose aggregations. Thus, of the four advantages listed above, only the last two require penguins to nest within pecking distance of neighbours.

Certain aspects of colonial breeding still need to be determined. One of these is the role of age in modifying behaviour. The study of LeResche & Sladen (1970) reported on certain aspects of the behaviour of young penguins between the ages of 3 and 7 years, but there is a need for a continuing study (such as the study by Richdale (1957) for 18 consecutive seasons on the Yellow-eyed penguin). It is supposed, for example, that most young penguins first nest at the colony periphery, and subsequently move in towards the centre as sites become available, but to confirm this the positions of individual penguins within a colony need to be documented over a long period of time. Individual differences in factors such as feeding ability, aggressiveness, and social status also need to be related to age. Very little is known about feeding ability or the extent of competition for food, yet efficiency at feeding probably affects the date and weight at which a penguin comes ashore to breed, which in turn probably affects selection of nest site and mate, and physiological condition for breeding.

Although this study has been primarily concerned with intra-specific relationships of a colonial species, the Adelie penguin, the comparative significance of this behaviour cannot be ignored. In a group in which anatomical differences are slight (Stonehouse 1967b:131), behavioural differences become even more significant when analysing evolutionary relationships. Common display categories in different species of penguins include threat, advertisement, and meeting displays. For example, the "severe threat" of the Rockhopper penguin (Warham 1963:250) and the Tete of the Yellow-eyed penguin (Richdale 1951:34) are very similar to the Gape of the Adelie penguin. Likewise, the Sheepish Look (Richdale 1951:17 & 34) is very similar to the Sideways Stare, and the Glare (Richdale 1951:35) is very similar to the Point. Examples of advertising displays, similar to the Ecstatic display of the Adelie penguin, include the Advertisement posture and short call of the King penguin, *Aptenodytes patagonica* (Stonehouse 1960:26), Crowing in the Gentoo and the Chinstrap penguin, *Pygoscelis antarctica* (Bagshawe 1938:275), the Full Trumpet in the Yellow-eyed penguin (Richdale 1951:25), the Ecstatic of the Macaroni penguin (Downes et al. 1959:54), the male display in the Rockhopper penguin (Warham 1963:248), the Ecstatic display in the Magellanic penguin (Conway 1965:121), and Ecstatic Braying in the African penguin (Roberts 1940:250). Though they will not be listed, meeting displays similar to the Loud Mutual of the Adelie penguin have also been reported in several species of penguin.

There are many apparent similarities between the displays of different species, but also many differences. For example, the characteristic head waving of the Adelie penguin Loud Mutual display is apparently absent in the meeting displays of the Rockhopper (Warham 1963:248) and Royal penguins (Warham 1971:109), though it is present in the Macaroni penguin (Matthews 1929:589, Downes et al. 1959:54). In the Adelie penguin, the flippers are held by the side of the body, in the Rockhopper and Royal penguins they are waved up and down, and in the Macaroni penguin they are held back during this display.

The Ecstatic and Mutual displays of different species contain some overlapping components. Thus, the head waving that occurs in the meeting display of the Adelie penguin, occurs in the advertising displays of the Rockhopper (Warham 1963:248) and Royal penguins (Warham 1971:110). Furthermore, the flipper waving that occurs in the advertisement display of the Adelie penguin, occurs in the meeting displays of these other two species. In the Macaroni penguin, Downes et al. (1959:54) report that the "Ecstatic display is apparently identical with (the mutual) epigamic display".

It is possible that a study of the refinement of behaviour components during ontogeny may assist in the interpretation of evolutionary trends. Thus, in the development of the Adelie penguin there is a refinement in the calls associated with the Ecstatic and Loud Mutual displays, which are much less distinct in chicks than in adults. It seems that this distinction does not develop even in the adults of some species; e.g. Downes et al. (1959:55) state that the same display in Macaroni penguins functions both for territorial advertisement and for mutual recognition (see above), and Isenmann & Jouventin (1970) comment on the lack of specialisation of acoustic signals in the Emperor penguin, Aptenodytes forsteri, compared to the Adelie penguin. Another significant refinement of behaviour concerns allo-preening, an important component of social behaviour, though not a display. Allo-preening has been reported from several species of penguins, and occurs in Adelie penguin chicks, but is not performed by adults (see section 9.9).

In determining evolutionary relationships, similarities of behaviour components can be used to infer the behaviour of a common ancestor (Hinde 1970:667). A possible example occurs in the advertising displays of penguins, which may derive from a common evolutionary origin. However, the possibility of convergent evolution cannot be dismissed. When a behaviour component is missing in a species, this may represent a major divergence, or it may only represent a change of threshold levels. The latter may be controlled by a simple genetic system (see Lorenz 1958). For a full interpretation of evolutionary relationships information is needed in more detail and for a larger number of species than is available at present. There is also a need for standardised descriptions, because details in some of the older references are inadequate and confusing.

The descriptions of behaviour presented in this study provide a detailed account of behaviour associated with nest dispersion, the formation and maintenance of pairs, and the ontogeny of the Adelie penguin. It is hoped that the descriptions will provide a basis for extended known-age studies, and for comparative studies of different penguin species.

12.0 SECTION SUMMARIES

Section 1. INTRODUCTION (pages 1 - 7).

Section 2. TERRITORY (pages 8 - 15).

1. Each territory consists of a nest plus a small area around the nest that can be defended by a penguin standing in the nest.
2. Territories within a colony may be designated as peripheral or central. Isolated territories occur outside the colonies.
3. Within a colony there is no significant difference between the spacing of central and peripheral nests.
4. The number of neighbours varies with position in the colony and with time of season.
5. On flat ground, nests in the centre of colonies tend to be arranged hexagonally, so that each penguin has a maximum of six neighbours. This represents maximum use of the nesting area.
6. The location of nest sites may alter slightly through the season, and from season to season. Location varies most on flat uniform terrain. Nevertheless, the pattern of territory arrangement remains superficially similar.
7. There is no shortage in the total nesting area, but there is a limited number of central sites.
8. Compared to central territories, peripheral territories are exposed to greater disturbance from conspecific intruders and predators. Isolated territories are even more exposed than peripheral territories.

Section 3. BEHAVIOUR ASSOCIATED WITH TERRITORY (pages 16 - 31).

1. Behaviour is divided into two groups; elementary acts and displays.
2. Elementary acts include nest building, copulation, attack, escape, and avoidance behaviour.
3. Six threat displays and four sexual displays are recognised.
4. Threat displays include the Bill-to-Axilla display, Sideways Stare, Alternate Stare, Point, Gape, and Charge.
5. Sexual displays include the Ecstatic display, Bow, Loud Mutual, and Quiet Mutual displays.

Section 4. SEASONAL CYCLE OF BEHAVIOUR (pages 32 - 38).

1. There are two peaks in the number of penguins ashore and the incidence of behaviour through the season.
2. Penguins of different breeding status make different contributions to these seasonal peaks.
3. Successful breeders have only one major peak of territorial and sexual activity, in the occupation period prior to egg-laying.
4. Unsuccessful breeders and unmated penguins also have a second peak of activity in the reoccupation period.
5. The reoccupation period is a time when site and pair bonds among unsuccessful breeders and unmated penguins are established and stabilised.

Section 5. ACTIVITY CYCLES IN CONTINUOUS LIGHT (pages 39 - 44).

1. Even in continuous light there is still a regular fluctuation of light intensity and temperature.
2. Adelie penguins have no single period of rest, but are active throughout the 24 hours.
3. There is a tendency towards a reduced level of activity in the middle of the day, especially on warm midsummer afternoons.
4. The midday activity minimum may be associated with the low heat tolerance of Adelie penguins.

Section 6. PAIR AND BREEDING SITE TENACITY (pages 45 - 59).

1. Unsuccessful breeders and unmated penguins change sites and partners more readily than previously successful breeders.
2. Unsuccessful breeders and unmated penguins that maintain a site and partner for a period of time in the reoccupation period have a greater chance of retaining the same site and partner the following season.
3. Penguins (especially males) that obtain a site and partner in the reoccupation period also have a greater chance of breeding the following season than those that do not obtain a site or partner.

Section 7. BREEDING BIOLOGY (pages 60 - 88).

1. Successful breeders arrive at the breeding grounds earlier than unsuccessful breeders, and unsuccessful breeders arrive

earlier than penguins that remain unmated. Males arrive earlier than females.

2. The sex ratio of adults in the colonies is uneven (1.0 to 0.85) in favour of males, and this may be explained by the apparently higher mortality of females.

3. The incidence of unmated penguins is consequently higher in males than in females.

4. Egg-laying is synchronised with respect to arrival dates.

5. Some females were consistently late layers, others were consistently early layers.

6. The mean clutch size is smaller in peripheral compared to central nests, and smallest of all in isolated nests.

7. Incubation of the first egg is incomplete until the second egg is laid.

8. The two main causes of egg and chick mortality were predation and parental failure.

9. Losses were highest in single-egg clutches, at peripheral nests, and among eggs laid late in the season.

10. In 1968-69, the return of penguins, incidence of unmated penguins, adult mortality, clutch size, and breeding success at Cape Bird were all markedly affected by the persistence of sea ice along the western shores of Ross Island.

Section 8. CHICK BEHAVIOUR (pages 89 - 101)

1. Chicks are semi-altricial at hatching, and require a great deal of parental care.

2. Feeding and comfort behaviour develop first, followed by recognition of parents, locomotion, escape reactions, aggression, and finally sexual behaviour.

3. Chicks become independent of parental protection from climate and predators by the age of 21 days, when they may be left unguarded for many hours of the day.

4. Complete independence from the parents does not occur until the chicks depart for sea, at about seven weeks of age.

Section 9. SOCIAL COMMUNICATION (pages 102 - 133).

1. Three types of intra-specific encounters for territory defence are recognised; disputes over territory ownership, encounters with neighbours, and encounters with strangers.

2. Sequences of behaviour used in territory defence result from interaction between two (or more) penguins.
3. The different displays, Bill-to-Axilla, Sideways Stare, Alternate Stare, Point, Gape, and Charge, appear to represent increasing levels of aggressiveness, in that order. They represent a gradient in presentation of the bill.
4. Charge, Gape, and Point may be termed forward or repellent threat displays, while Alternate Stare, Sideways Stare, and Bill-to-Axilla are sideways or deterrent threat displays.
5. The most aggressive components of behaviour include moving forward, bill open, body forward, and head forward. These all assist in the presentation of the bill, the main weapon of attack.
6. Penguins show avoidance reactions when passing between occupied territories.
7. During pair formation, a female must approach a male on his territory. The female must overcome her reticence of approach, while the male must overcome his aggressiveness to strangers.
8. Bowing and Mutual displays are sexual appeasement displays that facilitate the maintenance of reduced distance between mates.
9. There is a gradient in the presentation of the bill between threat and appeasement.
10. In the displays of the Adelie penguin most ritualisation has occurred in connection with the head and bill.
11. Table 58 summarises some of the more important reactions of penguins on the breeding colonies.

Section 10. <u>DIFFERENCES IN AGGRESSIVENESS OF INDIVIDUAL PENGUINS</u> (pages 134 - 149).

1. Spatial relationships between individual penguins are activity dependent.
2. Prior to egg-laying, males appeared to be more aggressive than females. However, after egg-laying there appeared to be no difference in the responses of male and female.
3. Dominance relationships between neighbouring penguins were difficult to determine because of territorial rights. On its own territory, each penguin is dominant.

4. Encounters between individual penguins are peck dominance, not peck right.

5. Penguins crouched on their nests avoided facing another penguin's frontal aspect (or head region).

6. Penguins kept in cages established spatial and dominance hierarchies.

7. The aggressive responses of penguins to a model increased after egg-laying to reach a peak about chick hatching.

8. Penguins could be classified as average, above average, or below average in aggressiveness.

9. Most penguins with above average aggressiveness were located at territories in the centre of a colony. Penguins with below average aggressiveness tended to occur at the colony periphery.

10. Penguins with high aggressive scores also had higher breeding success.

TABLE 58 : Summary of Adelie Penguin Behaviour Described in this Study.

Behaviour	Description on page	Bill position	Situation	Function
Rest	16	horizontal	on or off territories	rest
Walk	17	horizontal	to or from shore	locomotion
Slender walk	17	raised	walking thro' colony	locomotion
Stone robbing	18	lowered	stealing nest stones	to obtain stones
Nest scraping	18	-	nest construction and pair formation	constructs and directs attention to nest
Stone rearranging	18			
Copulation	19	-	male and female at nest	transfer of sperm
Withdrawn crouch	20	lowered	attacked while incubating	protects egg
Peck	20	forward	territory defence	repel intruders
Flipper attack	20	forward	" "	" "
Charge	25	forward	" "	" "
Gape	25	forward	" "	" "
Point	24	forward	" "	" "
Alternate Stare	23	sideways	" "	deter intruders
Sideways Stare	23	sideways	" "	" "
Bill-to-Axilla	22	sideways	" "	" "
Ecstatic	26	raised	male alone at nest	attract females
Bow	27	lowered	male and female at nest	appeasement and strengthens pair bond
Quiet Mutual	30	raised	" " " "	
Loud Mutual				
-upright	29	raised	" " " "	
-forward	29	forward	arrival at nest	individual assertion

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14.0 REFERENCES

ALLIN, J.T. and BANKS, E.M. (1968): Behavioural biology of the collared lemming Dicrostonyx groenlandicus (Traill): I Agonistic behaviour. Anim. Behav. 16:245-262.

ANDREW, J.D. and ROBERTS, J.M. (1952): The pairing of Adelie penguins. Ibis 94:540-541.

ARMSTRONG, E.A. (1954): The behaviour of birds in continuous daylight. Ibis 96:1-30.

ASCHOFF, J. (1967): Circadian rhythms in birds. Int. orn. Congr. Proc. 14:81-105.

BAERENDS, G.P. (1950): Specialisations in organs and movements with a releasing function. Symp. Soc. exp. Biol. 4:337-360.

BAGSHAWE, T.W. (1938): Notes on the habits of the Gentoo and Ringed or Antarctic penguins. Trans. zool. Soc. Lond. 24:185-306.

BASTOCK, M. (1967): "Courtship: a Zoological Study". Heinemann, London. 220 pp.

BLEST, A.D. (1957): The function of eyespot patterns in the Lepidoptera. Behaviour 11:209-256.

BROWN, R.G.B. (1963): The behaviour of the willow warbler Phylloscopus trochilus in continuous daylight. Ibis 105:63-75.

BROWN, J.L. and HUNSPERGER, R.W. (1963): Neurothology and the motivation of agonistic behaviour. Anim. Behav. 11:439-448.

CHATFIELD, C. and LEMON, R.E. (1970): Analysing sequences of behavioural events. Jnl theor. Biol. 29:427-445.

COCHRAN, W.G. (1954): Some methods for strengthening the common X^2 tests. Biometrics 10:417-458.

COLLIAS, N.E. (1944): Aggressive behaviour among vertebrate animals. Physiol. Zool. 17:83-123.

CONWAY, W.G. (1965): The penguin metropolis of Punto Tombo. Animal Kingdom (Aug. 1965):115-123.

COTT, H.B. (1940): "Adaptive Coloration in Animals". Methuen & Co., London. 508 pp.

CROOK, J.H. (1961): The basis of flock organisation in birds. Pp 125-149 in "Current Problems in Animal Behaviour". (Eds. W.H. Thorpe and O.L. Zangwill). Cambridge University Press. 424 pp.

CULLEN, J.M. (1954): The diurnal rhythm of birds in the arctic summer. Ibis 96:31-46.

DAANJE, A. (1950): On locomotory movements in birds and the intention movements derived from them. Behaviour 3:48-98.

DARWIN, C. (1872): "The Expression of the Emotions in Man and Animals". Murray, London. 374 pp.

DILGER, W.C. (1956): Hostile behaviour and reproductive isolating mechanisms in the avian genera Catharus and Hylocichla. Auk 73:313-353.

DOWNES, M.C., EALEY, E.H.M., GWYNN, A.M. and YOUNG, P.S. (1959): The Birds of Heard Island. ANARE Rep. (B) 1:1-135.

ETKIN, W. (1964): Co-operation and competition in social behaviour. Pp 1-34 in "Social Behaviour and Organisation Among Vertebrates". (Ed. W. Etkin). University of Chicago Press, Chicago. 307 pp.

FICKEN, R.W. and FICKEN, M.S. (1966): A review of some aspects of avian field ethology. Auk 83:637-661.

GOLDSMITH, R. and SLADEN, W.J.L. (1961): Temperature regulation of some antarctic penguins. J. Physiol., Lond. 157:251-262.

GRANT, E.C. (1963): An analysis of the social behaviour of the male laboratory rat. Behaviour 21:260-281.

GRANT, P.R. (1968): Polyhedral territories of animals. American Naturalist 102:75-80.

HARRISON, C.J.O. (1965): Allopreening as agonistic behaviour. Behaviour 24:161-209.

HAZLETT, B.A. and BOSSERT, W.H. (1965): A statistical analysis of the aggressive communications systems of some hermit crabs. *Anim. Behav.* *13*:357-373.

HEDIGER, H. (1964): "Wild Animals in Captivity". Dover, New York. 207 pp.

HINDE, R.A. (1970): "Animal Behaviour. A Synthesis of Ethology and Comparative Psychology". 2nd ed. McGraw-Hill, New York. 876 pp.

HINGSTON, R.W.G. (1933): "The Meaning of Animal Colour and Adornment". Arnold & Co., London. 411 pp.

HUXLEY, J.S. (1938): Threat and warning coloration in birds, with a general discussion of the biological functions of colour. *Int. orn. Congr. Proc.* *8*:430-455.

ISENMANN, P. and JOUVENTIN, E.P. (1970): Eco-éthologie du Manchot empereur (*Aptenodytes forsteri*) et comparaison avec le Manchot Adélie (*Pygoscelis adeliae*) et le Manchot royal (*Aptenodytes patagonica*). *L'Oiseau et R.F.O.* *40*:136-159.

KEARTON, C. (1930): "The Island of Penguins". Longmans, London.

LACK, D. (1965): "The Life of the Robin". 4th ed. Witherby, London. 240 pp.

LACK, D. (1968): "Ecological Adaptations for Breeding in Birds". Methuen & Co., London. 409 pp.

LEHRMAN, D.S. (1959): Hormonal responses to external stimuli in birds. *Ibis* *101*:478-496.

LeRESCHE, R.E. and SLADEN, W.J.L. (1970): Establishment of pair and breeding site bonds by young known-age Adelie penguins (*Pygoscelis adeliae*). *Anim. Behav.* *18*:517-526.

LeRESCHE, R.E., WOOD, R.C. and SLADEN, W.J.L. (1970): Antarctic avian population studies, 1968-69. *Antarctic Journal of the United States* *5*:46-49.

LEVICK, G.M. (1914): "Antarctic Penguins: a Study of Their Social Habits". Heineman, London. 140 pp.

LILL, A. (1968): Spatial organisation in small flocks of domestic fowl. *Behaviour* *32*:258-290.

LORENZ, K.Z. (1958): The evolution of behaviour. Scientific American 199:67-78.

MARLER, P. (1956a): Behaviour of the chaffinch, Fringilla coelebs. Behaviour Supplement 5:1-184.

MARLER, P. (1956b): Studies of fighting in Chaffinches. (3) Proximity as a cause of aggression. Brit. J. Anim. Behav. 4:23-30.

MARLER, P. and HAMILTON, W.J. (1966): "Mechanisms of Animal Behaviour". Wiley & Sons, New York. 771 pp.

MARSHALL, A.J. (1960): The environment, cyclical reproductive activity and behaviour in birds. Symp. zool. Soc. Lond. 2:53-67.

MATTHEWS, L.H. (1929): Birds of South Georgia. Discovery Reports 1:561-592.

McFARLAND, D.J. and BAHER, E. (1968): Factors affecting feather posture in the Barbary Dove. Anim. Behav. 16:171-177.

MORLEY, A. (1943): Sexual behaviour in British birds from October to January. Ibis 85:132-158.

MORRIS, D. (1956): The feather postures of birds and the problem of the origin of social signals. Behaviour 9:75-113.

MÜLLER-SCHWARZE, D. (1968): Circadian rhythms of activity in the Adélie penguin (Pygoscelis adeliae) during the austral summer. Antarct. Res. Ser. 12:133-149.

NELSON, J.B. (1970): The relationship between behaviour and ecology in the Sulidae with reference to other sea birds. Oceanogr. Mar. Biol. Ann. Rev. 8:501-574.

NELSON, J.B. (1971): The biology of Abbott's Booby, Sula abbotti. Ibis 113:429-467.

NICE, M.M. (1962): Development of behaviour in precocial birds. Trans. Linn. Soc. N.Y. 8:1-211.

ORIANS, G.H. and CHRISTMAN, G.M. (1968): A comparative study of the behaviour of Red-Winged, Tricolored, and Yellow-headed Blackbirds. Univ. Calif. Publs Zool. 84:1-85.

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

PENNEY, R.L. (1968): Territorial and social behaviour in the Adélie penguin. *Antarct. Res. Ser.* *12*:83-131.

PETTINGILL, O.S. (1960): Creche behaviour and individual recognition in a colony of Rockhopper penguins. *Wilson Bull.* *72*:213-221.

REID, B.E. (1964): The Cape Hallett Adelie penguin rookery, its size, composition, and structure. *Rec. Dom. Mus.* *5*:11-37.

REID, B.E. (1965): The Adelie penguin (*Pygoscelis adeliae*) egg. *N.Z. Jl Sci.* *8*:503-514.

REID, B.E. and BAILEY, C. (1966): The value of the yolk reserve in Adelie penguin chicks. *Rec. Dom. Mus.* *5*:185-193.

RICHDALE, L.E. (1941): The Erect-crested penguin (*Eudyptes sclateri*) Buller. *Emu.* *41*:25-53.

RICHDALE, L.E. (1951): "Sexual Behaviour in Penguins". University of Kansas Press, Kansas. 316 pp.

RICHDALE, L.E. (1957): "A Population Study of Penguins". Clarendon Press, Oxford. 195 pp.

ROBERTS, B. (1940): The breeding behaviour of penguins with special reference to *Pygoscelis papua* (Forster). *British Graham Land Expedition 1934-37 Scientific Reports* *1*:195-254.

ROWELL, C.H.F. (1964): Comments on a recent discussion of some ethological terms. *Anim. Behav.* *12*:535-537.

SAPIN-JALOUSTRE, J. (1955): Quelques aspects de la vie du Manchot Adélie en Terre Adélie. *Acta XI Cong. Intern. Ornith.* 231-240.

SAPIN-JALOUSTRE, J. (1960): "Écologie du Manchot Adélie". Hermann, Paris. 211 pp.

SAPIN-JALOUSTRE, J. and BOURLIÈRE, F. (1951): Incubation et développement du poussin chez le Manchot Adélie, *Pygoscelis adeliae*. *Alauda* *19*:65-83.

SAPIN-JALOUSTRE, J. and BOURLIÉRE, F. (1952): Parades et attitudes caracteristique de *Pygoscelis adeliae*. *Alauda* *20*:39-53.

SCHENKEL, H. (1967): Submission; its features and function in the wolf and dog. *Am*. *Zoologist* *7*:319-329.

SLADEN, W.J.L. (1953): The Adelie Penguin. *Nature* *171*:952-955.

SLADEN, W.J.L. (1958): The Pygoscelid penguins. I. Methods of Study. II. The Adélie penguin *Pygoscelis adeliae* (Hombron & Jaquinot). *Falkland Islands Dependencies Survey Sci*. *Rep*. *17*:1-97.

SLADEN, W.J.L., WOOD, R.C. and MONAGHAN, E.P. (1968): The USARP bird-banding program, 1958-1965. *Antarct*. *Res*. *Ser*. *12*:213-262.

SLADEN, W.J.L. and LeRESCHE, R.E. (1970): New and developing techniques in Antarctic ornithology. Pp 585-596 in "Antarctic Ecology". (Ed. M.W. Holdgate). Vol. I. Academic Press, London. 604 pp.

SMITH, W.J. (1965): Message, meaning, and context in ethology. *American Naturalist* *99*:405-409.

STOKES, A.W. (1962): Agonistic behaviour among Blue Tits at a winter feeding station. *Behaviour* *19*:118-138.

STONEHOUSE, B. (1960): The King penguin, *Aptenodytes patagonica*, of South Georgia. I. Breeding behaviour and development. *Falkland Islands Dependencies Survey Sci*. *Rep*. *23*:1-81.

STONEHOUSE, B. (1963): Observations on Adelie penguins (*Pygoscelis adeliae*) at Cape Royds, Antarctica. *Int*. *orn*. *Congr*. *Proc*. *13*:766-779.

STONEHOUSE, B. (1967a): Occurrence and effects of open water in McMurdo Sound, Antarctica, during winter and early spring. *Polar Record* *13*:775-778.

STONEHOUSE, B. (1967b): The general biology and thermal balance of penguins. Pp131-197 in "Advances in Ecological Research". (Ed. J.B. Cragg). Vol.4. Academic Press, London. 311 pp.

STONEHOUSE, B. (1970): Adaptation in polar and subpolar penguins (Spheniscidae). Pp 526-541 in "Antarctic Ecology". (E.M.W. Holdate). Vol. I. Academic Press, London. 604 pp.

STOUT, J.F. and BRASS, M.E. (1969): Aggressive communication by Larus glaucescens. Part II. Visual communication. Behaviour 34:42-54.

TAVOLGA, W.N. (1970): Levels of interaction in animal communication. Pp 281-302 in "Development and Evolution of Behaviour". (Eds. L.R. Aronson, E. Tobach, D.S. Lehrman and J.S. Rosenblatt). Freeman, San Francisco. 656 pp.

TAYLOR, R.H. (1962): The Adelie penguin, Pygoscelis adeliae, at Cape Royds. Ibis 104:176-204.

TAYLOR, R.H. (1964): Adelie penguin rookeries in the Ross Dependency. Antarctic 3:566-570.

TAYLOR, R.H. and ROBERTS, H.S. (1962): Growth of Adelie penguin (Pygoscelis adeliae Hombron and Jacquinot) chicks. N.Z. Jl Sci. 5:191-197.

TENAZA, R. (1971): Behaviour and nesting success relative to nest location in Adelie penguins (Pygoscelis adeliae). Condor 73:81-92.

THOMPSON, D.H. and EMLEN, J.T. (1968): Parent-chick individual recognition in the Adelie penguin. Antarctic Journal of the United States 3:132.

TINBERGEN, N. (1948): Social releasers and the experimental method required for their study. Wilson Bull. 60:6-51.

TINBERGEN, N. (1959): Comparative studies of the behaviour of gulls (Laridae): a progress report. Behaviour 15:1-70.

VOWLES, D.M. and HARWOOD, D. (1966): The effect of exogenous hormones on aggressive and defensive behaviour in the ring dove (Streptopelia risoria). J. Endocr. 36:35-51.

WARHAM, J. (1958): The nesting of the little penguin Eudyptula minor. Ibis 100:605-616.

WARHAM, J. (1963): The rockhopper penguin, Eudyptes chrysocome, at Macquarie Island. Auk 80:229-256.

WARHAM, J. (1971): Aspects of breeding behaviour in the Royal penguin *Eudyptes chrysolophus schlegeli*. *Notornis* *18*:91-115.

WILSON, E.A. (1907): Aves. *British National Antarctic Exp. Rept. 1901-4 Nat. Hist.* *2*:1-121.

WYNNE-EDWARDS, V.C. (1962): "Animal Dispersion in Relation to Social Behaviour". Oliver & Boyd, Edinburgh. 653 pp.

YEATES, G.W. (1968): Studies on the Adelie penguin at Cape Royds 1964-65 and 1965-66. *N.Z. Jl mar. Freshwat. Res.* *2*:472-496.

YEATES, G.W. (1971a): Diurnal activity in the Adelie penguin (*Pygoscelis adeliae*) at Cape Royds, Antarctica. *J. nat. Hist.* *5*:103-112.

YEATES, G.W. (1971b): Observations on orientation of penguins to wind and on colonisation in the Adelie penguin rookery at Cape Royds, Antarctica. *N.Z. Jl Sci.* *14*:901-906.

YOUNG, E.C. (1970): The techniques of a skua-penguin study. Pp 568-584 in "Antarctic Ecology". (Ed. M.W. Holdgate). Vol. I. Academic Press, London. 604 pp.