Studies on the Behaviour and Reproduction of the Royal Penguin (*Eudyptes chrysolophus schlegeli*)

by

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A thesis submitted for the degree of
Doctor of Philosophy in the Australian
National University

April, 1970

The work reported in this thesis, except where specifically mentioned, was performed by the candidate during the period June 1966 to April 1970.

Graeme T. Smith.

Graeme T. Smith

PLATE 1

Plate 1a	A pair of breeding Royal penguins in the Sand Colony. The female is incubating.
Plate 1b	A pair of Royal penguins Flagging. The chick on the right has almost completed its moult.

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Acknowledgements

The work reported in this thesis was carried out while I was a biologist with the Antarctic Division of the Department of Supply. I am grateful to the Division for the opportunity to work on Macquarie Island, and for its support during my term as a biologist with it.

While I was in Australia, Professor J.D. Smyth kindly provided facilities at the Zoology Department, Australian National University.

The study was originally suggested by Dr. Robert Carrick of the Mawson Institute, and I am extremely grateful for his help and advice in organising the study, as well as for allowing me to use his own study birds.

My supervisor Dr. C.H. Tyndale-Biscoe gave me valuable help and criticism during the study, and Dr. S.J.J.F. Davies of the C.S.I.R.O., Division of Wildlife Research gave invaluable guidance and assistance. I am extremely grateful to both of them.

I wish to thank the members of the 1966 and 1967 ANARE Expeditions for the invaluable and unstinting help during my stay on Macquarie Island. Special thanks to my fellow biologists at Bauer Bay, Duncan MacKenzie (1966), Peter Ormay (1967) and Bill Merrilees (1967) for their help and companionship during the long days of the Royal's breeding season.

Mr. Ivan Fox, whose knowledge of Macquarie Island and photographic expertise gave me considerable help before my departure for Macquarie Island, deserves special thanks. I am also grateful for his considerable help in the preparation of the illustrations for this study.

I would also like to express my gratitude to Mr. Noel Call for his invaluable assistance in the preparation of the histological material, and Mr. G. McKinnon who kindly provided the maps of Macquarie Island and the Antarctic.

The Tasmanian Fauna Board kindly gave permission for the collection of the Royal penguins for the reproductive study.

CHAPTER 1 - REVIEW OF THE LITERATURE

I. Introduction.

The penguins (family Spheniscidae) are widely distributed in the Southern Hemisphere. The distribution is circumpolar in the Antarctic and sub-Antarctic regions, and ranges north to the southern coasts of Africa, Australasia and South America, where the range extends northwards up the western coast, and across to the Galapagos Islands. The Galapagos penguin (Spheniscus mendiculus) is the most northern species, while the Emperor (Aptenodytes forsteri) and the Adelie penguins (Pygoscelis adeliae) are confined to the Antarctic.

Although most species of penguins are found in the warmer zones of the Southern Hemisphere, and in many cases close to inhabited coasts, comparatively little is known about their biology. By contrast, the biology of the penguins of the remote sub-Antarctic islands and the Antarctic continent is well documented for a number of species.

This anomalous situation is probably a result of the great interest shown in the Antarctic regions following Cook's voyages (1768-71 and 1772-75), and the comparatively limited number of species found in these regions.

Roberts (1958) has listed the numerous expeditions to the Antarctic since the seventeenth century. A brief history of Antarctic expeditions has been given by Schell (1965).

II. General Review.

Biological research in the Antarctic has been reviewed briefly by Mackintosh (1964) and Ingham (1964), and Roberts (1959) has reviewed the work of British ornithologists in the Antarctic.

Research on penguins can be broadly divided into two periods. The first period can be considered to start with the first monograph on penguins by Pennant (1768), and to end in 1945. Little detailed work was done until the start of the present century when there was an upsurge in interest in the Antarctic and sub-Antarctic regions, which resulted in a number of detailed papers on the natural history of the penguins in these regions.

Accounts of the Adelie penguin (Pygoscelis adeliae) were given by Wilson (1907), Murray (1909), Gain (1913), Levick (1914, 1915), Ardley (1936), Murphy (1936), and Falla (1937). The Emperor penguin (Aptenodytes forsteri) was studied by Wilson (1907), Murray (1909), Gain (1913) and Falla (1937), and the King penguin (Aptenodytes patagonica) by Wilson (1907), Murphy (1936) and Falla (1937). Accounts of the Antarctic penguin (Pygoscelis antarctica) were given by Wilson (1907), Murray (1909), Gain (1913) and Bagshawe (1938), and the Macaroni penguin (Eudyptes chrysolophus) by Gain (1913), Matthews (1929) and Murphy (1936), while the Gentoo penguin (Pygoscelis papua) has been studied by Murphy (1936), Bagshawe (1938) and Roberts (1940). Kearton (1930) gives and interesting but highly anthropomorphic account of the Jackass penguin (Spheniscus demersus), and Murphy (1936) has reviewed the other Spheniscus species.

Since 1945 there has been a greater emphasis on more detailed studies on specific aspects of the biology of penguins, with an increasing emphasis on the use of banded birds. The classic work on a banded population was that of Richdale (1951, 1957), who started work on the Yellow-eyed penguin (Megadyptes antipodes) in 1936. While a number of penguins of the sub-Antarctic and Antarctic have been studied in increasing detail, it is the Adelie penguin that has received most attention. An example of the intensity of these studies may be seen in the papers in Antarctic Bird Studies (1968), which covers such topics as Territorial and Social Behaviour (Penny), Circadian Rhythms (Muller-Schwarze), Biochemistry of Egg and Blood Serum Proteins (Feeney et al), Salt and Water Metabolism (Douglas) and Feeding Preferences (Emison).

III. Aspects of penguin biology.

A. Introduction.

A brief review of aspects of the biology of colonial penguins relevant to my own study will be given, followed by a more detailed review of the Royal penguin literature.

(1) Ecology. The detailed ecology of the penguins has been almost entirely confined to their terrestrial phase, which in the migratory species occupied only a minor portion of the year.

Of the penguins which breed in densely packed colonies, detailed accounts of the dynamics and chronology are available on the Adelie penguin at Hope Bay and Signy Island (Sladen, 1958), Phoque Island (Sapin-Jaloustre, 1960) and at Cape Royds (Taylor, 1962 and Stonehouse, 1963). These aspects of the ecology of the Emperor penguin have been studied by Prevost (1961), of the King penguin by Stonehouse (1960), the Rockhopper penguin by Warham (1963), and the Antarctic penguin by Sladen (1955).

These workers have found that, with the exception of the King penguin, the breeding cycles are highly synchronised and are regular from year to year. The early and late breeding King penguins probably show some synchrony, which is masked by the extended breeding season. They also found that there is a marked division of labour among the breeding males and females, and although the details vary, that there is a general similarity in the long incubation and guarding (of the chicks) periods.

Maturity is delayed in these species. Some Adelie penguins start breeding at three years of age (Sladen et al, 1966), Royals at five years (Carrick, 1964), and captive King penguins at six years (Gillespie, 1932). While the age of first breeding has not been determined in the other penguins it is apparent that all have a delay in the attainment of sexual maturity. Associated with the delayed sexual maturity are later arrival into the colony and differences in behavioural activity in the colony.

The limited amount of information on the Macaroni penguin (Downes et al, 1959) and the Erect-crested penguin (Richdale, 1941 and 1950) suggests that the breeding seasons of these two penguins are similar to other migratory colonial penguins.

(2) Behaviour. While many general descriptions of the behaviour of penguins have been given, little detailed analyses of the behaviour of penguins have been done. Sapin-Jaloustre and Bourliere (1952) give quantitative data on the seasonal frequency distribution of a number of displays of the Adelie penguin. Qualitative interpretations of displays, based on the situations in which they occur, have been done on the Yellow-eyed

penguin (Richdale, 1951), the Adelie penguin (Sapin-Jaloustre and Bourliere, 1952; Sladen, 1958; and Penney, 1968). These authors have also noted differences in behaviour with age.

(3) Reproduction. Little work has been done on the reproduction of penguins. Roberts (1940) has shown that in the Gentoo penguin there is a rapid increase in the size of the testes and ovaries at the beginning of October. Free spermatozoa were seen for about six weeks before regressing rapidly, and the ovaries showed a similar trend.

The gonads of the Emperor and Adelie penguins (Prevost and Bourliere, 1955) were shown to have a very rapid increase in size before breeding, followed by a rapid regression. The peak of the cycle was maintained for only a short time.

Sladen (1958) gave some data on the gonads of the Adelie penguins, some of which supported his age classification.

IV. Review of the Royal penguin literature.

A. Investigations prior to 1945.

The Royal penguin was first described by Finch in 1876 (Peters, 1931) and was named Eudyptes schlegeli. However, it is now considered to be the light-faced Macquarie Island form of the Macaroni penguin. E. c. chrysolophus.

During the period 1873 to 1918 the Royal penguin was extensively exploited for its oil. No detailed work was carried out on the Royal penguin during this period, although brief accounts were given of the general biology by Scott (1892), Hamilton (1894), and Bickerton (1897) (quoted in Falla, 1937 and Cumpston, 1968).

Wilson (1907) gave a brief account of his short visit to a Royal penguin colony in 1901. Tullock (1916) gave a brief account of the penguins on Macquarie Island and Falla (1937) summarised the data on the Royal penguin collected by the Australian Antarctic Expedition in 1911-13, and the B.A.N.Z.A.R. Expedition of 1929-31. The work of these authors may be summarised as follows:

The Royal penguin was migratory, spending September to April on land, and the rest of the year at sea. By the middle of September the first birds arrived on the island to commence breeding. The colonies were situated on large, barren and rocky areas, and the birds built shallow nests of stones. Egg laying began about mid-October. Tullock (1916) observed that two eggs were laid, the first being infertile, but Falla (1937) and previous authors thought that only one egg was laid. The incubation period lasted about six weeks, and the first egg was hatched about the end of November. Both parents shared the guarding and feeding of the chicks, and after being deserted by their parents the chicks formed creches. After about two months the chicks went to sea. In February the one year old birds came ashore to moult, and the breeding birds arrived in March to moult. All birds had finished moulting in mid-April.

The breeding season of the Royal penguin was very regular, a fact capitalised on by the 'oilers'.

B. Later work.

Since 1945 Carrick has been the only worker to study the Royal penguin (Carrick 1964, 1967 and 1969). He has been carrying out a long-term ecological study in two small adjacent colonies of approximately 1000 breeding birds. About 500-1000 young are fledged each year, and a total of 7400 chicks have been banded from

1955, when he began his study to 1966, and their life histories have been recorded since 1962. Large scale banding of chicks was also carried out in three other colonies, and searches were made in these and other colonies to check on dispersal from the natal colony.

In the 1965 and 1966 seasons pilot studies were carried out to determine the relation of weight on arrival, and weight changes of parents and chicks during the breeding season, to ultimate breeding success. These studies were carried out on known age birds older than seven years, and a small number of unknown age birds. In 1967 this program was expanded and large numbers of unknown age birds were banded and weighed on arrival. All known age birds older than five years old were also weighed on arrival.

Carrick (1964, 1967 and 1969) reviewed the results of this study, and the following account was taken from these papers, supplemented by personal comments from Carrick.

The annual cycles are very regular and synchronous, with a constancy of return by adults to their former nest sites, and of immature birds to their natal colony. Dispersal was seen mainly in the one year old birds,and as they aged, birds returned to their natal colony. After the winter migration the males returned to the colony first, followed a week or two later by the females. About one to two weeks after the return of the females the eggs were laid. Eggs were laid throughout October with a peak on the 20th and 22nd of the month. Two eggs were laid at an interval of four days, and both were fertile, although the first, which is smaller, was usually discarded. The males may stay with the females for up to 10 days after the laying of the first egg.

After this the male departed for sea, returning about 19 days before hatching to take over the incubation from the females. The females returned about a week before hatching time (cf. Ch.3), and the males guard the chick for about two to three weeks after hatching before departing for sea. During this time the female made frequent trips to sea to collect food for the chick. On the departure of the males the chicks form small creches until their moult and departure to sea in late January.

One year old birds came ashore briefly in December. Birds of each older age group arrived earlier, stayed longer, and progressively approached full breeding status, becoming attached first to a particular area, and later to a nest site and mate.

The attainment of sexual maturity was delayed, there being a considerable overlap in the level of breeding activity in the age groups up to seven years old. A few four year old birds are ashore at egg laying late in October, 3.5% of the five year old males ashore by egg laying have mates that lay, and 8.5% of the five year old females lay. Nearly all seven year old birds are ashore by egg laying, but only 41% of the mates of the seven year old males lay, while 60% of the seven year old females lay. By ten years of age, 20% of the males had not bred, while only five percent of the females had not laid. All older birds had bred, but the numbers are too small to make the increase in breeding success from the ten year old birds significant.

The percentage of eggs that hatch increases with age, but is only approximately 50% for both males and females at ten years of age.

No five year old bird had succeeded in fledging a chick, and in 1965-66 only 7 out of the 27 chicks hatched by known age parents 6-10 years old were reared successfully. The overall fledging success is about 40%.

Carrick (1967) states that the earliest returning birds are the older successful breeders, and that these birds weigh most on arrival. The arrival weight is of particular importance in the females who not only lay the eggs, but are ashore for nearly five weeks after their arrival. The minimum arrival weight of a hen is 4.2 kg, and better fat reserves may bring it up to 6.3 kg. The cocks go up to 7.0 kg. Hens lighter than 4.8 kg rarely lay, and most do not settle or stay ashore long. Those weighing 4.8 kg and over usually lay, but their incubation performance is related to age and previous 'experience' rather than to weight alone, above the 4.8 kg threshold. First breeders, whatever their age, are less successful than older birds, and 5 or 6 year olds compare unfavourably with those that defer the attempt to a later age.

Carrick (1967) considers that the breeding performance of a Royal penguin is a function of its social status, in which feeding status is the most important, for that is what determines the date and weight at which a bird comes ashore, which in turn determines how soon it acquires the experience and good nest site and mate that lead to success. The best nest sites are away from the periphery and thus safer from predators. There is, however, plenty of suitable ground for each colony to expand, and only their inability prevents peripheral nest site holders from laying.

Carrick (1967) explains the dynamics of the colonies in terms of food supply and feeding status. The latter determines which birds will first acquire the adequate fat reserves and attain the gonad development that enables them to come ashore early and secure an equally dominant breeding status. The long periods of starvation undergone by the breeding birds are explained in terms of the time and energy budget for these birds. By December when the chicks are being fed, and late January when they go to sea, plankton production is maximal, and competition presumably relaxes, for even the youngest and most subordinate birds are able to visit the colony.

It must be pointed out at this stage that Carrick's postulated explanation of the dynamics of the Royal penguin colony is based on very slender evidence. There is no evidence that there is a dominance hierarchy with regard to feeding, which is presumably what Carrick implies by his use of the term feeding status. Further, there is little evidence to suggest that the acquisition of fat reserves influences the onset of migration, or affects the gonad cycle, two factors which affect breeding success.

There is no evidence to suggest that the frequency and duration of visits by breeding birds is necessarily governed by the abundance of the food, as there is only a correlation between the time spent at sea and the abundance of zooplankton shown by Foxton (1956).

V. Aims of the study.

The breeding season of the Royal penguin shows a great deal of regularity in timing from season to season, and the activities during the season are highly synchronised.

There is a marked delay in the onset of sexual maturity, a cohort increasing its status (definition in Chapter 2) and hence its breeding potential with age. Within a cohort there is a considerable variation in the status achieved by individual birds.

The basic problem in this study was to find out what influences the degree of status a bird achieves in a particular breeding season, and hence its breeding potential. In more precise terms, it was hoped to find what factors influence a bird's ability to secure both a territory and a mate, and having achieved both, a permanent nest site and mate, and also what factors determine whether a pair can breed, or lay an egg.

The two most important factors were thought to be individual variation in the behaviour and the degree of gonad development.

In 1966 it was planned to study the behaviour of groups of known age birds of both sexes. In 1967 those birds studied in 1966 which returned were to be observed again. In addition the behaviour of a group of mature breeding birds was to be observed. The gonad cycle of breeding birds was to be studied and the condition of the gonads of birds of known age on their arrival at the rookery.

From this work it was hoped to show:

1) That certain displays were of functional significance in obtaining a nest site and a mate, as well as being of importance in successful breeding.

2) By comparison of both groups and individuals studied in both years, that these displays changed (in frequency, intensity, etc.) with age, and that these changes could be correlated with changes in status.

3) The gonad cycle of breeding birds, and that the state of development of the gonads increased with age.

4) The relative importance of gonad development in breeding success by a comparison of the gonads of known age birds with breeding birds, and the actual breeding success of known age birds.

5) The relative importance of both behaviour and reproductive development on the status and breeding potential.

6) Attempt to use these data to explain the dynamics of the Royal penguin during the breeding season.

CHAPTER 2 - METHODS

I. Introduction.

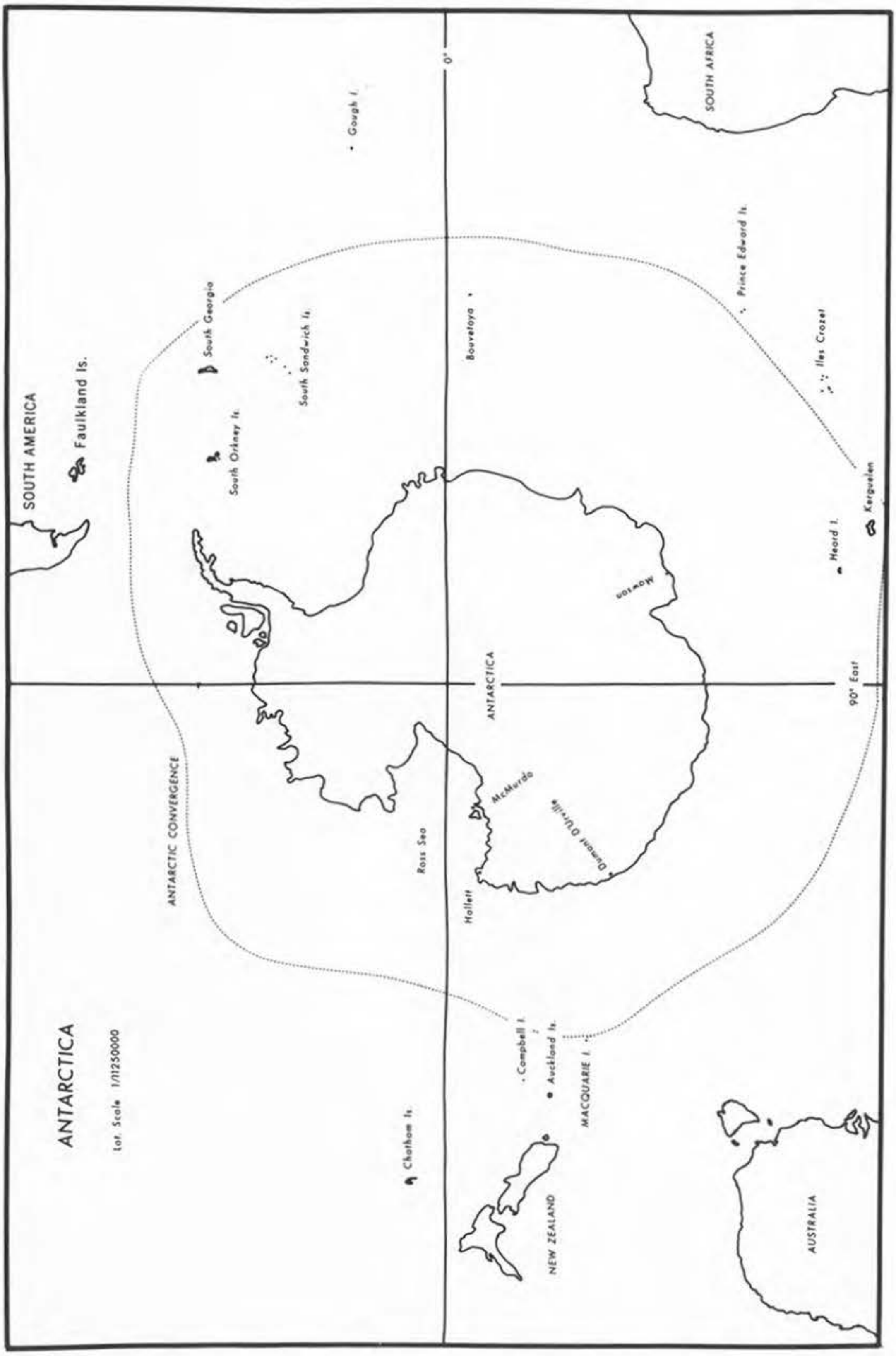
This investigation was carried out at the Bauer Bay rookery (see Map 2), which is also the rookery Carrick is using. The rookery has two colonies - the Sand Colony, which is about 150 yards inland, and the Inland Colony, which is about 50 yards to the north-east of the Sand Colony (see Plate 2).

The Royal penguins from the rookery came ashore near the mouth of the creek, and walked to the Sand Colony via a gap in the sand dunes on the seaward side of the rookery. Royals going to the Inland Colony walked around the north side of the Sand Colony, and then down a well worn track to the Inland Colony.

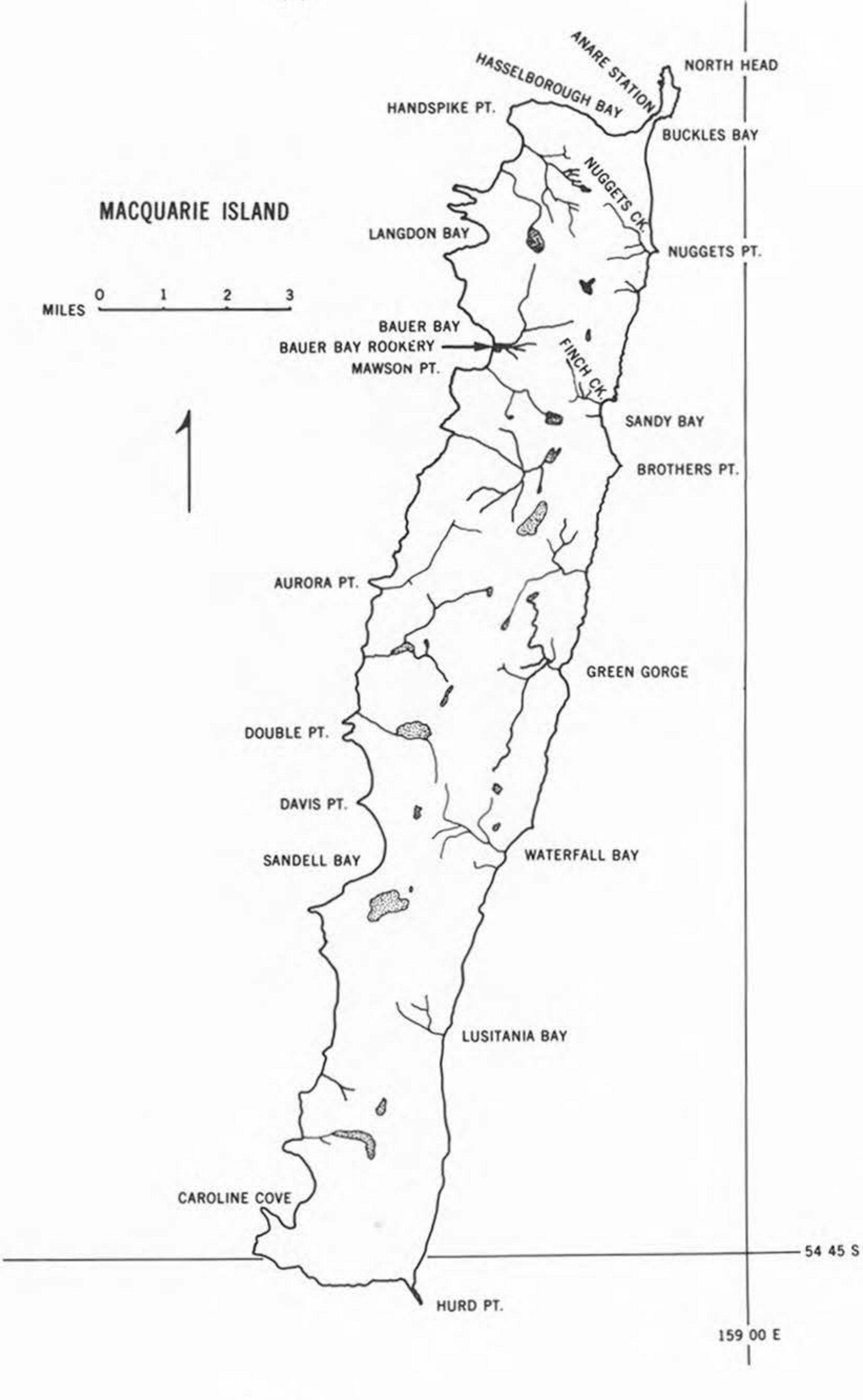
In both years, the Sand Colony had a grid of numbered, yellow stakes dividing it into squares (36 sq. ft.), and a blue stake in the centre of each square (see Plate 2a). The position of a bird was given as a quadrant of a given square. The Inland Colony had an irregular grid of marked stakes, and the position of a bird was given as a distance and direction from a particular stake, (e.g. 2 ft. N.E. of Q) (see Plate 2b).

In 1966 a trapping system was built in the gap between the rookery and the beach, but the trap was out of sight of the Sand Colony and the landing beach. Long fences guided the inward and outward going birds into the traps, and gates were placed in the fences so that the birds could move through the trapping area without actually entering the traps. The movement of the Royals was not affected by this trapping system, as they usually moved in groups. The trapping operator waited until a group of birds had entered the trap before processing them, which was normally done before the next group arrived.

The effect of trapping on the behaviour of the birds was unknown, but it appeared to be slight at the start of the breeding season. The birds which had already been trapped


ANTARCTICA
Lat. Scale 1/11250000
SOUTH AMERICA
Faulkland Is.
South Georgia
South Orkney Is.
South Sandwich Is.
Gough I.
0°
SOUTH AFRICA
Bouvetoya
Prince Edward Is.
Iles Crozet
Heard I.
Kerguelen
Mawson
ANTARCTICA
90° East
McMurdo
Dumont D'Urville
Hallett
Ross Sea
ANTARCTIC CONVERGENCE
Chatham Is.
Campbell I.
Auckland Is.
MACQUARIE I.
NEW ZEALAND
AUSTRALIA

MAP 1


MACQUARIE ISLAND
MILES
0
1
2
3
ANARE STATION
HASSELBOROUGH BAY
NORTH HEAD
HANDSPIKE PT.
BUCKLES BAY
NUGGETS CK.
LANGDON BAY
NUGGETS PT.
BAUER BAY
BAUER BAY ROOKERY
MAWSON PT.
FINCH CK.
SANDY BAY
BROTHERS PT.
AURORA PT.
GREEN GORGE
DOUBLE PT.
DAVIS PT.
SANDELL BAY
WATERFALL BAY
LUSITANIA BAY
CAROLINE COVE
54 45 S
HURD PT.
159 00 E

MAP 2

once, showed great hesitancy when approaching the trapping area for a second time, and some by-passed the traps altogether, when going into the colony. This behaviour was only seen in breeding birds who were feeding chicks.

Using Carrick's data, it was assumed that all unbanded birds in 1966 were older than eleven years, and experienced breeders. The oldest and most experienced birds arrived at the rookery earliest in the season. For convenience, I have used the symbol UK to denote unbanded birds. The symbol KA was used to denote banded, known age birds, which does not imply that the birds were non-breeders. When the term KA breeding birds was used, it was used to mean breeding birds older than six years old, unless otherwise stated, although Carrick has shown a small percentage of five and six year old birds may breed. Non-breeding birds were those birds younger than seven years old, with the above reservations.

The following definitions were used:-

Rookery and Colony. In line with Penny's 1968 definition, the terms Sand or Inland Colonies were used, but the Bauer Bay rookery.

Mate. A bird was said to have a mate if it was observed standing alongside another bird throughout a period of observation, that is, if it was paired. The term could only be applied loosely, because the strength of the pair bond between two birds couldn't be judged until they had been observed over a long period of time, that is, for one or more breeding seasons in the case of old, experienced breeding birds. In KA birds, the pair bond could be so weak that the pair would only stay together for a few hours.

Territory. Penny (1968) defined territory as "any space that an Adelie defends, for which it shows distinct affinity and within which the breeding birds nest". This definition could be applied to the Royal penguin. However, the term was broadened to include any site a Royal occupied during a period of observation. The strength of a bird's affinity, or ability, to defend a site or territory in the colony could only be shown during a series of observations.

Breeding Status. A bird was said to have breeding status if it had a stable territory and mate for the duration of the breeding season.

II. Reproduction.

During the 1967 breeding season (September to December), 103 males, and 98 females, were collected (see Appendix I for details). These birds fell into two classes.

A. Breeding birds.

On September 30, 1967, approximately 100 UK males, weighing between 5500 and 6000 grams were marked on the chest with a black, enamel paint spot. On October 5, approximately 70 UK females, weighing over 5000 grams, were marked with a yellow paint spot on the chest. Successive samples of five birds each were collected from both groups during the season.

B. Non-breeding birds.

Only small samples of known age birds were collected, as these were important in Carrick's continuing, long term studies. Samples of one to six year old birds were collected on their arrival at the colony, and samples of four to six year old birds were collected on their departure. Collection on arrival gave the reproductive state of the bird at that time, and it was hoped that collection on departure would give some indication of what changes had taken place during the time the birds were ashore. This was considered the best method of sampling, considering the limitations on the sample size.

C. Techniques.

The gonads were taken from all birds, and were immediately fixed in Schaudinn's solution for two days, and then stored in 80% alcohol. Schaudinn's solution was used because the formalin had polymerised, and could not be reconstituted. On returning to Australia, the gonads were blotted dry, and weighed to the nearest 0.1 gm. The length of the testes was measured to the nearest 1.0 mm., but the width was not taken, as all testes were cut longitudinally prior to fixation. The diameter of the six largest follicles was measured to the nearest 0.1 centimeter, and the median diameter was used in atretic and ovulated follicles.

Histological sections were prepared for all testes. Small sections, approximately 2 mm. thick, from the left testis, were placed in a 1% iodine solution for several hours, to remove mercury precipitates. These sections were then transferred to water for several hours, and then placed in a 5% gelatin solution for 24 hours, before being blocked in gelatin. Sections, 10 μ thick, were cut with a freezing microtome. Different sections were stained with haematoxylin and Sudan IV in propylene glycol. From the haemotoxylin sections, the diameter (μ), amount of debris, and stage of spermatogenesis was scored for 20 tubules in each testis. Spermatogenesis was scored according to the following scheme:- Stage I - mainly spermatogonia; Stage 2 - primary spermatocytes with some secondary spermatocytes; Stage 3 - mainly secondary spermatocytes; Stage 4 - mainly spermatids; Stage 5 - a few spermatozoa; Stage 6 - abundant spermatozoa; Stage 7 - spermatozoa in the lumen. This scheme is similar to that of Braithwaite and Frith (1969). The amount of debris was scored as zero (-), low (+), moderate (++), and high (+++).

The relative amount and distribution of tissues stained with Sudan IV was obtained by using a Swift automatic point counter. The theoretical basis for the use of this instrument in obtaining the percentages of different components in a a section, was given by Chayes (1956).

III. Behaviour.

A. Selection of study birds.

To illustrate any changes in behaviour with age, large samples of birds of different ages, and of both sexes, are required. The maximum number of birds that could be observed in a day was about 35. Using these figures, and the arrival times of the different groups, a minimum sample of 12 birds per group was aimed for.

In the 1966 breeding season, groups of two to six year old birds, and groups of older, known age breeding birds of both sexes, were observed. To select the latter group, a list was made of all known age birds, more than six years old, which had laid, or whose mates had laid. From this list, the first 12 males, and first 11 females to arrive at the colony, were selected. By collecting the other known age birds, it was hoped to obtain a random sample with regard to the dates of arrival of a group. This attempt was only partly successful, as the sample size of the six year old birds was reduced, as they arrived shortly after the older, known age birds, and a larger sample could not be handled.

All birds were caught in the trapping area, and individually marked with yellow enamel paint on their backs. Yellow was found to give the best contrast on the blue-grey feathers, and although fading, was still plainly visible on most birds after three months. Evidence from a study of the Gentoo penguin indicated that enamel paint will last for at least eight months (pers. obs.)

In 1967, all the 1966 study birds who returned were once again observed. In addition, a sample of unknown age breeding birds was obtained. These birds arrived on September 24, and weighed between 5500 and 6000 grams, and it was assumed that they were older, experienced breeding birds. The mates of these birds were used as the female sample, but they were not marked in order to avoid disturbing the colony. This sample was obtained for comparison with the younger, known age breeding birds.

Two 6-year old males, and one 5-year old male, were also collected, along with twenty one 1-year old birds. Individual groups were called the UK group (unknown age, breeding birds), the 6+ year old group (known age birds, older than six years), and the 6 year old group (six year old birds), etc.

The details of the dates of arrival, sex, and age, are given in Appendix 2. Appendix 3 gives the number of birds, and the median and range of the arrival and departure dates for each group of both sexes. The number of birds returning in each group, those returning later in the season, and the median and range of the dates of their return, is also shown.

B. Methods of observation.

Like other colonial penguins, the Royal penguin could be observed from close range without being unduly disturbed, provided the observer moved slowly and quietly. In this study, observations were made from vantage points in the tussocks surrounding the colonies. In most cases, the colony could be approached through the tussocks, and the observer could remain at least partly hidden. While an observer appeared not to disturb the bulk of the birds in the colony, those birds on the periphery, and within a few feet of the observation point, would show slight signs of agitation, that is, would look around, and occasionally elongate their heads in the observer's direction.

Each bird was observed for 15 minutes a day. However, a number of factors (weather, other work, the need to return to base, etc.) sometimes prevented daily observations from being made. It was considered that a continuous fifteen minute observation would give a reasonable sample of a bird's behaviour in a day. All observations were made between 0800 and 1600 hours. In the early stages of the season, this was approximately two hours after sunrise, and two hours before sunset. To overcome the effects of diurnal variation, the time of observation for each bird in 1966 was randomised as far as possible. In 1967, all birds were observed at the same time of day.

In addition to these regular observations, general observations were made to describe all displays and unusual sequences of behaviour.

C. Seasonal changes in activity.

In 1967, daily observations were made on the frequency of Flagging and Copulation in the Sand Colony, to obtain a measure of the seasonal changes in activity.

Flagging is the most conspicuous, and one of the most frequent, displays, and was therefore the most easily counted. The total number of Flagging bouts in the Sand Colony was counted for five minutes at 1000, 1200, and 1400 hours. In order to even out the Flagging as a result of birds arriving in the colony, the figures obtained were averaged.

The number of copulations seen during the regular daily observations was recorded each day in 1967. As these observations were made from fixed sites at the same time each day, it was thought that this count would give a reasonable picture of the changes in frequency of copulation during the breeding season.

D. Methods of recording.

All regular observations were made on a tape recorder. All displays were given as symbols, which facilitated accurate descriptions, especially in rapid sequences. Cine film was also used to record certain aspects of the behaviour.

IV. General

In 1966, daily counts were made of the total population in the Sand Colony, and irregular counts of the number of females were made for the first three weeks of the breeding season. In 1967, daily counts were made of the total population for the first two weeks, and after that, at intervals of one to five days. The number of females was counted for the first two weeks. The number of birds incubating alone was counted until all the chicks were in creches, and irregular counts were then made of the number of chicks. The position, and presence or absence of a mate, was recorded for all study birds during their stay ashore, between 0700 and 0800 hours.

Carrick, in 1967, marked numbers of UK birds of both sexes with paint marks, which showed whether the birds were heavy or light in weight on their arrival. He assumed that all these birds would be experienced breeders, and he hoped to show whether weight on arrival influenced breeding success. In the 1967 season, I used these birds to demonstrate the presence of failed breeding birds during the late incubation and guard periods, and also to make observations on the behaviour of these birds.

CHAPTER 3 - GENERAL BIOLOGY

I. Introduction.

In this chapter a brief description is given of Macquarie Island, including its avifauna, and the topographical localities of the Royal penguin colonies.

In Chapter I a brief outline was given of the biology of the Royal penguin. The purpose of this chapter is to provide a more detailed account of the dynamics of the Royal penguin colonies at Bauer Bay during the study period. The breeding season was considered to be that period between the arrival of the first males, and the complete formation of the creches.

This account of the sequence of events taking place during the breeding season is based mainly on the Sand Colony in 1967, but some of the data from both colonies and seasons were grouped. The errors introduced by grouping data were not considered important, as the main aim was to give a general account of the breeding season in order to provide a background for the later work. An estimate of the temporal differences in events between colonies and seasons may be made by comparing the populations at different times during the season. It was possible to do this because the populations in both colonies were approximately the same, and should remain approximately the same at any given time. Comparison of the population figures indicated that in both seasons the Inland Colony was one to two days behind the Sand Colony, and that the 1967 season was one to two days ahead of the 1966 season. The longest time difference was three to four days between the Sand Colony in 1967 and the Inland Colony in 1966.

The work of Sladen (1958), Penny (1968), and others, has shown that the annual cycle of the Adelie penguin was highly synchronised, and was essentially the same as that of the Royal penguin. Because the seasonal activities of the Adelie were so synchronous, Sladen (1958) was able to divide the annual cycle into six fairly distinct periods (i.e. Occupation; Incubation; Guard and Reoccupation; Creche; Dispersal and Departure). Although there was a small overlap between these periods, each one described the major activities taking place during that period.

Observations on the Royal penguin showed that the breeding season could similarly be divided into fairly well defined periods. These periods were called the Occupation, Laying, Incubation, Guard and Creche Periods.

The time span of the five periods for the 1967 season is as follows:

Occupation Period: September 19 to October 12
Laying Period: October 13 to October 30
Incubation Period: October 31 to November 19
Guard Period: November 20 to December 13
Creche Period: December 14 to January 31

The data used in defining these periods are given below.

II. Results

A. Macquarie Island.

Macquarie Island is situated on Lat. 54.45°S, Long. 159°E. It is approximately 400 nautical miles south-west of the New Zealand sub-Antarctic islands. Auckland and Campbell Islands, 400 miles to the north-east are the nearest islands (Map I).

1. Geography.- The island is 21 miles long, with its main axis running 15° east of north. The maximum breadth is three miles, and the area is 46 square miles. Geologically, Macquarie Island is probably a horst block which has been subjected to extensive marine erosion (Mawson, 1943). The result is a long, narrow plateau bounded on all sides by a

steep escarpment. From the foot of the escarpment a narrow coastal terrace extends to the sea. The coastal plain is most clearly defined on the northern half of the east coast, where it has been uplifted approximately 40 feet above sea level to form a well defined terrace which may be up to 400 yards wide. In other areas the coastal plain is narrow, and in a few places the escarpment falls directly to the sea.

The level of the plateau rises slightly from the northern end where the general level is about 800 feet, with peaks up to 1200 feet, to the southern end, with a general level of 1000 feet and peaks up to 1400 feet. The surface of the plateau exhibits the typical features of a well glaciated topography, and is dotted with lakes, the largest of which is 113 acres (Map 2).

2. Meteorology.- Law and Burstall (1956) have summarised the meteorology of Macquarie Island. The climate could be described as wet, cloudy, windy and cold. Rain, snow and hail are frequent, but generally light, and give an annual precipitation of 40 inches, occurring on about 310 days. Fogs and misty conditions occur frequently in all seasons. Completely cloudless skies are uncommon, and the average daily sunshine is approximately two hours.

The warmest month is January, and the coldest is June. The mean daily maxima for January and June are 46.7°F and 40.0°F respectively. The mean daily minima for these months are 34.1°C and 41.1°C. The annual range of the mean monthly temperatures is 6.8°C. The daily and seasonal temperature ranges are small, and show little variation from year to year.

The mean relative humidity is 88%, with approximately half the observations greater than 90%.

Macquarie Island lies in the zone of the westerly depressions. Sixty seven percent of all winds were from the sector 255° to 345°. The average wind speed was 20 knots.

3. Vegetation.- There is only a small number of plant species - 38 vascular plants and 41 Bryophytes. There are no trees or shrubs, and only one woody species. There are five vegetation formations; the tundra, or feldmark, is found mainly on the plateau in regions exposed to light wind velocity. The other four formations, fen, bog, sub-glacial herb field, and grassland, are confined to the coastal plain.

The dominant formation is the grassland, which is formed of wet tussock grass up to four feet high. The dominant tussock grass is <u>Poa foliosa</u>. The other dominants in this formation include <u>Stilbocarpa polaris</u> (Macquarie Island Cabbage), and <u>Poa hamiltoni</u>, which is confined to the vicinity of the penguin rookeries. This formation is the most conspicuous, and grows in the most favourable sites on the island. It covers all the steep plateau slopes, and the lower elevations, and extends up to 1200 feet in sheltered sites (Taylor, 1955).

4. Avifauna. - The southern ocean may be divided into two zones by temperature and salinity characteristics - the Antarctic and sub-Antarctic zones. The sub-Antarctic zone, in which Macquarie Island is situated, is sharply bounded in the south by the Antarctic convergence, and, in the north, by the less sharply defined sub-Tropical convergence.

The sub-Antarctic is a zone of cold water, rich in nutrient salts and plankton. The land masses are small and widely separated.

Ecologically, the boundaries of the zone are fairly distinct, especially the Antarctic convergence, and although the avifauna is fairly uniform within the zone, there are distinct changes across the boundaries (Murphy, 1936; Serventy, 1960).

The avifauna is dominantly marine, with a dipauperate land-bird fauna. The number of species of marine birds is small, but the abundance of food, and the limited number of terrestrial nesting sites, gives rise to large, high density populations, especially during the breeding season.

There were seventeen indigenous marine birds breeding on Macquarie Island. The two indigenous land birds are now extinct. Four introduced land birds are now breeding on the island, and a total of 31 birds from both north and south of Macquarie Island have been recorded as casual visitors (Law and Burstall, 1956; Keith and Hines, 1958).

There were four species of penguins: the King, Gentoo, Rockhopper and Royal.

King penguin (Aptenodytes patagonica). There was one large colony of 10,000 breeding birds at Lusitania Bay. The colony is situated on a raised boulder beach close to the shore. No detailed work has been done on this colony, but observations showed that the yearly cycle was similar to that described by Stonehouse (1960), for King penguins at South Georgia.

Gentoo penguin (Pygoscelis papua). The Gentoo is sedentary, and forms small colonies of 50 to 700 breeding birds throughout the island. The colonies are usually situated on dry, grassy areas of coastal plain, although a few were situated up to 400 feet up the escarpment. The sites of the colonies change every year. The breeding population is approximately 12,000 birds. No detailed work has been done on the biology of this penguin.

Rockhopper penguin (Eudyptes crestatus). The colonies were small and numerous, and were usually situated in rocky areas close to the sea. Occasionally, colonies could extend up into the tussocks above the coast. The biology has been studied by Warham (1963).

Royal penguin (Eudyptes chrysolophus schlegeli). The Royal penguin is endemic to Macquarie Island. It is a medium sized penguin, being about 18 inches tall. The golden superciliary plumes extend to the midline on the forehead, and the colour of the face varies from white to black (Macaroni condition), with intermediate forms being the most common.

The Royal penguin is migratory, spending the winter at sea, and returning in late September to breed in densely packed colonies.

1. The Colonies.- The 36 colonies (Carrick, 1964) may be divided into five types, based on their location.

(a) Talus cones associated with stream outlets from the plateau. There were 14 colonies situated on the talus cones, spreading from the beach to the neck of the cone(Pl. 3a).

(b) Tussock flats adjacent to the beach. There were eight colonies of this type, including the largest colony at Hurd Point (Pl. 3b)

(c) Tussock areas in valleys inland from the beaches. There were six colonies of this type, five being closely associated in one area.

(d) Boulder coast. These colonies were small, and normally associated with Rockhopper penguin colonies.

(e) Upland. There were two upland colonies; one at Caroline Cove, which was on an uplifted area some 600 feet above sea level, and the other about 800 yards inland, and about 400 feet above sea level at the head of Finch Creek. All these colonies, with the exception of the Sand Colony at Bauer Bay (see later), were on stony ground, poorly drained, and adjacent to a stream.

The two study colonies (Sand and Inland) were situated at Bauer Bay, approximately five miles south west of the main base (see Map 2).

The Sand Colony was situated on an eroded sand dune, sloping to the west. This was the only colony with a sandy substrate (Pl. 2a). The Inland Colony was approximately 40 yards to the north of the Sand Colony. It was on a raised boulder beach surrounded by large tussocks (Pl. 2b).

III. The breeding season.

A. Occupation period.

The occupation period began with the arrival of the first males in late September. It was characterised by a rapid growth in the population, and the formation of pairs. The end of the period was marked by a fairly sudden decrease in the number of birds arriving at the colony, and the laying of the first egg on October 12.

The first males arrived at Bauer Bay on September 19, 1967 (September 21 in 1966), but during the first week only 29 males had arrived at the Sand Colony. However, after September 24, the number of males arriving at the colony increased rapidly.

It was noticed that in both seasons two groups of males formed in the Sand Colony. The first arrivals formed a group on the east side of the colony, and about a week later, another group formed on the west side. The colony grew by the expansion and filling in of these two groups. In the Inland Colony the males were evenly distributed, and there was no apparent reason why the early arriving males should prefer to congregate in these two areas.

The first female arrived on September 27, 1967 (October 1, 1966), but the rapid increase in the number of female arrivals did not begin until October 3. By this date approximately 80% of the breeding males were ashore (Fig. 1). The number of males continued to increase until October 6, when approximately 95% of the breeding males were ashore. This rapid growth of the total population continued until October 12, when nearly all the breeding birds were ashore. By the end of this period only a few birds were not paired.

The increase in the number of study birds was not as pronounced, owing to the predominance of known age birds (Fig. 2). More than half the study birds older than five years arrived during this period.

B. Laying period.

The Laying period extended from October 13 to October 30. To obtain these dates, the frequency distribution of the dates of the laying of the first eggs by the 46 study birds, was calculated (Fig. 2). Only one first egg (that of a six year old female, whose mate was five years old) was laid outside this period.

The slight increase in the total population between October 13 and 21 (Fig. 1) was due to the arrival of the non-breeding, known age birds (Fig. 2). After October 21 there was a slight decrease, because of the first departures of the breeding males. From October 25 to 30, 560 birds (56%) left the colony (Fig. 1). The bulk of these birds were breeding males (note the corresponding rapid increase in incubating birds (Fig. 1)).

More than half of the study birds older than three years arrived before the end of this period, and more than half the birds older than four years arrived before October 22 (peak of egg laying, Carrick, 1964). These dates compare well with Carrick's (1969) data.

Of the 66 males that arrived before the end of this period, 56 also left before the end of the period, 34 in the main out flow. Of these 34 birds, only 13 had mates who had laid, which indicates that there is a tendency for the non-breeding males to depart at approximately the same time as the breeding males. The same tendency was also seen in the non-breeding females. By the end of the laying period, the majority of birds in the colony were incubating females, with a few, known age birds (male and female), on the periphery of the colony (Fig. 1).

At this point, it is convenient to consider the temporal relationships between the arrival of the 12 UK study males (1967), the arrival of their mates, the laying of eggs, etc. These males were selected because they arrived earliest, although one bird did not breed, owing to its failure to get a mate. The dates and intervals used are median figures.

All the males arrived on September 24, and their mates arrived on October 6 (12 days interval), and laid their first eggs on October 17 (11 days interval). The males departed on October 26, 9 days after the laying of the first egg (Fig. 2). The departure of nearly all the breeding males during a five day period emphasises the close synchrony in the timing of events in the breeding season.

Carrick (1964) gave the peak of egg laying at the Bauer Bay rookery between October 20 and October 22. However the peak in these study birds was between October 17 and October 19. The cause of this was the disproportionate influence of the UK birds, whose median first egg date was October 17. The interval between a female's arrival, and the laying of the first egg decreased, as the date of arrival became later. This was most noticeable in the mates of the UK males. The significance of this will be discussed in the next chapter.

Towards the end of the laying period, a number of mobile, unknown age females was seen. The cause of their failure to breed was not known. Of the 24 female study birds that laid eggs, 5 deserted their nests between October 27 and October 31, but the reason for their failure was not established.

C. Incubation period.

This period extended from October 31 to November 19. During this period, the population was mostly incubating females, and later, incubating males (Fig. 1). The date of the hatching of the first chick on November 19, 1967, indicated the end of this period.

The drop in population between November 8 and 13 was a result of the failure of the incubating females to continue hatching their eggs (Fig.1). Eighteen of the twenty five study females, who had laid, failed in this way during the period. Observations of Carrick's marked, breeding birds showed that the increase in the total population seen towards the end of this period, was due mainly to the return of failed breeding males, and some females (qualitative observations only). Appendix 3 also shows that non-breeding, known age study birds started to return during this period (note also the levelling out in Fig. 2)

All study birds older than three years had arrived by the end of this period, and the first of the two year olds had also started to arrive towards the end of the period.

On November 8 the first breeding male arrived back in the colony to resume incubating, and by November 16, 50% of the males had returned. The first of the UK study birds arrived on November 10, and by November 17 half of them had returned. Those breeding males whose females had failed to continue incubation, remained at their nest sites.

D. Guard period.

The Guard period extended from the date of the hatching of the first chick, to the start of the departure of the guarding males (November 20 to December 13). The majority of the non-guarding birds were failed breeders (observation of Carrick's marked breeding birds). The date of the first hatching was calculated from the time the first chick calls were heard. The total population during this period continued to increase until November 28, and remained approximately at this level until December 8, when it began to decrease. During this period all the two year old birds had arrived and departed, and the majority of the known age study birds, who returned to the colonies, had arrived (Appendix 3).

The number of guarding birds continued to fall towards the end of this period (Fig. 1), while the number of chicks increased rapidly from November 24. By the end of November all the chicks were hatched.

The females returned about hatching time, and fed the chicks with their first food. The mates of the UK males returned between November 21 and November 30 (median date November 26). This corresponded to a range of 36-43 days after the laying of the first egg. The median interval was 40 days, which was only one day longer than the period given by Carrick (1964) for the interval between the laying of the first egg and hatching (incubation period was 35 days, and the interval between the first and second egg, 4 days). Those females who had previously failed, or whose mates had failed (i.e. had deserted their nests), remained with their mates. Using the UK sample of both males and females, Figure 2 shows the mean length of the periods ashore, at sea after egg laying, and before the departure of the males. The date of hatching was taken as 39 days after the laying of the first egg, although the actual day of hatching was not observed in order to avoid disturbing the birds. Figure 2 shows that the females stayed an average of two days after their arrival at hatching time, but their following visits are only indicated approximately because observations were made only once a day.

E. Creche period.

This period started when the first males deserted their chicks (Fig. 1). All guarding males had departed by December 21, leaving 175 chicks. The UK males departed between December 7 and December 17 (median date December 13). The deserted chicks formed small groups(Plate 7d). By December 21 there were two groups of approximately 60 chicks, and a number of smaller groups, in which the numbers ranged from five to fifteen chicks. Some chicks were on their own, and in general, the creches were not compact.

Between December 13 and December 21, 380 birds left the Sand Colony. Only 160 of these birds were guarding males, and the rest were failed breeding birds, and the non-breeding birds.

By December 21 the colony consisted of 175 chicks in creches, some breeding birds feeding their chicks, and 200 older birds, made up mostly of one and two year old birds, with a few failed and non-breeding birds.

From about the middle of the incubation period to the end of the observations in mid-December, there were a number of birds on a rocky outcrop adjacent to the landing beach. There was a considerable variation in the numbers of birds observed there from day to day, ranging from 20 to 70 birds. The birds were of all age groups, and from observation of the study birds, it appeared that some birds returning later in the season, spent some time (one to two days) on the rocks, after leaving the colony, and before going to sea. Some birds returning from sea landed on the rock, but from the data of the study birds, none stayed there any length of time before moving up into the colony.

IV. Discussion.

The results obtained, confirmed Carrick's (1964, 1967) statement that the breeding season is highly synchronised. This was illustrated by the rapid fall in population when the males return to sea. Carrick's statement on the relationship between age and date of arrival was also confirmed. Appendix 3 shows that the median date of arrival became earlier as age increased, but there was a considerable overlap between the age groups. With the exception of the two year old birds, all males in all age groups began to arrive before the females, and this also applied for the median date of arrival. There was only a small difference between the median dates of arrival of age groups younger than six years.

In general, the pattern of activities of the eleven pairs of UK birds, agreed with those described by Carrick for breeding males and females. However, there were some differences in the actual periods spent incubating by both males and females. Carrick stated that both males and females incubated for about 19 days, and that the males might stay with the females until the 10th day of incubation. If one supposed that the average period the males stayed with the females is 5 days, then it would follow that the males spent about 14 days at sea before returning to take over the incubation. My own results showed that the UK males stayed 5 days after the laying of the second egg, that the females incubated for 26 days before being relieved by their mates who had spent 21 days at sea, and that the males incubated for a further 9 days before hatching (calculated from the date of the first egg). The females arrived back about this calculated hatching time. The main difference between Carrick's and my findings, was the greater time spent at sea, and the resulting shorter time spent incubating before hatching. This difference might be a result of the fact that my birds were among the first to arrive in the colony at the beginning of the season, and consequently could have lost a greater percentage of weight than the birds arriving later in the season. This would mean they would require a longer period at sea to build up their fat reserves. The birds on which Carrick obtained his data would almost certainly have arrived later in the season, and would not have lost as much weight before they left for sea.

Carrick also stated that the females arrived about one week before hatching. My own data do not agree with this, as the earliest arriving female appeared 36 days after laying the first egg, and the median interval was 40 days.

The work of Downes et al (1959) on the Macaroni penguin (E. e. chrysolophus) on Heard Island, and that of Warham (1963) on the Rockhopper penguin (E. crestatus) on Macquarie Island, shows that the annual cycle of these two Eudyptes species is almost identical to that of the Royal penguin. The general pattern of activities of the breeding males and females was the same as that of the Royal penguin, and the period spent incubating by males and females is similar to Carrick's data.

Warham (1963) states that all female Rockhopper penguins had returned to their mates before hatching (usually about two days before), while Downes et al (1959) states that female Macaroni penguins usually return just before hatching, although some return just after hatching. The results of these workers, together with my own data, suggest that there may be more variation than Carrick implies, when he states that females return a week before hatching.

The annual cycle of the Adelie penguin (Pygoscelis adeliae) has been studied by a number of workers (Sladen, 1958; Sapin-Jaloustre, 1960; Taylor, 1962; Stonehouse, 1963; Penney, 1968). They found that the breeding is short and synchronised, and that the pattern of activities of breeding was similar to that found in the Royal. The changes in population were the same, and these workers also found that the second peak in the population during the guard stage was a result of the return of the failed and non-breeding birds.

The pattern of activities of the breeding birds, while similar to those of the Royal, showed a number of differences. In the Adelie penguin, both males and females returned to the colony at the start of the breeding season at approximately the same time. The females usually left within a day of the laying of the second egg, and the males then incubated for about two weeks before being relieved by the females, who then incubated for a further two weeks. The males incubated for less than a week before hatching. Either the male or the female could be on the nest when hatching took place. After hatching, the frequency of the relief shifts increased, with the male and female taking turns to guard, and to collect food for the chick.

Sladen (1955) showed that the Chinstrap penguin (Pygoscelis antarctica) had a regular sequence of incubation periods. This pattern differed from that of the P. adeliae, and also from the Eudyptes spp. The pair stayed together for about five days after the laying of the second egg, and then either the male or the female would depart for sea. The bird that took the first incubation shift incubated for about 10 days, and then spent about 7 days at sea, and then a further shift of about 7 days on the nest. The other mate did two shifts of about one week, and the end of the second period was approximately at hatching time.

The Emperor penguin (Aptenodytes forsteri) (Stonehouse, 1953; Prevost, 1961) also has a well defined and synchronous breeding season, with a marked division of labour between the breeding males and females. After egg laying (single egg in May), the females departed, leaving the male to incubate the egg for about two months. The females returned at about hatching time, and the males departed for sea, where they spent two to three weeks, returning to help the female guard and feed the chick.

The King penguin (Aptenodytes patagonica) (Stonehouse, 1960) has an extended breeding season, which is not synchronised (see above). However, the breeding birds show a well defined division of labour, as both males and females take two periods of incubation before hatching, and after hatching, take turns in guarding and feeding the chick.

Thus, it has been found that the colonial penguins, with the exception of the King penguin, have evolved regular and highly synchronised breeding patterns, which, in general, are very similar in their sequence of events. All the species have evolved a well defined division of labour between the males and females which is very similar. The exception to this is the Emperor penguin, in which the male does all the incubating during the Antarctic winter.

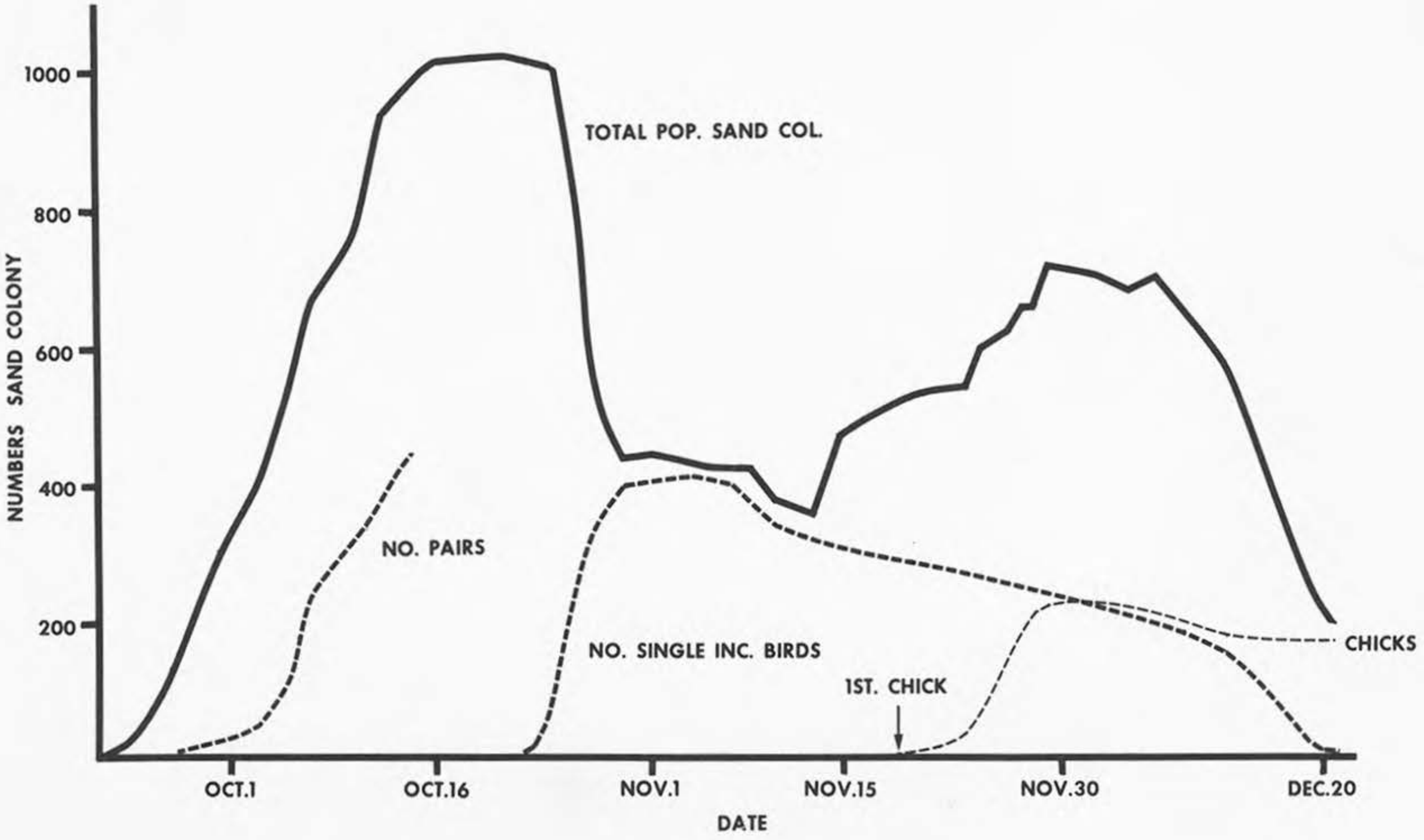
The similarity in breeding seasons is probably a result of the similarity in food resources. Foxton (1956) has shown that during the winter, the plankton production is at a very low level in the sub-Antarctic and Antarctic waters, but that the production increases rapidly to a maximum in December, and again in late January. The regular and synchronised breeding in these penguins, and the marked division of labour between the males and females, probably evolved to make the most efficient use of the available food resources (Carrick, 1967).

FIGURE 1

The changes in the total population of the Sand Colony in 1967, from the arrival of the first males until all the breeding males had departed on December 21. This figure also shows the number of pairs present from September 27 to October 14, and may be considered to show the arrival of the females during this period.

The rapid increase in the number of single incubating birds (female) shows the synchronised departure of the breeding males. After approximately October 10 this graph shows the number of incubating, and later guarding males.

The number of chicks present in the colony is also shown.



1000
800
600
400
200
NUMBERS SAND COLONY
TOTAL POP. SAND COL.
NO. PAIRS
NO. SINGLE INC. BIRDS
1ST. CHICK
CHICKS
OCT.1
OCT.16
NOV.1
NOV.15
NOV.30
DEC.20
DATE

FIGURE 2

This graph shows the changes in the number of study birds present in the rookery, and the distribution of the first eggs laid by the study birds (The data from both seasons are grouped).

The diagram illustrates the periods spent ashore by the 11 UK study males and their mates. The dates of the arrival of the males and females are median dates, as is the date of the laying of the first egg. The date of hatching was assumed to be 39 days after the laying of the first egg (see text).

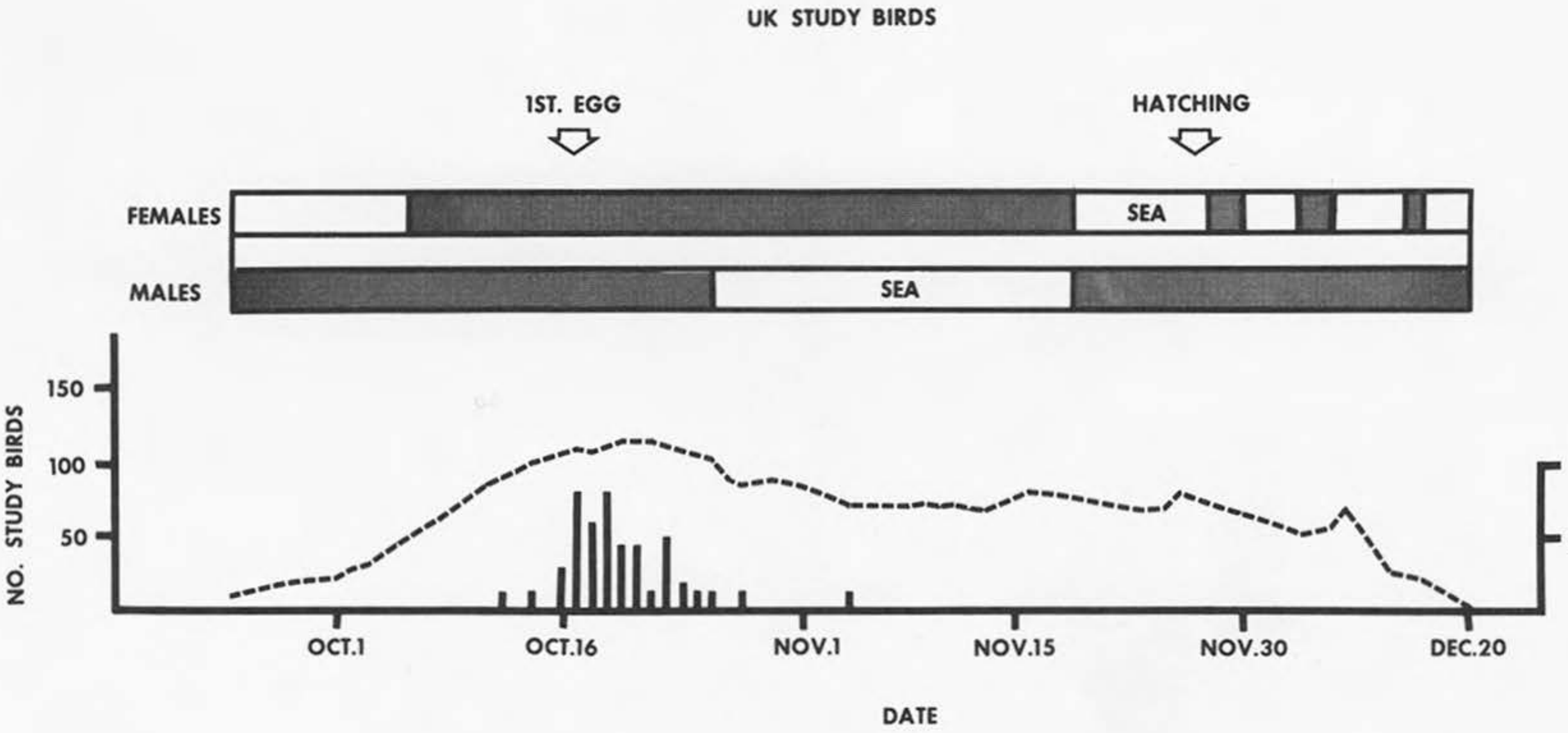

UK STUDY BIRDS
1ST. EGG
HATCHING
FEMALES
SEA
MALES
SEA
150
100
50
NO. STUDY BIRDS
5
NO. EGGS
OCT.1
OCT.16
NOV.1
NOV.15
NOV.30
DEC.20
DATE

PLATE 2

Plate 2a	The Sand Colony with its grid of numbered yellow stakes. The blue stakes are in the centre of the grid squares. The photograph was taken in late September before the arrival of the females. The area occupied by the males is approximately the extent of the breeding area in the colony. In the top left hand corner is the stream mouth where most of the Royal penguins come ashore.
Plate 2b	The Inland Colony with its irregular grid of stakes. The photograph was taken before the arrival of the females.

PLATE 3

Plate 3a	A typical Royal penguin colony situated on a talus cone and extending up into the stream valley.
Plate 3b	The Royal penguin rookery at Hurd Point. The photograph was taken at about 700 feet above the colony which is approximately 23 acres, and has about 500,000 breeding birds.

CHAPTER 4 - REPRODUCTION

I. Introduction

The migratory habits of the Royal penguin prevent the investigation of the full gonad cycle of the breeding birds. Only the degree of development on arrival, the changes taking place in the two or three weeks prior to egg laying, and the changes after egg laying, can be examined. Investigation of the cycle in non-breeding birds is similarly restricted.

The aims of this section of the study were:

Firstly, to determine the changes in the gonads from the time of arrival until the end of the guard stage.

Secondly, to determine the relationship between the gonad cycle of the breeding and non-breeding birds.

Thirdly, to attempt to obtain an estimate of the percentage of birds in each age group that were physiologically capable of breeding.

II. Results

A. Breeding females.

From the females marked on October 5, samples of five birds each were collected from birds on arrival at the colony, at the start of the laying period, early in the incubation period, and at the end of the guard period. (Data are given in Appendix 4).

The Royal penguin has a typical avian ovary. In breeding females, the ovary has a large number of follicles, a small number of which are distinctly larger than the rest. After ovulation, the follicle collapses, and the follicular epithelium increases in size to form a pale, yellow body, the corpus luteum (used only in a descriptive sense), which may be recognized up to two months after ovulation. After ovulation the other follicles become atretic. A follicle was considered atretic if the epithelium was shrivelled, and/or it had lost its spherical shape.

1. Ovary Weights.- The changes in the mean ovarian weight during the breeding season are shown in Fig. 3. The mean weight increases rapidly prior to ovulation, and decreases rapidly in the two weeks after ovulation. By December 8, only a small, further decrease was seen.

2. Follicles.- By assuming that the smaller corpora lutea was the largest of the follicles, and the larger corpus luteum was the second largest follicle, the changes in the mean size of the largest, the second largest follicle, etc., could be followed throughout the season. For convenience, the largest follicle was called the F1 follicle, the second largest the F2 follicle, etc. The results of this analysis are shown in Fig. 4. The pattern is the same as that for the ovarian weight.

The large follicles were greater than 1 cm in diameter, and the largest follicle seen before ovulation was 4.2 cm in diameter. The mean, and range, of follicles greater than 1 cm, 2 cm, 3 cm, and 4 cm for the samples taken on October 5 and October 13 are shown in Table I. Comparison of Fig. 4 and Table I shows that on arrival, females have two large follicles of approximately the same size, and a smaller F3 follicle. One bird had five large follicles.

On October 13, two of the females had the first egg in their lower oviducts. In Fig. 4, the upper line for F1 is for the three birds who had not ovulated, and the lower line is for all five birds. All birds had three very large follicles. Four of the females, including the two birds who had ovulated, had four large, pre-ovulatory follicles each. None of the follicles of the females who had ovulated were atretic.

On October 23 all females had ovulated twice, one having the second egg in the uterus. All follicles were atretic, and all except the F3 follicle had shrunk. The diameter of the F3 follicles ranged from 1.4 cm to 3.7 cm, the largest being from the female with the egg in the uterus. On November 3, the F3 follicles showed a large decrease in diameter, and the F1 and F2 follicles a slight decrease, while the F4 to F6 follicles showed no change. All follicles showed a further, slight decrease on December 8.

B. Non-breeding females of known age.

1. Ovary weights.- The mean ovarian weights, with standard deviation and range, are shown in Table 2. These are for birds in the age groups one to six years, on arrival, and of birds in groups four to six, on departure. The range and mean of the dates of arrival and departure of the collected birds is also given.

On October 11, two six year old birds had ovarian weights of 5.99 gm and 28.8 gm respectively, and on October 28, another two six year old birds had ovarian weights of 1.8 gm and 64.6 gm. The wide variation in ovarian weights in birds arriving on the same day was general, and no relationship was found between the date of arrival and the ovarian weight. There was a wide range of ovarian weights in each age group, but the mean weights increased with age.

There was no relationship between the date of departure and ovarian weight. The mean weight of the ovary was not significantly smaller than that on arrival.

2. Follicles. - No follicles were seen in the chicks or the one year old birds. In the two year old females, one had no follicles, the other two had only four small follicles. None of the three year old females had more than eight small follicles, and all females older than three years had a large number of small follicles. The mean number, and range, of the large follicles is shown in Table 1. The number of large follicles increased with age, and the mean number of large follicles in the six year old females was not different from that of the breeding females

on arrival. However, the range was larger, owing to one female having a small ovary (1.8 gm) with no large follicles.

After egg laying rapid re-absorption takes place in all the follicles in the breeding females. Evidence was found that re-absorption had started in five and six year old females before their arrival. The F1 follicle in two 6-year old females arriving on October 11 and October 14 respectively, were atretic. The diameter of these follicles was 3.0 cm and 3.3 cm respectively. All the follicles were atretic in two 5-year old females arriving on October 20 and October 21. None of these birds had ovulated.

In departing females evidence of re-absorption was only found in those birds with large follicles. One 6-year old females leaving on November 10 had ovulated twice, and was thought to be a successful breeder being relieved by her mate. Another six year old female~~s~~ leaving on October 24 had ovulated twice, and had the second egg in the lower oviduct. The reason for this bird's failure is not known. Two 5-year old females returning to the rookery on November 2 had atretic follicles, one having two corpora lutea, while the other had only one.

3. Comparison of breeding and non-breeding females.

If the ovary of a female on arrival is more developed than the least developed ovaries in the breeding females, then that bird could be said to be physiologically capable of breeding. If this assumption is valid the percentage of females in different age groups that are physiologically capable of breeding may be calculated. Comparison of the data for the breeding and non-breeding females show that 0% of the four year olds, 20% of the five year olds, and 59% of the six year old females are capable of breeding.

C. Males

1. Breeding males. - Samples of five males each were collected on arrival, before pairing, after pairing and before egg laying, after egg laying, during incubation, and during the guard period. All females collected with the males were birds marked on October 5.

The weight of the testes before egg laying was not significantly different, and in all males the left testis was heavier than the right. The weight of both testes became much smaller after the egg laying. Subsequent samples showed only a slight further decrease in weight (Fig. 5). The changes in the length of the testes were similar to those seen in the weight (data not given).

2. Non-breeding, known age males. - The mean weight of both testes increased with age, and the mean weight on departure was smaller than that on arrival (Table 3).

3. Histology of the testis. - The histological data are presented in Appendix 5. The calculations of the relative amounts of the different tissues stained with Sudan IV, is not accurate, owing to the method of fixation. They can only be used to indicate the presence of lipoidal matter, and to give a rough idea of the amount, and distribution. Absence of staining does not necessarily mean that there was no lipoidal material present before fixation.

(a) Breeding males. The data for the breeding males are given in Appendix 5 and summarised in Figure 6. The changes during the breeding season are illustrated in Plates 4 to 6. Before the females began to lay, the tubules were at their maximum diameter, and there was no significant difference in the mean diameters. The median stage of spermatogenesis increased from stage five to stage six after arrival. Only a small amount of interstitial tissue was stained with Sudan IV, and there was zero to low amounts of debris in the lumens. Between the laying of the eggs and the departure for sea, there was a profound change in the testes. The tubules showed a marked decrease in diameter, the lumens became packed with debris, and the median stage of spermatogenesis decreased to two. Massive steatogenesis was evident from the rapid increase in the relative amount of tubule tissue, and debris stained with Sudan IV. There was a slight increase in the relative amount of interstitial tissue stained with Sudan IV.

Subsequent samples (November 10 and December 8) showed that the diameter of the tubules had decreased slightly, and that the stage of spermatogenesis remained constant. The debris had cleared from the lumens, and the tubules were free of staining. The amount of interstitial tissue stained with Sudan IV had increased on November 10, but had decreased again by December 8.

(b) Non-breeding known age birds. The histological data for these birds are given in Appendix 5. In arriving males, the mean diameter of the tubules increases with age. There is an overlap in the ranges between birds two to six years old. The median stage of spermatogenesis increased with age, while the amount of debris, and the amount of Sudan IV staining in the tubules, decreased. In the departing four to six year old males, there was no difference in the mean, and range, of the tubule diameter, nor in the stage of spermatogenesis. The amount of debris was variable, while the amount of staining was greater in the six year old males.

(c) Comparison of breeding and non-breeding males. Th testis cycle is at its peak when the breeding males arrive at the colony, and it is maintained until about the time when the females lay. The testes then undergo regression. This is characterised by the shedding of the spermatids and

and spermatocytes into the lumen of the tubule, creating large amounts of debris, and the tubules collapsing and undergoing massive steatogenesis. Comparison of the mean testis weight for different age groups on the mean dates of arrival, shows that they fall approximately on the curve for the breeding males. Comparison of the histological data shows a similar relationship on a given date. This would suggest that all males go through a testis cycle at approximately the same time.

By comparing the data from the known age birds with that for the breeding birds, it is possible to obtain some idea of how far spermatogenesis has proceeded before the commencement of regression, whether there is a time difference in the cycles, and what percentage of birds in each age group have testes which have achieved full spermatogenesis. The latter may be compared with Carrick's (1969) data to see the effect of reproductive development on delayed maturity.

(i) Six year old males. Five males arriving in mid-October had testes similar to those seen in the breeding males at that time. The testis of a male arriving on October 28 had a maximum spermatogenic stage of 5, and regression may have just started. It is unlikely that a complete spermatogenic cycle would have been achieved. Four males leaving at the end of October had testes similar to those of the breeding males, and probably had a full spermatogenic cycle. A fifth bird showed no sign of regression, and as the maximum stage of spermatogenesis was four, it is unlikely that this bird would have completed the spermatogenic cycle before regression started. There is no apparent difference in the timing of the testis cycle between the six year old and breeding males. A maximum of 82% (9/11) of the six year old males may have achieved full spermatogenic activity.

(ii) Five year old males. Eight males were collected, on arrival, between October 5 and November 5, and four on departure in late October. The testes of three of the departing males were in regression, similar to that of the breeding males at this time, and may have achieved full spermatogenesis. The testes of all the other birds were similar to the testes of the breeding males on arrival. It is possible that at least the first three males collected (October 5, 10, and 14), may have completed a full spermatogenic cycle. Possibly 25% to 50% of the five year old males achieve full spermatogenic activity.

By comparing the stage of the testis cycle of the five year old birds, with that of the breeding males, at various times during October, it would appear that at least some of these males have a cycle which is up to three weeks later than that of the breeding males.

(iii) Four year old males. Fifteen four year old birds were collected, on arrival, between October 5 and October 31. The range of the tubule diameters overlapped, and the median stage of spermatogenesis showed a slight trend to increase later in the month. Only one bird showed full spermatogenesis (October 30), and only one bird showed evidence of regression (October 22).

Seven males were collected, on departure, late in October, and the testes of three had started to regress. The range of the maximum stages of spermatogenesis was four to six. The other birds were similar to the arriving birds.

It appears that in the majority of four year old males, the testes are developed to between stages four and six of the spermatogenic cycle before regression starts. Only one bird out of twenty one reached full spermatogenesis.

The delay in the testis cycle is similar to that in the five year old birds.

(iv) Three year old males. Eight three year old males were collected, on arrival, between October 18 and November 10. The testes of four of the males had started to regress. The median stages of spermatogenesis ranged from four to five, and none of these birds had completed a full spermatogenic cycle.

The mean stage of spermatogenesis of the other four males ranged from four to six, and considering the date of collection, it is unlikely that they would have achieved full spermatogenesis.

The stage of spermatogenesis in these testes was less than that seen in the arriving breeding males, and this would indicate that their testes cycle is about one month behind that of the breeding males.

(v) Two year old males. The testes of the five males collected on November 18 and 19 were regressing. The maximum stage of spermatogenesis ranged from four to five, and these birds did not achieve full spermatogenesis.

(vi) One year old males. The maximum stages of spermatogenesis ranged from one to four, and there was abundant debris in the lumens. These testes were probably in regression, not having achieved full spermatogenesis. The lack of Sudan IV staining was probably due to the small size of the testes, which allowed all the lipoidal material to be dissolved.

D. Copulating pairs. - Two pairs of breeding birds were collected, after copulation, on October 17 and 18. Both females had ovulated once, and the testes of both males had commenced regression. One pair of failed breeding birds was collected, after copulation, on December 8. The female had ovulated twice, and the gonads were not different from the breeding birds at this time. One four year old pair were collected after a copulatory attempt on Nov. 10. The testis had a maximum spermatogenic stage of five, and the ovary had no large follicles (Appendices 4

5)

III. Discussion.

Owing to the migratory habits of the Royal penguin, this investigation of the gonad cycle in breeding birds was limited to the two to three weeks prior to egg laying. Samples were also collected during the six weeks after egg laying. The changes in the gonads during this period are similar to those described in the Gentoo penguin in South Georgia (Roberts, 1940), the Emperor and Adelie penguins (Prevost and Bourliere, 1955), the Fulmar (Marshall, 1949), and the Short-tailed Shearwater (Marshall and Serventy, 1956).

The females arriving at the rookery in early October have three to five large follicles which grow rapidly prior to ovulation. The two largest follicles ovulate, leaving two distinct corpora lutea. There were no atretic follicles after the first ovulation and before the laying of the first egg, but after the second ovulation all the follicles were atretic and small, except the F3 follicle, which was still large. As the largest F3 follicle, after two ovulations, was found in the female with the second egg in the uterus, it is possible that atresia begins some time after the laying of the first egg, and before the second ovulation. It is unlikely that the Royal penguin is capable of producing more than two eggs. A similar situation is reported in the gull, Larus thayeri (Smith, 1966). Three egg clutches are rare in the closely related Macaroni penguin, (E. c. chrysolophus) (Downes et al, 1959), and further laying is not induced if the eggs are taken immediately after the laying of the second egg (Gwynn, 1953). The Rockhopper penguin (E. crestatus) occassionally lays a third egg, but will not produce another egg if the first two are lost (Gwynn, 1953).

Two eggs is the normal clutch for all the Eudyptes penguins. In three species (E.c. chrysolophus, E.c. schlegeli, and E. sclateri) only the second egg is incubated. E. atratus and E. crestatus frequently incubate the first egg, while E. pachyrhynchus normally incubates both eggs (Falla et al, 1966). It is possible that in this genus there has been an evolutionary trend towards a single egg clutch However, more comparative work needs to be done within the genus to establish if this trend exists.

The breeding males' gonads were almost at the peak of the cycle on their arrival at the rookery. Full spermatogenesis was reached shortly after arrival, and was maintained until just prior to egg laying, after which rapid regression took place. This sequence is similar to that found in the Short-tailed Shearwater (Marshall and Serventy, 1956). These authors suggested that the rapid onset of regression may have been related to the fact that in the Short-tailed Shearwater, the male takes the first incubation period. They assumed that the cholesterol positive lipids found in the regressing tubules may be involved in the synthesis of progesterone. This suggestion was supported by the work of Lofts and Marshall (1959), who found evidence of progesterone in regressing tubules.

The Emperor penguin (Aptenodytes forsteri) and the Adelie penguin (Pygoscelis adeliae) both have rapid regression after breeding, and in both species the males take the first incubation period. The Royal penguin male does not take the first incubation, but it does take turns in incubating with the female in the few days after the laying of the second egg and before the departure for sea. While it is possible that in some birds progesterone may be associated with incubation behaviour, independently of prolactin (Lehrman, 1961), it may be that the progestins found in regressing tubules may be an intermediate step in the metabolic pathway from cholesterol to androgens, and to estrogens, and thus may be entirely unrelated to the incubation in the male. The control of incubation in this bird remains speculative.

In most female birds the gonad cycle lags behind that of the males. In some birds the rapid final growth of the follicles, and ovulation, is influenced by stimuli received in the nesting area (review by Lehrman, 1961). There is no direct evidence that the final rapid growth of the follicles, and ovulation, in the Royal penguin is influenced by such factors. There is, however, some suggestive indirect evidence. One heavy, early arriving female, who did not have a stable mate or territory, was found, on departure (October 31), to have three large atretic follicles (largest was 32 mm in diameter), and no corpora lutea, which suggests that stimuli from the mate and territory may influence ovulation. The size of the largest atretic follicles in this bird, and the fact that the interval between arrival and egg laying decreases with a bird's later arrival, suggests that nest site stimuli may be minimal in influencing the final growth of the follicles.

The gonad cycle in non-breeding birds has been studied in only a few species. Wright and Wright (1944) found that in one year old Red-winged blackbirds, the cycle was later, and the testes smaller, than in adults, even in those birds that had reached full spermatogenesis. One year old Great-tailed grackle males were similar (Selander and Hauser, 1965). Johnston (1956) studied the testes cycle in one to three year old, and adult Californian gulls. In these birds the testis cycle reached a peak earlier, the testes became larger, and the spermatogenic cycle more complete, with increasing age. Similar cycles probably occur in the Fulmar, (Marshall, 1949), and the Short-tailed shearwater (Marshall and Serventy, 1956).

Little work has been done on the ovarian cycle in non-breeding birds. The work of Johnston on the Californian gull suggests that the ovarian cycles are similar to the testis cycles in adult males. The limited data on the gonad cycle of immature Royal penguins shows that similar changes to those mentioned above, take place with age in the Royal penguin, although the extended period of immaturity in the Royal emphasises the gradual sexual development.

All male Royal penguins have a testis cycle which, with age, approaches that of the breeding birds in timing, the size of the testes, and the stage of spermatogenesis reached. The small size and variability of the sample made comparison with the breeding birds difficult, but it is likely that the testis cycle of the two and three year old males may be up to a month later than that of the breeding males.

There is a cycle in the ovaries of females older than three years, and possibly in the one to three year old birds on a microscopic scale. The ovarian cycle in the non-breeding females is later than that of the breeding females. It is difficult to compare the cycles of the breeding and non-breeding females, but it is probable that the cycle of the non-breeding females is even more delayed than that seen in the males.

In both males and females there is no relationship between the condition of the gonads and the date of arrival at the rookery. It is obvious that factors influencing the vernal growth of the gonads, and migration, are not directly related. There is no evidence to suggest what factors may be responsible for the delayed and incomplete gonad cycles.

The attempt to calculate the percentage of birds in each age group physiologically capable of breeding was crude, but given that the basic assumption was reasonably sound, then the calculation at least provides a useful working figure

FIGURE 3

This figure shows the mean weight (in gms) of the ovaries of successive samples of five females taken throughout the season, and the standard deviation of the samples (vertical lines). The standard deviation of the sample collected on December 8 was too small to be shown.

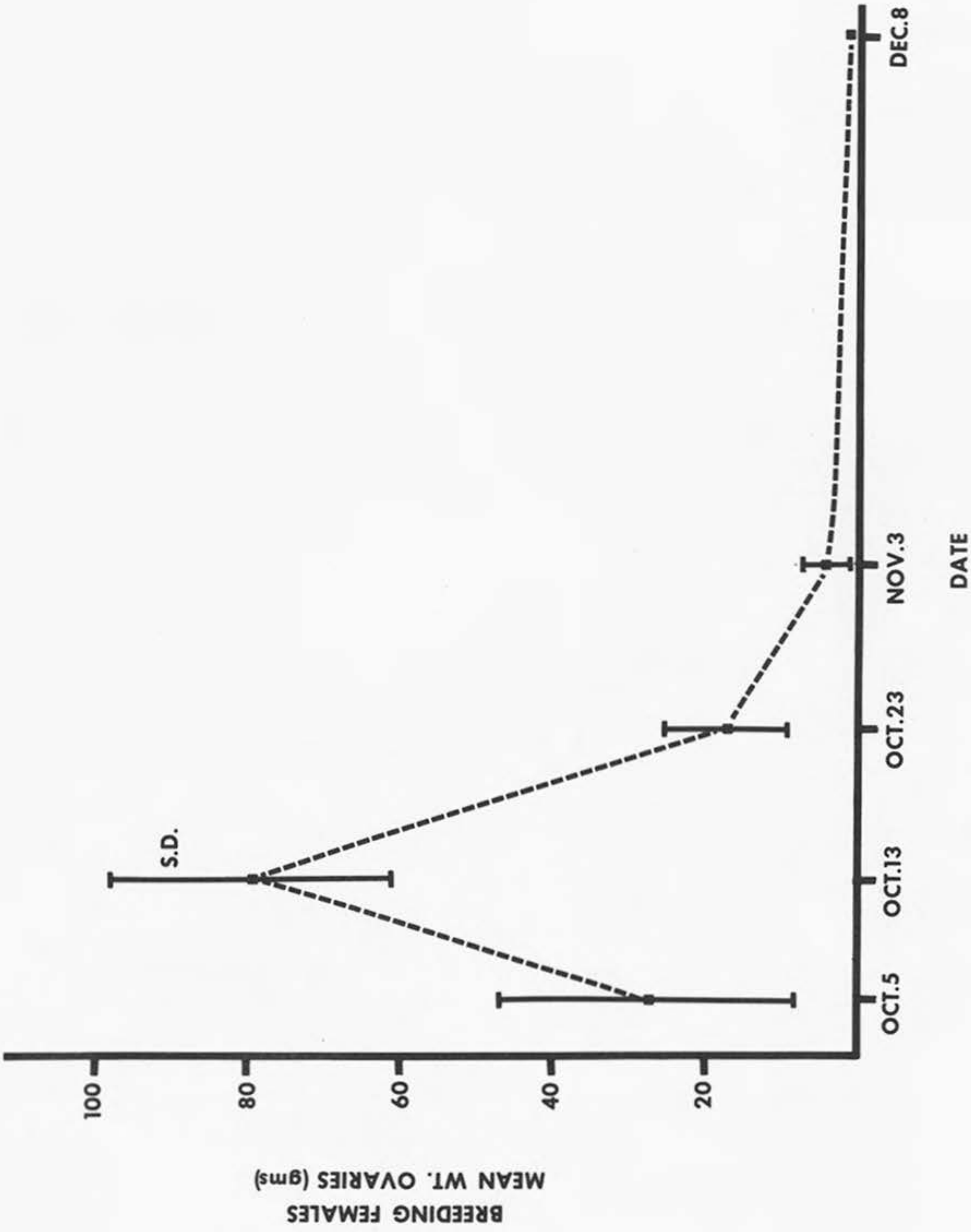
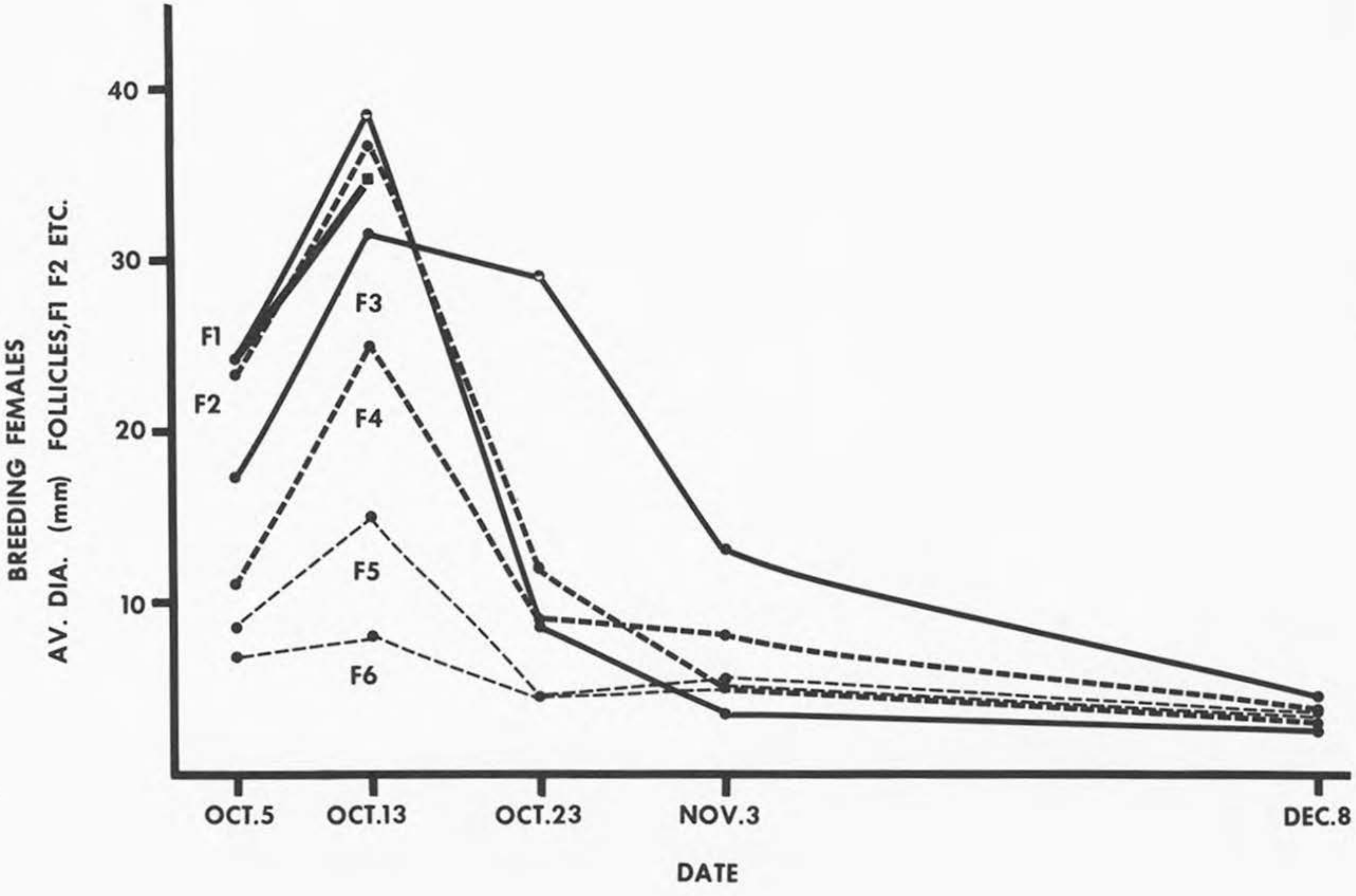

BREEDING FEMALES
MEAN WT. OVARIES (gms)
100
80
60
40
20
S.D.
OCT.5
OCT.13
OCT.23
NOV.3
DEC.8
DATE

FIGURE 4

This figure shows the mean diameter (mm) of the six largest follicles on the ovaries of successive samples of five breeding females collected during the season. F1 is the largest follicle and F6 the smallest.

The top line for the F1 follicle, from October 5 to October 13, is for the three females in the sample who had not ovulated, and the bottom line is for the two females who had ovulated once.


BREEDING FEMALES
AV. DIA. (mm) FOLLICLES,F1 F2 ETC.
40
30
20
10
F1
F2
F3
F4
F5
F6
OCT.5
OCT.13
OCT.23
NOV.3
DEC.8
DATE

<u>FIGURE 5</u>

The average weight (gms) of the right (lower line) and left testes of successive samples of five breeding males collected during the season. The standard deviations are shown as vertical lines.

The standard deviation of the sample collected on December 8 was too small to be shown.

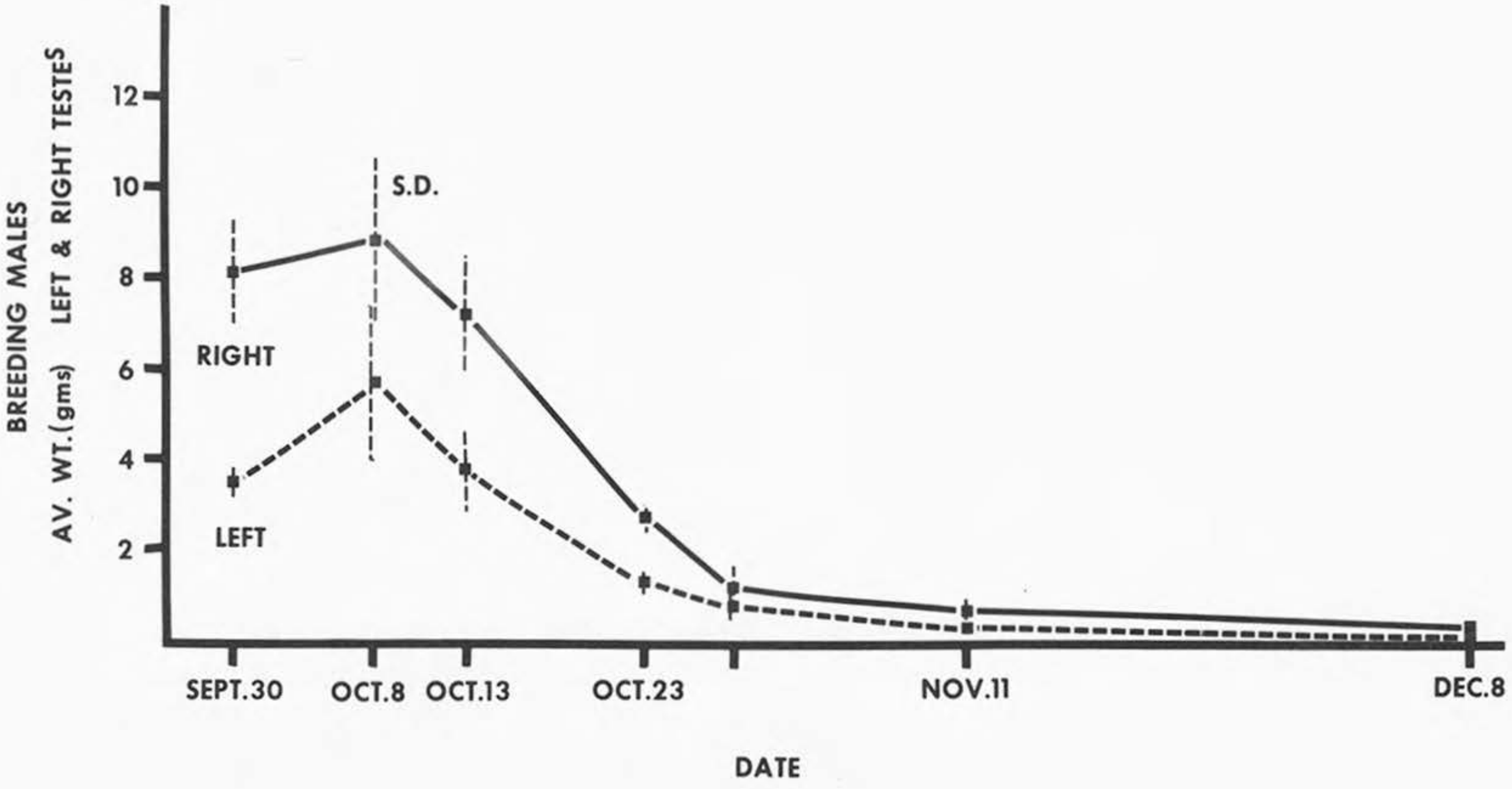

BREEDING MALES
AV. WT. (gms) LEFT & RIGHT TESTES
12
10
8
6
4
2
S.D.
RIGHT
LEFT
SEPT.30
OCT.8
OCT.13
OCT.23
NOV.11
DEC.8
DATE

FIGURE 6

The histological data from the left testes of the breeding males collected during the season.

A. The mean and range of the diameters (μ) of the tubules. The range is indicated by the vertical line.

B. The median and range (vertical lines) of the stages of spermatogenesis.

C. The mean relative percentages of the interstitial tissue (INT), tubule tissue (TUB) and lumen (LUM) stained with Sudan IV, and taken from the left testes. In the case of the lumen it is the debris within the lumen that is stained with Sudan IV.

D. The mean and range (vertical lines) of the amount of debris in the lumen of the tubules.

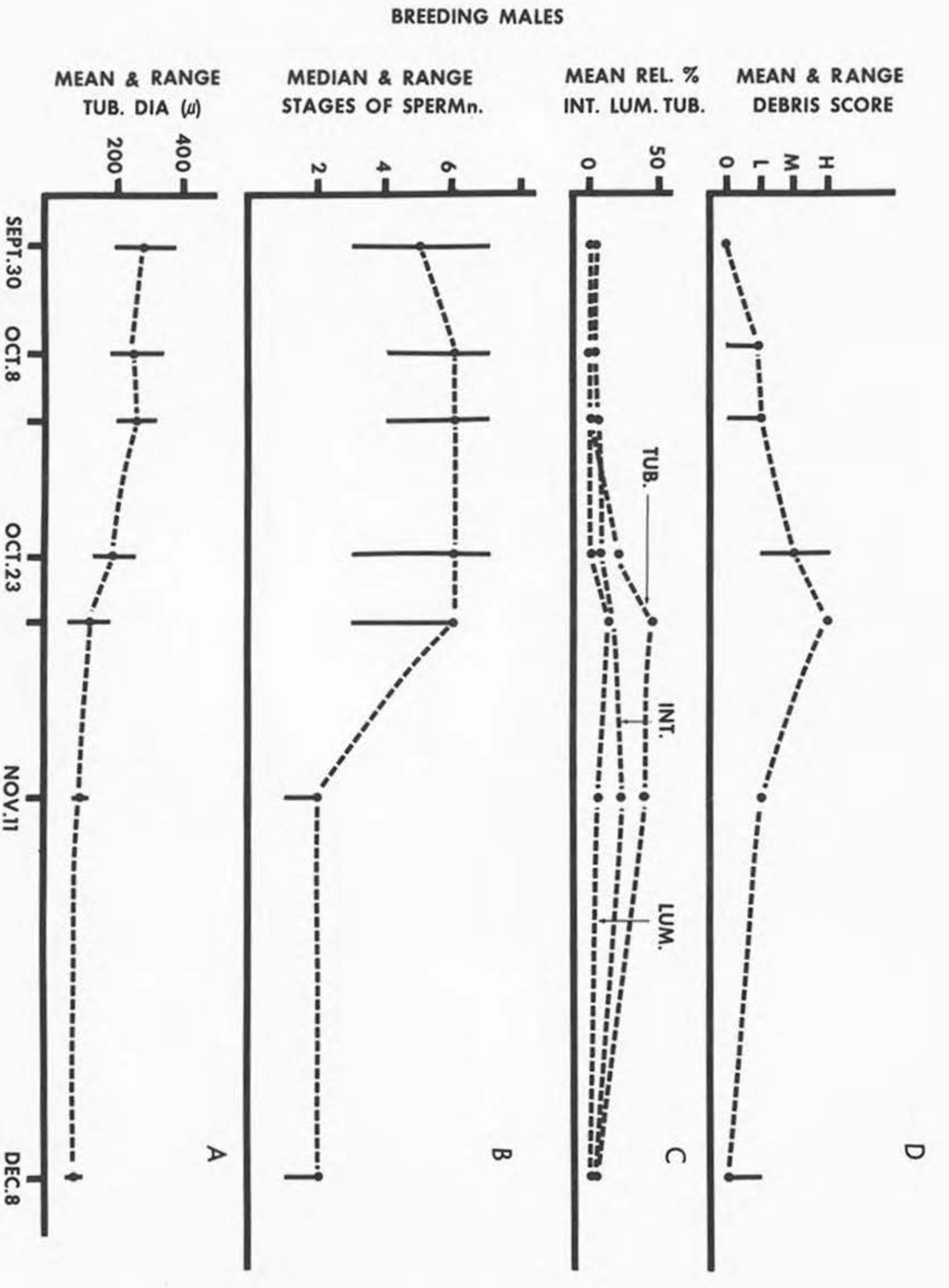

BREEDING MALES
MEAN & RANGE
TUB. DIA (μ)
200
400
MEDIAN & RANGE
STAGES OF SPERMn.
2
4
6
MEAN REL. %
INT. LUM. TUB.
0
50
MEAN & RANGE
DEBRIS SCORE
0
L
M
H
TUB.
INT.
LUM.
A
B
C
D
SEPT.30
OCT.8
OCT.23
NOV.11
DEC.8
DATE

TABLE 1

The mean number and range of the large follicles in the size classes < 10 mm etc. for all females collected on arrival and departure from the rookery.

* Collected on October 5.

** Collected on October 13.

Mean number and Range of Follicles in the different size classes

	Age	< 10 mm	<20 mm	<30 mm	<40 mm
	UK*	3.5 (3-5)	2.0 (1-4)	0.4 (0-2)	0.0 (-)
	UK**	4.2 (3-5)	4.2 (3-5)	3.0 (1-0)	0.2 (0-1)
A	6	3.3 (0-5)	1.9 (0-4)	0.5 (0-2)	0.0 (-)
R	5	1.3 (0-4)	0.3 (0-3)	0.1 (0-1)	0.0 (-)
R.	4	0.2 (0-1)	-	-	-
	3	-	-	-	-
	2	-	-	-	-
	1	-	-	-	-
D	6	2.0 (0-3)	0.8 (0-2)	0.4 (0-2)	-
E	5	1.0 (0-4)	0.3 (0-2)	-	-
P.	4	0.2 (0-1)	-	-	-

TABLE 2

The mean weight (gms) and standard deviation (SD) of the ovary of all known age females collected on arrival and departure from the rookery. The mean and range of the dates of arrival and departure are given.

Age	Av.Date Arr.	Range Date Arr.	Av.Date Dep.	Range Date Dep.	Av. ov. Wt. (gms)	SD Ov.Wt.	Range Ov.Wt
6	19.X	11-28.X	-	-	29.05	21.49	1.82-53.71
5	23.X	6.X-6.X1	-	-	9.61	12.32	2.09-45.87
4	20.X	5.X-2.X1	-	-	2.82	1.04	0.93-4.88
3	6.X1	29.X-8.X1	-	-	2.03		0.69-3.91
2	21.X1	19.X1-22.X1	-	-	0.69		0.39-0.64
1	14.X11	-	-	-	0.25		0.22-0.27
6			26.X	18.X-10.X1	16.21	17.56	1.51-49.05
5			28.X	22.X-4.X1	4.40	4.88	1.28-21.50
4			29.X	22.X-30.X	1.56	0.49	1.16-2.21

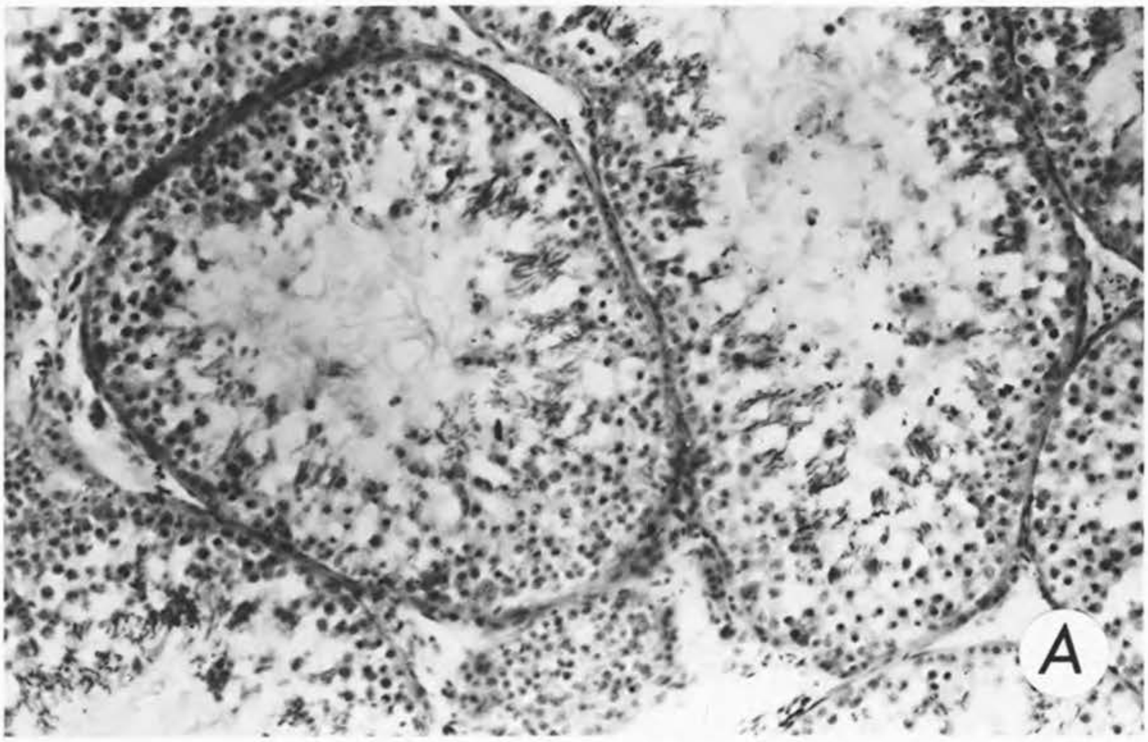
TABLE 3

The mean weight (gms) of both testes with their standard deviations (SD) for all known age males. The mean dates of arrival and departure for each age group is given. The number in each group is given in Appendix 1.

Age	Mean date of arrival	Mean date of departure	Mean wt (gms) left testis	S.D. wt. left testis	Mean wt (gms) right testis	S.D. wt. right testis
6 yr	16.X		4.3	1.8	2.1	0.8
5 yr	19.X		4.0	1.4	2.7	0.9
4 yr	21.X		2.5	1.0	1.4	0.8
3 yr	4.X1		1.0	0.5	0.5	0.2
2 yr	21.X1		0.6	0.3	0.2	0.1
1 yr	14.X11		0.2	-	0.1	-
6 yr		28.X	1.8	0.6	1.0	0.3
5 yr		26.X	1.8	0.7	0.9	0.5
4 yr		29.X	1.5	0.7	0.7	0.4

PLATE 4

Plate 4a	Section of the testis of a breeding male on arrival at the rookery on September 30 (X 200). The section is stained with haematoxylin. The material in the lumen of the tubules is gelatin.
Plate 4b	Section from the same testis as in Plate 4a, stained with Sudan IV (X 200). Note deeply stained interstitial cells.


A

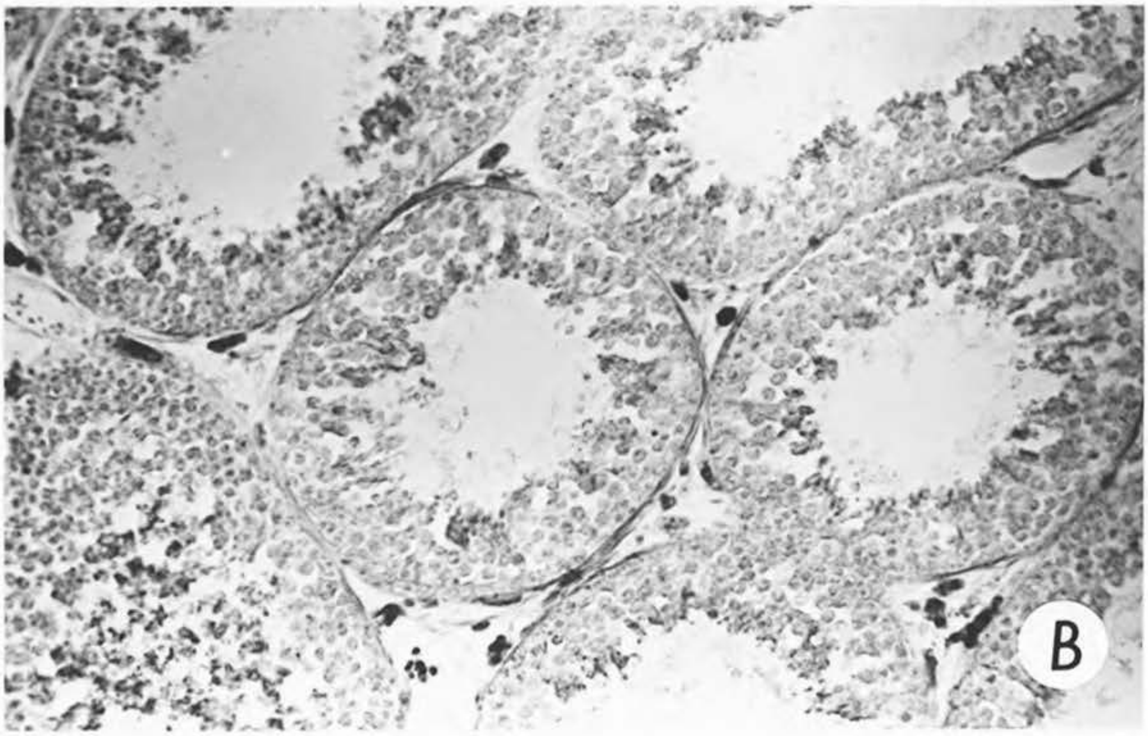

B

PLATE 5

Plate 5a	Section of the testis of a male leaving the colony on October 28 (X 200). It is stained with haematoxylin.
Plate 5b	The same testis as in Plate 5a, stained with Sudan IV (X 200). Note staining of debris in lumen and tubule tissues.

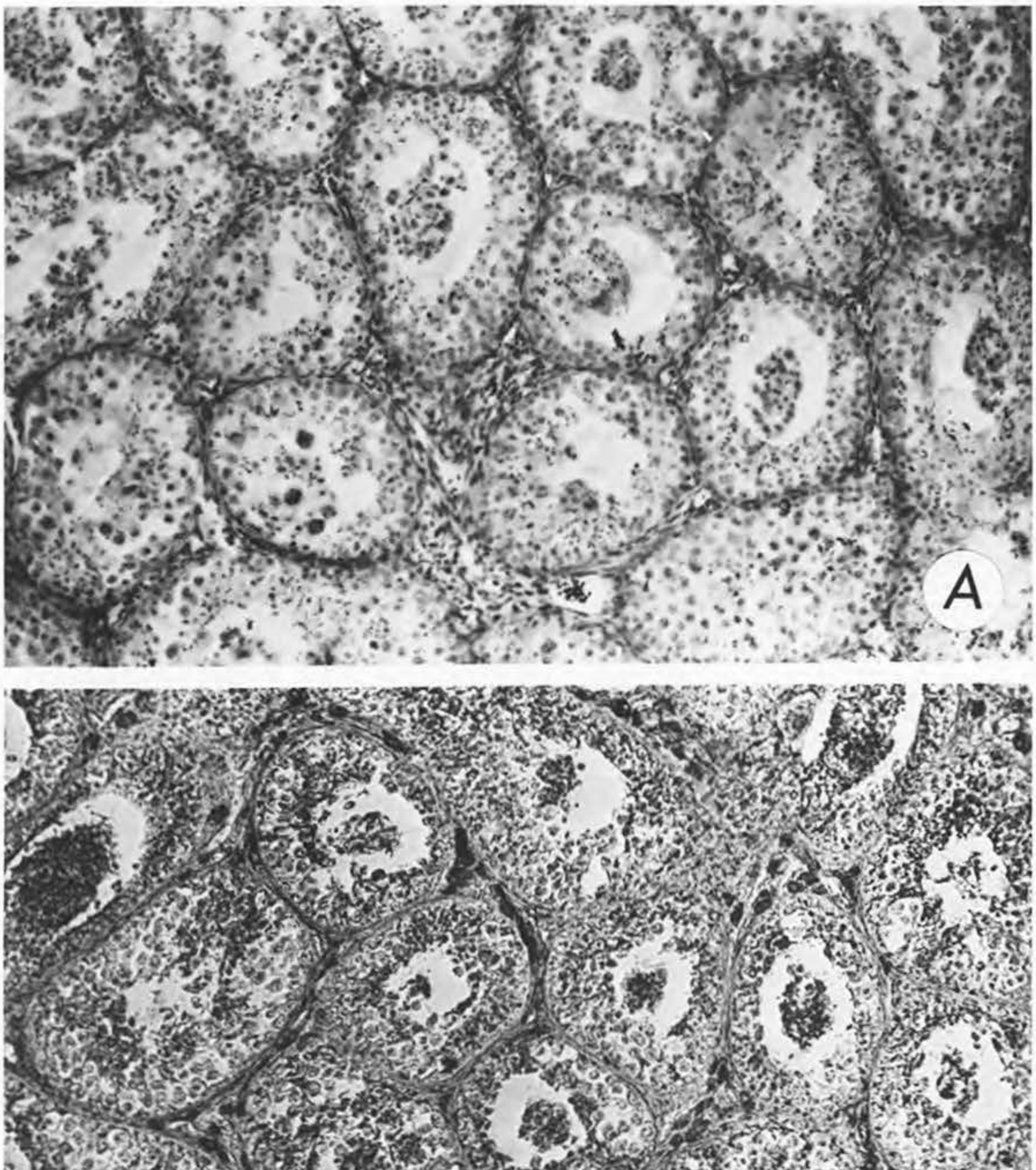
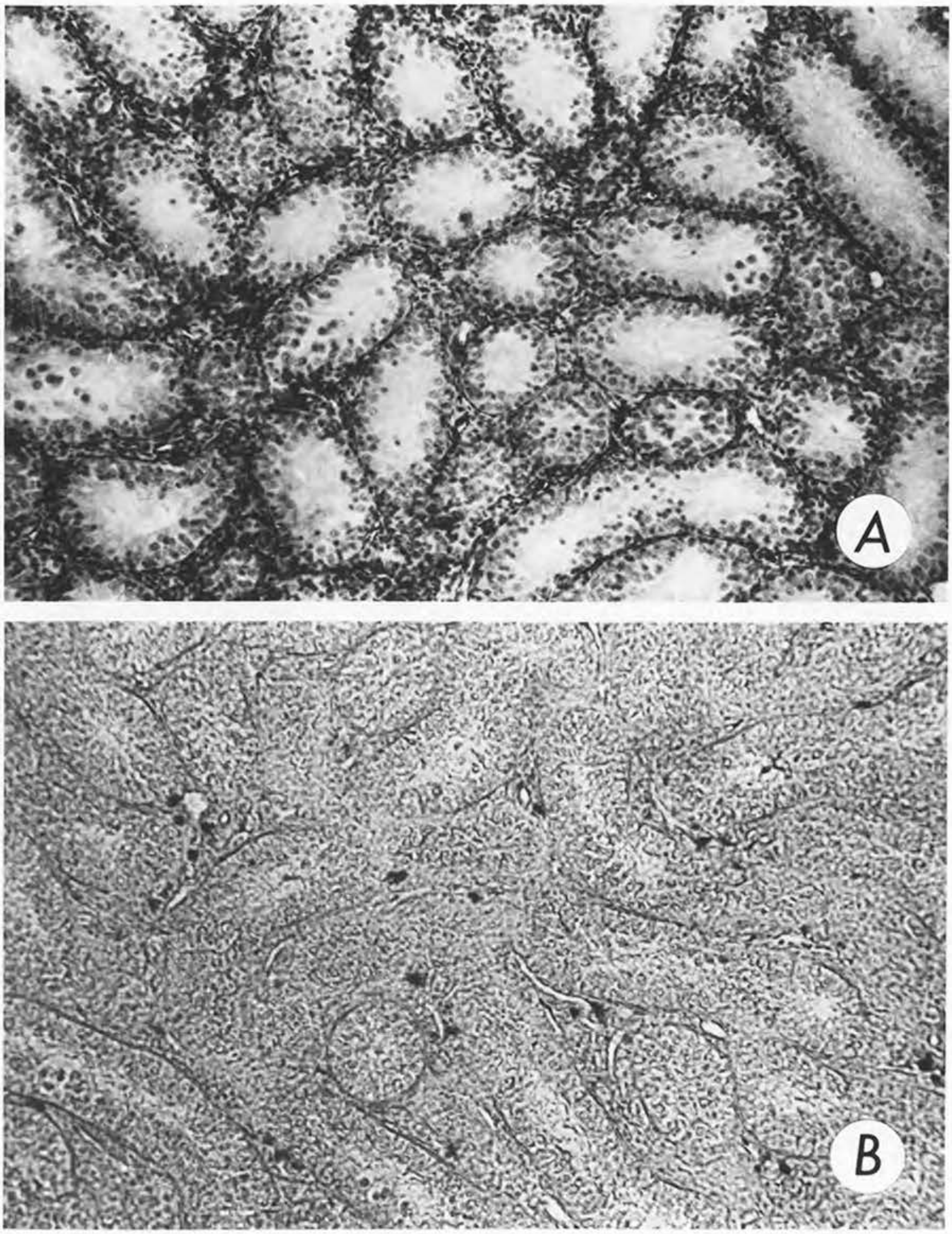

A
B

PLATE 6

Plate 6a	A section of a testis of a breeding male, collected on December 8 (X 200). It is stained with haematoxylin.
Plate 6b	A section of the same testis as above (X 200), stained with Sudan IV. The dark spots are melanocytes.


A
B

CHAPTER 5 - ETHOGRAM

I. Introduction.

The behaviour of the Royal penguin is classified into elements of behaviour, behavioural pattern and display situations. All the displays are described in terms of the elements of the behaviour, the position or movement of the body, head, wings and tail. Differences in feather posturing were only seen during Incubation, Running, and the Elongation Waggle. The supercillary plumes did not appear to be used actively in displays, and in contrast to the Adelie penguin (Wilson, 1907; Sladen, 1958; and Penny, 1968), the eyes were not used in displays.

The elements of the behaviour, and the displays, are diagramatically illustrated on a fold-out page inside the back cover.

II. Elements of the behaviour.

The positions in which the various parts of the body were held are described below.

A. The body.

The body has three basic postures:

1. Short (s). The head rests on the shoulders, and the body is slightly hunched.
2. Medium (m). The body is not hunched, and the neck is slightly elongated.
3. Long (l). Both body and neck are elongated. These body postures may vary from horizontal to the ground to upright.

B. Wings.

The positions in which the wings were held were placed arbitrarily in nine categories:

1. Horizontal forward (hf). The wings are horizontal to the ground in front of the bird, with the inner surfaces of the wings parallel.
2. 45° forward (45f). The wings are in front of the bird and at 45° to the ground, and the inner surfaces of the wings are parallel.
3. Forward (f). The wings are placed on the lateral sides of the abdomen.
4. Side (s). The wings are along the flanks of the body.
5. Slightly out (sl). The wings are a few degrees away from the flanks.
6. 45° (45). The wings are at 45° to the ground, with the inner surfaces of the wings facing the flanks.
7. Horizontal (h). The wings are approximately horizontal to the ground from the flanks, and the plane of the wings is approximately vertical.
8. 45° back (45b). The wings are approximately horizontal to the ground, with the plane of the wings roughly vertical, and projected 45° back.
9. Parallel back (pb). The wings are approximately horizontal to the ground, with the outer surfaces of the wings parallel and projected backwards.

C. The head.

The positions of the head are assigned arbitrarily to seven categories.

1. Vertically down (vd). The head is pointing vertically towards the ground.
2. 45° down (45d). The head is pointing 45° to the ground.
3. Horizontal (h). The head is horizontal to the ground.
4. 45° up (45u). The head is pointing 45° up from the horizontal.
5. Vertical up (vu). The head is pointing vertically up.
6. 45° back (45b). The head is pointing to the back and 45° from the horizontal.
7. Parallel back (pb). The anterior surface of the head is parallel to the back of the bird.

D. The bill.

The relationships of the mandibles were in four categories.

1. Bill closed (bc). The mandibles are together.
2. Bill slightly open (b sl o). A small gap between the mandibles.
3. Bill half open (b $\frac{1}{2}$ o). The distal ends of the mandibles are approximately one and a half inches apart.
4. Bill open (bo). The bill is wide open.

E. The tail.

There are three positions of the tail:

1. Tail down (td). Normal position of the tail.
2. Tail up (tu). The tail is held vertically up, exposing the cloaca.
3. Tail vertically down (tvd). The tail is vertically down.

III. Behaviour patterns.

The behaviour has been grouped roughly to facilitate description, and does not constitute any causal or functional grouping. In naming the various displays an attempt was made to use a word, or phrase, to describe what the bird was doing, and to avoid functional or motivational interpretation.

A. Basic postures.

1. Short sit (SS) (Plate 7c). The body is short, and the wings vary from forward to horizontal. The head is from 45° down to horizontal, and the bill closed. The bird rests on the tarsi, occassionally on its feet, and rarely, has its feet crossed.
2. Medium stand (MS). The body is medium, and the wings are from the side to 45° back. The head varies from 45° down to 45° up.
3. Long stand (LS) (Plate 8a). As in 2, but the body is long.
4. Incubation sit (IcS) (Plate 7a). The body is short and hunched forward, with the wings to the side, and the

head is vertical down to horizontal. The bird's feathers are fluffed, and the incubation patch is folded over the eggs.

5. Sleeping (SL). The body is short with the bill tucked under the right or left wing from the dorsal side. Occasionally the bill is outside the wings. Rarely, the bird rests the side of its head on the upper chest with the bill pointing to the midline.

6. Lying (L). As in 1, but horizontal to the ground, with the feet under the body.

B. Locomotion.

1. Walking (WA). The bird moves with a slow, shuffling gait. The body rolls from side to side, and the body posture varies from short to long. The wings are from the side to 45° back, and the head varies from 45° down to 45° up.

2. Hopping (HO). The body varies from medium to long, the wings from horizontal to 45° back, and the head is horizontal. In rocky areas the hop is preceeded by the bird bending forward, half way down to the ground. The body is straightened as the hop starts.

3. Running (R) (Plate 8b). The body is long, the head horizontal, the chest thrust forward and the wings from the side to 45° back.

4. Tobogganing (T). This is the fastest form of terrestrial locomotion, and is only observed in birds escaping. The bird falls on its chest and propels itself with its wings and feet. The wings are the main driving force.

5. Swimming (SW). Three distinct forms of swimming are seen in the Royal penguin.

   a) Paddling. The body is low in the water, the neck is elongated vertically, and the head is horizontal. The wings beat in unison.

   b) Submarine swimming. The body is straight, the head retracted onto the shoulders. The feet trail behind, and the wings beat rapidly.

   c) Porpoising. As in b). When the bird leaves the water the wings are held close to the flanks.

C. Comfort movements.

The classification of the comfort movements is based on McKinney's (1965) classification.

1. Shaking movements.

   a) Elongation Shake (EL SH). The body is stretched from short to long, and the wings from their original position to 45^{o} back. In the long position, the head is horizontal to 45^{o} up from the ground, and is shaken rapidly from side to side. The body is then retracted to the short or medium position, and the wings to their original position.

b). Elongation Flap (EL FL). As in a), but the wings are moved only. They are moved rapidly in unison in the horizontal plane, and may move from 45^o back to 45^o forward, or may either move from 45^o forward or back to the horizontal.

c) Elongation Waggle (EL WAG) (Plate 8c). As in a) with the addition of wing movement. The feathers are fluffed as the bird changes its body posture from short to long. The wings move as in b), but they move from 45^o back to 45^o forward. The wing movements are not in unison, and the head is turned to the side with the wing in the forward position. The whole body surface ripples when the head and wings are being moved. Rarely, the tail wags rapidly at the commencement of the movements of the head and wings, but usually only when these movements have stopped.

d) Head Shake (H SH) (Plate 14c). The head position varies from 45^o down to 45^o up. The head is shaken rapidly from side to side.

e) Tail Shake (T SH). This involves rapid movement of the tail to each side.

f) Leg Elongation (LE). From the lying position, one leg is extended back and forward several times.

g) Shoulder Shrug (SH SH). One shoulder is lifted and lowered once or twice.

2. Stretching movements.

   a) Tension Press (T P) (Plates 9a and 9b). A stretching movement in two parts, usually performed together, but may be performed independently.

      Part One (Plate 9a). The wings are moved back until they touch the distal end, and at the same time the body is inclined forward and the neck elongated forward with the head tilted upwards about 45^{o}. At the end of these movements the bird may gape (see below), and there may be a pronounced concave upwards curve in the neck. The body then returns to its original posture. If Part Two follows, (Plate 9b), the wings go to the forward position, and appear to be pressed against the body, while at the same time the body straightens, and the head goes to the vertical position. The neck is not elongated. Usually this display ends with a Sniff, (see below).

   b) Gape (G). The bill is from half to completely opened. The head may be horizontal to vertical, and may be moved in any direction between these two positions while Gaping.

   c) Swallow (SW). The bill is closed and swallowing-like movements are seen in the throat.

d) Nibble (NI). This involves a slight opening and closing movement of the bill.

e) Nibble Swallow (NI SW). Swallowing and Nibbling are performed together.

f) Sniff (SN). This is a sharp inhalation and/or exhalation of air.

3. Cleaning movements.

a) Scratch(SC) (Plate 8d). The bird stands on one leg, and the other leg is brought around the outside of the wing, the head is lowered, and the bird scratchs various parts of its head.

b) Foot Pecking (FP). The bird nibbles at material adhering to its feet.

c) Shoulder Rubbing (SH R). The bird rubs the side of its head on its shoulder.

d) Bill Washing (BW). The bird dips its head in water, and as the head is lifted from the water it is moved rapidly from side to side.

e) Combing (CO) (Plate 9c). The bird has its head on its shoulder, with the bill facing the side. The head moves in a curve across the feathers, with the bill closing at the end of the movement. The bird may repeat this movement several times. The head is then turned to the front, and moved from 45^{o} up to the vertical.

4. Preening.

   a) Nibble Preening (NI P) (plate 9d). The bird nibbles individual feathers, or draws them through the bill, in localized parts of the body.

   b) Stropping Preening (S P) (Plate 10a). This involves vigorous stroking of whole areas of the body with an open beak. A variation of this is Honing, where the bird strokes the inner surface of the mandible down the leading edge of the wing.

   c) Social Preening (SO P). This is Nibble Preening of the head region of another bird, usually the mate. For the individual bird, this may involve preening the mate(PM), being preened by the mate (PBM), or mutual preening (MP).

   d) Oiling Preening (OP). The oil gland in the Royal penguin is situated above the root of the tail, and is covered by a patch of white feathers. These feathers can be erected, and expose a brush of feathers on the papilla, surrounded by a small area of bare skin. Oiling Preening occurs when the bird draws these feathers through its beak, or rubs the side of its head on the oil gland. Other areas of the body are then preened, or rubbed with the side of the head.

5. Bathing. No detailed observations were made of this activity. It involves rapid

movements of the head, wings, feet and tail while swimming. The bird somersaults, or lies on one side while doing these movements.

D. Displays.

1. Rounded Neck Wings Forward (R N W F) (Plate 10b). The head is bowed forward from the body, and approximately half way to the ground. The wings are in the 45° forward position. The profile is rounded, though there could occasionally be a kink in the neck. This posture may be accompanied by braying.
2. Rounded Neck (RN). As in 1, with the wings by the side to 45°. There is no braying.
3. Neck Horizontal Wings Forward (N H W F). As in 1, but with the neck elongated and horizontal to the ground. May be accompanied by braying.
4. Long Curved Stand (L C S) (Plate 10c). The body is long, with the head held forward at approximately 45°. Occasionally the neck is concave upwards. The wings are 45° back, and may be moved to the horizontal and back. The profile is a smooth curve. This posture is always accompanied by braying.
5. Vertical Stand (VS) (Plate 10d). The body and the head is vertical. The wings are

from horizontal to 45^{o} back. Always accompanied by braying.

6. Head Down Under (H D U) (Plate 11a). The head is lowered to the ground with the beak pointing to the back, and the anterior surface of the bill parallel to the ground. The profile is almost circular. Usually accompanied by braying.

7. Flagging (F) (Plates 12-14). The body is short to long, the wings at the side to parallel back, and the head from vertical down to parallel back. The head is moved deliberately from side to side. The arc from the median plane of the bird varies from 45^{o} to 180^{o}. The movement of the head from the median plane to one side and back again to the median plane is called a Flag, and Flagging is a bout of Flags. In recording Flagging the number of Flags, and the position of the body, head and wings was recorded. Flagging may be accompanied by braying.

8. Head Flick (H FL). As in 1, but the head is flicked over the shoulders. The number of flicks varied from one to five. There is no braying.

9. Head Wobble (HW) (Plate 12a). The head is lowered towards the ground and is vibrated rapidly in a small arc. The wings

are at the side, but may be 45° forward or back. The head is usually close to the body, but occasionally it is well forward from the body, and may be moved from side to side while vibrating. The vibrations may start as soon as the head is moved downwards, or when the head has stopped moving. This is a variable and sometimes complex display, but the common form (subjective) is that of the initial description. For ease of recording, all displays involving movements of the head towards the ground, and vibration of the head, were combined together. This display may be accompanied by braying.

10. Looking Around (LA) The body is short to long, the wings at the side to horizontal, and the head horizontal to 45° up. The head is turned to one side and back. May be repeated a number of times, to one or both sides.

11. Rapid Looking Around (RLA) (Plate 11b). The body is medium to long, the wings at the side to 45° up. The head is turned rapidly from side to side with short pauses, generally when the head is turned to the side, or is pointing to the front. The general appearance is of a jerky movement.

12. Bobbing (B). Body medium to long. The head is generally horizontal and is moved up and down a few times.

13. Wing Quiver (WQ). The body is short to long, the wings at the side to 45^{o}. Either one or both wings are vibrated rapidly for a short time in a small arc.

14. Quiver (Q). This involves rapid vibration of the head in a small arc, but is not associated with movement of the head towards the ground. It appears to be identical to the vibration seen in Head Wobbling.

15. Head Down (HD). The head is lowered to anywhere from the chest to the ground, and almost immediately brought back. The wings are at the side.

16. Head Vertically Down (HVD). The body is from medium to long, the wings at the side to 45^{o}. The head is pointed vertically down, but is sometimes tilted to one side.

17. Excretion (EX). The bird leans forward, raises its tail to vertical, excretes, lowers and shakes it tail, and regains its original posture.

IV. Display Situations.

A. Copulation (COP)

The following description gives the sequence of actions leading up to a successful copulation. The variations will be given later.

The male, which approaches from any direction, crowds up closely to the female, with his wings in the horizontal forward position, quivering, and around the female. His head is from 45° down to horizontal, and is quivered over the top of the female's head. The female's body is from short to medium, with the wings at the side to 45° back, and the head 45° down to 45° up (Plate 11c). The female lies down, and the male climbs onto the female's back. By this time her head and tail are vertically up, and her cloaca everted. Once he has mounted, the male has his head bowed to the head of the female, and his wings are 45° forward. The male's head quivers around the head of the female, and his wings move slightly in and out. He gradually moves backwards until he is over the pelvic region of the female, by which time he is lying along her back. His head is still quivering, and his wings are beating on either side of the female. In this position the male depresses his tail down vertically over the female's exposed cloaca, and he moves his tail rapidly from side to side. Ejaculation takes place when the male presses his tail over the cloaca of the female. The male's tail then relaxes, and he stands up, slides, or hops off the female. The female continues to lie for a short time with her head horizontal and her tail vertical. The semen may be seen on the opening of the cloaca, which contracts rythmically. After a short time the female lowers her tail and stands up.

Copulation has been divided into three parts: firstly, the Copulation Prelude (CP) (Plate 11c), which ends with the female lying down; secondly, the Copulation Attempt (CA), which starts when the male mounts the female, and ends with the apposition of the cloacae; and thirdly, the Apposition (APP) of the cloacae and ejaculation.

The sequence of actions may stop at any point after the male starts to crowd up to the female. The time taken to perform the Copulation Prelude and Attempt is extremely variable.

If the female does not lie down the male may attempt to force her down. Occasionally he succeeds, but usually the female moves away. Occasionally the female lies down, but does not lift her head and tail when the male mounts her. In these cases the male usually hops off, after a short time. In two observations the male persisted for some time, and finally the female lifted her tail and 'successful' copulation took place. In copulations during the guard stage no semen was seen.

Two cases of abnormal copulation were seen. The first case involved a pair of birds during the laying period. No Copulation Prelude was seen, and the Copulation Attempt was made with the male lying on the ground facing the female. The second case involved a pair of unbanded birds. Both performed a copulation attempt on a lying chick.

B. Agonistic behaviour.

Agonistic behaviour has been defined by Verplank (1957) as' a broad class of behaviours that include all attack, threat, appeasement and flight behaviour'. Using this definition, the following behaviour patterns may be classified as agonistic behaviour.

1. Threat (TH) (Plates 15a and 15b). Threat behaviour involves the orientation of the head, or the whole body, towards another bird. It is very variable, and ranges from a movement of the head with a closed beak towards another bird, to full elongation of the whole body with an

open bill and accompanied by braying. The initial body posture may vary from short to long, and the wings from at the side to 45° back. When the bird elongates forward towards another bird, the wings are brought forward and used as props (Plate 15b). Elongation towards another bird may be repeated a number of times, and may also involve pecking at the other bird. These attempted pecks rarely contact. On returning to its former position after an elongation, the bird withdraws its head along the ground, usually rotating it 45° to 90°, and as the head nears the body, it is turned to one side so that one eye is still directed towards the other bird. The head is then raised, and the wings may be moved from the side to 45° back.

When threatening a passing penguin, skua or human, the bird's body is long, the wings 45° back, and the head held forward. The head bobs in and out towards the other penguin, etc. This behaviour may be accompanied by braying.

2. Aggression (AGG) (Plate 15c). The most common form is similar to threat, but involves physical contact. The birds lunge at each other with open bills, while braying and attempting to grab one another's bills. If one, or both birds succeed, each bird attempts to twist the other's head. This may be repeated a number of times. The final withdrawal is the same as in threatening.

If, when threatening, a territorial bird only orientates his head towards another bird, he may strike the other bird with the wing on that side, if the other bird elongates close enough to him.

In birds without a territory, a bird who has been threatening or aggressing towards another bird may turn its body side on to the other bird, and at the same time keep its head orientated towards it. It would hit the other bird with its wing. A bird that turns side on nearly always flees if the other bird continues to threaten it.

Males may show aggressive behaviour without any apparent provocation.

3. Fighting (FI). Both birds stand face to face, with chest out and pushing each other, while hitting with their wings, and pecking. The positions of both birds vary, and the initiative passes quickly from one bird to the other.

Pecking involves grabbing a bunch of feathers and twisting them. In beating, both wings move in unison (Plate 11d).

4. Fleeing (FL) (Plate 15d). This is the same as for running. The head is usually 45° up.

5. Chasing (C). Both birds run, and if the pursuer catches the other bird it pecks it, and hits it with its wings. The other bird does not attempt to retaliate but tries to get away. Occasionally a bird may toboggan if it cannot escape by running.

6. Submissive Posture (SU) (Plate 11d). The bird lies with its bill tucked under its chest.

7. Head Push (HP). The bill is pointed vertically to the ground, and the head is elongated. This was only observed in incubating females trying to fend off birds taking stones from their nests.

C. Nest building (NB).

The Royal penguin nests are small hollows in the substrate, and may be filled with grass, stones, etc. To scrape a nest the bird lies and digs with one foot. This movement means that the bird slowly rotates, thus making a circular hollow.

Birds may also collect soil by pushing their open bills into the ground and collecting a bill full of soil, and carrying it back to the nest. This is most commonly seen in incubating birds who elongate forward, dig, and then deposit the soil immediately in front of them (Plate 7b).

Some birds may also collect stones, bones, etc., and may collect grass from the edge of the colony.

V. Comparison of Eudyptes spp.

Warham (1963) has described the displays of the Rockhopper penguin in relation to the situations in which they occur. There is a close similarity between the displays of the Rockhopper and Royal penguins.

The display Warham calls Quivering is very similar to Head Wobbling in the Royal, but his reference to grass, etc., being placed to one flank suggests that Warham is combining the two displays I called Head Wobbling and Quivering. Quivering in the Royal is usually associated with the placement of material in the nest. It may be preceeded by bending the head to the ground, but this movement is much slower than that seen in the Head Wobble.

Bowing (Warham) is also similar to the Head Wobble, but without the vibration, and seems to be more akin to my Head Down display. Warham's Shoulder-hunched attitude is the equivalent of my Round Neck Wing Forward. His Trumpeting display is the same as my Long Curved Stand, while his Vertical Trumpeting is the same as my Vertical Stand display. His Male display is the same as Flagging, and in both species Copulation and agonistic behaviour was the same.

From Warham's descriptions it appears that the main difference between the two species is the frequency with which the displays are given.

The brief description of the displays of the Macaroni penguin given by Downes et al (1959), indicates that they are similar in form to those of the Royal.

Richdale (1941) gives a brief description of the behaviour of the Erect-crested penguin (*E. sclateri*). The form of the displays is the same as that of the other *Eudyptes* spp.

It is probable that all the *Eudyptes* penguins have basically the same behavioural repertoire, but more detailed descriptions are needed to show any differences in the form of the displays.

PLATE 7

Plate 7a	Incubating females in the Sand Colony. Note how the spacing closely approaches hexagonal close packing which gives the highest density of birds in a given area.
Plate 7b	Incubating bird digging. A distinct trench is made around the nest, and the material from the trench is used to build a mound around the nest scrape (Plate 7a).
Plate 7c	A pair of failed breeders in the typical SS posture. The birds are in the Inland Colony.
Plate 7d	A typical small creche in the Sand Colony, surrounded by adult birds, one of which is pecking a chick. Some of the adults are failed breeding birds, while others are non-breeding birds.

Plates 7-15 were taken by I. Fox from enlargements of positive, 16 mm black and white film.


A
B
C
D

PLATE 8

Plate 8a	A bird on the periphery of the Sand Colony in the LS posture. Note the skua in the bottom left of the picture. It may have been the cause of the bird's elongation.
Plate 8b	A bird Running (with wings horizontal) through the Sand Colony. Two birds are threatening it.
Plate 8c	Elongation Waggle. Note that the left wing is forward of the body, and the head is also turned to the left side.
Plate 8d	A bird Scratching the side of its head.

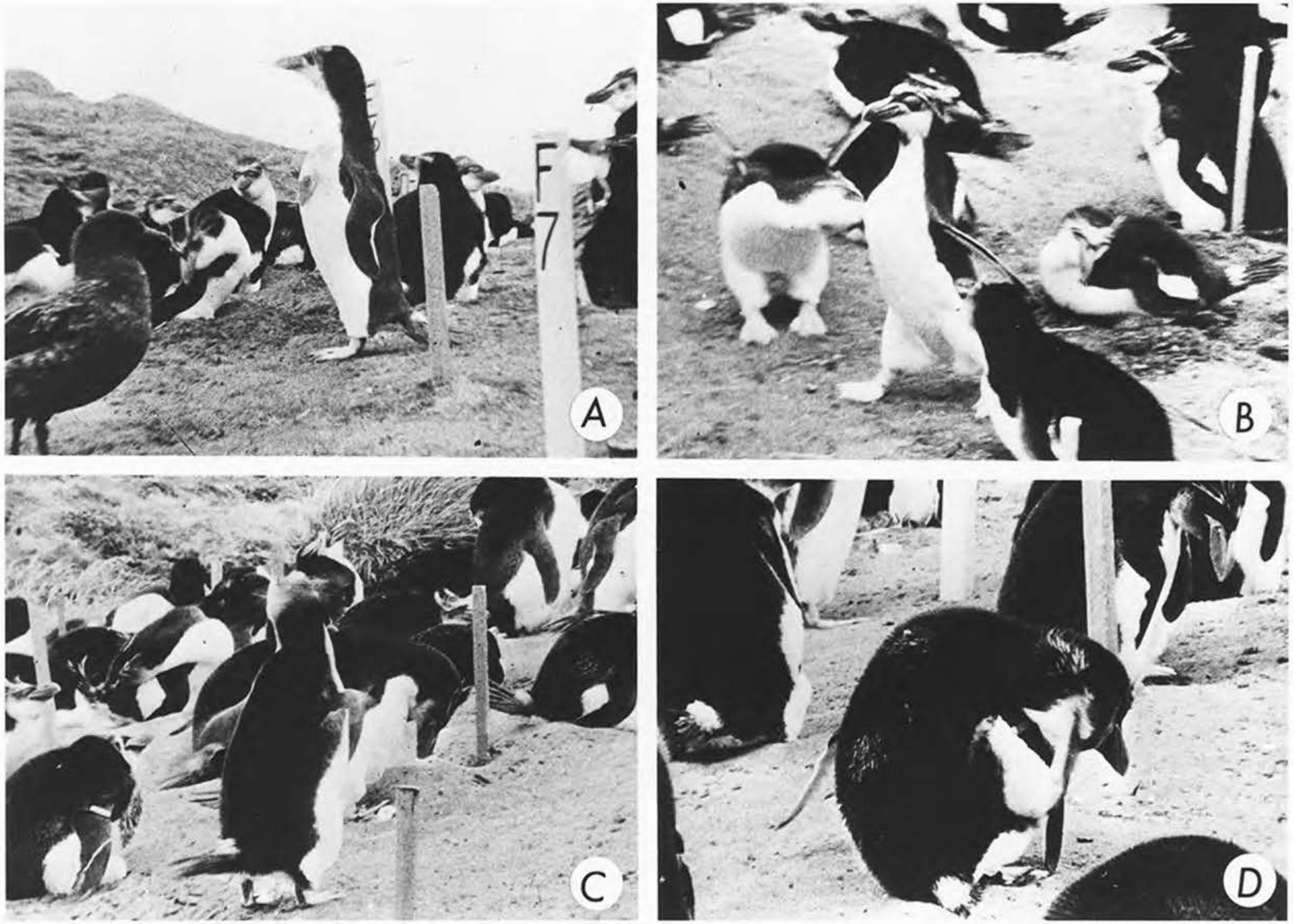

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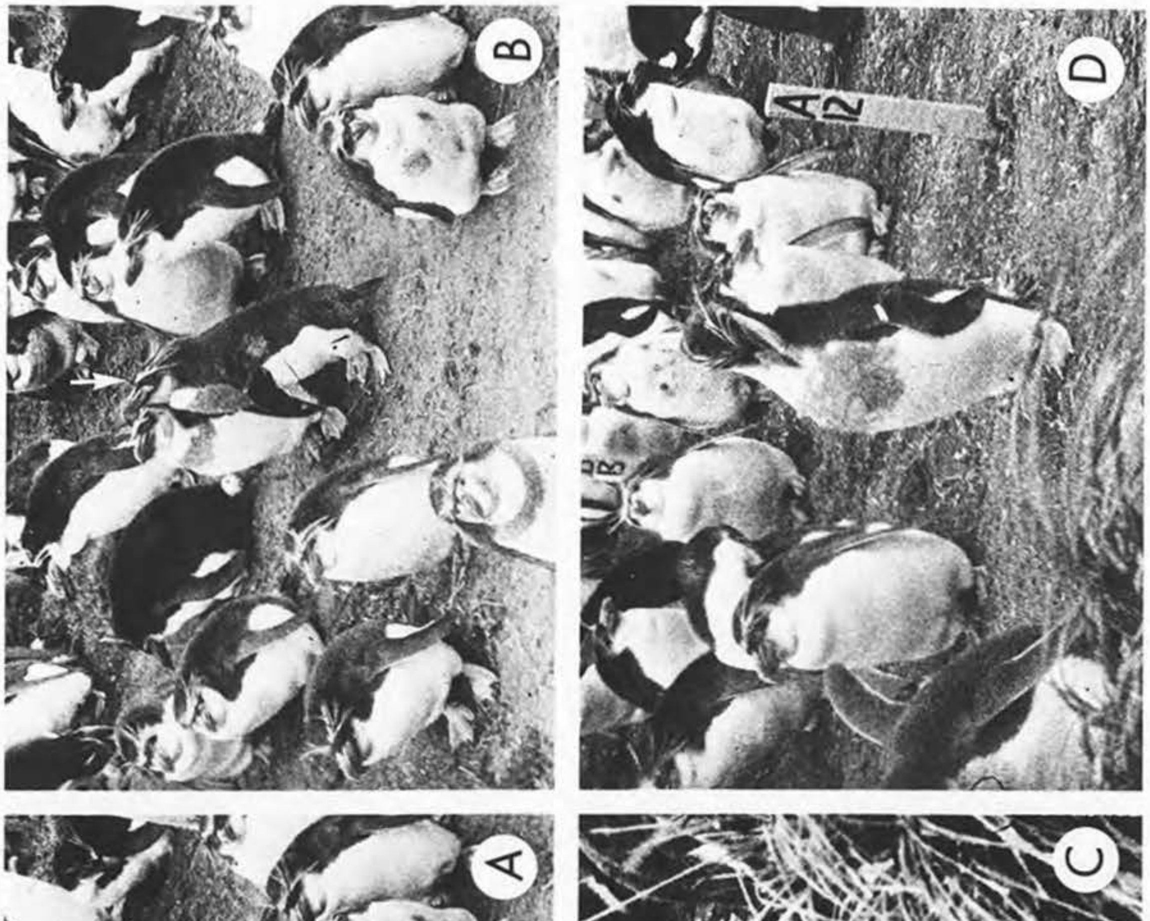
PLATE 9

Plate 9a	The Sand Colony prior to egg laying. The bird in the centre (arrowed) is doing a Tension Press, part 1. Note that the birds in the top centre and top left (arrowed) have eggs. The postures are typical for birds with their first eggs.
Plate 9b	A Tension Press, part 2 (arrowed), performed by the bird in Plate 9a.
Plate 9c	A bird Combing.
Plate 9d	A bird Nibble Preening the upper chest.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B

PLATE 10

Plate 10a	An incubating bird stropping its wing with its bill.
Plate 10b	A female (arrowed) approaching her mate in the Rounded Neck Wings Forward (RNWF) posture. The mate (back view, arrowed) is in the Long Curved Stand (LCS), with his wings forward. Note that the neighbouring birds are in the LCS posture with their wings 45° back.
Plate 10c	Two birds in the LCS posture with their wings 45° back.
Plate 10d	A bird (arrowed) performing a Vertical Stand (VS) after a HW display and before Flagging. Its mate, on the left, has commenced to Flag.

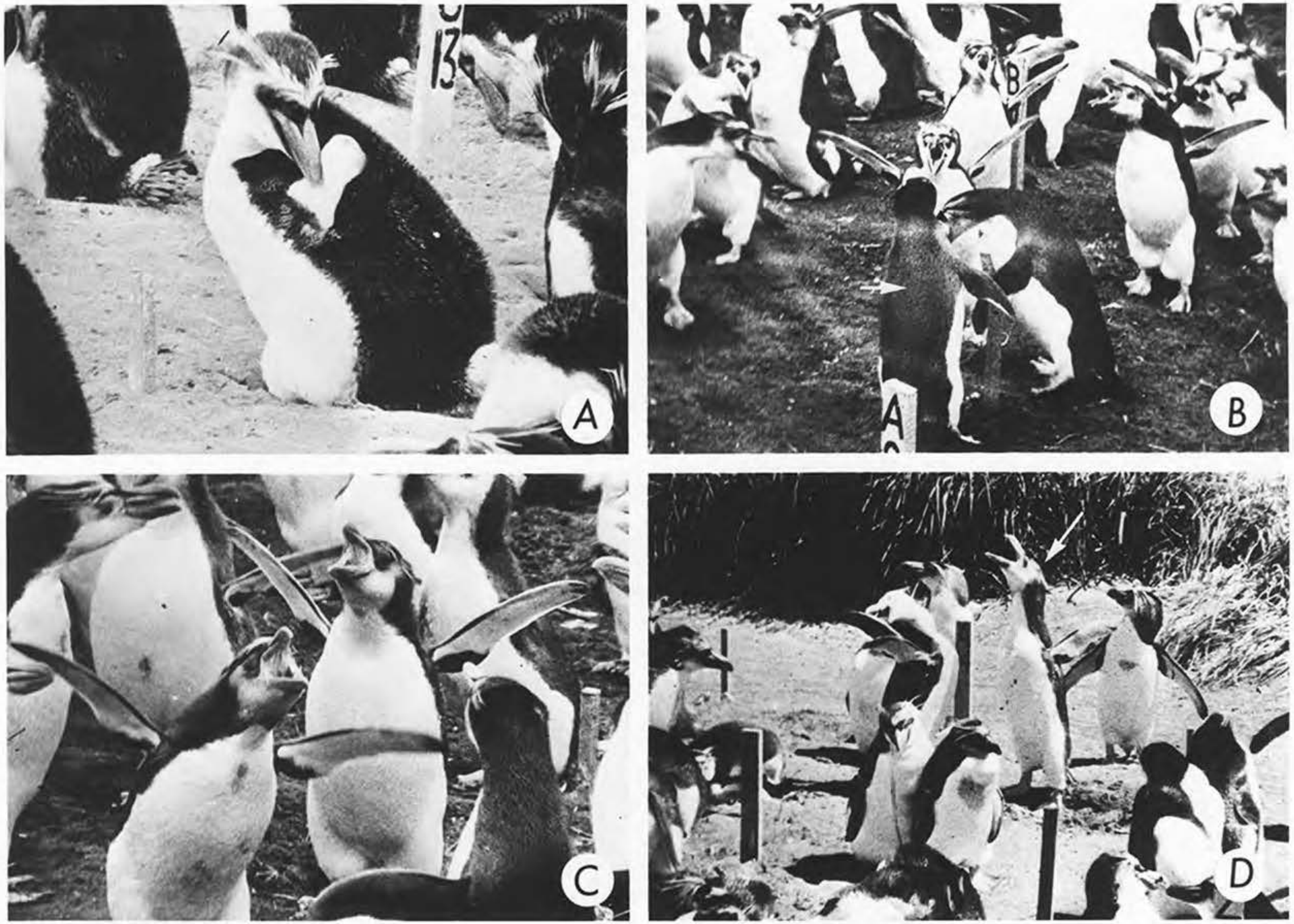
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PLATE 11

Plate 11a	An incubating bird in the Head Down Under (HDU) posture.
Plate 11b	A bird on the periphery of the Sand Colony performing a Rapid Looking Around.
Plate 11c	A Copulation Prelude.
Plate 11d	A non-breeding male pecking and beating an incubating female who is in the Submissive posture with her head turned to her left. The mate of the male is standing behind him looking on.

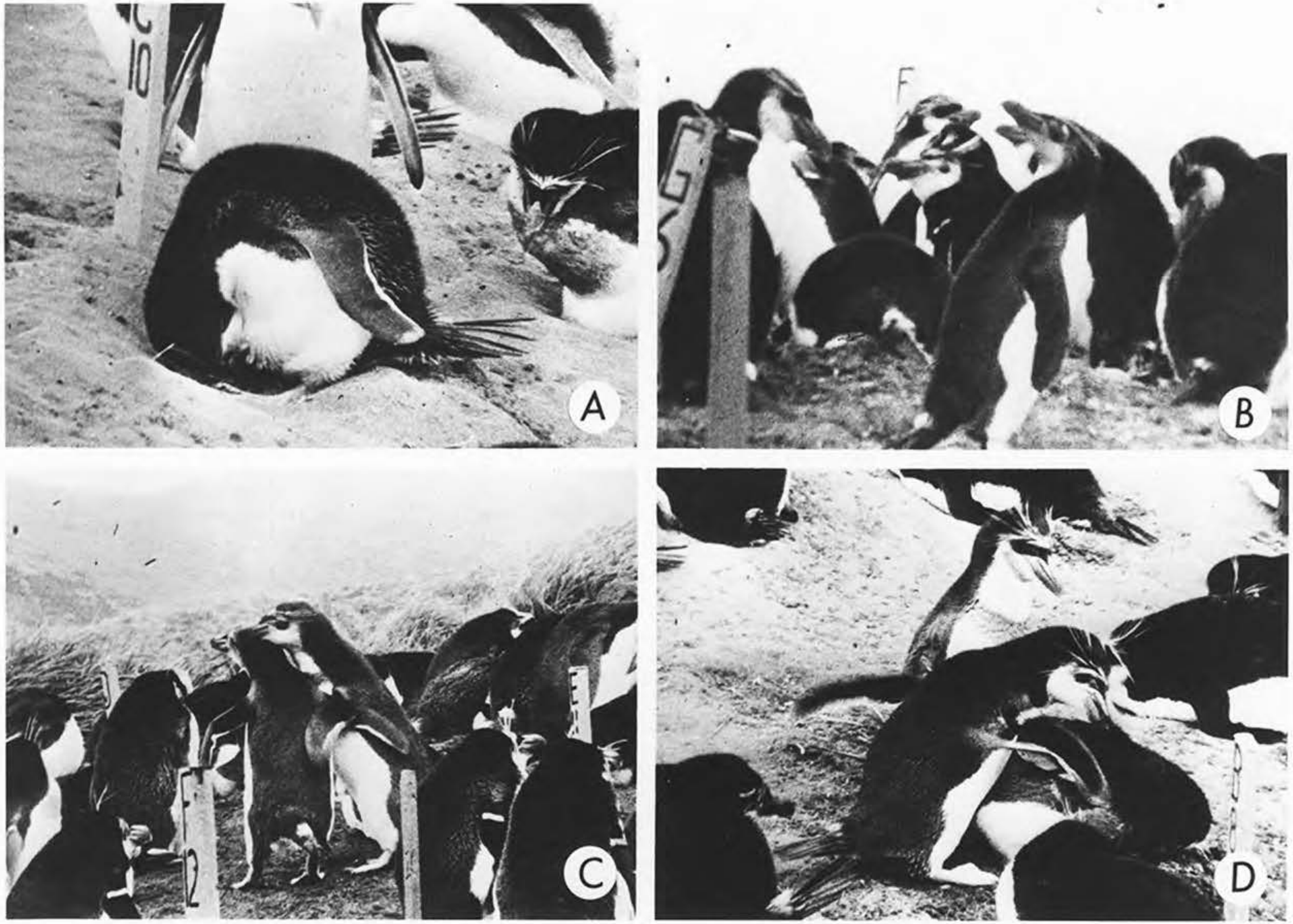
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PLATE 12

The first of three plates illustrating the Head Wobble display (HW), followed by a short bout of Flagging (F). The pair of birds is in the Inland Colony.

Plate 12a	Both birds performing a HW display. The male is on the left. Note that in both birds the wings are by the sides.
Plate 12b	The male is moving his head up from the HW. His wings have already moved to the 45° back position. The female has already started to Flag, as her HW display was shorter than the male's.
Plate 12c	The male is now elongated (LS) and his head is vertical, and has just started to move to his left for the first Flag. Note the modified posture of the female, which is a result of her attempt to keep the egg at least partially covered. Compare this with the posture in Plate 2B.
Plate 12D	The male has now moved his head to the furthest point to his left.

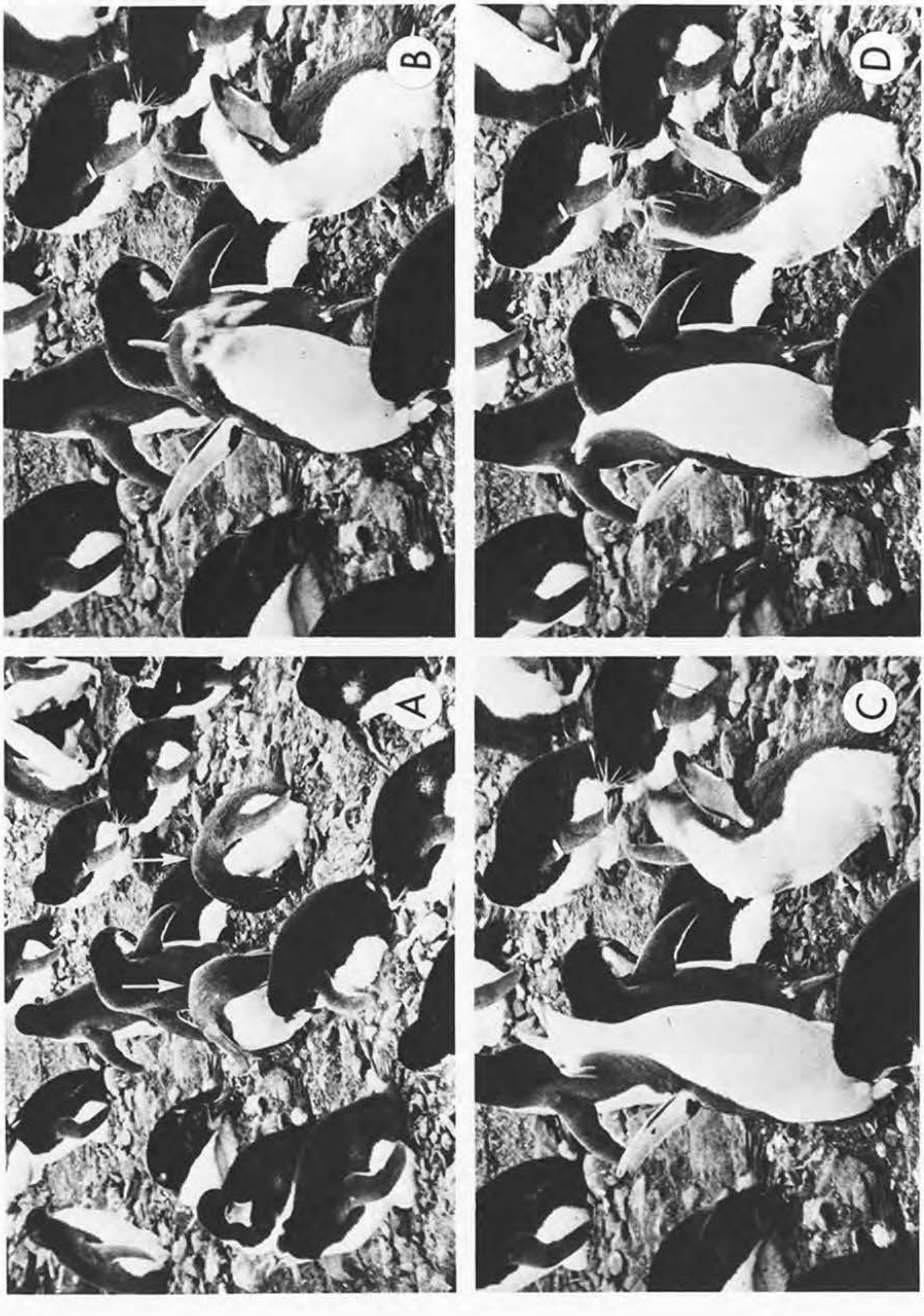
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PLATE 13

Plate 13a	The male's head is now a vertical arc, which completes one Flag.
Plates 13b-d	The male is performing another one and a half Flags.


A
B
C
D

PLATE 14

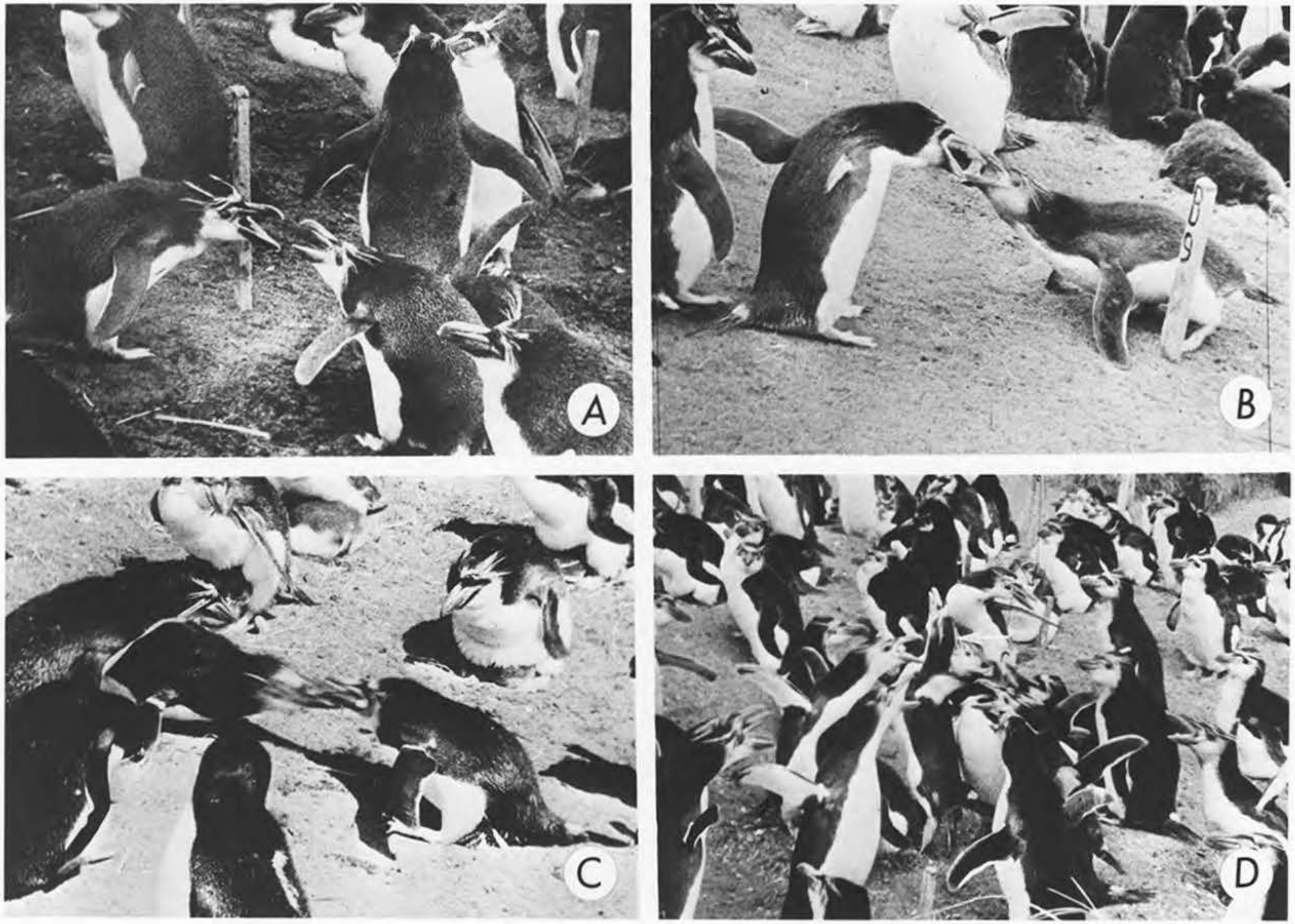
Plate 14a	The end of the third Flag by the male. The head is now 45° up, and he has stopped braying. The female has stopped Flagging and is resuming her former posture. Her wings are horizontal.
Plate 14b	The male is resuming his former posture and the wings are now horizontal. He is doing a Head Shake.
Plate 14c	The female is doing a Head Shake.
Plate 14d	The female has almost returned to the full Incubation Sit and the male is in the Short body posture with his wings 45°.

Note the lack of response by the neighbouring birds to these displays. One incubating female (Plate 13) threatened the pair.


B
D
A
C

PLATE 15

Plate 15a	Weak threat between two birds with their bills open and wings horizontal.
Plate 15b	Threat. The bird on the right is using its wings as props while elongating forward towards the other bird. The other bird has its wings 45° back.
Plate 15c	Aggression. The bird on the left has elongated completely forward and caught the other bird's open bill.
Plate 15d	A bird (arrowed) fleeing through a crowd of birds. Some are in the LCS posture, and others closer to the bird are threatening it. Note the Long body posture and the vertical head. The left wing is 45° back. The wings moved from 45° back to the sides after the bird had passed through the group of birds.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CHAPTER 6 - QUANTITATIVE ASPECTS OF THE BEHAVIOUR

I. Introduction

In the last chapter the postures and displays of the Royal penguin were described. In this chapter these postures and displays will be put into context by a description of the behaviour of the Royal penguin during the breeding season. The description of the breeding season will be qualitative, and will describe the behaviour of the breeding birds. Reference will be made to non-breeding birds where appropriate. The changes in the frequency of Flagging, copulation, Head Wobbling and threat behaviour during the season will also be described.

Quantitative aspects of the behaviour of different age groups of both sexes will also be discussed.

II. Results

A. Seasonal account of the behaviour.

Descriptions of the behaviour seen during the breeding season will be given, using the same framework as that used in Chapter I.

1. Occupation period. When a bird arrived on the beach it usually spent a few minutes preening before moving to the rookery. On the way to the rookery birds sometimes picked up stones, bones, etc., and carried them into the area of the colony.

During the first week males arriving in the colony did not display (see later), and any males already in the colony did not respond to the arrival of another male. During this period only Comfort behaviour was seen.

After September 24, when an increasing number of males was arriving daily, there was a greater number of males that would display on arrival at the colony, and those birds already in the colony displayed more frequently in response.

Typically, a male arrived at the periphery of the colony, walked around it for a short distance in the Neck Horizontal Wings Forward (NHWF) (with braying) posture, walked to a position nearest what was assumed to be his previous territory, and then ran through the colony towards his nest site. As he approached his territory he again assumed the NHWF (with braying) posture, and as he approached closer, would change his posture to the Rounded Neck Wing Forward (RNWF) posture (Plate 10b). On reaching his territory he would Head Wobble and Flag, accompanying both displays with braying (Plates 12 to 14). He could continue to Head Wobble and Flag for up to thirty minutes. Occasionally a male would assume the Vertical Stand (VS) (with braying) posture (Plate 10d) between the Head Wobble and Flag displays.

As the male passed through the colony the other birds would threaten him. Some would attempt to peck him (Plate 15d), but it was not common for a bird to actually connect when attempting this. The males around his territory would assume the Long Curved Stand (LCS) posture (Plate 10c), and from this posture most birds would Flag, although some birds adopted the VS posture before starting to Flag.

After the initial display the male would collect nesting material. This appeared to be common behaviour in the Inland Colony, but in the Sand Colony it was unusual. Seven out of eight birds observed on arrival at the Inland Colony collected nesting material, while only one in twelve birds in the Sand Colony did so.

By October 1 the only birds not displaying on arrival at the colony, or stimulating their neighbours to display, were those birds whose territories were on the periphery of the colony.

The density of the colony appeared to affect the number of Head Wobble and Flag displays given by males on arrival at their territory, or given by neighbouring birds. The clearest example of the effect of density was observed on October 2. Two males entered the colony within a few minutes of each other. One male took up a position five feet from the nearest neighbouring bird. After the initial display the male only gave two Head Wobble and Flag displays within five minutes, and none of the neighbouring birds displayed. The other male took up a position where the density was nearly at a maximum (birds forming a close hexagonal packing pattern (Plate 7a)). After the initial displays the male, and his two nearest male neighbours, Head Wobbled and Flagged continuously for five minutes. Quantitative data on this point are limited. On September 24 and September 25, when there were approximately 40 birds in the colony, 16 males were observed on arrival. These birds gave an average of 1.2 Head Wobbles and Flags. In only two cases did neighbouring birds respond after the initial display, one giving five Head Wobbles and Flags, and the other giving two. On September 30, when there were approximately 320 birds in the colony, three males gave an average of four Head Wobbles and Flags, and in each case, at least one neighbouring bird displayed, with an average of one Head Wobble and Flag each. On October 6, when there were approximately 550 birds in the colony, four males gave an average of five Head Wobbles and Flags, while the neighbouring birds gave an average of two each.

While this evidence is limited, it does suggest that the density of the neighbouring birds does have an effect on the number of Head Wobbles and Flags given.

After arrival males would settle down in the Short Sit (SS) posture, occasionally performing Comfort movements, threatening neighbouring birds, and giving infrequent Head Wobble and Flag displays, while awaiting the arrival of the females. Sometimes they collected nesting material. The twelve UK breeding birds were observed collecting nesting material on an average of one day each (range 0-3 days). Although most birds in the Sand Colony had a nest scrape, in 1967 fifteen males were not seen to begin nest digging until the arrival of the females.

The exact position of a male's territory could change as more males arrived in the colony. One male's territory gradually moved about 10 feet in five days before becoming stationary. Usually the movement was only a few feet, and presumably was a result of the increasing density, and consequent readjustment in the colony.

The females started to arrive on September 27 in 1967. The female's approach to the territory was the same as that described for the typical male. However, when the female ran through the colony, all the birds she passed, as well as the neighbouring birds of the mate, assumed the Long Curved Stand posture. This contrasted with the behaviour on the arrival of the males, when only neighbouring birds assumed the LCS posture. The mate adopted the LCS posture, and as the female approached, moved his wings 45^{o} forward (Plate 10b). When the female had arrived, the male performed the Head Wobble and Flag displays, occasionally preceeding the F display with a Vertical Stand display. The neighbouring birds usually Flagged after the LCS, while some performed a few HW and F displays.

The pair would continue the Head Wobbles and Flags for up to 10 minutes, halting when the male lay down to dig a nest scrape. Some pairs continued to display while the male dug the nest scrape, with the male either displaying while lying down, or standing up to display during bouts of digging. After five to ten minutes of digging the male stopped, and the pair sat side by side in the SS posture.

On a number of occasions two males were standing in the LCS posture, with their wings 45^{o} forward. On these occasions the female approached one male, Head Wobbled and Flagged towards him, and then moved off in the RNWF posture to the other male, which she stayed with.

Two behavioural variations were seen in the reactions of the males to the females. On three occasions copulation took place immediately after the arrival of the female. On four occasions the male responded to the arrival of the female by pecking her, to which the female responded with a HW display. In one of these cases, the male pecked the female 25 times in 20 minutes.

After the arrival of the female both birds collected nesting material. This behaviour was seen on an average of one day (range 0-4) per pair, for fifteen pairs of birds. The bird returning to the nest would place the material at the feet of its mate, and then Quiver. There was rarely a response to this display by the receiving bird, whether male or female. When there was a response, the bird would place its head above the material, and also Quiver.

If the male or female walked a short distance from the nest it always returned in the RNWF posture, and the mate responded with a HW and/or a F display.

The main displays seen in the mated pairs were the HW and/or F displays. These might be given on their own, with the mate, or in response to the mate (see later for more details).

The male continued to threaten neighbouring birds. The female, however, rarely initiated threat behaviour, and usually ignored, or occasionally displayed mild threatening behaviour, towards any neighbouring bird her mate was threatening.

Fighting and chasing was only seen during the latter half of the Occupation period. Fighting was rare, and usually involved only two males, although on two occasions three and four males were involved. The fights were spectacular, and could last up to thirty minutes. Both birds were pecked severely by neighbouring birds. The fight usually ended with one bird fleeing, being chased for a few yards by the other bird.

Although it was only possible to determine the sexes in a few cases, chasing appeared to involve a male chasing a female. These chases could take place over a distance of fifty yards around the colony, and in one case involved a pair, although the cause was unknown.

The number of copulations increased towards the end of this period, and ranged from a brief copulation prelude to complete copulation. Copulation was usually preceeded by HW displays by both the male and female, and at the end of the completed act, the male might Head Wobble or assume the RNWF posture, although he usually assumed the SS posture.

2. Laying period. There was no significant change in behaviour before laying, although the amount of activity in the colony was lessened.

Only one case of actual egg laying was observed, and in this instance the posture adopted was the same as that for excretion. After the laying of the first egg the male or female stood over it, and in some cases the incubation fold was slightly lowered. No care was taken of the first egg, and it was often quickly lost. In the Sand Colony these eggs often rolled down the colony, where they were collected by some birds. One birds was seen with six eggs in its nest scrape. Usually they were pecked at and broken, or collected by skuas or wekas.

After the laying of the second egg the full incubation posture was seen (Plate 7a). Both males and females took turns in incubating the egg until the departure of the males. In the change-over during incubation, the incubating bird elongated, and raised the incubation fold, exposing the egg. The other bird pointed its head towards the egg, and the incubating bird walked slowly backwards away from the egg. The bird which was about to start incubating walked forward over the egg in the RNWF posture, and proceeded to roll the egg under itself with its bill. Once the egg was in position the bird settled into the Incubation Sit. The other bird assumed the Head Vertically Down posture while its mate was settling down to incubate.

During this period a number of birds which had apparently lost their mates and/or territories would run through the colony, sometimes creating quite a disturbance. Those birds not directly involved reacted with a lot of Bobbing and Looking Around, which was the general reaction of birds to a disturbance within the colony.

3. Incubation period. After the departure of the male the females continued incubating. In the Sand Colony they built up their nests by digging sand from around the nest area (Plate 7b). Gradually the nest would become elevated above the general level of the rest of the colony, and would be surrounded by a ditch. This activity was most

pronounced during and after heavy rain. Behaviourally the females were very inactive, and only rarely threatened neighbouring birds, or performed a Head Wobble and/or Flag display.

It was not uncommon for non-breeding males to attack an incubating female, pecking and beating her . These attacks could last for up to ten minutes, but the female would not attempt to retaliate and would adopt the Submissive (SU) posture (Plate 11d). If these non-breeding males had mates, they would also occasionally join the males in pecking and beating the incubating female. On a few occasions non-breeding males actually attempted to copulate with incubating females.

During the incubation period females, and later incubating males, were seen to adopt the Head Down Under (HDU) (with braying) posture (Plate 11a), sometimes followed by Flagging. The Head Push (HP) display was only given by incubating females in the Inland Colony. In the few instances this display was seen it appeared to be a response to a male bird attempting to take stones from the incubating female's nest.

On their return to the colony the males went straight to their mates, and the displays given were the same as those given by the pair on the arrival of the females. The neighbouring incubating females greeted the male in the LCS posture.

The length of time between the arrival of the male and the departure of the female varied from three minutes to four hours. Usually the male took over the incubation within a few minutes of his arrival, while the female stood beside him until she departed. After displaying with the female the male would sometimes walk away from the nest, and attack one or more of the neighbouring incubating females before returning in the RNWF posture to take over the incubation.

During the latter stages of this period it was noticeable that some of the males approached a number of females before settling down on their territories, or moving to the periphery of the colony. Presumably the mates of these males had failed, and the males were looking for them. Like the females, the males rarely displayed during the incubation period.

During the period of male incubation the non-breeding birds were very mobile around the periphery of the colony. These non-breeders approached birds of the opposite sex in the RNWF posture. The outcome of these approaches was variable. Sometimes they resulted in aggression, with one bird fleeing, and sometimes in the birds sitting together. Occasionally they resulted in mutual preening, followed by the birds sitting together, or the approaching bird would attempt to preen the other bird who would then flee. These temporary pairings were ephemeral.

4. Guard period. The return of the females around the hatching period was accompanied by the same displays as those described for the arrival of the females at the beginning of the season. The females took over the incubation or the guarding of the chicks, and the males sometimes collected nesting material.

Later in the guard stage the guarding males did not respond to the arrival of a neighbouring male's mate, and only failed (see below) or non-breeding birds responded with the LCS and F displays. The behaviour of the failed breeding birds was similar to that seen during the occupation period.

During the latter stage of this period the chicks performed all comfort movements with the exception of oiling preening.

5. Creche period. During this period the colony was composed mainly of one and two year old birds, failed breeders, and chicks, with a few feeding adults. Little behaviour was seen on the few days on which observations were made during this period.

During this period one year old birds were seen to give all the displays listed in Chapter 5, with the exception of Flags, Neck Horizontal Wings Forward, Fighting, Copulation and nest building. Flagging, however, was seen in some birds kept in a small enclosure.

Chicks were seen to threaten and attack other chicks, as well as threaten adult birds, during this period. One chick was seen to approach another chick in the RNWF posture, but it lost the posture before reaching the other chick.

The size and structure of the creches varied from ones in which the chicks were well spread out, or huddles of standing chicks (Plate 7d), to some where the chicks were lying in a heap. The creches were surrounded by adult birds, mainly failed breeders, and/or had adults dispersed throughout them. Sometimes these birds pecked any chick that wandered too close, and the chicks usually ran straight back into the creche.

Earlier workers (Murphy, 1936) assumed that the adult birds around a creche acted as guardians of the chicks in the creches. Sladen (1958) has shown that these birds are unsuccessful breeding birds who have returned to their former nest sites, or non-breeding birds possessing unoccupied nest sites. He considers that their aggression towards wandering chicks is "not to persuade them to return into a creche, but to keep them away from their own territory".

My own observations support this conclusion. While the Royal and Adelie penguins show no evidence of communal behaviour in relation to the creches, it is possible that the territorial behaviour of these birds, at this stage, has an indirect effect in helping to maintain the creches.

6. General Comments. Although comfort behaviour did not appear to be correlated with any particular situation, there were some observations that indicated the possible factors eliciting some of these displays.

(a) Elongation Waggle. Sharp noises, such as hands being clapped, or sharp banging near a colony, would cause nearly all the birds to perform an Elongation Waggle. A skua diving on a section of the colony would also elicit this display, after the initial threat display towards the skua. This would suggest that an Elongation Waggle is a reaction to a frightening stimulus.

During the Incubation period, the Elongation Waggle was common. During this period, when the birds' feathers were fluffed, and in dry, windy weather when there was a lot of sand blown over the Sand Colony, the incubating birds could be seen with large amounts of sand between their feathers. During these conditions, numerous Elongation Waggles were seen, and quantities of sand were removed from the birds' feathers. Primarily, it would appear that this action was a function to remove debris from the feathers.

(b) Combing. This action was only seen after heavy rain, when the feathers were covered with droplets of water. It was followed by Swallowing. This indicated that the action may function as a means of the bird collecting drinking water, as there was no other supply of clean water during the penguin's period ashore.

(c) Head Shaking. This action usually followed most displays, while Swallowing and Nibble Swallowing usually followed preening. Nibble Swallowing could be the swallowing of debris collected while Preening. It is not known why Head Shaking should follow most displays.

B. Seasonal changes in Behaviour.

Observations made during the 1966 season showed that there were considerable changes in the amount of activity in the colonies during the breeding season. The most obvious differences were seen in the frequencies of Flagging and Copulation, and also in threat behaviour and Head Wobbling. Because of these observations, daily counts were made of Flagging and Copulation during 1967. Seasonal changes were also obtained from the regular behavioural observations of Flagging, Head Wobbling and threat behaviour.

1. Flagging. The frequency distribution of Flagging in the Sand Colony during the 1967 breeding season is shown in Figure 7a, and for the grouped study birds, in Figure 7b.

The distributions are similar, and the rapid increase may be a result of the Flagging of birds arriving in the colony, and the reaction of the birds already in the colony. The fact that the frequency began to decrease well before the population slowed down can probably be explained by the fact that the numbers of paired birds were increasing, and once birds were paired they were less likely to Flag. The low frequency during the Incubation period reflects the

the low level of Flagging seen in incubating birds, which made up the bulk of the population at this time. The second increase is mainly a result of the failed breeders returning to their territories. This may be seen by comparing the total number of Flags given by males number 6,7,8,13 and 15 (all failed breeders) in 1967, with the number of Flags given by other birds in the group (Appendix 6, Tables 1 and 2). This fact was further confirmed by counting 263 Flag displays in 25 minutes during this period. One hundred and ninety eight of these displays were given by failed breeding birds, and 54 by breeding birds, while only 11 were given by the non-breeding birds. In the study birds, the slight and probably insignificant increase during the Guard period is a result of the small number of failed breeding birds in the sample.

2. Copulation. Figure 8 gives the frequency distribution of Copulations during the period of observation in the 1967 breeding season. This graph includes both incomplete and complete acts. The frequency of copulations was high between October 7 and October 16 (the low frequency on October 11 was probably a result of the heavy rain and strong north-east winds on that day). The low frequencies during the Incubation period were a result of the non-breeding birds, while the increase in frequency during the Guard period was a result of the failed breeding birds.

The rapid increase in frequency at the start of the season was associated with the rapid increase in the number of females in the colony, and this, when considered with the rapid decrease in copulation after the start of the egg laying period, indicates that most copulation takes place well before egg laying, and probably shortly after the arrival of the females.

3. Head Wobble. Figure 9a shows the frequency distribution of Head Wobbles for the study birds in 1967.

The lack of any marked increase in the guard period was a result of the small number of failed breeders in the study birds. The totals for the failed birds, shown in Appendix 6, indicate that these birds have higher frequencies than successful breeding birds. The major difference between Head Wobbling and Flagging is that although the initial rapid increase is the same as that for Flagging, the frequency remains high until October 12, before showing a rapid decrease. The observation that there appeared to be an increase in Head Wobbling prior to Copulation may explain the longer period of high frequency of this display.

4. Threat behaviour. Figure 9b shows the frequency distribution of threat behaviour taken from all study birds in 1967. It was noted above that the females showed little threat behaviour, and therefore it was expected that the frequency distribution of threat behaviour would be dominated by that of the males. The increase was mainly a result of the increasing number of males in the colony. The slow decrease to the end of the laying period, after the majority of males had arrived, indicated that as the males became settled and their territories better defined, there was less threat behaviour, and this decreased to a minimum after the departure of the males. The slight increase later in the season was a result of the return of the males.

Comparison of the amount of threat behaviour shown by breeding and failed breeding birds (Appendix 6, Table 1) shows that the failed breeders do not show more threat behaviour than successful breeding birds.

5. Comparison with other penguins. The marked changes in the frequency distribution of the HW and F displays, and copulation, can be considered as a consequence of the short, highly synchronised breeding season of the Royal penguin.

Sapin-Jaloustre (1952, 1960) has shown that almost identical frequency distributions occur in the Ecstatic (la position extatique), and Mutual (la parade mutuelle) displays, and copulation, of the Adelie penguin in Adelie Land. The qualitative work of Sladen (1958) and Penny (1968) on the Adelie, indicates similar changes in frequency. The Adelie, like the Royal, has a short, highly synchronised breeding season.

The work of Prevost (1961) on the Emperor penguin, suggests that a similar frequency distribution may be found in the displays of the Emperor penguin, which also has a synchronised breeding season, although the breeding season is longer than that in the Adelie and Royal penguins, as a result of the extended winter incubation.

No qualitative data are available on the frequency distributions of the displays of penguins with less synchronised breeding seasons.

The writer's observations of the Gentoo penguin (Macquarie Island), indicate that the period of egg laying extends over about four weeks, and not as Carrick (1967) states, three to four months. The laying period is therefore fairly restricted, but not as much as in the Royal penguin. Gwynn (1953) also noted a fairly restricted laying period in the Gentoo penguin on Heard Island. My observations of the behaviour of the Gentoo penguin suggest that the frequency distribution of the Bowing and Trumpet displays, and copulation, are similar to those found in the displays of the Royal and Adelie penguins, but as a result of the longer breeding season, the changes are not as pronounced.

The work of Stonehouse (1960) suggests that the early and late breeding King penguins may show similar changes in the frequency distribution of their displays to those of the Gentoo penguin.

C. Quantitative differences in behaviour.

1. Introduction. In species with delayed breeding maturity associated with progressive improvement in "breeding status", corresponding changes in the type, form and frequency of displays important in the attainment of full "breeding status" would also be expected. If these changes can be demonstrated, then it is a reasonable hypothesis that the displays play a part in attainment of full "breeding status".

It is the purpose of this section to examine the frequency of all displays recorded, to demonstrate if there are changes with age or sex, and later to examine any changes in more detail.

The data from the behavioural observations were quantified and summarised, and are presented in Appendix 6. The total numbers of each display, and the number of observations made, are given for each bird, as well as the group totals.

Not all the displays described in the previous chapter were seen in the systematic observations, and Sniffing, as well as postures SS, MS, and LS are ommitted from the list. Even allowing for the differences in the number of observations for different birds, there is a great deal of individual variation in each group. This is well illustrated by the data for the UK males, which was the most homogeneous group. As well as the individual variation, there is variation between the different age groups in both sexes.

To clarify the differences seen in Appendix 6, calculations were made of the percentage number of days on which each display was observed (Table 4). Using this method, even the most common displays had a relatively low percentage occurrence, but this does not alter the importance of the display. The percentage occurrence for Flagging and Head Wobbling in UK males is less than that seen in the 6+ year old males. This is, in part, a result of the UK males' longer period ashore at the start of the breeding season, when little or no displays are given, and also a result of the longer period after egg laying, when the frequency of Flagging and Head Wobbling is also low.

The percentage occurrence of the Comfort movements varied widely, and there were no definite age or sex differences. Of the most frequent movements (P, EL WAG, SW and HSH), P and EL WAG were concerned with the maintenance of the body surface, while SW commonly followed a bout of preening. Head Shaking commonly occurred after other displays. The percentage occurrence of the rest of the comfort movements was low, and they were of no apparent significance.

The percentage occurrence of social preening was low. However, three to five year old males and females had a distinctly higher percentage occurrence of MP, while in

PM only the males had this pattern.

Threat behaviour was classed according to whether it was directed towards the mate (THM), a neighbouring bird (THNB) or a passing bird (THPB). In all these divisions, the percentage occurrence tended to be higher in the younger age groups. In all cases males had a higher percentage than females.

Threat towards a neighbouring bird was more frequent than towards a passing bird. The low percentages of threat towards a passing bird in the UK, 6+ and 6 year old birds is probably a result of their better nest sites, which results in less movement of birds past them.

In the displays F, HW, HFL and HD there was a general increase in percentage occurrence with age, and the males showed higher percentages than the females. The RNWF display, although showing a low percentage occurrence, was more frequent in the three to five year old birds of both sexes.

Of the other displays, only WA and R showed any changes with age, the percentage occurrence decreasing with age in the birds, and being similar for both sexes. These displays are a measure of the increasing ability of birds to secure a stable territory as they age.

The results of this preliminary analysis show that the displays F, HW, HFL, HD, TH, PM, MP and RNWF, because of the age and/or sex difference, may be important in the attainment of full breeding status. All threat displays were grouped, and in the case of F, HW and TH, their high frequency (Appendix 6) may be important in the attainment of full "breeding status".

In order to examine the age and sex differences in the displays listed above in more detail, the percentage number of days on which a display was seen was calculated for two situations - with and without a mate. These two situations were chosen because in the comparatively homogeneous environment of a Royal penguin colony, these were the only situations in which a bird could be classed objectively. (Refer to Chapter 2 for discussion on the use of the term 'mate').

2. Age differences. The age differences in the displays were examined in two ways. Firstly, the data for each display, in each of the groups in the two situations, were compared with those of the next oldest group, using the Mann-Whitney U test (Siegel, 1956). The results of this analysis are given in Table 5. Secondly, the regression coefficient "b" was calculated for each display against age, in the two situations (Table 6).

Table 5 shows that in only 13 of the 154 pairs was there a significant difference between adjacent age groups. However, all the values for "b", except that of TH for males with a mate, were significantly different from zero at the 5% level of significance. Positive values of "b" would be expected in those displays whose functions were important in the attainment of full "breeding status". In the cases of RNWF, MP and PM, negative values of "b" were obtained. Earlier in the chapter it was noted that these displays are often associated with the approach of one bird to another, and therefore higher frequencies of these displays would be expected in those birds without a mate who were actively seeking one, i.e. non-breeding birds. The bulk of non-breeding birds are younger than six years old, and the number with mate increases with age, hence the negative value of "b". The differences between males and females in the pattern of frequencies of PM and MP is a result of the non-breeding females less frequently initiating social preening, but responding to the PM's of the males.

The negative values of"b" for threat without a mate, in both males and females, is a result of the greater mobility of the non-breeding birds, which brings them into contact with strange birds. The positive value of "b" for threat with a mate may be a result of the increased aggression, and/or greater tendency to react to any intrusion into a territory by a neighbouring bird, as a bird obtains a more secure territory with a mate.

There is no apparent explanation for the negative values of "b" for HD in females in both situations.

3. Sex differences. The data for each group in each situation, for both sexes, were compared, using the Mann-Whitney U test (Table 7), and the values of "b" were tested for significant differences (Table 8).

In the no-mate situation the comparison of the 6+ year old groups is not valid, as only two females were without mates. In the younger age groups there was no pattern of significant differences.

In the situation with a mate there was, in general, no significant difference between the males and females in birds younger than six years. In the older age groups significant differences were only found in HW, TH, F, HD and HFL. These results indicate that the occurrence of F, TH and HD is significantly greater in males, while there is no significant difference in the HW and HFL, except in the six year old birds.

In comparing regression coefficients, the only information gained is whether the degree of change of the dependent variable (percentage occurrence of a display), compared with change in the independent variable (age), is significantly greater or smaller in one of the groups.

In the no-mate situation the values of "b" are significantly greater in the males for all displays except RNWF, which is not significantly different. Therefore, although in general the differences between the males and females of the same age are not significant, they summate, and are expressed in a significant difference in the values of "b", which shows that the changes with age are more pronounced in the males.

In the with-mate situation only the values for threat are not significant. The "b" values for the males are significantly larger, except for HW and RNWF. This is important in the case of HW, in view of the (above) apparent relationship between HW and copulation.

4. Differences in situation. The two situations were compared using the Mann-Whitney U test for all groups, and the values of "b" were also tested for significant differences (Tables 5 and 8).

In only one of the significant differences was the frequency higher in the no-mate situation. Only in the HW display was there a consistently significant difference between the age groups in both sexes. The lack of a significant difference in the 6+ and 6 year old groups of females was a result of the small number of days spent without a mate. To a lesser extent this also applied to HD and HFL.

Only in the UK and 6+ (breeding males) year old groups was threat significantly different between the two situations. This tends to support further the above statements on the effect of a mate and territory on threat behaviour.

The values of "b" for all displays (except HD for females) for both sexes with mates, are significantly greater than the no-mate situation, which indicates an increasing effect of the female on the frequency of the displays of the male.

5. Summary. The analysis of the effect of age, sex and situation on the eight displays has shown that there is either a decrease or an increase in the frequency of all displays in both sexes with age, and that except for HW and RNWF the changes are greater in the with-mate situation for both sexes.

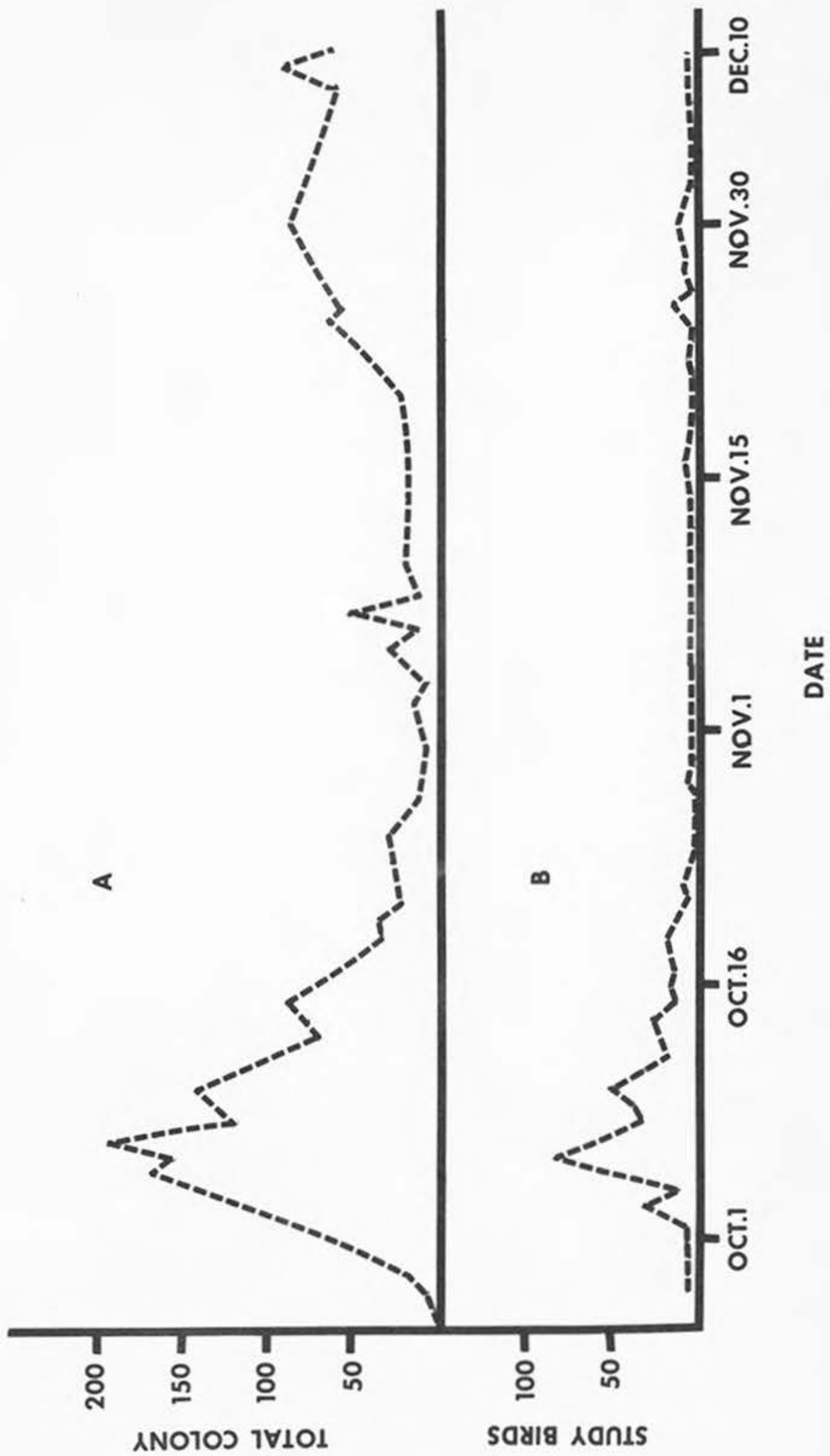
The displays PM, MP, RNWF, TH without-mate, and HD for females, show that the frequency decreases with age. In the cases of PM, MP and RNWF this trend was explained by the fact that non-breeding birds frequently approached other birds in attempting to obtain a mate. In the case of threat in the no-mate situation, this trend was a result of the increased mobility of the non-breeding birds.

The comparison of the individual groups, using the Mann-Whitney U test, has shown that the trends with age are gradual, and that, in general, there are no differences between the sexes or situations. However, significant differences were noted in the birds older than five years old (generally breeding birds) in the F, HW, HD, HFL and TH displays, with regard to differences between the sexes. In these displays consistent differences were also seen in mate/no-mate comparisons.

In the preliminary analysis, eight displays were considered possibly significant in the attainment of full "breeding status". From the above analysis it is apparent that three displays (PM, MP and RNWF) may function in the formation and maintainance of the pair bond. The significance of the other five displays will by analysed in more detail in the next chapter.

FIGURE 7

Figure 7a	The frequency distribution of the Flag display in the Sand Colony during the season. The daily values represent the average number of Flag displays seen during three 5-minute observation periods per day, during the 1967 season.
Figure 7b.	The frequency distribution of the Flag display during the season, obtained by grouping the data from all study birds.


A
B
NO. F
TOTAL COLONY
NO. F
STUDY BIRDS
200
150
100
50
100
50
OCT.1
OCT.16
NOV.1
NOV.15
NOV.30
DEC.10
DATE

F7

FIGURE 8

The frequency distribution of the number of copulations per hour, during the 1967 season. Incomplete and complete copulations are grouped.

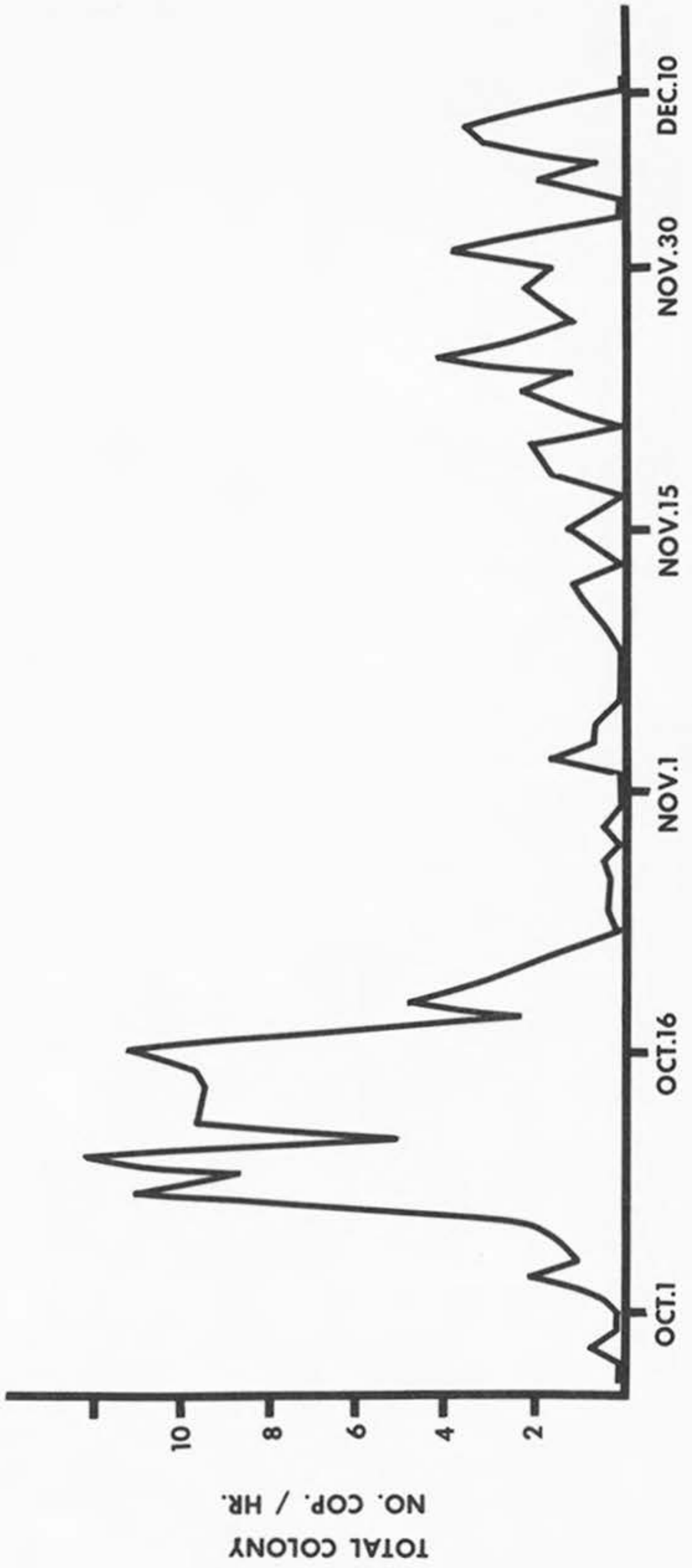

TOTAL COLONY
NO. COP. / HR.
10
8
6
4
2
OCT.1
OCT.16
NOV.1
NOV.15
NOV.30
DEC.10
DATE

FIGURE 9

Figure 9a	The frequency distribution of the Head Wobble display during the season, obtained by grouping the data from all the study birds.
Figure 9b	The frequency distribution of the Threat displays. The data were obtained from the study birds.

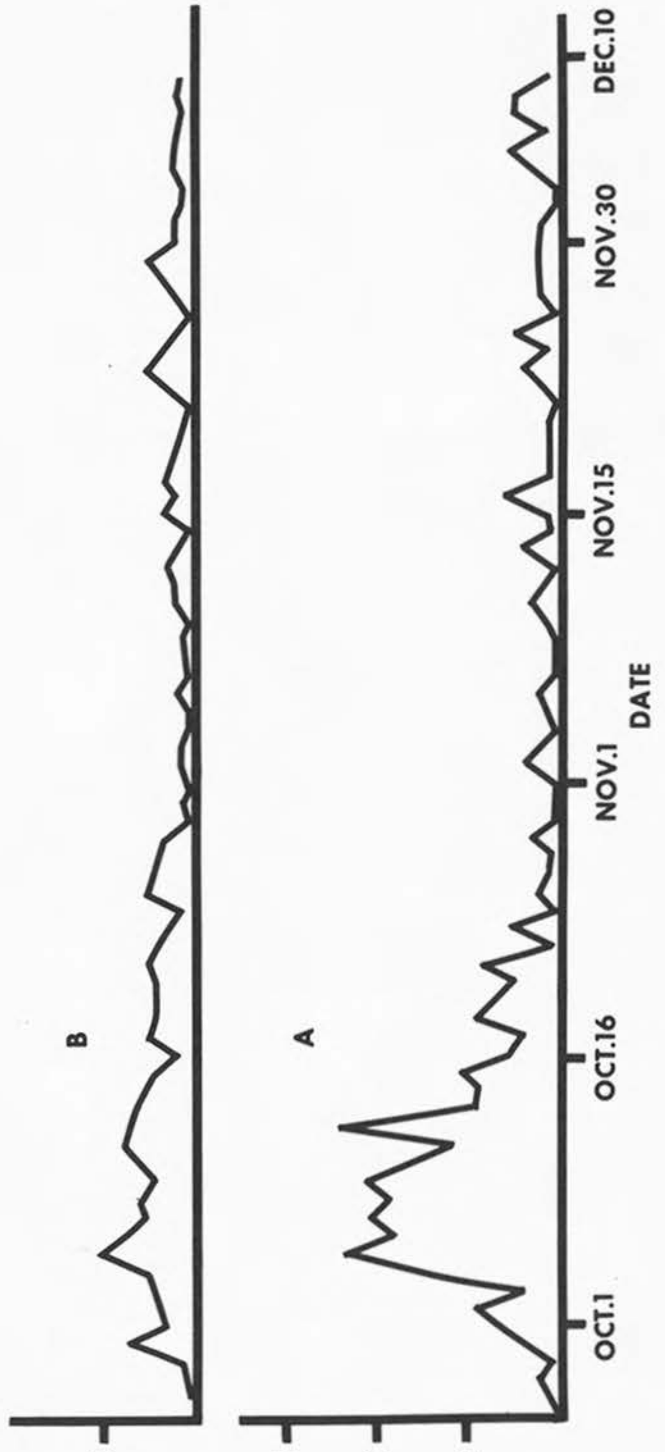

STUDY BIRDS
NO. TH
50
B
NO. HW
150
100
50
A
OCT.1
OCT.16
NOV.1
NOV.15
NOV.30
DEC.10
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TABLE 4

The percentage number of days that each of the displays listed was seen for each age group, in both males and females. 1966 and 1967 data grouped.

	Males							Females						
Behav	UK	6+	6	5	4	3	2	6+	6	5	4	3	2	1
F	17	26	27	18	18	9	-	7	4	2	8	3	-	-
HFL	14	20	18	15	13	7	-	9	4	6	4	3	2	-
HW	32	42	44	30	37	23	5	24	16	16	19	15	5	-
HD	14	21	14	25	17	17	9	13	9	13	14	15	2	-
ELWAG	20	35	42	53	48	53	37	29	20	36	36	46	44	20
ELFLAP	0	1	2	7	4	7	-	2	1	4	6	1	3	3
ELSH	1	-	-	1	1	2	2	0	-	2	1	-	3	-
TP	4	2	6	3	3	8	2	3	2	4	3	3	2	-
TP1	1	1	-	1	2	2	-	-	1	-	-	1	-	-
TP2	1	3	3	4	4	8	7	4	3	8	6	5	5	-
SL	26	17	12	19	21	16	14	16	10	13	19	14	8	3
L	-	1	-	-	-	-	-	-	1	-	-	-	-	-
P	46	50	53	71	71	63	53	48	36	56	59	67	37	33
PM	8	6	4	18	21	15	-	9	4	5	9	12	-	-
PBM	1	4	3	8	8	6	2	7	3	3	6	8	-	-
MP	8	8	4	19	15	14	-	9	8	12	12	15	-	-
G	2	8	10	11	8	10	2	3	1	4	9	6	5	-
SW	15	40	31	56	50	59	4	27	7	39	33	38	42	-
NISW	4	4	2	13	6	14	19	2	1	9	10	6	11	-
NI	0	1	4	2	2	3	-	-	-	-	3	1	5	-
HSH	23	39	39	42	39	42	33	22	6	42	29	37	33	3
THPB	13	15	19	29	24	36	33	19	13	22	17	22	27	10
THNB	29	40	28	50	40	48	39	23	13	20	22	26	33	30
THM	0	1	-	3	8	5	-	-	-	-	1	2	-	-
CM	9	5	6	15	9	13	7	3	5	8	7	8	10	-
WA	7	13	18	29	32	50	46	9	9	31	36	43	50	44
R	-	-	3	4	3	8	4	0	1	2	10	8	8	-
EX	2	4	5	5	8	7	9	2	2	4	4	6	8	3
RNWF	0	1	-	5	8	4	2	0	1	4	10	8	3	3
LCS	1	1	-	2	2	1	-	-	-	1	1	1	-	-
COP	1	1	1	3	4	4	-	2	1	2	2	2	-	-

TABLE 5

The percentage number of days on which the listed displays were seen, was calculated for each study bird. The data for each pair of groups listed (UK males and 6+ year males etc. and UK males with and without a mate etc), were compared using the Mann-Whitney U test. Significant differences are shown; * (p 0.05), ** (p 0.01), *** (p 0.001) if the older group or the mate situation is significantly greater than the other group. The symbol + is used if the reverse is true. The dash (-) indicates no significant difference at p 0.05.

		No mate						Mate						Mate - No mate						
		UK/6+	6+/6	6/5	5/4	4/3	3/2	UK/6+	6+/6	6/5	5/4	4/3	3/2	UK	6+	6	5	4	3	2
MALES	F	-	-	*	-	-	*	-	-	-	-	-	-	-	+++	-	-	-	**	-
	HW	++	-	*	-	-	-	-	-	-	-	-	-	*	-	*	***	**	-	-
	TH	-	-	-	-	-	-	-	-	-	-	-	-	*	*	-	-	-	-	-
	HFL	-	-	-	-	**	-	-	-	-	-	-	-	-	-	-	*	-	**	-
	HD	-	-	-	-	-	-	*	-	-	-	-	-	-	-	-	*	*	**	-
	RNWF	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	PM							**	-	-	-	-	-							
	MP							**	-	-	-	+								
FEMALES	F		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	-
	HW		-	-	-	-	-		-	-	-	-	-		-	-	***	**	**	-
	TH		-	-	-	-	-		-	-	-	-	-		-	-	-	-	-	-
	HFL		-	-	-	-	-		-	-	-	*	-		**	-	*	**	-	-
	HD		-	-	-	-	*		-	+	-	-	-		-	-	**	**	-	-
	RNWF		-	-	-	-	-		-	-	+	-	-		-	-	-	-	-	-
	PM								-	-	-	-	-							
	MP								-	-	-	-	-							

TABLE 6

The regression coefficients b for the percentage of days on which a display was seen against age in the mate, and no mate situations. The number of birds in each sample, and the standard deviation of the regression coefficient b (Sb) are given. The significance of b at the p 0.05 is given (S), if b is not significant (NS).

SITUATION

Females						Males					
Sit.	Dis.	No. Birds	b	Sb	Sig^n.	Sit.	Dis.	No. Birds	b	Sb	Sig^n.
NM NO MATE	F	86	0.15	0.67	S	NM	F	105	6.38	0.88	S
	HW	86	-0.42	0.86	S		HW	105	7.83	0.94	S
	TH	86	-3.98	2.50	S		TH	105	-4.67	1.43	S
	HFL	86	0.68	0.53	S		HFL	105	3.81	0.71	S
	HD	86	-0.58	1.18	S		HD	105	1.50	0.79	S
	RNWF	86	-0.75	1.26	S		RNWF	105	-0.79	0.70	S
MATE	F	70	0.88	0.65	S	M	F	77	1.69	1.15	S
	HW	70	2.42	1.74	S		HW	77	0.65	1.42	S
	TH	70	0.23	1.63	S		TH	77	0.08	1.56	NS
	HFL	70	1.54	0.80	S		HFL	77	2.10	1.13	S
	HD	70	-0.69	1.54	S		HD	77	0.21	1.25	S
	RNWF	70	-1.60	0.77	S		RNWF	77	-1.47	0.92	S
	PM	70	-2.91	1.43	S		PM	77	-4.86	1.37	S
	MP	70	-3.52	1.47	S		MP	77	-3.85	1.29	S

TABLE 7

Comparison of the percentage number of days on which a display was seen, for males and female in the mate, and no mate situation. The statistical test used was the Mann-Whitney U test. The level of significant difference is shown in the table. In all cases the male were significantly greater than the females.

		UK	6+	6	5	4	3	2
No mate	HW		-	-	0.05	-	-	-
	F		-	-	0.001	-	-	-
	TH		-	-	-	-	0.05	0.01
	HFL		-	-	-	0.05	-	-
	HD		-	-	-	-	-	-
	RNWF		-	-	-	-	-	-
Mate	HW	-	-	0.05	-	-	-	
	F	0.025	0.025	0.05	0.05	-	-	
	TH	0.05	0.05	-	-	-	0.025	
	HFL	-	-	0.025	-	-	-	
	HD	0.05	0.025	-	-	-	-	
	RNWF	-	-	-	-	-	-	
	PM	-	-	-	-	-	-	
	MP	-	-	-	-	-	-	

TABLE 8

The values of p for significant differences in the value of the regression coefficients, b, for the four comparisons in the listed displays.

M = Male F = Female
(M) = Mate situation (NM) = No mate situation

	Display							
Comparison	F	HW	TH	HFL	HD	RNWF	PM	MP
M(M)-M(NM)	0.001	0.001	0.001	0.001	0.001	0.001		
F(M)-F(NM)	0.001	0.001	0.001	0.001	0.05	0.01		
M(NM)-F(NM)	0.001	0.001	0.05	0.001	0.001	0.05		
M(M)-F(M)	0.001	0.001	0.05	0.001	0.001	0.05	0.001	0.05

CHAPTER 7 - ANALYSIS OF THE BEHAVIOUR

I. Introduction.

Using the age, sex and situation differences in the displays as a basis, I proposed that a number of displays played a part in the attainment of full breeding status. In this chapter I propose to analyse the displays in terms of their function and causation, in order to interpret more accurately the differences in frequency of the displays found in the different age and sex groups.

Tinbergen (1959) outlined the methods which can be used to interpret field observations in terms of the causation and function of the displays.

Ideally, the study of causation is an investigation of the internal and external factors which cause an animal to act in a particular manner. To explain fully the causation of behaviour, rigorous experimentation is required, and because of this, the deduction of causation from field data is best thought of in terms of gross motivation.

A number of workers have shown that much of the behaviour seen in fishes and birds may be explained in terms of the presence of two or more conflicting tendencies (Hinde, 1953; Andrew, 1956, 1957; Morris, 1958; Stokes, 1962; Kruijt, 1964; and Blurton Jones, 1968). It may be said that 'tendency' implies that an animal is likely to behave in a particular manner. The causal factors of the behaviour are partially present at least, but in the initial stages of analysis the term tendency has the advantage of not requiring the causal factors to be specified (Hinde, 1966).

Conflict behaviour is considered to be the result of the activation of two or more incompatible tendencies, and its expression is variable. It may take the form of Intention movements, Ambivalent behaviour, Compromise behaviour, etc. (Hinde, 1966).

The two main behavioural groupings that have been studied in terms of the conflict theory are Agonistic and Courtship behaviour.

Moynihan (1955) showed that threat postures in the Black-headed gull were the result of the varying strengths of the tendencies to attack and flee from a rival. Stokes (1962) found that in the agonistic behaviour of the Blue tit "...of the nine elements of agonistic posture, only two were predominantly indicators of the fleeing tendency". All the other elements showed some attack tendency, as well as a fleeing or staying tendency. He could find no combination of elements that would always indicate attack, fleeing or staying, and considered that each element is itself the result of the action of the three tendencies.

Hinde (1953, 1954) and Morris (1958) have shown that courtship behaviour is the result of a conflict between the tendencies to attack, flee and behave sexually.

The conflict theory of behaviour has been a valuable model in helping to understand the motivation of behaviour. However, as Hinde (1966), Blurton Jones (1968) and Simpson (1968) have pointed out, it suffers from a number of faults, and cannot be applied universally. Despite its inadequacies it still remains a useful theory in the initial stages of analysis.

The function of a display may be deduced from the situation in which it occurs. This method is highly subjective, and may lead to errors or simplication of interpretation. Like the study of causation it requires rigorous experimentation, but as Tinbergen (1959) has pointed out, the "natural experiment" can be of great value in interpretation.

Finally it must be stressed that this study is purely observational, and as such the conclusions must be tentative.

II. Causation.

Tinbergen (1959) sets out three methods for the analysis of the causation of displays - Form analysis, Temporal association, and Situation analysis. All these methods will be used.

A. Form analysis.

1. Introduction. The basic assumption of this method is that the elements of a display act as indicators of a particular tendency. Therefore if an element of attack behaviour is seen in a display it can be assumed that this element is an indicator of an attack tendency. The method involves looking for elements of a display which are also elements of attack, fleeing, sexual, or feeding behaviour, etc. It requires only a precise knowledge of the displays of a species, and has been used in the analysis of motivation by a number of workers (Andrew, 1956; Hinde, 1953; Morris, 1958; Tinbergen, 1959; Stokes, 1962; and Blurton Jones, 1968).

As Tinbergen (1959) and Stokes (1962) have shown, the reliability of an element as an indicator of motivation is variable. Another difficulty in deducing the tendency expressed by an element is that an element may be used in more than one situation. The Hammering position in the Blue tit is seen in both feeding and attacking. On the basis of form, this element may indicate either an attack or feeding tendency (Blurton Jones, 1968).

Despite these objections, form analysis still remains a useful method in preliminary analysis of behaviour, and also for comparison with other methods.

2. Analysis. The displays of the Royal penguin will be analysed in terms of attack, fleeing and sexual tendencies. It must be noted that fleeing is rarely seen in breeding birds, and it is likely that a tendency to stay is very strong.

The posture of the male during copulation is the strongest expression of the sexual tendency. The elements are as follows: the wings at the start of the copulation attempt are 45° forward, and at the point of apposition are horizontal forward. The movement of the wings forward of the body is therefore assumed to be an expression of an increasing sexual tendency. During the copulation attempt the head is bowed to the level of the feet. Increasing depth of the bow is therefore assumed to be indicative of an increasing sexual tendency. During the copulation attempt the head is vibrated over the head of the female, and this vibration is assumed to be an expression of the sexual tendency.

The attack tendency is most strongly seen in fighting. In fighting the Royal uses its wings to beat an opponent, and the wings are moved to the 45° or parallel back position before being moved forward. The wing position is therefore assumed to indicate the strength of the attack tendency - the further the wings are held towards the back the stronger the tendency. The elongated body is also considered an expression of an attack tendency - the more elongated the body the stronger the tendency (cf. fleeing).

In fighting the position of the head depends on whether the opponent is above or below it, and is therefore very variable. It is of no use as an indicator of the attack tendency.

The bill is open in both fighting and aggression, and may be considered an indicator of an attack tendency. However the reliability of the open bill as an indicator is dubious in view of Stokes (1962) finding that in a Blue Tit in an aggressive situation, an open bill indicated a greatly reduced probability of attack, and a corresponding likelihood of escape, while in a non-aggressive situation, an open bill indicated a slightly increased likelihood of attack.

Fleeing from an attacking bird was rarely seen. On all occasions the bird elongated to the long body posture with the chest thrust out and the head vertical. The position of the wings varied from the 45° to horizontal position. Birds running through the colony adopted a similar posture, but with the head horizontal. If attacked, the birds moved their heads to the 45° up or vertical position, and moved their wings to the side position. The position of the head above the horizontal is therefore considered an expression of the fleeing tendency, while the movement of the wings towards the side is thought of as a reduction in the attack tendency, with the increased fleeing tendency expressed by the movement of the head above the horizontal.

The long body posture is seen in both attack and fleeing, and is therefore not a reliable indicator of either tendency. The general reaction of a bird to a disturbance in the colony is to elongate to the long body posture and look around. This response obviously prepares the bird for either flight or fight, should either be necessary, and a long body may therefore indicate a conflict of attack and fleeing tendencies.

The presence of a staying tendency can only be seen in those situations in which attack or fleeing are normally evoked but do not appear, e.g. incubating birds that were attacked, but which did not retaliate or move away. The only response in this situation was to adopt the SU posture. A staying tendency may also be inferred from the failure of breeding birds to flee when attacked.

3. The displays. The motivation of the displays will be examined by comparing the elements of the displays with those listed above. The use of the terms strong, moderate and weak are subjective.

(a) Head Wobble (HW). The main elements of the Head Wobble (head bowed towards the feet and vibration of the head) are assumed to indicate a strong sexual tendency. The strength of the tendency is assumed to increase with increasing depth of the bow and duration of the vibration. The sexual tendency is also assumed to be indicated by the position of the wings forward of the body. Evidence that an attack tendency is present is assumed when the wings are towards the back of the bird.

(b) Rounded Neck Wings Forward (RNWF). The position of the wings and head are assumed to indicate the presence of a sexual tendency (less than that in HW), and the forward position of the head a weak attack tendency.

(c) Neck Horizontal Wings Forward (NHWF). The elongated neck, horizontal to the ground, is assumed to indicate an attack tendency (greater than in RNWF), while the forward position of the wings indicates a weak sexual tendency (less than in RNWF).

(d) Vertical Stand (VS). The vertical head, long body and wings 45° back are assumed to be an expression of both attack and fleeing tendencies.

(e) Head Down (HD). The movement of the head towards the ground is assumed to indicate a weak sexual tendency. This display is considered to be a low intensity HW display

(f) Head Flick (H FL) The elements of this display are the same as in Flagging, and it is considered to be a low intensity Flag display with similar motivation.

(g) Round Neck (RN) The bowed head indicates a weak sexual tendency.

(h) Long Curved Stand (LCS) The forward elongation of the head and position of the wings is assumed to indicate a strong attack tendency, while the upward pointing head indicates a weak fleeing tendency. The forward position of the wings in some Long Curved Stands indicates a weak sexual tendency. The long body (see above) is assumed to be indicative of a conflict between the attack and fleeing tendencies.

(i) Flag (F). This highly variable display is assumed to be capable of expressing a wide range of the strengths of the competing tendencies. The strength of the attack tendency can be gauged from the wing position, and a fleeing tendency is indicated by the position of the head above the horizontal. The body posture is assumed to be indicative of the strength of the conflict between the fleeing and attack tendencies.

The most conspicuous element of the Flag display is the flagging of the head. This flagging is characterised by the constancy of the time taken per flag, regardless of the length of the bout, which suggests that Flagging has developed a typical intensity. This typical intensity, together with the prominent supercilliary plumes, suggests that this movement is ritualised.

There are three different movements of the head in the Royal penguin which may have become ritualised into Flagging - the vibration of the head in copulation, the shaking of the head when biting in fighting, and head shaking. In the first case it would be associated with a sexual tendency, in the second with an attack tendency, and in the third it would not be associated with a major tendency. However, as Hinde (1966) has pointed out, there may be a motivational change, and the movement may have come to be governed by different causal factors to those to which it was originally related. The motivation of Flagging cannot be deduced in this analysis.

(j) Agonistic. The strength of the attack tendency in threat behaviour may be judged by the degree of elongation towards the other bird, and by the degree to which the beak is opened (see above for comments on the value of the open beak as an indicator of an attack tendency). The position of the wings cannot always be used as an indicator, as they may be used as props when the bird elongates forward. The relative strength of the attack tendency in two birds engaged in a threat display may be gauged by the position of the wings at the end of the display. If the wings were 45° back, then the attack tendency was stronger in that bird, than in the bird that had its wings by the side.

In mobile birds, fleeing is usually preceeded by a threat display. The potential loser re-orientates its body away from the other bird while maintaining its head face on, and elongating the body. Slight movements away may be associated with this movement. The re-orientation and the elongation of the body is indicative of an increasing fleeing tendency. By analogy, the turning of the head to one side when withdrawing from a threat display could be indicative of an increasing fleeing tendency.

4. Discussion

The analysis of the form of the displays shows that there are conflicting tendencies, or that conflicting tendencies can be expressed in them, e.g. HW and LCS. The wide variability of some of the displays (HW and F) suggests that these displays may be of use in indicating subtle changes over a wide range of strengths of conflicting tendencies. This is obviously important if a bird uses these displays to communicate its motivation to another bird.

From the analysis it would appear than the main tendencies are attack and sexual, with a relatively weak fleeing tendency, which is probably inhibited by a strong staying tendency, although this tendency can only be deduced from the lack of fleeing in situations where fleeing would be expected.

B. Temporal association.

1. Introduction. The second method listed by Tinbergen (1959) is that of temporal association of displays.

Tinbergen argues that the basis of this method rests on the empirical fact than an animal does not suddenly change from one motivational state to another in a constant environment, e.g. a feeding bird does not flee suddenly unless a flight provoking stimulus appears suddenly. Therefore displays which show close temporal associations have common causal factors.

There are a number of difficulties in the application of this method, as pointed out by Andrew (1956), Tinbergen (1959), Hinde (1966), and Blurton Jones (1968). Rarely is the environment constant. The display of bird A may stimulate bird B to display, and this display may affect the following display of bird A. This difficulty may be overcome, by the use of dummies, but as Tinbergen (1959) has shown, dummies cannot always be used. Another difficulty is that a display may not be followed by a 'pure' expression of one or the other of the tendencies with which it is normally associated. Hinde (1955-6) found that the pivot display is followed on 68% of occasions by agonistic behaviour, and by sexual behaviour on only 8% of occasions However, other evidence suggests that a sexual tendency is important in the display

Andrew (1956) has shown that displays may occur together, not because they share common causal factors, but because they both have a low priority, and can only occur in the absence of strong tendencies to behave in other ways. He explains the irregular toilet behaviour in *Emberiza* spp. by assuming that the causal factors for the behaviour are always present, but can only be expressed when the conflicting tendencies inhibit each other. This is the dis-inhibition hypothesis, which has be supported further by the detailed studies of Sevenster (1961).

2. Results. Two methods of analysis using temporal associations were used - association with a 'pure' tendency, and sequence analysis.

(a) Association with a 'pure' tendency. As a result of the rarity of fighting and fleeing, the only 'pure' tendency that could be used was the sexual tendency. It is assumed that a Copulation Prelude, Copulation Attempt and complete copulation were all expressions of a relatively 'pure' sexual tendency, and therefore the displays associated with copulation are assumed to have a sexual tendency.

The degree of temporal association between various displays and display sequences, and between copulation, for males and females, is shown in Table 9, by significant values of X^2 (chi-squared) (method in Siegel, 1956). In the males highly significant values are obtained for the HW display, both when preceeding and following copulation, and for the RNWF display when preceeding copulation. The display sequences HW/F, HW/HFL, and the displays LCS and F have significant negative values of X^2. In the females there is a significant positive value of X^2 for the display HW following copulation.

In the displays of the female to which the male appears to respond with a CP, the HW display had a significant positive value for X^2, while the display sequence HW/HFL had a negative significant value.

The significant positive value found for the HW and the RNWF displays confirms the results of the form analysis for motivation of these displays. The significant negative values for the LCS and F displays, and the HW/F and HW/HFL display sequences, confirm the lack of, or low value of the sexual tendency found by the analysis of form in these displays.

The negative value for HD in the displays of the females after copulation does not indicate unequivocally that there is no sexual tendency present, but rather it may be argued that in view of the small number (three) of displays seen after copulation, it is a measure of the weakness of the sexual tendency. The dominance of HW after Copulation indicates that the sexual tendency is usually relatively high after Copulation, and only rarely is it weak, and in that case HD may be seen instead of HW.

(b) Sequence analysis. If displays are associated in time, then it can be assumed that they have a similar motivation. To test the degree of association between displays, the number of times a display followed eight displays (F, HW, HFL, RNWF, LCS, PM and MP) was calculated. To decide whether the observed association between the various pairings differed from that expected in a random association, the chi-square values were calculated for each pair, using the total number of sequences in which each display featured, and the total of all sequences.

The data for all breeding males (UK and 6+) were grouped for the no-mate and mate situation. Table 10 shows the significant values for chi-squared ($p < 0.05$) of the males. Those marked with a plus are more common than expected, and those with a minus, less common

The data for the breeding females and the non-breeding birds are not given, as they do not differ from that of the breeding males.

In the males, the pattern of significant values for chi-squared are similar in both the no-mate, and mate situations.

The chi-squared values for HW show that this display is rarely followed by HW, TH, HD, C, MP or PM. The lack of a positive association with TH confirms the form analysis. The negative values for HW and HD indicate that a relatively strong expression of the sexual tendency is rarely followed by another strong or weak expression of this tendency.

In the previous section it was concluded that the sexual tendency was still relatively strong after copulation. If this conclusion is correct, then the negative X^2 values for the HW and HD displays following the HW display indicate that the HW display is a relatively weak expression of the sexual tendency compared with copulation.

Negative values were found for Comfort movements (C), Nest building (NB), Mutual preening (MP) and Preening the mate (PM).

The disinhibition theory postulates that when conflicting tendencies are in balance, and when the displays associated with these tendencies are prevented from appearing as a consequence, then those displays with a low priority that would normally be suppressed, may appear.

On the basis of this theory it may be concluded that the significant negative values for C, NB, PM and MP indicate that the HW display is not a conflict display, although, as it has already been pointed out, it may show evidence of an attack tendency under certain circumstances.

The positive association between the HW and F displays contrasts with the hypothesis of an attack tendency for F, and suggests that the head flagging is a ritualised movement of the head vibration seen in copulation. This suggests that head flagging is an indicator of the sexual tendency.

There is a significant positive association between Flagging and HW, TH, and C in the no-mate situation. There is a significant negative association between Flagging and HFL and F.

The temporal relationship between Flagging and HW and TH suggests that Flagging is an expression of a conflict between the sexual and attack tendencies, and depending on which tendency is stronger, Flagging may be followed by either HW or TH. The close temporal association between Comfort movements and Flagging suggests that in some cases the conflicting sexual and attack tendencies are in balance, thus allowing the Comfort movements to appear in an apparently irrelevant situation.

The X^2 values for TH show a significant positive association with HW, and a significant negative association with F, while in the mate situation there is a significant positive association between TH and C and NB. These results may be interpreted by assuming that TH is a conflict display resulting from the conflict between the attack and staying tendencies. If these two tendencies are in balance, then displays with a lower priority may occur. The positive association between TH and HW, C and NB may be interpreted on this basis.

The values of X^2 for the associations with HFL may be interpreted by assuming that the HFL display, like the F display, is an expression of a conflict between the sexual and attack tendencies. The differences between the mate and no-mate situations suggest that the sexual tendency is stronger in the mate situation, while the attack tendency is stronger in the no-mate situation.

The motivation of the displays deduced from the sequence analysis confirms the results found from the form analysis, and in the case of the F display, gives a greater insight into the motivation.

C. Situation Analysis

1. Introduction. The situation in which a display occurs may give some indication of the motivation of that display. Thus in the Royal penguin threat displays are mainly seen between neighbouring birds, and presumably are caused by slight incursion over the boundaries of the tightly packed territories. In this situation it is assumed that the tendencies to attack and flee (or stay) are present, and in some kind of balance.

2. Discussion. The Long Curved Stand is only seen on the arrival of a bird into the colony, and the display is always orientated towards the new bird. From the situation and orientation of the display it is apparent that a strong attack tendency is present, and probably a fleeing or staying tendency as well.

The fact that a bird using the LCS display to its mate changes its wing posture from 45° back to 45° forward, further suggests that the wings forward is an expression of a sexual tendency.

RN and RNWF are only seen when one bird is approaching another. A bird may walk a few feet away from its mate, and then return in the RN or RNWF posture, or a bird approaching a strange bird may use these postures. The approach of one bird to another usually elicits TH, but when the bird approaches in a RN or RNWF posture TH is rare. The fact that a bird approaching even a strange bird in RN or RNWF is rarely attacked suggests that these displays may inhibit attack. It is suggested that it is the sexual tendency in these displays which inhibits attack. This conclusion is supported by a number of observations of a female arriving in the colony being attacked by its mate. On all occasions the female responded to the attack with HW, which on other evidence is thought to be an expression of the sexual tendency.

The sequence NHWF, RNWF and HW is used by a bird approaching its mate. When approaching the mate through the body of the colony the bird adopts the NHWF display, and as it gets closer changes to RNWF, and finally a HW on arrival. A bird moving through the colony to reach its mate makes a determined dash, which suggests the presence of an attack tendency, and in a large colony it would be advantageous if the bird could inhibit attacks from the birds through which it passes. Form analysis suggests that NHWF is an expression of both an attack and sexual tendency, which would be expected in this situation, provided that the above assumption that the expression of a sexual tendency inhibits aggression, is correct. In the final few feet before reaching its mate the bird changes from NHWF to RNWF. It is clear that in this situation the need for a strong attack tendency is limited, while at the same time the need to inhibit aggression from the mate is increased. Therefore the bird changes to the RNWF posture, and finally ends with a HW.

The HW display is the most common display of the Royal penguin, and is given in a variety of situations.

In the form analysis of the HW display it was assumed that the duration of the display was an indication of the strength of the sexual tendency. If this is correct, then there should be significant differences in the duration of HW displays given in different situations. To test this the Median test (Siegel, 1956) was used to examine the differences in the duration of the HW display in the UK study birds, in the mate and no-mate situations. The median (Md) duration of the HW display, preceeding or following other displays, and in relation to the reaction of the mate, was tested, and the results are given below.

Before the Arrival of the Mate

	Md	No. Obs.
HW alone	4	82
HW/HW	4	8
HW/F	4	238
HW/HFL	3.5	18
HW/TH*	4	22
After the Arrival of the Mate		
HW - MNR	4	125
HW/F - MNR	4	82
HW/HFL - MNR	4	37
HW R. to HW of mate	5	32
HW MR with HW	4	19
HW with mate	5	36
HW/TH*	4	25
TOTAL	4	724

Range 0.01-0.17min.

* Preceeded or followed by a TH. R=Response
MNR= Mate no response (to HW of mate etc.)
MR = Mate responds (with HW to the mate's HW)

No significant differences were found between any of the groups using the Median test. While only a few HW displays preceeding copulation were timed, these, plus subjective observations, suggested that the HW displays preceeding copulation did not differ in duration from those in other situations. The lack of significant differences suggests that it is unlikely that the duration of the HW display can be used as an indication of the strength of the sexual tendency.

The diversity of situations in which the HW display is given makes it difficult to deduce motivation. However, the subjective impression that the frequency of this display increases prior to copulation, and the increased frequency during the reuniting of the pairs, lends further support to the assumption that the display is sexually motivated.

Form analysis also suggested that the HW display may also express a conflict between the attack and sexual tendencies when the wings are 45° back. This suggestion is supported by the observations that the HW display with the wings 45° back was only seen on the arrival of the mate, or when the display followed a TH. These observations also lend support to the assumption that the wings are an indicator of the attack tendency.

The Flagging display is characterised by the variability of its form, its close temporal association with the HW display, and the diversity of situations in which it is displayed.

From the form and sequence analysis of this display it was concluded that there was a conflict between the sexual, attack and fleeing tendencies, and that the four elements of the display act as indicators of these tendencies. Further evidence of the motivation of these elements should therefore be obtainable from a comparison of the elements of the displays given in different situations.

Despite the diversity of the form of the display, there appeared to be a relationship between the elements of it - with an increasing number of flags per bout, the body tended to change from the SS to the LS posture, the head from horizontal to 45° back, and the wings from the side position to parallel back.

In order to examine this relationship, and to establish if differences in the elements in the display could be used to gain further information on the motivation of the elements, 189 Flagging displays were analysed in the UK study males before the arrival of the mates. These birds were chosen because they formed the most homogeneous group, providing a reasonably large sample of flags in a situation that was as constant as any other that could be used.

Calculations were made of the number of bouts of Flagging for each score of the three elements, for bouts of 1, 2, 3...n flags per bout. These data are presented in Appendix 7. They confirmed the changes in the elements with an increasing number of flags per bout, as mentioned above.

To test that these changes were significant the Contingency Coefficient C was calculated for the elements head, body and wings, against the number of flags per bout. The values for C for all three elements were significant at the $p < 0.001$ level. This shows that the frequency distribution for the scores in each element, against the number of flags per bout, are significantly different.

Kendall's Coefficient of Concordance W was used to test that the changes in the scores for each element with an increasing number of flags per bout went in the above mentioned direction. The value of W was 0.296, which was significant at the $p < 0.001$ level.

These results show that with an increasing number of flags per bout, there is a significant trend for the body to go from the SS to the LS posture, the wings to move from the side to the parallel back position, and the head to move from the horizontal to the 45° back position.

While there is a significant relationship between the elements of the display, there is a great deal of variation. For example, the SS posture was seen in Flagging displays in which the number of flags per bout varied from one to eleven. Examination of the Flagging displays given by the UK study birds when with a mate, and when incubating or guarding the chicks, showed the same trends, with variability in the scores for the elements.

This analysis indicates that the motivation of the elements cannot be determined from an examination of the elements of the Flagging displays in different situations. I consider that this is a result of the broad catergorization of the situations. If the situations could be defined more accurately it may be possible to gain information on the motivation of the elements.

The significant association between the scores of the elements and the number of flags per bout indicates that the strength of all the tendencies change together. It would therefore appear valid to use the number of flags per bout to compare the strength of the tendencies of the Flagging display in different situations.

To test this the median (md) number of flags per bout was calculated for the breeding males in a number of situations. The results are given below.

Situation	Md. Flags/bout	No. obs.
Arriving in Colony	5	107
Before Arr. of Mate	4	189
With Mate	3	97
Incubating	4	54
Guarding	5	50
Failed Breeders	6	95

The medians were compared using the Median test (Siegel, 1956).

The largest median was seen in the failed breeding males. Presumably the failed breeding males (in cases where the female has failed to continue incubation), on return to their territories, have to re-establish their claim to them, and on the return of the mate, to strengthen the pair bond, or if the female does not return, to attempt to attract another mate. In such situations both attack and sexual tendencies would be expected to be high.

The median of birds arriving in the colony was not significantly smaller than that of the failed breeders ($p < 0.05$). In such a situation one would expect that the attack, fleeing and sexual tendencies would be high. The males with a mate had the smallest median, which was significantly ($p < 0.05$) smaller than all the other medians. In this situation one would not expect attack or fleeing tendencies to be strong, and one would expect the sexual tendency to be expressed in the HW display, which is common in this situation.

The three other situations may be considered to be intermediate, because in them the males are without a mate, but on established territories. The medians from these three situations are not significantly different ($p<0.05$ level) from each other, but are significantly smaller than the failed breeders and the arriving birds, and are significantly greater than those of the males with mates.

Breeding females flag infrequently, and the number of flags is not large enough to compare with those of the males. However, the association between the elements of Flagging appears to be the same, and in the small sample obtained, the medians are not significantly different from those found in the males in similar situations.

This evidence seems to support the hypothesis that the Flag display is an expression of a conflict, mainly between the attack and sexual tendencies, with a weaker fleeing tendency present.

In the section on sequence analysis the close temporal association between the HW and F displays was demonstrated. Because of the assumed sexual tendency in both displays, it was thought that the duration of the HW display may influence the length of the bout of the following Flag display. To test if there was any relationship between the duration of the HW display and the number of flags per bout, Kendall's Coefficient of Concordance W was calculated for 240 HW displays which were followed by F displays, given by the UK study males ($W=0.40$, $p < 0.001$). This shows that the distribution of the number of flags per bout does not vary with the duration of the HW display, and therefore the duration of the HW display does not influence the number of flags per bout in the Flag display.

While the duration of the HW display does not appear to affect the following F display, there is a change in the temporal relationship of the two displays, from the no-mate to the with-mate situation. The data for all the breeding males in the two situations are given below:

	NM	M
Total No. HW	619	648
Total No. F	400	170
HW foll. by HW	18(3%)	54(8%)
HW foll. by F	328(53%)	152(24%)

The number of HW displays given in the two situations is approximately the same, while the number of F displays shows a marked decrease. There is a small increase in the number of HW displays following the HW display, and while the percentage of HW displays followed by an F display decreases, the percentage of the F displays that follow the HW display does not change.

These data suggest that with the female present there is a decrease in the effect of the factors (presumably they are still present), affecting the strength of the attack and fleeing tendencies, and therefore reducing the likelihood of the HW display being followed by a F display. The sexual tendency is expressed by the HW display.

These temporal relationships provide little further evidence of the motivation of the displays.

D. Discussion

The motivation of the displays has been analysed using three methods: form analysis, temporal association and situation analysis. These methods have yielded similar results, and the displays will now be discussed with regard to the results of the three methods and the resultant difficulties in interpretation.

The form analysis of HW indicated that this display was primarily an expression of a sexual tendency which may also be associated with an attack tendency. The temporal association of HW and copulation supported this conclusion, while the situation analysis supported that the wing 45° back is an expression of an attack tendency. The fact that TH was followed by HW on more occasions than expected by chance suggests that the threat display is in conflict with the tendencies to attack and stay put, and that when these tendencies are in balance the HW display can be expressed.

It is suggested from the form analysis that the duration of the display may be an indication of the strength of the attack tendency. However there was no significant difference in the duration of HW in the duration of HW in different situations. Unfortunately there were no timed HW's preceeding copulation. It would be expected that these would be the longest, as copulation is assumed to be the strongest expression of the sexual tendency, but observations did not indicate that they were appreciably longer, and it is probable that duration is not an indication of strength.

The form analysis of the wing, body and head elements of the Flag display, indicates that both attack and fleeing tendencies were present. However the motivation of the head flagging could not be deduced from the form analysis. The fact that copulation took place less than expected after HW/F or F suggested that there was little sexual tendency. However the close temporal association of HW and F displays, and the fact that 83% of all Flag displays given by the UK males were preceeded by a HW display, suggested that there was some sexual tendency present, and it was postulated that the head flagging was ritualised from the head vibration seen in copulation.

Flagging which follows HW is a continuation of the uplifting of the head at the completion of the HW (Plate 12), and there is not time break, both displays being linked by a continuous movement. On the basis of temporal associations F should be an expression of a sexual tendency. However, attack, and possibly fleeing tendencies make their appearance. It could be argued that the causal factors for both sexual and attack behaviour are present, with the sexual tendency being most strongly aroused. This will reduce the likelihood of the expression of the attack tendency, allowing the HW display to take place, which may reduce the sexual tendency and allow both the attack and reduced sexual tendencies to be expressed in F. However, as the evidence of an attack tendency in the HW display is rarely seen, and the duration of the HW does not appear to be an indication of the strength of the sexual tendency, and has no influence on the length of the bout of Flagging, this suggestion is unlikely to be correct, and the causal factors for the close temporal association of these displays remains speculative.

The form analysis of the NHWF, RN, RNWF and LCS displays was supported by the situation analysis. The low frequency of these displays in the study birds did not permit sequence analysis, although the comparison of the displays associated with copulation supported the conclusion that there was a sexual tendency present in the RNWF, as suggested from the form analysis.

III. Function

The analysis of the function of displays is more difficult than the analysis of motivation from observational data, because of the almost complete lack of responses, other than a response to a display with the same display. Before attempting to interpret the function of the displays, the seasonal changes in frequency will be examined, as they will give some information that will assist in the functional interpretation.

A. Seasonal frequency distribution.

The seasonal frequancy changes will be examined in the following displays: HW, F, TH, HD and HFL. The total numbers of each display were grouped for each age/sex group. Two groups of breeding males(UK and 6+) were used, while all the data from females which had laid an egg in either one or both seasons were grouped. The data for both seasons were grouped for the non-breeding age/sex groups.

1. Unknown age breeding males (No. =12). The frequency distribution of the F, HFL, HW, HD and TH displays are shown in Figure 10. All displays have a peak in the latter half of the occupation period. However, in the case of the HD and HFL displays, the frequencies are so low that they will be omitted from further discussion.

The frequency changes can be related to the events taking place in the colony. The rapid increase in frequency occurs when most of the breeding males are already in the colony, and the number of females arriving in the colony is starting to increase. The peak of HW and F was on October 4 to 5, which was one to two days before the median date of the arrival of the females (October 6), and they had decreased to a low level before the median date of the first egg (Oct. 17).

The frequency distribution of F in the sample is similar to that found in the Sand Colony, except that the peak was reached two days later, and the decrease was not as rapid. Both these differences were caused by the later arriving birds. The distribution of HW is similar, except it has a higher and broader peak, with a slower decrease in frequency after the peak. The frequency of TH was much lower than that for HW and F, and there was no distinct peak, as there was for HW and F displays, but rather a broad, irregular hump.

The distribution of these displays was also calculated in relation to the date of arrival of the female, and the first eggs (Figures 11 and 12 respectively). The frequency distribution of the F display in relation to the arrival of the mates, shows an increase five days before the arrival of the mates, which is approximately the time when the number of females arriving in the colony starts to increase. From this time the distribution is irregular, but the peaks become smaller and are insignificant eight days after the arrival of the mates. The arrival of the mates does not influence the frequency of the display.

The frequency distribution in relation to the laying of the first egg is similar to that in Figure 10, and as in Figure 11, the frequency has started to decrease before the median day of arrival of the mates, and shows no evidence of being influenced by their arrival.

The frequency distribution of the HW display, in relation to both the arrival of the females and the laying of the first eggs, is similar to that in Figure 10 except that on both the second day of observation of the males with mates, and the median date of arrival of the mate, there is a sharp spike in the distribution which is assumed to be caused by the arrival of the females.

The frequency distribution in both Figures 11 and

12 is similar, and does not show any evidence of being affected by the arrival of the females.

2. Known age breeding males. The frequency distribution of F and HW is shown in Figures 13 and 14. The distribution has been adjusted to the day of arrival, because of the wide spread of arrival dates.

The TH distribution is not shown, but it is similar to that of the UK males. The HW and F distributions are similar to those in the UK males, but more irregular, owing to the greater heterogeneity of the group. The distributions were also recalculated in relation to the date of arrival of the mate and the date of the first egg (Figure 15). The distribution before and after the date of the first egg is similar to that found in the UK males, except that there is no spike on the median date of arrival of the females. However, the maximum frequency is reached on this day. In the distribution around the time of the arrival of the females there is a sharp spike on the day of arrival of the mates, in the HW distribution. In the F distribution the peak occurs two days before day 0, and the frequency decreases to a minimum.

3. Breeding females. The data for 35 females which laid eggs were grouped, and the frequency of HW and F was plotted from the day of arrival (Figure 16).

The frequency of both displays is low when compared to the males. There is no change in the F distribution, but in the HW distribution the frequency is high for three days after the arrival, before decreasing to a low level.

4. Non-breeding birds. Because of the wide variation in the dates of arrival and the length of stay in the colony found in the non-breeding birds, the distributions were plotted from the day of arrival for each age/sex group. Because of the low frequencies, the distributions of TH, HD and HF displays were not plotted.

(a) Males. The frequency distributions for F and HW are shown in Figures 13 and 14 respectively. There is an increase in frequency with age for both the HW and F displays, with HW more frequent than F. The frequency for both displays is much lower than for the breeding males. There is no regular distribution for either display, and the distribution becomes more irregular in the younger birds.

(b) Females. Only the HW display was frequent enough to warrant plotting (Figure 17). The frequencies are low for all age groups, and the distribution irregular.

B. Functions.

1. Head Wobble (HW). In analysing the motivation of the displays it was suggested that the expression of the sexual tendency in the HW, RNWF and NHWF displays may inhibit attack. Inhibition in this sense is more properly thought of as reducing the probability that a bird will respond to a given stimulus in a particular manner. In this case the adoption of a sexually motivated display will reduce the probability that neighbouring birds will react to it aggresively.

It is suggested that the HW display functions in this way because observations and the frequency distribution in relation to the arrival of the female shows that HW increases in frequency at this time, and that attack by the male is rare, but when this does occur the females always responds with a HW. In Chapter 5 a case was recorded where a male pecked his mate 25 times in 20 minutes. On each occasion the female responded with a HW. In this case the female did not stop Head Wobbling until the male had stopped pecking, and each time the female raised her head at the end of a HW the male started pecking. The fact that the female did not stop Head Wobbling until the male had ceased pecking may support the inhibitory theory, but the large number of attacks over a long period would also suggest that the HW was not very effective. However the rarity of this sequence of events suggests that only extremely aggressive birds attack their mates, and in these cases a lot of Head Wobbling is required to stop the attacks. It may be supposed that the initial HW displays are sufficient to inhibit the mate's attack in most cases. When the male returns to take over incubation from the female, the HW display is given by both birds. Frequently, however, the male will walk away from his mate and attack a neighbouring bird. I suggest that this is evidence of an attack tendency being present in the male on his arrival, and that the male is inhibited from attacking his mate by her HW, and that this attack tendency is "redirected" towards neighbouring birds (Moynihan, 1962). The frequency distribution may be explained, in part, by assuming that the increase in frequency of HW is a response to the increasing attack tendency associated with the increasing density as a result of the arrival of the females. The decrease in frequency is a result of the decreased attack tendency as the territories become more stabilized and the males adapt to the presence of their mates.

A sexually motivated display like the HW could also be expected to give information to the mate on the sexual state of a bird, and the close temporal association between HW and copulation would support this.

Head Wobbling in the male may also stimulate the final development of the female as the follicles undergo a rapid increase in size after she arrives in the colony. On the other hand, the decrease in HW after the arrival of the females suggests that this may not be so. I conclude that evidence supports the hypothesis that the HW display functions as an appeasement display in reducing the probability that other birds will attack the displaying bird, and also that it conveys information on the sexual state of a bird, and may sexually stimulate the other bird. These functions would also aid the formation and maintainance of the pair bond.

2. Flag (F)

I consider that the Flag display functions as a territorial advertisement display. This conclusion is based on the following facts. The frequency distribution is not affected by the arrival of the mates, and in the 6+ year old males the frequency had decreased before the arrival of the females. The increase in the frequency of the display is related to the increasing density resulting from the arrival of the females. The rapid decrease may be explained as for the HW display. As noted above, the Flag display in males on their arrival at the colony increases in frequency and intensity with the increasing density. Frequency of Flagging in failed breeding males is higher than in the successful breeding males, which suggests that the Flag display is used to strengthen their claim on their territories. Also the Flagging display in females has a very low frequency.

This evidence, taken together with the motivation of the display, suggests that the Flag display functions as a territorial threat display, and in attracting females to an unpaired territorial male.

3. Threat (TH). Threat displays are mainly seen between neighbouring birds, and between territorial birds and other birds passing through the colony, and therefore functions in territorial defence. Threat seen between non-territorial birds would appear to be a defence against intrusion into a bird's individual space.

4. Long Curved Stand (LCS). LCS is given only by a resident bird on the arrival of another bird in the colony, and is orientated towards the incoming birds. It appears to function as a threat display to keep birds away from the territory.

5. Round Neck Wing Forward (RNWF). This display is only seen on the approach of one bird to another, and the rarity of aggression after such an approach suggests that this display may act as an appeasement display similar to the HW display.

It is obvious that in the densely packed Royal penguin colonies there must be a mechanism(s) for reducing aggression that is normally present under such conditions, in order that successful breeding might take place. At the other extreme, fleeing must also be modified. Both these tendencies, if taken to extremes, will lead to breeding failure.

While the strong expression of these tendencies would be a disadvantage during the breeding season, they are obviously valuable while the bird is at sea. Under these circumstances it would be an advantage to reduce the direct expression of the attack tendency, using 'non-violent' displays to express this tendency, while at the same time having displays which would reduce the probability of attack.

The development of a strong staying tendency in response to the possession of a territory would reduce the fleeing tendency. Therefore in the Royal penguin there is a strongly sexually motivated display (HW) which is thought to function in reducing the probability of attack, while the F display has developed as a variable, yet highly distinctive territorial display, which functions as a threat display and in attracting females. The RNWF display enables the close approach of birds by inhibiting attack, while the LCS displays function in repulsing arriving birds. These displays communicate the motivation of a bird, while at the same time help to avoid excessive aggression or fleeing.

FIGURE 10

The frequency distribution of the F, HFL, HW, HD and TH displays for the UK study males during the Occupation and Laying periods of the 1967 season.
The number of birds in the group and the number of observations is given in Appendix 6.

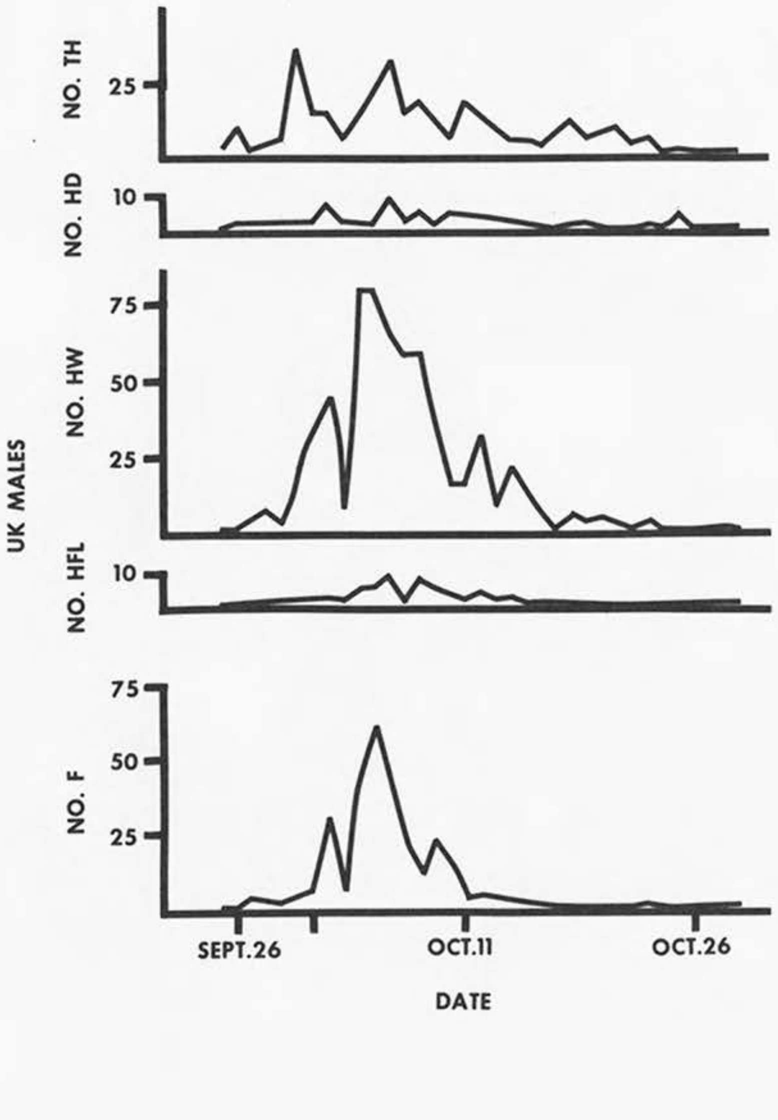

UK MALES
NO. TH
25
NO. HD
10
NO. HW
75
50
25
NO. HFL
10
NO. F
75
50
25
SEPT.26
OCT.11
OCT.26
DATE

FIGURE 11

The frequency distribution of the F, HW and TH displays of the UK study birds, before and after the arrival of the mates. Day 0 is the first day the male was observed with the mate.

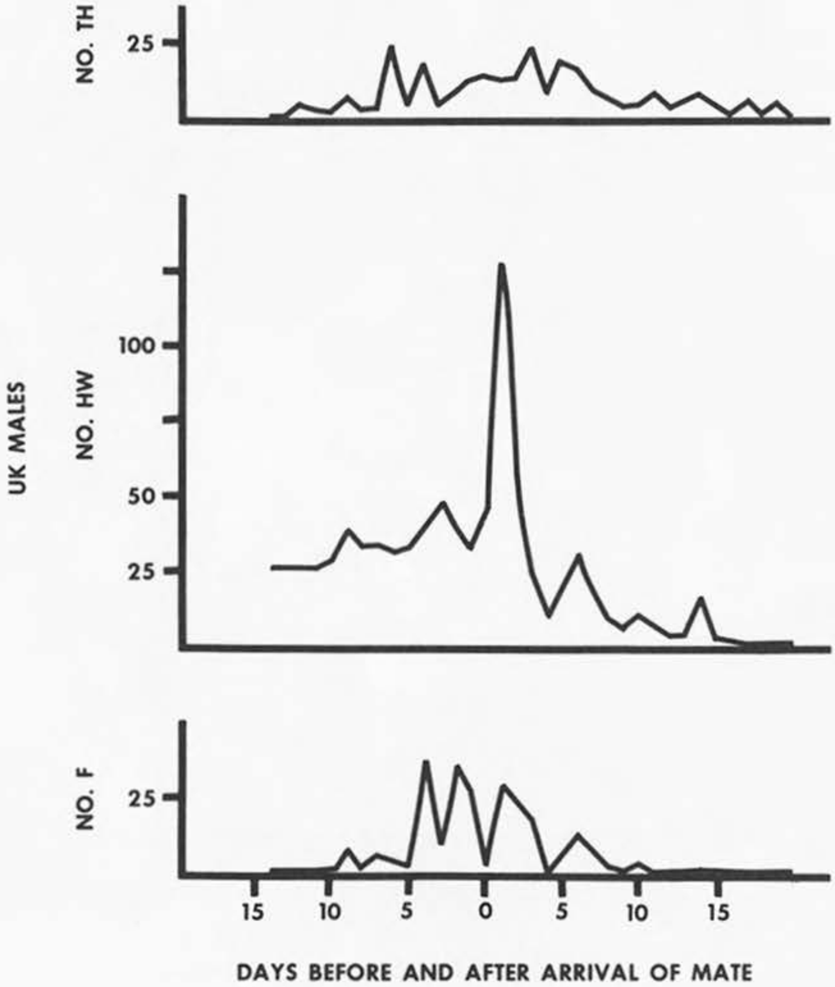

UK MALES
NO. TH
25
NO. HW
100
50
25
NO. F
25
15
10
5
0
5
10
15
DAYS BEFORE AND AFTER ARRIVAL OF MATE

FIGURE 12

The frequency distribution of the F, HW and TH displays given by the UK study birds before and after the mates laid their first egg. Day 0 is the first day of observation after the first egg was laid.

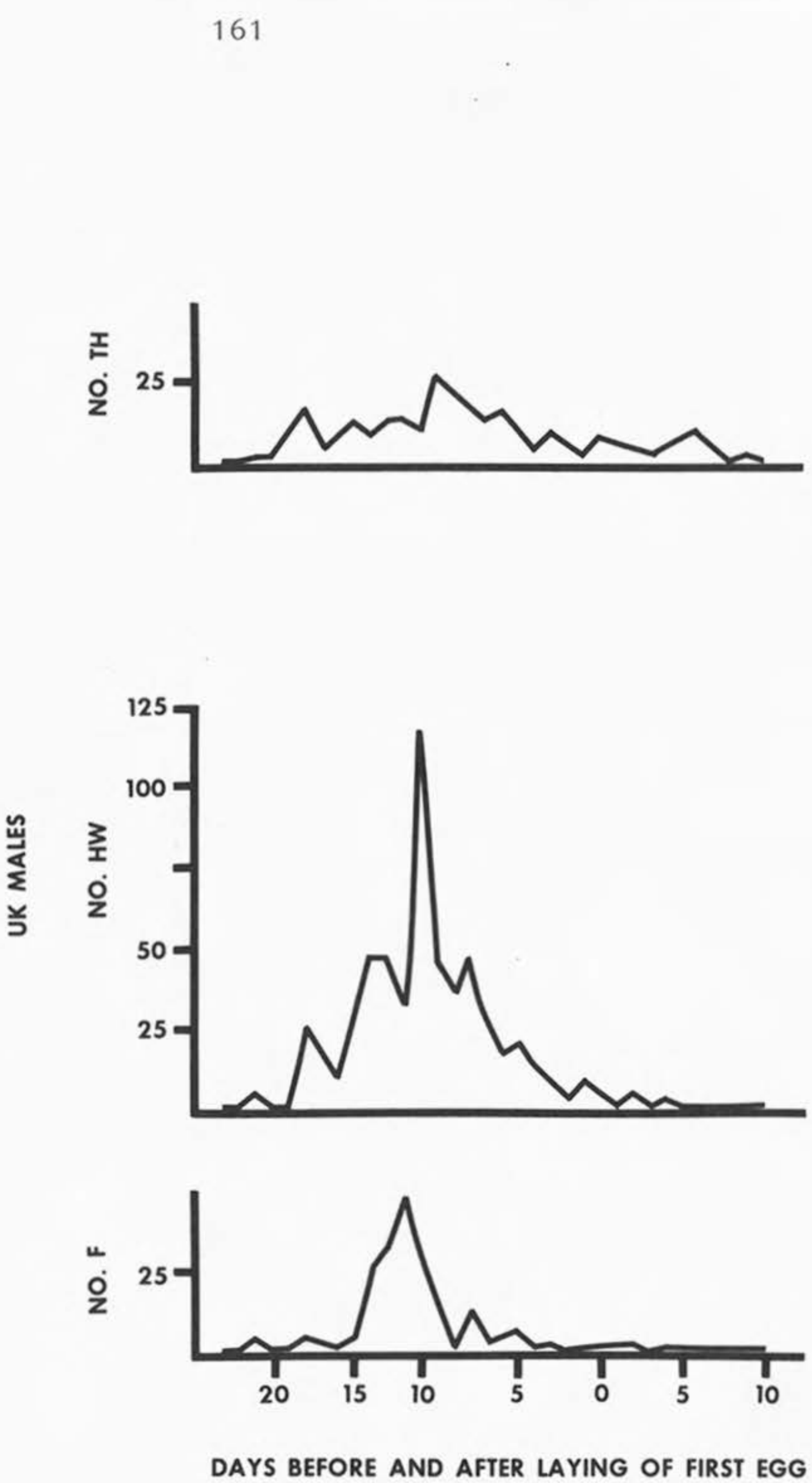
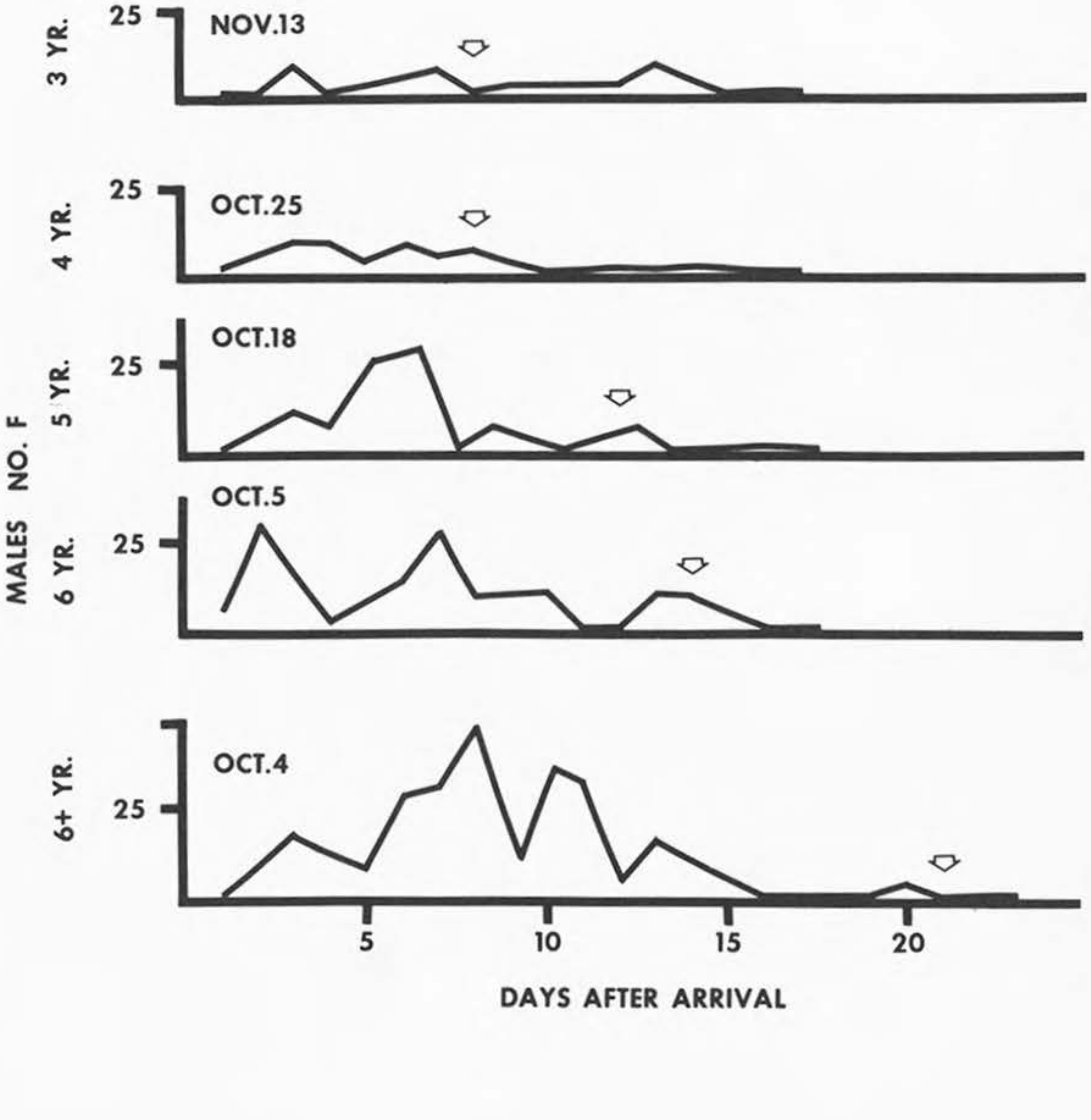

UK MALES
NO. TH
25
NO. HW
125
100
50
25
NO. F
25
20
15
10
5
0
5
10
DAYS BEFORE AND AFTER LAYING OF FIRST EGG

FIGURE 13

The frequency distribution of the Flag display for the six+, five, four and three year old males after their arrival in the rookery. The data from 1966 and 1967 were grouped. The arrow indicates the median number of days after arrival that the males in the different age groups left the rookery. The date given on each group is the median day of arrival for that group.


25
NOV.13
3 YR.
25
OCT.25
4 YR.
OCT.18
25
5 YR.
MALES NO. F
OCT.5
25
6 YR.
OCT.4
6+ YR.
25
5
10
15
20
DAYS AFTER ARRIVAL

<u>FIGURE 14</u>

The frequency distribution of the Head Wobble display for the six+, five, four and three year old males after arrival in the rookery. The data from 1966 and 1967 were grouped. The arrow indicates the median number of days after arrival that the males in the different age groups left the rookery. The date given on each group is the median day of arrival for that group. The number of males in each group, and the days of observation, are given in Appendix 6.

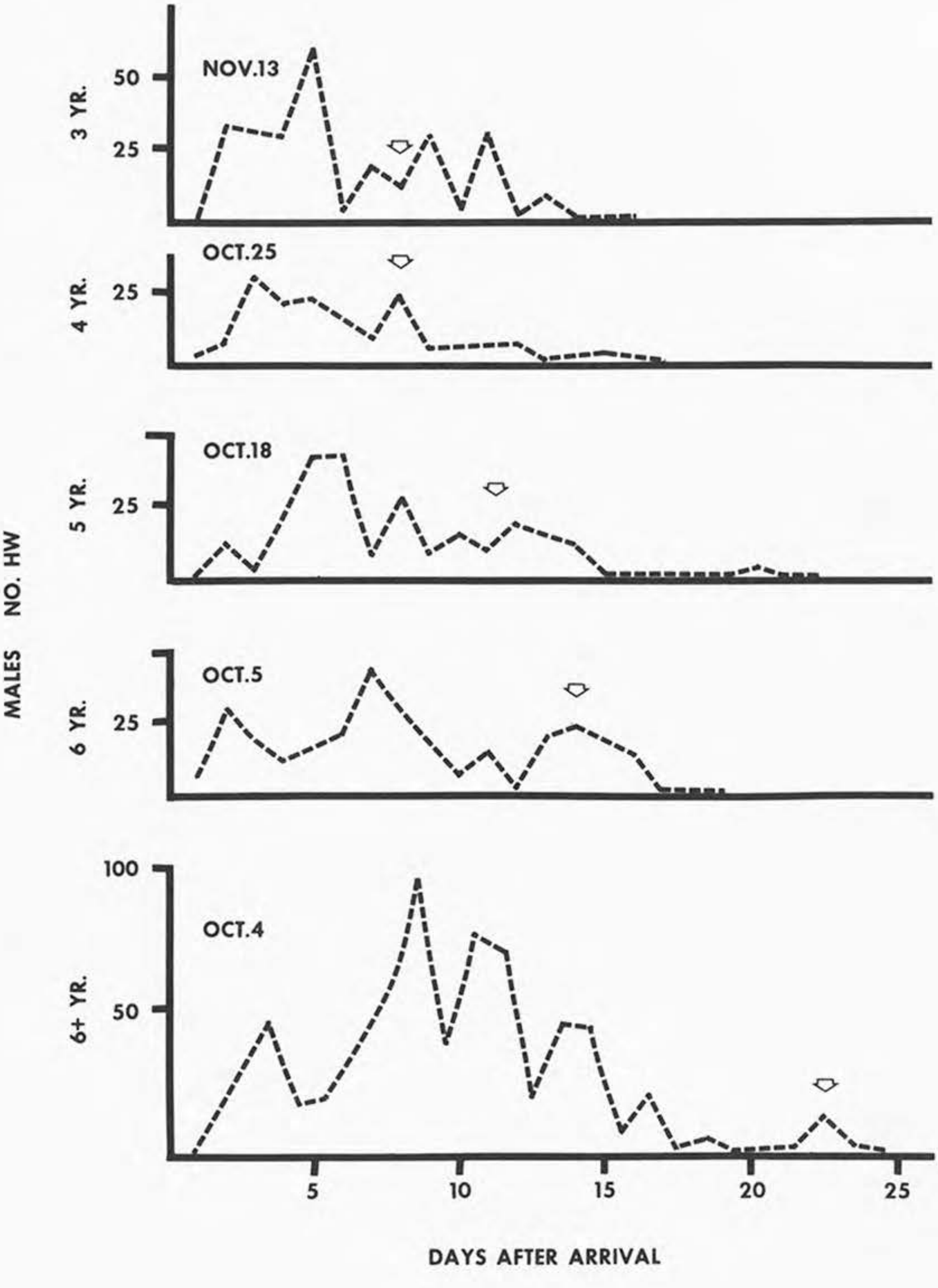

MALES NO. HW
3 YR.
50
25
NOV.13
4 YR.
25
OCT.25
5 YR.
25
OCT.18
6 YR.
25
OCT.5
6+ YR.
100
50
OCT.4
5
10
15
20
25
DAYS AFTER ARRIVAL

FIGURE 15

The frequency distribution of the HW and F displays for the six+ year old males before and after the arrival of the mate, and before and after the mate had laid the first egg. Data from the 1966 and 1967 seasons were grouped. Day 0 is the first day the male was observed with the mate, and after the first egg was laid.
The number of males and the days of observation are given in Appendix 6.

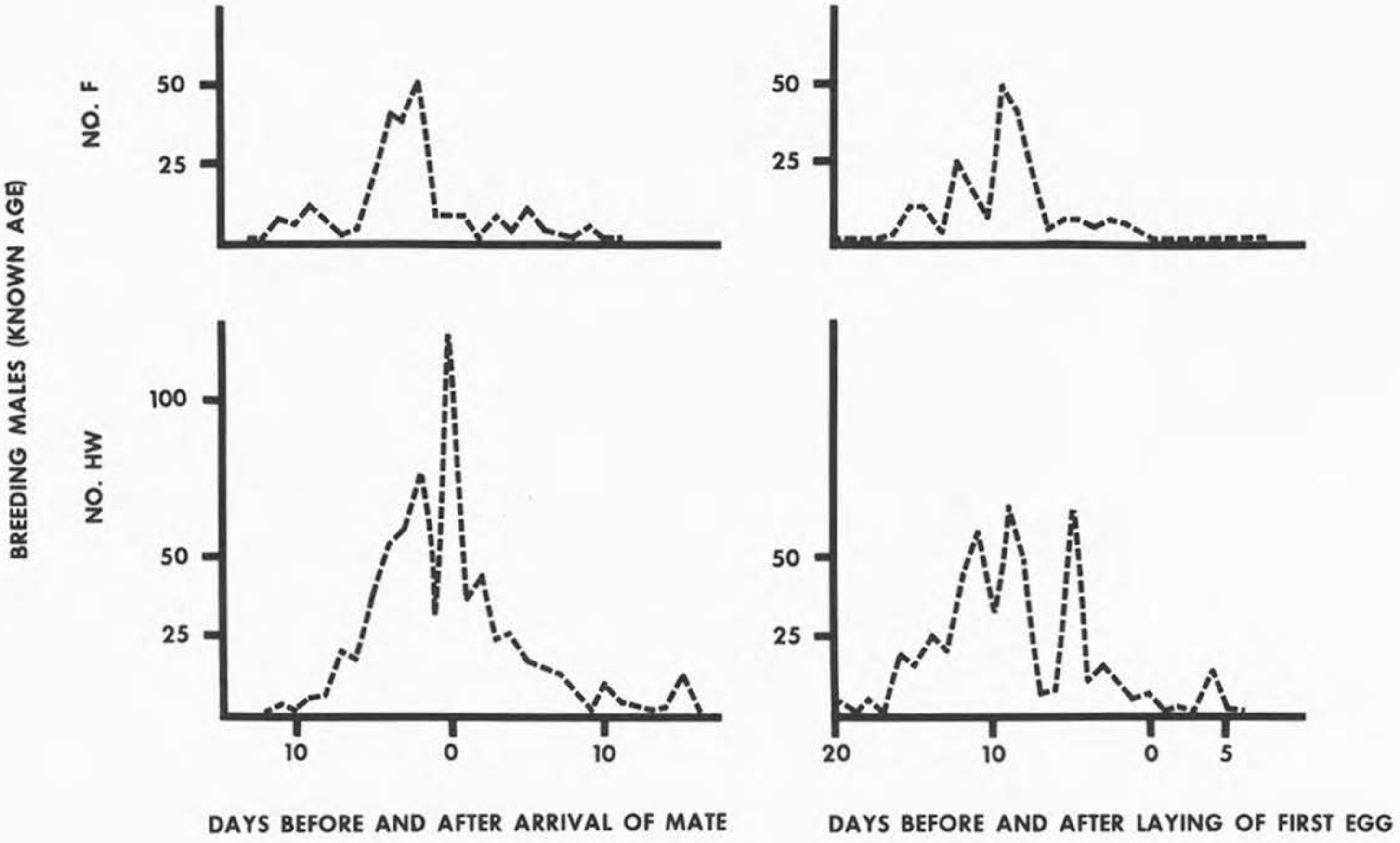

BREEDING MALES (KNOWN AGE)
NO. F
50
25
50
25
NO. HW
100
50
25
50
25
10
0
10
20
10
0
5
DAYS BEFORE AND AFTER ARRIVAL OF MATE
DAYS BEFORE AND AFTER LAYING OF FIRST EGG

FIGURE 16

The frequency distribution of the HW and F displays given by the breeding females after arrival. The data from both seasons were grouped.

The number of females and the days of observation are given in Appendix 6.

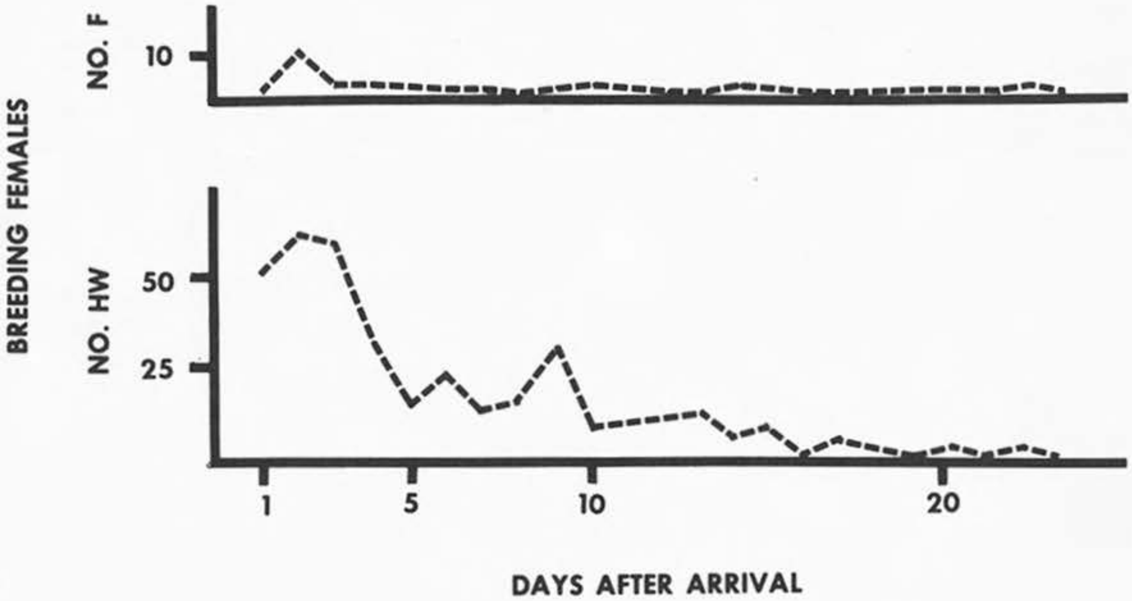

BREEDING FEMALES
NO. F
10
NO. HW
50
25
1
5
10
20
DAYS AFTER ARRIVAL

FIGURE 17

The frequency distribution of the HW display given by the six, five, four and three year old females after arrival.
The arrow indicates the median day after arrival that the females departed from the rookery.
The date for each group is the median date of arrival for that group. The data for both seasons were grouped. The number of females and the number of days of observation is given in Appendix 6.

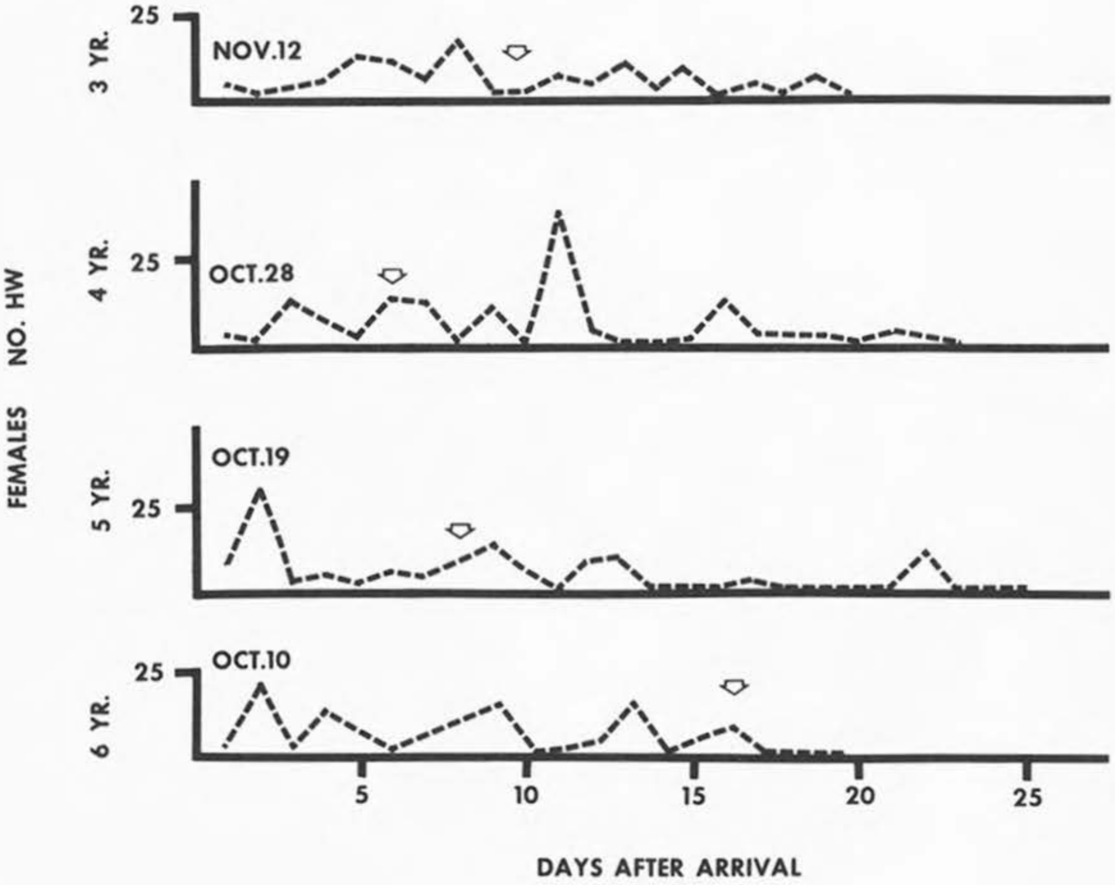

FEMALES NO. HW
3 YR.
25
NOV.12
4 YR.
25
OCT.28
5 YR.
25
OCT.19
6 YR.
25
OCT.10
5
10
15
20
25
DAYS AFTER ARRIVAL

TABLE 9

X^2 values for the displays and display sequences, preceeding and following copulation in the males. Also the X^2 values for the displays in the female following copulation and those displays of the female that appear to stimulate the mate to start copulation. All X^2 values are significant at the p 0.05 level.

	MALES		FEMALES	
	DIS.PREC.COP.	DIS.FOLL.COP.	DIS.FOLL.COP.	DIS.STIM.COP.
HW	+38.6	+32.1	+31.5	+11.1
HW/F	-5.9			
HW/HFL	-5.9			-5.4
HD			-8.8	
F	-4.2			
HFL				
RNWF	+48.1			
PM		-5.1		
MP				
C		-5.1		
TH				
WA			-5.5	
P		-5.1		
LCS	-5.9			

TABLE 10

X^2 values for displays following 8 displays in the No mate and mate situations for all breeding males (UK and 6+ year old).

X^2 values are significant at the p 0.05 level.

		HW	F	TH	HFL	HD	RNWF	LCS	C	NB	WA	MP	PM
No mate	HW	-41.2	+78.5	-28.6	+18.1	-5.9	-	-	-18.1	-	-		
	F	+9.1	-29.5	+11.2	-5.4	-	-	-	+8.7	-	-		
	TH	+22.3	-34.8	+12.1	-8.0	-	-	-	-	-	-		
	HFL	-	+4.1	-	-	-	-	-	-	-	-		
	HD	+8.4	-11.6	-	-	-	-	-	+4.5	-	-		
	RNWF	-	-	-	-	-	-	-	-	-	-		
	LCS												
Mate	HW	-20.3	+43.2	-14.2	+30.8	-	-	-	-18.7	-4.1	-	-9.4	-6.8
	F	+4.3	-5.2	+5.7	-5.1	-	-	-	-	-	-	-	-
	TH	+12.7	-19.3	+8.5	-13.7	-	-	-	+5.4	+5.2	-	-	-
	HFL	+5.4	-	-	-	-	-	-	-	-	-	-	-
	HD	-	-5.4	-	-	-	-	-	-	-	-	-	-
	RNWF	-	-	-	-	-	-	-	-	-	-	-	-
	LCS	-	-	-	-	-	-	-	-	-	-	-	-
	MP	-	-4.7	-	-	+4.5	-	-	+6.8	-	-	-	-
	PM	-	-	-	-	-	-	-	-	-	-	+9.5	-

CHAPTER 8 - STATUS, BEHAVIOUR AND REPRODUCTION

I. Introduction.

The population changes in the Sand Colony during the breeding season were examined briefly, and were later used as a framework for describing the behaviour and the frequency distribution of the displays. Quantitative aspects of the differences in the displays were examined, and the motivation and functions of the displays were examined within the different age groups of males and females.

In addition the gonad cycles of breeding males and females were determined, and the condition of the gonads of known age, non-breeding birds, on their arrival at the rookery, was related to the cycle in breeding birds.

The purpose of this chapter is to draw all these data together, and to attempt to relate them to a bird's breeding status. Before doing this the subject of status will be examined in more detail.

II. Status.

A. Introduction.

Breeding status has been defined as the possession of a permanent territory and mate for the duration of a breeding season (Chapter 2). For a Royal penguin to breed successfully it was necessary for the bird to have a permanent territory, and a mate with whom it had a pair bond strong enough to enable successful breeding to take place on the territory. A bird was considered to be a successful breeder if, in the case of a female, it laid two eggs, or in the case of a male, its mate had laid two eggs. This is a 'minimal' definition of success, as ultimately, success must be determined by the production of a fledgeling that is capable of surviving its first winter at sea. After this its survival is not dependent on its parents.

Although all Royal penguins may be said to have some status in the colony, the degree of status attained in a particular breeding season is dependent on how successful each bird is in obtaining the two basic requirements.

Three parameters of status were calculated: territorial tenacity, position of territory and strength of the pair bond. Territorial tenacity was calculated by finding the mean number of days each study bird spent on a particular position in the colony. Position of territory was determined by calculating the percentage number of days that each study bird was situated in the breeding area. The breeding area was defined as that area of the colony occupied by incubating females on November 9, 1967. This date was chosen on the assumption that the best territories would be occupied by the more experienced breeding birds, and that these birds would be surrounded by less experienced breeding birds. In addition, if the females of the less experienced pairs were going to fail to continue incubation before the arrival of their mates, they were most likely to do so before this date. Therefore the area in the colony occupied by breeding females on November 9 gave a good indication of the best breeding area in the colony. The third parameter was calculated by finding the mean number of days spent with each mate.

B. Results.

The data (Appendix 8) were examined in three ways: firstly, the median and range for each parameter in each group was calculated (Table 11); secondly, the data for adjacent age groups, in both males and females, were compared, using the Mann-Whitney U test (Table 12); and thirdly, the regression coefficient 'b' was calculated for each parameter against age (Table 13).

The regression coefficients 'b', for all parameters for both sexes, are significantly different from zero, and show that for both sexes, the ability to attain a secure territory in the breeding area, and to form a stronger pair bond, increases with age.

(1) Males. These changes are examined in more detail in Tables 11 and 12. In each group the median of the mean number of days spent at each site increases slowly up to the six year old males. The range of the means increases more rapidly.

The difference between the 6 and 6+ year old males is significant, and because of the greater breeding success (see below) of the 6+ year old males, the difference is considered biologically significant.

The difference in the medians of the 6+ and UK groups is a result of the earlier arrival of the UK group, and, to a lesser extent, the failure of some of the 6+ group to secure a stable territory, which is also the reason for the greater range.

The ability to form a pair bond shows a similar trend. The large range for the UK males was the result of one male having a territory but no mate.

The median percentage of time spent in the breeding area shows a gradual increase up to 100% at 6+ years, and an increasing number of males older than three years spent 100% of their time in the breeding area.

Observation showed that the breeding area after egg laying was tightly packed with no apparent vacant territories, and it is probable that two and three year old males that had territories in the breeding areas were in territories left vacant by failed breeding birds. This was probably true, to a lesser extent, for the four to six year old males.

(2) Females. The trends seen in territorial tenacity and pair bond are similar to those seen in the males, except that the rapid increase is seen from the five to the six year old birds. The percentage time spent in the breeding area is similar to that of the males.

The method of collecting the data has an inherent error. For birds with a reasonably stable territory the method of obtaining the position and presence, or absence, of a mate each day is satisfactory, but for younger birds, this method gives a misleading picture, as most of these birds are mobile and constantly shifting their positions in the colony. Thus the range of the average number of days spent at each site gives a more accurate picture of the changes with age.

Carrick (1969) found that birds up to three years old move around the periphery of the colony at random, whereas the four to seven year old birds tend to become attached to a restricted area, where they subsequently establish a "breeding site".

The data presented are in agreement with Carrick's statement, although no data have been presented on the attachment to a restricted area in the colony. Although these data, and Carrick's statement, give the impression of a continuous improvement with age, this is far from being true for an individual bird. The limited data available over two seasons (not given) indicate that birds may lose status although a year older.

III. Status and behaviour.

A. Introduction.

It has been shown that in a number of displays frequency changes with age, and also that the status of a bird changes with age. If one or more of the displays function in the attainment of a territory and a mate, then there should be a positive correlation between the displays and the status of a bird.

B. Relationships between status and the displays.

Regression coefficients 'b' were calculated for the frequency of the HW and F displays against the parameters of territorial tenacity (T), and pair bond (M)(Table 14). The data are given in Appendices 8 and 9.

With only two exceptions, the values of 'b' for the correlation of the frequency of the displays in the mate/no-mate situations, and also the values for these situations combined, against territorial tenacity and pair bond, are positive. Males and females in the no-mate situation had negative values of 'b' for the regression of the HW against the parameter M. The male value was not significantly different from zero.

The positive values of the regression coefficient 'b' for Flagging in all situations, against the parameters T and M, support the conclusion that this display functions in the attainment of a territory, and in attracting a mate. The negative values of 'b' for the HW display in the no-mate situation further support the conclusion that this display functions as an appeasement display.

The values of the regression coefficient 'b' give the general relationship between the frequency of the two displays and status. The frequency measure is the percentage number of days on which a display was given, which provides an adequate measure of the basic frequency of a display, although it does not give any indication of the absolute frequency. This is illustrated by the graphs of the frequency distribution (Figures 10, 13, 14, and 17). The differences in the absolute frequency are a result of the fact that the UK and 6+ year old birds are more likely to display a number of times during an observation period. To overcome this, the percentage number of days on which more than two Head Wobble and/or Flag displays were given was calculated for all birds. The median of the percentage number of days for each group was calculated, and is presented in Table 15.

The data for the females show that the median percentage for both displays is zero, with the exception of the Head Wobble display in the four and six year old females in the with-mate situation, and the six year old birds in the combined situation. These data are reflections of the low frequency of the displays. There is no apparent reason why the median in the four year old females should be greater than zero. In the six year old females it may be related to the sharp increase in the parameters of status seen between the five and six year old females, particularly in the pair bond parameter. The functional significance of the Head Wobble display lends support to this idea.

The median percentage of days on which more than two Flag displays were given was zero for males with a mate, and for males younger than six years old without a mate. The median for the six+ year old males was larger than for the six year old group. The median for the UK group was smallest because of the proportionally greater amount of time spent in the colony before the arrival of the mates (see above). The increase in the median percentage in the six year old males, a year before there is a rapid increase in status, is probably related to their earlier arrival which provides them with a more intensive stimulus environment to which they respond.

Because of the close temporal association between the Head Wobble and Flag displays there should be a close relationship between the changes in the median percentages of the two displays and age. This is true for the no-mate situation, but in the with-mate situation there is a trend for the median percentage of the HW display to increase with age up to five years, and then increase rapidly up to six years.

In the with-mate situation the changes in percentage parallel the changes seen in the status parameters, except that, as with Flagging, there is a rapid increase from the five to the six year old males.

These changes are to be expected if the pair bond function of Head Wobbling is correct.

The increase in the median percentage between the five and six year olds for both the Head Wobble and Flag displays, suggests that in addition to the effect of a more intense stimulus situation, the birds may, in fact, be more active in their attempts to secure a territory and mate. Some of them are successful, but as a group, the increase in status is not significant.

C. Summary.

A positive relationship was found between the parameters (territorial tenacity and pair bond) and the Head Wobble and Flag displays, with the exception of the Head Wobble in the no-mate situation. This was to be expected on the basis of the function of the two displays, that is Flagging functioning as a territorial threat display as well as for attracting unpaired females, and Head Wobbling functioning, not only as an appeasement display, but also for the maintenance of the pair bond. The use of the median percentage of days on which a display was seen more than twice, to give a more accurate measure of the absolute frequency, supports the conclusions from the regression analysis. This measure demonstrates the very low absolute frequency of the two displays in females in comparison with the males, and is particularly apparent for the HW display in the with-mate situation.

Carrick (1969) states that it is the male who establishes a territory, and the female who finds a mate among the unpaired males with a territory.

The relationship between the frequency of the behaviour and status supports his statement, as well as indicating that the males are more overt in the maintenance of the pair bond. The marked increase in the frequencies of the displays without a corresponding increase in status, from the five to the six year old birds, suggests that six year old birds may be more active in seeking a territory and a mate.

IV Reproduction and behaviour.

A. Introduction.

In the temperate zone birds which breed annually have a marked gonad cycle. Correlated with the changes seen in the gonads during the breeding season are changes in the behaviour of the birds, e.g. the taking up of a territory by the male, pair formation, mating, nest building, and incubation etc., (Armstrong, 1947; Guhl, 1961; Lehrman, 1961).

The changes in the behaviour are considered to be partly a result of the changes in the level and type of hormone present in a bird at a particular stage of the breeding season. The extensive literature on the effect of hormones on behaviour has been reviewed by Beach, 1948; Lehrman, 1961; Guhl, 1961; Davis, 1964; Young, 1964; and Van Tienhoven, 1967.

While generalisations can be made on the effect of hormones on behaviour, there are exceptions, and there appears to be no clear cut relationship between the level of a particular hormone and the frequency of a particular display.

Both gonadal and pituitary hormones may affect behaviour independently or synergestically (Aronson, 1965). The pathways by which hormones affect behaviour are diverse, and a particular hormone may have more than one effect, or may influence a response in several ways (Hinde, 1966).

The action of a hormone on behaviour may be induced or modified by other stimuli, both internal and external. The work of Lehrman (1965) on the Ring dove (Streptopelia risoria) and Hinde, (1965 and 1967) on the Canary (Serinus canaria) indicates the complex interaction of internal (i.e. hormones acting independently or synergistically) and external (i.e. presence of mate, nesting material, etc) factors which govern successful reproduction in these birds. As Hinde (1965) has pointed out, sexual behaviour cannot be treated in isolation, owing to the causal and functional relationships of other aspects of reproduction that are essential for successful reproduction to take place.

In this section it is proposed to attempt to relate the changes in the frequency of the displays of breeding birds to the changes in the gonads, and to attempt to explain the differences in frequencies of displays in the non-breeding birds in terms of their gonadal condition. However it is clear that the lack of both reproductive and behavioural data from the same individuals places restrictions on the deductions from such a comparison.

B. Gonadal and behavioural cycles in breeding birds.

In 1967 samples of unknown age birds were used for the reproductive and behavioural studies. These birds were assumed to be old, experienced breeding birds (see above). In Chapter 3 the high degree of synchrony in the breeding season was demonstrated, and it is assumed that the gonad cycle in the UK study birds is the same as that found in the breeding birds in the reproductive study.

It is therefore possible to deduce the possible effect of the gonadal condition on the seasonal frequency of the displays. As the frequency of the displays in the females was very low, and showed no seasonal variation, the discussion will be confined to the males.

The UK study males act as their own control, as these birds were observed during both the Occupation and Laying periods, as well as during the Incubation and Guard periods. During these two periods of observation there was a profound difference in the state of the gonads.

(1) Head Wobble and Flag displays. The close temporal association and the similarity of the frequency distribution of these displays enable them to be discussed together.

Before the arrival of the females the frequency of both displays is low, but with increasing numbers of females entering the colony there is a rapid increase in the frequency of the displays, reaching a peak well before all the females have arrived (Fig.1). The frequency then decreases to the initial level before egg laying, and these low frequencies are maintained until the birds depart for sea. The distribution for Flagging (and presumably Head Wobbling) in the colony was similar, and during the Guard period the frequency increases again. This increase was a result of the increasing number of failed birds in the colony. The data in Appendix 6 show that the failed breeding birds have a higher frequency of the displays than the successful breeding birds, and that the frequency in the former is similar to that shown by the same birds at the start of the breeding season.

Thus, during a period when the testis cycle is at a peak, the frequency of these displays is both high and low, but later in the season, when the testes are regressed, the frequency of these displays in failed breeding males is again high, while in the successful breeding males it is low.

Had the gonad condition of the males been a dominant factor influencing the expression of these displays, then the frequencies of the displays should have been high during the period prior to egg laying, and should have been low in both failed and successful breeding birds later in the season.

These facts indicate that the gonadal condition of the males has little influence on the expression of the displays. As the stimulus situation (increasing density and the arrival of the females) is similar in both periods, it may be concluded that it is the stimulus situation that affects the frequency of the displays.

The low frequency of the Head Wobble and Flag displays in successful breeding birds suggests that internal (pituitary or gonadal hormones) or external stimuli (that is tactile stimuli from the egg or chick) acting independently or synergistically, may reduce the tendency of these birds to give these displays.

(2) Threat. Compared with the Head Wobble and Flag displays, the frequency of threat is relatively low. The frequency is higher during the Occupation period after the arrival of the females, and is low during the laying period. During the Incubation and Guard periods the frequency of threat is low, and there

is no difference in the frequency between the failed and successful breeders.

Thus, the increase in the frequency during the Occupation period while the testis cycle is at a peak, and the low frequency during the Incubation and Guard periods in both failed and successful breeding males, suggests that the gonadal condition influences the likelihood of Threat behaviour being displayed.

(3) Copulation. The pattern of the frequency distribution of copulation in the colony was similar to that seen for Flagging, the main difference being that the high frequencies were maintained until just after the start of egg laying. The frequency of copulation, although increasing during the Incubation and Guard periods, was less than that in the Occupation period. Complete copulation was seen throughout the season, in both pairs with two eggs, and in failed breeding birds. Examination of the gonads of three pairs of breeding birds collected after copulation suggested that the gonads of birds copulating at any time during the season do not differ from the gonads of breeding birds.

The decrease in the frequency of copulation after egg laying correlates with the commencement of regression in the gonads, and suggests that copulation is dependent on gonadal condition. However, the increase in the frequency of Copulation later in the season, while not as great as that seen after the arrival of the females, indicates that copulation is not dependent on gonads being at the peak of their cycle, but that the probability of occurrence of copulation is affected by the condition of the gonads.

Examination of the percentage of Copulation Preludes that proceeded to full Copulation during the different periods of the breeding season, gave the following results.

PERIOD	No. C.P.	No.C.P.-App
Occupation	327	196(60%)
Laying	74	37(50%)
Guard	57	12(21%)

The median duration of the Copulation Preludes that did not proceed to full Copulation, and those that did, in the periods before the peak of egg laying and after, are given below

	Md. C.P.(0.01min)	No.Obs.	Md. C.P.-App(0.01min)	No. Obs.
Before E. Lay	0.11	63	0.18	29
After E. Lay	0.10	98	0.16	13

There was no significant difference (Median test, $p < 0.05$ level) between the Copulation Preludes in the two periods, in both those that did not proceed to full Copulation and those that did. The difference between the median duration of those Copulation Preludes that did and did not proceed to full Copulation was significant at the $p < 0.05$ level.

These data show that to achieve full Copulation the male must perform the Copulation Prelude for a longer time, and the decrease in the percentage of Copulation Preludes that proceed to full Copulation after egg laying, indicates that the sexual tendency in the male decreases after egg laying.

If the sexual tendency in the males decreases after egg laying, it is probable that it also decreases in the female, and that the decrease in the frequency of copulation after egg laying may be a result of the interaction of the behaviour of the males and females.

In conclusion, it is suggested that the probability of occurrence of copulation is dependent on the condition of the gonads, and that its actual occurrence is determined by other factors, either internal or external.

C. Non-breeding birds.

The generally low frequency of displays in the non-breeding birds (Fig. 13 and 14) cannot be directly related to the condition of the gonads, and is probably a result of the lack of appropriate stimulus situations.

It has been assumed that the stimulus situations during the Occupation and Guard periods are similar. If this is so, then a higher frequency of the F and HW displays in the one to three year old birds would be expected. The failure to see one year old birds Flag in the colonies, and the low frequency in the two and three year old birds, suggests that this is not so. However, observation of intense HW and F displays by two and three year old males in response to the arrival of females, and the intense HW and F displays given by two 1-year old birds in a crowded enclosure, suggests that the threshold for these displays in young birds may be high, and a more intense stimulus is needed to elicit them.

It would appear that the major factor stimulating the displays in breeding birds is the stimulus situation (increasing density, arrival of females etc.) which is responsible for the frequency of the displays.

Only in the Threat display and copulation was there any evidence that gonad condition played any role. In the younger birds there was some slight evidence to suggest that the frequency of the HW and F displays is affected by a higher threshold, which is probably not affected by gonad condition.

V. Breeding success.

Breeding success is dependent on reproductive maturity and behaviour. It is therefore possible to obtain an idea of the influence of these two major factors on the breeding success of the different age groups by comparing the percentage of successful breeders in each age group, and the percentage that are thought to be reproductively mature.

Carrick (1969) has shown that with increasing age there is an increasing percentage of birds in each age cohort that lay (females), or whose mate lays (males). In Chapter 4 a calculation was made of the number of males and females in each age cohort that were physiologically capable of breeding. These data, together with Carrick's data, are presented below.

	% With Eggs (Carrick)		% Physiologically Capable (CH.4)	
AGE	♂	♀	♂	♀
4	0.0	0.0	4.5(1/22)	0.0(0/17)
5	3.5	8.5	25.0(3/12)	20.0(5/25)
6	20.0	42.5	82.0(9/11)	59.0(8/13)

My original data are in brackets.

There is no significant difference between the number of males and females thought to be physiologically capable of breeding in the different age groups (original data analysed with the Fisher Exact Probability Test, Siegel, 1956). There was no significant difference between the four and five year old females, and the five and six year old females. The difference between the five and six year old males was significant at the $p < 0.05$ level. The difference between the four and six year old birds for both males and females was significant at the $p < 0.05$ level.

These data show that both males and females mature at the same rate, which support the same conclusion reached by Carrick on the basis of the percentage number of males and females in each cohort present at egg laying.

To obtain an idea of the influence of reproductive maturity and behaviour on breeding success, a comparison was made of the data on the numbers of males and females though to be reproductively mature in the different age groups with the numbers of males and females in the in the study birds that bred. These data are given below.

NUMBER OF BIRDS THAT BRED

AGE	♂	♀
4	0/21(0%)	0/22(0%)
5	0/18(0%)	3/24(13%)
6	1/13(8%)	7/10(70%)

There was no significant difference between the number of females that bred in the different age groups and the number that were thought to be physiologically mature. In the males there was no significant difference in the four and five year old males, but in the six year old males the number that was thought to be physiologically mature was significantly greater than the number that bred ($p < 0.05$).

The females and males mature at the same rate, and it is assumed that the difference between the percentage of an age cohort that breed, and the percentage that are physiologically capable of breeding is a result of behavioural factors.

There is no significant difference between the two samples in the four, five and six year old females, and it is assumed that physiological and behavioural development is in step. Six year old males were more physiologically mature than these breeding successes indicate, and this must be a result of behavioural factors.

In the section on status it was found that the females showed a marked increase in status between five and six years of age, while a similar increase in the males was found a year later. Carrick's data show a similar trend, the increase in the percentage of breeding females between five and six years old being 8.5% to 42.5%, while in the males the increase is from 3.5% to 20%, and in the seven year old males, it is 41%.

From this it can be assumed that although the males and females mature at the same rate, it is much more difficult for the males to secure a territory and attract a female than it is for a female to find a mate with a territory.

VI. Summary.

The term status has been used to denote the success a bird had during the breeding season in obtaining the two basic requirements for breeding success, that is, a stable territory and a mate, and also its success in obtaining these requirements in the breeding area of the colony.

The analysis of the status of birds of different age groups confirmed the increase in status with age found by Carrick (1969). Further, the importance of status in breeding success was confirmed by comparison with Carrick's data on the percentage of males and females with eggs (i.e. successful breeding birds). As with the parameters of status, the percentage of breeding females shows a marked increase from five to six years of age. In the males a significant increase in status does not occur until the males are older that 6 years. This was reflected in the breeding success of the males. The males did not breed as successfully as the six year old females until they were seven years old, and it was not until they were 11 years old that they bred as successfully as the females.

The differences in the frequency of the F and HW displays with age, correlated well with the changes in status, and provide further support for the functions of these displays. The increase in the frequency of the HW and F displays seen in the six year old males, without an increase in status, suggested that these birds, while more active behaviourally in seeking a territory and a mate, had more difficulty than the females of the same age had in finding a mate with a territory. This is suggested by the greater status and breeding success of the six year old females.

The effect of gonad condition on the frequency of behaviour was examined by a comparison of the gonad condition and the frequency of the displays during the season in the breeding males. While changes in the gonad condition are obviously related to changes in hormone levels, the term gonad condition was used, as there was no evidence of the hormones, or their concentrations, associated with the gonad condition.

The comparison of the behavioural and reproductive data suggested that the gonad condition in the breeding males did not have any apparent influence on the frequency of the HW and F displays. Their frequency appeared to be more dependent on the stimulus situation. However, Threat and Copulation did appear to be influenced by gonad condition, probably by affecting the threshold for the displays, the expression of the displays being finally determined by the stimulus situation.

In the non-breeding birds there appears to be some evidence that there is an internal mechanism, probably not influenced by the gonad condition, that influences the threshold for the HW and F displays.

In the final section of the chapter it was concluded that both males and females mature physiologically and behaviourally at the same rate, and that the difference in the breeding success between the males and females is a result of the greater difficulty that the males have in establishing a permanent territory and attracting a mate. This difficulty is probably influenced by their later arrival, which in itself is probably influenced by factors at sea which are unknown.

TABLE 11

The median and range of the mean (in brackets) at the parameters (PAR), Territorial tenacity (T), pair bond (M), and the percentage number of days spent in the breeding area (%BA) for males and females. The one year old birds were not sexed and are placed with the males.

		Age							
Sex	Par	UK	6+	6	5	4	3	2	1
M	T	33(32-34)	12(3-32)	3(1-21)	3(1-13)	2(1-7)	1(1-5)	1(1)	1(1)
	M	21(0-27)	12(2-20)	2(0-14)	2(0-7)	2(0-5)	1(0-2)	0(0-1)	0(0)
	%BA	100(100)	100(0-100)	59(0-100)	40(0-100)	46(0-100)	0(0-63)	0(0)	0(0)
F	T	22(19-27)	16(3-20)	8(1-20)	2(1-11)	1(1-6)	1(1-2)	1(0)	
	M	22(19-27)	16(2-20)	15(2-20)	1(0-11)	1(0-4)	1(0-5)	0(0-1)	
	%BA	100(100)	100(0-100)	70(0-100)	0(0-96)	4(0-75)	0(0-75)	0(0-50)	

TABLE 12

Comparison of the data in adjacent age groups for each parameter (T = territorial tenacity, M = Pair bond, %BA = percentage number od days in the breeding area) using the Mann-Whitney U test.
p 0.001(***), p 0.01(**), p 0.05(*).
The older age group is significantly larger in each case.

		Age						
Sex	Par	$\frac{\text{UK}}{6+}$	$\frac{6+}{6}$	$\frac{6}{5}$	$\frac{5}{4}$	$\frac{4}{3}$	$\frac{3}{2}$	$\frac{2}{1}$
M	T	***	**			***		
	M	***	***			***	**	
	%BA		***			***	**	
F	T	**		**		**	***	
	M	**		***		**	***	
	%BA			*			***	

TABLE 13

The values of the regression coefficients b, for each parameter (T = territorial tenacity, M = pair bond, %BA = percentage time spent in the breeding area) against age, the number of birds, the SD of b (Sb), and the statistical significance (Sign) of b being greater than zero at the give percent level (S).

Sex	Par.	No.	b	Sb	Sign.
M	T	108	+19.03	1.79	S
	M	108	+15.17	1.33	S
	%BA	108	+12.53	1.44	S
F	T	111	+19.68	1.68	S
	M	111	+21.94	1.91	S
	%BA	111	+12.49	1.33	S

TABLE 14

The regression coefficients, b, for percentage number of days the HW and F displays were seen (t), and also in the mate (m), and no mate situations (nm) against the values for the parameters, Territorial tenacity (T), and pair bond (M) for all study birds. The standard deviation (Sb) and the number of birds is given. The significance (S) at p 0.05 is also given.

Sex	Comp	b	Sb	No.	Sig^{n}.
M	T-HW t	+ 1.9	0.3	108	S
	T-F t	+ 1.2	0.1	108	S
	M-HW nm	- 0.0	0.0	108	NS
	M-F nm	+ 0.5	0.4	108	S
	M-HW m	+ 3.2	0.4	108	S
	M-F m	+ 2.1	0.4	108	S
F	T-HW t	+ 1.6	0.3	111	S
	T-F t	+ 0.3	0.1	111	S
	M-HW nm	- 0.1	0.1	111	S
	M-F nm	+ 0.3	0.3	111	S
	M-HW m	+ 0.1	0.1	111	S
	M-F m	+ 0.2	0.1	111	S

TABLE 15

The median percentages for each group of the frequency of the HW and F displays calculated from the percentage number of days on which more than two of both displays were seen for each study bird.

T = Data from the total number of days of observation.
M = Data from the days with a mate.
NM = Data from the days without a mate.

		Age							
	DIS.	UK	6+	6	5	4	3	2	1
Males									
T	HW	31	30	21	0	8	0	0	0
	F	12	13	13	0	0	0	0	0
M	HW	25	25	38	11	4	8.5	0	0
	F	0	0	0	0	0	0	0	0
NM	HW	23	20	14	0	0	0	0	0
	F	9	19	14	0	0	0	0	0
Females									
T	HW	0	10	0	0	0	0	0	
	F	0	0	0	0	0	0	0	
M	HW	0	0	0	0	0	0	0	
	F	0	0	0	0	0	0	0	
NM	HW	0	0	11	0	6	0	0	
	F	0	0	0	0	0	0	0	

CHAPTER 9 - DISCUSSION

I. Introduction

The data from this study have been analysed in terms of population rather than the individual. This method of analysis was adopted because of the large, individual variation in the age/sex groups studied. The data in Appendix 6, especially those for the UK males, give an indication of this variation. Initially attempts were made to find age differences on an individual basis, especially between the birds studied during both years of the study. However the variation made this almost impossible, and the population method was adopted. Part of this difficulty was a result of the the period of observation being too short to give sufficient data on each individual.

In discussing the various factors affecting breeding success, and the possible mechanisms affecting delayed maturity, it is convenient to consider separately the terrestrial and marine phases of the annual cycle. Data are only available for the terrestrial phase, and the factors operating at sea are as yet speculative.

II. Terrestrial phase.

A. Introduction.

The terrestrial phase of the annual cycle of the Royal penguin is occupied with breeding and moulting. All age groups come ashore for a period before returning to sea to gain the extra fat reserves required for the moult.

The dynamics and chronology of the breeding seasons during the study periods confirm Carrick's results, and in addition, illustrate the high degree of synchrony achieved by the breeding birds. The breeding season is very similar to that of other colonial and migratory penguins (Chapter 3). The regular and synchronous breeding seasons, together with the similar pattern of male and female incubation periods, suggests that this type of annual cycle has evolved to make the maximum use of similar environmental factors, in particular, the limited period of maximum food availability in the sub-Antarctic and Antarctic waters, thus ensuring that the offspring have the greatest chance of survival.

It is noticeable that in the non-breeding birds there is a tendency to return to the colony for a time between their initial period ashore and their final return for the moult. This sequence is similar to that seen in the breeding birds, and it possible that there is a basic pattern of activity present for both, which, with increasing age in the non-breeding birds, becomes more synchronised with the breeding population.

The Royal penguin, in common with other penguins and many other sea birds, has a delayed onset of sexual maturity. Delayed maturity has no doubt evolved as one mechanism by which a population can regulate its numbers. The mechanisms by which delayed maturity is achieved have received little attention from other workers, and it was the aim of this study to attempt to obtain information on reproduction and behaviour, which were thought to be the two major factors by which delayed maturity was achieved. This was attempted by relating the reproductive and behavioural data to age, the independent variable, and by seeing how they differed with age, and their possible affects on breeding success.

B. Influence of age.

Age is correlated with a number of aspects of the Royal penguin's biology, namely, date of arrival, gonad condition on arrival, behaviour, status and breeding success. The question posed is how these factors, and their possible inter-relationships with age, affect breeding success.

1. Date of arrival. The date of arrival at the colony will affect a bird's chances of breeding successfully. The breeding males arrive at the colony first and establish territories. Thus birds arriving later will be forced to attempt to establish territories on the periphery of the colony where they will be subjected to greater interference, and the possibility of predation. These factors may affect breeding success, and although they have not been demonstrated in the Royal penguin, subjective observation indicates that it is possible. Penney (1968) found no definite external causes for the lower success rates of Adelie penguins breeding on the periphery of the colonies, and suggested that they were the result of inexperience due to age.

Another effect of later arrival on breeding success is that a bird has a reduced chance of obtaining a reproductively mature mate.

In Chapter 8 it was suggested that the stimulus situation within the colony influenced the frequency of the Head Wobble and Flag displays. Thus the date of arrival will affect the stimulus situation into which the birds arrive,and birds arriving after egg laying will have a diminished stimulus situation and will consequently display less. Whether this lack of stimulus, and the resulting lower frequency of displays affects the possibility of securing a territory and mate is not known. This factor does not have any influence on birds arriving during the late Incubation and Guard periods, which provide a stimulus situation similar to that earlier in the season.

Therefore, while the date of arrival probably has some influence on breeding success, it cannot explain the fact that birds arriving after the peak of egg laying have almost a complete breeding failure.

2. Gonad condition.

With age, an increasing percentage of birds reach full gonad development, and the time lag of the cycle decreases. The gonad cycle appears to be independent of the time of arrival, although it is possible that the factors affecting time of arrival may also influence the timing of the gonad cycle.

Gonad condition has no apparent effect on the frequency of the Head Wobble and Flag displays, although it may affect the probability of occurrence of Threat and Copulation. This appeared true for the non-breeding birds, and it is unlikely that the gonad condition had any influence on breeding success via behaviour.

Reproductive development has a direct influence on breeding success. The breeding failure of birds younger than four years old is a result of their lack of reproductive maturity, which would account for Carrick's (1969) failure to find any breeding four year olds. However there is a small percentage of males, and probably females, whose failure to breed was not a result of reproductive immaturity.

The reproductive data indicate that males and females mature at the same rate, which confirms the same conclusion by Carrick (1969). Four to six year old females have a breeding success commensurate with the percentage of physiologically mature birds within those age groups, and the same applies to the four and five year old males.

Six year old males, and probably other old males, are significantly less successful in breeding than the percentage that are reproductively mature. This difference is a result of behavioural factors. Also, in the Yellow-eyed penguin (Richdale, 1957) and the Kittiwake (Coulson, 1966) the females are more successful than males among the younger breeders, and it is probable that the males are inhibited by behavioural factors.

3. Behaviour. The frequency of a number of displays is affected by age. The two most important displays, Head Wobble and Flag, which function in territorial acquisition and pair formation, increase with age, while TH, RNWF, MP and PM displays decrease with age.

While it is apparent that the frequency of the HW and F displays in breeding birds is not affected by gonadal condition but mainly by the stimulus situation, the frequency, however, may be modified by other factors, as shown by the lower frequency of displays in successful breeding birds compared with the failed breeding birds. The lower frequency of displays in the non-breeding birds may in part be related to the stimulus situation, but the low frequency of the younger non-breeding birds during the late Incubation and Guard periods suggests that internal factors also have an influence on frequency.

(a) Pair formation. Carrick (1969) has shown that the female usually finds a mate among the single territorial males. However, stable pair bonds may form before a territory is gained. Penney (1968) found a similar situation in the Adelie penguin. Both Penney (1968) and Richdale (1951) found that in the Adelie and Yellow-eyed penguins respectively, prior to the formation of a stable pair bond, 'trial' pairings are found, the duration of which was variable. Pair formation in the Yellow-eyed penguin may take place at any time during the season, and is a lengthy process.

As in other penguins, pairing in the Royal penguin is preceeded by a definite sequence of behaviour, that is, the approach by one bird in the RNWF posture, followed by the PM or MP, and then with both birds settling down together in the SS posture. This may be followed by further social preening, and/or HW displays. Most pairings are ephemeral, and from the data on periods spent with a mate, it can be inferred that the formation of a stable pair bond is a long-term process. Nothing is know of what causes a bird to attempt to form a pair with another bird, or why these pairings break up. The process of pair formation may be considered to take place in two stages. The first period is during the first three years of life when the birds are mobile around the colony, and are ashore for short periods. During these periods the birds gain experience in sexual recognition, and in the behaviour required to approach another bird. The second period is the time when the birds settle in a particular area of the colony. During this period the birds will learn to recognise individuals and gain further experience in 'social behaviour', and through a process of familiarity, more permanent pair bonds will be formed.

The notion that the formation of a stable pair bond is a long term process involving the gradual familiarization of the two birds is supported by the reduced breeding success after the loss of a mate (Carrick, 1969), while in the Kittiwake, the effect of a loss of mate on subsequent breeding success can be seen for two years (Coulson, 1966).

Probably the acquisition of a stable territory proceeds in a similar way. While it is easy to postulate a learning process (experience), there is no evidence to suggest how it operates, nor is there any evidence to show how the HW or F displays, which have been postulated to function in the attainment of territory and a mate, operate given the low frequency of these displays in the non-breeding birds.

4. Status.

Status is correlated with age, and obviously influences breeding success, but it is not the only factor, as a bird with a stable territory and mate may fail to breed because of late arrival or lack of reproductive maturity.

C. Conclusion.

Breeding success is related to age, and it is the influence of age on the other parameters that determines whether a bird can breed successfully. Basically, breeding success is determined by reproductive maturity. Given a mature reproductive system, it will be dependent on behavioural factors which will influence the attainment of a territory and a mate. If is not know if the gonads influence behaviour or vice versa. These factors are only applicable if the bird arrives at the colony early in the season. If it arrives later its gonads, or those of its mate, may have started to regress, and breeding will therefore be impossible. It is probable that the stimulus situation may influence a bird's ability to gain a territory and a mate, and thus time of arrival may be important from a behavioural point of view.

III. Marine phase.

It is apparent from the consideration of the factors affecting breeding success that both date of arrival and gonad condition may be influenced by factors operating at sea. The two main factors operating at sea are considered to be photoperiodism and food abundancy.

A. Photoperiodism.

Changing photoperiodism has been shown to affect a number of facets of avian biology. Farner (1967) has shown that the proximate factor initiating the gonad development in a number of annual breeding birds in the temperate zone is photoperiodism. It has also been shown to induce migratory behaviour and fat deposition, although these processes are not dependent on each other (Marshall, 1961; Van Tienhoven, 1968). Increasing photoperiodism is also one of the factors stimulating the spring bloom in zooplankton (Foxton, 1964).

Thus it is apparent that photoperiodism plays an important role in the initiation of the avian breeding season.

B. Food.

Little is known of the effect of food shortage on the testis cycle (Marshall, 1961; Lofts and Murton, 1968). However, Lofts and Murton (1966) showed that food shortage may impede spermatogenesis in the Wood pigeon, and it is possible that food shortage early in the period of testis development may have some effect in delaying the cycle. Food shortages have been found to inhibit the development of the follicles (Marshall, 1961).

Food shortage will obviously affect the amount of fat deposited. However, it does not affect the onset of migration (King and Farner, 1963; Lofts, et al, 1963).

Foxton (1956) gives data on the seasonal abundance of zooplankton in the sub-Antarctic waters. The abundance starts to increase in early September, reaching a peak in late November, and a second peak occurs during February becoming minimal again by the end of March.

C. Influence of food and photoperiodism.

No evidence is available for the influence of increasing photoperiodism on gonadal development, migration or fat deposition in the Royal penguin. However the regular and highly synchronised cycle suggests that factors influencing the time of the breeding cycle must be highly regular, and it is probable that photoperiodism is the only environmental factor that is regular enough.

The delay seen in the gonad cycles, and the dates of arrival of the non-breeding birds, may be a result of a higher threshold of response to the increasing photoperiodism.

Food may possibly have a modifying effect on the onset of migration and on the gonad cycle. However if the dates of arrival of the known age birds and the seasonal abundance of zooplankton (Foxton 1956) are compared, it is found that there is a decreasing number of Royal penguins at sea, while there is an increasing food supply.

Even allowing for the return to sea of large numbers of semi-starved breeding birds, it would appear unlikely that food availability is the major factor affecting the delayed arrival of the non-breeding birds. This is given some support by the early arrival of young birds with low weight, which indicates that high fat reserves are not essential for migration.

The gonad cycle of the non-breeding birds is delayed in comparison with the breeding birds, more so in the females than in the males. While the greater delay in the cycle of the females may be affected by food availability it is unlikely that the delay in the gonad cycles is a result of food availability, as the delay is relatively short and there is little difference between the age groups.

Consideration of the dates of arrival and the abundance of zooplankton suggests that food doesn't influence whether a bird achieves full gonad development.

Carrick (1967) states that individuals that are dominant at sea will be first to acquire adequate fat reserves, and attain the gonad development that will enable them to come ashore early and secure an equally dominant breeding status.

The method of feeding in the Royal penguin is not known and there is no evidence to suggest that there is a feeding dominance hierarchy, and as Skutch (1967) has pointed out, it is highly unlikely that a bird which can feed itself after a few weeks at sea should take a number of years (in the case of the Royal penguin five or more) to become efficient enough at feeding to gain the fat reserves required for successful breeding.

It would therefore appear more likely that it is not feeding ability, per se, that governs how rapidly a bird can put on adequate fat reserves, but rather it is the response to those factors (increasing photoperiodism?) that induce more active feeding.

Carrick (1967) has further implied that acquiring fat reserves influences the development of the gonads. Obviously in breeding birds these two factors are correlated, but there is no evidence to suggest that food influences the testis cycle, while it may have some effect on the ovarian cycle.

Therefore, while there is no direct evidence for the factors influencing the development of the gonads, acquiring of fat reserves and the onset of migration, it is suggested that age differences in these factors are affected by a physiological regulating mechanism rather than feeding ability, although food availability may modify the effect of this mechanism.

IV. Deferred maturity.

Long lived sea birds are characterised by low reproductive rates, long incubation and fledgling periods, and delayed maturity. Delayed maturity has been demonstrated in the Short-tailed shearwater (Marshall and Serventy 1956), the Yellow-eyed penguin (Richdale, 1957), the Arctic tern (Cullen, 1957), the Kittiwake (Coulson, 1966), the Adelie penguin (Sladen, 1966), the Gannet, Sula bassona (Nelson, 1966) and others, reviewed by Lack (1968).

Lack (1954, 1966 and 1968) has argued that bird populations are regulated mainly by food, through the effect of density dependent mortality outside the breeding season, and the characteristics of long lived sea birds are adaptations through natural selection to make the most efficient use of the relatively low abundance of food. Ashmole (1963) postulated that the food shortage during the breeding season was more important. However there is no conclusive evidence to show when food shortage is critical. Lack considers that delayed maturity has evolved in response to a food shortage, because on an average, those individuals which start breeding at the normal age for the species, eventually leave more offspring than those which start when younger. Birds which breed at a younger age may lack the 'experience' and feeding ability to successfully raise the chick, and it may also reduce the chances of survival.

Wynne-Edwards (1962) suggests that bird populations maintain their population level below that which would lead to overfeeding of the food resources. He suggests that they are able to do this through a homeostatic mechanism by which a population regulates the numbers entering the breeding population (group selection). Thus, on Wynne-Edward's hypothesis, maturity is a consequence of group selection which will determine how many members of the population should breed each year, i.e. regulating the reproductive rate to the mortality rate.

As Lack (1966) pointed out, there is no evidence to support the idea that birds that breed early reduce their chances of survival, and therefore leave few offspring, nor is there evidence that birds that breed later leave more offspring, although this is suggested, as in the Yellow-eyed penguins (Richdale, 1957), the Kittiwake (Coulson, 1966) and the Royal penguin (Carrick, 1967), birds breeding for the first time are less successful.

Lack (1968) suggests that younger birds lack the feeding ability and experience to breed as successfully as older birds. While experience undoubtedly is important, the idea that the younger birds are less efficient feeders does not appear to be valid as already pointed out.

There is no evidence to support Wynne-Edward's suggestion that delayed maturity is a result of the younger birds being prevented from breeding.

The presence of delayed breeding in a large number of sea birds, and others, suggests that it is an important mechanism in helping to regulate populations, and as Carrick et al (1962) have pointed out, the Elephant seal provides an excellent example of how delayed maturity may function in population regulation. Almost all the discussion and research on delayed maturity (e.g. Lack, 1968; Wynne-Edwards, 1962) has been focused on the possible factors influencing the evolution of delayed breeding, but little has been done on how it operates.

Delayed maturity can be considered to be just one mechanism that has evolved to regulate a population whose food supply is relatively low in relation to the size of the population.

I suggest that delayed maturity was achieved through the evolution of a maturing physiological mechanism, or mechanisms, that inhibited full spermatogenesis and probably delayed the gonad cycle, as well as affecting the threshold for the response to the migratory stimuli. It is also suggested that those stimuli affecting fat deposition and also the threshold affecting the probability of display were controlled by this mechanism, and that the action of these mechanisms may be modified by the availability of food. The operation of such a mechanism would aid the interpretation of the dates of arrival, condition of the gonads, and the behaviour observed during this study.

Having set the time of arrival and the condition of the gonads, the birds' behaviour, once in the rookery, is restricted by a high threshold for at least the HW and F displays.

Thus the complex interaction of time of arrival, state of the gonads, and behaviour, coupled with the highly synchronised breeding, prevents the younger birds from breeding.

The asynchrony of the cycles in the non-breeding birds has the advantage that the breeding is not interfered with by the presence of large numbers of non-breeding birds. The individual bird gains an increasing amount of experience of the colony, and of social contact with birds of its own age, and in smaller numbers than if the birds had all arrived at the same time. This would appear to have the advantage of limiting intraspecific strife by having smaller numbers of mobile birds, and also by having similarly aged birds of similar experience.

Wynne-Edwards regards the variability in the age of first breeding as being explained by group selection rather than by being evolved through natural selection. While some of this variability is undoubtedly genetic, the influence of modifying environmental factors cannot be overlooked, and it would seem that such variability has the advantage of allowing a population to maintain, more easily, a dynamic equilibrium within a dynamic environment.

Thus in the Royal penguin we can postulate that the pattern of periods spent ashore, the behavioural repetoire and the basic gonad cycle are all present at birth, i.e. genetically determined, and that with increasing age under the controlling influence of a regulating physiological mechanism, these facets of the Royal penguin gradually approach the adult condition, modified by the individual's experience, and such environmental factors as food availability.

Such a mechanism allows a bird to attain the maximum experience with birds of a similar age, while at the same time, minimises intraspecific strife. There is also the advantage that breeding birds can come ashore to breed without being interfered with, or having to waste time and energy in defending their territories from mobile non-breeding birds.

SUMMARY

The dynamics and chronology of the Bauer Bay rookery were described. There is a rapid influx of breeding males in late September followed about a week later by the breeding females. The majority of the breeding birds are ashore by mid-October and the population remains fairly constant until the breeding birds leave the colony during the last week in October. Egg laying commences about mid-October, with a peak about October 20. The breeding males leave about 10 days after the first egg is laid. The males return to resume incubation about mid-November, and hatching occurs about one week later. The females return at about hatching time to give the chick its first feed, and they continue to feed the chick until about mid-December, when the males leave and the chicks form creches. Both parents then feed the chicks.

One year old birds come ashore in December, and with age, the older birds come ashore earlier. There is a tendency for the non-breeding birds and failed breeding birds to return to the colony during the Incubation and Guard periods, and this gives rise to a second peak in the population graph.

The gonads of the breeding males on arrival are almost at the peak of spermatogenesis, spermatozoa being produced shortly after arrival. The follicles of the breeding females increase rapidly in size after arrival in the colony. The gonads undergo a rapid regression after the first eggs are laid.

The gonad cycle of the non-breeding birds is independent of the time of arrival at the rookery. With increasing age the gonad cycles show greater development and by six years of age, only a small percentage of birds do not have

complete cycle. The percentage number of males and females in each class that are reproductively mature was calculated from a comparison with the breeding birds.

The behaviour of the Royal penguin was described in terms of the elements of the displays, the displays proper and the display situations. Descriptions were given of the behaviour seen in the rookery during the season. The seasonal distribution of Flagging, Head Wobbling, Threat and Copulation are given, and all except Threat show a marked peak after the females start arriving and a rapid decrease before egg laying. The differences in the frequency of all displays for the different age/sex groups were described. Eight displays were found to have significant differences in frequency between age groups, and/or males and females (i.e. Head Wobble and Flagging, Head Down, Head Flick, Rounded Neck Wings Forward, Threat, Preening the Mate and Mutual Preening). The Head Wobble and Flag displays were considered to be the most important because of their high frequency and the diversity of situations in which they were seen. These differences were analysed in more detail, in terms of the effect of age, sex and the presence or absence of a mate. Changes in frequency with age were gradual. The decrease in the frequency of the Threat display with age was considered to be a consequence of decreased mobility, while the decrease in frequency of Mutual Preening and Preening the Mate and Rounded Neck Wings Forward was related to the greater number of pairings, mainly ephemeral, found in the younger birds, as these displays were used during the initial approach (RNWF) and after the approach (PM and MP)

The causation and function of the displays was analysed. Causation was analysed using form analysis, temporal association and situation analysis. The results of these analyses gave essentially the same results, and showed that the Head Wobble display was essentially the expression of a sexual tendency, while the Flag display was a conflict display between the sexual, attack and fleeing tendencies.

The other displays were also analysed in terms of the presence of absence of the tendencies to attack, flee or behave sexually.

The function of the displays was deduced from the frequency distribution of the displays, and from the situation in which they were given. The Head Wobble display (and other displays with a sexual tendency) was thought to act as an appeasement display, as well as in communicating the strength of the sexual tendency. The Flag display was considered to be a ritualised territorial threat display, as well as functioning in attracting females to the males.

Status was defined and changes in the parameters of status (territorial tenacity, pair bond and percentage time spent in the breeding area of the colony) with age showed that they increased slowly until the six year old females, and the six+ year old male group. These parameters correlated with the frequency of the Flag and Head Wobble displays and gave further support to the assumed functions of these displays. The changes in status of the males and females with age correlated with the data on breeding success.

Comparison of the behavioural and reproductive data suggested that the frequency of the Flag and Head Wobble displays was not influenced by gonad condition, and that the stimulus situation (arrival of females and increasing density) in the colony was the most important factor influencing the frequency.

It was concluded that breeding success is limited by reproductive maturity, and after maturity is achieved, breeding success is dependent on arrival into the colony at the right time, and the ability to attain a territory and a reproductively mature mate. It was suggested that delayed maturity is achieved by a maturing physiological mechanism that affects the threshold for the response to those factors initiating gonadal development and migration, and once in the colony, it influenced the threshold for the displays, especially the Head Wobble and Flag displays.

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APPENDIX 1

Reproduction. The number of males and females, collected on arrival and departure from the rookery on the given dates, is shown. The total number of birds collected in each group, and on each day, is also given.

* Birds collected in the rookery
** Two pairs collected after copulation
\+ Chicks taken from UK sample on that day
\++ Pair collected after copulation

	Arriving																Departure									
Age	UK		6		5		4		3		2		1		CH		UK		6		5		4		Total	
Sex	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Date																										
30.1X	5																								5	
5.X		5			1		1	1																	2	6
6.X						2		1																		3
8.X	5*																								5	
10.X				2	1		2																		3	2
11.X			1	2																					1	2
13.X	5*	5*																							5	5
14.X				1	1		3																		4	1
15.X			4																						4	
18.X	2	2**							1											2		1			3	5
19.X							2	2																	2	2
20.X					1	1		1																	1	2
21.X						2		1													1				1	3
22.X				1			1												1			3	1	1	3	5
23.X	5*	5*				1																			5	6
24.X					1															1	1	2			2	3
27.X																			2			3	1	2	3	5
28.X			1	2													5		2		2	1	2	1	12	4
29.X							1			1														1	1	2
30.X					1		4	1												1			1	2	6	4
31.X							1											1	1			3	1		3	4
2.X1					1	2	1	2		1															2	5
3.X1		5*																								5
4.X1						1																1	1		1	2
5.X1						1			3	1															3	2
6.X1					1	1																			1	1
7.X1									3	5															3	5
10.X1																				1						1
11.X1	5*						1+	1+	1																7	1
19.X1											5	3													5	3
8.X11	6*	6*													2+	1+									8	7
14.X11													2	2											2	2
TOTAL	32	28	6	8	8	11	16	10	8	8	5	3	2	2	2	1	5	1	6	5	4	14	7	7	102	98

APPENDIX 2

Study Birds. The age, sex, and date of arrival of the study birds in 1966, are listed in order of arrival at the rookery. The numbers given are those painted on each bird on arrival. The band numbers are not given. The numbers painted on the 1966 study birds that returned in 1967, and the dates of arrival, are given. The birds studied in 1967 only are also listed, except the 21, one year old birds collected between December 8 and 14. These birds were not sexed.

1966 No.	1966 Age	Sex	Date Arr.66	1967 No.	Date Arr.67
1	10	M	25.1X		
2	6	"	"		
3	"	"	26.1X		
4	5	"	27.1X	22	6.X
5	6	"	"	35	11.X
6	"	"	"	13	25.1X
7	10	"	1.X	15	2.X
8	9	"	"		
9	"	"	2.X	14	30.1X
10	5	"	"		
11	"	"	"		
12	9	"	"		
13	"	"	3.X		
14	"	"	4.X		
15	"	"	"		
16	4	"	5.X	23	6.X
17	6	F	"		
18	8	M	"		
19	10	"	"		
20	8	"	6.X	29	9.X
21	11	F	"		
24	"	"	9.X		
25	"	M	"		
26	4	"	"	40	14.X
27	"	"	10.X		
28	"	"	"	21	5.X
29	9	F	11.X		
30	4	M	"		
31	9	F	12.X		
32	10	"	"		
33	6	M	13.X		
34	"	F	"	30	9.X
35	"	"	"	26	9.X
36	4	"	14.X		
37	"	"	"	36	11.X
38	9	"	"		
39	6	"	"		
40	7	"	"		
41	11	"	"		
42	"	"	"	34	10.X
43	9	"	15.X		
44	8	"	16.X		
46	5	"	17.X		
47	"	M	18.X		
48	"	"	"	24	7.X
49	4	"	"		
50	"	"	"		
51	"	F	"		
52	5	F	18.X		
53	"	"	"	48	22.X
54	"	"	"		
55	"	M	"		
56	"	F	"	45	20.X
57	"	M	"	38	13.X
58	"	"	19.X		
59	"	"	"		
60	4	F	"		
61	5	"	"	33	10.X
62	4	M	20.X	20	5.X
63	5	"	"	43	16.X
64	"	F	"	25	8.X
65	4	"	"		
66	5	"	"		
67	4	M	24.X		
68	"	"	"		
69	5	"	"	37	13.X
70	4	F	25.X	28	9.X
71	5	"	"	46	20.X
72	4	"	"		
73	5	"	"		
74	"	"	"		
75	4	M	"	27	9.X
76	"	F	28.X		
77	"	"	"	47	22.X
78	"	"	"		
81	"	M	26.X		
82	"	F	"	44	17.X
83	"	M	"		
84	"	"	"		
85	"	F	"	72	19.X1
86	"	"	29.X	49	24.X
87	5	"	"	32	10.X
88	3	"	"		
89	4	M	3.X1		
90	"	"	"		
91	"	F	"	39	13.X
92	"	M	5.X1	52	27.X
94	"	F	8.X1		
95	3	"	"		
96	4	"	"		
97	3	M	"		
98	5	F	8.X1		
99	3	"	"		
100	"	M	"		
101	4	"	"		
102	"	F	"		

APPENDIX 2 Continued

1966 No.	1966 Age	Sex	Date Arr.66	1967 No.	Date Arr.67
103	3	M	6.X1		
104	"	F	9.X1		
105	5	M	"		
106	3	F	10.X1	58	7.X1
107	"	M	"		
108	"	F	"		
109	"	"	11.X1		
110	"	M	"		
111	"	"	"		
112	"	F	"		
113	5	"	"		
114	"	M	"		
115	2	F	"		
116	3	M	"		
117	"	"	"	42	16.X
118	"	"	12.X1		
119	"	F	"		
120	"	M	"	55	31.X
121	"	"	"		
122	"	"	13.X1		
123	"	"	"		
124	2	F	"		
125	3	"	"	53	30.X
126	"	"	"		
127	"	"	"	41	15.X
128	"	M	14.X1		
129	"	"	"		
130	"	"	"		
131	"	F	15.X1	56	5.X1
132	"	"	14.X1		
133	"	M	"	51	26.X
134	"	"	"		
135	"	"	"		
136	"	F	"		
137	"	M	"		
138	"	F	15.X1	50	25.X
139	"	"	"		
140	2	"	16.X1	54	31.X
141	5	"	18.X1		
142	2	M	20.X1	59	11.X1
143	"	F	"	64	13.X1
144	"	"	21.X1	57	6.X1
145	"	M	22.X1	67	15.X1
146	"	"	"	74	20.X1
147	"	"	23.X1		
148	"	F	24.X1		
149	"	M	"	62	12.X1
150	"	F	"	65	14.X1
151	2	M	26.X1		
152	"	F	"	73	20.X1
153	"	M	"	69	17.X1
154	"	F	"		
155	"	M	"		
156	"	F	"	71	18.X1
157	"	"	"	60	11.X1
158	1	M	28.X1	68	16.X1
159	2	F	"	70	18.X1
160	"	"	"		
161	"	"	"		
162	"	"	"	61	12.X1
163	"	"	"		
164	"	"	"		
165	"	M	30.X1	63	13.X1
166	"	"	"	66	14.X1
167	"	"	"		
	UK	M		1	24.1X
	"	"		2	"
	"	"		3	"
	"	"		4	"
	"	"		5	"
	"	"		6	"
	"	"		7	"
	"	"		8	"
	"	"		9	"
	"	"		10	"
	"	"		11	"
	"	"		12	"
	5	"		16	4.X
	"	"		17	"
	"	"		19	"
	4	"		18	"

APPENDIX 3

Study birds. The number of males and females, and the median and range of the arrival and departure dates for each group, is shown. (The data for both years is grouped.) The median and range of the dates, and the number of birds who returned to the rookery later in the season, is also shown.

Age Group	Sex	No. Arr.	Arr. dates Range	Date Arr. Median	Dep. Dates Range	Date Dep. Median	No. Ret.	Ret. Dates Range	Ret. Date Median
UK	M	12	24.1X	-	25.X - 27.X	26.X	11	10.X1 - 24.X1	17.X1
UK	F	11	30.1X - 9.X	6.X	10.X1 - 24.X1	17.X1	-	-	-
6+	M	20	25.1X - 11.X	1.X	18.X - 3.X1	25.X	13	13.X1 - 2.X11	21.X1
6+	F	14	6.X - 16.X	12.X	27.X - 23.X1	4.X1	9	8.X1 - 3.X11	18.X1
6	M	13	25.1X - 16.X	6.X	5.X - 31.X	20.X	6	5.X1 - 25.X1	22.X1
6	F	10	5.X - 20.X	11.X	25.X - 13.X1	28.X	10	25.X1 - 9.X11	3.X11
5	M	18	2.X - 11.X1	18.X	3.X - 3.X1	27.X	14	3.X1 - 16.X11	30.X1
5	F	23	6.X - 19.X1	19.X	14.X - 9.X11	30.X	20	19.X1 - 20.X11	27.X1
4	M	21	5.X - 8.X1	24.X	6.X - 20.X1	31.X	17	16.X1 - 9.X11	6.X11
4	F	22	14.X - 8.X1	28.X	24.X - 1.X11	5.X1	17	23.X1 - 16.X11	29.X1
3	M	27	6.X1 - 20.X1	13.X1	13.X1 - 1.X11	20.X1	9	21.X1 - 20.X11	9.X11
3	F	26	20.X - 20.X1	12.X1	1.X1 - 3.X11	20.X1	10	30.X1 - 20.X11	9.X11
2	M	12	16.X1 - 30.X1	25.X1	22.X1 - 3.X11	1.X11	4	3.X11- 14.X11	7.X11
2	F	17	11.X1 - 28.X1	26.X1	12.X1 - 3.X11	28.X1	4	3.X11- 9.X11	7.X11
1	M & F	21	8.X11- 14.X11	9.X11	8.X11- 14.X11	9.X11	-		

APPENDIX 4

Female Reproduction. The age and date of arrival of all females collected is shown here. Also shown is the weight of the ovary in grams, the diameter of the four largest follicles, and any corpora lutea present (in mm.). 1 is the largest follicle, 2 the second largest, etc. C.P.1 is the smallest corpus luteum, C.P.2 is the largest corpus luteum.

AT = atresia. Those birds marked with a + have atretic follicles, and those with - have no atretic follicles.

- * UK breeding females collected after copulation
- ** Four year old female collected after copulation
- \+ Breeding female collected on departure, who did not have mate (see text)

A = arriving. D = departing. C = In colony.

DIAMETER OF FOLLICLES AND CORPORA LUTEA (MM)

Age	Date	Ov.Wt (gms)	1	2	3	4	C.P.1	C.P.2	AT.
UK(A)	5.X	14.9	23	18	12	8			-
"	"	19.5	26	24	18	8			-
"	"	13.7	22	19	11	8			-
"	"	25.9	28	24	17	7			-
"	"	65.3	33	31	30	26			-
" (C)	13.X	91.4	42	40	31	24			-
"	"	88.9	38	35	33	26	28		-
"	"	47.1	36	29	23	8			-
"	"	95.7	39	38	34	25	22		-
"	"	74.2	36	36	32	28			-
" (C)	23.X	14.4	25	8	7	7	11	9	+
"	"	19.2	37	8	5	4	15	9	+
"	"	5.6	14	14	3	3	11	7	+
"	"	23.9	34	10	5	5	12	8	+
"	"	21.4	34	4	4	4	10	9	+
" (C)	3.X1	2.6	9	5	5	4	4	3	+
"	"	2.7	14	7	4	3	4	2	+
"		11.5	20	16	9	8	5		+
"	"	2.0	10	9	6	5	7	6	+
"	"	2.3	13	4	4	4	6	3	+
" (C)	8.X11	1.1	4	4	4	4	2	2	+
"	"	1.1	4	3	3	3	3	3	+
"	"	0.8	4	4	4	3	2	2	+
"	"	1.2	4	4	3	3			+
"	"	1.9	5	4	4	4	4	4	+
6(A)	10.X	29.9	29	24	16	10			-
"	"	23.2	24	22	22	17			-
"	11.X	5.9	16	16	11	10			-
"	"	28.8	30	25	16	8			+
"	14.X	53.7	33	28	24	20			+
"	22.X	6.5	17	11	8	6			-
"	28.X	64.6	36	33	28	19			-
"	"	1.8	5	5	5	5			-
6(D)	18.X	19.8	25	22	19	5			+
	"	5.2	13	13	5	5			+
	24.X	49.1	37	33	9	8	15		+
	30.X	5.6	18	13	8	8			+
	10.X1	1.5	7	4	3	3	5	4	+

DIAMETER OF FOLLICLES AND CORPORA LUTEA (MM) Continued

Age	Date	Ov.Wt (gms)	1	2	3	4	C.P.1	C.P.2	AT
5(A)	6.X	45.9	32	29	26	19			-
"	7.X	9.8	18	12	8	8			-
"	20.X	4.8	16	14	6	6			+
"	21.X	2.5	6	6	6	6			-
"	"	10.7	18	17	11	8			+
"	23.X	2.2	6	6	6	5			-
"	2.X1	3.5	16	5	5	4	8	4	-
"	"	2.1	7	7	6	6			-
"	4.X1	2.3	6	6	6	6	7		-
"	5.X1	5.9	12	7	7	7			-
"	6.X1	2.8	6	6	6	5			-
5(D)	22.X	10.7	20	18	18	11			+
"	"	2.2	6	5	5	4			-
"	"	2.5	7	7	6	5			-
"	24.X	3.1	9	5	5	4			-
"	"	3.2	13	8	6	6			+
"	27.X	2.5	11	8	4	4			+
"	"	1.8	6	6	5	4			-
"	"	21.5	26	22	15	13			+
"	28.X	3.7	19	7	7	4			+
"	"	2.6	11	8	6	6			+
"	31.X	2.3	12	7	5	3			+
"	"	1.3	4	4	3	3			-
"	"	2.7	9	9	5	5			-
"	4.X1	4.7	13	9	8	8			+
4(A)	5.X	1.9	11	5	5	5			-
"	6.X	1.5	6	5	5	5			-
"	19.X	2.8	9	6	6	6			-
"	"	4.9	14	10	7	7			-
"	20.X	2.7	8	7	6	6			-
"	21.X	3.4	8	7	7	7			-
"	30.X	3.1	7	6	6	6			-
"	2.X1	0.9	5	4	4	4			-
"	"	4.2	8	7	7	7			-
4(D)	22.X	1.2	5	5	5	5			-
	27.X	1.5	6	4	4	4			-
	"	1.4	8	7	6	5			-
	28.X	1.2	4	4	4	3			-
	29.X	2.2	11	9	7	6			+
	30.X	2.1	4	5	5	4			-
	"	1.6	6	6	5	5			-
3(A)	29.X	0.7	4	4	4	3			-
	2.X1	1.3	7	6	5	5			-
	5.X1	1.2	4	4	4	3			-
	7.X1	3.0	6	6	6	6			-
	"	2.3	7	6	6	6			-
	"	3.9	8	6	5	5			-
	8.X1	0.7	6	5	4	-			-
	"	1.8	6	6	6	5			-

DIAMETER OF FOLLICLES AND CORPORA LUTEA (MM) Continued

Age	Date	Ov.Wt (gms)	1	2	3	4	C.P.1	C.P.2	AT
2(A)	19.X1	0.4	4	3	3	2			-
	22.X1	0.6	4	4	3	3			-
	"	0.4	-						
1(A)	14.X11	2.0	-						
	"	2.0	-						
CHICK	8.X1	0.03	-						
UK(C)*	17.X	46.6	38	30	25	8	24		-
" *	18.X	70.1	39	35	26	7	19		-
" *	8.X11	1.0	5	5	5	4	2	2	+
" +	31.X	32.8	32	30	11	10			+
4 **	10.X	1.3	4	4	4	4			-

APPENDIX 5

Histology of the testes. The age, and date of arrival of all males collected in 1967 is shown. The relative proportion of interstitial tissue, tubule tissue and lumen, with and without Sudan IV staining, is shown. Lumen stained with Sudan IV refers to the debris in the lumen. The median and range of the stages of spermatogenesis, the amount of debris in the lumen and the mean and range of the tubule diameters (µ), are also given. Debris is scored as zero (-), low (+), moderate (++), and high (+++).

* UK breeding males collected after copulation

** Four year old male collected after copulation

\+ Sample collected on departure

Age	Date	No lipid			With lipid				Stage of S. gen Md	Stage of S. gen range	Debris	Mean Tub.Dia. µ	Range Tub.Dia. µ
		Int	Tub	Lum	Int	Tub	Lum	Other					
UK	30.1X	13	123	54	7	0	0	3	5	4-6	-	256	220-300
"	"	14	135	34	14	0	0	3	6	5-6	-	286	260-330
"	"	8	141	46	2	0	0	3	6	5-7	-	327	280-390
"	"	16	125	50	8	0	0	1	5	4-6	-	324	280-380
"	"	17	140	29	8	1	0	5	4	3-5	-	224	180-260
"	8.X	24	122	49	2	0	0	3	5	6-6	+	232	200-290
"	"	21	128	43	5	0	0	3	6	5-7	-	229	200-270
"	"	15	137	45	1	0	0	2	6	5-7	+	282	250-340
"	"	17	135	37	2	0	0	9	6	5-7	-	245	200-290
"	"	10	146	32	7	0	0	5	5	5-6	-	278	240-310
"	13.X	5	130	50	7	0	0	8	5	4-5	-	267	230-320
"	"	11	106	63	19	0	0	1	6	5-7	+	259	220-300
"	"	9	135	37	15	0	0	4	6	5-7	+	258	210-310
"	"	8	142	46	3	0	0	1	6	5-6	-	257	220-300
"	23.X	7	113	27	25	24	1	3	6	5-6	++	165	130-190
"	"	8	32	37	27	91	1	4	5	5-6	++	196	130-240
"	"	10	129	38	1	18	0	4	6	3-7	+++	197	180-240
"	"	8	79	48	13	49	0	3	6	4-7	++	211	180-270
"	"	4	106	56	12	18	0	4	5	5-6	+	216	200-270
" +	28.X	6	122	26	22	14	0	10	5	3-6	+++	150	120-180
"	"	6	16	4	26	104	40	4	5	3-6	+++	158	130-190
"	"	10	0	0	48	112	24	6	3	3-5	+++	97	90-120
"	"	8	0	0	30	108	48	8	3	3-5	+++	98	80-120
"	"	4	0	0	30	130	30	6	3	3-5	+++	120	100-150

APPENDIX 5 Continued

Age	Date	No lipid			With lipid				Stage of S. gen Md	Stage of S. gen range	Debris	Mean Tub.Dia. µ	Range Tub.Dia. µ
		Int	Tub	Lum	Int	Tub	Lum	Other					
UK	10.X1	8	12	8	42	106	18	4	2	1-2	+	101	80-130
"	"	6	44	4	60	66	12	8	2	1-2	+	103	100-110
"	"	8	0	0	42	122	22	6	2	1-2	+	106	100-120
"	"	4	102	18	51	15	3	7	1	1	+	90	80-110
"	"	16	42	14	36	76	4	14	1	1-2	+	87	80-100
"	8.X11	49	133	10	0	0	0	8	2	1-2	+	80	60-120
"	"	49	136	7	0	0	0	8	2	1-2	+	81	70-100
"	"	62	119	7	0	0	0	12	2	2	-	76	70-90
"	"	56	130	8	0	0	0	6	2	2	-	62	50-70
"	"	5	64	1	73	43	0	4	2	2	-	83	70-110
6	11.X	10	144	33	11	0	0	2	6	5-6	-	305	230-350
"	15.X	8	137	39	11	0	0	5	6	5-6	-	235	210-280
"	"	6	138	35	13	4	0	4	6	5-6	-	303	260-340
"	"	10	146	41	1	0	0	2	5	5-6	-	236	190-280
"	"	8	148	37	5	0	0	2	6	5-7	+	229	200-290
"	28.X	8	127	36	13	6	4	6	5	4-5	+	217	190-270
6+	27.X	6	2	0	22	124	38	8	2	2-5	+++	134	100-160
"	"	4	2	3	30	130	23	8	4	2-5	+++	145	100-160
"	28.X	5	151	22	15	0	0	7	6	5-6	++	233	190-290
"	"	6	140	20	24	2	2	6	5	4-6	+	202	180-220
"	31.X	5	136	31	23	0	0	5	4	4-5	+	221	180-280
5	5.X	17	122	48	11	0	0	2	4	3-4	+	275	230-330
"	10.X	8	128	51	10	0	0	3	5	4-6	+	268	220-290
"	14.X	5	137	49	7	0	0	2	5	4-5	+	204	170-220
"	20.X	6	136	39	14	0	0	5	5	5-6	-	235	190-280
"	24.X	6	130	50	10	0	0	4	6	5-6	+	268	220-330
"	30.X	8	126	46	10	0	0	10	5	4-6	-	256	210-290
"	2.X1	16	130	46	6	0	0	2	4	4-5	-	204	170-240
"	5.X1	2	110	40	26	10	0	12	4	4-5	-	149	110-200
5+	21.X	16	143	28	12	0	0	0	4	4-5	-	231	200-270
"	22.X	4	107	24	21	32	6	6	5	2-6	+++	155	120-200
"	24.X	8	118	32	24	12	0	6	6	5-7	+++	215	200-230
"	28.X	7	127	32	25	1	1	8	6	3-6	+++	179	120-127

APPENDIX 5 Continued

Age	Date	No lipid			With lipid			Other	Stage of S. gen Md	Stage of S. gen range	Debris	Mean Tub.Dia. µ	Range Tub.Dia. µ
		Int	Tub	Lum	Int	Tub	Lum						
4	5.X	17	129	41	5	0	0	8	4	3-5	-	266	230-320
"	10.X	14	127	48	1	0	0	10	4	3-5	-	218	160-270
"	"	6	142	48	4	0	0	0	5	3-6	-	255	220-300
"	14.X	9	132	56	0	0	0	3	5	2-5	-	225	200-270
"	"	9	135	51	2	0	0	3	5	4-6	-	245	210-290
"	"	7	126	52	9	0	0	6	5	5-6	-	259	220-300
"	19.X	17	126	56	0	0	0	1	4	3-5	+	231	200-290
"	"	15	142	40	0	0	0	3	4	4-6	-	227	200-270
"	22.X	9	62	30	21	60	13	5	5	5-6	+	265	200-300
"	29.X	4	110	40	28	8	0	10	5	5-6	-	222	190-270
"	30.X	12	130	44	8	0	0	6	5	5-6	-	217	180-260
"	"	2	122	49	20	0	0	7	5	4-6	-	207	180-240
"	"	20	138	31	0	0	0	11	6	5-7	+	235	190-280
"	"	12	140	32	8	0	0	8	6	5-6	+	214	180-270
"	31.X	4	117	51	19	5	0	4	4	4-5	-	218	180-260
4+	22.X	18	120	59	1	0	0	2	5	4-5	+	225	200-280
"	27.X	18	138	39	2	0	0	3	5	5-6	+	174	150-200
"	28.X	8	100	50	20	14	0	8	6	5-6	+	227	200-260
"	"	6	131	51	6	0	0	6	4	4-5	+	226	180-270
"	30.X	5	128	45	17	0	0	5	4	4-5	+	198	160-240
"	31.X	7	45	15	26	96	4	7	5	5-6	+	185	120-340
"	4.X1	6	124	30	26	10	0	4	4	3-4	+	124	90-160
3	18.X	10	111	66	5	0	0	8	4	4-5	-	221	190-290
"	5.X1	5	112	64	15	0	0	4	4	4-5	-	224	200-240
"	"	12	90	38	26	26	4	4	4	3-4	+	137	90-160
"	"	10	98	63	21	0	0	8	5	3-6	-	159	120-180
"	7.X1	8	104	26	26	16	10	10	4	2-5	+	146	110-170
"	8.X1	2	70	44	36	44	0	4	4	2-5	+	173	150-200
"	"	11	118	36	13	10	4	8	4	2-5	+	144	100-170
"	10.X1	6	126	52	8	0	0	8	5	2-6	+	226	180-270
2	18.X1	17	127	36	0	0	0	20	4	2-5	++	147	110-180
	19.X1	24	122	42	0	0	0	12	4	2-5	+++	170	130-200
	"	4	86	32	40	20	10	8	4	2-5	+++	140	110-190
	"	5	92	17	33	35	15	3	4	1-5	+++	102	90-140
	"	17	78	9	49	32	9	6	3	1-4	++	99	80-120

APPENDIX 5 Continued

Age	Date	No lipid			With lipid			Other	Stage of S. gen Md	Stage of S. gen range	Debris	Mean Tub.Dia. μ	Range Tub.Dia. μ
		Int	Tub	Lum	Int	Tub	Lum						
1	14.X11	88	82	24	0	0	0	6	2	1-4	+++	118	100-160
"	"	74	88	32	0	0	0	6	2	1-4	+++	114	90-160
CHICKS	8.X11	No tubules developed											
UK*	18.X	15	143	38	1	0	0	3	4	4-5	+	222	190-250
" *	"	4	91	61	26	12	0	8	5	5-6	++	205	180-230
4 **	10.X	6	130	40	18	0	0	6	4	4-5		219	170-250

APPENDIX 6

Study birds. The number of daily 15 minute observations on each study bird, and the total number of listed displays seen for each bird, is shown. The column on the right hand side of each group gives the totals for each display in the group, and the total number of observations. THPB, THNB, THM are threats towards a passing bird, a neighbouring bird, and the mate, respectively.

* Failed breeding birds.

TABLE 1

	UK Males 1967													UK (Males (IC)											
Bird No.	1	2	3	4	5	6	7	8	9	10	11	12	Tot	1	2	3	4	5	6*	7*	8*	9	10	11	Tot
No. of Obs.	32	29	33	31	33	31	33	29	31	33	34	32	381	29	27	21	25	24	21	16	25	27	27	26	268
Behav.	Totals													Totals											
F	56	15	7	22	24	2	5	31	3	8	65	56	294	2	7	2	2	1	19	6	11	1	3	1	55
HFL	14	8	9	11	4	1	6	2	4	3	11	3	76	0	0	0	2	0	3	1	3	0	0	2	11
HW	88	62	20	63	52	8	17	43	40	45	110	93	641	0	2	0	10	0	52	7	19	0	3	3	96
HD	17	8	18	5	22	15	14	7	5	5	19	14	149	2	6	5	7	5	6	1	0	1	3	0	36
BLWAG	11	2	8	6	11	15	11	6	4	12	18	12	106	9	6	3	8	3	11	2	4	7	5	5	63
BLFLAP	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
BLSH	0	0	0	0	1	0	1	0	0	0	0	3	5	0	0	0	0	0	0	0	0	0	0	0	0
TP	2	1	2	0	0	2	0	2	0	3	0	3	15	1	0	0	0	0	0	0	0	0	1	1	3
TP1	0	0	0	1	0	0	0	0	0	0	1	0	2	1	0	0	0	0	0	0	0	0	0	0	1
TP2	1	0	0	0	0	1	0	0	1	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	1
SL	21	26	7	7	20	0	22	29	3	15	24	22	196	0	4	6	4	1	2	10	15	3	2	4	51
L	0	0	0	0	0	0	0	0	0	7	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0
P	23	36	37	23	17	33	39	30	24	13	30	32	337	9	18	8	16	3	10	9	19	7	7	6	112
PM	4	6	1	5	3	10	2	1	3	0	3	0	38	1	1	0	4	0	1	1	4	0	0	2	14
PMB	2	0	1	0	0	1	0	2	0	0	0	0	6	0	0	1	0	0	0	0	0	2	3	1	7
MP	0	1	2	2	3	8	7	3	4	2	6	0	38	0	1	0	5	0	1	0	5	2	1	2	17
G	0	6	0	0	1	0	1	0	0	1	1	2	12	0	0	0	0	0	0	0	0	0	0	0	0
SW	9	4	4	7	5	8	5	6	7	0	4	5	64	3	0	0	1	1	0	0	0	1	0	0	6
NISW	2	3	0	2	1	2	0	0	2	10	1	2	25	0	0	0	0	0	0	0	0	0	0	0	0
NI	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
HSH	5	14	7	14	19	4	10	7	5	9	19	16	129	3	3	1	2	2	8	1	1	1	0	4	26
THPB	6	9	8	2	5	1	2	1	5	10	7	10	66	2	1	3	2	1	3	0	4	1	0	6	23
THNB	28	17	8	38	30	16	14	31	25	9	6	22	244	2	1	0	8	0	2	0	5	3	0	1	22
THM	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1
CM	8	21	4	3	17	2	3	3	1	1	13	0	76	3	7	2	3	1	1	0	1	1	1	3	23
WA	5	2	4	0	11	1	5	4	0	3	6	4	45	0	0	0	0	0	0	0	0	0	0	1	1
R	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EX	1	2	1	0	1	2	0	1	0	2	1	1	12	0	0	0	0	0	0	0	0	1	0	0	1
RNWF	0	0	0	0	1	1	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	1
LCS	1	0	0	0	0	0	0	0	0	0	0	3	4	0	0	0	0	0	2	0	0	0	0	0	2
COP	0	1	0	0	0	2	2	0	0	0	2	0	5	0	0	0	0	0	0	0	0	0	0	0	0
HDU	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	3	0	5

APPENDIX 6

TABLE 2.

1967

	6+ year Males							Incubating				6 year Males									5 year Males						4 year Males			
Bird No.	13	14	15	29	31	35	Tot.	1̇3	1̇5	29	Tot.	16	17	19	22	24	37	43	38	Tot.	18	20	21	40	52	Tot.	42	51	55	Tot.
No. of Obs.	31	23	21	19	14	17	125	24	18	22	64	1	4	14	6	17	7	13	15	77	10	13	21	12	1	57	16	16	13	45
Behav.	Totals											Totals									Totals						Totals			
F	18	28	10	2	7	8	73	7	12	0	19	1	0	13	0	33	0	19	17	83	2	32	10	6	0	50	7	5	6	18
HFL	3	16	1	0	2	0	22	0	2	0	2	0	0	5	0	19	0	3	11	38	1	3	6	2	0	12	1	3	1	5
HW	28	102	11	3	14	8	166	6	11	0	17	0	0	23	0	54	0	26	42	145	1	59	42	13	0	115	13	16	11	40
HD	16	19	11	4	7	1	58	3	5	1	9	2	1	4	0	4	0	5	4	20	3	7	17	3	1	31	8	13	12	33
ELWAG	13	14	8	5	9	3	52	4	9	4	17	0	4	5	2	10	1	4	8	34	4	12	9	6	2	33	3	8	7	18
ELFLAP	0	0	0	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
ELSH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TP	2	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	1	0	1	2	0	0	1	0	0	1	0	1	0	1
TP1	0	0	0	0	0	0	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
TP2	2	1	0	1	0	0	4	0	0	1	1	0	0	1	0	0	0	1	1	3	0	0	1	0	0	1	0	3	0	3
SL	6	13	4	6	1	1	31	5	4	1	10	0	0	2	0	5	0	6	1	14	0	2	5	0	0	7	2	4	2	8
L	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P	21	7	45	12	13	10	108	10	15	13	38	3	3	15	7	17	5	9	9	68	4	18	22	9	0	53	16	20	9	45
PM	1	4	1	3	0	1	10	0	0	0	0	0	0	3	0	3	0	5	0	10	0	2	5	3	0	10	1	2	0	3
PBM	2	0	4	3	0	0	9	0	0	0	0	0	0	0	0	1	0	1	0	2	0	0	1	0	0	1	3	1	0	4
MP	3	5	4	2	0	2	16	1	2	0	3	0	0	0	0	1	0	6	2	9	2	2	3	1	0	8	7	3	1	11
G	4	1	0	0	1	0	6	0	0	0	0	0	0	0	0	0	0	1	0	1	2	0	2	0	0	4	2	1	0	3
SW	4	8	4	4	0	1	21	1	0	1	2	0	2	1	0	0	0	0	4	7	0	0	5	0	0	5	2	1	1	4
NISW	0	1	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1
NI	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HSH	15	15	3	5	5	4	47	1	3	1	5	0	4	5	3	5	1	2	2	22	1	4	4	0	0	9	0	3	2	5
THPB	9	8	5	0	3	9	34	8	7	3	18	1	0	4	2	1	0	2	5	15	2	5	3	0	2	12	6	4	2	12
THWB	27	27	14	11	7	1	87	6	7	4	17	0	1	7	2	9	0	4	9	32	3	12	20	5	3	43	10	4	2	16
THM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	4
CM	22	7	1	10	0	2	42	9	2	2	13	0	2	8	0	0	0	0	1	11	0	9	16	1	0	26	0	0	0	0
WA	11	3	7	1	5	3	30	1	0	0	1	0	6	6	1	1	0	2	3	19	3	0	13	2	4	22	2	6	6	14
R	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
BX	1	2	2	0	0	0	5	1	0	1	2	0	0	1	0	1	0	0	2	4	0	0	2	0	0	2	0	1	0	1
RNWF	0	0	0	0	2	0	2	0	0	0	0	0	0	1	0	0	0	0	0	1	5	0	1	0	1	7	0	3	5	8
LCS	0	0	0	0	1	0	1	1	1	0	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1
COP	0	1	1	0	0	0	2	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	0
HDU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 6

TABLE 3

1967

	3 year old male								1 year old (males and females)																					
Bird No.	59	62	63	66	69	70	74	Tot.	1	5	6	7	8	10	11	14	15	16	17	18	20	21	22	24	26	27	28	29	30	Tot.
No. of Obs.	9	6	3	5	2	6	6	37	1	1	2	1	1	3	2	2	1	1	1	1	3	2	1	1	1	2	1	1	1	30
Behav.	Totals								Totals																					
F	0	1	1	0	0	0	0	2	0																					0
HFL	1	0	0	0	0	0	0	1																						0
HW	11	2	3	0	0	0	0	16																						0
HD	14	0	2	1	0	2	1	22													2		2							4
ELWAG	5	4	6	4	2	2	2	27		2	1					1	1						1			1				7
ELFLAP	0	1	0	0	0	0	0	1																						0
ELSH	0	0	0	0	0	0	0	0																						0
TP	0	0	0	0	0	0	0	0																						0
TP1	0	0	0	0	0	0	0	0																						0
TP2	2	1	0	1	0	0	2	6																						0
SL	1	3	0	0	0	1	0	5												1										1
L	0	0	0	0	0	0	0	0																						0
P	8	6	1	4	2	5	12	39				1		4	1	4	1				1									12
PM	3	0	0	0	0	1	1	5																						0
PBM	1	0	0	0	0	0	0	1																						0
MP	0	0	0	0	0	1	1	2																						0
G	0	0	0	0	0	0	0	0																						0
SW	2	0	0	1	1	1	0	5																						0
NISW	0	0	0	0	0	0	0	0																						0
NI	0	0	0	0	0	0	0	0																						0
HSH	8	1	0	2	1	0	1	13							1															1
THPB	4	3	2	2	0	1	3	19							2						6	1	1							10
THNB	12	2	5	6	4	1	6	43						3												1			1	5
THM	2	0	0	0	0	0	0	2																						0
CM	2	3	0	0	0	0	0	5																						0
WA	9	13	8	8	4	11	3	64	4	1					2	4					11	3				3		2	5	35
R	0	0	0	0	0	0	0	0																						0
EX	0	0	0	0	0	0	0	0							1															1
RNWF	1	0	0	0	0	0	0	1	1																					1
LCS	1	0	0	0	0	0	0	1																						0
COP	1	0	0	0	0	0	1	2																						0
HDU	0	0	0	0	0	0	0	0																						0

APPENDIX 6

TABLE 4

1966

	6+ year males													6 year males					5 year males													
Bird No.	1	7	8	9	12	13	14	15	18	19	20	25	Tot.	2	3	5	6	Tot.	4	10	11	48	55	57	58	59	69	105	114	47	63	Tot.
No. of Obs.	23	14	15	14	14	14	12	13	11	12	11	8	161	14	13	7	15	49	11	1	3	2	6	12	7	4	11	23	19	2	3	94
Behav.	Totals													Totals					Totals													
F	10	18	14	65	10	21	4	4	24	13	17	7	207	6	31	21	15	73	35	0	1	0	0	9	1	0	7	0	4	1	1	59
HFL	3	8	11	16	6	13	3	3	6	4	6	1	80	2	6	1	11	20	8	0	0	0	1	2	0	0	1	3	13	2	0	31
HW	21	32	56	104	38	59	33	24	54	21	18	27	487	17	34	24	47	122	38	0	5	0	3	16	4	0	19	13	51	4	2	155
HD	13	19	9	11	6	8	12	16	14	10	3	8	129	2	7	8	26	43	18	0	14	9	3	10	3	8	17	24	36	2	2	146
ELWAG	10	6	14	8	3	7	13	7	11	7	11	4	101	0	14	11	8	33	12	0	7	7	11	11	7	10	15	9	24	3	6	122
ELFLAP	1	0	0	0	0	0	0	1	1	0	0	0	3	0	1	1	1	3	0	0	2	0	1	1	1	0	2	1	2	0	0	10
ELSH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	3
TP	0	0	0	0	0	0	1	0	2	0	1	0	4	3	2	1	1	7	0	0	1	0	0	0	0	0	0	2	1	0	0	4
TP1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
TP2	0	2	0	0	0	0	1	0	1	1	1	0	6	1	0	0	0	1	0	0	1	0	2	2	1	0	1	0	0	0	0	77
SL	16	16	3	11	17	6	3	3	6	1	0	1	83	11	0	7	1	19	13	0	0	0	15	11	6	0	8	13	19	0	0	85
L	4	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P	40	18	29	36	23	24	29	28	19	19	6	8	279	48	30	13	19	110	31	2	15	2	10	25	21	12	30	50	40	0	10	248
PM	0	1	2	4	3	0	1	0	0	0	0	0	11	0	0	0	1	1	2	0	0	0	2	2	19	0	3	20	2	0	2	52
PBM	1	1	1	0	1	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	1	0	1	1	0	7	8	0	3	21
MP	1	2	0	2	2	0	6	0	0	0	0	0	13	0	0	0	0	0	7	0	0	0	1	0	5	0	6	15	6	0	1	41
G	0	7	14	21	3	5	9	10	0	5	12	5	91	10	11	11	5	37	0	0	0	0	0	4	3	0	13	29	9	0	3	61
SW	33	22	23	19	12	27	21	11	12	20	25	9	234	31	13	19	25	88	20	2	3	4	11	19	20	9	22	25	33	7	11	186
NISH	4	0	2	0	3	0	1	0	0	0	1	0	11	0	0	6	0	6	0	0	0	0	1	3	4	0	3	3	6	1	2	23
NI	2	0	0	0	0	0	0	0	0	0	0	1	3	4	2	1	0	7	3	0	0	0	0	0	0	0	0	0	0	0	0	3
HSH	15	10	33	13	15	26	18	29	13	13	13	10	208	42	23	11	23	99	11	1	17	4	10	10	25	8	38	20	34	6	9	173
THPB	7	4	0	2	1	4	0	3	5	1	2	0	29	3	4	2	7	16	8	0	1	4	4	21	2	3	2	16	11	2	0	74
THNB	23	26	22	28	30	24	11	3	30	7	3	4	211	4	8	2	35	49	22	0	3	3	20	24	10	5	16	21	26	1	0	151
THM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	00	2	1	1	0	0	5
CM	0	0	1	3	0	9	2	0	0	0	0	0	15	0	0	0	2	2	2	0	1	3	0	0	0	0	16	9	12	0	0	43
WA	21	3	3	3	0	6	0	1	4	0	0	1	42	3	5	19	3	30	2	4	8	8	20	14	4	17	22	14	7	3	0	123
R	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	1	0	1	0	0	0	5
EX	1	0	1	1	0	1	0	0	2	1	0	1	8	1	2	4	0	7	1	0	0	0	3	0	0	0	2	4	0	0	0	10
RNWF	1	0	0	0	0	0	0	0	0	0	0	2	3	0	0	0	0	0	0	0	0	0	1	6	0	0	0	0	1	0	0	8
LCS	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	2
COP	0	0	0	0	0	2	0	0	0	1	0	0	3	0	0	0	1	1	0	0	0	0	0	0	1	0	3	1	4	0	0	9
HDU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 6

TABLE 5

1966

	4 year males																
Bird No.	16	28	30	49	50	62	67	68	75	81	83	84	89	90	92	101	Tot.
No. of Obs.	1	4	3	6	11	2	9	5	1	4	4	11	11	11	14	12	99
Behav.	Totals																
F	0	0	0	0	3	0	0	1	0	0	2	7	0	6	6	1	26
HFL	0	0	0	0	2	0	0	2	0	1	0	2	1	13	2	2	25
HW	0	11	0	0	5	0	3	7	0	1	11	23	4	43	19	15	142
HD	0	1	0	11	10	0	9	7	0	1	5	15	9	11	7	15	101
ELWAG	1	3	1	3	5	0	5	2	0	4	9	12	8	10	14	13	90
ELFLAP	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	2	6
BLSH	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2
TP	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	3
TP1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2
TP2	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	2	4
SL	0	2	0	0	2	0	4	5	0	3	1	7	1	9	9	3	46
L	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P	1	5	2	20	28	0	54	13	0	8	8	29	28	33	39	27	295
PM	0	0	0	3	5	0	17	5	0	2	6	5	2	6	10	0	61
PBM	0	0	0	0	2	0	1	3	0	1	0	0	2	3	2	0	14
MP	0	0	0	0	5	0	8	3	0	4	0	3	7	2	6	1	39
G	0	0	0	0	1	0	2	0	0	0	2	1	6	0	0	2	14
SW	0	1	1	9	10	0	21	7	0	2	3	13	13	15	31	26	142
N1SW	0	0	0	1	3	0	1	3	0	0	0	2	5	1	1	0	17
N1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0	3
HSH	0	1	0	12	10	0	9	8	0	1	6	12	21	19	19	14	132
THPB	1	1	0	2	3	0	8	1	0	0	2	11	2	2	5	7	45
THNB	0	0	0	12	15	0	41	5	0	0	16	16	2	14	22	25	168
THM	0	0	0	2	2	0	6	1	0	0	0	1	0	0	0	1	13
CM	0	0	0	3	0	0	8	0	0	6	6	4	3	0	9	1	34
WA	2	7	0	18	7	0	13	3	0	2	6	20	31	11	17	19	156
R	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	1	4
EX	0	0	0	0	0	0	0	0	0	0	4	2	2	0	3	0	11
RNWF	0	4	0	0	0	0	1	0	0	0	3	0	3	0	0	1	12
LCS	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2
COP	0	0	0	0	1	0	0	0	0	0	0	2	0	3	0	1	7
HDU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	3 year males																				
Bird No.	100	103	107	110	116	117	118	120	121	122	123	128	129	130	133	134	135	137	97	111	Tot.
No. of Obs.	4	18	8	4	8	16	11	1	9	9	2	2	14	2	10	1	10	10	14	5	158
Behav.	Totals																				
F	0	17	0	1	0	0	0	0	0	1	0	0	2	0	7	0	0	1	4	7	40
HFL	0	11	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	12	1	4	31
HW	0	61	2	4	30	1	19	0	2	3	0	0	12	0	9	0	1	60	17	26	247
HD	9	37	9	7	8	16	20	0	23	14	0	0	4	0	7	0	5	4	8	14	185
ELWAG	7	34	4	7	9	8	15	2	4	17	0	0	4	2	18	0	12	17	11	9	180
ELFLAP	0	1	0	1	5	1	0	0	2	0	0	0	0	0	0	0	2	1	1	1	15
BLSH	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
TP	0	2	0	0	2	2	0	0	2	3	0	0	2	0	1	0	0	2	3	1	20
TP1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	3
TP2	0	1	0	1	2	1	0	0	0	2	0	0	0	0	0	0	1	0	2	1	11
SL	0	22	0	0	18	5	0	0	3	2	0	4	5	1	6	0	0	3	5	0	74
L	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P	7	39	14	6	19	57	11	12	20	17	3	4	24	9	34	0	36	14	37	10	373
PM	5	10	7	0	4	0	4	0	8	3	0	0	1	0	2	0	1	1	5	2	53
PBM	0	5	2	1	1	2	1	1	0	0	0	0	0	0	0	0	0	3	1	0	17
MP	4	9	6	4	4	3	5	2	6	0	0	0	2	0	3	0	4	1	8	2	63
G	0	2	5	1	1	2	3	1	1	0	0	0	2	9	2	0	9	1	4	2	45
SW	7	33	14	11	8	26	19	2	12	40	3	2	12	3	19	0	16	16	21	23	287
N1SW	0	6	0	0	1	6	5	0	2	0	3	0	2	0	3	0	19	2	2	1	52
N1	0	1	1	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	6
HSH	3	28	7	15	15	16	12	2	16	17	1	0	10	0	7	0	14	8	22	12	205
THPB	1	10	8	1	2	15	8	1	0	4	0	2	7	0	9	0	6	2	15	7	98
THNB	9	48	12	4	3	23	14	0	15	7	1	0	20	1	21	0	26	11	23	7	245
THM	0	0	0	0	0	0	6	0	1	0	0	0	0	0	1	0	0	2	4	0	14
CM	2	5	2	2	3	3	5	0	1	2	0	0	4	0	2	0	1	0	3	0	35
WA	47	21	30	19	7	27	35	0	42	20	5	0	11	0	32	0	38	10	39	14	397
R	1	5	0	1	0	3	0	0	2	0	0	0	0	0	1	0	2	2	6	0	23
EX	0	1	0	1	1	0	0	0	2	1	0	0	0	0	1	0	3	0	2	2	14
RNWF	0	0	0	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	6	1	11
LCS	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
COP	1	5	4	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	2	15
HDU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 6

TABLE 6

1966

	2 year males												2 year females																	
Bird No.	142	145	146	147	149	151	153	155	165	166	167	Tot.	115	124	140	143	144	148	150	152	154	156	157	159	160	161	162	163	164	Tot.
No. of Obs.	3	10	9	5	3	8	7	3	2	2	4	56	2	4	1	5	8	3	7	4	2	2	4	4	4	2	6	1	3	62
Behav	Totals												Totals																	
F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HFL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
HW	0	13	1	0	0	0	0	0	0	0	0	14	0	0	1	3	0	0	2	0	0	0	0	0	0	0	0	0	0	6
HD	0	13	0	1	3	5	8	0	0	2	1	33	0	0	0	2	2	3	0	0	0	2	3	1	0	2	0	0	0	14
ELWAG	0	12	3	0	1	7	10	2	2	0	0	37	0	6	1	5	4	4	1	4	1	0	6	3	2	0	6	0	0	43
ELFLAP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
ELSH	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	2
TP	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
TP1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TP2	0	0	0	0	1	1	2	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	3
SL	0	3	4	1	0	4	2	0	0	0	5	19	0	0	0	5	2	0	0	1	0	0	5	0	0	0	1	0	0	14
L	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P	0	18	8	5	1	25	19	9	2	1	2	90	6	25	0	0	19	5	3	3	1	0	7	5	5	0	4	0	0	83
PM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PBM	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
G	0	0	4	0	0	0	0	0	0	0	0	4	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	3
SW	0	17	4	1	4	13	14	3	1	0	0	57	5	8	1	1	10	3	1	2	1	0	6	7	3	0	2	0	1	51
N1SW	0	1	0	1	0	3	5	1	0	2	1	14	0	0	0	0	4	0	1	0	0	0	3	0	0	0	0	0	0	8
N1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	3
HSH	0	13	1	0 0	4	10	11	0	1	3	1	44	1	6	1	1	6	1	3	4	1	0	6	3	6	0	0	0	0	39
THPB	0	6	7	3	2	3	7	1	0	0	2	31	0	2	0	2	4	0	2	5	2	0	3	4	0	0	2	0	0	26
THNB	0	12	6	5	3	13	12	2	3	1	0	57	1	1	0	7	11	5	5	7	0	4	8	1	2	4	0	0	0	56
THM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	3	0	0	3	0	0	10
WA	0	1	1	0	0	0	0	0	0	0	0	2	4	16	4	16	20	19	21	6	0	0	12	8	6	2	11	0	0	145
R	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	0	1	0	0	5
EX	0	1	0	0	0	3	1	0	0	0	0	5	0	1	0	0	1	0	1	0	0	0	1	0	1	0	0	0	0	5
RNWF	0	3	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	12	0	0	0	0	1	0	0	0	0	13
LCS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HDU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 6

TABLE 7

1967

	6+ year females				6 year females							5 year females							4 year females						3 year females										
Bird No.	26	30	34	Tot	46	25	32	33	45	48	Tot	23	27	28	36	39	47	Tot	41	50	56	58	53	Tot	72	54	57	60	61	64	65	67	71	73	Tot
No. of Obs.	31	19	36	86	20	16	16	26	21	6	105	3	19	11	22	4	8	67	12	23	20	15	9	79	6	9	3	4	1	11	8	3	7	8	60
Behav	Totals				Totals							Totals							Totals						Totals										
F	0	0	1	1	1	0	3	1	0	0	5	0	3	0	3	0	0	6	1	6	0	9	0	16	0	0	0	1	0	0	0	0	0	0	1
HFL	0	0	1	1	0	0	4	2	1	0	7	0	7	0	12	0	6	25	1	1	3	8	0	13	0	0	0	0	0	0	0	0	0	0	0
HW	3	7	2	12	5	16	31	6	8	3	69	0	14	2	34	0	24	74	10	27	9	42	15	103	0	7	1	1	0	1	3	0	0	2	15
HD	13	13	3	29	1	10	11	5	9	0	36	0	4	3	7	0	6	20	6	7	3	7	10	33	0	7	3	0	0	7	2	0	1	3	23
BLWAG	9	8	10	27	14	7	6	5	10	0	42	0	1	2	5	2	5	15	5	16	5	8	5	39	5	10	2	3	2	4	1	2	5	4	38
BLFLAP	1	1	0	2	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	2	0	0	0	0	0	0	0	0	1	0	1
BLSH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TP	1	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	2
TP1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TP2	2	0	0	2	0	1	0	0	4	0	5	0	0	2	0	1	1	4	3	0	1	2	1	7	0	1	0	0	0	0	0	0	3	0	4
SL	7	2	8	17	4	2	0	8	4	2	20	0	3	4	3	0	4	14	0	7	13	6	2	28	0	3	4	0	0	3	1	1	1	1	14
L	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P	27	21	27	75	22	17	23	10	10	1	82	0	20	5	9	3	3	40	12	16	18	11	10	67	7	12	2	3	2	15	14	4	12	5	76
PM	3	6	1	10	0	1	0	3	1	0	5	0	0	3	0	0	1	4	1	2	1	0	2	6	0	0	0	0	2	6	0	0	0	1	9
PBM	0	1	0	1	0	0	1	3	1	0	5	0	3	0	0	0	0	3	0	5	1	3	1	10	0	1	0	0	1	2	0	0	0	0	4
MP	2	7	2	11	1	3	0	1	5	2	12	0	5	2	0	0	2	9	4	4	8	2	5	23	0	0	0	0	0	12	0	0	0	4	16
G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	1	3	7	0	1	0	0	0	0	0	0	0	0	1
SW	1	3	1	5	2	2	1	1	3	0	9	0	0	3	1	0	0	4	2	1	0	1	1	5	0	0	2	0	0	1	0	0	0	0	3
N1SW	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1
N1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HSH	3	3	2	8	0	3	3	0	2	0	8	1	5	5	1	0	7	19	1	1	2	3	2	9	0	0	0	0	0	0	0	0	0	0	0
THPB	6	3	4	13	9	3	4	2	3	1	22	0	1	6	1	0	5	13	2	7	3	4	0	16	2	1	3	0	1	2	2	1	1	4	17
THNB	5	3	17	25	8	1	2	9	3	2	35	0	0	0	2	0	0	2	2	7	8	10	2	29	1	0	0	1	1	2	7	0	1	4	17
THM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2	1	0	0	0	0	0	0	0	0	2	3
CM	12	0	2	14	1	3	3	6	1	0	14	0	4	0	4	0	2	10	0	0	5	0	0	5	0	2	0	0	0	0	0	0	0	0	2
WA	2	2	0	4	1	1	6	1	3	0	12	3	3	2	9	3	2	22	8	11	6	16	5	46	6	16	9	2	7	9	8	2	6	9	74
R	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	1	1	0	4	0	6	0	0	1	0	2	1	0	0	0	0	4
EX	0	0	0	0	1	0	1	0	1	0	3	0	0	1	1	0	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
RNWF	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	9	0	1	5	16	0	1	1	0	0	0	1	0	0	2	5
LCS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
COP	1	1	0	2	0	1	0	0	0	0	1	0	1	0	1	0	0	2	0	3	0	0	0	3	0	1	0	0	0	1	0	0	0	1	3
HDU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 6

TABLE 8

1966

	6+ year females												6 year females					5 year females														
Bird No.	21	24	29	31	32	38	40	41	42	43	44	Tot	17	34	35	39	Tot	66	46	52	53	56	61	64	71	73	74	87	98	113	141	Tot
No. of Obs.	10	10	7	6	6	5	6	4	6	6	10	76	17	14	11	12	54	10	4	3	7	2	20	13	11	1	6	4	9	4	5	99
Behav.	Totals												Totals					Totals														
F	6	3	1	1	0	0	1	0	0	2	0	14	0	0	1	5	6	0	0	0	0	0	1	0	0	0	0	0	1	0	0	2
HFL	11	4	0	3	0	0	6	1	1	6	1	33	0	0	0	2	2	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2
HW	16	12	1	20	2	2	21	2	5	58	1	140	2	1	1	9	13	0	4	0	1	0	16	1	0	0	0	0	4	1	0	27
HD	6	5	1	2	9	0	5	3	2	12	2	47	9	0	1	6	16	1	3	0	2	0	13	8	2	0	0	0	10	3	2	44
BLWAG	3	4	3	4	2	0	1	1	2	2	11	33	3	0	3	2	8	4	5	2	6	0	14	10	11	3	1	7	7	3	2	75
BLFLAP	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	3	4	0	0	0	1	0	0	8
BLSH	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	4
TP	1	0	0	1	1	0	0	0	0	0	0	3	1	0	0	1	2	0	0	1	0	0	0	1	2	1	0	0	0	0	0	5
TP1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TP2	0	0	0	1	0	0	0	1	1	0	1	4	0	0	0	0	0	0	1	0	4	0	3	1	3	0	0	0	1	0	0	13
SL	3	3	0	5	0	0	0	2	1	3	4	21	6	0	0	0	6	2	4	0	0	0	5	1	0	0	0	0	2	3	1	18
L	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P	6	8	10	14	12	1	5	4	6	6	36	108	15	0	0	3	18	24	14	3	15	0	28	27	32	1	14	9	12	8	10	197
PM	2	3	0	0	1	0	0	1	0	0	0	7	3	0	0	1	4	0	0	0	2	0	3	3	0	0	0	0	0	0	0	8
PBM	9	4	0	0	1	0	2	0	0	0	0	16	3	0	0	0	3	1	0	0	0	0	1	0	0	1	0	0	0	1	0	4
MP	0	1	0	3	0	1	4	0	0	1	0	10	7	0	0	0	7	0	0	0	2	0	7	5	0	2	0	0	1	2	1	20
G	0	0	0	0	0	0	0	20	1	0	11	32	8	0	0	0	8	0	13	0	0	0	1	3	2	0	0	0	5	4	0	28
SW	19	17	6	9	5	0	8	4	11	10	11	100	2	0	3	2	7	6	8	1	15	0	23	17	11	3	8	4	24	3	5	128
NISW	0	0	0	1	0	0	0	0	0	0	1	2	1	0	0	0	1	0	0	0	0	0	4	5	5	0	1	3	4	0	0	22
NI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HSH	12	13	4	7	3	2	2	1	2	22	9	77	9	0	1	0	10	5	8	1	10	0	24	18	7	1	4	5	10	1	3	97
THPB	1	4	2	2	2	1	0	2	1	4	4	23	2	0	1	2	5	5	0	0	1	0	5	6	14	1	4	2	3	0	5	46
THNB	5	2	4	6	2	0	5	2	6	6	5	41	3	1	0	6	10	5	3	0	0	0	14	12	7	4	1	2	2	0	5	55
THM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CM	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0	3	3	0	0	0	4	0	0	0	0	0	0	0	0	10
WA	0	2	0	1	4	0	1	0	0	2	16	26	3	0	1	3	7	16	4	0	22	0	7	10	19	0	0	3	10	14	10	115
R	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	4	4	0	0	0	2	0	0	0	3	0	0	0	0	0	2	7
EX	0	0	0	0	2	0	0	0	0	0	2	4	0	0	0	0	0	1	0	0	0	0	2	1	0	0	0	2	0	0	0	6
RNWF	0	0	0	2	0	0	0	0	0	0	0	2	0	0	0	1	1	3	0	0	1	0	0	3	0	0	0	0	0	0	0	7
LCS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	2
COP	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
HDU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 6

TABLE 9

1966

	4 year females															
Bird No.	36	51	65	70	72	76	77	78	82	85	86	91	94	96	102	Tot
No. of Obs.	12	4	4	1	4	10	4	3	1	1	5	10	4	6	15	84
Behav	Totals															
F	0	0	0	0	0	0	1	0	0	0	2	0	0	0	1	4
HFL	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	3
HW	1	0	0	0	0	1	10	0	0	0	0	3	0	0	31	46
HD	11	0	2	0	1	7	7	2	0	0	5	9	2	7	28	81
BLWAG	10	1	15	0	3	4	14	2	1	0	11	3	3	3	18	88
BLFLAP	0	0	0	0	0	1	2	0	0	0	3	1	1	0	1	9
BLSH	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	2
TP	0	2	0	0	0	0	0	0	0	0	0	2	3	0	1	8
TP1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TP2	0	0	0	0	2	0	0	1	0	0	0	0	0	1	1	5
SL	2	0	2	0	0	5	4	0	0	0	2	2	1	2	11	31
L	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P	41	3	7	0	5	26	10	4	0	0	21	35	6	45	35	238
PM	3	0	0	0	0	3	1	0	0	0	0	0	0	3	2	12
PBM	0	0	0	0	0	0	1	0	0	0	0	0	0	2	4	7
MP	6	0	0	0	0	2	0	0	0	0	0	1	0	0	8	17
G	0	0	0	0	4	10	0	0	0	0	1	5	4	1	1	26
SW	19	2	5	0	0	5	13	5	2	0	6	5	10	21	27	120
NISW	8	1	0	0	0	0	2	1	0	0	2	2	2	2	1	21
NI	0	0	0	0	0	0	0	1	0	0	0	2	1	0	0	4
HSH	13	1	1	0	0	13	7	5	1	0	16	7	0	13	25	102
THPB	5	0	0	0	0	13	0	1	1	0	1	2	0	1	6	30
THNB	12	0	2	0	2	3	8	1	0	0	13	4	3	2	6	56
THM	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CM	8	0	0	0	0	0	0	1	0	0	9	0	0	1	4	23
WA	36	0	26	0	13	17	27	8	0	0	17	14	22	7	22	209
R	3	0	3	0	1	4	2	1	0	0	0	0	2	3	0	19
EX	0	0	0	0	0	0	1	1	0	0	1	1	2	1	1	8
RNWF	4	0	2	0	0	1	2	0	0	0	1	2	0	0	0	12
LCS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
HDU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	3 year females																	
Bird No.	88	95	99	104	106	108	109	112	119	125	126	127	131	132	136	138	139	Tot
No. of Obs.	13	7	13	12	2	2	11	7	4	2	4	8	17	1	8	7	1	119
Behav	Totals																	
F	1	0	0	0	0	0	4	0	0	0	1	0	0	0	0	0	0	6
HFL	0	0	0	0	0	0	3	1	0	0	1	0	0	0	0	0	0	5
HW	5	1	23	1	0	0	24	6	0	0	0	0	10	0	1	0	0	71
HD	23	7	16	15	1	0	14	9	3	0	3	14	6	1	0	0	0	112
BLWAG	3	3	11	9	1	0	9	8	3	6	4	16	8	1	9	8	0	99
BLFLAP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
BLSH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
TP	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	4
TP1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
TP2	0	2	0	0	0	0	0	1	0	0	1	1	0	0	2	0	0	7
SL	14	3	8	0	0	2	15	5	0	0	8	0	9	0	4	0	0	68
L	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P	19	13	41	24	8	0	21	8	5	0	3	4	27	6	27	25	0	231
PM	2	2	5	2	0	0	5	3	1	0	0	4	7	0	0	0	0	31
PBM	2	0	0	0	0	0	1	2	4	0	0	1	3	1	1	0	0	15
MP	0	1	11	1	0	0	3	2	3	0	0	2	14	2	1	0	0	40
G	0	3	0	0	7	1	6	2	0	0	0	12	0	0	0	0	0	31
SW	8	9	17	20	8	1	19	10	8	0	1	7	10	0	8	4	1	131
NISW	0	2	3	2	0	0	0	0	0	0	0	2	1	0	0	0	0	10
NI	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	3
HSH	15	5	25	16	5	0	15	10	11	0	1	20	15	1	6	11	1	151
THPB	1	0	7	9	1	0	3	1	0	0	3	3	8	0	4	5	0	45
THNB	5	0	15	5	1	0	4	8	4	2	5	4	9	0	8	5	1	76
THM	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
CM	2	0	2	1	0	0	6	1	0	0	3	0	6	0	0	0	0	21
WA	5	22	39	24	7	0	10	20	27	7	15	19	20	2	10	6	2	235
R	0	0	2	1	1	0	0	2	1	2	0	0	1	0	5	1	0	16
EX	0	1	1	1	0	0	1	1	1	0	3	0	1	0	0	1	0	11
RNWF	2	0	3	1	0	0	0	1	0	2	0	0	2	0	2	0	0	13
LCS	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2
COP	4	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	5
HDU	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 7

Analysis of 217 Flag displays given by the UK study males before the arrival of their mates. The Flag displays were classed according to the number of flags per bout, and the number of displays in each class was divided according to the score for each of the other three elements (EL. SC).

	EL. SC.	No. flags/bout											
		1	2	3	4	5	6	7	8	9	10	11	12
BODY	SS	33	67	43	22	4	3	1	1	1			
	MS	1	4	7	8	4	3	–	2	–	1		
	LS	–	–	2	2	5	–	–	1	–	–	–	2
HEAD	vd	–											
	45d	–	1										
	h	30	50	19	11	–	–	–	1				
	45	3	17	25	14	3	2	–	–	–	–	–	1
	v	1	2	7	6	8	3	–	1	–	1	–	1
	45b	–	1	1	1	1	1	–	2	1			
	pb	–	–	–	–	–	–	1					
WINGS	s	10	15	4	3	1	–	1					
	sl	2	3										
	45	3	6	7	3								
	h	12	20	7	3	3							
	45b	7	27	33	23	9	6	–	3	1	1	–	2
	pb	–	–	1	–	–	–	–	1				

APPENDIX 8

The average number of days each bird spent at a site (D/S), the average number of days spent with each mate (D/M), and the percentage of time spent in the breeding area (%BA), is listed for all males (♂) and females (♀) in the different age groups (6+, 5 etc.) The data from both years are grouped.

AGE SEX	D/S	D/M	%BA
UK♂	16.5	21.0	100
	16.0	21.0	100
	17.0	21.0	100
	33.0	27.0	100
	11.3	22.0	100
	34.0	23.0	100
	33.0	11.5	100
	17.0	19.0	100
	16.0	24.0	100
	33.0	20.0	100
	33.0	20.0	100
	33.0	0.0	100
6+♂	32.0	11.0	100
	25.0	20.0	100
	23.0	17.0	100
	19.0	16.0	100
	3.8	1.5	73
	2.8	2.0	0
	10.0	14.0	100
	7.3	12.0	100
	12.0	4.3	100
	12.5	7.0	100
	11.5	14.0	100
	11.5	12.0	100
	11.0	16.0	100
	11.5	6.0	100
	10.0	5.0	100
	11.5	14.0	100
	12.0	8.0	100
	15.0	13.0	100

AGE SEX	D/S	D/M	%BA
6♂	1.0	0.0	0
	1.7	0.0	0
	5.7	2.5	88
	1.0	1.0	17
	18.0	14.0	100
	2.2	0.0	0
	4.0	2.3	0
	8.0	3.7	0
	2.7	3.0	68
	2.8	0.0	59
	1.4	0.0	100
	14.0	8.0	100
	21.0	7.5	100
5♂	1.4	2.5	10
	4.7	2.0	0
	3.8	7.5	78
	13.0	6.0	100
	1.0	0.0	0
	7.5	3.0	87
	1.0	0.0	100
	1.3	0.0	0
	1.4	1.3	100
	1.3	0.0	0
	3.3	2.5	0
	5.3	2.0	100
	4.0	6.0	83
	1.4	1.0	13
	1.6	1.0	0
	2.0	1.3	67
	3.0	7.3	4
	5.0	6.5	92

APPENDIX 8 (cont.)

AGE SEX	D/S	D/M	%BA
4♂	3.2	2.8	94
	2.3	3.0	81
	6.5	4.0	8
	1.0	0.0	0
	3.3	1.0	10
	3.0	3.0	0
	1.1	1.5	0
	1.7	2.0	0
	1.6	2.0	82
	3.8	2.7	33
	1.0	0.0	0
	1.6	2.0	73
	2.0	1.0	67
	1.0	0.0	0
	1.5	1.0	83
	1.7	1.3	40
	2.1	1.7	46
	2.0	1.7	67
	6.0	3.0	100
	2.5	5.0	87
	2.1	3.0	62
3♂	4.7	1.1	0
	1.0	0.0	0
	1.2	0.0	0
	1.0	0.0	0
	1.0	0.0	0
	1.0	1.0	0
	1.1	1.3	0
	1.5	1.0	17
	1.7	2.2	63
	1.5	1.5	33
	1.0	1.0	20
	1.1	1.1	9
	1.5	1.0	0
	1.1	1.5	0
	1.0	0.0	0
	1.1	1.1	56
	1.2	1.0	46
	1.0	0.0	0
	1.0	0.0	0
	1.1	1.0	6
3♂ cont.	1.1	1.1	50
	1.1	1.2	8
	1.0	0.0	0
	1.1	1.1	0
	1.1	1.0	30
	1.5	1.5	20
	1.0	1.0	29
2♂	1.0	1.0	0
	1.2	1.0	0
	1.1	0.0	0
	1.2	0.0	0
	1.0	0.0	0
	1.1	0.0	0
	1.1	0.0	0
	1.0	0.0	0
	1.0	0.0	0
	1.0	0.0	0
	1.0	0.0	0
UK♀	21.0	21.0	100
	21.0	21.0	100
	21.0	21.0	100
	27.0	27.0	100
	22.0	22.0	100
	23.0	23.0	100
	23.0	23.0	100
	19.0	19.0	100
	24.0	24.0	100
	20.0	20.0	100
	20.0	20.0	100

APPENDIX 8 (cont)

AGE SEX	D/S	D/M	%BA
6+♀	18.0	18.0	100
	9.0	17.0	100
	20.0	20.0	100
	11.0	20.0	100
	5.0	8.0	100
	18.0	9.0	100
	17.0	13.0	100
	19.0	16.0	100
	15.0	20.0	100
	2.3	3.8	85
	15.0	12.0	100
	21.0	19.0	100
	21.0	20.0	100
	3.0	15.0	0
6♀	20.0	20.0	0
	6.3	18.0	0
	18.0	17.0	100
	7.3	7.3	0
	8.0	12.0	100
	1.2	2.5	0
	19.0	19.0	100
	9.5	18.0	100
	1.3	7.0	41
	3.3	2.5	100
5♀	1.0	0.0	0
	11.0	21.0	96
	3.5	6.5	50
	5.8	5.7	91
	1.0	0.0	0
	3.0	1.5	0
	1.7	1.3	0
	2.6	1.2	0
	3.7	3.0	27
	1.0	0.0	0
	2.0	1.0	0
	1.0	1.0	0
	1.9	5.0	80
	2.0	2.3	31
	1.4	0.0	73
5♀	1.0	0.0	0
	1.2	0.0	17
	1.3	0.0	0
	2.3	4.0	89
	1.0	1.0	40
	1.4	1.6	0
4♀	1.3	1.0	7
	2.3	2.6	60
	2.5	3.8	22
	1.4	1.6	75
	3.0	2.6	67
	2.6	2.4	0
	5.5	3.0	0
	1.6	0.0	0
	1.1	0.0	22
	1.1	1.0	0
	1.0	0.0	0
	1.2	0.0	0
	1.6	1.3	55
	1.3	2.0	0
	1.3	0.0	0
	1.0	0.0	0
	1.0	0.0	0
	1.0	0.0	0
	1.4	1.0	46
	1.0	1.0	25
	1.3	1.0	25
	1.7	2.5	60
3♀	1.2	1.0	38
	1.5	1.0	0
	1.0	1.0	22
	1.0	1.0	0
	1.4	1.1	6
	1.8	1.3	0
	1.0	1.0	11
	1.2	1.2	0
	1.0	1.1	0
	1.6	2.0	57

APPENDIX 8 (cont)

AGE SEX	D/S	D/M	%BA
3♀ cont	1.3	1.0	75
	1.3	2.2	46
	1.2	2.5	43
	1.0	1.0	33
	1.0	1.0	0
	2.2	4.5	73
	1.0	1.0	0
	1.0	0.0	14
	1.0	0.0	0
	1.0	1.0	0
	1.0	1.0	0
	1.0	0.0	0
	1.9	1.3	5
	1.0	1.0	0
	1.1	1.2	0
	1.1	0.0	18
	1.0	0.0	0
2♀	1.0	0.0	0
	1.0	0.0	0
	1.0	0.0	0
	1.0	0.0	0
	1.0	0.0	0
	1.0	0.0	0
	1.0	0.0	0
	1.0	0.0	0
	1.0	0.0	0
	1.0	0.0	0
	1.0	0.0	50
	1.0	0.0	0
	1.1	1.1	0
	1.0	0.0	0
	1.0	0.0	0
	1.0	0.0	0
	1.0	0.0	0

APPENDIX 9

The percentage number of days on which the HW and F displays were seen for all study birds in the mate and no-mate situation.

AGE	NO MATE		MATE		AGE	NO MATE		MATE	
SEX	%F	%HW	%F	%HW	SEX	%F	%HW	%F	%HW
UK♂	46	55	46	46	6♂	100	0	–	–
	20	30	42	58		0	0	–	–
	18	25	20	50		9	18	66	66
	0	0	35	59		0	0	–	–
	50	60	25	42		33	66	46	54
	20	10	0	36		0	0	–	–
	25	25	0	20		50	50	0	44
	50	43	13	50		44	89	0	33
	14	29	8	92		0	17	100	100
	25	33	0	33		62	77	–	–
	17	25	45	73		57	57	–	–
	43	52	–	–		38	63	14	57
						–	–	25	50
6+♂	10	10	17	50					
	20	20	54	77	5♂	25	0	25	25
	66	50	10	0		38	38	60	100
	33	33	0	0		20	20	0	46
	18	36	33	66		–	–	8	17
	40	40	11	22		0	0	–	–
	25	58	14	43		56	33	50	50
	17	50	0	50		0	0	–	–
	83	83	14	43		33	33	–	–
	75	88	40	80		0	0	50	100
	40	80	25	75		0	0	–	–
	86	100	40	40		0	0	0	25
	0	33	13	75		25	25	13	25
	17	33	20	40		0	0	20	60
	50	50	25	50		0	0	0	0
	40	60	33	50		0	0	100	100
	60	60	0	20		33	30	0	20
	100	100	17	50		0	0	0	23
						0	0	23	38

AGE	NO MATE		MATE	
SEX	%F	%HW	%F	%HW
4♂	50	50	25	42
	0	0	15	46
	0	0	33	33
	0	0	–	–
	50	50	50	50
	0	0	0	0
	0	0	0	100
	0	0	0	0
	0	0	0	0
	29	29	25	50
	0	0	–	–
	0	0	0	43
	33	66	0	30
	0	0	–	–
	0	0	0	50
	–	–	25	25
	43	43	25	75
	0	0	0	29
	0	50	22	56
	25	25	30	60
	0	0	14	43
3♂	0	66	0	40
	17	17	–	–
	33	33	–	–
	0	0	–	–
	0	0	–	–
	0	0	0	0
	25	0	0	0
	0	0	–	–
	33	33	20	50
	0	0	0	66
	25	0	0	100
	0	0	0	57
	0	8	0	0
	0	0	0	50
	–	–	0	0
	0	0	0	33
	17	17	0	66
	0	0	–	–
	0	0	–	–
	0	0	25	50
3♂ cont	0	0	0	0
	17	17	75	50
	0	0	–	–
	0	0	0	50
	0	0	75	33
	0	0	20	60
	0	0	25	100
2♂	0	0	–	–
	0	0	0	66
	0	13	–	–
	0	0	–	–
	0	0	–	–
	0	0	–	–
	0	0	–	–
	0	0	–	–
	0	0	–	–
	0	0	–	–
	0	0	–	–
6+♀	–	–	0	22
	–	–	0	33
	–	–	0	0
	–	–	30	60
	0	0	38	63
	–	–	17	17
	–	–	20	100
	–	–	0	25
	–	–	0	20
	–	–	20	60
	–	–	0	25
	–	–	0	40
	–	–	20	80
	0	0	0	100

APPENDIX 9 (cont)

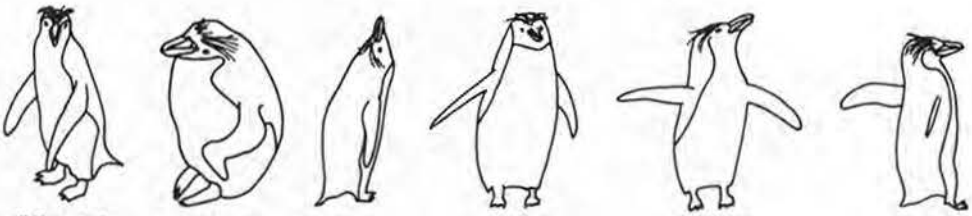
AGE	NO MATE		MATE	
SEX	%F	%HW	%F	%HW
6♀	-	-	6	25
	-	-	20	70
	-	-	11	33
	0	0	0	22
	-	-	0	25
	-	-	0	17
	-	-	0	10
	-	-	0	20
	0	0	0	100
	25	50	-	-
5♀	0	0	-	-
	0	0	8	25
	-	-	0	18
	-	-	8	46
	0	0	0	0
	-	-	0	71
	0	0	0	25
	0	0	0	0
	0	0	0	50
	0	0	-	-
	0	0	-	-
	25	0	0	50
	-	-	-	-
	0	0	11	33
	0	0	0	25
	0	0	-	-
	0	0	-	-
	0	0	-	-
	0	0	-	-
	0	0	20	40
	0	25	-	-
	0	0	-	-

AGE	NO MATE		MATE	
SEX	%F	%HW	%F	%HW
4♀	11	0	0	66
	29	0	20	27
	0	0	0	29
	0	0	44	55
	0	0	0	43
	0	0	0	25
	0	0	33	66
	0	0	-	-
	0	0	-	-
	0	0	-	-
	0	0	-	-
	0	0	-	-
	0	0	0	13
	0	0	50	100
	0	0	-	-
	0	0	-	-
	-	-	-	-
	20	0	-	-
	0	0	0	100
	0	0	0	0
	0	0	0	0
	0	0	13	50
3♀	0	0	0	100
	0	0	0	0
	25	0	-	-
	0	0	-	-
	0	0	0	17
	0	0	0	33
	0	0	-	-
	0	0	0	0
	0	0	0	33
	0	0	33	100
	0	0	0	100
	0	0	0	50
	0	0	0	0
	0	0	0	0
	-	-	0	0
	50	0	22	55
	0	0	0	100
	0	0	0	0

APPENDIX 9 (cont)

AGE	NO MATE		MATE	
SEX	%F	%HW	%F	%HW
3♀	0	0	–	–
cont	33	0	–	–
	0	0	0	0
	0	0	0	20
	–	–	0	0
	0	0	0	0
	0	0	0	0
	0	0	–	–
2♀	0	0	–	–
	0	0	–	–
	0	0	–	–
	0	20	–	–
	0	14	–	–
	0	0	–	–
	0	0	–	–
	0	33	–	–
	0	0	–	–
	0	0	–	–
	0	0	–	–
	0	0	–	–
	0	0	0	0
	0	0	–	–
	0	0	–	–
	0	0	–	–
	0	0	–	–

THE ELEMENTS AND BEHAVIOR PATTERNS OF THE ROYAL PENGUIN



45° FORWARD(45f) FORWARD(f) SIDE(s) 45°(45) HORIZONTAL(h) 45°BACK(45b)

WINGS

VERTICAL DOWN(vd) 45° DOWN (45d) HORIZONTAL(h) 45° UP(45u) VERTICAL UP(vu)

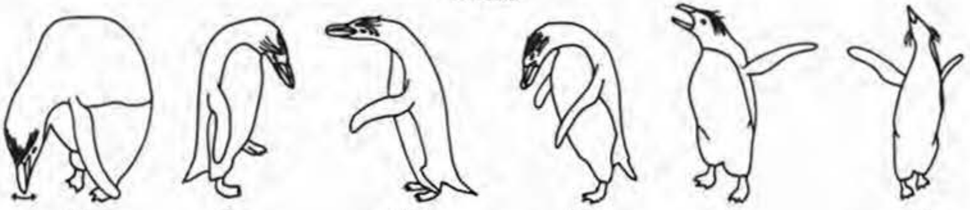
HEAD

SHORT(s)-SS) MEDIUM(m)-MS LONG(l)-LS INCUBATION SIT(IcS) RUNNING

BODY

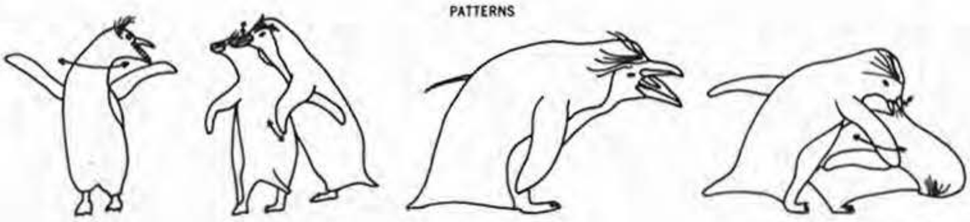
ELSH ELWAG TP1 TP2 HDU

PATTERNS



HW RN NHWF RNWF LCS VS

PATTERNS



F CP TH AGG SU

PATTERNS