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Sexual Behavior in Penguins

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by

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My last but not least tribute is to my wife, constant companion of the majority of my excursions, who rendered invaluable service in the field. It was frequently her lot to grapple with irate penguins with snapping mandibles, scratching claws, and worst of all, whirring flippers, while I attended to other matters. Such tasks, added to the arduous tramping and climbing involved, made heavy demands on both stamina and courage. The rigors of the long "campaign," however, were ever gallantly borne, and the privations patiently endured. She carefully read the manuscript, as written, and offered many useful suggestions when I could not see the wood for the trees.

Preface

"It is far more important nowadays to work out the life-history and habits of a beetle or a caddis-fly than to form extensive collections or make new 'records' " (Russell, 1938: vi).

"Life-history data are becoming increasingly more important as a basis for the classification of birds, and the amateur bird student who gathers these data, has become a most valuable ally to the museum taxonomist" (Mayr, 1946: 229).

The above quotations amply illustrate how the study of birds and other animals has advanced from the old-time conception of concentration on classification and work in the laboratory. Today, as long as it is efficiently carried out, observation in the field is a necessary adjunct of biological science, and, further, because of the work of a large army of field ornithologists the principles of vertebrate behavior are beginning to emerge with some clarity.

Passerine birds, as exemplified by the researches of such keen students as Mrs. Margaret M. Nice, Mr. David Lack, and Mr. H. Eliot Howard, have supplied much of the detail which has led to this advance. Other families of birds lower down the scale have also contributed important and unexpected information, but on penguins and petrels, very little work of a continuous nature, with the exception of that of Mr. R. M. Lockley, has been undertaken. It is hoped, therefore, that this monograph on penguin behavior, supplemented by my own detailed observations on six species of petrels, will in some small way contribute towards the filling in of this gap in our knowledge of the behavior of the more primitive birds.

Although the main text covers only the first ten years of research, field work on the Yellow-eyed Penguin will continue for many years. Since I have completed the paper, two more seasons have passed—seasons which have provided further important information. For example, one mated pair has remained intact for nine consecutive years and another for seven; the first case of inbreeding has been discovered, a brother and a sister from the same clutch four years earlier having mated and reared one chick; and finally, one penguin has been observed for 12 years and nine others for 11 years, so that these two groups are at last 15 and 14 years old respectively.

"It is almost an absolute necessity that one should become familiar, or perhaps better, intimate with an organism, so that he *knows* it in somewhat the same way that he knows a person, before he can hope to get even an approximation of the truth regarding its behaviour" (Pearl in Russell, 1938: 17).

I can truthfully say that I *know* my penguins and Royal Albatrosses, and from this knowledge one feature of bird behavior, in particular, has been very forcibly brought home to me. It is the strong individual variation in behavior and the urgent need for recognizing this in any attempt at deductive thinking.

An endeavor has been made to cover as much of the pertinent literature as possible, and considerable energy and time have been expended in acquiring by means of microfilms and library interloans many of the papers needed. In New Zealand, however, literature dealing with modern aspects of animal behavior is almost nonexistent, a handicap which, I hope, has to some extent been overcome. At the same time, some important papers and books I have not been able to consult, or, if they have been in my possession on loan, the time available has been far too short for adequate study. I may add that only those works actually mentioned in the text are listed at the end; many other publications were consulted, some of which, although not quoted, had an important influence, consciously and unconsciously, on deductions made.

In the text many of the subheadings in the different chapters are identical, so that a certain amount of repetition has been unavoidable. Again, data relative to the unemployed birds could not be restricted entirely to the chapter dealing with this class of bird, and therefore reference to the unemployed birds appears throughout the book. Finally, certain individuals, as for example the female 73 and the female Erect-crested Penguin, have supplied so many aspects of behavior that their frequent mention has been a necessity. I trust that these repetitions will not prove tedious to the reader.

Several writers have had considerable influence on my thought. Among those to whom I am indebted the most are Mrs. Nice, Dr. S. Charles Kendeigh, Dr. G. K. Noble, and Dr. Robert C. Murphy in America, Dr. Julian S. Huxley and Mr. David Lack in England, and Dr. N. Tinbergen in Holland.

I am fully conscious that the story which follows is by no means complete. There are many imperfections. I sincerely trust that the various points raised, the deductions made, and the criticisms offered, will be a spur to prick the ambitions of others to labor in the same field, examining critically from a new angle not only my own work but also that of their other predecessors and contemporaries. Further, I have tried to approach the subject with an open mind, endeavoring to avoid the influence of established ideas, and for this reason have been somewhat critical in testing theories already published.

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Chapter I

Scope of the Study

General. Technique. Review of Previous Investigations. Definitions of Structural Features and Emotional Aspects. General Definitions. Summary.

THIS MONOGRAPH is primarily a survey of sexual behavior in penguins throughout the year, with special reference to the Yellow-eyed Penguin, *Megadyptes antipodes* (Hombron and Jacquinot). Comparison is made, however, with other species of penguins and with the findings of workers who have studied penguins. Previous publications, both scientific and popular, have dealt mainly with penguins found in large colonies, and it has been erroneously assumed that all penguins behave in the manner of these colonial, and largely migratory, birds. Further, in these studies, of a more or less casual nature, no observer has, I think, for more than one season studied birds in the wild state. Moreover, as far as I am aware, no one has banded these migratory penguins in large numbers and determined their matrimonial status in succeeding seasons. Interpretation of behavior under such conditions, with no knowledge of the previous history of the birds under study, is most difficult.

The expression "sexual behavior" is intended to convey the widest possible meaning. Provided that it has some sexual basis, even if only of a social character, it includes relations between members of the same or opposite sexes, and actions of both aggressive and love-habit nature.

The following account is based on ten seasons of intensive field work on the Otago Peninsula, New Zealand, from August 1936 to May 1946. In all, 973 visits were made to several colonies, each about 20 miles from Dunedin, the most widely separated colonies being 20 miles apart. Further, as indicated at the beginning of Chapter IX, I almost lived with the Yellow-eyed Penguins in the 1939-40 season. At the same time, a similar study was made of a trio of the Erect-crested Penguin,* *Eudyptes sclateri* Buller, and of several nests of the Little Blue Penguin, *Eudyptula minor* (Forster). In this way, my observations on sexual behavior in penguins, as described herein, were consolidated. Finally, it was also possible to work out and obtain most of my photographic records.

It seems desirable to present detailed descriptions of sexual behavior as observed and interpreted by myself in the sedentary Yellow-eyed Penguin and also in the migratory Erect-crested Penguin. Comparison of my observations with those of other observers is difficult, for, as already stated, these investigators have worked mostly on unmarked birds or, when marked, on birds known for no more than one season. Further, my principal study has concerned a sedentary species which is present on the breeding grounds intermittently in the winter months, whereas most of those observed elsewhere are in large colonies and are migratory. Although the Erect-crested Penguin is migratory and my observations were not made in a large colony, I nevertheless gained first-hand information in regard to much of its sexual behavior.

The observations summarized here concern 88 male and 96 female penguins which were found breeding for a minimum of one season. In addition, 31 of these males were unmated, in one season or more, after having once bred. As many of the penguins returned to the same area year after year, some 292 matings were recorded.

The sex of the penguins was determined by visiting the nests daily for two consecutive seasons during the span of egg deposition. After examining the vent of the bird or birds present, I obtained a fairly safe indication of the sex of each. This test was subsequently checked by noting definite sexual behavior patterns. Final confirmation came when a bird, accidentally killed, was dissected, and because Yellow-eyed Penguins change their mates

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*See Richdale, 1941b: 26, and Marples, 1946: ii, for use of this name.

Fig. 1. "Unemployed" male of breeding age standing in nest, October 11. By that date practically all eggs had been laid.

Fig. 2. Female 70 brooding nine-day-old chicks, November 14.

frequently it was possible to trace accurately the sex of every bird that had lived in that particular colony in the research period. Sex differences are more fully discussed in Chapter IV.

TECHNIQUE

All birds handled were securely marked with aluminum bands on which the numbers were stamped in four places. This enabled me to read from a blind as far as 36 meters away, with the aid of a telescope, the numbers on the birds' tarsi no matter in which direction they turned—a very important point. Further, I did not have to show myself and thereby upset their natural behavior. In addition, the more important individuals carried a colored celluloid band for quicker identification. Finally, all birds were foot-marked so that, should the bands come off, the identity of the bird would not be lost.

It is not possible with the Yellow-eyed Penguin as it is with the Adélie Penguin, *Pygoscelis adéliae* (Hombron and Jacquinot), to walk up to a group of penguins and make photographic records of many types of behavior in a short time. In the first place, the Yellow-eyed Penguin is not found in large colonies and, secondly, the species usually flees at the sight of man, and certainly will not develop a true behavior pattern in his presence. A blind is absolutely necessary, a fact which will come as a surprise to many readers. Practically all the types of behavior described further on were observed and worked out from a blind (fig. 3) and photographs, too, were taken under similar conditions. In the case of the Erect-crested Penguin, however, a blind was not required, because, if care were taken, my presence only a few feet away did not disturb the normal actions of the penguin.

In the course of the research there were times when it was necessary to catch the birds. Naturally that interfered with normal reactions, but, on these occasions, the birds were not being watched for behavior patterns. For example, the weights acquired for Tables 11-13 and Graph D were taken in the tenth year of study after the behavior research had been completed. The birds watched on the landing beach in the winter of 1939 (Appendix I) were not aware of my presence. I arrived before they did in the afternoon and left without being observed when it was dark.

The weights just mentioned were taken from breeding birds. Since the Yellow-eyed Penguin will not desert its eggs or chicks, no records were lost in that way. The method of weighing was to place the bird in a sugar-bag and then use a spring balance accurate to a quarter of a pound.*

My notes became voluminous, for I have made it a rule to record as much detail as possible even though the details might seem irrelevant at the time. *In other words, I endeavored to see and record exactly what the bird did.* There were subsequently many occasions when I was pleased that I had adopted such a plan.

The detailed part of the research, involving the 292 matings already mentioned, was confined to four main colonies and their subsidiaries. It was felt, however, that in working out interrelationships between colonies a greater number would be an advantage. Accordingly the five remaining breeding areas outside the limits of the four main areas were included and visited each season, though on fewer occasions. This proved to be a wise procedure.

Observation in the first season was much in the nature of a reconnaissance; only two colonies were under consideration, with 66 visits to each of eight nests. In the next four years there was a great concentration of effort, 691 visits being made to colonies. These visits covered all periods of the year. Some visits were made at night and some in daytime. Subsequently, activities were restricted to the last five months of the year, August to December inclusive.

PREVIOUS INVESTIGATIONS AND OBSERVATIONS

There is considerable literature concerning penguins, especially in reference to those inhabiting Antarctica and the sub-Antarctic regions. The most important parts of this have been ably sum-

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*As balances marked in the metric system and suitable for use in the field were improcurable, it was necessary to use an instrument marked in avoirdupois. I have consequently retained these units herein.

marized by Murphy (1936: 329-471), supplemented by his own field work. To this writer I am indebted for much of the material used in endeavoring to work out, for comparative purposes, the behavior of species unknown to me in the flesh.

Additional papers have been produced by Falla (1935: 319-326, and 1937: 32-113), Bagshawe (1938:185-306), O'Brien (1940: 311-324), and Roberts (1940a: 195-254). The last is epoch-making, for it is the first serious attempt to analyze penguin behavior in detail and to theorize thereon in the light of modern conceptions of animal behavior. Bagshawe's contribution has also been of great value.

My own earlier papers* (1940: 180-217, 1941a: 265-287, and 1941b: 25-53) dealing largely with life history, are somewhat anthropomorphic, and suffer from a lack of understanding of penguin behavior. By 1944 my ideas on penguin behavior had crystallized and I set out to commit them to writing, at the same time applying my observations to the theory of animal behavior. My first efforts produced "Courtship and Allied Behavior in Penguins" (1945a: 305-319, 37-54), and "Pair-formation in Penguins" (1946: 133-156, 215-229).

DEFINITIONS OF STRUCTURAL FEATURES

Crown.—In a narrow circle around the eyes are sulphur feathers which broaden to a band averaging 10 mm. in width, called the "crown." This runs across the back of the head from gape to gape, encircling each eye en route.

Forehead.—The area confined by the crown and the base of the bill is a mixture of yellow feathers streaked with dark lines running in the same direction as the bill. This will be called the "forehead."

Eyes.—The eyes themselves during the major emotional attitudes develop a staring appearance, being widely stretched open so that the honey-yellow iris and the pink around the outer edge of each eye are prominent.

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*As I shall be frequently referring to my previous penguin papers, 1940, 1941a, 1941b, 1945a, and 1946, only the year and page number, in parentheses, e.g., "(1940: 79)," will be given.

Crest.—This term is often confused with "crown," which applies only to the Yellow-eyed Penguin. "Crest" describes the yellow head feathers which, as they proceed backwards, protrude from the head of birds belonging to the genus *Eudyptes.* Although such patches are not confused with the "crests" of *Eudyptes,* it should be noted that the Gentoo Penguin, *Pygoscelis papua* (Forster), has large conspicuous white patches above the eyes joined by a narrow white band over the head.

DEFINITIONS OF EMOTIONAL ASPECTS

Love-habits.—This term will cover any behavior not of an aggressive nature adopted by one sex towards the other whether in the breeding season or not, and whether by breeding or unemployed birds.

Courtship.—In this paper "courtship" is synonymous with love-habits.

Habits of Aggression.—These are the antithesis of love-habits and denote any antagonistic behavior whether intra-specific or inter-specific.

Mutual.—This term implies that two birds are indulging in love-habits together. It does not necessarily indicate that these love-habits are identical. Frequently one may content itself with "throbs" and "shakes" in response to more intense behavior by the other.

Keeping Company.—To me this phrase seems to express exactly how two birds of opposite sex behave towards each other under certain conditions. It is not intended necessarily to convey the meaning usually assigned to it in describing human relationship, i.e., that marriage will follow.

Fond of Company.—The Yellow-eyed Penguin is a highly social species, a fact which is particularly noticeable among unmated birds. Individuals of this group rarely remain alone if they are aware that other birds, mated or unmated, are in the vicinity. "Fond of company" will express this characteristic.

Mating.—The word "mating" is here used to signify that two birds have definitely started family life together for the ensuing season but not necessarily that coition has yet occurred. The condition of being mated then continues at least till the end of the breeding season. "Mating" is not synonymous with "coition."

Mated Pair.—When I am referring to two birds which are known to be mated this expression will be used.

Pair.—This will indicate that there is reason to believe that two birds together, apparently with some affinity towards each other, are of opposite sex. At the time, it is not known to the worker whether they are mated. Some of these pairs will actually be mated, but others will not be. The real status cannot definitely be decided till they produce an egg.

Pair-formation.—This is the process by which two birds of opposite sex come together and subsequently mate for at least one season and breed.

Divorce.—When two birds of a mated pair in the previous season return to the colony, and at least one mates with a third bird, a divorce has occurred.

GENERAL DEFINITIONS

Unemployed.—I have used this word to describe all penguins which at the time an observation is made, are without eggs or chicks when other birds have eggs or chicks. The term "non-breeding" does not cover this group, but includes birds that have lost eggs or chicks.

Colony.—The term "colony" is generally intended to convey the impression of large closely packed groups of breeding birds such as exist in some gulls, cormorants, and migratory penguins. The Yellow-eyed Penguin, however, breeds in small scattered groups and sometimes even in single breeding pairs. The use of the term "colony" has been widened to include any community of Yellow-eyed Penguins and really indicates a breeding area.

SUMMARY

This monograph is based on a ten-year study of the sexual behavior of the Yellow-eyed Penguin, *Megadyptes antipodes* (Hom-

bron and Jacquinot). Eighty-eight males and 96 females which mated 292 times were observed. Observations were made also on unemployed birds. All birds were banded and a blind was used to observe important behavior. Recent publications on penguins are summarized and terms to be employed in this monograph are defined.

Chapter II

An Analysis of Types of Behavior

Categories of love-habits—social value, pair-formation value, family value. Categories of habits of aggression—social value, pair-formation value, family value, against predators, warning. Types of behavior—love-habits, including salute, sheepish look, throb, excited shake, open-yell, half trumpet, welcome, full trumpet, arms act, mutual-preen, kiss-preen, bowing, ecstatic; habits of aggression, including tête, open-yell, sheepish look, glare, physical force; and substitute activities, including preening, fiddling with nesting material, sleeping, love-habits of higher emotional valency than preening, a fourth category of substitute activities. Substitute activities in other species. Summary.

In penguins, behavior may be divided into two broad groups. The first concerns all those types of behavior which come under the heading of love-habits, and the second concerns habits of aggression. The next point that will be observed is that both of these types of behavior may be manifested in several different ways at any period throughout the year. It will be observed, too, that the sexual status of the birds involved will range from that of penguins behaving towards each other with no matrimonial significance at all, to that of those which definitely have an affinity, or, at least, a temporary understanding, and finally to that of mated birds with families.

In all these classes of penguins, love-habits are similar, although those of the first class are fewer in number and not so intense. I propose, therefore, to assign three functional values to love-habits used by penguins—social, pair-formation, and family. Similarly, habits of aggression have different functions under different circumstances. Finally, both love-habit and aggressive behavior may be noted when abnormal circumstances call them into play. Such behavior has been described as substitute activity.

CATEGORIES OF LOVE-HABITS

Social Value.—Love-habits of this value concern the behavior of two or more birds in which the factors of age and sex do not enter at all. The birds are all merely casual acquaintances and gather because they are "fond of company"—a strong characteristic in the Yellow-eyed Penguin (1941a: 274, and 1946: 134). Normally, only the less intense types of love-habits are employed.

The incidence of social behavior may be observed between two or more individuals in the water just off the landing ground. It is common, too, on the landing ground itself when the birds are standing about before proceeding to their various camps or nests. It is seen, in addition, on the breeding ground where two or more unemployed birds may congregate. Breeding birds on their way to their nests, should they pass such a group, will be greeted socially with love-habits which have no higher significance than social value.

Other examples are as follows: The unemployed male Z14 was once found in the company of two fully fledged chicks in the absence of their parents (1946: 135-136); a juvenile* female completed her first molt in the company of two nearly fledged chicks (Chapter X); well-acquainted males may enter or leave the water together (Appendix I); and the same is true of females, adult or juvenile, and of mixed groups.

There is some overlap, however, between social and pair-formation behavior. At times the observer is unable to decide which type he is watching, and it seems highly probable that behavior beginning socially may grade into that which has pair-formation value.

Pair-formation Value.—Any use of a love-habit, whether by a single bird or more, which may lead to the formation of a pair has

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*Though in such a context some ornithologists might prefer "juvenal," the form "juvenile," favored by the dictionaries, is used in this book for both noun and adjective.

this value when love-habits are being performed. Before the observer can hope to make anything like accurate deductions of this value, he must first of all know the sex of the birds which he is watching; next he should be aware of their previous history; and, finally, a knowledge of the subsequent history of the actors will be of great assistance. I fail to see how anyone making casual visits to penguin colonies or how anyone even by remaining there for the whole of one season only, can hope, with certainty, to attribute pair-formation value to behavior under observation.

Family Value.—Whenever a mated pair is together, no matter at what period of the annual cycle, mutual love-habits involving all types will be performed. Mutual behavior between a mated pair is particularly pronounced when the individuals meet after an absence, whether in the non-nesting or in the nesting season. It is quite likely, therefore, that love-habits with family value act as a bond to keep the mated pair intact (Chapter III).

When the chicks are dependent on their parents, mutual behavior between adults and offspring will also occur. All this has family value and is fully described in Chapter IX.

CATEGORIES OF HABITS OF AGGRESSION

Social Value.—Intra-specific aggression which is not directed towards either a potential rival or a potential enemy would seem to have social value. Age and sex are not influencing factors. It is merely "quarrelsome" or "playful" behavior, with each bird standing its ground, and there is no law requiring retreat without retaliation.

This behavior is prevalent when birds are standing about in groups. Two may suddenly tête,* but this is seldom followed up by physical force. Another bird, especially if unexpectedly touched by a neighbor, will "open-yell" at its supposed annoyer. Again, when the birds are playing around in the water both these aggressive actions are prevalent; the tête, however, under these last

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*Types of behavior such as "tête" are described subsequently in this chapter.

circumstances, is more frequently supplemented with one or two slaps of the flipper by each bird (fig. 4).

Pair-formation Value.—In this type of aggression age and sex are definite factors. It is confined to adults of breeding age and is directed against potential rivals which might possibly cause the loss of the all-important sex-partner, and the intruding bird not only fails to retaliate but also retreats. A male attacks a potential rival male and the female remains inactive, or a female attacks a potential rival of her own sex and the male remains inactive (1941a: 272, and Appendix V). There is no question of defense of a territory or of a nest site. In some cases, the pair with affinities towards each other have not even reached that stage. Should a nest site have been selected, the behavior may occur some distance from it. If an intruder, say another male, does appear at the nest site, the latter is not the direct object of defense, but the aggressor is rather concerned with retaining the sex-partner or potential sex-partner.

Aggression with pair-formation value is observed when trios are formed, examples of which are given in Chapter VI. Briefly, two birds of opposite sex which are mutually attracted towards each other are engaged in love-habits with pair-formation value. Not far away is a bird, usually a male, which is the object of aggression by the similarly-sexed partner of the pair and which does not retaliate. The other member of the trio remains a passive spectator.

The "injured" male adopts the "glare" simultaneously facing his rival, and then the "sheepish look" as the latter comes a little closer. If there is no retreat, the male of the pair takes a step or two forward. Should this be ineffective, he will grasp his annoyer by the back of the neck with his bill and thrash him with his flipper. After some little time the intruder may return, only to receive similar or more forceful treatment.

The phenomenon of trios seems to be confined only to adults. I have never known a juvenile to take part, although one or more of these youngsters will hover around in the neighborhood of adults performing love-habits (Chapter II). This behavior is quite different from, and must not be confused with, the trio type. One member of the pair, however, will attack a juvenile should it approach too closely.

Family Value.—During the incubation and chick stages, fear of the loss of the sex-partner does not seem to arise. Anxiety for the safety of the eggs or chicks will cause the guardian—of either sex—to threaten or attack any intra-specific intruder, irrespective of sex. If both guardians are present they will attack in unison.

After the chicks are old enough to leave the nest, some occupy a new site a little distance away. Under such circumstances, trespass by an intra-specific intruder on the old nest site does not disturb the parents. Should the intruder, however, come near the chicks in their new position, the parent or parents are immediately on the alert. It seems, then, that it is not so much the nest site that is being defended but what is in it.

The foregoing is exemplified by the behavior of the female 115 towards her potential enemy, the unemployed male 692 (1941a: 278). On the approach of 692, she advanced a little in front of her chicks and "glared" silently. Bird 692 performed the "full trumpet" and was about to proceed closer, but 115 forestalled him with an "open-yell," which doubtless she would have followed up with physical force, had not her mate, Z12, arrived and upset further reactions. The mated pair, in unison, then forcibly ejected 692.

Some weeks later, 115 was followed from the beach by the unemployed male 104. When near her unguarded chicks, she suddenly turned and barred further progress with an "open-yell," followed by a "glare." Seventeen minutes later, Z12 arrived. Both males greeted each other, simultaneously facing each other, with a most dignified "salute," after which, to use Guthrie-Smith's apt phrase (1914: 61), 104 "sloped off" and so ended the episode.

As to potential inter-specific penguin enemies, not much evidence is available. The only other species I have seen with the

Yellow-eyed Penguin is the Erect-crested Penguin. Outside the chick stage, or if away from the nest, the Erect-crested Penguin is tolerated, but I have not seen any mutual behavior of a social nature. If guarding chicks, or if incubating, the Yellow-eyed Penguin will act aggressively towards the Erect-crested Penguin. In the instance I observed, had not the latter fled, the Yellow-eyed Penguin would probably have used her flippers.

Against Predators.—Predators of the Yellow-eyed Penguin include several exotic mammals including man. In other species of penguins, such predatory birds as the Southern and Antarctic skuas, *Catharacta skua maccormicki* (Saunders) and *Catharacta skua lönnbergi* (Mathews), the Giant Petrel, *Macronectes giganteus* (Gmelin), and the Sheath-bill, *Chionis alba* (Gmelin), may be added.

If a mammal approaches too near to the Yellow-eyed Penguin an "open-yell" will result, and the flipper will be used if the animal is close enough. I once observed a lamb gambol up, evidently intent on bunting the penguin, which "open-yelled," hit the lamb on the nose, and then carried on with its preening. Such animals as ferrets, *Mustela putorius,* and stoats, *Mustela erminea,* do not seem to attack adult Yellow-eyed Penguins, but ferrets have killed the Little Blue Penguin in the burrow. The Yellow-eyed Penguin is obviously able to defend itself on land.

Should man approach too closely, he is met with ominous passes from the bill, and, provided the bird does not flee, these will be supplemented by the use of the flipper, if the bird is close enough. If a chick squeaks when handled, a parent which has fled will usually return and "open-yell" at its annoyer. One male, 28, if he saw me coming and was not in charge of the chicks, would place himself between me and the chicks and "glare" at me. If I touched a chick he would immediately attack me with bill and flipper. This is the only adult that has behaved in that manner.

Warning.—Huxley (1938a: 431) classifies characters concerned with "threat" and "warning," the latter indicating "possession of weapons, nauseous taste, or other unpleasant properties, normally directed against enemies of other species." There would appear to be nothing of this nature in the Yellow-eyed Penguin, but it may be observed in the Royal Albatross, *Diomedea epomophora sanfordi* Murphy.

About a month after hatching, a Royal Albatross chick is no longer guarded by a parent. If a potential enemy, such as a Skua, appears the chick sits upright in its nest (1939: fig. 7) on its tarsi, rapidly snaps its mandibles, and simultaneously makes a gulping noise. Should the Skua approach further, vile-smelling oil will be ejected. In the case of the Skua, which fears the oil, the snapping and gulping are a true warning, for they signify the possession of unpleasant properties.

Types of Behavior

Love-Habits

Salute (fig. 5).—As far as I have been able to ascertain, it is usually the male which adopts this attitude. A bird apparently interested in a female will stand from six to fifteen feet away with his back to her and, according to the human observer, will seem to be quite indifferent to her presence. He must, however, be fully conscious of her, for suddenly he turns around and, with neck arched, with beak nearly touching the ground, and with flippers pushed out stiffly in front of him, he rapidly walks up to and past her with quaint little steps, stops with his back to her, and thrusts his beak straight up to the sky, with his neck fully stretched, and with his flippers still thrust out in front. Reaching to his full height he maintains this position for about five seconds before slowly lowering and turning the head, almost simultaneously looking over one shoulder as if to gauge the effect. It should be noted that when the head is lowered, it is accomplished by the contraction of the neck, the bill still pointing upwards, and the latter not being lowered till the bird slowly turns his head to look over his shoulder. Even then the bill is lowered only slowly.

Frequently, I have seen the demonstration confined to a single "salute." On other occasions, the male will again walk past the female, but not so far, and repeat the procedure. After that the pair may start to preen each other, and love-habits in varying degrees may follow. Further still, the "salute" is sometimes performed several feet in front of the second bird (fig. 6; 1946: pl. 27).

To judge from the literature, the Yellow-eyed Penguin is the only penguin which "salutes." This behavior certainly does not occur in the Erect-crested Penguin nor is it very likely that it occurs in the genus *Eudyptula.*

The "salute" may be used in all three values of love-habits as described earlier in this chapter. Socially, as indicated below, it may be observed on such occasions as when males "salute" each other, when birds "salute" in the water and just after landing, when juveniles "salute," and, finally, when even nestlings do it.

Males will "salute" each other as in the case of 104 and Z12 (Chapter II). A further example, involving the males 721 and 61 (Appendix I), occurred in the winter on July 9 on the beach and must merely have been a greeting, for both, to my knowledge, had been acquainted with each other for at least four years.

The "salute" with the head and neck only pointing towards the sky, is also frequently performed in the water when there are a number of birds playing close inshore. Again, the first arrival at a colony in the winter, whether in the water or on shore, may "salute" or be "saluted" by the second arrival. It is a common sight also to witness a bird which has emerged from the water approach and "salute" the nearest individual of a group already ashore. In all these cases I was unaware of the sex of the active bird.

The "salute" may be used by one or more curious juveniles which congregate in characteristic fashion around a pair indulging in love-habits on the landing ground. First one and then another will walk quickly past not only the male, but the female as well, and "salute" until pecked off the premises by the irate male. The sex of these juveniles I have never determined, so that the act may be, and probably is, performed by either sex. The "salute" of the juveniles probably has social value, possibly being a premature appearance of love-habits, or it may be merely a case of suggestion stimulated by observing such actions in adults.

I have twice witnessed a chick ninety days old perform the "salute" before its nest mate, but here again I did not know the sex.

It seems obvious that the "salute" has definite pair-formation value, being probably the beginning of actions leading up to the formation of a pair. As the males are very much in excess of the females, strong intra-sexual competition exists during pair-formation activities; it may be for this reason that the "salute" is more in evidence with males. Females, however, do perform the "salute." (See Appendix I, under 23 July, 23, 29, and 30 August. The female mentioned "saluted" two of her male suitors, but not the one with which she ultimately formed a mated pair.)

Family value of the "salute" is exemplified by the behavior of Z12 and 115 (Chapter IX).

Sheepish Look (fig. 7; see also 1945a: fig. 3).—The bird stands up off its tarsi but does not stretch itself up to its full height as in the "salute" or the "full trumpet." The flippers are pushed out stiffly straight forward, at an angle of 45° to the ground, but it is the appearance of the head which characterizes the attitude. The neck, instead of lying normally contracted between the shoulders, is half stretched upwards, but not fully as in the "salute." The head is then hung so that the bill, pointing downwards, lies almost parallel to the foreneck. Frequently the head is held to one side (1945a: fig. 3), while the sheepishness of the whole attitude is accentuated by the wide-opened staring eyes, and the raising of the feathers of the crown and forehead.

This and the next five types of behavior do not appear to be in the repertoire of the Erect-crested Penguin, nor, as far as I can tell from the photographs of Wilson (1907), Levick (1914 and 1915), Gillespie (1932), Murphy (1936), and Falla (1937), of the species there depicted.

The "sheepish look," which is usually, though by no means always, adopted by the female, is very common after the birds remain ashore in the daytime in August, till about the middle of the incubation period. It may occur at any time when a bird returns to its mate at the nest, though one is not certain to see it included in the elaborate ritual that takes place during the change of guard. In the early winter months it may be witnessed when the birds perform love-habits either at the nest site or on the landing ground. From the end of July to the beginning of the pre-egg stage in August, it becomes increasingly common. Finally, it occurs in the period of molt, particularly between mated pairs and pairs "keeping company."

Throb (fig. 8).—This action, beginning with rapid pulsating movements of the skin and feathers at the base of the neck and top of the breast, is really a further development of the "sheepish look." The bill, raised to the sky at an angle of 45° and sometimes a little further, is opened slightly, vibrated very slowly, and a noise resembling a series of chuckles issues from the base of the throat. The crown is raised slightly.

The "throb" is common to both sexes and is frequently heard at irregular intervals when two birds of a pair, or a mated pair, are together. It may signify the commencement of a bout of intense emotional activity, or it may be the final act after intense activity before the pair subsides to a spell of passiveness. On other occasions, the periods of inactivity may be broken for a few moments by "throbs" only, with no behavior of greater intensity.

Shake (fig. 9).—The head is usually turned well round to one side so that the bill is almost parallel to the ground and there is a right angle at the throat, though sometimes the bill is lowered to form a 45° angle. Simultaneously, the crown and forehead feathers are raised considerably, the eyes are widely opened, the flippers are raised halfway between the "arms forward" and the "arms sideways" position, and the bill is partly opened. Quickly following all these actions, the bill slowly opens, quivers slightly, increases in momentum till the whole head is being violently "wobbled" from side to side, while at the same time a vibrating noise issues from the throat. The whole scene may culminate in a "full trumpet," or the "welcome," or it may subside altogether,

Fig. 3. The blind in position before an incubating penguin.

Fig. 4. Social behavior in the water. The two birds on the right are "têting" and slapping at each other.

to be repeated a few moments later. On other occasions the "shake" is either silent, or carried out with only very slight vocal accompaniment. During the entire performance, the bird stands off its tarsi with the tail and under parts clear of the ground. There are numerous variations of this attitude, for the several parts of the bird used are not always in the same position.

Both sexes perform the act, which is quite common at the pre-egg stage. The bird on the nest, whether male or female, will indulge in quite violent "shakes" as soon as it sees its partner begin to pick up nesting material. In this case, the back and neck are arched, and the bill is pointing to the edge of the nest. The "shake," though prominent at the pre-egg stage, is also commonly used by a mated pair during the breeding period and occasionally in the period of molt.

At the nest of the male Z12 and the female 115 (see Chapter IX) the male frequently performed these "shakes" before the female, and many times finished up with a "full trumpet." On a number of occasions, when Z12 was feeding the chicks in the presence of the female, the latter broke into "shakes," sometimes silent and of very slight intensity and at other times very violent and with full vocal effects. Usually the result was the interruption of the feeding to allow the male to respond, generally with "throbs," "shakes," and "half trumpets."

Excited Shake.—Externally this appears to be an extension of the "shake," but it is an entirely different action. The stance and the position of the flippers are the same as for the "shake," but the eyes do not stare so much. The head and bill, instead of being vibrated vigorously, have a tendency to bob up and down, first to the left side and then the right. The bill points to the ground and is partly open, and an acute angle is formed at the throat. The crown and forehead feathers, especially the former, are raised more conspicuously than in any of the other attitudes. Vocal accompaniment is quite loud, with a simultaneous movement of the feathers and the skin as in the "throb." The head and bill are frequently raised to the "half trumpet" position, resulting in the assumption of the latter attitude.

Actually, the "excited shake" followed quickly by the "half trumpet" attitude makes a composite action frequently used. The "excited shake" is a very emotional attitude and is indulged in by both sexes, but not until both are definitely interested in each other, which does not necessarily mean that they are going to mate. It is common with mated birds at the nest from the pre-egg stage to the departure of the chicks, in the period of molt, and when the birds are at their camps or nesting sites in the winter.

Open-yell (fig. 10).—On some occasions, a bird, without any preliminary actions, breaks into what I term the "open-yell." Standing off its tarsi, it leans forward with the body at least 45° to the ground, with the neck stretched out in a similar line, and with the head bent slightly forward off that line. The mandibles are then opened as far as possible, with the eyes staring to their fullest extent. As it lunges forward, the bird emits a yell at the top of its voice. The flippers are sloped down at 45° from the shoulders and are halfway between the "arms forward" and "arms sideways" positions.

This love-habit does not seem to have social value. In pair-formation it does not occur until the members of a pair are well disposed towards each other, and is employed mostly during the "welcome" ceremony, after one bird has returned from the sea to find the other at the nest site.

The main function of the "open-yell," as a love-habit, is within the family group and as such has family value. A bird will break into the "open-yell" when, on the nest, it suddenly sees its partner returning from fishing (Chapters VIII and IX); when it performs part of the "welcome" ceremony (fig. 12); and when it has returned from the sea, at the post-guard stage, to observe the chicks issuing from their hiding place clamoring for food.

Half Trumpet (fig. 11).—This is the commonest behavior of all the love-habit activities, and consists of "throbs," and what appear to be half-hearted trumpets. Standing off its tarsi, the bird leans forward slightly, with its head still a little further forward. The mandibles are half open, emitting fairly loud continuous noises, which are difficult to define, while, at the same time, "throbbing" occurs at the base of the neck. The flippers are pushed forward while hanging down at an angle of 45° from the shoulders, with the inner surfaces facing each other. Closely associated with the "half trumpet," as already explained, is the "excited shake."

The "half trumpet" may be heard at almost any time when a mated pair, and sometimes when two birds "keeping company," are found together. It is part of the "welcome" ceremony, and will last for some considerable time after that is finished. In the period of molt, a pair or mated pair will suddenly break into this activity for a few moments, standing so that the bills almost touch each other. At the pre-egg stage, and whenever any love-habits are taking place in the winter, when a pair or mated pair happens to stay ashore for the day, it is very common. For example, during one important episode on record, two birds continued the "half trumpet" behavior at frequent intervals nearly all day (Chapter III).

Welcome (fig. 12 and 1941a: fig. 6).—To give the "welcome" the birds stand in exactly the same position as for the "half trumpet," except that the mandibles are open as far as possible, the eyes are staring widely, and a much louder and a greater volume of noise issues forth. The vocal sound emitted bears a close resemblance to the "full trumpet," except that there is less of the pretty musical warbling and a preponderance of "yelling." With the first outburst over, the birds will subside to the "half trumpet," to the "excited shake," to the ordinary "shake," to the silent "shake," to the "throb," and finally, to the "sheepish look," before once more breaking into the "full trumpet." The foregoing is the order of the actions, if all are performed, but some are frequently omitted. Then again, the renewed "welcome" is often preceded by all or some of the actions in the reverse order, beginning usually with the "throb." Occasionally, either bird may indulge in a "full trumpet" during this "welcome" ceremony. The "welcome" is usually given several times, after which change of guard is effected if at the egg or small-chick stage. After the change, further "welcomes" may occur together with some of the other actions of the ceremony, but the dominant activity is the "half trumpet."

Even though the Yellow-eyed Penguin appears to be the only penguin which indulges in this type of "welcome," all other species probably have a comparable ceremony when two birds, held together by some strong bond, such as the joint ownership of a nest, meet. In the Erect-crested Penguin, and no doubt in the other members of this genus, the ceremony is most intense and includes the "ecstatic" (1941b: 47-50). With the genus *Eudyptula*, the ceremony occurs at night in the burrow, and whatever actions take place are accompanied by weird alternating inspiratory and expiratory sounds. In the Adélie and Ringed Penguins, *Pygoscelis antarctica* (Forster), the ceremony resembles that of the genus *Eudyptes*, but in the Gentoo Penguin "bowing" and hissing seem to be the chief features. For the genera *Aptenodytes* and *Spheniscus,* I cannot discover much about the procedure, although neck- and bill-rubbing is possibly a feature in the latter species (Murphy, 1936: 459).

In the Yellow-eyed Penguin, the "welcome" is given whenever one bird arrives at the nest and finds its partner there, whether in the winter after both have been at sea for the day, or in the pre-egg stage, when one or both may go off to sea and return separately that day, or in the incubation period, when one partner may stay away for as long as five days, or in the chick stage, especially when one bird guards the chick in the daytime, or finally, in the period of molt, when a bird has discovered its mate which has preceded it to the molting site.

As far as I have been able to discover, the "welcome" is entirely the prerogative of mated birds in all species. It is quite likely, also, that a pair which is "keeping company" may indulge in this behavior, but I have not had the opportunity to watch this group thoroughly enough to be positive.

Full Trumpet (fig. 13).—A bird seldom breaks directly into the "full trumpet," for it is generally the culminating point of one or more of the preceding types of behavior. Standing only on its toes with the tarsi and legs erect and in line, with the tail and underparts quite clear of the ground, with the flippers thrown stiffly forward at the "arms forward" position, with the head thrust straight towards the sky, with the line from the chin through the breast to the vent forming the arc of a circle, and with the line running from the back of the head to the tail a definite hollow, the bird opens its mandibles, and the vast volume of trilling sound that issues forth is fantastically suggestive of the tremolo of giant crickets, and is musical to a degree. All this time, with the mandibles vibrating rapidly, the feathers and skin at the base of the neck and top of the breast, too, are pulsing vigorously in and out. A near view shows that the muscles from each shoulder down the back to the tail are contracting in rapid rhythm. At the commencement of the majority of the "full trumpets" the flippers are held out behind the bird at 45° from the shoulder, being brought through to the "arms forward" position only after several heaves of the top of the breast, and after some vocal sound has been emitted.

Trumpeting is evidently performed in all penguins with the exception of the genus *Eudyptula.* I have no evidence that this genus performs love-habits outside the burrow. If this is so it could hardly trumpet inside. The incidence of trumpeting in the Yellow-eyed Penguin is fully discussed in Chapter VII. In all species where it occurs it seems to take place at all times of the year, and although it has family and pair-formation value it appears to be used more often with social significance.

It should be noted that trumpeting is really an individualistic type of behavior by a single bird very frequently alone, but it will also occur with the mate alongside; it is only occasionally part of a ceremony in which both are participating. For this reason, I think Armstrong (1942: 133) has read too much emotional value into the behavior of the captive King Penguin, *Aptenodytes patagonica* J. F. Miller, which he saw trumpeting alongside another bird. Further, I do not think the bird was "posturing" in the sense of "displaying" before a second bird. To me, this bird's trumpeting is an individualistic action which for some reason we do not yet understand.

Gillespie (1932: opp. 44) gives a good figure of trumpeting in the King Penguin, and Wilson (1907: 18) describes it for the Emperor Penguin, *Aptenodytes forsteri* G. R. Gray. In the latter someone has called it "bugling." It seems, too, that trumpeting in this genus is semi-musical (Wilson, *loc. cit.*; Matthews, 1929: 591; Gillespie, *op. cit.*: 45), as in the Yellow-eyed Penguin. In the genus *Pygoscelis*, this cry, which is called "crowing" (Bagshawe, 1938: 201 and 275) or "braying," is quite harsh. A good picture of braying in the Gentoo Penguin is given by Falla (1937: fig. 33) and by Bagshawe (*op. cit.*: pl. II, fig. 4). Further examples are the paintings by Ménégaux (1907: pl. III, fig. 4, and pl. V, fig. 8). As Falla's picture portrays a Gentoo Penguin over an egg and Ménégaux's picture a bird in charge of young about a month old, it is obvious that in the Gentoo Penguin, as in the Yellow-eyed Penguin, the "full trumpet" or "braying" occurs at all times during the breeding season.

I do not agree with Roberts (1940a: 250, fig. 5) that his picture is of a Ringed Penguin crowing. It is obviously drawn from Bagshawe's picture (1938: pl. VI, fig. 3) and contradicts Bagshawe's caption that the penguin is yawning and stretching. This is a common attitude in the Yellow-eyed Penguin and in the Erect-crested Penguin, and is also figured and similarly described for the Adélie Penguin by Levick (1914: fig. 3) and by Gain (1914: pl. I, fig. 4). Bagshawe (*op. cit.*: pl. VI, fig. 2), however, gives a photograph of the Ringed Penguin about to crow, and in the text (p. 275) describes the action and states that the bird is alone.

In the Adélie Penguin, the "full trumpet" is figured in many places—e.g., Wilson (1907: fig. 39), Murray (1909: opp. 248, third plate), Levick (1914: fig. 32, and 1915: pl. VI), Gain (1914: pl. I, fig. 6), and Falla (1937: fig. 50). The whole attitude is beautifully illustrated by Ponting's picture (1921: 239) showing three single birds performing the action. Similar behavior by two other birds apparently side by side, and possibly a mated pair, is difficult for one not on the scene to interpret correctly. They appear to be trumpeting, but if they are a mated pair, they may be at the peak of the "ecstatic" ceremony during the process of changing guard.

It has rather puzzled me that in practically all the numerous pictures showing the "full trumpet" in the Adélie Penguin the bill is closed. In the Erect-Crested Penguin and especially in the Yellow-eyed Penguin, it is almost impossible to snap a photograph like that, for vocal accompaniments are taking place before the head points to the sky. For that reason, the "full trumpet" in the Adélie Penguin, as shown, for example, in Ponting's picture, might be a different attitude.

In Murray's picture, just mentioned, the bill of the bird is slightly open and the caption reads, "An Adélie calling for its mate after commencing the nest." Levick's description (1914: 46) of this attitude clearly signifies that calling is part of it in spite of the lack of evidence in photographs.

The "full trumpet" of the Adélie Penguin is not the "salute" of the Yellow-eyed Penguin, for in the first place the latter does not keep its head raised for more than five seconds, whereas in the former the time is evidently much longer. Secondly, the Yellow-eyed Penguin always "salutes" another bird, whereas the "full trumpet" is usually a solitary business performed in most cases by a bird on a scoop.

In the Erect-crested Penguin, braying is a very raucous affair. It will be noted that braying occurs either when a bird catches the first glimpse of its partner returning from the sea (1941b: 48), or sometimes with no apparent stimulus when it is alone (*op. cit.*: 45-46). No doubt braying is performed by all species of *Eudyptes*, a view which is supported by Falla's picture (1937: fig. 87) of two Rockhopper Penguins, *Eudyptes crestatus* (Miller), indulging in the "ecstatic" and also by Matthews' description (1929: 589) of the "ecstatic" by two Macaroni Penguins, *Eudyptes chrysolophus* (Brandt). He also mentions that the bray is much deeper and harsher than in the Gentoo Penguin. Kearton (1930: 53) gives an excellent picture of the "full trumpet" in the African Penguin, *Spheniscus demersus* (Linnaeus), which seems to indicate that it may happen in the other three members of the genus. Finally, in the "full trumpet" in all species, as far as I can tell from pictures, the flippers are held from the sides of the bird at varying distances and heights.

In summary, it is apparent that, in the other species, as with the Yellow-eyed Penguin, trumpeting occurs throughout the year. Murphy (1936: 349) states that in the King Penguin it is not confined to the courting period and in the Magellan Penguin, *Spheniscus magellanicus* (J. R. Forster), it takes place in the water (*op. cit.*: 439). Levick (1915: 83) has noted it in the Adélie Penguin when out on the sea ice, while I have observed it in the Erect-crested Penguin at all times when ashore (1941b: 25 *et seq.*). Dr. R. A. Falla has kindly sent me a photograph taken during the Mawson expedition, of the Adélie Penguin adopting its characteristic "full trumpet." This bird was occupying an empty scoop while others were attempting to cover chicks at least three weeks old. It is therefore quite clear that the "full trumpet" is retained in this species at least well into the breeding season.

Arms Act (fig. 14).—I first witnessed this performance at 4:57 p.m. on 4 September 1937, two weeks before the first egg appeared, on the landing ground, where the male was practicing it on the female. The former had already given the impression that he was searching for a mate, when he suddenly went up to the female, whose back was to him. He pushed his breast up against her back, at the same time putting the front of his neck on the back of hers, and pressed heavily. All this time the male's flippers, vibrating rapidly, were one on each side of the female and protruding in front of her. It appeared as if he were trying to "put his arms around her." The female submitted to this treatment for a while and then moved away.

When I first saw this action it puzzled me very much, and continued to do so in subsequent seasons, for I had not seen a repetition of the performance in the Yellow-eyed Penguin. On 31 March 1939, however, I observed similar rapid movements of the flippers and the pushing of a male's neck on to a female's in the Erect-crested Penguin (1941b: 35). As the female was prostrate on the nest and had obviously been stimulated by the male, it was apparent that this was the beginning of behavior leading to coition, and my thoughts immediately reverted to the Yellow-eyed Penguin pair on 4 September 1937. It should be remembered that on my many visits to the nests of the Yellow-eyed Penguin in the ten years when I observed them, I never witnessed coition, although I had been present at night as well as in the daytime.

In January 1940, I several times saw attempts to copulate both by the male and the female Erect-crested Penguins (*op. cit.*: 49), scenes which convinced me that the male Yellow-eyed Penguin was trying to persuade the female to copulate with him on the night in question. In Appendix I, it may be noted that the male 721, on 16 July, 16 August, and 24 August, pushed his breast up against the female 70. On the last date there seemed to be keen activity on the part of the three males concerned, for 721 twice pushed himself against 70; on the first occasion he exercised some considerable force, which the female withstood for some time before turning away. With all the foregoing information in hand, and in view of the circumstances surrounding 721 that winter, I am sure that his action had coitional significance.

A photograph by Kearton (1930: 64) shows a pair of African Penguins apparently performing the "arms act." Similar behavior, with the variation of crossed bills, has been noted in the King Penguin by Matthews (1929: 590), Gillespie (1932: 96-97), and Murphy (1936: 349). In the Gentoo Penguin, coition is described by Bagshawe (1938: 193) and Roberts (1940a: 209), and in the Adélie Penguin by Gain (1914: 21) and Murphy (1936: 393). The remarks of all these writers corroborate my belief that the "arms act" is the beginning of coition. The act itself is figured in the Gentoo Penguin by Ménégaux (1907: pl. IV, fig. 5) and Bagshawe (1938: pl. I, fig. 4), in the Adélie Penguin by Gain (1914: pl. III, fig. 14) and Roberts (1940a: fig. 18), and in the Ringed Penguin by Wilton (1908: pl. XVIII, fig. 57).

Mutual-preen (fig. 15).—This term indicates that two birds are preening each other. Sometimes while one bird is preening itself a neighbor will assist it. One bird may bend forward and preen the breast of another, which responds by preening the top of the head of the first.

Kiss-preen (fig. 16).—A common action occurs when two birds simultaneously preen each other's throats and upper necks.

The last two types are common actions of a mated pair wherever they may happen to be together, and nearly always take place after major love-habits. Chicks, as they begin to acquire their feathers, will also indulge in the practice, and, when well fledged, will do so with their parents. This has family value.

Pair-formation value is noted when two birds "keep company" or are mutually disposed towards each other. When unattached birds, or for that matter, mated birds from different pairs, are in close proximity, they will "mutual-preen" and "kiss-preen" at any time of the year. This has social value. Such behavior is not followed by the more intense love-habits.

A perusal of the literature indicates that this minor behavior is common to all species. My own observations on the Erect-crested Penguin indicate that this behavior is prevalent among mated pairs in the genus *Eudyptes*, far more so than in the Yellow-eyed Penguin.

Bowing.—As this attitude does not occur in the penguins which I have studied in the field I cannot describe it fully. The reader is referred to Murray's (1909: opp. 246) photograph of an Emperor Penguin for behavior which I regard as true "bowing." In the Yellow-eyed Penguin, however, there are occasions when birds may give the impression that they are "bowing."

For example, the female 115 frequently bent over to inspect a chick that was lying flat on the ground (fig. 17 and 1941a: pl. 51). At the nest at the pre-egg stage, the bird standing alongside the one on the nest might at times bend over towards the other, but I do not regard this as "bowing." It is really only an inquiring attitude. When exploring among or under rocks, these birds always bend over after the manner of "bowing." In fact, "bowing" seems to be an attitude that is involved in many normal actions, largely owing to the build of the birds. For example, when they are racing along at the beginning of the "salute," this "bow" is very pronounced, but it does not seem possible for a penguin to proceed in any other way under such circumstances. It is difficult to interpret behavior of other species as seen only in photographs, but I strongly suspect that "bowing" is caused mainly by structure.

There is no "bowing" in the Erect-crested Penguin. Certainly the male when bringing sticks and other objects to the female on the nest used to bend down and put them at her feet, but sometimes when he was between the rocks in such a position that his head was level with the nest he merely stretched up and deposited the material. During part of the elaborate "ecstatic" ceremony these birds used to bend over and sway in unison (fig. 19 and 1941b: fig. 8), but this is hardly "bowing."

However, in three species—Emperor, King, and Gentoo Penguins—"bowing" does seem to have significance; in all the others, as far as I can tell from the literature, it has the same value as in the Yellow-eyed and the Erect-crested Penguins. Certainly, in the latter it is the more noticeable in love-habit ceremonies at the nest. Hence Levick's (1914: fig. 55) picture of Adélie Penguins changing guard I would not call "bowing."

In the genus *Aptenodytes*, I would suggest, "bowing" is equivalent to the "salute" in the Yellow-eyed Penguin and has the same function. With the Emperor Penguin, my contention is supported by Murray's (1909: opp. 246) picture of two birds "bowing," and also by his description of circumstances when "bowing" occurs (*op. cit.*: 245). Gain (1912: 482 and pl. I) gives similar evidence, and his caption for the figure is "Emperor Penguin saluting." In the King Penguin, the best evidence is supplied by Falla (1937: 47), who remarks that if two groups pass each other "they all stop, bow, and then move on again." It is obvious that the kind of "bowing" which occurs in the Yellow-eyed and Erect-crested Penguins occurs also in the genus *Aptenodytes*, as, for example, when a bird feels inquisitive (Gillespie, 1932: 62).

In the Gentoo Penguin, judging by the observations of Matthews (1929: 586), Bagshawe (1938: 185 *et seq.*), and Roberts (1940a: 218), "bowing" does have an emotional value higher than that of "salute" and seems to be part of the love-habits at the nest. "Bowing" appears also to have "salute" value as explained by Bagshawe (*op. cit.*: 221, 222, 251), who remarks that he observed "immature birds bowing to each other—just for friendship's sake."

In summary, my impression is that "bowing" has been given in books a significance which is not apparent in the field and that undue emphasis has been placed on the attitude as one of the more intense love-habits.

Ecstatic (figs. 18 and 19; see also 1941b: fig. 8).—This behavior has already been described in detail (1941b: 48). It always concerns two birds and passes through two phases during which the flippers are not retained at the sides but are actually moving all the time. The first involves head-to-sky behavior coupled with braying and excited neck-twining (fig. 18). The second concerns bending over in unison towards the ground while simultaneously braying and twisting the head (fig. 19 and 1941b: fig. 8). Sometimes the birds touch the nest with the beak and sidle around the nest using it as a pivot. Then the entire ceremony, or modification thereof, is repeated one or more times according to the degree of emotion at the moment. Such variations are fully explained in the 1941 text (1941b).

As confusion has arisen over the use of the word "ecstatic" it is necessary to state clearly how I here employ the term. The "ecstatic" requires the participation of two birds and has pair-formation and family value only. The "full trumpet," on the contrary, is performed mainly by one bird alone, but may occur when two birds are together. Although it has family and pair-formation value, it occurs frequently when it has only social value.

Further, it is sometimes used as a substitute activity. Actually, the function of the "full trumpet" is not completely understood.

The confusion is due to Levick's use of the term "ecstatic" to cover both types of behavior. In his book (1914: 42-43) he describes the "ecstatic" in the one instance thus: "Both perhaps would assume the 'ecstatic' attitude, rocking their necks from side to side as they face one another (fig. 26)." These remarks are then supported by the figure quoted. Further on (*op. cit.*: 46-47, and fig. 32) and in his report (1915: 82-83), the "ecstatic" attitude which he describes is totally different and seems to be what I term the "full trumpet." His final reference to "Figs. 26 and 32, Adélies in ecstatic attitude" (1914: 47), clearly signifies that he has not grasped the difference between the two. In his report (1915: 83), however, he mentions only the second type and cites Wilson's drawing (1907: fig. 39) as his source.

Levick's first use of the phrase, as depicted in his figure 26, coincides with my original interpretation of the term as indicated in my paper on the Yellow-eyed Penguin (1941a: 269), and my experience in the field with the Erect-crested Penguin had already served to strengthen it. My first impression on observing the mutual behavior of the latter at its nest was the striking resemblance it bore to the behavior described by Levick for the Adélie Penguin. Murphy (1936: 392) and Huxley (1930: 68) have applied the term in this sense. Others have employed it in the second sense, as, for example, Falla (1937: 77) and Roberts (1940a: 219) for the Adélie Penguin and Bagshawe (1938: 201) for the Gentoo Penguin. In regard to the Ringed Penguin, however, Bagshawe (*op. cit.*: 275) uses "ecstatic" in both senses.

When Roberts' paper (1940a) reached me towards the middle of 1941, my paper on the Erect-crested Penguin (1941b) was already in press. It was not till then that I noticed that the word "ecstatic" was being used for what I was calling the "full trumpet" (1941a: 270).

There is another matter which requires clarification. Prior to the completion of his paper, Dr. Roberts had written inquiring about the "ecstatic" attitude in the Erect-crested Penguin and as we, unknown to each other, attached different meanings to the term, that part of my letter quoted at the foot of page 219 of his 1940a paper is misleading. It is a description of the "salute" and not the action to which Dr. Roberts applies the term "ecstatic" nor of the action to which I apply the term "full trumpet."

Looking back on my paper on the Erect-crested Penguin (1941b), I fear, after having given penguin behavior more thought, that I have caused some confusion by using certain terms in a somewhat different sense from that employed in the present paper. In the earlier paper, the term "ecstatic ceremony" always applied to what is here termed "ecstatic." At the time of writing the earlier paper I had not begun to use for the Erect-crested Penguin the term "full trumpet." Consequently, what I *then* termed "ecstatic" and "ecstatic attitude" I should now term "ecstatic" when performed by two birds together, but *when performed by a single bird* I should now term it "full trumpet."

According to my interpretation of the term "ecstatic," the Yellow-eyed Penguin does not indulge in this behavior. Certainly, during the "welcome" ceremony, sometimes during the "full trumpet," and usually during the "excited" and ordinary "shakes," the behavior is very emotional, but the ecstasy does not compare with that which I have often seen displayed between a mated pair of Erect-crested Penguins (1941b: 47-49).

That two species of *Eudyptes* at least perform the "ecstatic" is evident from Matthews' excellent description (1929: 589) concerning the Macaroni Penguin and from Falla's picture (1937: fig. 87) depicting the Rockhopper Penguin. It would seem justifiable, therefore, to assume that the Drooping-crested Penguin,* *Eudyptes pachyrhynchus* G. R. Gray, and the Royal Penguin, *E. schlegeli* Finsch, also adopt the attitude.†

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* See Marples, 1946:ii.

†From 9 January to 26 February 1948 when on an expedition to the Snares Islands, I was able to study the behavior of the Snares Island Crested Penguin whose systematic status is as yet not ascertained. Its love-habits closely resemble those of the Erect-crested Penguin and include the "ecstatic," which is employed in exactly the same way.

It is rather curious that so many of the pictures portraying the "ecstatic" in the Adélie Penguin show the bills closed or only slightly open, for example, Wilton (1908: pl. XXXIII, fig. 101), Murray (1909: 244), Levick (1914: fig. 26), Gain (1914: pl. 1, fig. 5), and Falla (1937: fig. 54). A person might be tempted to think that this is another attitude, but Falla's (*op. cit.*: fig. 51) and Ponting's (1921: 240) pictures belie that idea.

The behavior under discussion is also adopted by the Ringed Penguin. This is verified by the photographs of Wilton (1908: pl. XVIII, fig. 56) and of Bagshawe (1938: pl. VI, fig. 5, pl. VII, figs. 3 and 4). The description of the latter's pictures in the text (p. 275) further indicates that the behavior is the "ecstatic." None of the writers already mentioned in this paper give any suggestion that the "ecstatic" occurs in the Gentoo Penguin. Roberts (1940a: 219) is the only one who indicates that it is not present.

In the remaining species it seems to be absent, for there is no suggestion of it in the work of Wilson (1907) or Gillespie (1932) for the King Penguin, or of Kearton (1930) or Murphy (1936) for the genus *Spheniscus*. Finally, it would be difficult to imagine birds of the genus *Eudyptula* performing it in the burrow.

I think enough has been said to make it clear that the "ecstatic" may be seen at any time when the birds come ashore in the spring till the end of the molt. Thus Roberts' statement (1940a: 219) that it is confined to the pre-laying period cannot be substantiated, especially in view of Falla's (1937: fig. 54) photograph which shows an incubating pair of Adélie Penguins performing the "ecstatic." In any case, it is my experience, as shown in this paper, that *very little penguin behavior is confined to any particular period.*

In summary, the "salute," "full trumpet," and the "ecstatic," as far as I can tell from my own field work and the photographs and descriptions of others, are not performed by all penguins. The "salute" appears to be used only in the Yellow-eyed Penguin. The "full trumpet" and allied forms are seen in all genera except

Eudyptula. The "ecstatic" is adopted only by the genus *Eudyptes,* the Adélie and the Ringed Penguins.

Habits of Aggression

Tête (fig. 20).—A bird may make a threatening pass as though to peck at the head of another, but the thrust rarely reaches the mark. The second bird replies with a similar peck and both finish up facing each other, with bills wide open and with tips almost touching. One or both may give one or more of these thrusts at the other with vocal accompaniments of the "open-yell" type before finally turning away, apparently no longer interested. Sometimes the flipper is used in conjunction with the "tête," but contact is rarely made.

This behavior with the occasional use of the flipper is the nearest approach to mutual outright fighting I have seen in the Yellow-eyed Penguin. As far as I can tell, stand-up fights, during which each opponent attacks the other, seem to be confined to the three species of *Pygoscelis,* and apparently have pair-formation value largely (Levick, 1915: 61-70, and others; Bagshawe, 1938: 203, 275).

The "tête" seems to be a common type of social aggression in all genera, except *Eudyptula* and *Spheniscus,* for which I can find no evidence but this may be due to a paucity of observation. Falla (1937: fig. 103) gives a good picture of two Royal Penguins "têting" when not at the nest, in circumstances typical of the Yellow-eyed Penguin. In penguins nesting in closely packed colonies, bickering involving the "tête" is common. Finally, as far as I can tell, the "tête" has social significance only.

Open-yell (fig. 10).—This action is commonly seen as aggressive behavior in the Yellow-eyed Penguin (Chapter II). It is used with social value and family value, and as a threat against predators, but does not appear to be employed with pair-formation value.

Sheepish Look (fig. 7).—As aggressive behavior, the only occasions when I have observed it, this type of behavior seemed a

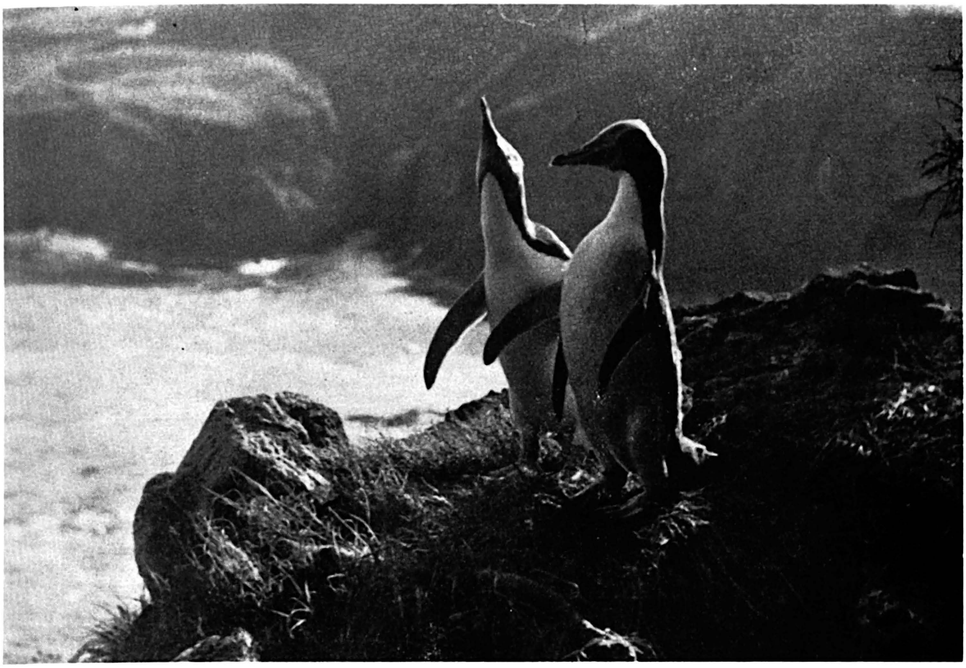

Fig. 5. Salute. Male Z12, on the left, has returned from fishing. He "salutes" female 115, which is 20 meters from the nest. The response is the "gawky" attitude. The chicks are 38 days old and are still being guarded.

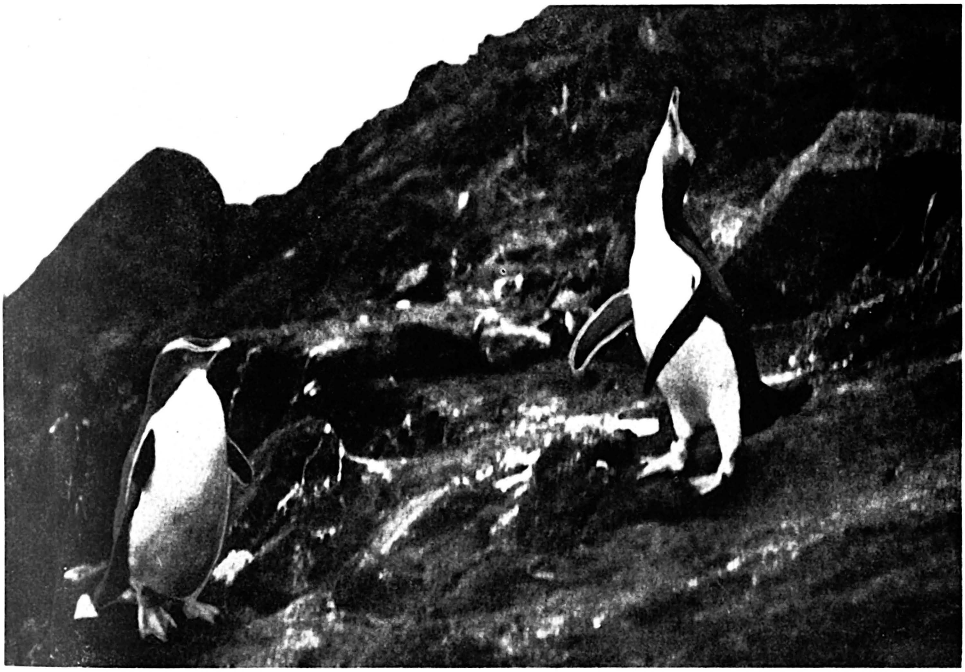

Fig. 6. Salute. Male 721, on the right, "salutes" female 70. This time he does not pass the bird "saluted" but stops in front.

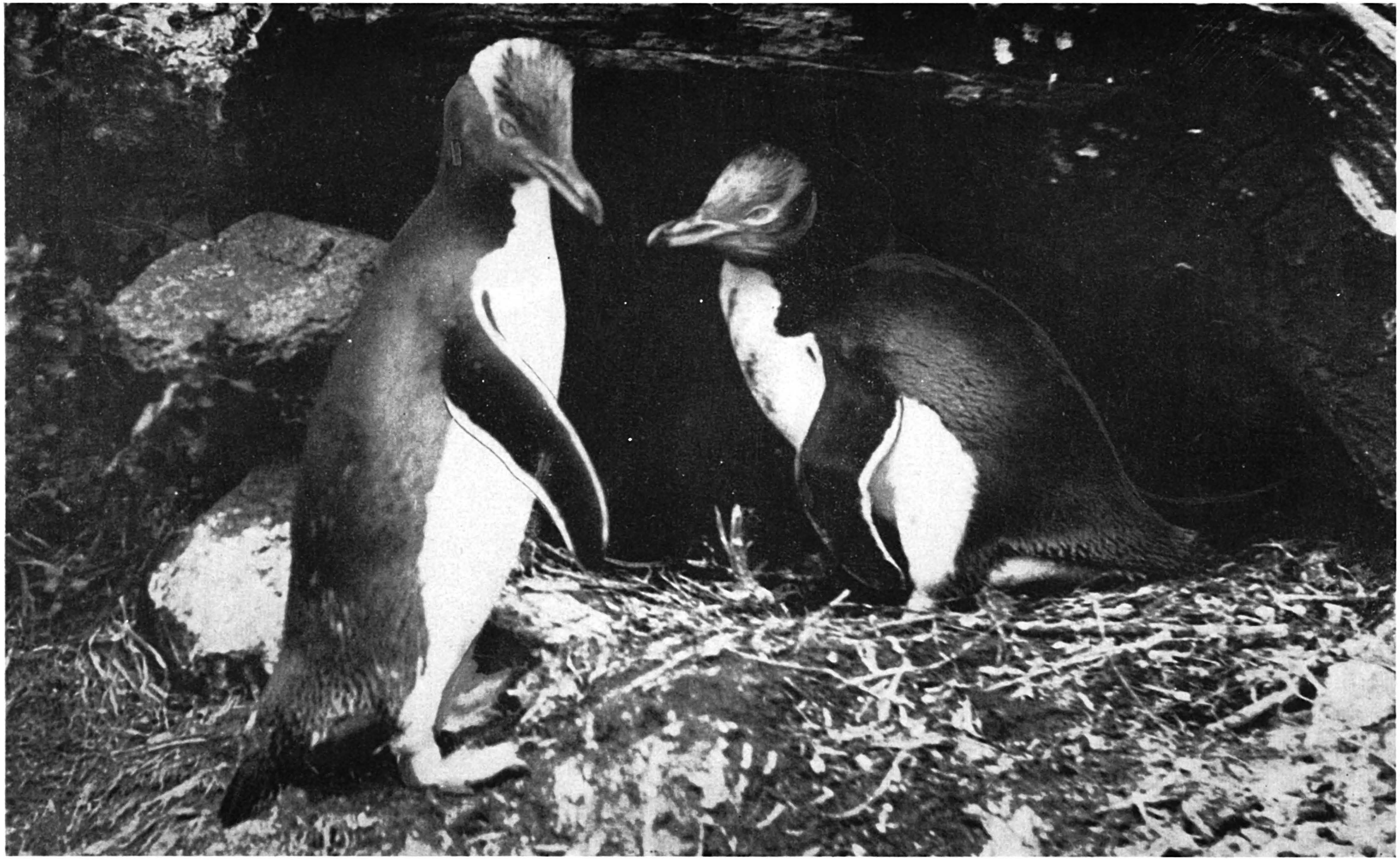

Fig. 7. Sheepish look. The male, performing the act, has just returned from the sea. The female is covering the chicks, eight days old.

threat following the use of the "glare," after an intruder in a trio had approached a little too closely to the pair (Chapter II). Under these circumstances, the "sheepish look" has pair-formation value.

Glare (fig. 21).—The position of the bird is exactly the same as that employed for the "open-yell," except that the bill is closed and pointed downwards towards the source of danger. The "glare" is used with pair-formation value and family value, and as a threat against predators, but does not seem to have social value. It is generally followed by the "open-yell" and, if need be, then by physical force. The "open-yell," however, does sometimes precede the "glare," more especially when the danger appears suddenly.

Physical Force.—This term implies the use of either bill or flipper, or both, in direct action. Physical force may follow the employment of any of the foregoing acts of aggression and is employed in activities of a social nature, against potential rivals, against potential penguin enemies, and against predators.

SUBSTITUTE ACTIVITIES*

"Substitute activities appear when the reaction evoked by external and internal stimuli is blocked, either by an antagonistic reaction, or by the lack of stimulation for the next reaction of the chain, or by exhaustion of the normal reaction" (Tinbergen, 1939a: 231).

This definition of substitute activities encompasses three categories (*op. cit.*: 225-228). In the first the animal is under the influence of two antagonistic drives, the simultaneous expression of which is a physical impossibility. For example, with the approach of a human being too close to the young there is an urge to flee and at the same time an urge to remain and protect its offspring. In many kinds of birds neither urge prevails, and preening takes place instead.

The second category occurs when an action in a chain is frustrated. This is seen in substitute feeding as part of the courtship

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*In his latest discussion of this subject, Tinbergen (1947: 56) has decided to use the term "displacement reaction" in preference to "substitute activity."

of the male Snow Bunting, *Plectrophenax nivalis subnivalis* (Brehm), when the female refuses copulation initiated by the male.

The third type follows upon the exhaustion of the normal reaction to stimuli. An example is of a Whitethroat, *Sylvia communis communis* Latham, which feigns injury when disturbed at the nest. It may repeat the action several times and then sit down somewhere and start to preen.

SUBSTITUTE ACTIVITIES IN THE YELLOW-EYED PENGUIN

In the Yellow-eyed Penguin, substitute activities resemble those just noted and, in addition, there seems to be a fourth category which will be discussed later. There are several types of behavior which occur as substitute activities in conjunction with love-habits and habits of aggression.

Preening.—Preening seems to be the commonest of all types of substitute activities. It is most prevalent in quiescent periods between those occasions when intense love-habits are performed by mated pairs and pairs "keeping company." After one penguin "salutes" another without eliciting a response, the initiator almost invariably proceeds to preen itself before making another attempt. Reference to Appendix I will indicate the frequency of preening after periods of activity much of which ended in frustration for the initiator.

In addition to the foregoing, there are cases of preening following aggressive behavior. For example, a bird may be disturbed by a potential rival, a potential penguin enemy, or a potential predator. After the appropriate aggressive reaction to the situation, this bird may perform the "sheepish look" and the "throb." Sometimes it may "half trumpet" or may even emit a "full trumpet." Following these it will preen itself. Including preening, all these love-habits which occur subsequent to the exhaustion of normal aggressive reactions appear to be substitute activity.

Fiddling with Nesting Material.—In the Yellow-eyed Penguin, this takes place either at the nest or nest site and, as far as I can tell, only at the pre-egg and incubation stages. This behavior may occur also in the winter months, but I have not had the chance to observe it. Nest sites certainly hold fresh material, including green vegetation, at this period.

Two sets of circumstances prevail when nesting material is handled as a substitute activity. In the first instance, there may be a single bird of either sex at the nest, on which occasion fiddling with nesting material is quite often accompanied by a little "shake." The latter action, which is also a substitute activity, is far more prevalent at the pre-egg stage than at the incubation stage. The second instance occurs at the pre-egg stage and possibly in the winter when both members of a pair are at the nest. The bird off the nest in quiescent periods may pick up and drop nesting material aimlessly and the bird on the nest may fiddle with sticks.

Sleeping.—After acts of aggression and the subsequent substitute activities following the intrusion of a human being, a bird may close its eyes either in a standing or a sitting position. Further, after a period of intense love-habit behavior between the female 70 and her three attendant males (Appendix I), the eyes would be closed. "Sleeping" will also occur at the conclusion of spasms of intense love-habits by two birds at a nest site.

Love-habits of Higher Emotional Valency than Preening.—An indication of the incidence of these, applicable to aggressive behavior, has been given above. Further evidence is supplied by the action of the mated pair Z12 and 115 after they had ousted the unemployed male 692 from their nest site (Chapter II). Their love-habits following these acts of aggression were far more intense than usual and would seem to have the significance of substitute activity. There was also comparable behavior by the female 65 after she had ejected the usurping female 73 from the side of her mate, which was occupying the nest (1941a: 272). This resort to love-habits, belonging to quite a different drive, after acts of aggression, would appear to be a method by which the birds adjust themselves to normal conditions.

These higher love-habits are also used as substitute activity other than subsequent to acts of aggression. Outstanding examples are the puzzling behavior of isolated unemployed males ashore, in the daytime, when other birds are breeding (Chapter VII), and the employment of the "full trumpet" on many occasions by breeding birds in the chick stage (Chapter IX).

A Fourth Category of Substitute Activities.—Observations on the behavior of the Yellow-eyed Penguin reveal what appears to be a fourth category of substitute activities not included in Tinbergen's definitions. When the chicks are at the post-guard stage and able to wander about freely away from the nest, the vigor of their pleadings for food, once the parent's supply is finished, becomes a source of embarrassment. On such occasions, the harassed adult will indulge in various love-habits which are often quite intense. Here the stimuli are set in motion by the pleadings of the chicks, and the parents, being unable to respond with food, perform what appears to be substitute activity.

This category is similar to Tinbergen's third one in which exhaustion of the normal reaction to stimuli produces substitute behavior. In this latter case the initiator performs the substitute behavior, but in my proposed new category it is the object of the action initiated.

Summary.—Substitute activities in the Yellow-eyed Penguin occur in several situations: (1) They may arise from two antagonistic drives as exemplified by a parent in charge of chicks. Torn between the desire to flee and the urge to safeguard the chicks, the parent does neither, but something else. Of course, there are some individuals which will not flee and which vigorously guard their young. (2) A substitute activity may result from a lack of stimulation for the reaction to be expected next in the usual sequence, as when a bird preens itself after failing to obtain a response to a "salute." (3) After the "welcome" ceremony and change of guard have been effected in the incubation period, the bird on the nest will fiddle with straw and sticks. The relieved bird may preen itself just outside the nest. These seem to be substitute activities caused by the exhaustion of normal reactions. (4) As previously noted regarding the chick's demand for food, a parent may be physically unable to respond to stimuli. This causes the adult to substitute another activity.

SUBSTITUTE ACTIVITIES IN OTHER SPECIES

In regard to the other species, there is not much published material concerning substitute activities, although they may be as common as in the Yellow-eyed Penguin.

A striking instance which comes to mind is the behavior of Levick's hooligan cocks (1914: 97), which were apparently unemployed, for it is difficult to believe that birds with family ties would act as they did. In the Yellow-eyed Penguin, the unemployed are law-abiding and commit no greater "sin" than forming the odd male of a trio. Apparently, the "hooligans" consist first of all of unmated birds and later of males that have lost their nests, if Levick's deductions are correct. It would seem, then, that, denied a natural outlet for their normal functions, a substitute is found in riotous behavior.

Gillespie (1932: 103) relates how two King Penguins changed guard and how the relieved bird came back once or twice before finally going off to the water. That seems like a case of substitute activity. Next comes Wilson's experience with the Emperor Penguin (1907: 11), in which he found that adults, even if unemployed, had to brood something even if it were an addled egg, a dead chick, or a lump of ice. Gillespie (1932: 101) believes there is a similar tendency in the King Penguin.

My own experience with the Erect-crested Penguin makes it manifest that substitute activity exists in this species. In between their extremely intense love-habits there were periods of "self-preening," "mutual-preening," and "kiss-preening." Whenever relieved from his position on the nest, whether an egg was present or not, the male would rush around and collect sticks, which he placed at the feet of the female. This occurred also in the period of molt and would seem to be a substitute activity (1941b: 49). Another interesting episode was the arrival of the female to find her place alongside her partner usurped by an intruder (*op. cit.*: 40). There was no apparent sign of recognition by the mated pair. The female began to preen herself and after a little while the male on the nest commenced to reach for sticks, adding them to the nest. It seems to me that both these actions should be considered as substitute activity, since the mated pair could not perform the normal "welcome" ceremony.

DISCUSSION OF SUBSTITUTE ACTIVITIES

Tinbergen (1939a: 225-228) in discussing the origin and function of substitute activities indicates that they are of wide occurrence in birds and other animals. Nice (1943: 155-156) has noted the behavior in the Song Sparrow, *Melospiza melodia euphonia* Wetmore, and points out (*op. cit.*: 214) that it occurs in the Black-headed Gull, *Larus ridibundus ridibundus* Linnaeus, when a mate refuses to leave the nest after incubation has commenced, resulting in the disappointed partner's bringing a further supply of nesting material. Palmer (1941: 80-83) describes preening, playing with nesting material, scrape-making, and courting behavior under certain conditions in the Common Tern, *Sterna hirundo hirundo* Linnaeus, as substitute activities. Lack (1939b: 188 and 1943: 32) gives examples in the English Robin, *Erithacus rubecula melophilus* Hartert, and Hochbaum (1944: 20) in ducks (Anatidae). Makkink (1936: 26-28 and 1942: 35-40) indicates that, in the Avocet, *Recurvirostra avosetta* Linnaeus, and the Oyster-catcher, *Haematopus ostralegeus* Linnaeus, respectively, pseudo-sleeping, which occurs after aggressive behavior, is probably a substitute activity. Rand (1943: 167-170), after relating instances in several North American birds, suggests that these activities be called "irrelevant behavior."

Finally, two papers dealing with substitute activities, one each by Kortlandt and Tinbergen, are reviewed by the latter (1946: 259-260). It is concluded that "the 'sparking over' activities result when an internal drive is blocked, yet forces the animal to do something. This block may have different causes; it apparently has to express its drives in movements once the former are activated."

In the Royal Albatross* I believe that the male, which is ashore at the pre-egg stage far more frequently than the female, is there because of a coitional urge. In other words, he is waiting for the female. Some of these males build nests of an excellent quality soon after arrival. There is no real need for them to do so, for the female can and does, if need be, build the nest by herself a few hours before the egg is laid. To me, the male's nest-building is a substitute activity. A further instance concerning the Royal Albatross occurs just after change of guard whether egg or chick is present. The relieved bird will sit down only a foot away, pluck grass, and place it around itself as if on the nest.

My suggested fourth category of substitute activities probably occurs in all petrels at the post-guard stage. For example, in the Royal Albatross, the chick will sometimes vehemently plead for further food when the parent's stock has been exhausted. At this point the adult may perform one or more types of love-habits and may even proceed to "mouth" its offspring. In the Diving Petrel, *Pelecanoides urinatrix* (Gmelin), after I had watched a chick being fed (1943a: 39),† the parent retired and then returned to nibble the chick. Judging by their prolonged cries the chicks of the Sooty Shearwater, *Puffinus griseus* (Gmelin), persistently harass their parents after having been fed, but I was never successful in observing the reaction of the adult. As soon as the electric torch was switched on, the parent bird reverted to ordinary behavior, but I could see the chick still in its beseeching attitude.

It would seem that in birds which feed their young at long intervals, chicks at the post-guard stage subsequent to feeding may be the cause of substitute activity. This does not apply, however, in

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*Facts mentioned in this and subsequent chapters relative to the Royal Albatross and unaccompanied by a reference, may be found more fully described in a recent monograph.

†As I shall be frequently referring to my published petrel papers, 1939, 1942a, 1942b, 1943a, 1943b, 1944a, 1944b, 1944c, 1945b, and 1945c, only the year and page number will be given.

the Bronze Cormorant, *Phalacrocorax chalconotus* (Gray), and the Stewart Island Cormorant, *Phalacrocorax huttoni* Buller, which I have watched. The young, especially when almost fully fledged, are so fiercely persistent in the way they half fly and half run after their parents that the latter necessarily feed hurriedly and immediately take refuge in flight. Thus the occasion for the substitute activity previously discussed does not arise.

In conclusion, it appears that when "circumstances prevent an activated drive from discharging itself into the adequate instinctive actions" (Tinbergen, 1942: 80), release from the situation is afforded by substitute activities which belong to quite another drive. This is true of penguins, albatrosses, and other petrels in the same way as indicated by several other investigators in their own particular fields.

SUMMARY

Love-habits are classified according to three values—social, pair-formation, and family. The first type occurs among all birds irrespective of age or sex; the second concerns adults only, engaged in forming a potential mated pair; and the third takes place only within the family group. Fourteen types of love-habits are described: (1) The "salute" seems to occur only in the Yellow-eyed Penguin. (2) The "sheepish look," "throb," "shake," "excited shake," "open-yell," and "half trumpet" are probably peculiar to the Yellow-eyed Penguin but, at the same time, there seems no doubt that a comparable set of actions obtains in other penguins. (3) The form of "welcome" described is referable to the Yellow-eyed Penguin only, but doubtless all species have a "welcome" ceremony, which will be the same in function but different in form. (4) The "full trumpet" is adopted by all penguins except perhaps the genus *Eudyptula.* (5) The "arms act" probably occurs in all species. (6) "Mutual-preen" and "kiss-preen" are minor love-habits applicable to all species. (7) True "bowing" occurs only in the King, Emperor, and Gentoo Penguins. (8) The "ecstatic" is employed by all species of *Eudyptes,* and also by the Adélie and Ringed Penguins. Habits of aggression are divided into five groups—those with social value which occur among all birds irrespective of age or sex, those with pair-formation value which are confined largely to trios, those with family value which are directed against potential penguin enemies when eggs or young are being cared for, those against predators which may be employed at all times by all birds, and those relative to true "warning," which is not found in penguins. Five habits of aggression are described: (1) The "tête" and "physical force" occur in at least several of the other species. (2) The "open-yell," "sheepish look," and "glare" are confined to the Yellow-eyed Penguin. Substitute activities as defined by Tinbergen are examined in penguins and are found to exist in the same way as he found for other species. In addition, there is suggested a fourth class; as, for instance, when a parent penguin is unable to respond to the pleadings of chicks for food, it does something else instead. Finally, the application of substitute activities to petrels and cormorants is investigated.

Chapter III

Pair-Formation

Pair-formation in the Yellow-eyed Penguin in winter months, in pre-egg stage, in molt, in breeding season prior to mating. In other species. Allied behavior in pair-formation, including affinity, divorce, flirtation, period of receptivity, sex recognition, function of head feathers. Discussion. Summary.

Before beginning the discussion of the difficult subject of "courtship" in the Yellow-eyed Penguin, I should like to quote Huxley's note (1914:491) which appears in his classic paper, "The Courtship Habits of the Great Crested Grebe (*Podiceps cristatus*)": ". . . the word *Courtship* is perhaps misleading as applied to the incidents here recorded. While Courtship should, strictly speaking, denote only *ante-nuptial* behavior, it may readily be extended to include any behavior, by which an organism of one sex seeks to 'win over' one of the opposite sex. It will be seen that the behavior of the Grebe cannot be included under this. 'Love-habits' would be a better term in some ways; for the present, however, it is sufficient to point out the inadequacy of the present biological terminology."

A discussion of "courtship" behavior in the Yellow-eyed Penguin is subject to the limitations noted by Huxley. "Courtship" in the human species takes place prior to marriage and is preparatory to that state, but the so-called "courtship" in birds frequently involves actions which occur in both mated and unmated individuals. Moreover, they may be noted at all times of the year and are not necessarily confined to behavior preparatory to pair-formation, copulation, or ovulation. This is true of such birds as penguins and petrels, hence the desirability of adopting some such terminology as suggested by Huxley. The term "love-habits" will be used as defined in Chapter I.

The term "display" as employed by others when referring to penguins is apparently synonymous with love-habits. The word seems better reserved for describing the behavior of such birds as the Peacock, *Pavo cristatus* Linnaeus, or the Birds of Paradise (*Paradiseidae*), the conspicuous plumage of which is very noticeable during a ceremony. To my mind "display" denotes a preconceived idea which some authors, mainly those who write about bird display in general, have tried to fit into the behavior of penguins.

PAIR-FORMATION IN THE YELLOW-EYED PENGUIN

In the Yellow-eyed Penguin there is evidence that, at almost any time of the year, pairs are formed, which subsequently lead to the rearing of families. This may occur in the winter months; it may be a hurried affair at the pre-egg stage, after the birds have begun to stay ashore in the daytime; it may begin in the period of molt; or it may commence in the breeding season for other birds, but with the participants not actually breeding until the succeeding season.

Pair-formation in Winter.—A considerable number of newly mated pairs are formed in the winter months. Occasionally, members of a mated pair fail to return in the molting period, but the majority that disappear do so in the winter. Others again separate by divorce, so that the deserted member of the mated pair then has to find a new mate. A female has little difficulty, but the problem is not so simple for the male. In addition to mated males, there are always a number of unmated males of breeding age which contest the situation with the former. All these males, which are in excess of females, are on pair-formation missions in the winter.

The situation is still further complicated by a number of young birds, preponderantly males, reaching breeding age. In all cases noted in my records, these young birds of either sex, whether mated to older birds or to those of their own age, have been discovered already mated at the beginning of the pre-egg stage. The fact remains that, at the end of August, the beginning of the pre-egg stage, most of the females, whether they have bred before or not, are already mated.

The following examples supply corroborative evidence of the foregoing statements. In the "drama" of the female 70, and the three males (Appendix I), I was in possession of certain facts concerning the past history of each bird. I feel certain that 70, during those winter months of 1939, was interested in the whole affair, although she frequently appeared indifferent. But were the three male rivals on an equal footing, or was 61 securely mated to 70 all the time? In spite of appearances I am inclined to think that the latter was the case. At some time in the winter of 1937, birds 70 and 721 mated when their partners of 1936-37 did not return. When both happened to be on shore on the same day that winter, they always spent the night together on the site where their nest was ultimately built, and this site was in a different place from either one of those that these birds had occupied in 1936-37. Yet, in 1938-39, on the dissolution of their partnership, each returned to its first nest with a new mate which was secured during the winter of 1938.

Further examples of winter pair-formation concern the male 37 on two occasions and the male 14 on one (Appendix IV), the mating of Z12 and 115 (1941a: 275), and, finally, the mating of Z14 and Z18 (Chapter III).

Pair-formation in the Pre-egg Stage.—When the pre-egg stage arrives, the great majority of the males which are observed ashore alone and which eventually breed already have mates. They are not ashore in the expectation that a congenial partner will fortuitously turn up and appropriate them.

This is exemplified by the following case: In the early part of the shore period in the spring of the seasons of 1938-39 and 1939-40, the male 39 was found alone whenever I visited the colony in the daytime. An observer unacquainted with the previous history of this bird probably would have concluded that 39 was waiting to be found by a female, whereas we know that 39 and 2 were mated both before and after the two seasons under consideration. Judging from the evidence which I have, concerning this and other mated pairs, the female 2 must have spent some nights with 39, and probably an odd day when I was not in the colony. Further, I have plenty of evidence to substantiate the fact that the behavior of 39 and 2 was not peculiar to them alone.

It will be realized, therefore, from the evidence just given and more to follow that at the beginning of the pre-egg stage most of the breeding pairs are already formed. Of the 292 matings over the ten-year period only seven, to my knowledge, were effected at the pre-egg stage. Three of these, even, were doubtful and a fourth was most unusual.

Examples are as follows: It will be noted in Appendix V that on 29 August 1940, birds 72 and 75 were apparently mated, but that when I returned to the colony on 14 September, bird 65 had secured 72. This was the first occasion on which I had seen a partnership dissolved after the penguins had begun to stay ashore during the day at the end of August. It is just possible, however, that this was an instance of "flirtation" by 75, which had lost her mate many months earlier.

A second case occurred in 1941-42. Birds Z13 and Z15 had reared two chicks together in the 1940-41 season. On 21 September 1941, I visited Colony Z at 10 a.m. for the first time that season and found Z13 and Z15 together at a good nest many meters from the old one. Seven days later the male 102, which had been unemployed the previous year, and Z15 were together at a totally different part of the colony. On 5 October bird 102 was sitting on a normal egg, and on an abnormal one which measured 44 x 38.5 mm. and weighed 38 grams. This egg was the smallest I have ever seen, and the smallness may have had something to do with this extraordinarily sudden change of partnership. It is worthy of note, too, that the small egg was the first one laid (fig. 22 and 1946: pl. 19).

In the case of the two females 18 and 29 (Appendices II and III) there is a strong probability that each acquired her new mate at the beginning of the pre-egg stage. Finally, it is even more probable that the mating of the male 28 and the female 25 (Appendix IV) was a hurried affair.

In the tenth year of study a very definite example of pair-formation during the pre-egg stage occurred, but, owing to my movements, was probably abnormal. The incident, however, does show that the formation of pairs takes place in the pre-egg stage. It should be remembered, though, that the foundation of the new alliance, about to be described, may have been built at an earlier period. In other words, there may have been an affinity between the two penguins concerned. Certainly, each member of the newly mated pair was known to the other before the week in which they mated.

This is an account of the events leading to this unusual realignment of individuals. At the western end of the biggest colony a track leads to a side colony more than two hundred meters distant. This area is quite distinct, but birds inhabiting it and the end of the main colony leave the beach at the same point and, therefore, meet each other sooner or later.

On 30 August 1945 the male 932 and the female B41 were together at a nest in the side colony where they had been mated for the two previous seasons. I weighed both of them and, like many other mated pairs that had been similarly treated, they apparently were undismayed. On 3 September the male A10 was alone at his nest in the western end of the main colony where he had nested with the female 944 in the previous year—both were then two years old and the eggs did not hatch. That day there was no sign of 932 and B41. On 9 and 15 September A10 and 944 were together and 932 and B41 were again absent.

Now, at 11 a.m. on 22 September, the female B41 was found on a scoop without nesting material in a second side colony half a mile away at the opposite end of the bay. On reaching the first side colony, I found 932 and 944 together at B41's old nest indulging in vigorous love-habits. There was no evidence of the displaced A10. On 29 September there was an egg in the scoop at the second side colony, presumably laid by B41; no other female, to my knowledge, was available that could have laid it. In the first side colony 932 was on a single egg laid fully two days earlier.

Subsequently it was found that 944 was mated to 932, that only one egg was laid, and that it failed to hatch. Female B41 remained unmated in her newly found colony and laid no second egg in her scoop. Not until 19 October was A10 seen again. It is highly significant that he was found not in the western end of the main colony, but under a gorse bush some 40 meters from 932 and 944. His excreta were yellow, indicating that he had been ashore since the previous day at least. My long experience with penguins signifies plainly the reason for this. I doubt that A10, on 19 October not quite three years old, had ever been in this side colony before, and he was not there by accident. He had met 944 at the landing and had followed her along the track towards her new home, where he had been ejected by 932. Further, he had not deserted 944.

My deductions from the evidence are that B41 abandoned her colony, leaving 932 unemployed. The latter met 944 on the landing ground and some time within the short period of seven days managed to entice her to his nest and form a mated pair.

Pair-formation in Period of Molt.—There are sufficient examples of mating having taken place in the period of molt to prove that it is a normal occurrence. A number of parents disappear, probably because death has intervened, in the short interval between the time when the chicks enter the water and the time of appearance of the adults ashore for the molt, so that the surviving birds may quickly become involved in pair-formation activities. Further, divorce may occur and be followed by the mating of one partner with a third bird.

Instances of pair-formation in the period of molt are the following: The movements of the males 721 and 60, and the female 676, were known up to the incubation period (Appendix I). Subsequent movements are less well known but, at the end of the season, 60 and 676 molted together in a sub-colony and eventually mated, rearing chicks in the three succeeding seasons. It is just

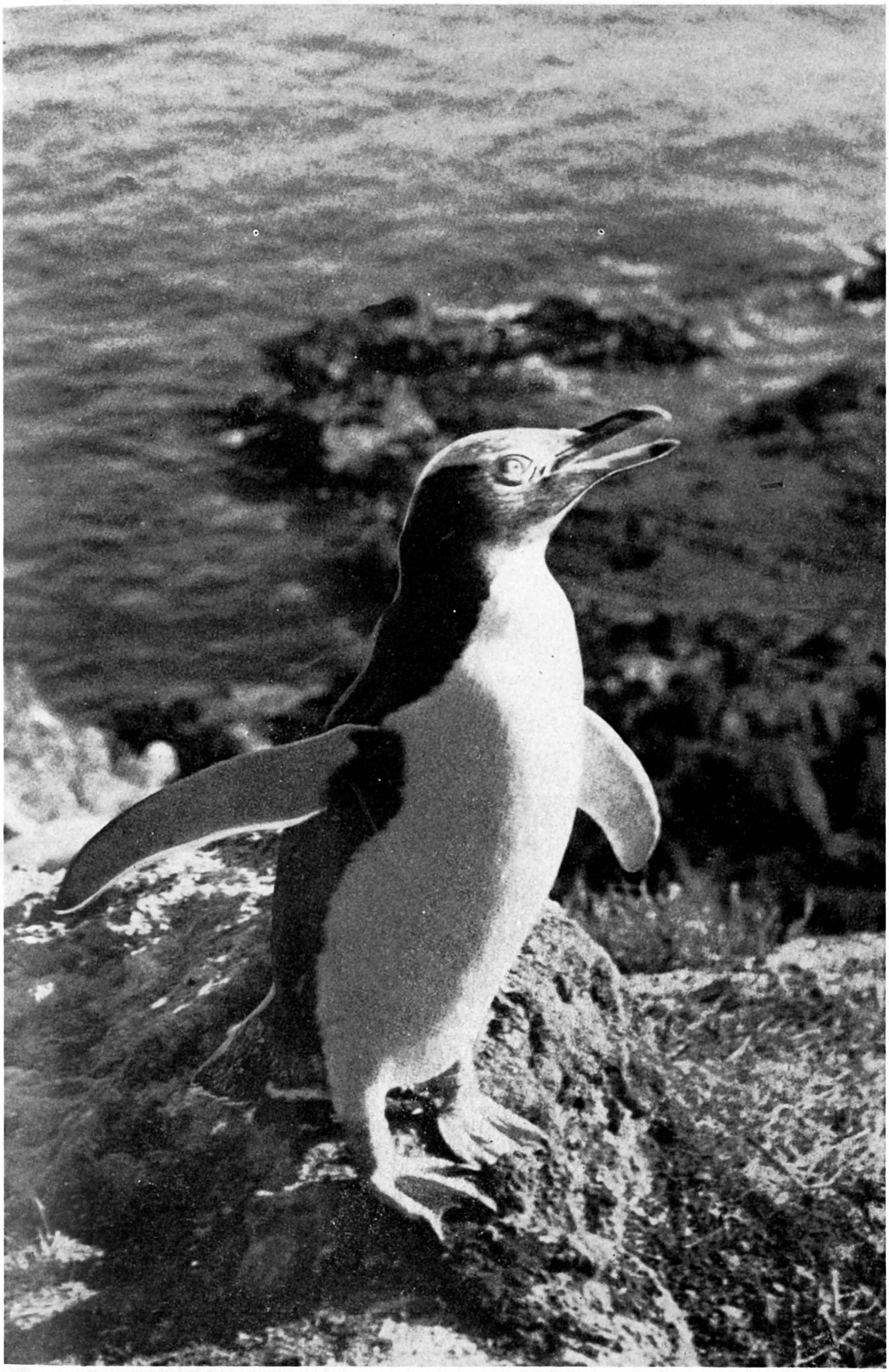

Fig. 8. Throb. Male Z12 "throbs." The chicks, 66 days old, have just been fed.

Fig. 9. (at left) Shake. Male Z12 "shakes" when he sees female 115 feed the chicks, which are 49 days old.

Fig. 10. (below) Open-yell. In this case the action is a love-habit forming part of the "welcome" ceremony.

possible that these birds may have mated a little before they molted.

A good example is that of the old female 4 and the young three-year-old male 52, which molted together in 1939, near the female's nest, where she had just reared chicks. In 1939-40 they mated and reared a family and were still together in 1943-44. The female's former mate had disappeared. But the best case of all—the one which I was able to follow with the least possibility of error—is that of the female 73 and the male 72 (Chapter III and Appendix V).

Pair-formation in the Breeding Season Prior to Mating.—When the breeding season arrives and until the chicks have entered the water, breeding birds appear to remain faithful to their domestic duties, as exemplified by the behavior of Z12 and 115 (Chapter IX). Probably, however, acquaintances are formed at this period which result in a future mated pair; the affair between the male 72 and the female 73 (Chapter III and Appendix V) furnishes evidence in support of this view.

Behavior resulting in the formation of pairs, however, does definitely take place in the breeding season, when the chief actors are not the breeding birds but the unemployed members of the community. These birds arrange themselves in pairs; some arrangements endure only a few days, others last several weeks, and still others last the whole season with both birds molting together. A part of this last group will actually become mated and will breed in the subsequent season. Up to the eighth year of study I had no record of such efforts resulting in a mated pair. Subsequently, however, there were three cases (Chapter VII), which clearly establish the fact that when two birds favorably disposed towards each other "keep company" their love-habits have pair-formation significance even if the birds do not mate.

When mated birds are tending eggs or young they usually do not participate in the more serious love-habits outside the family group. Such behavior is usually restricted to the unemployed section of the community. The latter section, therefore, forms a good medium through which to watch the protracted behavior that ultimately leads to the formation of a mated pair. Apparently, a breeding urge keeps these unemployed penguins ashore in the daytime—though they are not ashore every day—in the incubation stage and well into the chick period. Much of their activity may take place at a camp site in the evenings after they return from the sea. From approximately the middle of the chick period many of the pairs break up, with only a few of the more serious ones continuing.

Two examples of this phenomenon of "keeping company" in the breeding season follow. The first is a continuation of the story of the two males 1 and 20, and the female 18 in the winter of 1939 (Appendix II). After failing to mate with 18, bird 20, on 22 September and 26 September 1939, was observed close to the mated pair, 1 and 18, but by 4 October and thereafter he was inhabiting another part of the colony altogether. The proximity of the unmated 20 to the newly mated pair clearly indicated that bird 1 had supplanted bird 20 and that he had become the odd member of a trio.

In September 1940, that is to say in the next breeding season, male 20 appeared to be mated with the two-year-old female 636, but although a good nest was made, and occupied by both birds at the pre-egg stage and for a time after eggs had been laid by other birds, 636 produced none. It is significant that this nest was only sixty meters from birds 1 and 18. Birds 20 and 636 molted together in February 1941. I worked an entire day in the colony when these two were together at this period. At irregular intervals, they indulged in all the love-habits except the "welcome" and "full trumpet." Obviously, they had been "keeping company" the entire season. I fully expected this pair to mate in September 1941, but when the time came 636 was found mated to 15, at a sub-colony a half mile away. Bird 20 was again left unmated.

In September 1942, after being unemployed for three years and remaining in the neighborhood of 18, male 20 at last mated with 18. The rôles were reversed; it was now the turn of male 1 to become unemployed and the odd member of a trio. As the latter was discovered loitering near 20 and 18 on September 11 and September 19, it was obvious that he had not deserted 18.

On 3 October, after other birds had commenced incubation, I found male 1 and the two-year-old 940 indulging in love-habits. They had not built a nest. A young three-year-old, B46, which persisted in taking up a position too close to the pair, was frequently pecked to a safer distance by 1, whose "property rights"* were being infringed. This pair did not succeed in mating.

For the three years beginning in 1942, male 1 was not far away from the mated pair 20 and 18. In the period of molt in 1945, male 20 died. In the following spring, bird 1 again mated with his former partner 18 close to their old nest site.

The second example is a unique set of happenings observed in the tenth year of study and is given in Table 1.

In Table 1 the period involved is that from the time when the earliest eggs were being laid to the time when the earliest chicks

TABLE 1

Pair-formation Behavior of a Group of Eight Unemployed Penguins

Date	Camp site	♂	♀
Sept. 16	A1	980	976
Oct. 14	A1	961	T34
	A2	980	K14
Oct. 21	A1	961	976
	A2	980	K14
Nov. 18	B1	979	K14
Nov. 25	A3	961	B52
Nov. 30	B1	979	K14
	B2	M24	976
Dec. 7	B1	979	K14
	B2	M24	976
Dec. 14	A2	961	B52

Age of birds:

Two-year-olds: ♀♀ 976, T34, K14, ♂ 980
Three-year-olds: ♀ B52, ♂♂ 961, 979
Four-year-old: ♂ M24

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*The term "property rights" is defined in Chapter VI.

were being left unguarded. Weekly observations began on 16 September and ceased on 26 December. The intervening dates when no birds were present are not given and, judging by the amount of excreta at the camp sites, there were birds ashore during my absence. Two sub-colonies (A and B), approximately three-quarters of a mile apart, and reached by the same channel of water, are involved. To date not one of the eight birds has bred. Bird B52 in the previous year "kept company" with bird 892, which is known to be a male, so that B52 is probably a female. Being cognizant of the sex of B52, we, therefore, know the sex of the other seven.*

Table 1 shows plainly how unstable pair-formation is among unemployed birds which "keep company." The male 961 had three partners in six weeks, and the female 976 had three in nearly eleven weeks. Two of the females, K14 and 976, were lost to the males of Colony A because they shifted to Colony B. This also indicates that they were not very strongly attached to the males with which they were "keeping company," and, further, that a male does not follow a female to another colony but is dependent on her returning to him if the pairing continues. An idea is gained, too, of the way in which any given individual meets a number of other penguins, and it should be remembered that there were breeding birds in these sub-colonies which probably became acquainted with many of the unemployed members.

In conclusion, it would seem that a considerable amount of "flirtation" occurs, especially among the unemployed, before a mated pair is formed. Moreover, it will be surprising if any of the pairs seen on 7 December and 14 December are maintained till the following breeding season.

A further case of pair-formation cannot conveniently be placed under any of the four previous headings, but is of considerable interest in connection with pair-formation in penguins. It concerns

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*In the seasons 1946-47 and 1947-48, six of these young birds were mated to other birds not named in Table 1 and in circumstances which made determination of their sex definite. All were correctly determined in 1945-46.

the male 692, which I had known for seven seasons—from 17 November 1938—and which in all that time had not been mated. In that period several other males were unmated, but each had been mated at least twice. For some reason 692 had not mated, although, in each season, he had built an exceptionally good nest for a penguin. On several occasions I saw him spend a considerable amount of time in the company of other unemployed males. On another occasion he made advances to the female 115, which had two chicks (Chapter II). At last at 10 a.m. on 3 April 1943, I discovered him indulging in love-habits with Z18, a young female only two weeks past her first molt; Z18 was responding with "sheepish looks." When I next visited the colony in the succeeding September, Z18 was mated to Z14. Two eggs were laid which later proved infertile, the usual fate of eggs laid by two-year-old females. Bird 692 remained unmated.

On 7 March 1943, Z14, which had been unemployed all that season, was at the western end of the colony and had never been seen at the eastern end near the nest of 692. In November 1942, Z18 was banded near the nest of 692. All three would leave the water at the same spot and ascend a common track before branching off to their respective camping sites. Up until 3 April 1943, at least, Z18 went in the direction of 692. At some time in the winter, Z18 and Z14 formed an attachment and began "keeping company"; Z18 was taken to the area of Z14, which was new to her, and she subsequently nested there. The initial stages of this "keeping company" state-of-affairs occurred either on the landing ground or on the common track, or on both. Bird 692 was probably present once or twice, but possibly the process of "getting acquainted" and "feeling well-disposed towards each other" occurred in his absence. No doubt on one of these occasions Z18 was persuaded to ascend the strange branch track. Following these events, the more intense love-habits probably took place and Z18 probably continued to ascend this track when she landed alone. Thus it will be seen that the formation of this mated pair was definitely begun in the winter.

PAIR-FORMATION IN OTHER SPECIES

There is little information available concerning pair-formation in other species of penguins. Most of the information which is available refers to migratory species from the time when they come ashore after the winter sojourn at sea, and the beginning of egg-laying. My own experience with these species is also limited, being confined to the behavior of a trio of Erect-crested Penguins and to some observations on the Little Blue Penguin.

Pair-formation in the Winter Months.—The majority of the remaining sixteen species of penguins spend the winter at sea, a circumstance which makes it almost impossible to gather direct information at that season. In regard to the resident species, little has been noted, although I judge that their behavior closely resembles that of the Yellow-eyed Penguin. My own observations (1940: 182-184) on the Little Blue Penguin indicate that behavior resulting from its love-habits occurs in winter; and that probably, therefore, pair-formation also occurs in that season.

In the period of time spent at sea, I do not think behavior occurs which leads to pair-formation, either in the sedentary or migratory species. I have watched banded penguins land many hundreds of times, and only rarely have I seen two birds, known to be mated, land together, either when feeding chicks or in the winter or in the pre-egg stage. When landing has coincided, close watching has indicated that members of a mated pair have met by chance just off the beach. Similarly, in regard to the Gentoo and the Ringed Penguins, Bagshawe (1938: 231, 250, 283) has proved definitely that members of a pair in either of these species do not fish together, for the members of a pair return to the nesting sites at different times.

In reference to the Adélie Penguin, Murray (1909: 249) states "there is good reason to suppose that the pairing is done before the birds leave the sea," but he does not give his reasons. Nimmis (Falla, 1937: 39) thinks that the Emperor Penguin was invariably found in couples, not only in the period of molt, but in the winter as well, but no evidence is given of his knowledge of the sex of the birds. It should be remembered that the Yellow-eyed Penguin is "fond of company" irrespective of sex and age so that it would be justifiable to assume that the Emperor Penguin is similarly disposed.

In summary, little is known about pair-formation in the winter months, in both the migratory and sedentary species of penguins, other than the Yellow-eyed Penguin.

Pair-formation in the Pre-egg Stage.—Most writers who have discussed pair-formation think that it is effected in the migratory species after the birds return from their migration, and before the eggs are laid. For example, Levick (1914: 32) remarks, "There is no evidence that any pairing had taken place on or before the march, and the birds had all the appearance of being quite independent." Murphy (1936: 376) states that in the Gentoo Penguin, "Pairing does not take place during migration but only after the selection of nesting territory." In the northern part of its range, the Gentoo Penguin is a sedentary species; possibly it forms mated pairs in the same way as the Yellow-eyed Penguin does in the winter. Roberts (1940a: 200), who holds the same view as Murphy, records that when the Gentoo Penguin comes ashore at the beginning of the season "there is nothing in their behaviour at this time to suggest that they are already formed into pairs," and goes on to say that it is not long before pairs begin to appear. On page 204 he notes further that "none of the family Pygoscelidae arrive at their colonies already paired." Bagshawe, however, records the opposite opinion (1938: 226, 229, 287) and thinks that both the Gentoo and Ringed Penguins arrive at the rookeries already mated.

I think that if large numbers of mated pairs of some migratory species are banded and examined in the succeeding season, many will be found to be mated to the same partner in each of the two seasons. I am of the opinion, like Bagshawe, that the migratory species arrive mated, although the two members of a mated pair may not necessarily arrive at the nesting ground on the same day. Thus, although out of touch in the winter, they are nevertheless mated. I base my opinions on the behavior of a mated pair of Erect-crested Penguins (1941b: 35-36). These birds returned to a given spot, their old nest, not together, but seven days apart, the female first.

If the two members of a mated pair do not consort together at sea, it follows that individuals of mated pairs of migratory penguins are unlikely to arrive at their breeding area at the same time. This would explain why, when migratory penguins first reach their nesting grounds, observers fail to note any behavior indicating that the penguins are in pairs. Nevertheless, if the literature is examined carefully, it will reveal evidence that some birds are already mated before arrival (see Chapter VI). It also seems to me that the nesting site is the rendezvous and has the function of acting as a bond to keep the mated pairs together.

The foregoing is referable to birds which return and remate. In addition, others will return which have lost their partners through death and still others possibly through divorce. This means that new alliances will be finalized at the pre-egg stage. As, in all probability, once penguins have passed the wandering stage of youth there is a tendency to inhabit a restricted part of a colony, the factors of affinity and previous acquaintance would have a bearing on many new alliances. If so, pair-formation would not be a sudden affair.

Besides the old breeding birds, there will be present in any colony also a number of young birds ready to breed for the first time. Among these, pairs may be formed, although not necessarily, without the influence of any previous factors. Young birds appear to take up residence in a colony as the result of following older residents to a particular area. There they associate and become acquainted with the other residents and perform love-habits with them, probably in the first place only with social value, but sooner or later love-habits with pair-formation significance will occur. All this sequence of events need not necessarily take place in one short pre-egg period. It is quite possible, as in the Yellow-eyed Penguin, that preliminaries are commenced at least one season earlier and that these young birds return to their newly found residence after the winter.

The foregoing manner of pair-formation is known to take place in the Yellow-eyed Penguin (earlier in Chapter III), but for the other species of penguins there is actually insufficient evidence to make certain how pairs are formed. Concerning these other species, statements and inferences in the literature that mated pairs are formed suddenly at the pre-egg stage are actually only assumptions. To clarify these important points, observations on banded birds are sorely needed.

Pair-formation in Period of Molt.—Any information regarding pair-formation in the period of molt in species of penguins other than the Yellow-eyed Penguin is of a very slender nature. My data (1941b: 34-35) on the Erect-crested Penguin, those of Bagshawe (1938: 279) for the Ringed Penguin, and of Kearton (1930: 94) for the African Penguin, suggest that the formation of pairs may commence in this period of molt.

Pair-formation in the Breeding Season prior to Mating.—In the literature there are some observations which suggest that birds not breeding begin pair-formation when other birds are breeding. These unemployed birds are at least "keeping company," but there is no direct evidence that they eventually mate in the succeeding breeding season.

Falla (1937: 50) notes that on 4 December 1930 at Macquarie Island, a few pairs of King Penguins, towards the outskirts of the rookery, "were still engaged in courtship." Possibly some of these pairs remained unemployed and behaved subsequently as does the Yellow-eyed Penguin. In regard to the Adélie Penguin at Cape Denison on 5 January 1931 he was puzzled (*op. cit.*: 77) by "the aimless behaviour of five pairs of penguins occupying empty scoops" when other birds had chicks at least two weeks old. From time to time these unemployed pairs indulged in self-exhausting displays of love-habit behavior, including the "full trumpet" and the "ecstatic." Falla judged that all this behavior was abnormal, but in the light of similar behavior by unemployed pairs of Yellow-eyed Penguins at the same stage of the breeding cycle, I do not think his judgment is tenable. Really the unemployed Adélie Penguins were acting normally, even supposing some of them had lost eggs or chicks. A careful perusal of Falla's remarks (*op. cit.*: 91 *et seq.*) about the Rockhopper Penguin indicates that in this species unemployed birds "keep company" in the breeding season and possibly begin forming pairs. A similar state of affairs is recorded in the life histories of individual pairs of Gentoo and Ringed Penguins as noted by Bagshawe (1938: 249 *et seq.*).

In regard to the species which have come within the scope of my own field work, I have found fresh green leaves pulled into burrows, empty at the time of observation, and unemployed pairs of the Little Blue Penguin present during the day, when other birds are breeding. All this indicates a state of "keeping company" and is circumstantial evidence that pairs might be forming. My work on the mated pair of Erect-crested Penguins that had lost their egg also focuses attention on the possible behavior of unemployed pairs in the process of mating.

ALLIED BEHAVIOR IN PAIR-FORMATION

Pair-formation in penguins is associated with interrelationships of the various members of a penguin community, irrespective of their matrimonial status. These interrelationships have a definite influence on the formation of mated pairs and pairs which "keep company." Therefore observers, working on individual birds of whose previous history they know nothing, draw erroneous conclusions when—as frequently is the case—they infer that the beginning and the end of pair-formation are taking place while they happen to be watching. Many of the observations on alleged pair-formation have been made on penguins already mated.

Affinity.—Two instances are known to me in which a penguin several seasons before it managed to mate with the object of its desire, showed a distinct preference for another bird already mated. One instance concerns a female and the other a male, and each occupied the previous nesting site of the newly acquired mate.

The first instance was the affinity shown by the female 73 for the male 72, when the latter was mated to the female 65. As far back as 25 September 1939, I found 73 with 72 at his nest just before the eggs were laid. I was fortunate enough to witness the arrival of the rightful mate 65, and the ejection of 73 by 65 (1941a: 272). In the autumn of 1941, the female 65 disappeared, immediately after her chicks entered the water. Female 73 quickly deserted 74, joined 72 at his nest, molted with him, and in the spring of 1941 mated with him (Appendix V). This new partnership remained constant for the succeeding three years, after which 73 lost her life in a rabbit trap.

Bagshawe (1938: 212) gives an instance of a male Gentoo Penguin having intercourse with a strange female. When his mate came up, the "lawful" female attacked both, and the strange female was very subdued. This is in keeping with the law of "property rights" as it concerns penguins, and it will be remembered that 73 did not retaliate under similar conditions. Bagshawe's account is strongly reminiscent of the behavior of 65 when she found the female 73 with her mate, and could well be interpreted as a similar instance of affinity.

The second instance observed by me concerns the male 20, which had shown evidence for three years that he was interested in the female 18, before eventually mating with her (Chapter III).

Further examples of the possible influence of affinity in pair-formation is first that of the mating of Z12 and 115 (1941a: 275). Bird Z12 was already known to 115 at the time 122 disappeared. Another case is that of the male 37 (Appendix IV). Both his newly acquired mates were previously known to him.

A final example occurred in my tenth year of study. On 8 August 1945, the male B10 was found near his nest with a large rock on top of him. He had been dead up to two weeks. In the previous seasons he had been mated to the female 35. The nest was well lined with sticks, giving the impression that 35 was with him at the time of the accident, but of course one cannot be sure; he may have been divorced before that. On 30 August the female 35 was found mated to 28 not far away. I cannot say for certain whether this union was effected prior to or subsequent to 8 August. I do know, however, that 35 and 28 had been in the colony for at least nine years and that they landed at the same spot, and traversed the same path to their camps over that period; they were no strangers to each other. For three of those years—from 1941 to 1943—28 was unmated, and from what I know of penguin behavior he would attempt some sort of love-habits with 35. The intensity of these love-habits would depend on the susceptibility of the latter. In any case I would suggest that this behavior paved the way for the union of 1945-46.

In addition to the foregoing, there are other instances, concerning which I am not so fully informed, pointing in the same direction. I have now seen the result of the forming of a considerable number of mated pairs whose individual history, in the case of some birds, I can trace as far back as ten years. I am impressed by the fact that the individuals of many of these newly mated pairs have known each other for a long time. Before they were mated they were from time to time in each other's company, ostensibly performing love-habits of social value. It has occurred to me, especially on the evidence of the behavior of 73, 20, 69 (Chapter III), and others to a lesser degree, that affinities have developed. In addition, in some instances the love-habits have had pair-formation value which has not become effective till a later season. It seems to me, therefore, that the factor of affinity has a far greater influence on pair-formation than has been realized. Further, it is now also possible to understand better the meaning of "flirtations," discussed later in Chapter III.

As for the other species, the only evidence available concerns Gillespie's King Penguins (1932: 95-130). The female "Ann" seemed to develop an affinity towards the male "Bertrand," but six years went by before she eventually succeeded in mating with him. In that period, she was unmated three times, and it appears as if "Bertrand" accepted her because there was no other female available (see also Table 23).

Arising from the behavior of the female 18 and the male 20, as just narrated, is the problem of which sex takes the initiative in pair-formation. It appears that it may be either, although the initiative is usually limited to the male, which is the more numerous sex. It should be noted, too, that in the case of the male 20, this initiative occurred before the pre-egg stage and that this was true also of the female 73 (Chapter III).

From these two examples it may be observed that my use of the term "initiative" is different from that implied in the current definition of the word. My meaning refers to behavior of penguins either *before* they are well disposed towards each other or *before* they are mated, as was the case with 20 and 73. To me it seems that it is at this stage that observers should make a decision regarding the sex which takes the initiative in pair-formation, and, as already stated, in the Yellow-eyed Penguin it may be either sex.

In the literature, "initiative" and kindred terms are applied to penguins usually at the pre-egg stage, and, in my view, obviously *after* the birds have either mated or are "keeping company"—that is to say, *after* the individuals are favorably disposed towards each other. At this stage the behavior is definitely mutual, and is on a different footing from the earlier type. Mutual behavior is interchangeable; each sex takes its turn. The early type is one of the few occasions, in penguins, when behavior is unilateral, and it remains so until the passive bird is favorable towards the advances of the active bird; then the behavior becomes mutual.

Roberts (1940a: 203) remarks, referring to the Gentoo Penguin, that "*in the early stages* the initiative in courtship may be taken by birds of either sex." His observations were made on birds either already mated or "keeping company," and initiative in this case has a meaning different from that which I ascribed to it. Levick (1914: 35) infers that the female of the Adélie Penguin occupies a scoop, and relies on the initiative of the male to form a pair. Falla (1937: 77-81) has summarized the conflicting opinions of several observers regarding the behavior of the sexes in the Adélie Penguin at the pre-egg stage. Other than who is right and who is wrong, the observations tell us nothing about pair-formation, and the initiative suggested has occurred *after* the birds are well disposed towards each other.

In summary, true initiative that is unilateral occurs *before* birds are favorably disposed towards each other. Either sex may take this initiative, although it is usually taken by the male, which meets more intra-sexual competition when acquiring a mate. Initiative *after* the birds are well disposed towards each other refers to mutual behavior and is effected by either sex, according to circumstances.

Divorce.—The phenomenon of "divorce," which may be caused by the factors of affinity, dominance, and absence of mate, is a definite influence in the pair-formation of penguins. In this section, only the causes will be considered, other material being relegated to Chapter V, which deals with the retention of mates from year to year.

The first cause, that of affinity, is exemplified by the female 73, which divorced her mate 74 because of her affinity for the male 72 (Appendix V, and Chapter III).

The second cause is the factor of dominance, as indicated by the behavior of male 37, which, actuated by the loss of his mates, twice divorced the male 28 from his partners (Appendix IV). Another good example is the following in which it would seem that the two males, 51 and 39, were aware that they had lost their partners. An urge then caused them to develop love-habits which were strong enough to separate two females from their partners.

The male 39 and the female 2 were mated, to my knowledge, for six consecutive seasons from 1937-38 to 1942-43. Over the same period, and only a short distance away, were the male 34 and the female 27, also mated for six years. In 1942-43 the male 51, owing to the disappearance of his partner, remained unmated. Now, in 1943-44, the mated pairs were 51 and 2, and 39 and 27, leaving 34 unemployed, so that my two long outstanding partnerships were broken at one blow. The cause of the new arrangement cannot be stated with certainty, but it seems possible that 51, having been unemployed for a year, and being the youngest bird of all five, separated 2 from 39, and that the latter separated 34 from 27. It is significant that both 51 and 39 remained at their old nests and that the females 2 and 27 left their old nests. This strongly supports my statement that 51 and 39 were the active birds in appropriating a neighbor's partner. There is no evidence of any behavior by the females 2 and 27 comparable with that of 73 (Appendix V).

The third cause which may lead to divorce is the prolonged absence of some of the birds in the winter. This would allow more leeway to the forces of affinity and the determination of a mateless male. Such a development does not always follow, however. For example, in the winter of 1939 on the 28 nights I watched, the female 76 appeared on the landing ground six times and the male 135 five times, but on no night did they appear together. When the breeding season arrived they were still mated to each other.

In regard to other species of penguins, Gillespie again provides the only available information. In the King Penguin, divorce seems to develop much as in the Yellow-eyed Penguin, for of the twelve matings shown in Table 23, five were broken by divorce. By analogy with such evidence, and that supplied by the Yellow-eyed Penguin, it is possible to conclude that divorce is a factor in the pair-formation behavior of all penguins.

Flirtation.—In the Grebe, *Podiceps cristatus* (Linnaeus), Huxley (1914: 521) has noted what he calls "flirtation" between a mated bird and a stranger. The latter was soon driven away by the rightful mate, but the "erring spouse" was not attacked, being received again without anger. A similar state of affairs was observed also in the Black-tailed Godwit, *Limosa limosa* (Linnaeus) (Huxley and Montague, 1926: 17,23). In the Gentoo Penguin, however, Bagshawe (1938: 212) has recorded that "flirtation" occurred at the coition stage, when the returning spouse, which happened to be a female, arrived and drove off the usurping female before again accepting her erring partner. A perusal of Bagshawe's account of the life history (*op. cit.*: 249-264) of the Gentoo Penguin indicates that "flirtations" are common in that species.

In the Yellow-eyed Penguin I have not seen a great deal of "flirtation." The most interesting case is the "flirtation" of the female 73 with the male 72 and her ejection by the rightful partner 65 in the spring of 1939. Subsequent events, already noted, would signify that this "flirtation" did have a serious background. It could well be maintained that "flirtation" in penguins is more than a mere letting off of emotional energy and is probably an important agent in pair-formation. The effect is certainly difficult to gauge. Further, it is only because I have been able to follow the movements of the birds mentioned that I can explain the mating of 73 and 72. The case of 75 and 72 is also possibly an example of attempted pair-formation beginning with "flirtation" (Chapter III).

The behavior of the male 20 and the female 18, in the winter of 1939, was probably of greater import than "flirtation," for these two did mate in 1942. It is interesting to note, however, that in the interval between these two dates, 20, as an unemployed male, frequented the same area as 18 and her mate 1, and all three left the sea by the same path. Birds 20 and 18 must have met alone on many occasions, and 20 probably made advances to her. Whether the latter replied with a little "flirtation" I do not know. I do know, however, that there was an affinity between the two; thus "flirtation" probably did occur. If so, this is another case of "flirtation" ultimately leading to mating.

A third case of "flirtation" probably setting up an affinity and leading to pair-formation involves the male 69 and the female 75. At 6:15 p.m. on 29 September 1939 I found the unmated 69 alongside the female 75, which was covering her first egg. Bird 69 was in the normal position for a mate, and there was no evidence of any love-habits taking place. Not far away was the rightful mate 66, returning from the sea after a day's fishing. Unfortunately, not realizing the importance of 66, I caught him

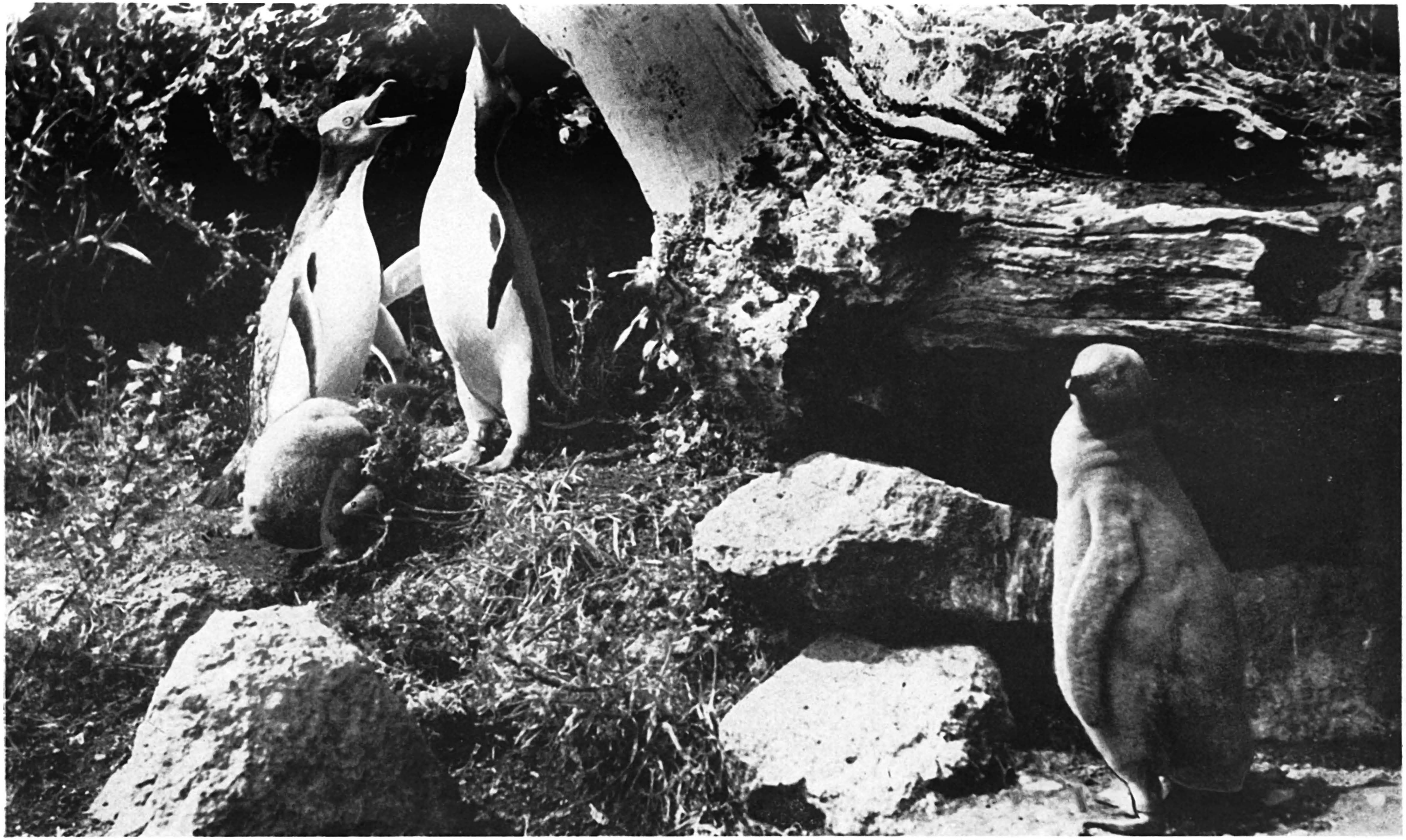


Fig. 11. Half trumpet. The bird on the left is performing the "half trumpet," whereas that on the right is engaged in the "full trumpet." This picture indicates clearly the meaning of the term "mutual behavior," which does not imply that each bird is doing the same thing. The chicks are 35 days old.

Fig. 12. Welcome. The culminating point in the "welcome" ceremony. The male on the left has just returned. The female is on the edge of the nest, with two eight-day-old chicks behind her.

to examine him, and thereby interfered with subsequent events that would have occurred when he reached his nest. That season 66 did not return to molt, and in the following spring 69 was found mated with 75, only to lose her to 720 the succeeding year.

In summary, these three cases indicate that "flirtation" in penguins is more than a discharge of surplus energy, and is a definite factor in pair-formation.

Influence of Period of Receptivity.—The term "oestrus" is strictly referable to mammals, although it has been used by many workers, including the writer, for birds. In this paper the term "period of receptivity" will be employed to denote that the bird has reached the peak of its sexual phase and is ready for coition.

It will be remembered that, in the Yellow-eyed Penguin, the majority of the mated pairs are formed previous to the pre-egg stage. This means that the period of receptivity, when the gonads are fully developed, is not necessarily a precursor of pair-formation. Some observers believe that pair-formation does not take place before the peak of the sexual phase, but these deductions were made on penguins whose earlier history was unknown.

Roberts (1940a: 210) postulates that "display before a female Gentoo with unenlarged ovary fails to produce any response," in that species. Murphy (1936: 340), in discussing Levick's notes on the mating of the Adélie Penguin, suggests that when a female responds to the approaches of a male, she is "nearing the oestrus condition, and the affair may proceed." In view of these two opinions, the following episodes will serve usefully in comparisons, and it should be kept in mind that Roberts (*op. cit.*: 227) found by extensive collecting that in the Gentoo Penguin, the gonads are enlarged at the beginning of the breeding season and soon regress. Presumably this is true of all species.

On 26 April 1941 I saw two young Yellow-eyed Penguins come ashore, each seventeen months old. Their sex was unknown to me, but judging by the large size of B14, the exceptionally small size of M16, and the shape of the latter's head, I think that

B14 is a male and M16 a female. Their weights were 13 pounds and 11¾ pounds respectively. A considerable amount of trumpeting occurred before landing, and on the beach "half trumpets" and "kiss-preening" were indulged in by both. As they entered the bushes I appeared behind them, causing both to race along a narrow track, where they halted in front of a friend. On my closer approach, B14, the more timid, bumped into M16, which immediately uttered a short trumpet and then continued with several "half trumpets." Bird M16 was unusually demonstrative, her behavior resembling that of birds at the nest just before the appearance of the eggs. I think that she was in the grip of emotions due to the aforementioned mutual love-habits. Now, this bird probably did not have an enlarged ovary, first because of her youth, and second because of the time of the year. Nevertheless love-habits had been aroused either by B14 or by his presence.

Probably a better example is that of the female 18 and the male 20 (Appendix II and Chapter III). These birds, whose previous and subsequent histories are known, were indulging in vigorous love-habits on 22 April 1939, shortly after their molt was completed. The female, which had just helped to rear two chicks, with the male 15, could not have had an enlarged ovary. The subsequent story of 20 and 18 indicates clearly that the episode of 22 April was a serious matter.

I regard the evidence afforded by 20 and 18 as very important, for it clearly demonstrates that a female will respond to a male, not her mate, when her ovary is not enlarged. There are other examples available. One concerns the female 115 and her mate 122 on 25 June 1939, when both stayed ashore for the day at their old nest site. Vigorous indulgence in mutual love-habits occurred all that day.

The migratory Erect-crested Penguin also indulges in mutual love-habits of a very intense nature, outside the pre-egg stage, when the ovary of the female cannot be enlarged (1941b: 47-49).

For example, on 24 January 1940, the female, on reaching her nest, had been preceded six days by her mate, whom she had not seen for three weeks. On 28 December previously they had pushed their addled egg out of the nest, and had given up domestic life for that season. When reunited on 24 January, intense mutual love-habits occurred, culminating in frantic fruitless attempts by the male to effect coition. This is not an isolated incident, for in the previous season, when the birds were halfway through their molt, attempted coition occurred, preceded by the usual elaborate love-habits (*op. cit.*: 34).

In summary, the foregoing examples definitely indicate that a female will respond to a male outside the period of receptivity. With the Erect-crested Penguin, the position as specified is slightly different, for both birds were already mated, but I would suggest that this species, in a normal colony, behaves, in this regard, in much the same way as the Yellow-eyed Penguin. Gonadal development is not a necessary precursor of pair-formation, although during that phase some mated pairs are doubtless formed; but this happens rarely in the sedentary Yellow-eyed Penguin. Presumably, in the migratory species, birds which have lost partners through death and divorced birds form newly mated pairs, not as a direct result of gonadal development, but because of their incomplete matrimonial status.

"Trial and Error" Theory of Sex Recognition.—"Just as a male Gentoo is unaware of sex differences and does not differentiate between males and females even in mating, so is a female normally unaware of sex, and attempts to dominate weaker birds. The essential differences in the behaviour of the sexes is that during the breeding season a male always tries to dominate weaker birds, while the female loses the dominating urge during the short period when fertilization must take place" (Roberts, 1940a: 212-213).

I find myself unable to agree with the remarks just quoted. They certainly do not apply to the Yellow-eyed Penguin, and in all my field work I have never seen anything suggesting that the Yellow-eyed Penguin does not know the sex of his neighbors; nor has there been any indication that a bird, whether male or female, dominates a weaker bird. The law of "property rights" certainly does exist, but this form of domination is in a different category. Further, a close study of Bagshawe's splendid paper on the Gentoo Penguin (1938) gives me the impression that the behavior of this species is very much akin to the Yellow-eyed Penguin's, and that possibly the relationship between the two is closer than suspected.

In the Yellow-eyed Penguin it has already been shown that pair-formation is usually effected before the pre-egg stage. Further, I have records of males which mated with early-laying females one season and late-laying birds in the next (Chapter VI). In pair-formation in the Yellow-eyed Penguin, therefore, the factor of the synchronization of the sexual periodicity in the two sexes, as apparently obtains in some species of birds, does not apply. The male is ready for the female when she is ready. Roberts (*loc. cit.*) does not think this is the case in the Gentoo and King Penguins.

It may be indeed that this synchronization obtains in some species such as the King Penguin, Little Blue Penguin, and the three northerly species of *Spheniscus.* In the Little Blue Penguin, the span of egg-laying is fully five months (my own observations), and a protracted period seems to occur in the King Penguin and also in the genus *Spheniscus.* It would seem desirable for individuals with a similar period of receptivity, unless there are other means of overcoming the difficulty, to mate.

In the Yellow-eyed Penguin, there is a fairly fine distinction between the "sheepish look" of the female and that of the male, and the realization of this during the fifth year of study has allowed me to distinguish the two sexes with some considerable accuracy. To the reader not familiar with the birds in the field, it is most difficult to explain this difference, for the ability to detect it is acquired only after long experience. The head of the female, as it breaks into the "sheepish look," presents a much rounder and more graceful appearance than that of the male, which appears rather ugly. This difference at length became apparent, even when the birds were at the nest and occupied in ordinary routine activities or posed in normal attitudes. The female still seemed to have that extra grace and roundness of the head. Further aids in sex determination are given in Chapter IV.

It is interesting to notice that McLennan (Nicholls, 1918: 127) when examining the Little Blue Penguin on Phillip Island, in Victoria, "detected a difference between the heads of the male and the female. It was hard to define, but, after closely inspecting a number of birds, both Tregellas and myself [Nicholls] were satisfied that the difference did exist." It is a noteworthy point also that Lack (1939b: 187) was able to distinguish fine differences in several of his female Robins by behavior and by structure.

After reading Nice's discussion (1937: 84, 215), in which evidence is given to prove that Song Sparrows "cannot tell the sex of one of their kind except by its behavior and notes, unless personally acquainted with each other," I endeavored to discover if this were true of the Yellow-eyed Penguin. If I am correct in my foregoing statements, that I can distinguish the sexes in the Yellow-eyed Penguin, it would seem to be a far easier task for the birds themselves.

On the other hand, Allen (1934: 180) states that the Ruffed Grouse, *Bonasa umbellus* (Linnaeus), is not cognizant of sex as such, even though there are external differences between male and female. Noble and Vogt (1935: 278-286), however, have found that in certain birds which are usually dimorphic, the male can distinguish sex differences even in stuffed specimens, and similarly, Chapman (1935: 516-519) has shown that Gould's Manakin, *Manacus vitellinus vitellinus* (Gould), can distinguish between stuffed female and male birds of its own species. Further, an observation of Vogt (1938: 22, 40) is important. It is "that Willets [*Catoptrophorus semipalmatus semipalmatus* (Gmelin)] are able to recognize the sex of other Willets without resorting to trial and error methods." Likewise, Makkink (1936:46) states for the Avocet "that the birds must be able to distinguish each other's sex already in the beginning of their meeting."

Lack (1940b: 279) has summarized the position regarding sex recognition as follows: "Some species discriminate the sexes readily, some have a generalized first reaction but discriminate at close quarters, in others some kind of dominance relation is perhaps involved. There are yet others in which the behaviour does not seem to fit into any simple pattern."

When I was watching the Yellow-eyed Penguin at Colony W in the winter of 1939, I noticed that some of the males usually "saluted" any female which happened to land. Now at this colony there were a number of birds from Colony B. One bird, in particular, the female 29, maintained an attitude of aloofness during the whole winter at W, and took not the slightest notice of any "salutes." Further, the behavior of the males indicated that they knew the sex of 29, and it is hardly likely that they were acquainted with her previously, since they belonged to Colony W (Appendix III). I do not think, however, that the "salute" is used to discover the sex of another penguin, for in my opinion that is known on sight, and I have already given instances (Chapter II) of males undoubtedly known to each other "saluting" each other. Again, throughout the whole winter of 1939, all females that were known to be breeding birds were continually "saluted" by males, sometimes with response and sometimes without.

The case of the male B14 and the female M16, just mentioned, indicates that two young birds, no more than one month past their first molt, knew each other's sex. They had never experienced the spring as mature individuals, so that it is not the alleged releasers of the pre-egg stage that has enabled them to discover each other's sex. If there are releasers for such purpose, then obviously they function at any time of the year. A further example is that of the old unmated male 692, and the young female Z18, only two weeks past her first molt (Chapter III). The male in this case discovered by some means the sex of a bird barely more than a juvenile.

In summary, I should like to say that I have given the "trial and error" theory considerable thought, have tested it out in the field, and am not at all convinced that it applies to penguins.

Further, in the Yellow-eyed Penguin, I have never seen any homosexual activity. If sex recognition were such a difficult matter, I would surely have seen some instance of such activity.

The Function of Head Feathers.—It should be noted that the various genera and species of penguins are recognizable by outstanding differences in the bill and other markings about the head and neck. Some writers have maintained that these latter features are used in display in courtship pattern behavior, or in what I call love-habits, implying that they are an aid to pair-formation. I find it difficult, however, to agree with their deductions. Is it not true that all this description of alleged display of head feathers, neck markings and so on, is depicting the behavior of birds *after* members of a pair are well disposed towards each other and frequently *after* the mated pairs are formed? I think so. It will have already been observed that this is true in the Yellow-eyed Penguin. I fear very much that these observers are endeavoring to explain the function of these marks in the light of preconceived ideas, realizing that certain birds do use a gaudy plumage for display purposes.

In the three species of penguins that I have studied in the breeding season—Erect-crested, Yellow-eyed, and Little Blue Penguins—I have not been able to discover any use of the head feathers or other marks for display. This means that in behavior before and after pair-formation, or after the birds are well disposed towards each other, markings on the head have no apparent function.

Gaudy plumes are absent from the head of the Little Blue Penguin, and I have not seen any other feature that is thought to be of use in display, as is judged to be the case in the Magellan Penguin (Roberts, 1940a: fig. 16). As the Little Blue Penguin is nocturnal when on shore, it might be argued that such markings could not be functional, as a partner could not see them in the dark.

In the Erect-crested Penguin, the crests are nearly always erect when the birds are on land, and are flattened only in rain, or when the birds are indulging in the "ecstatic" (1941b: 31, 38), or when one of them, as in the particular birds I had under observation, the male, flattens his crest after the manner of an aggressive horse putting his ears back when about to attack an intruder (*op. cit.*: 36). I could see no evidence that these birds used their beautiful crests for display purposes in any of their mutual love-habits. Roberts (1940a: 217 and fig. 9) states that the Ringed Penguin exposes the black ring on the throat in display, maintaining that this is one of the functions of these markings. Now the female Erect-crested Penguin, as part of the "ecstatic" and when thoroughly excited, used to put her head back exactly like the bird portrayed on the right side of Roberts' figure 9. The head was so placed at any time from her coming ashore in September until the end of the molt in April. The head was not held still, but was moved rapidly from side to side; the impression gained was that the bird seemed to be trying to put it back as far as possible. I do not think that this was an attempt to display any of the feathers of her throat. To my knowledge, the male never did this.

The Yellow-eyed Penguin, especially after the molt, has a beautiful sulphur-yellow crown, which it raises slightly in some of its love-habit behavior. The crown is raised in the "sheepish look" and the "shake," and it is also raised in aggressive attitudes. I have very carefully watched the use of the crown, but cannot find that it is employed for the purpose of attraction when performing love-habits. In these instances the positions of the bird are such that the crown would scarcely be visible to the bird opposite. I have stated (Chapter II) that in performing the "salute" a bird may pass another and "salute" with the back to it, so that the crown would be visible if the passive bird were looking, which it seldom is. The "salute," however, is not always given when the birds are in this position. They may be face to face. Further, the "salute" cannot be considered as an intense love-habit. If a Yellow-eyed Penguin were to bow before a second bird, the crown would be visible, and it might be conceded that the crown was used in display, but the Yellow-eyed Penguin does not bow. According to Roberts (1940a: 217 and fig. 19), the Gentoo Penguin apparently bows and displays its head patches to a mate, but is this either a prelude to pair-formation or an aid in stimulating love-habits after the mated pair is formed? I doubt if these interpretations apply.

I cannot see any evidence that these adornments of the head and neck have anything to do either with pair-formation or with subsequent love-habits, whether at the pre-egg stage or later. It seems to me that Murphy (1936: 334) has reached the correct interpretation, in regarding them as a recognitional area when penguins are in the water. He writes: "This is no doubt the explanation why strong differences in bill color, in the pattern of markings on head, and throat, and in the development of bright superciliary plumes, ear-patches and similar ornamentation, have been evolved through some sort of selection within the group."

Recognition of the species by the penguins themselves may be made possible by this means, when many are swimming on the surface of the water. It is thought that some land birds would be likely to confuse the species if there were not some distinguishing plumage, and that if a species were removed from related species, this distinguishing plumage would tend to disappear (Lack, 1940b: 282). This phenomenon has also been noted by Mayr (1942: 49). It is possible, therefore, that penguins need some recognitional factor, especially in the water, a point that may be particularly important for the migratory species which do not touch land for several months.

In conclusion, I suggest that head adornments in penguins have no function relative to love-habits, but may be useful at sea in enabling any bird to recognize any other as of its own species. In other words, the adornments are not concerned with sexual selection, but natural selection, and are of benefit to the species as a whole.

DISCUSSION OF LOVE-HABITS AND PAIR-FORMATION

Love-habits.—In penguins, love-habits, whether or not they concern breeding or unemployed members of the community, take place with equal intensity *during the entire period spent on the breeding grounds.* In sedentary species, such as the Yellow-eyed and the Little Blue Penguins, love-habits occur in the winter, but I find no record for the King Penguin or for those colonies holding sedentary Gentoo Penguins; this is probably due to a paucity of observations. The migratory species, when away from the breeding grounds, probably indulge in some form of love-habits. For instance, Levick (1915: 83) has noted the "full trumpet" of the Adélie Penguin far out on the sea ice, and if this species rests on the floes in its winter quarters it must surely indulge in emotional actions. But I do not think the function of these winter love-habits in migratory species serves as an emotional bond to keep the members of a pair together, for they are probably not in contact (Chapter III, and 1941b: 36). Such winter love-habits would seem to have some function or value to the species as a whole.

In petrels, with one important difference, a comparable situation exists. The difference concerns petrels at sea in the non-nesting season when there are indications, even though necessarily of an indirect nature, that mated pairs and pairs "keeping company" remain together at sea. Serventy (1941: 89) also holds this view and gives evidence in support of it.

Three outstanding incidents in my study of the Royal Albatross support the foregoing contention. The first is the frequent arrival of both parents together to feed the chick after having been there singly on the previous occasion (1942a: 258); the second incident suggests that a newly mated pair was formed at sea (*op. cit.*: 175, 262); and the third incident, which is more exact, is briefly as follows: a mated pair which lost their chick on 9 June 1945, at the age of 135 days, made their next two appearances on 9 October and on 7 November, and on each occasion the birds arrived together. Surely these three episodes suggest that members of mated pairs and pairs "keeping company" not only fraternize at sea, but also are able to find each other on their feeding grounds.

It is known that members of the family Diomedeidae perform love-habits at sea. They have been recorded for the Wandering Albatross, *Diomedea exulans* Linnaeus, by Murphy (1936: 558-559), and for the Black-footed Albatross, *Diomedea nigripes* Audubon, by Fisher (1904: 78) and by Dr. Loye Miller (private communication), who "watched two birds swim up to each other, raise the bills to the zenith, and utter a doleful groan." My second example, just quoted, also indicates that these love-habits not only may have pair-formation value but may result in a mated pair when the shore is reached.

As for the burrowing petrels, I know for certain that one, the Broad-billed Prion, *Pachyptila vittata* (Gmelin), is ashore in the non-nesting season (1944a: 206-209). The observed facts are that after an absence of approximately six weeks from the end of the breeding season, this species returned to its island home, occupied the burrows immediately in pairs, and performed love-habits, not only on the night of arrival, but on several days before returning to the sea. Subsequently, this behavior was continued sporadically until the breeding season began.

The arrival in pairs suggests that the birds were in contact at sea, and the employment of love-habits in the burrow signifies either that new pairs were being formed or else that previously mated pairs were maintaining the pair-bond. Probably both considerations apply, and their behavior would also seem to imply that, as in Diomedeidae, love-habits had been taking place at sea.

In view of what has just been said about the incidence of love-habits among penguins and petrels, an analysis of the functions of love-habits among birds in general will be profitable. There appear to be three such functions, and, further, this classification helps me to account for the ever-present love-habits in the Yellow-eyed Penguin—something that I previously (1946: 150-151) was unable to do.

The general consensus has been that love-habits which take place at the pre-egg stage are epigamic. This is certainly true when, as in the Ruff, *Philomachus pugnax* (Linnaeus), love-habits lead direcly to coition. But, among mated penguins, petrels, and some other birds, the love-habits used at the pre-egg stage are the same as those employed at any other time of the year; they do not lead directly to coition; and my own observations on the Royal Albatross (Chapter VI), and those of other workers on some other species of birds, indicate that there is absolutely no ceremony whatsoever immediately before coition. It seems better not to use the term "epigamic" for these cases. It would be more explicit to say that the first function of love-habits at the pre-egg stage is to "attune" members of a mated pair to a state that will make effective coition, fertilization, and ovulation. When the female reaches her periods of receptivity coition will occur immediately with the least possibility of failure. In other words, the love-habits have a gradual effect and keep the birds mutually stimulated during the whole of the pre-egg period; copulation occurs when the female is ready and not as the direct result of stimulation by the male.

The second function of love-habits, which is applicable to many types of birds from passerines on the one hand to petrels and penguins on the other hand, is bond-holding, and is more noticeable after coition has ceased. These love-habits appear to be exactly the same as for the first function, but they have no influence on either coition or ovulation. They are apparently designed to keep the mated pair intact where that is vital for the success of the family (Huxley, 1914: 516).

But among mated pairs of the Yellow-eyed Penguin this second function obtains also in the winter months. Thus in such species the bond-holding value is not only for the benefit of the family; perhaps, to these species, it is important that mated pairs should tend to hold together from season to season. Chapter V records that this happens in 82 per cent of the cases in the Yellow-eyed Penguin. The Royal Albatrosses are thought, according to my records, to remain mated for life; possibly from the evidence given in the two preceding paragraphs they fraternize at sea in the non-nesting season. If so, the opportunity for the employment of bond-holding love-habits would exist away from the breeding grounds as well. This is probably true of other petrels, in which, as we shall see, there is only a small percentage of divorce.

A further variation of the bond-holding function of love-habits is revealed by the behavior of the female Yellow-eyed Penguin 115 after she lost her mate (Chapter IX). For 51 days she continued her domestic duties unaided, followed by a further 45 days till her molt was completed. With no opportunity for mutual love-habits to act as a bond, 115 remained faithful to her family, even though, on the landing ground, she had to pass one or more eligible unemployed males which did make advances towards her (Chapter VII). It would appear then that another bond—a parental bond—was working for the success of the family. This bond probably resulted from the emotional attachment between the parents and chicks.

A final point to notice is that this second function of love-habits is probably working at the pre-egg stage simultaneously with the "attuning" function, especially in birds like penguins and petrels. In this way, disintegration of mated pairs is prevented at a crucial time in the breeding cycle—the time when the mated pair must remain intact so that fertilization may be effected. It is difficult, however, to differentiate between the two types, for one merges into the other.

The ill-effect of the breaking of the pair-bond at the pre-egg stage is demonstrated by the following three examples of nest failure (Chapter III). First, the female Z15 laid an exceptionally small egg, and, although she then laid a second one of normal size, neither hatched; second, the female 944 laid only one egg and it did not hatch; and finally, the female B41 not only laid merely one egg but also failed to secure another mate, even though unemployed males were available.

The third function of love-habits concerns bringing individual birds together so that they may become acquainted and in some cases ultimately form mated pairs. I have observed this in considerable detail among unemployed members, especially of the Yellow-eyed Penguin and the Royal Albatross. The tendency has also been noted in other penguins and petrels. Some of the performers in the Yellow-eyed Penguin were, it is known, not old enough to breed, but others in both the Yellow-eyed Penguin and the Royal Albatross were surplus males. If, at the pre-egg stage, these unemployed birds feel a breeding urge, the love-habits used may have similar value to those employed by the mated birds. Once the incubation and chick stages are in progress, however, this possible value must surely disappear. It is, therefore, necessary to search for another reason for the use of love-habits by unemployed penguins and petrels *after the mated birds have started incubating* and when all eggs for that season have been laid.

It seems to me that the function of these love-habits is to raise the participants to such a condition that they will, in the incipient stages, form a pair which will "keep company." In the Yellow-eyed Penguin, we know that this is what may and does happen (Chapters III and VII). Similarly, in the Royal Albatross, there is one definite record of love-habits between a pair "keeping company" in both the incubation and chick stages for other birds, resulting in the formation of a mated pair in the succeeding season (1942a: 175, 262).

Once the pair has been formed the continuation of the love-habits is bond-holding and tends to keep the pair together. Probably because the pair has never bred and members are not strongly attached to each other, many of these pairs are broken, but still a number do remain intact. When the next pre-egg stage arrives, the love-habits of those pairs which have remained together attain an "attuning" function as well.

In summary, love-habits among such birds as penguins and petrels when unemployed have three functions. The first is designed to allow birds to become acquainted and thereby facilitate the formation of a pair. Once that is effected, the continuation of the love-habits tends to act as a bond to keep the pair intact until the next breeding season arrives. If that is achieved, the love-habits will then have "attuning" value which will lead to the procreation of the species. As for the mated birds, the love-habits have two functions: (1) "attuning" value at the pre-egg stage; (2) bond-holding value at all times. The latter function keeps the mated pair intact: first, so that the "attuning" value may operate at the pre-egg stage; second, so that the family may survive, and, third, so that later, after the chicks have departed, the mated pair may keep together until the next breeding season.

As a result of the foregoing classification of love-habits some concluding remarks may be appropriate concerning the use of the term "courtship." It seems to me that if the word is to be employed it should be reserved to denote behavior that may lead to the formation of a mated pair. Many workers, however, use the word in reference to behavior which occurs after the pair is formed and which leads, directly or indirectly, to the union of the gametes and to ovulation. This may be conceded as legitimate provided it is clearly understood what the worker means; the term then cannot also be used for behavior prior to pair-formation.

This second use of the word "courtship" covers all sexual behavior between the sexes at the pre-egg stage, but, in some species at this period, the behavior is of two grades. One concerns ceremonies, often quite brief, which occur immediately before coition; and the second concerns earlier, more elaborate ceremonies which do not lead directly to coition. The first may be called pre-coitional behavior and the second "courtship" behavior. Examples of species in which both types occur are the Grebe, some gulls, the Avocet, and some passerine species (Chapter VI).

Whatever decision is made about the foregoing aspects of behavior, "courtship," in species where it obtains, is not an appropriate term for sexual behavior between a mated pair subsequent to the pre-egg stage. A knowledge of the foregoing facts, therefore, has caused me to employ the word "love-habits" to cover all three phases. This word may not be the best that could be chosen, but it does imply that the term "courtship" is misleading, and that the terminology needs revision in the light of recent widespread observations on the sexual behavior in birds at all periods of the annual cycle.

In summary, the word "courtship" may be employed to denote either behavior leading up to pair-formation or pre-egg behavior after the mated pair is formed. Similar behavior indulged in by mated pairs at other times is not "courtship." In some species, pre-egg behavior may be further subdivided into "courtship" and pre-coitional behavior.

Pair-formation.—"The problem of pair-formation is primarily that of recognition—specific and sexual" (Nice, 1943: 192). In penguins, specific recognition is aided by the fact that the head markings of the different species are distinctive (Chapter III). Where there is a tendency to generic resemblances further aid is afforded in preventing interbreeding by the evolution of different laying dates, and to some degree by geographical isolation, as exemplified by the Drooping-crested and the Erect-crested Penguins.

The former breeds around Stewart Island and on the southwestern end of the South Island of New Zealand. The latter breeds on Antipodes and Bounty Islands, which are approximately 400 miles in an easterly direction from Stewart Island. The laying dates of the Drooping-crested Penguin are in the end of July (my own observations) and of the Erect-crested Penguin, approximately mid-October, according to my records, which for six years give an average of 17 October and a range from 12 October to 21 October.

There is thus a difference of at least two months in the laying dates of these two closely related species. Any attempt at interbreeding would be frustrated, since the behavior patterns essential at the time of their respective pre-egg stages would not synchronize. These remarks are interesting in view of Mayr's statement (1942: 255) regarding the function of the "engagement period" in some birds. He writes, "The engagement is likely to be 'broken' if the behavior patterns of the two mates do not fit exactly. This is the

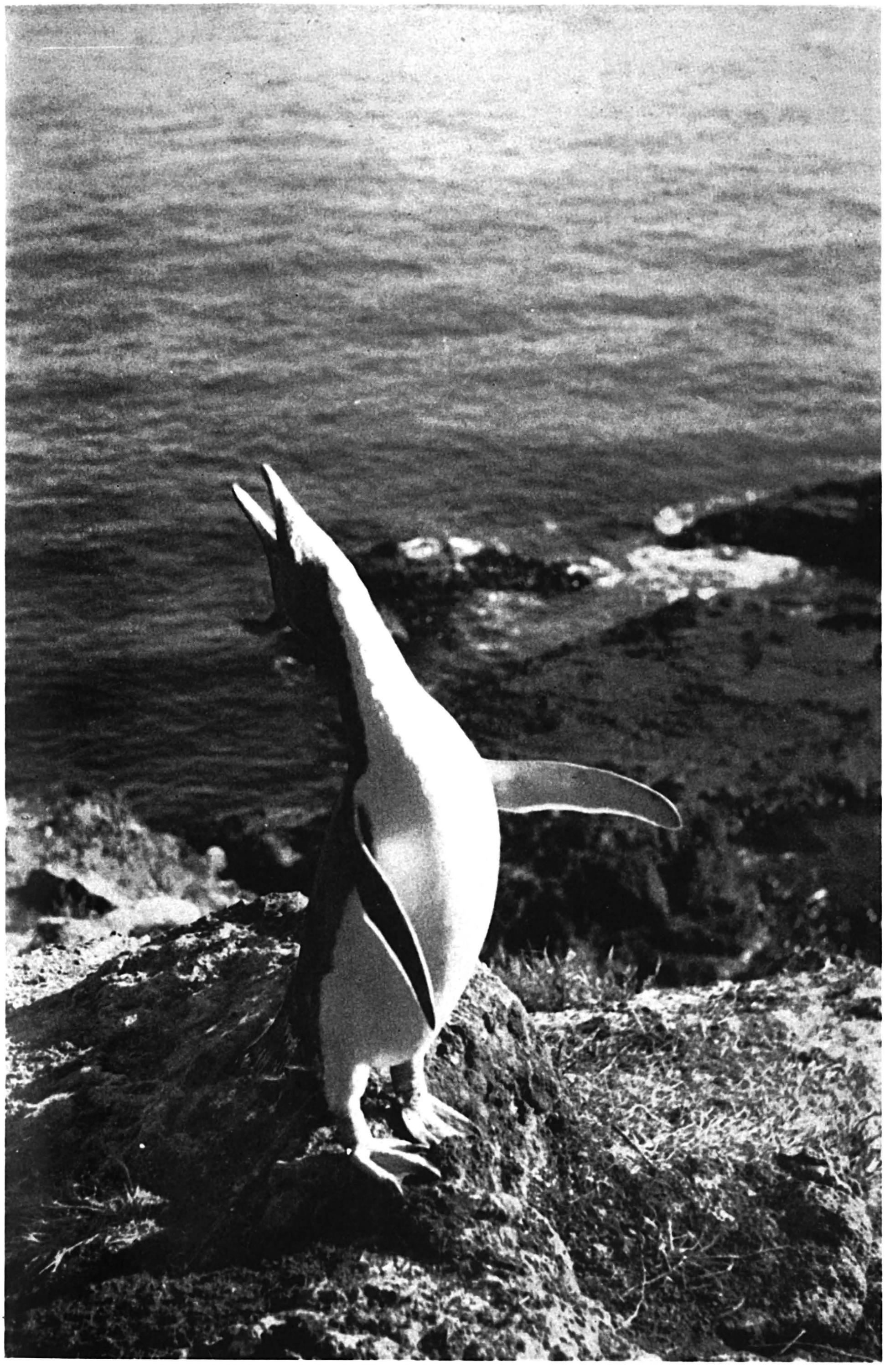


Fig. 13. Full trumpet. Male Z12 giving his last "full trumpet" the day before he was lost.

Fig. 14. Arms act. Female Erect-crested Penguin attempting to mount the male, January 7, 10 days after the egg had been ejected from the nest.

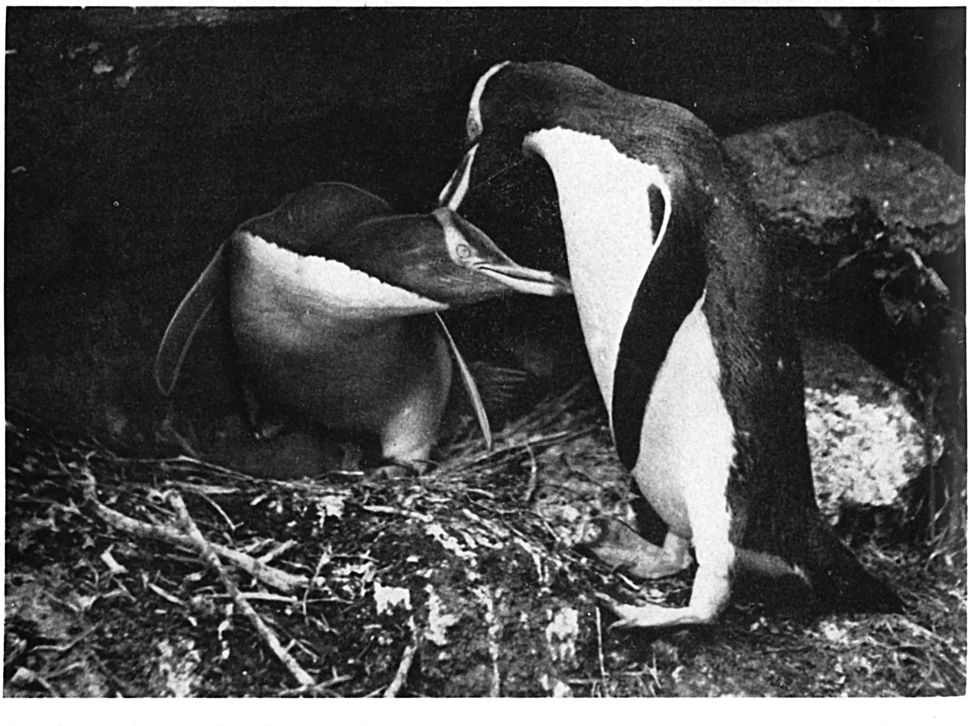


Fig. 15. Mutual-preen. Minor behavior after the "welcome" ceremony. The bird on the nest is straddling two nine-day-old chicks.

reason wild hybrids are rare in bird species with definite pair formation and engagement periods, but fairly common . . . in genera and families without pair formation."

A similar situation obtains between two species of *Pachyptila,* the Broad-billed and the Fairy Prion, *Pachyptila turtur* (Kuhl). On Whero Island there is a difference of two months between the peaks of their respective laying dates (1944c: 34). Moreover, since there was no overlap, it would be impossible for these two species to interbreed.

My views regarding sexual recognition are already stated (Chapter III). How the Yellow-eyed Penguin can discover sex, which he appears to know on sight and which is something apart from gonadal development, I have never been able to ascertain. Sex appears to be known also among young birds at least as early as the time immediately after the acquisition of their first adult plumage.

Further, the reader will have observed long before this that pair-formation in penguins is obviously not a hurried affair and my contention that it is a gradual development is in agreement with Lack (1940b: 279), who states: "I think it will prove exceptional to find pair-formation depending on a simple dominance mechanism or set of releasers." I should add, too, that, according to my limited observations, pair-formation in the Royal Albatross takes some considerable time, and does not occur within the short space of time between the arrival of the birds on the breeding area and the laying of the egg.

Further still, though I have never been able to follow the exact steps of pair-formation in the Yellow-eyed Penguin, the case of Z18 and Z14 (Chapter III) probably denotes the sequence of events in many instances. The matter is certainly not as simple as Armstrong (1942: 299) would have us believe: "Ponting (1921) describes how an Adélie penguin, newly arrived from the sea, inspected and rejected three possible partners and then courted a fourth." In the first place, Ponting did not know the sex of any of the penguins; secondly, he had no proof that the first and the last were actually courting; thirdly, he would, indeed, have been fortunate to arrive at the psychological moment a mated pair was being formed; and, fourthly, if he had, he would have been unable to recognize the fact. Hence his observation is worthless from the point of view of pair-formation.

In actual practice the precise moment of pair-formation in birds has rarely been witnessed and it certainly has not been observed in penguins. Good claims have been made for some birds as, for example, Noble, Wurm and Schmidt (1938: 26) for herons, *Nycticorax nycticorax hoactli* (Gmelin), Kendeigh (1941: 49) for the House Wren, *Troglodytes aëdon* Vieillot, Lack (1943: 61) for the English Robin, and Hochbaum (1944: 25) for the Canvasback, *Aythya valisineria* (Wilson).

In my experience with the Yellow-eyed Penguin there has never been a dissolution of a partnership in the incubation or in the chick stages. The majority of the mated pairs are formed between the time the chicks leave for the sea and the time when the birds stay ashore for the pre-egg period. My limited observations on the Little Blue Penguin point to the same procedure, but as my field work on the Erect-crested Penguin has involved birds already mated, I cannot decide about that species. It does seem, however, that the mated pair, entirely isolated, breeding under abnormal circumstances far from their usual breeding areas, did mate before arriving on their selected nesting station. They may, of course, have molted there in the previous autumn, for the Erect-crested Penguin is found at this period along the Otago coastline. In the spring, it is a rare occurrence to find an Erect-crested Penguin ashore in this area, and it would be even rarer to find two birds that would be willing to stay in this abnormal place and mate.

Many other species of birds appear to arrive on the breeding grounds mated, and this is certainly true of those mated for life, of which the Royal Albatross appears to be one. Those which arrive mated include the Herring Gull, *Larus argentatus argentatus* Pontoppidan, which Darling (1938: 30) thinks may also mate for life; the Black-headed Gull (Kirkman, 1937: 35); the Common

Tern (Austin, 1947: 1-2); the Gannet, *Sula bassana* (Linnaeus) (Armstrong, 1942: 6); and some ducks (Hochbaum, 1944). Further, Huxley (1923: 266) and Huxley and Montague (1926: 19) suggest that the Red-throated Diver, *Colymbus stellatus* Pontoppidan, and the Black-tailed Godwit respectively arrive mated if the pairs survive, whereas the others—those which have lost their mates and those which are unemployed—do not mate before migration.

In other species of birds, especially in those which tend to return to, or to breed in, the same neighborhood year after year, the influence on pair-formation of the factors of affinity, previous acquaintance, and divorce need careful investigation. Finally, in any study of pair-formation, the impact of the unemployed section on the alignment of mated pairs is most important. (See Chapter VII.) The status of these birds should be recognized, for each is without a partner and presumably, if of breeding age, each bird has a strong desire to obtain one.

In conclusion, the study of pair-formation is only in its infancy. "It is clear that we need many more detailed studies of marked birds from the first moment of meeting" (Nice, 1943: 204). Finally, it is not a general rule, which some writers would appear to think obtains among most birds, that pair-formation is closely associated with epigamic and "attuning" love-habits of the pre-egg stage, for pair-formation frequently takes place long before this.

SUMMARY

In the Yellow-eyed Penguin evidence is given that pair-formation may occur at any time in the year and that the majority of the mated pairs are formed in the winter. The same statement probably applies to the other species of sedentary penguins, but, in the migratory species, pair-formation cannot well take place at sea. "The problem of pair-formation in birds is primarily that of recognition—specific and sexual." Pair-formation in penguins and petrels has never been witnessed, although it has been witnessed in a few other birds. Six types of allied behavior in pair-formation are recognizable: (1) *Affinity.* This factor has, to my mind, a far greater influence on pair-formation in birds than is realized. (2) *"Divorce."* This may be caused by affinity, dominance, and absence of mate. (3) *"Flirtation"* is probably a definite factor in pair-formation. (4) *Period of receptivity.* In the Yellow-eyed Penguin, at least, pair-formation usually occurs before the peak of the sexual phase. (5) *"Trial-and-error" theory of sex recognition.* Penguins apparently can recognize the sex of another bird of its species on sight. My field observations give no support for "trial-and-error sex recognition" in the Yellow-eyed Penguin. (6) *Function of head feathers.* Head feathers are not concerned with pair-formation but are a means by which penguins recognize their own species. True initiative in penguins is unilateral and occurs *before* the birds are favorably disposed toward each other. Either sex may take the initiative. Among unemployed birds, love-habits may have three functions—to facilitate pair-formation, then to act as a bond until the pre-egg stage, and finally, to "attune" the birds for coition, fertilization, and ovulation. Among birds already mated, love-habits may be bond-holding at all times, and, in addition, at the pre-egg stage, "attune" the birds for coition, fertilization, and ovulation. The word "courtship" may be used to denote behavior either before or after pair-formation but does not seem to be applicable to post-egg behavior. The term "love-habits," therefore, is suggested to cover all three types.

Chapter IV

Sex Differences, Measurements, and Weights

Early Identification of Sex in Penguins. Measurements according to Sex. Weights according to Sex. Variations in Weight throughout the Year. Summary of Sex Differences. Discussion of Sex Differences and Measurements. Summary.

THE SUBJECT of this chapter is not strictly a part of sexual behavior but has an important bearing on it. Some writers (Hombron and Jacquinot, 1841: 320; Jacquinot and Pucheran, 1853: 156; Buller, 1888, 294; Sharpe, 1902: 138) have attempted to distinguish the sexes by a difference in plumage, but I am unable to confirm any such difference. The first two authors state of the female that *"le jaune de la tête est moins pur, moins vif."* These French voyagers were at the Auckland Islands in early March, a period when most breeding Yellow-eyed Penguins molt. The illustration in Jacquinot's Atlas (1842 and 1853: pl. 33, fig. 2) is, judging by the shortness of the tail, of a bird not long molted, and is probably the male described (1841: 320). The colors of the new plumage are particularly bright. Probably the female taken had not commenced her molt. In that event, the crown would be a sandy color. Certainly if both had just molted there would have been no noticeable difference in the color of the yellow feathers.

EARLY IDENTIFICATION OF SEX IN PENGUINS

The first season of observation passed without any progress whatsoever towards a solution of the problem of differentiation of sex. Something had to be done. In the second season I noted that when both birds were present at the nest during the daytime, between the laying of the first and second eggs and for a few days before oviposition, it was one particular bird that occupied the nest in the majority of cases and often in every case. Eventually, I arrived at one nest to find an egg obviously not long laid and covered with blood. One bird was badly smeared and the other was clean. That was a beginning. Having acquired these facts, I was bold enough to sex tentatively the mated pairs at the remaining seven nests.

In the laying span of three weeks of the third season (1938-39), I visited daily 30 mated pairs in three colonies and examined the vent of at least one partner, and of both if present, not long after each egg was laid. The procedure was repeated in 1939-40 on 26 mated pairs in four colonies. As the Yellow-eyed Penguin changes its mate frequently, it was not long before I could test my work. Not once have I had the mortification of seeing two "males" or two "females" mated.

Measurements of Sexes

Shortly after I began banding penguins I realized that there was considerable variation in size. It was therefore necessary to

Table 2

Measurements of Breeding Yellow-eyed Penguins

	Sex	n[1]	Mean mm.	δ[2] mm.	SE$_m$[3]	Range mm.
Bill	♂	66	55.14	1.52	0.18	51.00 to 58.75
	♀	70	53.76	1.79	0.20	49.25 to 57.75
Flipper	♂	66	215.19	3.70	0.46	207 to 223
	♀	70	206.35	5.05	0.60	197 to 215
Toe	♂	66	91.71	3.56	0.44	85 to 103
	♀	70	86.62	2.36	0.28	80 to 92
Tail	♂	42	64.00	4.71	0.72	56 to 77
	♀	47	60.72	5.42	0.79	45 to 71

Difference between Sexes:	Bill	1.38	± .28[4]
	Flipper	8.84	± .76
	Toe	5.09	± .52
	Tail	3.28	±1.07

[1] Number of individuals measured.
[2] Standard deviation of mean.
[3] Standard error of mean.
[4] Standard error of the difference.

TABLE 3

Classification of Measurements of Breeding Yellow-eyed Penguins

	Class interval mm.	Number of birds		Percentages	
		♂	♀	♂	♀
Bill	58.0 to 59.9	2		3	
	56.0 to 57.9	24	7	36	10
	54.0 to 55.9	30	24	45	34
	52.0 to 53.9	9	29	14	41
	50.0 to 51.9	1	8	2	12
	48.0 to 49.9		2		3
Flipper	220.0 to 224.9	7		11	
	215.0 to 219.9	32	3	48	4
	210.0 to 214.9	23	19	35	27
	205.0 to 209.9	4	18	6	26
	200.0 to 204.9		26		37
	195.0 to 199.9		4		6
Toe	101.0 to 103.9	2		3	
	98.0 to 100.9	0		0	
	95.0 to 97.9	11		17	
	92.0 to 94.9	19	1	29	1
	89.0 to 91.9	24	12	36	17
	86.0 to 88.9	9	36	14	52
	83.0 to 85.9	1	18	1	26
	80.0 to 82.9		3		4
Tail	76.0 to 78.9	1		2	
	73.0 to 75.9	1		2	
	70.0 to 72.9	2	2	5	4
	67.0 to 69.9	7	5	17	11
	64.0 to 66.9	8	6	19	13
	61.0 to 63.9	15	13	36	27
	58.0 to 60.9	6	8	14	17
	55.0 to 57.9	2	6	5	13
	52.0 to 54.9		6		13
	49.0 to 51.9		0		0
	46.0 to 48.9		0		0
	43.0 to 45.9		1		2

measure and weigh all birds whose sex was definitely known. In addition others were handled in the hope that subsequently their sex would be discovered, as eventually happened in many instances.

Measurements will be considered first. In measuring live birds the element of error tends to be great, but I have been as careful as possible. The measurement of the flipper is the most difficult to

TABLE 4

A Comparison of Differences in Measurements between Mated Pairs of Yellow-eyed Penguins

Bill		Toe		Flipper		Tail	
Interval of difference mm.	n[1]	Interval of difference mm.	n[1]	Interval of difference mm.	n[1]	Interval of difference mm.	n[1]
♂ longer							
						17 to 16	1
		15 to 14	2			15 to 14	1
5.75 to 6.5	6	13 to 12	4			13 to 12	1
4.75 to 5.5	4	11 to 10	3	22 to 19	3	11 to 10	5
3.75 to 4.5	12	9 to 8	10	18 to 15	15	9 to 8	1
2.75 to 3.5	10	7 to 6	18	14 to 11	22	7 to 6	5
1.75 to 2.5	21	5 to 4	33	10 to 7	22	5 to 4	9
.75 to 1.5	18	3 to 2	19	6 to 3	26	3 to 2	10
.5♂ to .5♀	19	1♂ to 1♀	11	2♂ to 2♀	14	1♂ to 1♀	8
.75 to 1.5	9	2 to 3	3	3 to 6	4	2 to 3	4
1.75 to 2.5	6	4 to 5	3			4 to 5	3
2.75 to 3.5	1					6 to 7	5
♀ longer							
Totals	106		106		106		53

[1] Number of pairs of birds.

make. From a point at the posterior edge of the armpit where the flipper joins the body, one end of a ruler was placed and allowed to extend over the top of the fully stretched flipper to the farthest point at the tip. To obtain the measurement of the toe, the left thumbnail was placed at the end of the toe joints. Allowing the ruler to touch the thumbnail, I measured the toe to the end of the claw. The length of claw varies according to the age of the bird and according to the rocky or sandy nature of the colony. By placing the ruler between the central rectrices as they leave the

TABLE 5

Table 4 Summarized in Percentages

Bill Intervals mm.	%	Toe Intervals mm.	%	Flipper Intervals mm.	%	Tail Intervals mm.	%
♂ longer							
6.5 to .75	67	2 to 15	84	3 to 22	83	2 to 17	62
.5♂ to .5♀	18	1♂ to 1♀	11	2♂ to 2♀	13	1♂ to 1♀	15
.75 to 3.5	16	2 to 5	6	3 to 6	4	2 to 7	23
♀ longer							

flesh, I measured the tail to the tip of the longest feather, which was not always a center one. The bill was measured with dividers extended from the basal edge of the culminicorn where it touches a thin piece of skin, to the tip.

In Graph A the measurements of the bill, tail, toe, and flipper of 136 breeding birds are given. To allow for errors in measurements class intervals of 2 mm., 3 mm., 3 mm., and 5 mm. respectively have been used. In Table 3 the percentages of each sex in the same class intervals are given.

In considering the significance of a difference between means the criterion has been accepted that it must be at least three times the value of the standard error of the difference. On this basis the measurements given in Table 2 are all significant, although that for the tail has not much to spare.

As indicated by Table 3, 83 per cent of the males have a flipper of from 210.0 to 219.9 mm., whereas 90 per cent of the females fall between 200.0 and 214.9 mm. With the toe, 65 per cent of the males are from 89.0 to 94.9 mm., and 77 per cent of the females are from 83.0 to 88.9 mm. For the bill, however, there is considerable overlap between the sexes. Ninety-five per cent and 86 per cent of the males and females respectively fall between 52.0 and 57.9 mm. In the intervals 54.0 to 57.9 mm., 82 per cent of the males are placed and from 52.0 to 55.9, 76 per cent of the females. Regarding the tail, of which there are fewer records, 86 and 68 per cent of the

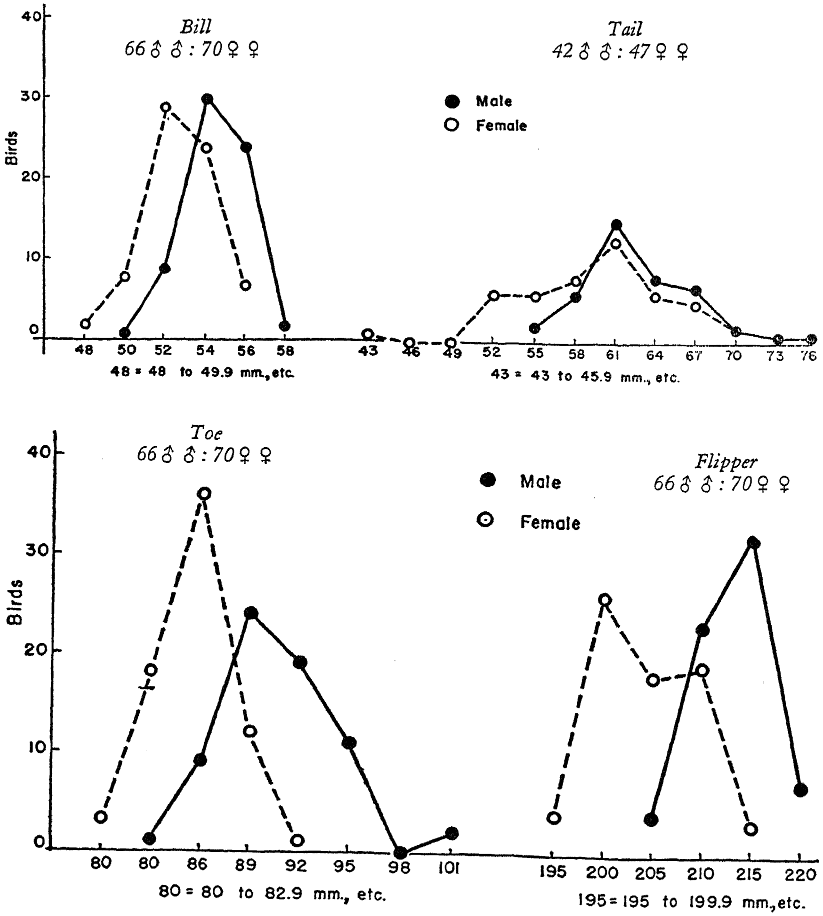
TABLE 6

Details of Eight Breeding Penguins

Number and Sex	Years observed	Number of mates	Number of seasons unemployed	Bill mm.	Toe mm.	Flipper mm.
20♂	8	3	3	51	85	212
75♀	8	4	..	56½	87	215
Z10♀	2	1	..	50	80	197
34♂	8	2	1	56¼	95	218
27♀	8	2	..	50¼	85	200
636♀	5	1	..	49¼	88	207
M29♀	1	1	..	49¾	88	204
A10♂	2	1	1	55¾	89	208

records of males and records of females respectively lie between 58.0 and 69.9 mm.

These differences are further amplified by Tables 4 and 5, which indicate that 84 per cent of the males have longer toes, 83 per cent longer flippers, 67 per cent longer bills, and 62 per cent longer tails. The corresponding percentages for females with longer measurements are 6, 4, 16, and 23. In between these two groups are a number of mated pairs between which the differences



GRAPH A: Measurements of Breeding Yellow-eyed Penguins are either nonexistent or small. A still further amplification of the differences between the sexes may be noted in Graph A.

Although the general rule is that the male is the larger sex, particulars in Table 6 make it clear that such is not always the case. Bird 20 is the smallest male and was smaller than his three mates 35, 5, and 18. To my knowledge Birds 34 and 27 were mated for six consecutive seasons. Birds 75 and Z10 are the largest and smallest females respectively. The females 636 and M29 are the only two breeding birds found with bills shorter than 50 mm. The male A10 is rather small, and since his mate also was small it was not until the latter mated with a bird whose sex was known that I was sure of the sex of A10.

In summary, it is apparent that the margin of difference between the bills of the sexes is not great enough to form a safe guide for tentatively estimating the sex of the Yellow-eyed Penguin. The more consistent differences in toe and flipper are more reliable.

WEIGHT OF SEXES

Wherever it has been possible to weigh a mated pair together, the female is usually the lighter. Care, however, must be taken, for several factors may upset this general rule. For instance, relative weights between the sexes will be changed if one of the mated pair has fasted longer in the winter or in the pre-egg stage. Other disturbing factors are the length of time that a particular bird has been incubating, or whether it has fed or is about to feed a chick. Finally, if the birds are at different stages in their molt their weights will not be comparable. All these factors affect weight, so that when an observation is made, a male, normally heavier than his mate, may be lighter.

A good example is the case of the male X16 and the female X15. When weighed near the end of the guard stage, X16 weighed 11¾ pounds, but he had been guarding his chicks all that day and the previous night. When X15 arrived, I weighed her before she fed the chicks. She registered 13 pounds. Now a penguin at this

Table 7

Weight Statistics for 119 Breeding Pairs

Number of pairs	Sex	Mean pounds	δ[1] pounds	SE$_m$[2]	Range pounds
80	♂	12.19	0.74	0.08	10.75 to 14.00
	♀	11.31	0.70	0.08	9.50 to 12.75
39	♂	12.63	1.00	0.16	10.75 to 14.75
	♀	11.61	0.98	0.16	10.00 to 13.75
	Difference	0.88		±0.11[3]	
		1.02		±0.23	

[1] Standard deviation.
[2] Standard error of mean.
[3] Standard error of the difference.

period delivers about one pound of food to the offspring, which means that if she had been weighed half an hour later she would have weighed approximately 12 pounds. If it had been 18 hours later still (the stage at which X16 was weighed), she would have been much lighter. A perusal of Table 12 will indicate that in the interval of 35 to 41 days, 20 females ranged in weight from 10 to 12 pounds, for an average of 10.87 pounds. This was the stage at which X15 was weighed, and her weight would have fallen within this range.

It is obvious, therefore, that if weights are to be used for comparison it should be made quite certain that the basis of comparison is the same for each sex.

The weights of the 80 mated pairs of penguins given in the first part of Table 7 were collected from the fourth week of incubation

Table 8

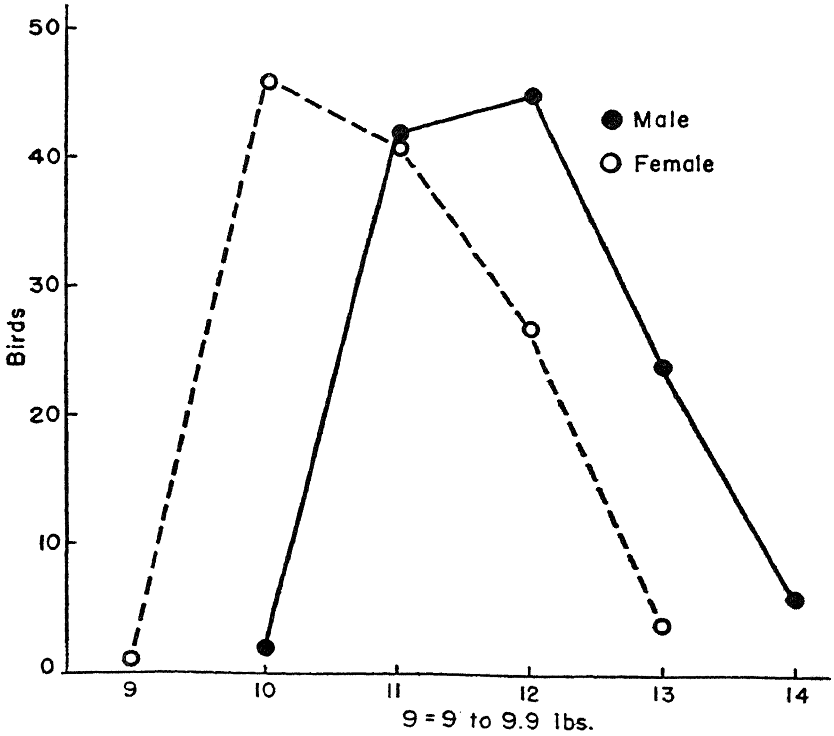
Classification of Weights of 119 Breeding Penguins

Class interval pounds	Number of birds		Percentages	
	Male	Female	Male	Female
9.0 to 9.9		1		1
10.0 to 10.9	2	46	2	39
11.0 to 11.9	42	41	35	34
12.0 to 12.9	45	27	38	23
13.0 to 13.9	24	4	20	3
14.0 to 14.9	6		5	

to the end of the guard stage at a period when the relative weights of the sexes were normal. The weights of each mated pair, however, were not recorded on the same day nor under equal conditions. For example, some birds must have been weighed shortly after change of guard and others at various times up to the change-over. It is hoped that the number of cases taken is sufficient to spread this variation evenly.

The 39 mated pairs whose weights are given in the second half of Table 7 were taken on the same day in the winter months. As far as I could tell, the conditions were equal.

As the difference between the sexes in the second set of weights is significant, clearly the male is on the average the heavier bird. It will be noticed that the difference between the weights of



Graph B: Weights of 119 Mated Pairs of Yellow-eyed Penguins the 80 mated pairs is also significant. This would seem to indicate that individual variations due to the method of weighing have been evened out. There is evidently about one pound of difference in the average weight between the sexes when they are weighed under equal conditions.

When the whole 119 pairs of weights are considered as in Table 8 it will be observed that there is considerable overlap. For example, there is an almost equal number of each sex in the interval 11.0 to 11.9 pounds. Eighty-seven (or 73 per cent) of the males occur between 11.0 and 12.9 pounds, and the same number of females between 10.0 and 11.9 pounds. Graph B further amplifies the foregoing remarks.

VARIATIONS IN WEIGHT THROUGHOUT THE YEAR

Each month an endeavor was made to collect as many weights as possible up to one hundred. It was not practicable to take a definite number of individual birds and follow them throughout the whole year. Some were handled a few times, others many times. Those factors militating against obtaining an even sample have been enumerated at the beginning of the previous section. It is hoped, however, that the results will indicate well-defined tendencies in weight fluctuations throughout the year. As the mean monthly weights of the sexes as signified in Graph C remain in a relation to each other that can be explained by observations made in the field, the sample taken is probably representative.

From 1 May to 23 August all birds of breeding age are counted whether or not they bred the previous or succeeding year. All were potential breeders, and failure to secure a mate in the breeding season does not interfere with the weights of these birds in the winter. At other times, however, the fact of being unemployed is likely to influence weights, so that such weights are excluded. From 24 August to 31 October only mated pairs are considered. Subsequent to that and up to the end of April, only either parents still attending chicks or those whose chicks have been successfully reared are included. Birds which lose chicks enter another category which influences weight.

Graph C is divided into 13 divisions, nine of which coincide with the months November to July inclusive. The remaining three months are divided into four parts. The first extends from 1 August to 23 August, which marks the end of the winter. In the second phase from 24 August to 15 September the sexes spend much time ashore fasting until the first eggs begin to appear about the latter date. Then from 16 September to 7 October the vast majority of the eggs are laid, with odd ones appearing after 7 October. In the last period from 8 October to 31 October all birds are incubating.

Beginning with January, it will be noted, the sexes weigh 12.35 and 11.25 pounds respectively. In February most of the chicks depart, leaving the parents time to fatten prior to the molt, which actually begins in the last week of the month, thereby causing the weight recorded in the graph to rise steeply. In March a large majority of the parents begin their molt, a fact which is reflected in the highest peak reached by the graph. By April, only a few of the breeding birds have yet to complete the molt. May includes only those birds which have completed their molt, many of which have not regained their normal weight. This results in the lowest weights reached by the penguins.

A complete recovery from reproductive and molting worries has been made by June, and is indicated by a fairly sharp rise to what probably is their normal weight. In July there is a further rise in weight. This apparently functions as a reserve drawn upon in periods of fast in the approaching pre-egg period. The weights of the birds continue to rise from 1 August to 23 August for both sexes, and it will be noted that the males increase in weight far more quickly. It will be remembered, too, that the males are the first to stay ashore in the daytime; that is to say, they indulge in fasting, generally speaking, before the females. As a result of this fast the mean weight for males drops steeply from 24 August to 15 September, so that for the first and only time the males are lighter than the females, which have remained the same as in the previous period.

From 16 September to 7 October, however, the mean weight for males has risen slightly and the mean weight for females dropped suddenly. This is due to the occupation of the nests by the females and to the departure of the males in the daytime for some food. For the remainder of October there is no change in weight for the males, but the mean weight for females drops a little further still. Eggs continue to be laid sometimes as late as 15 October, and there are large numbers of females which have not recovered from the fast that occurs just before and during egg-laying. By this last period, the males have mostly regained their normal weight. In November the weights of males rise further still, and the females manifest an improvement which occurs while the birds are incubating, in spite of the fact that some spend as long as five days on the eggs without relief.

Early in November the eggs begin to hatch and have finished towards the end of the month. Feeding chicks at this stage does not make very great demands on the parents. Each parent enters the water at least every second day and sometimes on consecutive days, enabling it to feed itself more frequently than during incubation.

As the chicks grow older, they require more and more food, so that just prior to the termination of the guard stage at the end of December, the parents are working hard. The effect of this extra strain is reflected by a decrease in weight. As soon as the chicks are left to look after themselves during the day while both parents fish, this strain is relieved. The task of feeding the chicks is easy for some time, and the second parent to return seldom has to disgorge much food. Theoretically, therefore, the weights of the adults should increase in January, and, as shown in the graph, this increase does occur. When the chicks are nearly fully fledged, however, and are beginning to demand from 1½ to 2 pounds of food each day, the strain on the parents theoretically is once more severe, and there should be a fall in weights in the final three or

Fig. 16. Kiss-preen. Further behavior following that shown in fig. 15.

Fig. 17. Female 115 bends down to inspect a chick, 35 days old. This act is not a love-habit nor is it "bowing."

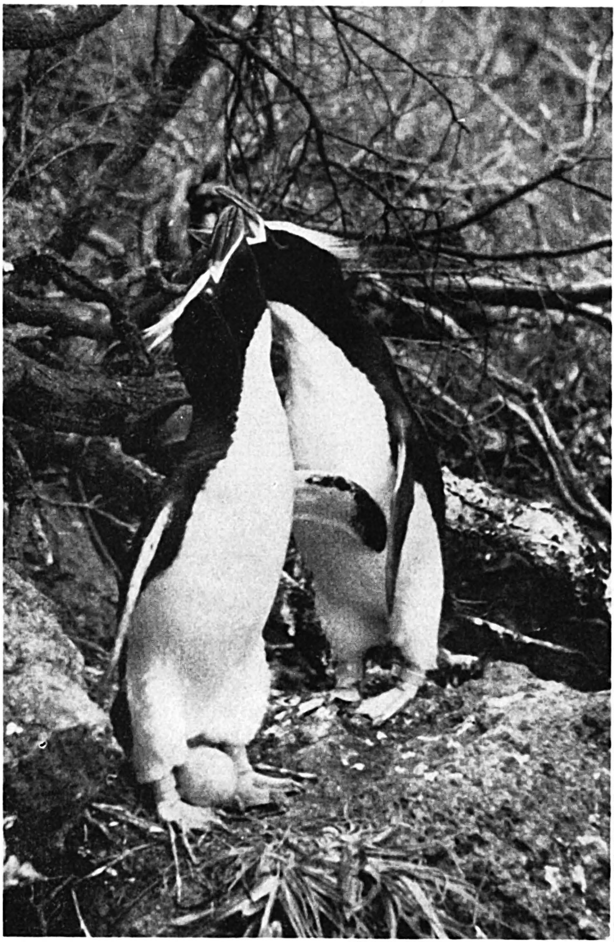


Fig. 18. Ecstatic. The position of the birds in the first phase of the attitude.

Fig. 19. Ecstatic. The same birds in the second phase of the "ecstatic."

four weeks the chicks are ashore. The number of January weights taken is not sufficient to draw a definite conclusion in this regard. Those for February contain some from feeding birds and also some from birds about to molt. If the weights of only these birds which still are feeding their young were included there would probably be a slight decrease from January as there was after November. For example, on 3 February 1940, three females with chicks weighed 11 pounds, 11 pounds, and 10¾ pounds, respectively, and on 5 February and 23 February two males weighed 10¼ and 11¾ pounds.

Tables 9 and 10 give the complete statistics of the weights of the sexes as shown in Graph C.

The weights of several individuals throughout the year will now be given. There is considerable fluctuation, but when read in conjunction with Graph C the result is usually easily interpreted.

On 14 September 1940 the late-laying female 73 weighed 14 pounds, which signified that she had not begun her period of fasting. Seven days later, however, she was down to 11¾ pounds, an indication that she had been ashore most of that week. On 28 September she weighed 11½ pounds but had had some food. When within two days of laying her second egg, on 5 October, she weighed only 10½ pounds, thus reflecting the stress of this period. On 17 November with one chick out of the egg and the other hatching, she weighed 12 pounds. As her excreta were white, she had just changed guard. Her mate 74, which was still with her, weighed 12¼ pounds, even though his excreta were discolored. This is an example demonstrating that although birds fast for some days in the period of incubation it must be a rest period. On 8 August, 74 weighed 13½ pounds and on 14 September 12¼ pounds, so that in between these dates, before he started occupying the nest at the beginning of the pre-egg period, he must have weighed more than 13½ pounds. On 28 September, he was down to 11 pounds, which was half a pound lighter than his mate on the same day.

The weight of male 34, of 17 pounds on 3 March 1939, was taken just after he had commenced his molt; that on 1 April of 9½ pounds, just after he had entered the water when the molt was completed; and that on 6 May was 12½ pounds. This pro-

TABLE 9

Monthly Statistics of Weights of Male Yellow-eyed Penguins

Month	Number of males	Mean pounds	δ[1] pounds	SE_m[2]	Range pounds
January	46	12.35	0.99	0.15	10.25 to 14.00
February	18	13.29	2.63	0.63	10.00 to 18.00
March	41	15.04	2.26	0.35	10.75 to 19.50
April	38	12.67	2.39	0.37	9.50 to 17.00
May	21	11.75	0.72	0.16	10.50 to 13.75
June	34	12.38	0.94	0.16	10.75 to 14.00
July	32	12.53	0.85	0.15	11.00 to 14.50
1 to 23 Aug.	44	13.79	0.80	0.12	12.00 to 15.50
24 Aug. to 15 Sept.	52	11.83	0.96	0.13	10.50 to 14.75
16 Sept. to 7 Oct.	73	11.95	0.69	0.08	10.50 to 14.75
8 to 31 Oct.	53	11.94	0.63	0.09	10.75 to 13.75
November	100	12.37	0.83	0.08	11.00 to 14.00
December	100	11.76	0.78	0.08	10.25 to 14.25

[1] Standard deviation.
[2] Standard error of mean.

TABLE 10

Monthly Statistics of Weights of Female Yellow-eyed Penguins

Month	Number of females	Mean pounds	δ[1] pounds	SE_m[2]	Range pounds
January	38	11.23	0.62	0.10	10.25 to 12.50
February	22	12.26	2.21	0.47	10.50 to 18.00
March	59	13.66	2.55	0.33	8.75 to 18.50
April	32	11.74	2.12	0.37	8.00 to 15.50
May	16	10.61	1.04	0.26	8.50 to 12.00
June	16	11.41	0.72	0.18	10.00 to 12.50
July	13	11.81	0.49	0.14	11.00 to 12.50
1 to 23 August	22	12.45	0.81	0.17	11.00 to 14.25
24 August to 15 Sept.	46	12.45	0.93	0.14	10.00 to 14.75
16 Sept. to 7 Oct.	74	10.75	0.77	0.09	9.00 to 12.75
8 to 31 Oct.	62	10.68	0.62	0.08	9.50 to 12.25
November	100	11.10	0.76	0.08	9.75 to 13.00
December	100	10.97	0.75	0.08	9.75 to 13.25

[1] Standard deviation.
[2] Standard error of mean.

gression gives some idea of the speed with which he had recovered. His weights of 10¼ pounds on 31 January and 5 February 1940 respectively when feeding two chicks are very low. At that time I thought that this was perhaps due to a decline in health, especially as his mate 27 on 5 February weighed 11¾ pounds, after having fed the chicks. Seven subsequent weights, averaging 12.64 pounds from 6 July to 8 December, made it clear that his health was sound. Further, he was still present in 1945-46. On 29 September 1940, he weighed 12½ pounds, but 27, which had just laid her second egg, weighed only 10¼ pounds.

Of further interest are the data for the young two-year-old female 616, which, on 29 September when the second egg was laid, weighed 10¼ pounds. On 26 October, after nearly five weeks' incubation, she weighed 12¼ pounds, an indication that she had recovered in that period. On 18 August 1940, just before the pre-egg stage, the male 28 weighed 15½ pounds, the heaviest weight recorded for any bird at such a period. On 15 September after some time ashore, he weighed 11¼ pounds. On this same day two other males weighed only 10½ pounds each.

Successive individual weights in the winter do not always show an increase. For example, the male 72 weighed 14 pounds on 3 June 1939, and 12½ pounds a week later. On 29 April, two weeks after he had molted, the male 28 weighed 14 pounds, and his mate 8 weighed 12 pounds. On 13 June they weighed 12 pounds and 10¾ pounds respectively. I cannot explain these data.

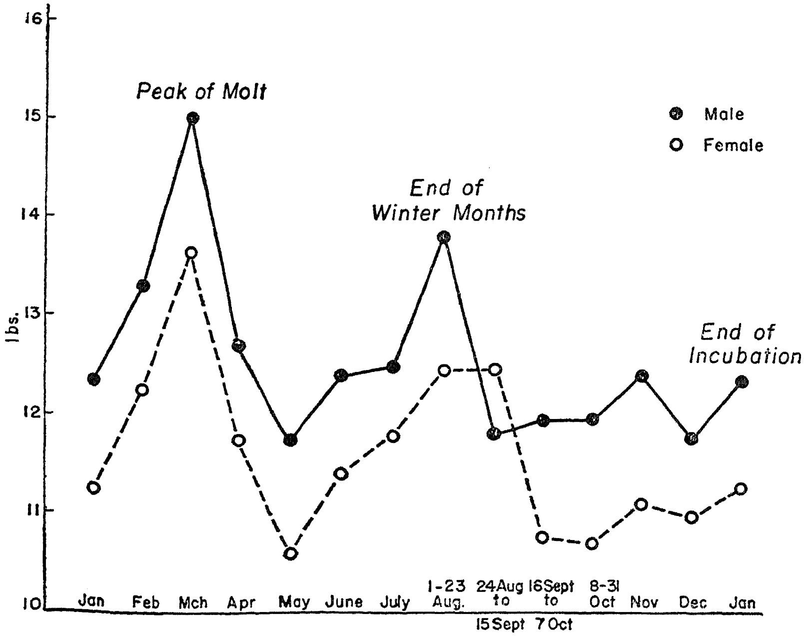
VARIATIONS IN WEIGHT IN RELATION TO LAYING OF FIRST EGG

In Graph C the monthly weights do not reflect the true correlation between the time the first egg was laid and the times before and after that event. For example, some of the females which had not begun to fast very assiduously till early October would be very heavy in the interval of 15 September to 7 October, thereby influencing the weights for that period.

In Tables 11 and 12 the weights of the sexes are given separately, divided into seven-day intervals from 56 days prior to deposition of the first egg to the end of the guard stage, when the chicks were abandoned during the day and both parents could fish simultaneously.

In Table 13 the differences between the weekly weights are analyzed statistically. Only seven of the 42 differences are significant. Six of them may be due to inadequate sampling, but one, that for the female between the intervals just before the first egg and just after, definitely is not. In the week before the first egg the females certainly tend to remain ashore, but in the next week, when the two eggs are laid, only odd females enter the water. This sudden and universal change in behavior is reflected in a marked difference in the mean weights of the two class intervals.

Speaking generally, there is little, if any, significant difference from week to week. Four other types of interval were employed.



GRAPH C: Mean Monthly Weights of Breeding Yellow-eyed Penguins throughout the Year

In weights taken at two-weekly intervals (Graph D), nine differences are significant out of 20; at three-weekly intervals, five out of 12 are significant; and the division of each stage into the equal parts gives five significant differences out of 10. It will be observed that as the intervals are widened the differences in weight tend to become more significant. A further tendency, however, is for important phases in the breeding cycle to be obscured.

In an endeavor to obviate this tendency a final broad grouping was made as shown in Graph E. All but one of the eight differences are significant, and the one exception is nearly so. One important point, however, is hidden. This is the fact that the females are heavier than the males for four weeks preceding the laying of the first egg, a phenomenon best appreciated by the use of weekly intervals as shown in Tables 11 and 12. In conclusion, Graph E indicates that there are several points from 56 days before the first egg to 48 days after hatching which manifest a significant difference statistically. Moreover, a close study of the behavior of the sexes during this period fully supports these statistics. There now follows a detailed description of this behavior in conjunction with the statistics.

Since the reader, if he so desires, may graph for himself the weekly intervals as recorded in Tables 11 and 12, I have thought it preferable to plot the two-weekly intervals. These will be found in Graph D. A further advantage of this last interval is the smoothing out of the curves, although a certain amount of information tends to become hidden in the pre-egg section.

Graph D begins towards the end of the winter months when the weights of both sexes are still increasing. The period from the forty-second day to the first day before the laying of the first egg is best discussed in weekly intervals, as a wider interval fails to reflect important changes in behavior. In the interval from the forty-second to the thirty-sixth day the males reach their heaviest weight, after which a steady decline occurs till the end of the interval from the seventh to the first day, when once more their weight begins to increase. From 40 days before the egg appears, not only do the males begin to stay ashore in the daytime, but they remain there for much longer periods than the females. Although some of the females stay ashore early they spend far more time at sea fishing than do their partners. Because of this fact the peak of weight of the females is not reached until the interval from the thirty-fifth to the twenty-ninth day.

The result of this phenomenon is that the weights of the two sexes towards the end of the interval from the thirty-fifth to the twenty-ninth day coincide. The females then begin to exceed the

Table 11

Mean Weekly Weights of Male Penguins from 56 Days before Egg is Laid to End of Guard Stage

Stage	Class interval days	Number of birds	Mean pounds	δ[1] pounds	SE$_m$[2]	Range pounds
Pre-egg	56 to 50	4	14.13	0.70	0.35	13.00 to 14.75
	49 to 43	2	13.38	0.22	0.16	13.25 to 13.50
	42 to 36	9	14.22	0.45	0.15	13.50 to 14.75
	35 to 29	10	13.82	0.83	0.26	12.50 to 15.50
	28 to 22	7	12.50	0.77	0.30	11.75 to 14.25
	21 to 15	13	11.96	0.46	0.13	11.00 to 12.75
	14 to 8	17	11.57	0.72	0.18	10.50 to 13.00
	7 to 1	17	11.47	0.50	0.12	10.50 to 12.25
Post-egg	0[3] to 6	20	12.04	0.61	0.14	10.75 to 13.00
	7 to 13	33	11.93	0.84	0.15	10.50 to 14.75
	14 to 20	16	11.90	0.73	0.18	11.00 to 13.75
	21 to 27	18	11.79	0.59	0.14	10.75 to 12.50
	28 to 34	21	12.33	0.91	0.20	11.25 to 14.00
	35 to 41	25	12.57	0.60	0.12	11.50 to 13.75
	42 to 48	20	12.27	0.61	0.14	11.00 to 13.50
Guard	0[4] to 6	31	12.51	0.85	0.15	11.00 to 14.75
	7 to 13	26	12.59	0.84	0.16	11.50 to 14.00
	14 to 20	27	12.12	0.91	0.18	10.50 to 14.00
	21 to 27	25	11.74	0.58	0.12	10.75 to 13.00
	28 to 34	22	11.47	0.59	0.12	10.25 to 13.25
	35 to 41	21	11.62	0.97	0.21	10.50 to 14.25
	42 to 48	12	11.91	0.83	0.24	10.50 to 12.50

[1] Standard deviation.
[2] Standard error of mean.
[3] Date of first egg.
[4] Date of hatching.

males in weight till the last week of the pre-egg period, when the weights are once more equal and the males regain the ascendancy. In the interval from the twenty-first to the fifteenth day, females are on the average slightly over one pound heavier than males. At this period, provided that the mated pairs are known and that one has some idea of the date in relation to the egg, it is possible to make a fairly reliable estimate of the sex of the individuals of any given pair. It is not even necessary to weigh the two birds. The heavy deposition of surplus fat, especially on each side of the center of the back, is an almost certain indication that the bird is a female. The male at this stage is thin and angular.

TABLE 12

Mean Weekly Weights of Female Penguins from 56 Days before Egg is Laid to End of Guard Stage

Stage	Class interval days	Number of birds	Mean pounds	δ[1] pounds	SE_m[2]	Range
Pre-egg	56 to 50	3	12.58	0.33	0.20	12.25 to 13.00
	49 to 43	2	12.75	----	----	12.50 to 12.75
	42 to 36	3	11.92	0.66	0.39	11.00 to 12.50
	35 to 29	4	13.81	0.72	0.36	12.75 to 14.75
	28 to 22	5	13.30	0.56	0.25	12.75 to 14.25
	21 to 15	11	13.05	0.62	0.19	12.00 to 14.00
	14 to 8	21	12.20	0.62	0.13	11.00 to 13.25
	7 to 1	18	11.57	0.63	0.15	10.50 to 12.75
Post-egg	0[3] to 6	39	10.42	0.52	0.09	9.00 to 11.50
	7 to 13	17	10.40	0.48	0.12	9.75 to 11.00
	14 to 20	22	10.76	0.55	0.12	10.00 to 12.25
	21 to 27	16	10.59	0.53	0.13	9.50 to 11.50
	28 to 34	16	10.94	0.79	0.20	10.00 to 12.25
	35 to 41	19	11.19	0.63	0.14	10.25 to 12.00
	42 to 48	21	11.29	0.61	0.13	10.25 to 12.50
Guard	0[4] to 6	34	11.46	0.62	0.11	10.00 to 12.50
	7 to 13	26	11.26	0.85	0.17	9.75 to 13.00
	14 to 20	24	10.84	0.67	0.14	9.75 to 12.25
	21 to 27	17	10.88	0.62	0.15	10.00 to 12.00
	28 to 34	27	11.27	0.94	0.18	9.75 to 13.50
	35 to 41	20	10.87	0.51	0.11	10.00 to 12.00
	42 to 48	22	10.43	0.52	0.11	9.75 to 11.50

[1] Standard deviation.
[2] Standard error of mean.
[3] Date of first egg.
[4] Date of hatching.

With the appearance of the first egg there is an abrupt change. In the interval from the seventh to the first day before the first egg, the males begin to seek food more often and the females tend to remain ashore. For some days after the first egg is laid, the females rarely enter the water and the males seldom stay ashore in the daytime. There are of course exceptions to this general rule. As a result of this change, the females reach their lowest weight level in the interval between the date of laying the first egg and 13 days thereafter. The males reach theirs before the egg is laid.

From these respective depression points the weights of both sexes gradually increase in the period of incubation until the highest peak in weight for the post-egg period is reached for both

TABLE 13

Differences in Weekly Means Taken from Tables 11 and 12

	Male			
Intervals	Difference pounds	SE$_d$[1]	Difference pounds	SE$_d$[1]
56 to 50 and 49 to 43	0.75	0.38	0.17	0.20
49 to 43 and 42 to 36	0.84*	0.22	0.73	0.38
42 to 36 and 35 to 29	0.40	0.30	1.89*	0.53
35 to 29 and 28 to 22	1.32*	0.40	0.51	0.44
28 to 22 and 21 to 15	0.54	0.33	0.25	0.31
21 to 15 and 14 to 8	0.39	0.22	0.85*	0.23
14 to 8 and 7 to 1	0.10	0.21	0.63*	0.20
7 to 1 and 0 to 6	0.57*	0.18	1.15*	0.17
0 to 6 and 7 to 13	0.11	0.21	0.02	0.15
7 to 13 and 14 to 20	0.03	0.23	0.36	0.17
14 to 20 and 21 to 27	0.11	0.23	0.17	0.18
21 to 27 and 28 to 34	0.54	0.24	0.35	0.24
28 to 34 and 35 to 41	0.24	0.23	0.25	0.25
35 to 41 and 42 to 48	0.30	0.18	0.10	0.19
48 to 42 and 0 to 6	0.24	0.21	0.21	0.17
0 to 6 and 7 to 13	0.08	0.22	0.20	0.20
7 to 13 and 14 to 20	0.47	0.24	0.42	0.22
14 to 20 and 21 to 27	0.38	0.22	0.04	0.21
21 to 27 and 28 to 34	0.27	0.17	0.39	0.23
28 to 34 and 35 to 41	0.15	0.24	0.40	0.21
35 to 41 and 42 to 48	0.29	0.32	0.34	0.15

*These differences are statistically significant.

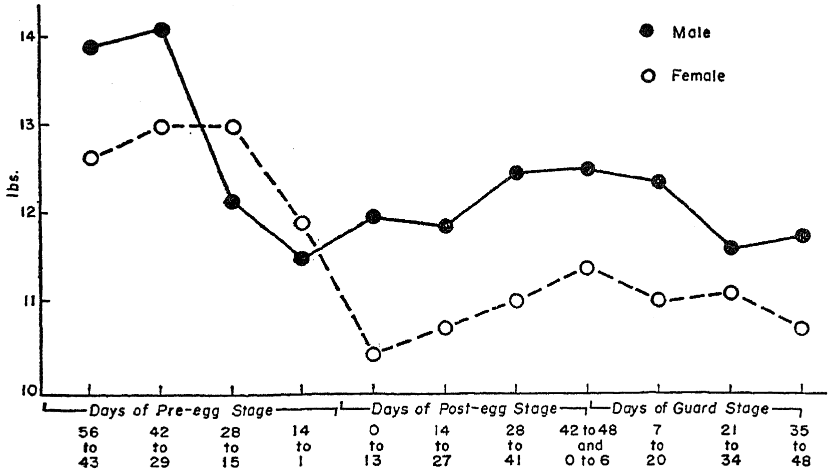
[1] Standard error of the difference.

sexes in the intervals of 42 to 48 days before hatching and from the day of hatching to six days thereafter. Soon after the parents begin to feed the chicks a decline in weight occurs. This indicates that even though the parents themselves acquire food daily, which they did not in the incubation stage, the additional task of feeding the chicks decreases the weight of the adults. At the end of the guard stage the adults have once more reached a low level, soon to be relieved when both birds begin to search for food together and leave the chicks to their own resources during the day.

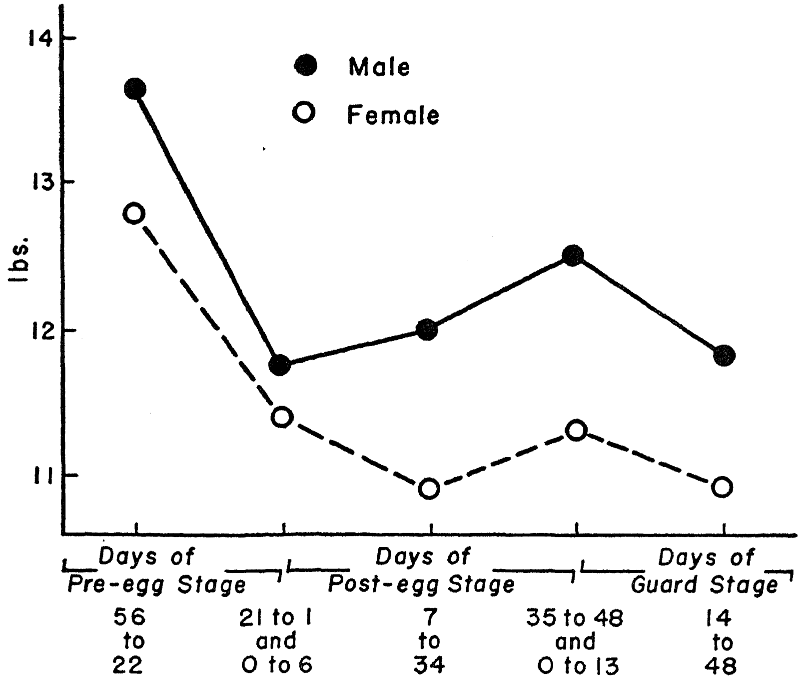
The graph for the guard stage tends to be irregular. This is the most difficult period in which to obtain an even sampling, as there is a great disparity in weight between a bird which has been ashore for nearly 24 hours and one that has just returned from the sea. The true test would be to weigh the birds at a definite period, say five or six hours after they had returned home. This, however, would be a colossal and almost impossible task.

SUMMARY OF SEX DIFFERENCES

The only certain way of sexing the Yellow-eyed Penguin, other than by dissection, is to examine the vent of both birds of a mated pair in the span of egg deposition. Subsequently, as mates are changed frequently, unsexed or doubtfully sexed birds will sooner or later mate with sexed birds. Failing the application of the above methods the following points will make fairly reliable tentative guides. Reliance placed on one is likely to prove faulty, but when a number can be assessed together for the one bird the conclusion is fairly sound. (1) At the end of the winter any exceptionally heavy birds are males. It is not safe to attempt to assess lighter penguins. (2) In the early days of the pre-egg stage the solitary bird at the nest in the daytime is usually a male. If the female is present with the male in the daytime the male is generally on the nest. (3) In the last few days before egg deposition the above roles are usually reversed. (4) In the second, third, and fourth weeks before the egg deposition the female is decidedly heavier than the male



GRAPH D: Mean Two-weekly Weights from 56 Days before Egg to End of Guard Stage



GRAPH E: Mean Weights at Wide Intervals from 56 days before Egg to End of Guard Stage and the deposit of fat on the female's back is so obvious that these two features are reliable guides to sex. (5) During the day, in the period between the laying of the two eggs, which is normally four days, there is, as a rule, only one bird at the nest. This bird is usually, but not always, the female. (6) In the first two weeks after the first egg the female is noticeably much lighter than the male. (7) At the incubation stage unemployed birds wandering about the colony, provided they are over two years old, are almost always males. Only rarely does a female wander about the colony at this time. (8) If these birds are discovered trumpeting, especially if solitary and from hidden positions in the bushes, it is further evidence that they are males. (9) Birds which are known to have had mates in a previous breeding season and are found without mates once all the eggs have been laid, are males. (10) From towards the end of the incubation period to a time just past the middle of the winter there is no definite way of deciding sex. The small birds are usually females, and the large birds, as a rule, are males. In the middle is a group composed of both sexes. The measurements and weights of these birds overlap. (11) When the birds are banded, males require a wider ring. This is a good index, but practice in applying the tests is necessary.

A striking testimony of the efficiency of these methods of estimating the sex of the penguins occurred in August 1945, when B10 was found dead with a large rock on top of him. On dissection he was definitely proved to be a male. From this fact has emerged a remarkable chain of discoveries. In the colony concerned, 29 male and 30 female mated birds have been under observation. Changes in partnership have been so numerous that by discovering the sex of B10 I now know for certain the sex of the 59 birds that are and have been breeding in the colony over a period of nine years. Not one of these birds had been wrongly sexed tentatively. The sexing of B10 also means that any new bird coming into the colony and mating with a present resident is sexed immediately.

DISCUSSION OF SEX DIFFERENCES AND MEASUREMENTS

Compiling data relative to the weights of birds in wild species has in the past received little attention. The taxonomist has been content usually with merely measuring his specimens. To explain this, Baldwin and Kendeigh (1938: 416) advance two possible reasons. The first may be the lack of a suitable portable weighing instrument. The second and more important reason is probably the recognized variability of bird weights and the consequent lack of appreciation of their importance. They state also that weights of birds are easy to obtain. Undoubtedly that is true of some species, but with the petrels and penguins on which I have been working the collection of weights is not easy. In fact, the gathering of data for Graphs C and D and Tables 11 and 12 was a colossal task.

In urging the need for bird weights Baldwin and Kendeigh remark (*loc. cit.*): "The weights of birds and the variations and fluctuations of these weights furnish criteria of considerable importance in the understanding of the physiological and ecological researches on the bird as a living organism. The physiology of the bird, its behavior, and the influence of the environment are interacting factors, no one of which can be understood without a knowledge of the two others."

Nice (1938: 1) has also advocated the need for weighing birds. In November 1937, at the Charleston meeting of the American Ornithologists' Union, she entered a plea to banders to "weigh their birds at every capture," and urged those already with data to analyze and obtain the greatest value possible from such data. She pointed out that weights of birds have two chief values. First, to visualize the size of a bird, it is just as necessary to know the average weight of a species as it is to know its length; second, there are many biological problems on which the weights of birds will throw light.

The authors named above have enumerated the most important sources of bird weights up to 1938, many of which deal with isolated weights of different species. Few provide data on fluctuations in weights over a period. It is this aspect of weights of birds with particular reference to seasonal variations that is pertinent to the present discussion.

According to Baldwin and Kendeigh (1938: 431, 435) most species show a maximum weight in winter and early spring and a decrease at the approach of the breeding season. Nice's observations (1937: 25-26) on the Song Sparrow show somewhat similar results. Marples (1942 and 1945) points out a similar trend in the Little Owl, *Athene noctua* (Scopoli), and in the Wax-eye, *Zosterops lateralis* (Latham).

Wolfson (1945: 109-121), however, objects that these generalizations are only partly true. He states that there exists in Juncos, *Junco oreganus* (Townsend), and other passerine birds which are migratory a significant correlation between an increase to a maximum body weight and the beginning of the spring migration. He produces convincing evidence in support of his contention. His impressive graph (p. 120) indicates that in the spring, migrants increase rapidly in weight, whereas residents continue to decrease. Further, he points out that the increase in the weight of the migrants is due to the deposition of fat, subcutaneously and intraperitoneally (p. 109).

The remarks of Wolfson are interesting in view of what happens in the Yellow-eyed Penguin. In this penguin there is not only a tendency to follow the same pattern of weight fluctuations as in migrant passerine species, but also a development of heavy deposits of fat as the breeding season approaches.

From the commencement of the winter to the onset of the pre-egg stage there is a gradual and steady increase in weight and fat deposition in both sexes. This is true not only of the group of penguins, as a whole, data from which were used to construct Graph C, but it is also true, in the main, of individuals which I was able to weigh several times in the period noted above. Further, although no birds were collected for autopsy, it was obvious that both sexes, and males in particular, were extremely fat by 24 August. Even the ability of these males to walk with their usual agility was impaired.

At the time when this fat is gradually accumulating, the testes are increasing in size as probably also is the ovary. The dissection of the male B10 and that of another bird killed by a fall of rock towards the end of the winter period, disclosed that the testes were much enlarged. The physiological state of the penguins eventually reached a condition that allowed them to stay ashore for a time without food and prepare for important functions at the pre-egg stage.

Probably there are external as well as internal factors that help to bring about these changes which culminate in the pre-egg stage. If so, these external factors, one of which is probably the increase in day length, apparently act differently on the sexes. The females reach their peak in weight and in deposition of fat later than the males and are later in beginning to stay ashore in the daytime; they do not, at first, fast as frequently as the males. Wolfson (1945: 110) found a comparable situation in his migrant passerines, a fact which explains why females arrive on the breeding grounds later than the males.

In summary, it will be seen that in the Yellow-eyed Penguin a steady increase in weight of body and in the deposition of fat precedes the pre-egg stage and that the females lag behind the males. The sexes, in this way, are prepared for the behavior patterns which will be released in the succeeding period. This preparation occurs at the correct time presumably because of the response of the endocrine glands to external factors in the environment. The response of the endocrine system then causes a change in the metabolism which results in an accumulation of surplus fat.

When the pre-egg stage arrives, a reversal in the relative weights of the sexes occurs. From the end of the fifth week before the advent of the first egg, the female Yellow-eyed Penguin becomes on the average heavier than the male and retains this advantage until just before the egg is laid. (See Tables 11 and 12.) The reason for this is twofold, as previously noted. It is not due to the unlaid eggs, which average about 136 grams and are laid four days apart.

The advantage in female weight in species where the male is the heavier during most of the year has been recorded elsewhere. When occurring just before the laying period, it has been thought to be due to the presence of the eggs (Nice, 1937: 27 and 1938: 7; Marples, 1942: 247). Another factor may be that the male's weight tends to decrease because of his greater activity, especially noticeable in species which are highly territorial. Such a possibility is suggested by Nice (1937: 25).

In species where only the female incubates there are records indicating that she continues to be heavier even after the eggs are laid and during the subsequent incubation (Nice, 1937: 26-27 and 1938: 7). Nice also quotes Riddle and Braucher as stating that there is an eight per cent rise in weight during incubation in pigeons and doves (Columbidae). From this she considers that the incubating period is not the arduous task that some people think. For the male, in species where he does not share the task of incubation (so far as records are available), his weight continues to decline. This is recorded for the Song Sparrow (Nice, 1937: 22) and the Little Owl (Marples, 1942: 247).

In the Yellow-eyed Penguin, incubation is shared equally by the sexes. The female remains lighter than the male throughout, and, in fact, at the beginning of the period she reaches one of her two lowest points of depression. This is due to an increase in fasting towards the end of the pre-egg stage and especially during egg-laying. From this low level the weight of the female rises steadily (Graph D) until the eggs are hatched. The male's weight also registers a steady increase. These facts support Nice's view that incubation is a recuperative period.

It would seem that where both male and female incubate, both gain in weight. Where the female alone incubates, the female only becomes heavier. A knowledge of what happens where only the male incubates, as in the Red-necked Phalarope, *Phalaropus lobatus* (Linnaeus), would be of considerable interest.

With the hatching of the chicks, all parents, whether male or female, which assist in feeding the young, appear to decrease in weight, indicating that such a period is one of stress. This statement applies to the Song Sparrow; the Tree Sparrow, *Spizella arborea arborea* (Wilson) (Nice, 1937: 27); apparently to the Little Owl (Marples, 1942: pl. 20); and certainly to the Yellow-eyed Penguin. (See Graph D.) With the last-named species the parents increase in weight again after the end of the guard stage. (See Graph C.)

Finally, weights in the period of molt should be considered. Immediately following the breeding season, in autumn, the molt commences in most species of penguins for both sexes. The greatest amount of fat is developed (it is greater than at the end of the winter months), and the heaviest weight of the yearly cycle is attained just as the molt commences; but on the completion of the molt the birds register the minimum weight for the year.

In regard to other species, Nice (1937: 22) indicates that Song Sparrows are undoubtedly at their lowest weight in August and September when the molt occurs. Beck found a heavy loss at this time in four domestic fowls (Nice, 1938: 7). In the Little Owl, Marples (1942: 247) thinks that the minor loss in weight he recorded in the autumn was due to molt.

The contrary view was held by Baldwin and Kendeigh (1938: 463), who say that "molting and renewal of feathers in August and September is not joined with a decrease in weight; rather there is an increase in weight at that time." In support of this, Laskey (Nice, 1938: 7) reports the "highest weight during the inactive period of molting" in male Mockingbirds, *Mimus polyglottos polyglottos* (Linnaeus). From information given later, a similar situation appears to obtain in the Broad-billed Prion, which seems to be heaviest in the period of molt immediately following the breeding season.

Prior to concluding, it will be pertinent to discuss the Broad-billed Prion and the Diving Petrel relative to their seasonal

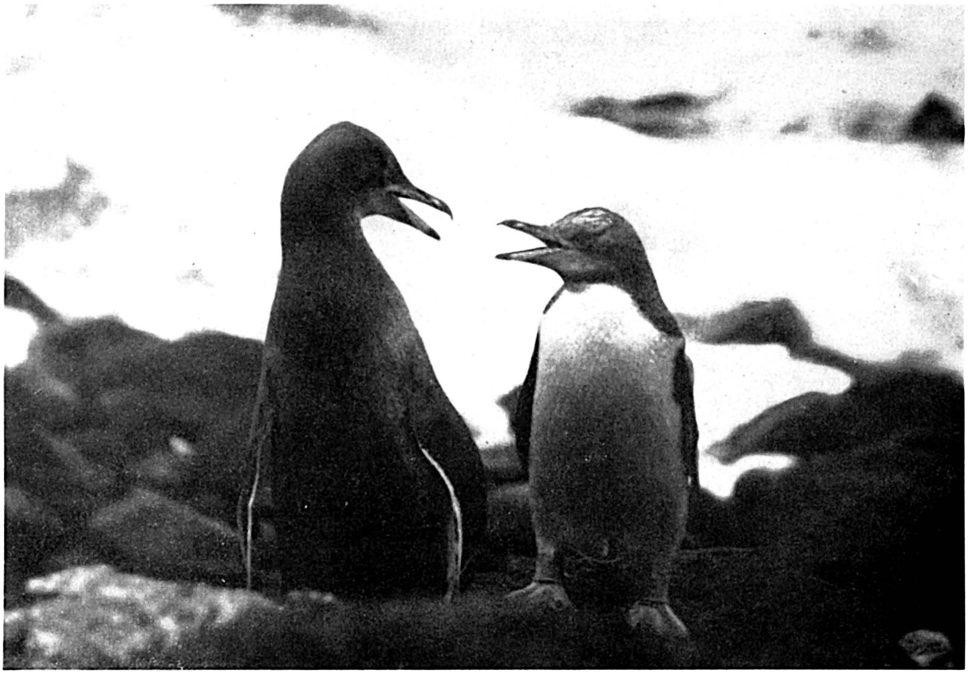


Fig. 20. Tête. The nearest approach to mutual outright fighting in the Yellow-eyed Penguin. Two juveniles are seen here.

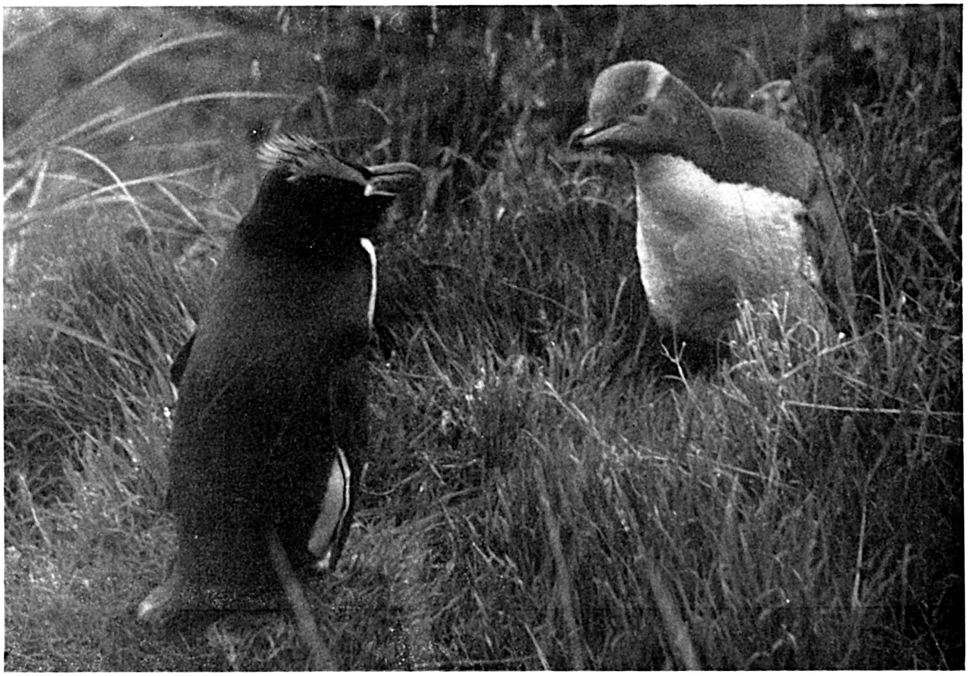


Fig. 21. Glare. Female 115, five days in molt, "glares" at female Erect-crested Penguin which is trying to impose her company on 115.

Fig. 22. On the left, a normal egg of the Yellow-eyed Penguin, approximately life-size; on the right, the only abnormal one the author has seen.

weights, of which a few scanty records have been made (Tables 14, 15, and 16).

TABLE 14

Statistics of Seasonal Weights of the Broad-billed Prion

Date	Remarks	Number of weights	Mean grams	δ[1] grams	SE_m[2]	Range grams
12 to 20 May		13	206.6	14.75	4.10	177 to 227
24 August to 2 September	laying begins end August	19	189.4	16.65	3.78	160 to 220
6 to 16 December	end of chick stage	27	189.8	17.65	3.39	170 to 235
7 February to 7 March	all in molt	22	197.2	13.70	2.87	172 to 224

[1] Standard deviation.
[2] Standard error of the mean.

TABLE 15

Difference in Weights in Table 14

Periods	Difference grams	SE_d[1]
between May and August	17.2	5.06*
" August and December	0.4	4.33
" December and February	7.4	3.73
" February and May	9.4	4.55
" December and May	16.8	5.02*

* These differences are statistically significant.
[1] Standard error of the difference.

TABLE 16

Statistics of Seasonal Weights of the Diving Petrel

Date	Remarks	Number of weights	Mean grams	δ[1] grams	SE_m[2]	Range grams
23 to 26 August	end of winter months	26	136.15	6.25	1.25	125 to 152
22 December to 30 January	chick stage	100	124.10	10.27	1.02	108 to 158

Difference 12.04 ±1.44*

[1] Standard deviation.
[2] Standard error of the mean.
*This difference is statistically significant.

Before attempting to interpret the tables it will be advisable to summarize briefly the annual cycle of the species concerned; more details are published elsewhere (1943a, 1944a, 1945b). As for the Prion, the period from 12 May to 20 May is the middle of the non-nesting season and, when handled, all birds, whose breeding status was unknown, had completed their molt. Records were possible because this species visits the shore at irregular intervals in the winter. The period from 24 August to 2 September marks the end of the pre-egg stage and the beginning of laying. One or two of the 19 birds weighed in this period were incubating, but the breeding status of the others was again unknown. The birds caught between 6 December and 16 December were all feeding chicks which were near the end of their stay in the burrows. Some adults were weighed before they had fed their chicks and others afterwards. As chicks may receive up to 80 grams of food in a night (1944a: 195), the range in weight of feeding adults is very wide. Finally, the period between 7 February and 7 March is one when the molting period occurs. On 7 February 1941, I was present on the island of Whero when the Broad-billed Prion made its first appearance on the island after the completion of the breeding season a little more than a month earlier. All individuals inspected were molting and all showed considerable wear on the toes, indicating that they were old birds. Their breeding status was unknown.

For the Diving Petrel only two periods in the annual cycle when weights were taken are available for comparison. The first extended from 23 August to 26 August, which probably represents the beginning of the pre-egg period. The birds were all caught and weighed at night just after they had landed. Some were known to be breeding birds, but others were unbanded. Those handled in the second period—22 December to 30 January—were all attending chicks, and were weighed either before or after they had fed the chicks. As in the Prion, there is, for this reason, a wide range in the weights of the parents.

In the light of this information, Tables 14 to 16 will be discussed. The difference between the December and February weights of the Prion, as shown in Table 14, is not significant as it stands, but when one realizes that the December weights of some birds include a quantity of undelivered food for the chicks, one perceives that the real difference would be much greater than as shown in Table 14, and possibly statistically significant. This suggests that the month at sea, in which the molt commences, constitutes a recovery period from the stress of feeding the young. When penguins molt they remain ashore and fast the whole time which, in many species, extends for more than three weeks.

In the period of molt, from 7 February to 7 March, the Prions were weighed on four separate dates. These weights do not show any significant difference, lending support to the views of Baldwin and Kendeigh that birds do not lose weight while molting.

In the Broad-billed Prion, the difference between the May and December weights, however, is significant, and, as May is the middle of the non-nesting season, the weights would probably have been much higher still at the beginning of the pre-egg stage, at approximately the end of July. This is also the condition in the Diving Petrel, a fact which indicates a significant difference between early pre-egg and chick-stage weights. It would seem therefore that weights in the two petrels under discussion rise in the non-nesting season to a peak at the beginning of the pre-egg stage as in migrant passerines and penguins, and drop to a depression point in the period when chicks are being fed.

Finally, Table 14 indicates also that, as in the Yellow-eyed Penguin, there is a depression point at the end of the pre-egg stage in the Broad-billed Prion. This is corroborated by the fact that there is a significant difference between the weight in May and that in late August.

In conclusion, it is obvious that not all species of birds reach their maximum weight in winter and then decrease as the breeding season approaches. Some, including the migrant passerine species, penguins, and at least some petrels, reach the maximum weight at the beginning of the pre-egg stage. The weight of incubating birds tends to rise; if a bird does not incubate, the weight tends to fall. Parents that feed the young also lose weight, but no data are available concerning parents that do not feed the young. In the period of molt, some birds, particularly penguins, certainly lose weight. On the other hand, there is evidence that others do not and that still others even gain weight. It is abundantly clear that knowledge of the weights of birds will aid in the solution of many physiologic and psychologic problems.

SUMMARY

Externally, there is little difference between the sexes in the Yellow-eyed Penguin. The sexes were first determined by an examination of the vent just after eggs were laid. Males averaged greater in weight and in linear measurements than females, but there was considerable overlap. Weights fluctuate considerably throughout the year. The peak occurs as the molt begins and the lowest depression comes when the molt finishes. From this point the weights rise steadily in the winter to another peak at the beginning of the pre-egg stage. In this period, the weight of males decreases, but for approximately four weeks the females are heavier than the males. The weight of the females begins to decline when the first egg is laid and reaches a low depression soon after. The weights of both sexes increase again during incubation followed by a fall to the end of the guard stage. After this there is another increase, followed by another decrease, in the last days when the chicks are ashore. Many species of birds are heaviest in winter, but migrant passerine species are heaviest immediately prior to migrating, by which time they are extremely fat. In those species for which data are available the sexes which incubate increase in weight during the process and drop again when young are being fed. In the period of molt some species apparently increase in weight, whereas others decrease in weight. Fluctuations in weights of petrels seem to follow the same pattern as those of the Yellow-eyed Penguin except that there appears to be no decrease in the period of molt.

Chapter V

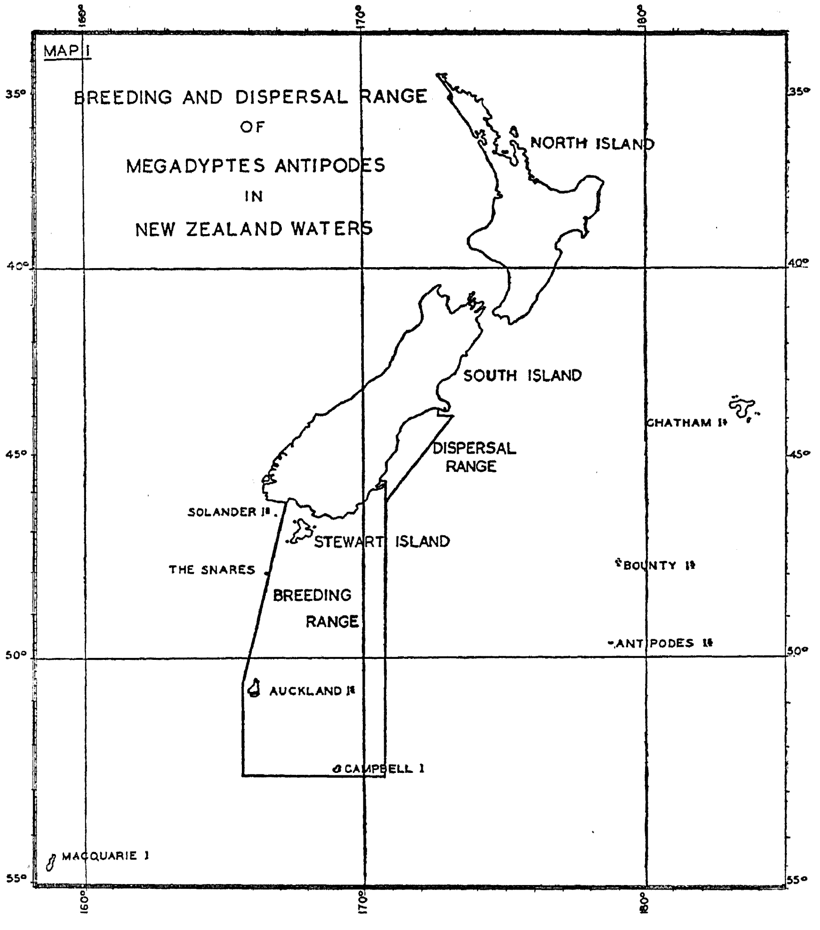
Sexual Behavior in Winter

Sexual behavior in the winter in the Yellow-eyed Penguin, including migratory status, general behavior, frequency of the sexes ashore, love-habits, retention of mates. Sexual behavior in winter in other species. Discussion of the length of the pair-bond, the question of re-mating, and sexual selection. Summary.

IN MOST SPECIES OF PENGUINS the winter stage is clearly defined, for it begins with the termination of the molt and ceases when the birds stay ashore during the day preparatory to egg deposition. In the King Penguin, however, the molt directly precedes the pre-egg stage (Gillespie, 1932), so that the winter stage, in this species, will extend from the day when duties with the chicks cease until the molt begins. The genus *Spheniscus,* except for the Magellan Penguin, varies also from the usual. The Peruvian Penguin, *Spheniscus humboldti* Meyen, and the African Penguin breed throughout the year; consequently with the information available it is difficult to assess their non-breeding season. Little is known about the Galapagos Penguin, *Spheniscus mendiculus* Sundervall, although it probably follows the pattern of the two previous species.

SEXUAL BEHAVIOR IN WINTER IN THE YELLOW-EYED PENGUIN

Migratory Status.—The Yellow-eyed Penguin is sedentary and not sea-going, as indicated by Guthrie-Smith (1914: 59) and Oliver (1930: 68), for it may be seen any evening in the winter at its own particular colony after it has come ashore for the night. Each individual does not come home every night; there are absences of one or more days. For example, in the "drama" of the three males and the single female (Appendix I) the homecoming of the birds was watched on 28 nights from 18 June to 1



September 1939. The female returned on 17 occasions and the males 15, 19, and 15 times respectively.

Where they go during the nights of absence is most difficult to ascertain, for a visit to all the colonies in turn will reveal that, as a rule, only birds belonging to that place will be found there. It is seldom that a resident from a neighboring colony calls. I feel certain, however, that these absentees spend the night ashore somewhere and not at sea, for years of watching indicate that during the last hour before dark few birds land. They appear to be very anxious to reach shore before darkness overtakes them, giving the impression that they have enemies in the water.

From 30 March to 30 August 1940, I watched 25 evenings at six colonies when as many as three were sometimes visited on the same evening; altogether 147 penguins were handled. No fewer than 133 were residents of the colony where found, nine were unbanded strangers, and only five were visitors from a neighboring colony. As there is evidence that the Yellow-eyed Penguin travels some considerable distance north and south of the Otago Peninsula in a short time, probably the missing residents spend their absent periods beyond the limits of the Peninsula.

General Behavior.—After the busy breeding season, during which a colony resounds with the "welcome" calls of returning parents, and after its more silent occupation by molting birds, the breeding area presents a forlorn aspect on winter mornings and early afternoons, when, as a rule, it is uninhabited. Birds do, however, sometimes stay ashore all day and, if two or more are associated, love-habits will occur (Appendices II and IV).

If ashore for the night, only birds mutually disposed towards each other proceed to a camp site in the bushes, which, in the case of a mated pair, may be their old nesting place or a subsequent new one some little distance away. If the pair is composed of individuals from different mated pairs of the previous season, the camp may be at or near the previous nest of one of the pair or in a different place altogether. If one of the pair be an old breeder and the other has not bred, the camp is usually, but not always, near the previous nest of the breeder. These remarks indicate that nest sites may be chosen in the winter.

The reader may obtain a good idea of general behavior at this period from Appendices I through IV. The first portrays typical behavior of a number of birds on the landing ground for 28 evenings; the second discusses the activities of two males and a female ashore all day early in the winter; the third gives an account of the aloofness displayed by a female visitor ashore only for resting; and the fourth describes the efforts of a male, which had lost his mate through death, in acquiring a new mate.

In the evening arrival of the sexes at the colony, there is no fixed order, since it is sheer chance whether the male or the female appears first. Rarely do individuals of a mated pair come in together and, therefore, two birds landing at the same time are not necessarily a "pair" in the sense of a mated pair, even if they happen to be male and female. Only an observer who knows his birds can decide that. An interesting incident of independent landing follows:

On 5 August 1945 the breeding male 884, and a breeding female not his mate, arrived at 3:40 p.m. and proceeded together to their respective nest sites. Twenty minutes later 942, the mate of 884, appeared by herself. At 5:10 p.m. their previous year's sole chick 994 left the water. It is not suggested that the yearling was still consorting with its parents, but it is odd that a whole family should land at the same colony on any one evening.

Frequency of the Sexes Ashore.—In Table 17, which covers the period from 1 May to 23 August, all the birds whose sex was known are listed. These are divided into those which were mated the previous season and those which were not. The last group includes old unmated males, and unmated two-year-olds of both sexes. Parents which had lost either eggs or young are retained in the first group. It can be seen that the ratio of males to females from mated pairs only is 104 to 68, and 131 to 71 if the unemployed are included.

As the eggs begin to appear just prior to the middle of September, more females than males are present, whereas more males than females were present in winter and the first part of the pre-egg stage. For September, 82 males and 97 females were handled—an advantage for the latter of 18¼ per cent. Not only is the female the dominant sex ashore in the interval when the two eggs are being laid, but she tends to remain ashore alone in the daytime for some days previous to the laying of the first egg.

The males, on the other hand, tend to go off to sea in the daytime at this period (Chapter VI).

From what has just been said, it will be observed that mated males are ashore 53 per cent more often than mated females. The difference would appear to be sufficiently great to rule out the factor of inadequate sampling. What is the significance of the male's being more frequently ashore than the female at this stage?

Two possible explanations offer themselves. The first is that the male may begin to feel the influence of the succeeding breeding season almost from the time the molt is finished. Such an influence could be inferred from the behavior of the male 37 (Appendix IV). It seems evident that, in many families of birds, the male is in a higher state of endocrine excitement for a much longer period than the female. This tendency is noted by Darling, who states (1938: 16) that "the males come into the preliminary stages of breeding condition a few days or possibly weeks, before the female." It may be, therefore, the beginning and the gradually increasing intensity of this phenomenon which causes male Yellow-eyed Penguins to come ashore more often. In addition, the deposition of nesting material in rudimentary nests would seem to be further evidence of early endocrine excitement.

The second explanation concerns the definite surplus of male Yellow-eyed Penguins. (See Tables 39-41.) There would appear to be no occasion for the female to worry about a mate, for there is always a male available. The situation is very different for the male, which has to face severe intra-sexual competition, but it

TABLE 17

Number of Birds of Each Sex Noted in the Winter Stage

	Mated birds		Unmated birds		Total birds	
Period	♂	♀	♂	♀	♂	♀
May	18	16	3	..	21	16
June	29	16	5	1	34	17
July	23	13	9	..	32	13
1 August to 23 August	34	23	10	2	44	25
Totals	104	68	27	3	131	71

should not be thought that a female Yellow-eyed Penguin never manifests a preference for a particular male. The female 73, for example, showed a strong inclination towards the male 72 (Appendix V and Chapter III).

Love-habits.—In the winter, breeding penguins of any given community may be divided into two broad groups—those which will retain the same partner for two consecutive seasons, and all other categories. A knowledge of these facts is important in assessing the incidence of love-habit behavior at this period. Further, it should be realized that on the whole of this portion of the population, the impact of the forces of affinity and divorce will have a greater influence than at any other time in the annual cycle, for at this time most of the newly mated pairs are formed.

As to love-habits with family value, only the first group will perform these—the function doubtless being to keep the mated pair intact (Chapter III). The second group of birds, which are without mates, will be largely concerned with love-habits with pair-formation value. Such behavior, however, will not be confined to unmated birds, but, as opportunity offers, will be directed also towards individuals which are already mated. The result is not always without success, for we know that divorces do occur. As to love-habits with social value, these will take place not only

TABLE 18

Annual Survival of Mated Pairs

	Pair broken because of					
	loss of one or both birds		divorce of one or both birds		Pair remains intact	
year	number	per cent	number	per cent	number	per cent
1937-38	5	62½	--	--	3	37½
1938-39	8	29	7	25	13	46
1939-40	18	50	5	14	13	35
1940-41	11	42	1	4	14	54
1941-42	6	25	3	12½	15	62½
1942-43	6	20½	4	14	19	65½
1943-44	5	19	4	15	17	66
1944-45	7	22	2	6	23	72
1945-46	16	41	4	10	19	49
Total	82	33	30	12	136	55

TABLE 19

Dissolution of 248 Mated Pairs from Season to Season

Number of mated pairs intact by the					
2nd	3rd	4th	5th	6th	7th season
136	69	34	19	7	1

among the potentially breeding birds but also among those which will be non-breeding members.

Retention of Mates.—As already noted, when the birds stay ashore in the daytime, at the beginning of the pre-egg stage, the great majority of the mated pairs have been formed. It is not, however, until the first egg has been laid that the observer is absolutely sure of the constitution of the mated pair. Hence it is not until then that the retention of mates or divorce from them can be certainly known. To discuss therefore, in this chapter, the subject of the retention of mates would appear somewhat premature.

Such a discussion is opportune, however, in order to understand more fully pair-formation and love-habit behavior as it exists in the winter. Briefly, the Yellow-eyed Penguin does not mate for life, although there is a tendency for mated pairs, if each member returns, to remain together. This has happened in 82 per cent of the cases. The causes of a dissolution in partnership are death, disappearance, and divorce.

Table 18 signifies that out of 248 matings in nine years, 136, or 55 per cent, remained intact in the succeeding season. Eighty-two, or 33 per cent of the mated pairs, were dispersed owing to

TABLE 20

Duration of Pair-bond in the Yellow-eyed Penguin

Years	Number of pairs	Years	Number of pairs	Years	Number of pairs
1	48	3+	10	6	2
1+	42	4	2	6+	3
2	13	4+	1	7	—
2+	19	5	2	7+	1
3	10	5+	4	Total	157

N.B. A plus sign means that the mated pair was in existence either when the first observation was made or was still a fact when the final observations closed.

death or disappearance of one or both of the mated pair. Thirty, or 12 per cent, were separated owing to divorce. This figure represents 18 per cent of the total of 166 mated pairs which returned to breed again in the succeeding year in the same colony. In 17 of these instances both members of the divorced pair re-mated with other penguins, and in 13 instances one member of the old pair was left unmated. All of the latter except two were males. These two females are the only females which have remained without a partner. They were divorced in the tenth year of my study (Chapter VII).

Of the 82 partnerships which were broken because of loss, 16 were broken because both birds disappeared and 66 because only one bird disappeared. Forty-one of the birds which returned mated with other birds, and 25, all males, were left unemployed for at least one season. This means that in 38 instances birds were left unemployed at least one season after having mated.

TABLE 21

Data on Times Individual Yellow-eyed Penguins Were Present for Breeding

Number of birds which were present		Male	Female	Total
once and not seen again		7	22	29
twice ” ” ” ”		10	17	27
three times ” ” ” ”		6	5	11
four ” ” ” ” ”		5	3	8
five ” ” ” ” ”		3	2	5
six ” ” ” ” ”		2	2	4
seven ” ” ” ” ”		2	1	3
eight ” ” ” ” ”		—	2	2
nine ” ” ” ” ”		1	—	1
	Total	36	54	90
once and not lost		23	10	33
twice ” ” ”		3	8	11
three times ” ” ”		6	6	12
four ” ” ” ”		2	1	3
five ” ” ” ”		4	4	8
six ” ” ” ”		4	4	8
seven ” ” ” ”		4	1	5
eight ” ” ” ”		5	2	7
nine ” ” ” ”		1	6	7
	Total	52	42	94

Table 20 gives some idea of the length of time the mated pairs remained intact. Of the 292 matings recorded, 157 distinct groupings of mated pairs were involved. Seventy-seven of these groupings lasted for from one to six years; the average was 1.7 years. The status of each of these birds was known prior to pair-formation and it was known also when the partnership was dissolved.

Regarding the rest of the groupings, 80 in all, the mated pair was either an accomplished fact when the records were begun or was still in existence in the tenth year of study. These mated pairs have lasted, to my knowledge, for from one to seven years, with an average of two years which in actual practice would be much higher. The seven-year-span, one of the six, all of the five, and the four-year spans are still intact. Table 19 includes further data on the rate of dissolution of the mated pairs as the years pass by.

Table 21 indicates that mortality among the females is much greater; this is particularly noticeable in the first two lines of the table, which show that 39 females were lost as against 17 males. It should be remembered that there is always a surplus of males in any colony. Many of these have mated only once, a fact that has greatly augmented the male total—shown in the first line of the second half of the table. The last line indicates that six females have nested nine times and are still in the colony. There are also nine males which have been present for nine years and one for ten years, but all except two have been unemployed for one or more seasons. (See also Table 22.)

Thirty-six male and 54 female penguins have not been seen again in their nesting colony after the mated pair was once broken. One or two of these have reappeared elsewhere, but that is a rare occurrence. I firmly believe that most of the disappearances are due to death. The bodies of eight males and 11 females have been recovered. This is just over 21 per cent of the total that has disappeared. As the chances of recovering bodies are small, the figure 21 per cent means that many of the other missing penguins died.

Table 22 gives particulars of 28 male and 12 female penguins whose breeding status is known from seven to ten years. A striking feature is the excess of males over females. This excess can be accounted for by the normal excess of males and the higher mortality among females.

A study of the table reveals considerable variation in the length of time that mates are retained. The male 721 had five mates in ten years, and was twice unemployed. The male 39 had only two mates in nine years and his only break in partnership was due to divorce. Another male, 738, had only one mate in the seven years. The male B20 had a different status in each of

TABLE 22

Duration of Pair-Bond in all Birds Known from Seven to Ten Years

Male	Duration of pair-bond	Years	Male	Duration of pair-bond	Years
721	+1,1,1,2u,3,2+	10	692	+7u,1+	8
1	+1,1,3,3u,1+	9	X10	3u,2,1,1u,1+	8
3	+1,5,1u,2+	9	40	+1,6—	7
15	+2,2u,5+	9	51	+1u,1,2,1u,2—	7
28	+3,1,3u,1,1+	9	52	1u,5,1u+	7
34	+6,1u,1,1+	9	155	5u,1,1+	7
37	+1u,2,1,5+	9	675	4u,3+	7
39	+6,3+	9	683	1u,2,2u,1,1+	7
72	+1,4,3,1—	9	720	2u,3,2+	7
20	+1,1,3u,3—	8	738	7+	7
21	+1,1,4,1u,1—	8	W18	2u,1,1,3+	7
36	+2,6+	8	Z13	+1,1,1u,4+	7
42	+2,3,2u,1—	8	Z14	+1u,1,2u,1,2+	7
64	+1,3,1u,3+	8	B20	+1u,1,1,1,1,1u+	6
102	+2,1u,5+	8	Total	29 males	
Female			Female		
2	+6,2,1+	9	73	+2,1,2,3—	8
4	+1,1,5,1,1+	9	75	+2,2,1,3—	8
18	+2,3,3,1+	9	76	1,6,1—	8
25	+2,1,1,5+	9	116	+3,1,4+	8
27	+6,3+	9	B13	6,1+	7
35	+1,1,3,3,1+	9	618	6+	6
16	+1,7+	8	Total	13 females	

Key:

+1, etc., means mated for one year, etc., and previous status unknown.
1+, etc., means mated pair still in existence.
1u, etc., means unmated for one season, etc.
1—, etc., means mated for one season, etc., and then lost or dead.

six years in which he was under observation. Only five of the 29 males listed have not passed a mateless season within my knowledge. Two have had mates for nine consecutive years; one of these males is still in the colony. One male, 692, went for seven consecutive years before acquiring a mate (Chapter VI).

Of the females not one has been left unmated. Bird 35 has had five partners in nine years, and five of the others have had four mates. Female 618, which produced eggs as a two-year-old and is a daughter of the male 3, has had only one mate (36) in six years and is still living.

With such frequent changes of partners as is shown by Table 22, one would expect to find the re-mating of several pairs after divorce. Seven years passed without anything of that nature occurring. In 1943-44, B20 and 78, which had been mated in 1941-42, again mated after having been separated and mated to other birds in the intervening year. The partnership did not endure, for in 1944-45, B20 mated with 76, and 78 with 721. The second case is the re-mating of male 1 and female 18 after a separation of three years (Chapter III).

In summary, in the Yellow-eyed Penguin the mated pairs tend to remain mated if the two members return. The liability to divorce is present to the extent of 18 per cent. Other causes of a break in partnership are death and disappearance. In spite of these factors, some mated pairs remain intact for a long time, whereas others have a different matrimonial status almost every year. Females have but little difficulty in acquiring a partner, but a male is apt to be left unemployed, since there is a surplus of his sex. Even under this handicap some males always have a partner and others seldom fail. Finally, re-mating, by the same birds after a divorce, occurs only rarely.

SEXUAL BEHAVIOR IN WINTER IN OTHER SPECIES OF PENGUINS

As practically nothing is known about the other species of penguins in the winter, no attempt will be made to follow exactly the headings used in the previous section on the Yellow-eyed Penguin.

Migratory Status.—Nine of the remaining sixteen species are migratory in the winter. This is indicated by Murphy (1936: 362, 390, 411, 422, 435, 445) for the Emperor, Adélie, Ringed, Rockhopper, Macaroni, and Magellan Penguins respectively. Tullock (1916: 94) makes it clear that the Royal Penguin is migratory. My own observations indicate a comparable state of affairs for the Erect-crested Penguin (1941b: 35) and for the Drooping-crested Penguin (data unpublished). One species, the Gentoo Penguin, may be either migratory or sedentary according to locality (Murphy, *op. cit.*: 369).

Of the remaining six, Murphy (*op. cit.*: 347) shows that the King Penguin is sedentary, that the African and Peruvian Penguins (p. 457) apparently breed throughout the year, so that it is difficult to say whether or not individuals are migratory, and that little is known about the Galapagos Penguin (p. 466), though it probably follows the pattern of the African and Peruvian Penguins. The Little Blue Penguin spends part of the winter ashore (1940: 181-184; Hursthouse, 1940: 121), but more detailed study is required. For the White-flippered Penguin, *Eudyptula albosignata* Finsch, I can find little information, although possibly its behavior is similar to that of the Little Blue Penguin.

Retention of Mates.—No data are available for the other species of penguins comparable with that which has been supplied for the Yellow-eyed Penguin. Even though the findings of Gillespie (1932: 95-130) are taken from birds in captivity, they probably reflect what actually happens in the wild state. Table 23 gives the annual matings as far as can be ascertained from his book.

A careful study of the table will indicate how closely the mating arrangements of the King Penguin resemble those of the Yellow-eyed Penguin. The former, likewise, does not mate for life, but there is a tendency for mated pairs to remain together for a period. One male was mated each season in seven years, and had three different mates, resembling such males as 39, 72, and 37 in the Yellow-eyed Penguin (Table 22). One re-mating after a divorce was recorded.

With regard to the remaining species, there is evidence that in at least two of them mates may be retained from one season to the next. This has been noted by me in the Erect-crested Penguin (1941b) and the Little Blue Penguin (unpublished observations). Regarding the latter, information supplied by Hursthouse (1940: 121) seems also to point in this direction. The records cover only two consecutive seasons, so that little is known about the duration of the bond or whether divorces obtain. It is suggested, however, that all species may conform to the pattern set by the Yellow-eyed and King Penguins.

Table 23

Annual Matings of the King Penguin
Gillespie (1932: 95-130)

Year	Mated birds	Egg date	Unemployed birds
1918	Charles & Ann	8 July	Bertrand, Dora, Erica
1919	" "	1 September	" " "
1920	" "	10 July	" " "
1921	Charles & Erica	6 June	Ann
	Bertrand & Dora	7 June	
1922	Charles & Dora*	15 June	Erica,* Ann
	Bertrand & Dora	1 August	
1923	Charles & Dora	18 June	Ann
	Bertrand & Erica	2 July	
1924	Charles & Dora	10 June	Erica died
	Bertrand & Ann	24 June	
1925	?		
1926	?		Charles died
1927	Bertrand & Dora		Ann

* Could Erica possibly have laid this egg?

A Discussion of the Pair-Bond in Birds

Duration of Pair-Bond.—The duration of the pair-bond in birds varies considerably from those like the Ruff, in which the sexes meet solely for coition, to those like some of the Anatidae, which mate for life. Lack (1940b: 269-272) has arranged these variations in five classes. His fourth class deals with the species which remain mated either for a single brood and then separate as in the House Wren (Baldwin, 1921: 237-238), or for one season before separating. The tendency is for the majority of this class to adopt the latter course (Nice, 1930: 70-72, and 1937: 88, and 1943: 182). That there may be considerable variation from this rule is well illustrated by Kendeigh (1941: 55). Lack's fifth class is composed solely of birds which mate for life.

The Yellow-eyed Penguin would seem to lie midway between Lack's fourth and fifth groups. In this species 82 per cent of the mated pairs that return remain intact for the second season. These partnerships have been observed to continue for as long as seven consecutive years. This degree of continuance means there is an 18 per cent divorce rate, which is an important and influential factor in the duration of the pair-bond. This type of pair-bond obviously does not fit into either of Lack's two last-mentioned classes. It is therefore necessary to establish an extra class in which are placed species tending to remain mated for some years but in which there is a definite element of divorce.

Judging by the evidence that has been presented concerning the King, Erect-crested, and Little Blue Penguins, it is possible that the other species of penguins also belong to this new group. Such a possibility would at least be a fruitful source of research.

An examination will now be made of the length of the pair-bond in petrels. Owing to the nature of the terrain and the consequent difficulties in recovering individuals of species nesting in burrows, it was not possible to obtain results with the same degree of accuracy as with the Yellow-eyed Penguin and the Royal Albatross. In Table 24, therefore, many of the figures preceding a plus sign would in fact be larger. Further, in all five species some of the pairs were found together, without eggs or chicks, either before or after a successful breeding season. These occurrences are not included in the table, which deals only with birds with eggs or chicks. The first three species were studied for five years, the fourth was studied for three, and the last for ten years.

In the Yellow-eyed Penguin, the percentage of mated pairs which remained intact for more than one season lies between 42.7 and 69.4 (Table 20). As it is definitely known that 115 of these 157 mated pairs in the proportion of 48 to 67, mated either for one year only or for more than one, there are 42 mated pairs whose status is in doubt. They mated at least once. On the basis of this proportion, one may assume that 18 of these 42 mated for only one year and 24 for more than one. On this basis the real percentage which mated for more than one year would be 54.1.

In the first three petrels noted, the percentage is lower than this, but in actual fact it would be much higher. In the Sooty Shearwater the survey had not progressed as far as the first three petrels, but the tendency is for the same pattern to be followed. A considerable number of pairs were found together again in the succeeding season but without eggs or chicks. The Royal Albatross

TABLE 24

Duration of Pair-Bond in Petrels

Number and percentage of pairs

Years	*Pelecanoides urinatrix* (Gmelin)	*Pachyptila turtur* (Kuhl)	*Pelagodroma marina* (Latham)	*Puffinus griseus* (Gmelin)	*Diomedea sanfordi epomophora* Murphy
1	15(10.2)	8(4.4)	7(3.6)	6(6.4)	1(12.5)
1+	87(59.6)	118(65.2)	142(73.6)	86(91.5)	
2	2(1.4)				
2+	26(17.8)	28(15.5)	25(12.9)	2(2.1)	
3	1(0.7)	1(0.5)			
3+	8(5.5)	14(7.8)	14(7.3)		1(12.5)
4					1(12.5)
4+	6(4.1)	9(4.9)	5(2.6)		
5+	1(0.7)	3(1.7)			
6+					1(12.5)
8+					1(12.5)
9+					1(12.5)
10+					2(25.0)
Total	146	181	193	94	8
Percentage more than one year	30.2	30.4	22.8	2.1	87.5

N.B. Percentages in parentheses.

seems to follow a different pattern; pairs may mate for life, for there has not been a single divorce. There was one case of re-mating after one of the partners had disappeared.

The foregoing seems to show that the duration of the pair-bond in the four burrowing petrels noted resembles that in the Yellow-eyed Penguin. This assumption is further supported by the fact that instances of divorce have been discovered in all four, although not to the same extent as in the Yellow-eyed Penguin. Obviously, there must have been other divorces which were not detected. Divorce in these species is therefore not an exceptional affair.

For other petrels the evidence, where available, appears to run along the same lines. Roberts (1940b: 158), who watched for two successive seasons, indicates that Wilson's Petrel, *Oceanites oceanicus* (Kuhl), tends to remain mated from season to season. Lockley (1942: 105, 232), who made wider observations, records the tendency to remain mated with occasional divorce in the Manx Shearwater, *Puffinus puffinus puffinus* (Brünnich). Finally, behavior resembling that of the Sooty Shearwater was observed by Lewis (1924: 87) on 44 banded birds of a closely allied species, the Short-tailed Shearwater, *Puffinus tenuirostris* (Temminck). One pair was found together for three consecutive years.

To what extent other birds mate for a period before divorce intervenes needs further investigation. It is difficult to trace the partners after separation, especially if the birds are numerous or widely dispersed. Terns and gulls may behave according to the pattern being discussed. For example, Austin (1947: 1) postulates that the Common Tern tends to remain mated from year to year and gives the percentage as 79.1. Tinbergen (1939b: 228) has noted the return of two out of seven pairs of gulls four years in succession but no divorces. Similar circumstances may apply to many of the Paridae (Odum, 1941: 317-318) in which one case of divorce has been reported (Kendrick, 1940: 309). Finally, Lorenz's Jackdaws, *Coloeus monedula* (Linnaeus), changed mates at times (Lack, 1940b: 271).

In summary, it would seem that, in addition to the Yellow-eyed Penguin and probably at least some of the other penguins, several species of petrels and some other birds like the Paridae, gulls, and terns may belong to the proposed new class for length of the pair-bond. They tend to remain mated for some time, but divorce is more than a chance occurrence. The Royal Albatross, however, on the slender evidence available, appears to belong to Lack's fifth class.

The Question of Re-mating.—The question now arises whether two individuals of a mated pair which are still mated in a second year have actually re-mated, or whether the relationship has been continuous. This has been discussed, with a list of examples, by Lack (1940b: 271-272). Much more detailed information is required, however, before definite rules can be formulated.

In one species at least, the House Wren (Kendeigh, 1941: 53), the rule is for a change of mates between broods in the same season. This rule obtains, but less frequently, in a few other species, as, for example, the Bluebird, *Sialia sialis* (Linnaeus), the Brown Thrasher, *Toxostoma rufum* (Linnaeus) (Nice, 1930: 70), and the Snow Bunting (Tinbergen, 1939c: 45). The more general rule, however, is for birds of this type to remain mated for the whole season (Nice, 1937: 85).

Nevertheless, mated pairs of House Wren do sometimes remate for a second brood and, though less frequently, for a second and even a third season (Kendeigh, *op. cit.*: 55). Nice (1937: 88) has noted only eight instances of re-mating from season to season in more than 200 pairs of Song Sparrows, and Kendeigh (*op. cit.*: 54) 13 per cent for male and 22 per cent for female House Wrens. It is commonly thought that re-mating is due to a tendency for some of the females to return to their former territory. It may also be due to personal attachment (Tinbergen, *op. cit.*: 46) and even to sheer chance (Lack, 1943: 60).

It is desirable, however, that this discussion should center around such birds as penguins and petrels whose procedure in pair-formation is on a pattern different from that of the foregoing species. As indicated by Lack (1940b: 272) very little has hitherto been discovered about this group.

Within my experience, re-mating among penguins and petrels is the normal procedure. If this were a matter of chance it would not happen so often, although doubtless chance does have some influence. More important factors in re-mating, however, are return to the vicinity of the previous year's activities, personal recognition, and personal attachment.

The theory often put forward that individuals of a mated pair tend to return to the previous nest site and, because of that, re-mate, is not the whole story. With penguins, which are not in contact on migration (Chapter III), return to the old neighborhood is a necessary prelude to re-mating. This is indicated by the few Yellow-eyed Penguins that have taken up residence in another colony and that have all acquired new mates.

The case may be a little different in petrels, for if, as suggested (Chapter III), the mated pairs are in contact on migration they should return together. If such a mated pair were banded and found together again on a different breeding ground this suggestion would be proved. Petrels may, of course, separate for a time, and as the breeding season approaches, return to the seas near the breeding grounds, recognize each other, and thus facilitate their re-mating when each member reaches land.

According to my observations, three species of penguins—Yellow-eyed, Erect-crested, and Little Blue—do return to the vicinity of the previous nest site. Further, my mated pair of Erect-crested Penguins, and subsequently the female alone, adhered rigidly to exactly the same nesting site for nine years. As for petrels, all six species I have studied return to at least the vicinity of the old nest. Some, however, nest a little distance away from the previous season's site. Lockley (1942: 70-76) and Lewis (1924: 87) have made comparable records for other species. Palmer (1941: 48) and Austin (1947: 3) also have published comparable observations on terns. Of course, with terns and gulls, the mated pairs may have returned together from their winter feeding grounds.

Judging by the behavior of the Erect-crested Penguin (1941b: 35-36) and of the Royal Albatross, members of a mated pair in migratory penguins and petrels do not usually reach land on the same day at the beginning of the pre-egg stage. As colonies of migratory penguins, in particular, are so populous it would seem an easy matter to acquire a different mate before the old one returned. In fact, there would be little chance of re-mating at all if return to the previous nest site were the only factor. As for the migratory penguins, what evidence there is so far, suggests that these species do re-mate rather than the reverse (Chapter VI).

This brings in the factors of personal recognition and personal attachment. Apparently in penguins, petrels, and other birds with comparable behavior individuals are capable of recognizing each other, as has been indicated by Lorenz (1937: 261). "It seems logical that if physiological rhythms are involved a pair of individuals who have successfully mated once and become adjusted to each other will be more likely to be attuned for nesting again than will two strangers" (Kendeigh, 1941: 53). Not only successful breeders but also those which have lost either eggs or chicks and which have "kept company" re-mate. It would seem, then, that a strong personal bond has developed between the paired or mated birds, so that once they recognize each other, re-mating is a natural result. This individual attachment has also been noted in gulls by Tinbergen (1939c: 46).

In the Yellow-eyed Penguin, as members of the pair or mated pair do keep contact in the non-nesting season, their period of mating is definitely continuous. Even so, divorce is frequent in this species. It is amazing, therefore, that one pair has remained united for seven years* and in a colony where there were plenty of unemployed birds desirous of a mate. Personal attachment would seem to be strong between these two. Other species, which

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*In the fourteenth year of study this pair was still intact, making eleven years in all.

appear to be in the same class as the Yellow-eyed Penguin, are terns (Palmer, 1941: 38-41; Austin, 1947: 1-3) and gulls (Tinbergen, 1939b: 228).

In summary, some birds, such as many of the highly territorial passerine species, re-mate in a second season only occasionally. In others, like penguins and petrels, where pair-formation takes place independently of territory, re-mating is the rule. Of the latter group, some are in contact in the non-nesting season, whereas others like migratory penguins are not. Recognition and personal attachment seem to be the most important factors. These factors cannot be effective unless the birds return to the vicinity of the previous nest site.

Little is known of the incidence of re-mating in birds after individuals of a mated pair have been divorced and mated to other birds in the interval. As already shown, re-mating to the same bird after divorce is rare in the Yellow-eyed Penguin. For the White-faced Storm Petrel, *Pelagodroma marina* Latham, I have one record and Lockley (1942: 181) gives another for the Manx Shearwater. Finally, Thomas quotes an instance in the Bluebird (1946: 154). It is worthy of note, too, that Austin (1947: 14) has not had a single case of re-mating after divorce in his numerous records on terns.

One important fact observed in penguins and petrels, within my experience, is that individuals of the divorced pair, whether mated to other birds or left unemployed, usually remain in the vicinity of their former nest. Thus the three factors, recognition, personal attraction, and nearness to the previous nest site, which have just been considered as the cause of re-mating in a succeeding season, are still present at least in some degree. Yet these former mates seldom re-mate. The separating factor is in the realm of conjecture. After his ejection by male 20, the behavior of male 1 for three years plainly indicated that he retained at least a personal attraction for the female 18. When 20 was removed by death, it developed that 18 was not averse to re-mating with her former mate 1 (Chapter III).

Sexual Selection.—Regarding true female choice, Huxley (1938b: 40) states that the type postulated by Darwin, in which a female deliberately selects one male from a number of rivals present at one time, does occur in some birds—namely the Ruff, Blackcock, *Lyrurus tetrix* (Linnaeus), various Birds of Paradise, and Gould's Manakin (Chapman, 1935: 486). There is little evidence of the occurrence of sexual selection in other circumstances. Noble and Curtis (1939: 2, 28, 44) have proved its existence in the Jewel fish, *Hemichromis bimaculatus* Gill.

Female choice seems to exist in some other birds. This is the view of Kendeigh (1941: 23, 48, 51), who states that House Wrens remain on their territories and that the females make a choice influenced by the song of the males. Lack (1944: 61) remarks that in territorial birds female choice could occur only at the pair-formation stage and this seems to apply to his Robins (1939b: 184).

In birds whose behavior is essentially mutual, as in penguins, the choice may be made by either sex. For example, in the Yellow-eyed Penguin, the female 73 definitely chose the male 72, but no other example is available owing to the difficulty in observing such behavior. This choice was not due to display, as in the Ruff, or to advertisement, as in territorial birds, but to an affinity formed at a much earlier date.

The female 73 was definite about the particular male she wanted, but the impression to the observer in the field is that other females are not usually so definite, being more inclined to accept a male, though not necessarily any male, which presses his attention hard enough. An example is that of the male 37 (Appendix IV). This aspect of pair-formation is closely paralleled in ducks as recorded by Hochbaum (1944: 32-33), who points out that there is severe competition among males for a mate. The female does not "select" one but shows willingness and accepts the male which succeeds, amidst competition, in taking up a position alongside her.

Concerning the question of intra-sexual selection in monogamous birds, Huxley (1938b: 35) points out that "intra-sexual selection will always exist when some members of a species remain unmated or fail to effect fertilization effectively." In the Yellow-eyed Penguin, there is certainly keen competition among males for possession of the females. The surplus of males is 24.9 per cent (Table 41) considering all penguins, both male and female, over two years old; if males only are considered, excess of unemployed over breeding males is 40.2 per cent.

For the House Wren, Kendeigh (1941: 45) gives 28 and 35 per cent of the males as non-breeding in the total population. In Robins, Lack (1940a: 319), counting males only, records 20 per cent for his own birds, and 19 per cent for Burkitt.

That intra-sexual selection exists among Royal Albatrosses and, by analogy, possibly among other petrels, is indicated by the behavior of three males towards a female Albatross which had returned without her mate (1942a: 175, 262). In my ten-year study of the Royal Albatross, there has always been an excess of resident males ready to compete for any available female. At the time of writing (1946) there were five mated and four unmated males, the latter constituting 44.4 per cent. Comparable data in other petrels are not available. There is a similar sort of competition apparently in several species of lizards (Noble and Bradley, 1933: 86-87).

In summary, true sexual selection exists in a few birds and a modified form in some others, but more research is required in order to determine exactly in how many kinds of birds it does exist. Intra-sexual selection appears to be widely prevalent in monogamous birds and probably insures, at least in the Yellow-eyed Penguin and the Royal Albatross, that every fertile female breeds. Males seek out the females primarily in the males' own interests. In this way, mating efficiency is evolved and maintained; it is helpful not only to the individual but is of general advantage to the species in its struggle for existence. Finally, as indicated by the female 73, there is also a measure of competition among the females themselves. The notion that there is female competition is supported by the evidence of Thomas (1946: 148) regarding the rivalry, at the pre-egg stage, between two female Bluebirds for one mate.

SUMMARY

Nine species of penguins are migratory; probably seven are sedentary and one may be either. Male Yellow-eyed Penguins are ashore 53 per cent more frequently than the females. In the Yellow-eyed Penguin, 82 per cent of the mated pairs which return re-mate, giving a divorce rate of 18 per cent. Death and disappearance are the other causes of a break in partnership. One mated pair has remained intact for 11 years; other penguins have had a different status nearly every year. Owing to a surplus of males, females seldom remain unmated. Even so, some males rarely fail to mate. In the other species, the meager evidence available suggests that the pattern described immediately above is followed. Gillespie's work on the King Penguin is the most informative. Penguins lose touch with each other in the water. In petrels, however, it is suggested that the mated pairs and pairs "keeping company" associate at sea. A new class for the nature and duration of the pair-bond is proposed. It includes species in which the mated pairs tend to remain mated for some seasons, with the factor of divorce more than a chance occurrence. Penguins, some petrels, the Paridae, gulls, and terns probably belong to it. Re-mating is rare in some birds. In penguins and petrels it is common and is facilitated by return to the vicinity of the old nesting site, recognition, and personal attachment. True sexual selection exists in some birds. Intra-sexual selection among males seems widely prevalent in monogamous birds and insures that most females breed. There may also be a measure of competition among females themselves.

Chapter VI

The Pre-egg Stage

Pre-egg stage in the Yellow-eyed Penguin, including first few days ashore, sexes at the nest up to the laying of the first egg, behavior of sexes ashore, choice of nesting site, territory and "property rights," dominance, why penguins stay ashore, influence of male on gonadal development of female, factors influencing egg-laying, appearance of eggs, love-habits, trios, two-year-old breeding birds. The pre-egg stage in other species. Discussion of the pre-egg stage. Summary.

The pre-egg stage extends from the day the penguins commence to stay ashore in the daytime to the laying of the last egg. Each end of the phase is well defined and is marked by a distinct change in the birds' behavior. In the previous period (winter) the dominating factor in the life of the Yellow-eyed Penguin was pair-formation. In the pre-egg stage all his activities hinge on the need for coition. This stage includes some cases of pair-formation, coition early and subsequently at periodic intervals, fertilization, and a short period between fertilization and the laying of the first egg.

First Few Days Ashore.—To determine the date when the penguins began to stay ashore in the daytime, detailed observations were carried out for four seasons—1936 to 1939. It was rare to find birds ashore before the beginning of the last week in August. By 27 August in a normal season, most of the birds are ashore. The year 1939 was late, following the worst season for penguins in my ten years of study.

In the early stages, if only one bird is present at the nest in the daytime, it is nearly always the male. Frequently both are together, in which case the male usually occupies the nest site. In order to find out something about the movements of the absent females, between 26 August and 1 September 1940, four nests were visited twice daily—at 9 a.m. and at 9 p.m. The results shown in Table 25 indicate that the behavior varies considerably.

In the daytime the male was present alone nine times, both were there six times, and neither eleven times. At night the figures were nine, eleven, and five respectively. Neither in the daytime nor at night was the female found alone. One record in the table indicates that the female may go off to sea and leave the male behind.

Another feature signifying that the male spends much time ashore at this early stage is his drop in weight (Chapter IV). For example, on 26 and 30 August 1945, I weighed ten pairs which had been ashore together at least for that day, with the following results: males, 12.3 (11-13¾) pounds; females, 12.8 (10-14) pounds. Eight of the females were heavier than their partners. Oddly enough, these ten pairs were the only birds ashore; no single birds were present. A casual observer would have concluded that the birds come ashore in pairs, but their respective weights indicate plainly that the males had been ashore alone when I was absent from the colony. Seven of these males caught on 17 and 18 August, just before the pre-egg stage, averaged 13.8 pounds and ranged from 13 to 14½ pounds, thus further substantiating my claim that they had been ashore.

TABLE 25

Day and Night Occupation of Nest Site in Early Stages

	Nest							
Date	Ridge		Lawyer		Camp		Hollow	
1940	Day	Night	Day	Night	Day	Night	Day	Night
26 August	♂	♂	♂	♂	A	A	♂	♂
27 August	A	♂	A	A	A	♂	♂	B
28 August	♂	B	A	B	♂	♂	B	B
29 August	B	B	B	B	♂	B	B	B
30 August	♂	♂	A	♂	B	B	A	A
31 August	♂	♂	A	B	B	B	A	A
1 September	A		A				A	A

Key: ♂ means ♂ alone.
B means both present.
A means both absent.

TABLE 26

Presence of Sexes Ashore in Daytime at Intervals of Seven Days prior to Laying of First Egg

Sex at nest	Class interval in days 35-29	28-22	21-15	14-8	7-1	Total
♂ alone	10	8	8	9	10	45
♀ alone	0	0	1	5	19	25
Both	8	14	32	58	118	230
Neither	8	19	18	13	21	79
Not identified	0	3	1	4	6	14
Total	26	44	60	89	174	393

Sexes at Nest up to Laying of First Egg.—Tables 26 and 27 represent 393 visits to 39 nests in the seasons of 1937-38 and 1938-39. The aim was to find out as much as possible about the behavior of the sexes at the pre-egg stage. All records were taken in the daytime before the return of the great majority of the sea-going birds between 3 p.m. and 5 p.m.; daily observations were not made. As soon as it was found that at least one bird was in occupation in the daytime, observations at each nest were commenced. After that, if the site were vacant the vacancy was recorded and is shown in the tables. Earlier absences were not recorded. Owing to their timidity, some birds were not identified. At other times it was impossible to ascertain which sex occupied the nest. Perhaps the position of the nest was not definite, perhaps neither was on it, or perhaps their timidity had caused them to move away from the nest-site before I could decide.

TABLE 27

Presence of Sexes Ashore in Daytime at Intervals of Seven Days prior to Laying of First Egg (Expressed in Percentages)

Sex at nest	Class interval in days 35-29	28-22	21-15	14-8	7-1	Total
♂ alone	38	18	13	10	6	11.5
♀ alone			2	6	11	6.5
Both	31	32	53	65	68	58.5
Neither	31	43	30	15	12	20.0
Not identified		7	2	4	3	3.5

TABLE 28

Sex of Bird on Nest in Daytime When Both Birds Are Present at Pre-egg Stage

Sex at nest	Class interval in days 35-22	21-15	14-8	7-1	Total
Male	5	10	22	21	58
Female	3	4	13	44	64
Not identified	14	18	23	53	108
Total	22	32	58	118	230

Of the 314 occasions when one or both birds were seen at the nest in the daytime the number of occasions increased from 18 in the 35-29 interval, from 25 in the 28-22 interval, from 42 in the 21-15 interval, from 76 in the 14-8 interval to 153 in the 7-1 interval. Conversely, the absences decreased accordingly as the date of egg deposition approached. It should be noted that once the penguins stay ashore they do not fast continuously; on 20 per cent of the visits the nests were left unattended.

Before the last week the female is rarely ashore alone and was found only once in the 21-15 interval. Strangely enough, the bird concerned was a very late layer. I have been unable to check up thoroughly the relation of the male's absence in the daytime at this stage to his return in the evening, but there is reason to think that he usually comes back. In 13 out of 19 of the cases of absence given in Table 26 the male was with the female next day. His absence in the other six cases does not imply his non-return on the night in between.

Both birds of a mated pair spend much of their time together

TABLE 29

Sex of Bird on Nest in Daytime When Both Birds Are Present at Pre-egg Stage (Expressed in Percentages)

Sex on nest	Class interval in Days 35-22	21-15	14-8	7-1	Total
Male	23	31	38	18	25
Female	14	13	22	37	28
Not identified	63	56	40	45	47

TABLE 30

Appearance of Sexes Ashore in Relation to Own Egg and to First Egg Laid by Earliest Penguin

	Own Egg		First Egg	
Sex	Mean days	Range days	Mean days	Range days
Male	24.7	11 to 40	16.3	—1* to 26
Female	20.0	7 to 38	12.3	—5* to 24

* The minus sign indicates that some birds were not seen ashore for the first time till after the first egg was laid for the season by the earliest-laying penguin.

at the nest in the daytime and their appearances gradually increase as the egg date arrives. The occupation of the nest by the sexes over the entire period, as shown in Tables 28 and 29, is approximately equal. Up to and including the interval from the fourteenth to the eighth day before the first egg is laid, however, it is usually the male which occupies the nest, but in the interval from the seventh to the first day the female is far more frequently on the nest. In the three-day interval before the first egg is laid she was, according to my records, on the nest 25 times against seven for the male. From the sixth to the fourth day before the first egg is laid the figures are 16 for the female and 10 for the male. These facts indicate plainly the relation of the nearness of laying and the more frequent occupancy of the nest by the female.

The information given in Table 30 is a little understated, for I have probably missed the first appearance of some of the birds. The first set of data indicates the relation between the appearance of the sexes ashore and the laying of their own egg. The second

TABLE 31

Relation of Arrival Ashore to Time of Laying

	Mated pair		Days ashore before egg		
Year	♂	♀	♂	♀	Laying date
1937-38	72	65	32	32	1 October
1938-39			25	22	30 September
1940-41			40	38	5 October
1938-39	39	2	24	9	18 September
1937-38	721	70	22	22	18 September
1938-39	61	70	22	22	20 September

set is in relation to the first egg laid that particular season by the earliest penguin.

The date of egg-laying of any particular female did not seem to have any effect on her early or late arrival ashore. It seemed to be influenced entirely by the individuality of the particular bird. Thus the first ashore were often the latest layers, as shown in Table 31.

Behavior of Sexes Ashore.—When both birds are ashore, much of the time is spent in inaction, just standing or sitting about. Sometimes they preen themselves and at other times they preen each other. Occasionally one of them goes through one or several of the less intense love-habits. The second bird quickly responds and sometimes the whole affair ends in a "full trumpet" by one or both birds, although more frequently in "half trumpets." The excitement then subsides to "mutual-preening."

The foregoing behavior being self-exhausting, calm is soon restored and may last for several hours. Typical behavior on such occasions is described in Appendix VI, between a mated pair seven days before the first egg appeared.

These periods of love-habits are more intense and more frequent in the morning and towards evening. The five or six hours in the middle of the day are relatively silent. Daylight and the exit of some of the birds for the sea, circumstances that lead to departure ceremonies, cause many pairs and mated pairs to indulge in love-habits. The evening activity becomes pronounced after the first bird has returned from the sea and the united pair perform the "welcome" ceremony. This may set off a pair which, though ashore all day, has been silent. The excitement seems contagious, and it is not long before pairs in the whole neighborhood are participating in love-habits.

All this behavior is entirely mutual, and I have no evidence that it is initiated by a particular sex. Either bird may be on the nest. As already stated, there is a tendency for the male to be in occupation more frequently at the beginning of the season, with the roles reversed as egg deposition approaches. This pattern, however, is not by any means rigid.

The bird on the nest, irrespective of sex, seems to act according to a definite pattern which is explained in Appendix VI. It sits down on the nest, shapes it, takes straw from the other bird, arranges it, and indulges in "shakes" when its partner picks up straw or when touched by its mate. The bird off the nest collects the straw and appears to be the more alert of the two.

The presence of a female is apparently not necessary for the building of a nest. The male 721 (Appendix I) built an excellent nest long before he enticed the two-year-old female 676 to his residence. In the succeeding year when still unmated he did not build a nest at all. A further example is that of the male 692 (Chapter III).

When a single bird of a mated pair is ashore alone, it almost invariably occupies the nest, usually adopting an incubating position. Normally the occupation is silent, but sometimes the males will indulge in "full trumpets," especially if the fashion has been set by unmated males (Chapter VII). I have not known the female to use the "full trumpet" under these conditions, but this fact may be due to a paucity of observations. Obviously, the collection of such data is not easy.

In the early days of the pre-egg stage, when a human being approaches, most, although not all, of the birds usually scuttle away. With the approach of egg-laying their demeanor changes, for they gradually become less easily scared and eventually re-

TABLE 32

Data Illustrating Changes in Nesting Sites

	1936-37		1937-38		1938-39		1939-40	
Nest	♂	♀	♂	♀	♂	♀	♂	♀
A			GW	63				
B	61	A						
C	B	70			61	70	61	70
D	721	C			721	63	721	676
E			721	70				
F			61	A			60	....

main at the nest, in most cases adopting the "sheepish look," sometimes indulging in little "throbs," or even a "glare."

Does Male or Female Choose Nesting Site?—Table 32 gives some idea of the change of nesting sites in a small group of penguins.

Evidence in favor of the male will be discussed first. In the case of the three males, 60, 721, and 61 (Appendix I), each individual certainly occupied a nesting site long before any female found her way there. The female 70 eventually mated again with 61, her previous season's partner, at his nest, but Table 32 shows that 61 did not originally initiate occupancy of this site, for 70 had been there in 1936-37 before she mated with 61.

The table should make it clear, however, that 721 took to Nest D the females 63 and 676 in 1938-39 and 1939-40 respectively. It is worthy of note, too, that as 676 was only a two-year-old in 1939-40, she could not have had any interest in a previous site.

Further evidence for the male is shown in Table 33, which covers three successive seasons. The females 4 and 30 each left her old nest and partner and mated with the neighboring male at his nest site.

Finally there is the action of the male 72 in returning to his nesting site of four years earlier and taking the female 75 with him (Appendix V). Obviously, this choice was the male's.

The case for the female opens with the activities of bird 4 as shown in Table 33 for 1939-40. Her partner 31 did not return to molt in 1939. The young male 52 passed through his second molt with her. Here is another instance of a young bird, this time a male, occupying the site of an old breeder.

TABLE 33

Data Illustrating a Change of Partners

Nest	♂ 1937-38	♀	♂ 1938-39	♀	♂ 1939-40	♀
A	3	4	3	30	3	30
B	31	30	31	4	52*	4

*A three-year-old bird.

Table 32 shows that the female 70 chose the site in 1938-39. Her new mate 61 had previously occupied two other sites which he abandoned in her favor. As further evidence for the female, in 1936-37 and 1937-38, 75 was mated to the male 67 at "Big Net." In 1938-39 and 1939-40 she retained the same place, but her partner was 66, from a nest not far away. Hence this female had nested in four consecutive years on the same site but with two different mates.

A final interesting example of female choice is that of X15, which in 1938-39 was mated to the male 684 at Colony S. In 1939-40, her partner was X16 at another colony five miles away. In 1940-41, she returned to her old nest at S with still another mate; therefore, at least in the last year she definitely chose the site.

An example of dual choice was provided in 1938-39, by male 74, which remained unemployed but built a nest at the "Fence." The same season the female 73 reared a family at "Mueh." In 1939-40, 74 mated with 73 at "Mueh." But in 1940-41, the same mated pair reared their second family at the "Fence," the old nest site of 74.

From the evidence presented it appears that the choice of the nesting site is not the prerogative of any one sex. This view is supported by many examples not given. Birds tend to return to the vicinity of their old nests. In the event of the non-return of their old mates they may be found, or followed, by other birds desirous of mating with them, which makes it appear that the owner of the nest made the choice.

On the other hand, because of the loss of a mate or even in the case of a divorce, a bird may be intercepted on the landing ground and encouraged to follow the suitor to his or her nest. A parallel case (Chapter III) is the mating of Z14 and the two-year-old female Z18, which was content to follow Z14 to his part of the colony. This practice also obtains among old breeding birds.

Further, there are unmated males which have not secured their first mate until they have been unemployed for one or more seasons after attaining breeding age. Usually they frequent one particular part of the colony. When they do become mated, the pair generally breed in the male's locality. Habit or conservatism, in this case, seems to be the ruling factor, and the indication is that the male has chosen the site and enticed his mate to it.

If a mated pair remain together for several seasons, they will, after a time, usually change their nesting site. There seems to be no apparent reason for this, nor is it possible to say which sex is responsible for the change. Subsequently they may return to the original site.

Territory and "Property Rights."—Mated penguins and some of those which "keep company" will defend the nest or potential nest site and its immediate vicinity by threatening and if need be attacking an intra-specific intruder. The "defended area" (Noble, 1939: 267) may be termed "territory." The defense is not necessarily confined to the breeding season but will occur in the winter whenever the site is being occupied. It will be observed, however, from the examples of defensive behavior, given in Chapters II and VI, that other factors are involved, so that the Yellow-eyed Penguin defends not only territory but also, at certain times, something apart from territory.

To cover all these phases of defense a new term, "property rights," is needed. A mated penguin's "property rights" may include its nest site, its nest and contents, its chicks out of the nest, or its mate. If unmated, it may claim "property rights" over a potential nest site or even over another bird of the opposite sex with which it is apparently attempting to form a pair and which seems to be favorably disposed towards the aspirant—in other words, a potential sex-partner.

Dominance.—Aggression and kindred subjects which are closely linked with dominance have already been discussed (Chapter II). As far as I can tell, there is no dominance between members of a mated pair, their behavior being essentially mutual. Evidence exists, however, which points to dominance with minor social value among other classes of penguins, and there is another type among individuals which are rivals in some respects.

Further, dominance is obscured by the factor of "property rights," which usually allows the possessor the privilege of pecking or attacking an intra-specific intruder without retaliation.

Dominance as possessing *social value* seems to exist only as a "supersedence" (see Chapter VI), and may be noted among a group of penguins standing about on the landing ground. In captivity, penguins might correctly or incorrectly indicate, as happens in ducks (Hochbaum, 1944: 35), that a "peck order" exists.

In *pair-formation* there would appear to be a definite element of dominance as exemplified by the history of the male 692 (Chapter III), which, it will be remembered, was seven years unmated even though he made efforts to secure a partner. In the eighth year, 692 mated with a young three-year-old and helped to rear a chick. His final success, as far as I could tell, was due to lack of competition—he was the last odd male in his colony.

Other males have remained unmated a long time. (See Table 43.) Yet there are still others which never fail to secure a mate. Table 42 shows that two males were mated for nine consecutive years, two for eight, and two for seven years. In addition, eleven others known from seven to ten seasons only occasionally failed to mate.

Finally, the case of the dominant male 37 (Appendix IV) further corroborates the foregoing deductions. This male secured a mate as a three-year-old and has remained mated for the eight years I have known him as a breeding bird. He has had three mates, the first two dying. His two last mates were divorced from the male 28. This statement is proved by the fact that 28 after each divorce was loitering near the newly mated pair, a characteristic feature of such a circumstance. (See Chapter VI.)

The cause of this state of affairs would seem to be a dominance factor. Males which are more dominant or assertive in pair-formation rarely fail to secure a mate even when one is lost. Others, such as 692, apparently lacking in pair-formation dominance, obtain a partner only with difficulty.

As already noted, I have been unable to detect any dominance between a mated pair at any stage of the annual cycle (*family value*). There is, however, one possible exception. Reverting to the history of the female 73, which developed an affinity for the male 72 while he was mated to the female 65 (Chapter III and Appendix V), one may find evidence that 73 had for several seasons been attracted towards 72, which did not seem to object to these advances. Now the question arises, was the female 65, while still alive, dominant enough to prevent her mate 72 from wandering away to 73? Again, another mated pair has remained mated for seven consecutive seasons and was still intact in the tenth year of study. It is just possible that a dominance relationship, as exemplified by these two cases, enables one partner to hold the other in spite of external attractions.

The foregoing relates to dominance as applied to adults. Between chicks there does not appear to be any sign of dominance when two healthy chicks are attended by both parents. Should, however, one of the parents disappear, the remaining adult is incapable alone of feeding two large chicks. A fight ensues between the chicks; one becomes dominant, receiving more and frequently all the food. This type of dominance I was able to work out in detail (1941a: 281).

In summary, it would seem that dominance does exist, under certain circumstances, in the Yellow-eyed Penguin. Socially there is little evidence other than "supersedence." From the point of view of pair-formation lack of dominance makes it difficult for some males to secure a mate, whereas others, which appear to have a high degree of dominance, seldom pass a year unmated. In family relations a bird may be dominant enough to prevent loss of its mate. Finally, one chick of a pair may become dominant under stress of hunger.

Why Do Penguins Stay Ashore?—To me the answer to this question revolves around the phenomenon of coition. It should be remembered that at the beginning of the pre-egg stage, which is towards the end of August, most of the birds are already mated.

It seems to me that the male's endocrine condition is ready for coitus at any time during the pre-egg stage and for that reason he must be ashore if he is to synchronize with the female when she is ready. This is a biological necessity. The male's presence at the nest is far more frequent, as shown by Table 26, and also by the fact that he becomes so light in weight. Further, when the first egg is about to appear the male is less often ashore and his absence is most marked between the laying of the eggs. This would seem to imply that the stimulus of coition has faded and that a new phase has set in. There is an urge to prepare for incubation. At this stage, too, the female tends to remain ashore because of the nearness of egg deposition. Her weight is relatively heavy; she is prepared physiologically and psychologically for the next step in the chain.

It will have been noticed that the male is absent sometimes in the pre-egg stage. Probably these absences occur at a period immediately after coition has been effected. If one may judge from observations of other species of penguins, coition occurs early in the period on shore and continues periodically until immediately before the first egg is laid.

I once thought that the birds stayed ashore for the purpose of guarding their nesting territory (1941a: 270), but now I do not think this is so. As already stated, the nest is left vacant for 20 per cent of the pre-egg period. Certainly there is evidence that if a nest site is abandoned by a pair it may soon be appropriated by another pair, such an occupation possibly occurring in the temporary absence of the real owners. If so, the assertiveness of the latter upon finding intruders present would be sufficient to establish their claims. Further, as the Yellow-eyed Penguin does not exhibit thieving propensities, there is no need to stay ashore to guard nesting material. Once an egg appears, a bird rarely leaves it, even though the first egg is not usually incubated until the second is laid.

Influence of Male on Gonadal Development of Female.—Although, as will presently be shown, females are mated to different mates in different seasons they still lay in the same relative order, generally speaking, whether the season is late or early. Further, the span of laying for all birds is short, averaging 23.6 days (Table 34) with a range, including extreme dates over ten years, from 11 September to 15 October. These figures indicate that different females reach the peak of their gonadal development at consistently different times in the pre-egg stage. If the males had a similar peak they would have to find a female where the two conditions coincided, resulting in several females, particularly in small colonies, being left unmated, but a female only rarely is left unmated. The truth is, as already noted, that the male can synchronize with the female when she is ready. Since changes in partnership due to loss or divorce are so frequent, this is a useful provision. Examples of the adaptability of the male to the female are as follows:

For six seasons the earliest laying female 2 was mated to the male 39. Her average laying date for eight seasons was 17 September. Over the same period the medium-laying female 27 was mated to the male 34. The average date of her laying was 25 September. At this time the male 51 was mated to the late-laying female 38. Her average for four seasons was 2 October.

In 1943-44, 51 mated with 2, which laid that year on 14 September. Male 39 linked up with 27, which laid on 24 September, 34 being left unemployed. In 1944-45, 2 laid on 12 September and 27 on 25 September, both retaining the same mates. In 1945-46, 34 mated with 2, which laid on 15 September, and 27, which was still mated to 39, laid on 20 September.

A further example is the male 683. In 1941-42, he was mated to a three-year-old, 616, which laid on 12 September, the second earliest date on record. In 1944-45, his mate was another three-year-old, B48, which laid her first egg on 8 October and the second on 12 October, the last that season, and among the latest for the ten-year period. In 1945-46, his partner was B13, which laid on 30 September.

The foregoing examples signify clearly that the laying date and gonadal development in the female are not influenced by the male, and that the male is able to switch from one female to another independently of these phenomena. In other words, the male is ready for the female at any time, whether she is a late or an early layer.

Factors Influencing Egg-laying.—Regarding events which stimulate egg-laying, I have not many positive data. Table 34 indicates that the laying span does not vary much from year to year.

The breeding season in the Yellow-eyed Penguin is long, commencing with the pre-egg stage at approximately 24 August and continuing to early in May when the latest breeding birds have completed the molt. If egg-laying were prolonged, some birds would molt in the winter at the risk of succumbing. Or, if they molted at the normal time their chicks would die from starvation. The principle of natural selection may explain why the egg-laying season should be somewhat restricted and should begin each year about the same time.

The weather over a long period does sometimes have a slight influence. The year 1938-39, being very wet and boisterous, could be considered abnormal. As a result, and apparently through a shortage in food supply, mortality among the chicks was exceptionally high, and the loss of breeding adults in the winter of 1939

TABLE 34

Annual Egg-laying Dates

Year	Number of nests	Extremes of Egg-laying dates	Laying span in days
1936-37	8	19 September to 9 October	21
1937-38	8	18 September to 5 October	18
1938-39	26	16 September to 5 October	20
1939-40	23	23 September to 15 October	23
1940-41	21	18 September to 9 October	22
1941-42	28	12 September to 6 October	25
1942-43	25	15 September to 10 October	26
1943-44	30	14 September to 6 October	23
1944-45	35	12 September to 12 October	31
1945-46	40	11 September to 7 October	27

TABLE 35

Sex on Eggs on Day Each Egg Appears

Sex on	Male	Female
First egg in the daytime	----	29
First egg the night following laying	9	13
Second egg in daytime	5	22
Second egg the night following laying	4	7

was far greater than usual. The molt was unduly protracted, and the number of strange penguins on the Otago coast, not only of the Yellow-eyed Penguin but also of four species of *Eudyptes*, far exceeded the number present in any other year of study.

Following all this was the late-laying season of 1939-40. Mortality among chicks and adults continued higher than the average but not so high as for the previous season. There was apparently a carry-over from 1938-39, and the laying season of 1940-41 was evidently also slightly affected.

As already noted, the influence of the male does not affect the date of egg-laying—nor, as far as I can tell, does the size of the colony. Isolated pairs nesting singly lay within the normal span. It appears, too, that practically all females, once they have attained the ability to produce eggs, are mated each year. In summary, it would seem that egg-laying is governed by a long breeding season which does not allow of much deviation.

Appearance of Eggs.—This section deals with the behavior of the sexes on each day the eggs were laid and on the days in between. Usually the interval between the eggs is four days, but it is sometimes five. Most of the records, which are not numerous, were taken in the daytime, but some were obtained after dark and after the sea-going birds had returned in the evening.

TABLE 36

Sex on Eggs during Deposition

In daytime				After dark			
Male		Female		Male		Female	
alone	both	alone	both	alone	both	alone	both
26	10	137	21	7	31	15	19
36		158		38		34	

It will be noted that in 29 instances the female was on the egg the day it was laid. As for the second egg, the male was in charge five times. In these instances the eggs were probably laid in the night when the male was with the female. His normal procedure would be to change guard after daylight and allow his partner to go off to sea. For example, at one nest the female was still guarding a single egg at 8 p.m. with the male alongside. At 7:50 a.m. the next day the male was alone, covering two eggs.

Table 35 indicates that, on the evening following the laying of the eggs, whether first or second, the female is not so often in charge, for the male takes his turn when he comes home.

Table 36 shows that the female almost monopolizes the nest in the daytime in the period of egg deposition even when both birds are present, as happens only occasionally. Obviously, too, the female rarely enters the sea for food in the period of egg-laying. In the evening, however, the situation changes, for the male then appears to do more than his share of guarding the egg. Either sex may stay away all night, but the female does so less often than the male; she was absent on only seven out of the 72 times when records were taken after dark.

In the daytime both sexes were present 31 times, whereas the single bird was there 163 times. Apparently the incentive, coition, that kept the birds together, no longer obtains. There is a need, however, for at least one bird to remain and guard the egg. Even so, I have two records of the single egg being left unguarded. This is difficult to explain, especially as one female was a "courageous" type, refusing to leave the nest, even at the pre-egg stage, at my approach. Moreover, for twelve consecutive days before the first egg she entered the sea only once for food.

The fairly rigid adherence of the female to the nest in the period of egg-laying has raised the query concerning her doings four days before the first egg. Out of 206 records taken on these four days the female was present 154 times, which is 75 per cent of the times. Between the laying of the eggs, if we exclude the days on which the eggs appeared, she was ashore 156 times out of 185, or 84 per cent of the times.

In this connection the activities of the female 38 in 1939-40, just before laying, are interesting. At 2 p.m. on 5 October neither bird was present. My next visit was at 11 a.m. on the 7th, when the male was alone on a good nest. At 11:30 a.m. the female landed from the sea and when I re-visited the nest at 1:30 p.m. she was sitting on it with the male preening her. At 11:15 a.m. on 8 October, she was alone with an egg, indicating that it had probably been laid between dawn that day and 1:30 p.m. the previous day.

Apparently the nearness of egg-laying does not prevent a female from entering the sea. It is more usual, however, for her to remain ashore as egg-laying approaches.

Love-habits.—As the majority of the breeding birds are already mated when the pre-egg stage begins, love-habits within the mated pair cannot have anything else but family value. Their first function will have bond-holding value to prevent disintegration of a mated pair at the crucial pre-egg stage. Their second function will have "attuning" value and will "attune" members of a mated pair to a condition when coitus will be effected, followed by successful ovulation. (See Chapter III.)

At the pre-egg stage, love-habits with pair-formation value are largely confined to the unemployed section, as exemplified by the behavior of the unemployed male 692 towards the mated female 115 (Chapter II). Even so, mated birds with an affinity towards a third bird may employ love-habits with pair-formation value. This was indicated by the behavior of the female 73 towards the male 72 (Chapter III).

As for social value, these love-habits are observed at the pre-egg stage when the various breeding birds meet on their way to and from the water. Unemployed birds will also indulge in these social habits with breeding birds.

Trios.—The formation of trios has puzzled me for many years, but I think that I can now interpret it. The whole behavior has pair-formation significance and there are four main types.

(1) A male whose mate has died and a mated pair.—When a bird has lost its mate through death, it requires a new mate, and, as already stated, if the survivor is a female, little difficulty is experienced. If it is a male, however, he is in immediate competition with a surplus of his sex and is often left unemployed for the season. As the pre-egg stage arrives, the urge to mate coupled with the lack of opportunity drives some of these males to pay attention to females already mated. In the incipient stages, conceivably such behavior may be the cause of some of the divorces. An example of this type of trio is as follows and concerns the male 61 whose mate had died, and the mated male 135 and female 76 in 1940-41.

The mated pair had been united since 1938-39 and the association endured until 1943-44, when 135 disappeared. The male 61 had been mated to the female 70 in 1938-39 and in 1939-40; 70 was killed by a vandal in the molt of 1940. All these birds had been known to each other for some years (Appendix I). Birds 61 and 70 nested approximately one hundred meters from the landing ground at the base of a steep cliff, while 135 and 76 had a nest 300 meters beyond them and over the cliff. Moreover, their track passed within a few yards of 61 and 70. Before the pre-egg stage of 1940, it is doubtful if 61 had ever been to the top of that cliff.

At 10 a.m., on 29 August 1940 I found 61 at the top of the cliff under some bushes approximately 54 meters from the nest of 135. Male 135 was at his nest alone as was usual at the beginning of the pre-egg period. The presence of unemployed 61 was clearly due to the influence of the mated pair and probably he had followed 76 to the top of the cliff. That day, at 3:30 p.m., I caught 76 (which weighed the enormous weight of 14¾ pounds) at the top of the cliff as she was proceeding to join 135. Next day, at 2 p.m., I found 61 at the entrance of the bushes of nettle in which 135 and 76 had their nest. Both birds were in occupation. Shortly after I had departed I heard a tremendous "open-yell," and the sound of flippers beating mercilessly on a penguin's back. Investigation revealed that 61 had entered the doorway and approached the mated pair. The infuriated 135 had driven him back to the doorway, and 135 stood some feet away adopting a very menacing "glare." Close behind him, taking no part in the incident, was 76. At 10 a.m. on 31 August 61 was still in the same place in the doorway and the mated pair were further back alongside a rudimentary nest.

On 5 October, when the egg-laying season was almost over, 61 was alone, sitting on a good nest at the base of the cliff. He had failed to secure a mate.

(2) A divorced male and a newly mated pair of which the female was his previous season's partner.—This type is different from the last. The male has been displaced obviously against his will and is frequently found in the daytime not far away from the newly mated pair. Had this male been uninterested he would have been at or near his previous year's nest site, which in the case of some divorced males was a considerable distance away. Interpretation of his behavior is difficult, but either he is endeavoring to obtain the co-operation of his former mate or conservatism is keeping him in the vicinity of her presence until he can adjust himself to the new circumstances. Once incubation begins, such a state of affairs does not last long. Examples of this class of trio, involving the loitering of a divorced male near a newly formed pair, are supplied by the displaced males 28 and 32 (Appendix IV), and the males A10 and 1 (Chapter III).

(3) Odd male and a pair when all three are unemployed.—This combination may be observed at any time in the breeding season, but is not apparent until the eggs have been laid by other birds. The female concerned is, in most cases, a two-year-old and the odd male has previously had no connection with her. Pair-formation, which may be the ultimate result of this group, is rarely achieved. A typical example is that of the male 1 and the female 940, constituting the pair, and the odd male B46 (Chapter III).

(4) An odd female and a mated pair.—Mostly because females are in the minority, they are not usually the odd member of a trio. This seems to occur only when a female has a decided pre-

ference for another male. Naturally, such a preference is difficult to detect, and I consider myself fortunate to have been able to trace the history of the breeding female 73, which had an affinity for a breeding male not her mate (1941a: 272, and Appendix V).

The foregoing classifications do not give all the possible groupings of trios, and there may be other types that have not been observed. All are closely bound up with pair-formation, although the second type is somewhat different in that it is a finale after a newly mated pair has been formed. In all cases, the odd bird, whether male or female, is subjected to aggression by the "injured" member of the pair and does not retaliate.

Two-year-old Breeding Birds.—Normally, both sexes of the Yellow-eyed Penguin are ready to breed at three years of age. A few of these three-year-old females produce a clutch which fails to hatch, and there were two cases (see Table 39) of females which, though "keeping company" with a male, did not lay. Whether three-year-old males are similarly infertile is impossible to determine on the evidence available. Possibly a few of the three-year-old males without attachments are unattached because they have not felt the mating urge.

Of the two-year-olds, 34, or 23.4 per cent of the 145 recorded, have attempted to breed. Five of these were males and 29 were females. Four of the males were mated to a female of their own age and the fifth to an older bird. Not one of the eggs laid by the partners of these males hatched. Two of the males, one mated to a two-year-old and the other to a four-year-old of proved fertility, failed to perform their share of the incubation. The females persisted in doing their part, but the eggs were left cold between the periods when they were not covered by the females.

Of the 29 females, 25 were mated to older males. Sixteen of these females laid two eggs each. In two cases both eggs hatched, in four only one, and in ten neither hatched. Nine birds laid only one egg each, of which only two hatched. Thus out of 41 eggs laid by 25 two-year-old females mated to older males, only 10, or 24.4 per cent, hatched.

In summary, it would seem that young females are likely to feel the mating urge a season earlier than the males of a similar age. This fact is not due to a dearth of such males, for they are actually more numerous than two-year-old females. (See Tables 37 and 44.) Furthermore, it is safe to say that the normal age at which breeding commences in each sex is three years.

TABLE 37

Breeding Two-year-old Penguins

Type of bird	Total	Percentage
Females mated to two-year-old males	4	11.8
Females mated to older males	25	73.5
Males mated to two-year-old females	4	11.8
Males mated to older females	1	2.9
Total	34	100

PRE-EGG STAGE IN OTHER SPECIES OF PENGUINS

First Few Days Ashore.—When penguins return to the breeding grounds after the winter two factors seem to influence their initial behavior. First of all, there is a tendency, particularly apparent among those which have bred previously, to return to the vicinity of their former nest site. This statement is supported by the evidence of Gain (1914: 32, 55) and my own banding experiences with the Yellow-eyed, the Erect-crested, and the Little Blue Penguins. Secondly, many birds are possibly still mated to their previous season's partner. This occurs in the three species on which I have worked (Chapter V), and also in the King Penguin in captivity (Gillespie, 1932: 95-130).

The literature shows that penguins on arrival have a definite goal, for many pass through an unfilled rookery to some point beyond, which is doubtless the site of their previous season's activities. Gain (1914: 15), for instance, states definitely that many female Adélie Penguins head for a well-known goal. Wilson (1907: 47) was puzzled why the first few dozen birds that arrived took up widely scattered positions, as if trying to avoid the proximity of a neighbor. If these birds were occupying well-known territory the phenomenon is easily understood. The assumption is supported by the behavior of my mated pair of Erect-crested Penguins (1941b: 35-36).

Most writers (Chapter III) regard penguins as unmated on arrival, but the writers have produced little evidence in support of their assertions. On the other hand, many remarks suggest that some penguins are mated at this time.

For instance, Levick (1914: 17) notes that on 16 October, twenty Adélie Penguins had arrived in the morning, and by 4 p.m. there were approximately a hundred. On 18 October "a fair number" began to build nests, which the females occupied while the males brought stones. Presumably some of the pairs were mated, and if so mating could hardly have occurred in the short two-day interval. Wilson (1907: 47) states that when only a few dozen had just arrived on 19 October, "One or two birds only had paired as yet."

Let us consider Bagshawe's careful records on the Gentoo and Ringed Penguins (1938). On 31 May and 24 June (pp. 226-227), in the winter when the Gentoo Penguin visited the colonies, Bagshawe thought that some were in mated pairs. In September, when the rookeries had been re-occupied, his daily observatons made him think that the birds were "already mated—possibly with the same mates as last season" (p. 229).

As for the Ringed Penguin (p. 279), on 10 November five or six pairs were mated only eight days after the first birds were seen. This observation is comparable to mine on the Erect-crested Penguin (1941b: 35-36) when the second bird of the mated pair arrived seven days later and joined its mate at once at the previous nest site. If these two Erect-crested Penguins represent fairly the behavior of migratory penguins on their return in the spring, one can see why observers have noted little among the early arrivals to indicate that they are already mated.

Writers seem to incline to the view that the arrival dates are fairly uniform. This assumption is supported by my own records of a female Erect-crested Penguin which, for eight years from

1939, arrived on the average on 25 September, with a range from 22 September to 27 September. When some observer is able to keep records, he will probably find that this rigid adherence to a timetable is a common pattern in the behavior of most individuals of migratory penguins.

Statements regarding which sex is the first to appear are contradictory; the contradictions probably result from lack of detailed observation. For the Adélie Penguin, Levick (1914: 19) and others state that the female appears first, whereas Gain (1914: 16) and others think that the male appears first. For the genus *Eudyptes,* Murphy (1936: 418, 430) and Falla (1937: 91) give evidence in favor of the male, but I have a single record for the female (1941b: 36).

Probably the truth is that the males, on the average, tend to arrive before the females and that the early females arrive long before many of the later males appear. There is the possibility, too, that some of the females arrive before their own mates. It is assumed that many of the pairs remain intact over the winter, as was the case with my mated pair of Erect-crested Penguins (1941b).

In the male Yellow-eyed Penguin, fat deposition reaches its maximum before it does in the female and at a time immediately before the birds stay ashore in the daytime; probably this occurs also in other species. Furthermore, the male probably feels the sexual urge before the female. These two factors possibly contribute towards driving the males ashore first on the average. Variation in this procedure will be due to individual differences. It will probably be found, too, that individual birds tend to arrive in the same order each season.

As in the Yellow-eyed Penguin, the migratory species apparently begin the pre-egg stage when far above their normal weight. This has been noticed in the Rockhopper Penguin by Murphy (1936: 430). Only once did I weigh the female Erect-crested Penguin. That was two days after her arrival when she scaled 12¼ pounds. Her normal weight was probably not more than eight pounds. The prevalence of fat was obvious, for the feathers of the lower part of the body reached almost to the ground and obscured the legs and tarsi, in great contrast to her appearance after several weeks of semi-fasting. In the sedentary species there is little information available concerning the pre-egg stage.

Sexes at Nest up to First Egg.—Once ashore, such highly migratory species as the Adélie Penguin (Levick, 1914: 51), the Ringed Penguin (Bagshawe, 1938: 283), and the genus *Eudyptes* (Murphy, 1936: 430; Falla, 1937: 91; Richdale, 1941b: 37) rarely re-enter the water. The Emperor and Magellan Penguins are probably in the same category, but lack of data makes it unprofitable to discuss them.

The evidence is contradictory as to which sex of the Adélie Penguin occupies the nesting site. During eleven visits between 5 October and 20 October, the male Erect-crested Penguin was either on or very close to the nest. The egg appeared on 21 October. My visits coincided with periods of quiescence. As the love-habits of this mated pair were performed rigidly with the few square inches of the nest site as a pivot, and as the nest was on the top of a small rock, the female must have been on the nest at times. Furthermore, with this mated pair coition could have occurred only at the nest.

Apparently because the male is at a higher sexual pitch in advance of the female he is more likely to occupy the nest in the early stages. As the female feels the urge for coition she will at times take charge, and as the day of egg deposition approaches this second urge will cause her to occupy the nest.

A close study of Bagshawe's story of the Gentoo Penguin (1938) will indicate that in behavior this species is different from its allies, the Adélie and Ringed Penguins. In fact, its behavior resembles that of the Yellow-eyed Penguin. Bagshawe's life histories (pp. 250-264) are given in considerable detail and plainly show that, as with the Yellow-eyed Penguin, both sexes spend much time in feeding in the pre-egg stage and that both may be absent from the colony for a period.

Roberts (1940a: 202-203) notes that the two sexes may occupy the nest and that both will collect nesting material. After allowing for individual differences, one may consider the procedure as similar to that in the Yellow-eyed Penguin, with the males more in occupation of the nest in the early stages and the females later. In conclusion, one cannot help wondering whether the Gentoo Penguin is really a sedentary species, for its pre-egg behavior closely resembles that of the sedentary group.

Of the remaining sedentary species little is known. The Little Blue Penguin (1940: 183) and the White-flippered Penguin (O'Brien, 1940: 315) seem to follow the pattern of the Yellow-eyed Penguin.

The interval between the arrival ashore and the laying of the eggs, generally speaking, seems to be three or four weeks. Table 38 summarizes fairly definite data on the subject.

TABLE 38

Duration of Pre-egg Stage in Penguins

	Date of		Interval	
Species	arrival	first eggs	in days	Reference
Gentoo	13 September	29 November	77	Bagshawe, 1938: 229, 247
Adélie	13 October	3 November	21	Levick, 1914: 17, 51
	12 October	9 November	27	Gain, 1914: 14, 24
Ringed	1 November	29 November	28	Bagshawe, 1938: 279, 282
Drooping-crested	18 July	early August	about 21	My own records
Erect-crested	♀ 26 September	21 October	25*	Richdale, 1941b: 37
	♂ 3 October		18	
Rockhopper	♂ end July	end August	31	Murphy, 1936: 430
	♀ 12 August		19	
			about a month	Roberts, 1940a: 215

*Between 1939 and 1946 six records are available for the duration of the pre-egg stage for the female. The average is 21.6 days and the range 20 to 25 days.

The reference to the Drooping-crested Penguin in Table 38 concerns a short visit to Jackson's Bay on the west coast of the South Island of New Zealand, from 21 to 25 August 1944. Local observation indicated that the penguins were just arriving on 19 July. It will be seen that the pre-egg stage is approximately three weeks long.

According to the precise records of Bagshawe (1938), the Gentoo Penguin in Grahamsland is somewhat of an exception. He gives the date of the complete occupation of the rookeries as 13 September (p. 229) and of the first egg as 29 November (p. 247).

Behavior of Sexes Ashore.—As in the Yellow-eyed Penguin, the love-habit behavior of the mated pairs at the nest when there is no interference from intruders is self-exhausting. The literature seems to point to this conclusion, and my observations on the Erect-crested Penguin (1941b) support it.

In the Yellow-eyed Penguin, the mated pairs, once at the nest, are not subjected to much interference. There is a little, however (Appendix V and Chapter VI). In some of the other species, fighting and thieving are prevalent as noted in the Gentoo (Bagshawe, 1938: 203, 213), in the Adélie (Levick, 1914: 22, 35, and others), and in the Ringed Penguins (Bagshawe, *op. cit.*: 275, 277). In the genus *Spheniscus*, Murphy (1936: 445) records pre-egg fighting in the Magellan Penguin, and Kearton (Murphy, 1936: 459) states that thieving is prevalent in the African Penguin.

The function of this fighting is difficult to discover; careful watching of banded birds over a number of seasons will be required to understand the function. Levick (1914: 35) considers it twofold. For one thing, it possibly has pair-formation significance and is concerned with defense of the sex-partner. The other function may concern disputes over territory and resistance to intra-specific enemies intent on stealing nesting material. The phenomenon of fighting is further elaborated later in this chapter.

Aggression or fighting of social value, apart from the values indicated above, seems to exist in the other species as it does in the Yellow-eyed Penguin. This is particularly noticeable in the bickering that exists in closely packed colonies, a condition that continues long after the need for defense of territory and a sex-partner has ceased. There must therefore be some other cause.

As in the Yellow-eyed Penguin, the sex on the nest seems to act according to a definite pattern. Some contend that the female brings the material. As penguin behavior is strictly mutual, those holding opposite views are probably correct also. That the female will also bring nesting material has been observed in the Gentoo by Roberts (1940a: 202-203), in the Adélie by Gain (1914: 15), and in the Erect-crested Penguins by me (1941b: 45).

There is little evidence on which to judge whether an unmated bird will occupy a nest site. It probably will. Bagshawe's observations (1938: 251) point in this direction. Then there are my unpublished records of a female Erect-crested Penguin occupying a nest alone for seven consecutive seasons (Chapter VI).

Does Male or Female Choose Nesting Site?—There is practically no information available on this question. Some observers have endeavored to decide on the evidence of one season's work, but without a knowledge of the movements of the birds the previous season it is hardly possible to decide. My work with the Erect-crested and Little Blue Penguins does not help in this connection.

Territory and "Property Rights."—A dearth of direct evidence makes it difficult to assess the incidence of territory and "property rights" in the other species of penguins. Probably the site of the nest is defended as in the Yellow-eyed Penguin. There was evidence of this in my mated pair of Erect-crested Penguins which threatened to attack a Yellow-eyed Penguin after that bird had unconsciously approached too closely to their nesting rock.

To what extent the mate and chicks are defended as distinct from the nest site is also difficult to say. Species that adopt the crèche system of guarding chicks are thought to pool their food. This, however, is not proved. Possibly parents may still continue to feed their own chicks. Regarding the behavior of unemployed birds towards a potential mate or nest site nothing is known.

Dominance.—Once again paucity of observation makes it difficult to discuss the other species of penguins. In my paper on the Erect-crested Penguin (1941b: 39) it was shown how a bird not a member of a mated pair stood alongside an incubating male and was dominant enough to prevent the female, when she returned from the sea, from changing guard. Further, in an earlier season, this same intruding Erect-crested Penguin was twice observed alongside the incubating female adopting dominant behavior. The female remained passive. When the mate of the female arrived the intruder retreated (*op. cit.*: 33). What appeared to be comparable behavior to this has been recorded in an unbanded Drooping-crested Penguin by me (1946: 134), and in a Gentoo Penguin by Bagshawe (1938: 193). It is useless to attempt to classify the type of dominance observed in the foregoing examples.

Why Do Penguins Stay Ashore?—It has already been stated that the chief urge which drives penguins ashore at the beginning of the pre-egg stage is the need for coition. Some arrive early, whereas others are still appearing when the first eggs are laid (Gain, 1914: 21). It may be, too, that in a densely packed colony it is necessary to hold the nesting site and to prevent nesting material from being stolen.

Apparently coition does not occur on migration (Murphy, 1936: 376, 392). Not long afterwards, however, it commences. Bagshawe (1938), dealing with the Gentoo Penguin, gives far more details than anyone else. His birds (p. 229) began the complete re-occupation of the rookeries on 13 September. He saw the first attempted coition on 19 September and the first complete act on 22 September, 68 days before the first eggs were noted. From the beginning of October he records its occurrence among marked mated pairs at the nest. Occurrences continued through October and November.

Gain (1914: 14-24) saw the first Adélie Penguin arrive on

12 October, disappear and return on 15 October, with the first coition on 28 October and eggs on 9 November. Levick's (1915: 65) three dates are 13, 16 or 17 October and 3 November. Gentoo Penguins arrived on 29 October, began to copulate on 3 November, and first laid on 18 November (Gain, *op. cit.*: 52-53). Regarding the Ringed Penguins, Bagshawe (1938: 279-282) saw them arrive on 2 November and copulate for the first time on 14 November. He found the first eggs on 29 November.

The foregoing dates are not all likely to be the first occurrences for, unknown to observers, coition probably took place earlier. The dates do show that once sufficient time has elapsed for members of old mated pairs to find each other and for new pairs to be formed, coition is effected almost immediately. How long it continues is difficult to assess, but probably until a day or two before the egg appears.

Bagshawe again is the most informative on this point. His four life histories (pp. 259-264), which ended in the production of eggs, do not record coition in the three days before this event. Of course, it may have taken place unobserved, for both birds of the mated pair were usually in occupation. He clearly indicates, however (pp. 248, 282) in both the Gentoo and Ringed Penguins, a definite decline in intercourse as the eggs begin to appear. Further, he also notes (p. 193) attempted coition when a female Gentoo Penguin was incubating her first egg. He concludes with the following important remark, "This was the only time we saw attempted intercourse when the female had an egg laid." Similarly, Roberts (1940a: 226) has records of a few cases of copulation after the eggs had appeared and one between parents which were feeding young approximately ten days old.

Influence of Male on Gonadal Development of Female.—There is little information available regarding laying dates of individuals in successive seasons and their changes of mates. In species where the span of laying time for all birds is short, as in the Yellow-eyed Penguin, doubtless the females lay in the same order annually. This is suggested by my female Erect-crested

Penguin which, for six years, averaged October 16.6, with a range from 12 October to 21 October.

Factors Influencing Egg-Laying.—As in the Yellow-eyed Penguin, climatic conditions do not seem to affect greatly the annual return and subsequent egg-laying of the migratory penguins. This is borne out by my long observations of a single female Erect-crested Penguin (Chapter VI). Climatic conditions do, however, in the more rigorous parts of the south, dictate that each phase of the breeding cycle should be within narrow prescribed limits. Individuals that tend to produce offspring that vary beyond these are ruthlessly obliterated.

Murphy (1936: 347) thinks that because the King Penguin is sedentary and that because the shores which it inhabits are not ice-choked, it may molt at any time, and that therefore phases of the breeding cycle are not restricted. The African, Peruvian, and possibly the Galapagos Penguins, which are more favorably situated still, breed twice a year (Murphy, *op. cit.*: 457), probably for the same reason.

In the Little Blue Penguin there is another variation. The egg-laying season extends, according to my observations, from the end of June to about 12 November. It should be remembered, however, that the chick stage lasts only eight weeks and the molt only fourteen days. These two facts tend towards a prolonged egg-laying season. On the other hand, the molt does not occur at any time but is restricted from late December to the end of the autumn. As against all this, the Yellow-eyed Penguin, which is sedentary, lives in mild waters and yet its breeding phases are restricted. It would seem, therefore, that the sedentary habits of the King Penguin and its milder climatic environment are factors insufficient to explain the protracted egg phase of the breeding cycle.

Appearance of Eggs.—In the sedentary species it would appear from the information available that, in the period of deposition of eggs, behavior resembles that of the Yellow-eyed Penguin. This apparently applies also in the migratory Magellan

Penguin, for the male seems to absent himself at least in the daytime after the first egg (Murphy, 1936: 447). As for the semi-migratory Gentoo Penguin, both male and female take charge of the first egg in turn for several hours. The female is rarely absent, but the male more frequently leaves his partner (Bagshawe, 1938: 265-266).

Members of a mated pair in the highly migratory species such as the Adélie (Levick, 1915: 65-66), the Erect-crested (1941b: 38-39), and the Macaroni Penguins (Matthews, 1929: 589) observe a rigid fast in the period of egg-laying. In the last two species the males take turns on the first egg, but in the Adélie Penguin, according to Levick, only the female incubates.

Love-habits.—Evidence is abundant to show that love-habits take place in the pre-egg stage in other species. Probably, as in the Yellow-eyed Penguin, all three values are involved. To enable a person to interpret these habits a person must know the history of the individual birds.

Trios.—The literature seems to indicate that there are trios in the other species. Gillespie's account (1932: 95-130) of King Penguins gives several examples of the attentions of unmated birds towards one of a mated pair. In the case of the divorced female "Ann" (p. 113), there is a striking resemblance in her behavior towards her lost partner then mated to another, and that of a divorced male Yellow-eyed Penguin to his former mate which had acquired a new partner. Murphy (1936: 349) also records "triangular complication" in the King Penguin.

In the Adélie Penguin (Levick, 1914, and others), fights have been noted between an odd bird and one member of a pair. The exact meaning of these is hard to assess without a more intimate knowledge of the birds concerned. Bagshawe's life-histories (1938: 249-264) of the Gentoo Penguin bring out the prevalence of trios. One pair in particular (pp. 256-258) would appear to be an unemployed couple unable to breed. An odd unemployed male came along and fought the paired male. This closely resembles the behavior in the third class of trio in the Yellow-eyed Penguin, except that in the latter there are no stand-up fights. Finally, a trio occurred in my Erect-crested Penguins (1941b), but I did not know enough about the birds to be able to explain it.

Young Breeding Birds.—Although information is fragmentary, probably no penguin breeds until it has reached at least its second year. The yearling stage of the Little Blue Penguin is so much like the adult that there may be an exception in this species.

Gillespie (1932: 128) gives evidence that in the King Penguins the breeding age is the fifth year. He also indicates that, as in the Yellow-eyed Penguin, love-habits may occur among young birds not able to breed.

DISCUSSION OF PRE-EGG STAGE

Coition and the Period of Receptivity.—"Physiological readiness for breeding depends on the maturing of the gonads in both male and female. The time when this development begins each year may be in early spring while the bird is still in its winter quarters and may be nearly completed by the time the bird arrives in May. Aside from the maturation process of the sex cells, there is the release of the hormones that exert a conditioning influence over the body as a whole and initiate the nervous processes that regulate the various steps in the reproductive cycle. It may well be true that these hormonal factors do not act in a complete manner until the birds arrive on the mating grounds" (Kendeigh, 1941: 44).

These words of Kendeigh summarize the physiological state of many species of birds at the onset of the pre-egg stage, which is frequently about a month before oviposition. The species concerned are then ready to pass through their own specific pattern behavior which will lead to fertilization and ovulation. For the migratory Snow Bunting, Tinbergen (1939c: 4) has analyzed this period into six distinct phases from the arrival of the males in flocks to the laying of the females. Others, as for example, Howard (1929), Marshall (1929), Huxley (1932), Lack (1939b), and Nice (1943), have made slightly different groupings, but all point to much the same type of behavior. Generally speaking, the pre-egg stage of these types is divided into a pre-coition and a coition phase. The latter lasts only a few days and it is at this time that coition is effected and continued to the end of egg deposition (Lack, 1939b: 190; Odum, 1941: 323; Nice, 1943: 218). Sometimes, however, coition ceases when the first egg is laid (Tinbergen, 1939c: 33).

But in other birds, the pre-egg stage is on a different coitional basis altogether. Coition occurs early and at intervals throughout the whole of this period. Penguins, as indicated earlier in this chapter, are in this category. But that is not all, for in the Yellow-eyed Penguin, at least, coition appears to cease a day or so before the eggs are laid. (See earlier discussion in Chapter VI.) This may well be the general rule in other species of penguins, although there are exceptions.

This penguin pattern behavior of frequent coition at the pre-egg stage plus cessation before the egg appears, also exists in the Royal Albatross. Further, in this species, it has been possible to work out the phenomenon in greater detail. Coition between mated pairs of Royal Albatrosses may occur as early as 27 days before the egg is laid. That the act is not performed continually is indicated by the fact that the breeding area is vacated by both birds for 54 per cent of the time in the pre-egg stage. In the rest of the time, the female is ashore only occasionally when coition usually takes place. It would seem that excessive coition is avoided because the internal state of the female prohibits the act except on well-spaced specific occasions.

In regard to coition in the Royal Albatross, the latest I have observed was a little less than two days before the egg is laid. Moreover, the male, counting all observations made on all birds throughout the ten years of observation, was absent on 75 per cent of these two days of the pre-egg period. This fact seems to indicate the passing of the coitional urge.

The foregoing remarks on the Royal Albatross apply to mated pairs only. Coition among unemployed birds is something quite different (Chapter VIII). Failure, therefore, to recognize these two groups in the field, will lead to faulty deductions.

Other species of birds which perform coition early are the Avocet (Makkink, 1936: 14), the Oyster-catcher and the Grebe (Huxley and Montague, 1925: 894; Makkink, 1942: 25, 60), the Canvasback (Hochbaum, 1944: 29), the Common Tern (Palmer, 1941: 64), and the Black-headed Gull (Kirkman, 1937: 197). In the last-mentioned, Kirkman states that coition may occur 30 days before egg-laying.

Makkink (1942: 55, 60) offers an interesting explanation for the occurrence in the Oyster-catcher of such early coition. In this species, it was observed seven weeks before the appearance of the first egg at a time when the birds were still in the flock and displaying all their sexual attitudes and activities. He remarks, "To my mind the act of copulation, which occurs so early in the season and then probably lacks the significance of fertilization, is just as suitable a means of getting acquainted with fellowbirds as any other activity. In this way all sexual activities play a more or less important role in the process of the formation of pairs."

Provided that the Oyster-catchers are not already mated when they appear in flocks near the breeding grounds and that pair-formation does occur at this time, this may be a reasonable explanation. In the Yellow-eyed Penguin and in the Royal Albatross, however, which are already mated in the great majority of cases at the beginning of the pre-egg stage, the explanation offered does not apply. Early coition in these species, if one assumes from the analogy of other species of penguins that it occurs in the Yellow-eyed Penguin, is due to some factor as yet unknown. It definitely has nothing to do with pair-formation, which occurs much earlier.

To recapitulate, I believe that, in general, species which do not usually retain the same mate from season to season allow coition from a point only a few days before the eggs are laid. Other species, which tend to retain the same mates from season to season, and which have mutual love-habits, permit coition early and periodically in the pre-egg stage. Finally, it is possible that, in many species of this group, coition ceases shortly before oviposition.

In many birds, especially those which are sexually dimorphic, love-habits occur at the pre-egg stage only and lead up to coition. In some instances, as in the Ruff, once that is effected the male takes no further interest in family affairs. In others, however, normal love-habits are distinct from coition; the latter does not take place as a direct result of the former; and coition occurs with but little accessory behavior.

Within my experience, this phenomenon is best illustrated by the Royal Albatross. Among the seven pairs of mated individuals which I have known for a period of ten years, never have I seen indulgence in the elaborate love-habit ceremonies mentioned in the literature. Coition I have witnessed frequently each season. Usually the male has been ashore for a day or two when the female arrives. Following this the two birds generally remain sitting close together for several hours, their most exciting action being a little "mouthing" of each other's neck and head. Eventually coition occurs without any accessory behavior and without any signals apparent to the human observer. Within half an hour both birds may fly and will be absent for several days.

As for penguins, Falla (1937: 91) makes the following important note about a visit to a Rockhopper Penguin colony on 3 December, "Pairing without much preliminary demonstration was observed at many of the new nests." Further, from Murphy's account (1936: 393) of coition in the Adélie Penguin, and from Bagshawe's (1938: 193 and 249 *et seq.*) of the same act in the Gentoo Penguin, it would seem that comparable behavior, as in the Rockhopper Penguin, applies in these two species. From these statements, and my own observations on love-habits in the Yellow-eyed Penguin at the pre-egg stage, it appears that if there is any patterned behavior prior to coition in penguins, the elaborate love-habits described in Chapter II are not part of such behavior.

Other workers have noted a comparable lack of ritual immediately before coition. For example, Lack (1939b: 190) remarks, "There is no courtship display leading up to copulation" in the English Robin. Southern (1938: 427, 429) has observed a comparable situation in the Common Tern, Tinbergen (1935: 19 and 1939c: 29) in the Phalarope and Snow Bunting, Kendeigh (1941: 50) in the House Wren, Whitman (1919: 7) in pigeons, Makkink (1942: 24-25) in the Oyster-catcher, Hochbaum (1944: 30) in some ducks, and Wilson (1946: 240) in Magpies, *Gymnorhina dorsalis* Campbell. Allen and Mangels (1940: 17) state that, in the Black-crowned Night Heron, the period preceding copulation is one of quiescence modified by a little activity. These remarks come close to describing what happens in the Royal Albatross.

In gulls (Darling, 1938: 43; Noble and Wurm, 1943: 192), in the Avocet (Makkink, 1936: 13-14), and in some passerine species (Stidolph, 1947: 80), however, there is apparently some ceremony. Finally, in the Grebe (Huxley, 1914: 508), there is another modification. This species has evolved distinct pre-coitional ceremonies which are performed on a special platform where eggs will subsequently be incubated. This platform is in a totally different place from the open water where the usual love-habits are performed.

In summary, it is evident from the foregoing that in a wide range of birds, coition is effected without accessory behavior. Love-habits which lead directly to coition are not as universal as has been supposed. It is probable, however, that many more birds than is thought indulge in a certain amount of pre-coitional behavior which is different from their usual or "attuning" love-habits of the pre-egg stage.

The question now arises as to which sex is the more eager for coition. As far as I can tell, after carefully watching the Royal Albatross, there is no difference at all. This seems to be the view of many workers, including Nice (1943: 198) writing of the Song Sparrow, Kendeigh (1941: 50) of the House Wren, Whitman (1919: 7) of pigeons, Tinbergen (1935: 21, 1939c: 29) of the Phalarope and the Snow Bunting, Allen and Mangels (1940:

17) of herons, Huxley (1924a: 131) of grebes, and Makkink (1936: 14-15, and 1942: 24-28) of the Avocet and the Oyster-catcher. Tinbergen (1939c: 29) thinks the view that the male is the more eager is wrong, such a view being fostered by the fact that the female's signals are difficult to observe and also by the fact that there is a long pre-coitional period in many species.

The next question concerns the duration of time when the male and female respectively are ready and eager for coition. There are two schools of thought on this matter. The first is that of Howard (1929: 74):

"A bird resembles a mammal. Throughout the cycle the male is physiologically prepared to conjugate, but the female is under stricter physiological control; her prior sexual condition corresponds to prooestrum, and her condition when the secondary physiological control is removed to oestrus."

The second is that of Allen (1934: 189-190), worked out on a lengthy study of the Ruffed Grouse in captivity:

"That birds are *not* like mammals and that the males are *similar* to the females in having a short definite mating period. The period may be longer than that of the female or it may be shorter; it varies with the species and with individuals, especially with age. . . . The whole framework of bird behavior during the breeding season is built around securing synchronization of the cycles in male and female. . . . If the species is rare, territories large, competition not severe—a lack of synchronized rhythm and resulting infertile eggs is likely to occur. The more common the species, and therefore the greater the competition and the smaller the territories, the greater the likelihood of absolute synchronization."

From this Allen goes on to postulate: "Final extirpation of species on the verge of extinction, such as the Heath Hen and the Passenger Pigeon, might well have been accomplished because of the lack of synchronization in the few males and females left towards the end of their existence."

In many species, covering a wide range of avian types, the facts seem to be vastly different from what Allen supposes. In groups which meet only for coition, as in the Blackcock, Lack (1939a: 295) suggests that the male has a longer period of sexual maturity than the female. Similarly, Chapman (1935: 486-487, 498) indicates that the male of Gould's Manakin is sexually active for four and possibly eight months.

In many species which form a pair-bond the male is, to use Huxley's words (1941: 201), "more constantly in the phase of sexual preparedness." This is supported by Marshall (1929: 655), by Tinbergen (1935: 8, 17, and 1939c: 30, 35) for the Phalarope and Snow Bunting, and by Hochbaum (1944: 26) for ducks. It also applies in penguins and in the Royal Albatross. In the latter species, the phenomenon is most marked, for the male awaits the dictates of the female from the time when he first appears ashore until shortly before the egg is laid, and on the few occasions when the female puts in an appearance, coition is consummated. This indicates clearly that, in the Royal Albatross, the period of receptivity in the female is not continuous.

Evidence has already been produced to show that, in the Yellow-eyed Penguin and possibly most other species of penguins, a male will mate with a female irrespective of her gonadal development, which does not limit the choice of any bird, male or female. Moreover, as in Palmer's terns (1941: 65), there are rarely any females of breeding age left unmated. This seems to be true also of the Royal Albatross. Likewise, in the Phalarope, Tinbergen (1935: 27) states that he did not see any unpaired males. Such a state of affairs would not be possible, especially in sparsely populated colonies, if synchronization of the sexes were essential in pair-formation and in coition. In these species, therefore, the following statement does not apply: "The value of large colonies has been interpreted as providing greater chances of one bird meeting another in the same sexual phase" (Noble and Wurm, 1943: 210).

In summary, penguins, albatrosses, and some other birds inhabit the breeding area from a point usually succeeding pair-formation to egg deposition in response to an innate urge which leads them on to coition, fertilization, and ovulation. Coition frequently does not occur as the result of special ceremonies. Pair-formation and gonadal development are normally separate phenomena, although the two may coincide. A short period of receptivity in both sexes, as postulated by Allen, is not the rule. Rather the assumption of Howard, that the female is ready for coition only at intervals but that the male is sexually prepared all the time, describes the more general state of affairs. Such an arrangement prevents excessive coition and also saves females, where there are small colonies or groups, from being left unmated, and therefore the species from possibly meeting the fate that has befallen the Heath Hen, *Tympanuchus cupido cupido* (Linnaeus), and the Passenger Pigeon, *Ectopistes migratorius* (Linnaeus).

Territory and Fighting.—"The theory of territory in bird life is briefly this: that pairs are spaced through the pugnacity of males towards others of their own species and sex; that song and display of plumage and other signals are a warning to other males and an invitation to a female; that males fight primarily for territory and not over mates; and finally that the owner of a territory is nearly invincible in his territory" (Nice, 1943: 151).

Penguin behavior differs considerably from this account of it and follows more closely the statement formulated for gulls, murres, *Uria aalge* (Pontoppidan), herons, etc. (Nice, *op. cit.*: 163) —birds which defend nesting station only. In the Yellow-eyed Penguin, at the pre-egg stage and in the winter, a nest site is defended even though the position is frequently complicated by the presence of a potential or actual sex-partner. Since unmated males often adhere rigidly to nest sites at these periods and continue to do so till well into the chick stage, territory seems to be actually defended, quite apart from defense of sex-partner or contents of the nest.

In densely packed colonies of migratory species of penguins the nest site probably is defended more rigidly. This appears to be particularly true of those species of penguins which have to guard their nesting material so that it will not be appropriated by neighbors. Even so, the sex-partner is usually present to create a complicating factor.

In the Royal Albatross, interest in the nest site seems to be a stage further removed. When on shore, whether single or not, the bird is not necessarily at the nest site. Further, at the pre-egg stage, as stated, there is a 54 per cent absence from the breeding area; there is far more concern over the defense of the sex-partner. What happens in other petrels I do not know.

This raises the question of sexual fighting which Tinbergen (1939c: 59) defines as "all fighting occurring shortly before and during the formation of sexual bonds." Details of this type of fighting, as it exists in the Yellow-eyed Penguin, are given in Chapter II. The all-important point is defense of the sex-partner and furthermore, both sexes, though it is usually the male, may participate in the fighting.

In the Yellow-eyed Penguin, however, the length of time in which sexual fighting may take place is not so restricted as in many of the passerine species. Pair-formation behavior in the former may occur at any time outside the incubation and chick stages for breeding birds and for the entire twelve months among unemployed birds. Coincident with these periods sexual fighting will occur should a bird approach a pair "keeping company." Similarly, old breeding birds which have not severed partnership may also be called upon to fight sexually.

The situation is similar in the Royal Albatross. The sex-partner is rigidly protected from a potential rival whether the pair is in the process of forming or whether the birds are already mated. The first group may spend two complete seasons together before actually producing eggs and all this time while ashore keep strictly to themselves, fending off any intruder. The second group need be on the alert only at the brief pre-egg stage.

It is not known whether the sex-partner in albatrosses is defended at sea in the winter. As it is possible that members of a pair or a mated pair may be together at sea, where love-habits have been observed comparable to those enacted ashore, defense of a sex-partner may also take place at sea.

From the foregoing it is clear that the defense of a sex-partner is something apart from defense of territory, although in defending the former the latter may also be defended. This statement conforms with Tinbergen's thesis (1939c: 67) that "fighting before and during the formation of sexual bonds serves (without the animal 'knowing' it) to secure objects or situations that are indispensable for reproduction." It should not be forgotten, however, that this situation exists in mated pairs of Yellow-eyed Penguins and Royal Albatrosses which have been mated for years and which are not contracting a "marriage" bond. This statement probably applies also to other species of penguins and petrels.

Tinbergen also thinks (1936: 6) that in some birds the sex-partner is more important than territory and that if so there will be a greater amount of "free fighting." This is especially true of the Royal Albatross and probably of the Wandering Albatross, and explains the fights and bickerings seen in albatross colonies, especially among the unemployed, after incubation has commenced. The foregoing remarks apply also, but to a lesser degree, to the Yellow-eyed Penguin and possibly to other species of penguins—for example, Levick's "hooligan" cocks.

Tinbergen (1936, 1939c) has shown that sexual fighting is not restricted to territory in some kinds of birds and animals. Some of these are ducks of several kinds, grebes, and the Avocet. In the Bitterling, *Rhodeus amarus*, fighting takes place in the vicinity of a fresh-water mussel (*Anodonta*) which moves about. Finally, in the Moose, *Alces alces* (Linnaeus), and the Red Deer, *Cervus elaphus* (Linnaeus), fighting occurs near the herd wherever it may wander. Even the highly territorial passerine species may sometimes, as is true of the Snow Bunting, leave the territory, and the male will fight in the presence of the female. Comparable observations have been made for the Willet by Vogt (1938:40), and for the Black-capped Chickadee, *Parus atricapillus* Linnaeus by Odum (1941: 326).

Fighting over territory, therefore, and over the sex-partner are separate phenomena. Davis (1940, 1941, 1942) is very emphatic in making this distinction.

A third type of intra-specific fighting described in Chapter II concerns potential penguin enemies. Such fighting occurs at the nest site as long as eggs or chicks are in occupation, and in the vicinity of the chicks after they are old enough to wander from the nest, should an intruding Yellow-eyed Penguin appear. I do not think fighting at the nest is fighting for territory, although the defense of territory is one of the results. Further, once the eggs are laid, concern over a potential rival seems to cease. Apparently it is recognized that such an individual has then no power to break the pair-bond. Under these circumstances, either one or both parents will attack the intra-specific enemy, even though the latter may be on a possible pair-formation mission (1941a: 278).

In the Royal Albatross the situation is a little different. Incubating birds may be surrounded and trampled on without protest by excited and screaming unemployed birds performing love-habits. This has been noted in the Wandering Albatross by Murphy (1936: 552). As in the Yellow-eyed Penguin, fear of a potential sex-rival seems to have disappeared. Finally, since the Royal Albatross chick is guarded for a relatively short period and thereafter is visited irregularly for feeding purposes only, fighting intra-specific enemies is practically nonexistent.

In summary, there are three main types of intra-specific fighting—territorial, over the sex-partner, and against penguin enemies. In the first it is usually the male which does the fighting, although females in some cases do help. In the second, generally male fights male and female fights female, when she is called upon to defend her rights. Finally, in the third, both sexes attack either singly or in unison. In conclusion, a feature to note in the Yellow-eyed Penguin and the Royal Albatross is the cessation of sexual fighting among breeding birds once the eggs have been laid. This lasts at least until the chicks have left the breeding grounds. Once that is effected, the mated birds may again be called upon to fight sexually.

Dominance.—The question of dominance is bound up with the phenomenon of "property rights" and also, as already shown, possibly with the formation of pairs. Nice (1943: 196-199) after discussing the varied views of many writers dealing with a wide range of species concludes: "Social dominance is something that can be observed and measured; sexual dominance is a postulate that might well be discarded until thoroughly studied. If the male drives or pecks or pounces on the female, these activities are his signals that he is ready for pair-formation. The female signals by posturing, trilling, etc. We do not have to say that one set of actions expresses dominance and the other submission. After all, in nature the female is free to come or go. If she really feared the male, she would stay away from him."

The statement about sexual dominance expresses exactly what happens in the Yellow-eyed Penguin and the Royal Albatross. It is difficult to believe, and this is supported by my observations on the Erect-crested Penguin (1941b), that any other procedure obtains in the other species of penguins. Evidently there is a need for studying the question more thoroughly in penguins, as in other birds.

In the Royal Albatross, as already stated, the female is not often ashore unless she feels the desire for coition. If she feared the male, one would think she would stay away. The female having once arrived, coition may occur immediately (the male is usually already present) or it may not occur for several hours. There is no ocular suggestion that the male is dominant over the female, nor is there any other evidence whenever the mated pair is together. Their behavior is essentially mutual.

Another instance is the mating of the female albatross whose mate failed to return (1942a: 175, 262). Three males, known to be unmated, courted her. She showed no sign of submissive behavior and in fact kept her suitors on the move. If there was any dominance she dominated the proceedings. Once again, had she feared these males she need not have come ashore as frequently as she did.

With penguins, the status of the female, as far as I can ascertain, is much the same. There is no sexual dominance within the mated pair. In the Yellow-eyed Penguin, I have not observed coition but in the Erect-crested Penguin I have seen unsuccessful attempts. There was no question of dominance in those and, further, each partner took a turn at mounting.

Since Nice's summary appeared, Noble and Wurm (1943: 215-217) have stated that in the Laughing Gull, *Larus atricilla* Linnaeus, "Successful copulations occur only after the male secures sexual dominance over the female"; they affirm that the female gets severely pecked and "does not attempt to peck back." This is different from the pattern followed by the Royal Albatross and by penguins.

What Nice describes as social dominance which can be observed and measured, she divides into three phases—supersedence, peck-dominance, and peck-right (*op. cit.*: 92).

The first phase occurs "when the approaching bird successfully usurps the position of the possessing bird" (p. 98). This may be observed in Goldfinches, *Carduelis carduelis* (Linnaeus), when feeding on a thistle head and in Wax-eyes feeding on a berry-yielding tree. One bird continually supersedes another. Comparable behavior may be seen in a group of Yellow-eyed Penguins occupying neutral ground, as, for instance, on the landing area, and doubtless exists among other penguins, but I am not sure of its occurrence in the Royal Albatross. "Supersedence," therefore, fits in with my social value of dominance as noted earlier in this chapter.

The second phase is "peck-dominance—a give-and-take relationship, often place-conditioned, in which the subordinate wins a number of the contacts." Finally, the third is "peck-right in which the dominance is rigid and independent of place." There is no evidence, within my experience, of the last two types of social dominance in the Yellow-eyed Penguin or the Royal Albatross.

The existence of these three phases of dominance in other birds is ably summarized by Nice (1943: 92-96).

In summary, in the Royal Albatross, in the Yellow-eyed Penguin, and probably in other penguins, dominance may be observed in a social way only in "supersedence." There is, however, a type of "peck-right" different from that just noted, which is intimately bound up with the phenomena of pair-formation and "property rights." In these two cases the potential rival or potential intra-specific enemy does not attempt to retaliate. As exemplified by the male 692, some males are less dominant in pair-formation matters than others, a fact which has also been noted by Whitman (1919: 28) in pigeons. Within the mated pair, unless one partner is dominant enough to prevent the other's mating with an outsider, there is no dominance on a sexual basis. Certainly, there is no such dominance of one sex by the other as was noted by Allen (1934: 180-199) or such as is ascribed by Roberts (1940a: 212-213) to the Gentoo Penguin.

Factors Influencing Egg-laying.—Factors influencing egg-laying may be grouped into two divisions—exteroceptive and proprioceptive. These have been discussed by many writers, notably by Marshall (1936a, 1942), by Huxley (1938b), and more recently by Davis (1942). For penguins, Roberts (1940a: 229-237) has given much space to the subject.

In the Yellow-eyed and Erect-crested Penguins, as already indicated, climatic conditions over a period of years do not have much influence. Roberts (1940a: 233) has arrived at comparable conclusions. In the Royal Albatross also, the return to land is surprisingly near the same date each year. The "bad" year of 1938-39 did have an adverse influence in the two succeeding years on the Yellow-eyed Penguin, but the Royal Albatross was not affected. In 1944-45, the Royal Albatross was decidedly late for the first and only time in nine years. That year, too, the Diving Petrel, the Fairy Prion, and the White-faced Storm Petrel were similarly retarded, but on the same island the early-laying Broad-billed Prion and the late-laying Sooty Shearwater were on time. Observations on these last five petrels covered five seasons to 1944-45. In 1941-42, the Diving Petrel averaged ten days early (1945b: 45), while the Sooty Shearwater was constant each season.

In conclusion, from the foregoing account of two species of penguins and six of petrels for from five to ten years, climatic conditions do not seem to affect the egg-laying dates a great deal. Variations occasionally occur, but all species are not affected in any one year. Further, the influencing factors may go back as far as the preceding breeding season, immediate local conditions on the breeding grounds not seeming to have any effect.

Since most birds come into breeding condition as the days gradually lengthen, the influence of increasing light is thought to stimulate the gonads through the anterior pituitary by way of the eye. A noted exception to this rule is the Emperor Penguin, which lays in July in total darkness. In addition, there are two New Zealand petrels, the Black Petrel, *Procellaria parkinsoni westlandica* Falla (Falla, 1946: 112-113), and the Grey-faced Petrel, *Pterodroma macroptera* (Smith) (Oliver, 1930: 135-136), which lay their eggs in early winter when the days are still shortening.

Much has been written concerning the thesis that love-habits after pair-formation, when the birds are on the breeding grounds, lead to synchronization of the male and female sexual cycles (Howard, 1929) and thereby help or are even necessary for ovulation (Marshall, 1929: 656; Huxley, 1938b: 17, 1941: 201, and others). It is also stated that in some cases the mere presence of a "companion" (Darling, 1938: 19-20) is sufficient, and that this companion may be either a male or another female. Two females confined together may both take to laying eggs (Matthews, 1939: 557). This is the reverse of what is normally accepted (Marshall, 1936b: 1057), that coition is needed before ovulation will occur. There are also records of isolated females laying, for example, Whitman's (1919: 9) for pigeons, and Allen's (1934: 185) for Ruffed Grouse.

In view of the foregoing, the behavior of my female Erect-crested Penguin which returned alone for seven years after the loss of the male is of interest. In five of those years she produced the usual two eggs, and in fact the dates were earlier than when the male was last with her, the second last laying being as early as nine days. In all that time she did not have the stimulus of her kind or the physical stimulus of coition. Certainly there were two breeding pairs of Yellow-eyed Penguins in the same colony, but they were some distance away and could only be heard. Moreover, by the time she laid, the Yellow-eyed Penguins were halfway through their incubation, and the only possible auditory stimulus on the Erect-crested Penguin would be the "welcome" ceremonies at the irregular times that change of guard was effected.

These facts are recorded not to refute what has already been established but merely to show that there are exceptions. A further interesting fact, already noted, is that if a late-laying Yellow-eyed Penguin female comes ashore early with her mate, the resulting love-habits do not cause her to ovulate earlier than usual. This state of affairs has been noted by Howard in the Reed Bunting, *Emberiza schoeniclus* (Linnaeus), and by Tinbergen (1939c: 21) in the Snow Bunting. Further still, a late-laying female penguin mated to a succession of different males does not, as a result, alter her relative laying date each season.

In summary, love-habits between mated birds at the pre-egg stage are thought to assist the synchronization of the male and female periods of receptivity and to lead to coition, which in turn has a beneficial effect on ovulation. Opposed to this conclusion is the normal ovulation of a single Erect-crested Penguin female without the stimulus of love-habits or coition. Further, a female Yellow-eyed Penguin is definitely not affected by the date of her arrival on the breeding grounds in the daytime or by the gonadal development of her mate.

Another thesis which has aroused considerable interest is that of Darling (1938), who suggests that a concentrated number of the same species, and the visual and auditory patterns exhibited by the activities of these assembled individuals, are indispensable to the reproduction of colonial birds (Allen and Mangels, 1940: 4). Darling remarks:

"The thesis of this essay is that the social group and its magnitude, in birds which are gregarious at the breeding season, are themselves exteroceptive factors in the development and synchronization of reproductive condition in the members of individual pairs of birds and throughout the flock" (p. 3).

"It is suggested that members of a flock and the visual and auditory patterns evoked act primarily on the nervous system by way of eye and ear, then on the anterior pituitary and from that seat of control on the testes and ovary" (p. 6).

From this he goes on to declare (p. 93) that "there is a threshold of numbers below which breeding does not take place." As evidence he instances (p. 86) that in 1936 three pairs of Razorbills, *Alca torda* Linnaeus, visited his island without breeding and that in 1937 there were 14 pairs which bred. Then he recalls the well-known habit of the Fulmar, *Fulmarus glacialis glacialis* (Linnaeus), which visits the site of a new colony for several years before breeding. In the meantime, the birds increase in numbers till a breeding threshold is acquired.

Without wishing to refute the foregoing thought-provoking ideas, I should like to point out first of all that some colonial birds will nest singly and without retardation of ovulation. Secondly, I believe there is another explanation why species when founding a new nesting station do not breed in the first year or so.

Regarding the first point the Erect-crested and Yellow-eyed Penguins will each nest singly and in keeping with normal laying dates. In the latter also there is no variation in breeding times, either in the separate colonies of the Otago Peninsula or in the much larger colonies on the Catlins coast approximately 100 miles farther south, or at Stewart Island, which is still farther south. Roberts has observed comparable circumstances in Gentoo and Rockhopper Penguins (1940a: 234). A friend has noted the nesting of a single pair of Drooping-crested Penguins on the South Island coast. With petrels, for many years a single pair of

Royal Albatrosses nested on the Otago Peninsula. Further, on a tiny island off Stewart Island, some 60 miles from the nearest breeding ground, I have found a single breeding pair with a chick of the Mottled Petrel, *Pterodroma inexpectata* (Forster). Finally, in New Zealand the Blackbacked Gull, *Larus dominicanus* Lichtenstein, near populated areas, nests in colonies; but in uninhabited parts of the country, especially in the south of Stewart Island, it breeds in single isolated pairs and, as far as I can tell, at the normal time.

With reference to the "threshold" hypothesis, what the observers did not know about the Fulmars, in particular, was their age and breeding status. Knowledge of these two points is extremely important in explaining the behavior of birds like penguins and petrels when forming new colonies.

Over a number of years during which I have been fortunate enough to watch the development of several new nesting stations of the Yellow-eyed Penguin, the age and breeding status of the individuals were known. They have consisted mostly of juveniles of both sexes (sex discovered subsequently), an occasional two-year-old female, a greater number of two-year-old males, and some older unemployed males which have usually not bred. Occasionally an old unemployed breeding male appears. At first the population is small, and there is no breeding *because there is no female of breeding age present.* That is the vital point. There is no question, in this particular instance, of a numerical threshold. As soon as a female reaches breeding age, breeding commences and, by this time, the population has increased, owing to the advent of the foregoing types of unemployed birds. Moreover, breeding birds, once established, rarely leave their colonies of residence, and for this reason do not appear in new colonies.

The foregoing are definitely observed facts regarding banded penguins. As for the petrels, however, my technique is not so definite, because of the difficulties of keeping a check on petrel movements. But I do know that in the six species I have studied intensively, breeding birds adhere strictly to their own vicinity.

This means that the Fulmars developing the new station were presumably not old birds.

Judging by the Diving Petrel, which does not breed until at least the second year, and according to my own observations and also those of Lockley (1942: 140-143), petrels normally spend some time as unemployed birds. The same is true of the Royal Albatross, which will pass even two years and possibly more on the breeding grounds before breeding.

It seems that young birds tend to wander and rarely return to their colony of hatching. The Diving Petrel is the only petrel I have recorded in which the young return, and Lockley has recovered a few young Manx Shearwaters. This behavior is true also of other birds, as, for example, the House Wren. Kendeigh and Baldwin (1937: 115) remark: "The evidence is fairly convincing that the immature birds do practically all the wandering into other regions and seeking of new areas in which to breed, while the adult birds almost invariably return to the immediate locality of their former breeding sites."

It may be, therefore, that Fulmars which develop a new station over a number of years without breeding are mostly young birds. If older birds are present they may be unemployed males, since there is probably a surplus of this sex. The reason for not breeding may be, not that there is lacking a numerical threshold, but that the *females*, at least, *have not attained breeding age.* I offer this merely as a suggestion for further research.

In view of the foregoing statements, the opinions of Fisher and Waterston are of considerable interest (1941: 252). They indicate that in a number of colonies of Fulmars each of which produced less than 10 eggs per year, an aggregate of 532 pairs laid only 126 (26.6 per cent) eggs. Colonies which produced less than 100 eggs each, aggregated 734 pairs that laid a total of 308 (41.8 per cent) eggs. Finally, in some of the larger colonies the percentage of eggs in relation to pairs of birds in residence is considered to be more than 75. From this Fisher and Waterston conclude (p. 255), "In general, the effect of numbers on the Fulmar's breeding cycle is parallel to the effect of numbers on the Herring-gull's cycle described by Fraser Darling."

The age and breeding status of the birds in the colonies considered were unknown. Instead of the percentage of eggs in the small colonies being low because of a small numerical threshold, could not the percentage have been low because of a scarcity of birds capable of breeding? This point needs investigation before the former statement can be regarded as correct. In the large, well-established colonies, especially as Fulmars are rapidly increasing, it is only to be expected that a greater percentage of older and therefore breeding birds are in residence.

Trios.—The question of trios, in which both sexes are involved on a sexual plane, has not received a great deal of attention in birds. It would seem to have a pair-formation significance and the odd member is usually attacked or threatened by the similarly-sexed partner of the pair.

It is evident from the literature that in the highly territorial species, trios are formed although they do not last long. Trespassing males apparently attempt to persuade females to come to their territory (Nice, 1943: 172).

In other species, especially in those in which pair-formation may take place at any time over a lengthy period before the eggs are laid, the odd member of the trio is more persistent in its attentions. It is this aspect of trios which I have been able to work out with a fair amount of detail. It is suggested that this should serve as a basis for further investigation.

At the pre-egg stage in penguins, trios are more in evidence, but after incubation commences breeding birds are seldom involved. Trios are then confined to the unemployed and may be observed at any time in the year.

This statement is also true of petrels, at least when they are ashore. At the pre-egg stage, mated pairs of Royal Albatrosses and pairs "keeping company" will be visited by an outsider which is warned off by the bird of its sex of the pair. These outsiders will also visit each other, so that this phenomenon of "visiting" is a common feature in an albatross colony.

It exists, too, in the smaller petrels. Unemployed members wander about a great deal and enter not only one another's burrows but also those of incubating birds. This is particularly noticeable in the Sooty Shearwater (1942b: 95 and 1944b: 97) and leads to the formation of numerous trios in the incubation and early chick stages when breeding birds are otherwise employed.

The observations of Lockley (1942) on the Manx Shearwater, and of several writers on the Fulmar, seem to point in the same direction. "Visiting" and trios are obviously common in these species. On one occasion (1943b: 105) I discovered that a member of a trio of White-faced Storm Petrels had its beak firmly fixed into the back of an intruder.

In conclusion, it would seem that the phenomena of "visiting" and of trios are intimately bound up with pair-formation. They are two of the means by which birds become acquainted with potential sex-partners. As individual penguins and petrels tend to adhere to a fixed neighborhood, there is every opportunity for the acquaintanceship to develop. Even if a mated pair does not result more or less immediately, an affinity between two birds may develop which, ultimately, at a more opportune moment, may end in pair-formation (Chapter V). On the other hand, it should be noted that many of these acquaintanceships and also of those pairs "keeping company" come to naught.

In regard to other birds, trios have been noted in Phalaropes by Tinbergen (1935: 27), the females being in the majority; in the Kentish Plover, *Charadrius alexandrinus alexandrinus* Linnaeus, by Selous (1906: 214-215); in the Grebe by Huxley (1924a: 131); and in Oyster-catchers by many observers. The exact significance of these is difficult to estimate. Huxley thinks that the Grebe intruding on the mated pair was a male which was warned off by the male of the pair.

SUMMARY

On the average, male penguins seem to arrive first on the breeding grounds. Some females, however, arrive before some males and even before their own mates. This is true of many birds and, in particular, of the Royal Albatross. In both the Yellow-eyed Penguin and the Royal Albatross, the male tends to occupy the nest first, probably because of his more tense sexual state. As the female feels the urge for coition she tends to occupy the nest. The approach of oviposition then causes her almost to monopolize the nest. Penguins which are entirely migratory seem to fast all the time at the pre-egg stage. The Yellow-eyed Penguin does not. Both sexes in the Yellow-eyed Penguin are absent 20 per cent of the time; in the Royal Albatross, 54 per cent. After arrival, the first factor which influences subsequent behavior in penguins and petrels is their return to the vicinity of their previous nest site. This allows members of a pair to recognize each other, and if the personal bond is strong enough, to re-mate. In birds like penguins and petrels, the pre-egg stage extends at least three or four weeks. Coition occurs early and frequently, usually until just before the eggs are laid. In some birds, the pre-egg stage is divided into a pre-coition and a coition phase. Coition occurs only in the latter phase and may last throughout egg-laying. In many birds coition takes place without accessory behavior. A number of writers think that neither sex is the more eager. Both these statements are particularly true of the Royal Albatross. Some workers believe both sexes have short definite periods for coition, so that two individuals cannot copulate unless their periods of receptivity synchronize. This is the view of Allen (1934). Others follow Howard (1929), who thinks that the male is ready all the time but that the female is not. This would seem to be the more general rule and is true of penguins and the Royal Albatross. Female Yellow-eyed Penguins lay in the same relative order each season. The laying date and gonadal development of the female are not influenced by the male. The male can mate with any female irrespective of these factors. This is also true of the Royal Albatross. In penguins and petrels, climatic conditions do not affect egg-laying dates to any extent. Increasing day length is thought to stimulate reproductive functions. As against this, some birds, including two species of New Zealand petrels, lay before the middle of winter. In the Yellow-eyed Penguin, the female dominates the nest in the period of egg deposition, being present 84 per cent of the days. Mated pairs of Yellow-eyed Penguins defend nest sites, contents of nest, chicks out of nest, and mate. Unemployed Yellow-eyed Penguins defend a potential nest site, a potential sex-partner, or both. These defended objects are called "property rights." Sexual fighting is "all fighting occurring shortly before and during the formation of sexual bonds" (Tinbergen, 1939c: 59). Sexual fighting is of short duration in many species of birds. Among breeding Yellow-eyed Penguins and Royal Albatrosses it ceases between the laying of the egg and the departure of the chicks but obtains at all other times when the birds are ashore. Among unemployed members of these two species, however, it may occur at any time in the year. Defense of the sex-partner in penguins and the Royal Albatross is something apart from territory, although, in defending the former, the latter is often defended. When the sex-partner is more important than territory, as in the Royal and Wandering Albatrosses, much "free fighting" occurs. That sexual fighting is not always restricted to territory, has been noted in some species of birds and other animals. Three types of intra-specific fighting are noted—for territory, in which the male usually does the fighting; over the sex-partner, in which male fights male and female fights female; against enemies, in which both sexes act in unison. Dominance in penguins and in the Royal Albatross is bound up with the questions of "property rights" and of pair-formation. In these species there is no sexual dominance within the mated pair. Dominance in the period of pair-formation probably occurs, as some males have great difficulty in securing mates. Social dominance exists only in "supersedence." As opposed to Darling's thesis (1938), some colonial birds will nest singly without retardation of ovulation. In view of this, the return of a female Erect-crested Penguin for seven years after loss of her mate is of interest. In five of those years she laid eggs at the normal time without the presence of any of her kind. When the Yellow-eyed Penguin is forming a new breeding station, failure to breed is not due to small numbers but to the absence of breeding females. It is suggested that the absence of breeding females may be the cause of the failure of Fulmars to breed when establishing a new station —not the lack of a numerical threshold. The phenomenon of trios among birds seems to have pair-formation significance. In species like penguins and petrels, trios occur at any time when the birds are on the breeding grounds. Trios are more in evidence among unemployed members of a community. In the Yellow-eyed Penguin, the normal breeding age is three years. Some breed at two years, the number being 22.8 per cent of all two-year-olds recovered. Only 35.7 per cent of the eggs laid, hatched.

Chapter VII

Unemployed Birds

Classes of unemployed Yellow-eyed Penguins. Incidence of love-habits in Yellow-eyed Penguins. Trumpeting among Yellow-eyed Penguins. Segregation. Unemployed birds in other species of penguins. Discussion of unemployment in birds. Summary.

As UNEMPLOYED MEMBERS of any species of birds form a distinct and important unit which must be differentiated from the breeding members of a community in any behavior study, it has been considered desirable to deal with the complete annual cycle of the unemployed Yellow-eyed Penguins in a single chapter. It is only towards the end of the laying season for breeding birds that the status of the unemployed penguins gradually becomes apparent. Before this, the unemployed members of a penguin community are difficult to distinguish, especially if they occupy nests, for they behave in exactly the same way as the breeding birds. Therefore, it is only when it is known that all eggs have been laid for that season, that those birds remaining without eggs are definitely unemployed.

CLASSES OF UNEMPLOYED IN YELLOW-EYED PENGUINS

Tables 39 and 40 deal only with the four main colonies, except for the first two seasons, when only two and three colonies respectively were watched. Records for the first three years are sparse, for, even though unemployed were present, I was not aware of their status, and, further, some time elapsed before observations, of young birds marked as fledglings, were collected. These facts amply demonstrate that, for this type of research on behavior, it is not until the third or fourth season that the observer's data warrant his making deductions. In working out percentages, therefore, in Table 40, I am taking into account only the last

TABLE 39

Breeding and Non-breeding Adult Penguins

		Birds not "keeping company"					Birds "keeping company"				
		Males of breeding age		Two-year-olds			Two-year-olds		Three-year-olds	Males of breeding age	
Year	Pairs of breeding birds	old breeders	others	♂	♀	sex unknown	♂	♀	♀	old breeders	others
1936-37	8										
1937-38	31			1				1		1	
1938-39	36	2	2	4		9	2	2			
1939-40	26	7	6	9	2	10		1		1	
1940-41	24	6	12	0	1	1		1		1	
1941-42	29	10	6	4	0	3					
1942-43	26	9	8	7	0	3					
1943-44	32	6	13	2	1	3	1	6		4	1
1944-45	39	3	13	9	2	5		4	1	2	3
1945-46	41	3	15	2	2	8	1	4	1		4
Total	292	46	75	38	8	42	4	19	2	9	8

seven seasons. It should be realized, however, that even in these seasons a few unemployed birds were probably missed.

Breeding Males Temporarily Unmated and Not "Keeping Company."—Each season, in all colonies and sub-colonies, there are usually male penguins which have bred at least once and which have failed to secure either a mate for breeding or a non-breeding female with which to "keep company." In seven seasons

TABLE 40

Data from Table 39 Expressed in Totals and Percentages (1939-40 to 1945-46)

Type of bird	Total	Percentage
Breeding birds	434	64.8
Birds not "keeping company"		
old breeding males	44	6.6
males which have not yet bred	81	12.1
two-year-old males	33	4.9
two-year-old females	8	1.2
two-year-olds, sex unknown	34	5.0
Birds "keeping company"		
two-year-old males	2	.3
two-year-old females	16	2.4
three-year-old females	2	.3
old breeding males	8	1.2
other males	8	1.2
Total	670	100.0

the number has varied annually from 2.9 to 13.5 per cent of all birds more than two years of age with a mean of 7.7 (Table 41). When all adults, including two-year-olds, are considered, the mean is 6.5. The small percentage in 1944-45 and 1945-46 was due to the unprecedented influx of young breeding females. It should be noted that there are also additional old unmated breeders but that these have been "keeping company" with non-breeding females.

Table 42 gives some idea of the number of times 38 male penguins failed to secure a mate in the research period. The figures include only times subsequent to when a male was first mated. Further, only those birds on which four observations have been made are considered. It may be seen that, on the average, a breeding male is unmated once in every five years. Nine, or 24 per cent of these males, to my knowledge, secured a mate each season. Two males were successful for nine consecutive seasons, at the end of which one was found dead and the other was still thriving; their early history is unknown.

Males Which Have Not Acquired Their First Mate.—These birds are more than two years old and, as indicated in Table 41, are slightly more numerous than the previous class. Their number has varied annually from 8.1 to 17.9 per cent of all birds

TABLE 41

Percentages of Breeding and Non-breeding Penguins More than Two Years Old

		Unmated males			
		not "keeping company"		"keeping company"	
Year	Breeding birds	old breeders	others	old breeders	others
1939-40	78.8	10.6	9.0	1.6	
1940-41	71.7	8.9	17.9	1.5	
1941-42	78.4	13.5	8.1		
1942-43	75.5	13.0	11.5		
1943-44	72.7	6.8	14.8	4.6	1.1
1944-45	79.6	3.0	13.0	2.0	3.0
1945-46	78.8	2.9	14.4		3.9
Mean	75.4	7.7	14.1	1.4	1.4

more than two years of age, with a mean average of 14.1 per cent for seven seasons.

Table 43 records 51 males of this class, together with the number of years necessary for each of them to acquire a mate. The mean is 2.45 years. As 33 of these records are incomplete, the true mean will be somewhat higher than shown.

The story of male 692, which was unmated for at least seven years, has already been narrated (Chapter III). Another interesting case is that of B15, which lived for the six years of his life in the colony where he was hatched before he was accidentally killed. Several of the birds included in the table "kept company" with the two-year-old females some time before being finally mated.

Table 42

Data Relative to Occasions When Breeding Males Are Mated and Unmated

Number of males	Years of observation	Times	
		mated	unmated
1	10	8	2
2	9	9	0
2	9	8	1
1	9	7	2
2	9	6	3
2	8	8	0
3	8	7	1
1	8	6	2
1	8	5	3
2	7	7	0
1	7	6	1
2	6	5	1
4	6	4	2
2	5	5	0
4	5	4	1
1	5	1	4
1	4	4	0
2	4	3	1
3	4	2	2
1	4	1	3
38	Aggregate times birds were respectively mated and unmated	199	50
	Percentage	80	20

TABLE 43

A Total of 51 Unemployed Males More than Two Years Old That Have Not Acquired Their First Mate

Number of years unmated	1	2	2+	3	3+	4	4+	5	5+	6	7+
Number of birds	10	9	14	4	6	3	1	1	1	1	1

Two-year-old Males Not "Keeping Company."—In any colony in any year there may be a number of birds which have reached the age of two years. One hundred and eleven, or 76.6 per cent, including both sexes, have remained unemployed (Table 44), whereas 34, or 23.4 per cent, have attempted to breed (Table 37). Twenty-nine, or 85.3 per cent, of the latter are females.

Of the non-breeding two-year-olds, 22.5 per cent "kept company," but the majority seemed to remain unattached. According to Table 40, 11.1 per cent of all adults are of this type, the majority being males.

The different classes of unemployed two-year-olds banded in all colonies in the ten years are listed in Table 44. Of these classes 33.3 per cent are males and definitely without attachments. In addition, there are 37 per cent whose sex was not ascertained, partly because they were not seen subsequently, and partly because they were still two-year-olds at the time of writing. If the males of these were added to the first group the percentage would probably exceed 60.

This means that the number of unattached two-year-old males

TABLE 44

A Total of 111 Unemployed Two-year-old Penguins of Both Sexes

Birds not "keeping company"			Birds "keeping company" with					
			two-year-olds		old breeding birds		other adults	
♂	♀	Sex unknown	♂	♀	♂	♀	♂	♀
38	8	42	4	4	—	8	—	7
33.3	7.2	37.0	4.5	4.5		7.2		6.3

is high. Only a further 4.5 per cent made any pretensions at breeding by "keeping company" with females of their own age.

The number of two-year-old males concerned with producing eggs is given in Table 37. The percentage is low, only 14.7 of breeding two-year-olds. Therefore, it would appear that two-year-old males show a greater tendency to remain unmated than do the females.

Two-year-old Males "Keeping Company."—There are only four instances of this type in my records, and each bird was with a two-year-old female. This fact coupled with the five records (Table 37) of a two-year-old male mated to a female clearly indicates how seldom young males develop the mating urge.

All of the four males "keeping company" were discovered in the period of incubation for breeding birds. Each was ashore in the daytime and each was going through love-habits common to breeding birds at the pre-egg stage. No attempt was made to build a nest.

At the time of writing, one pair of the foregoing is still at the two-year-old stage. As for the remaining six birds, I was unable to follow their doings in detail, but four of them were subsequently mated to different penguins altogether.

Old Breeding Males "Keeping Company."—These birds, of which there are nine instances (Table 39), have bred at least once in a previous season. In eight instances, the bird with which the male was "keeping company" was a two-year-old female, and in the other instance it was a three-year-old female. In three of these instances, involving two two-year-old females and the three-year-old female, the attachments, which began, to my knowledge, as early as the pre-egg stage and possibly in the preceding winter, led, in the succeeding breeding season, to three mated pairs which produced eggs. All three pairs in the preliminary season built good nests and went through all the love-habits of old breeding birds. When they did lay, two of the pairs retained approximately the same site, but the third pair shifted approximately 80 meters away through thick vegetation reached only by a tortuous track; in this instance, obviously, the bond between the pair was strong.

Males More Than Two Years of Age Which Have Never Mated, "Keeping Company."—Eight birds, of which seven were "keeping company" with two-year-olds and one with a three-year-old, come under this heading. Altogether 138 males more than two years old have failed to mate, 121 of which did not "keep company" with any other female (Table 39). This leaves 17 which were partly able to satisfy the breeding urge by "keeping company" with a non-breeding female, but one should remember that many others were inhibited from doing so owing to a dearth of females.

Two-year-old Females Not "Keeping Company."—Of 56 two-year-old females the sex of which has been ascertained (Tables 44 and 37), 29 produced eggs, 19 "kept company," and only eight remained unattached. This state of affairs is due to the activities of a large number of unmated males in search of a mate, so that these young females are in great demand. The behavior of these unattached females is usually of a social nature but not always so, for at any time up to the succeeding breeding season, they may be seen indulging in love-habits, chiefly the less exciting ones, with other males.

As three-year-olds these females were always either mated or "keeping company," but I am not able to say exactly when the mated pair was formed; in most instances it was probably in the winter preceding laying. For example, note the case of Z14 and Z18 (Chapter III).

Two-year-old Females "Keeping Company."—This type of bird is not common, there having been only 19 altogether as against four for the males. Four were "keeping company" with males of the same age, eight with old breeding males, and seven with old males that had never bred.

Three-year-old Females "Keeping Company."—It was not until the ninth and tenth years of study that my only two records of this type were made. One was "keeping company" with an old breeding male with whom she reared two chicks in the following year when a four-year-old, and the other with a three-year-old male that had not bred. As far as I could tell, no eggs were laid when these two females were three-year-olds. From these two examples, it seems possible that occasionally a female is unable to lay eggs until she is almost four years of age. Further, as has already been noted, a few other three-year-olds have produced eggs which did not hatch.

Unattached Females Which Have Once Bred.—Up until the tenth year I had no record of a breeding female being left unattached. Then two such females suddenly appeared, but the circumstances seem to be extraordinary. There is evidence that both produced at least one egg. The two females are B41 (Chapter III) and W45.

Birds Which Have Lost Eggs.—These birds automatically join the unemployed group once their eggs are lost. Some of these birds are still mated in the succeeding season, but there is a tendency to separate and to disappear from the colony. Eggs are lost mostly through failure of both to hatch; this is the usual fate of those laid by two-year-olds. Only rarely does this happen to older females. Occasionally the eggs are ejected from the nest.

Birds Which Have Lost Chicks.—Chicks are lost for various reasons, especially if the weather is exceptionally wet in the first week after hatching. The behavior of the parent birds which have lost their young resembles that of birds which have lost their eggs. Once again, in assessing penguin behavior, birds of these last two classes must be distinguished from the non-breeding groups.

In summary, a colony of Yellow-eyed Penguins may be divided into twelve classes of unemployed birds. Until these classes can be recognized by an observer there is a great deal of penguin behavior which cannot be understood. As the need for recognizing unemployed birds is applicable to other species of penguins as well, one can see why so many faulty deductions have found their way into the literature.

INCIDENCE OF LOVE-HABITS IN YELLOW-EYED PENGUINS

According to classification of unemployed birds in the last section, this group may be divided into those penguins "keeping company," those which apparently would like to "keep company" but lack the opportunity, and finally those which appear indifferent.

Birds "Keeping Company."—As has already been noted, many unemployed birds are in pairs some of which build good nests whereas others merely occupy a camp site. In still others, the attachment is far more ephemeral. All these birds "keeping company" perform love-habits characteristic of breeding birds at the pre-egg stage, a condition which lasts as long as the nest or camp site is occupied. Further, the "welcome" ceremonies and change of guard probably take place when individuals of such a pair meet again after a sojourn at sea, and coition also probably occurs. It is obvious, therefore, that the love-habits of this group definitely have pair-formation value, even though the association only occasionally results in a mated pair.

Birds Not "Keeping Company" Because of Lack of Opportunity.—This group includes all the old unmated breeding males, some of the males which have never bred, and a few of the two-year-old males. Their behavior indicates plainly the presence of an urge to acquire a mate. The first to become conspicuous are the old breeding males which are noticeable in the winter and at the pre-egg stage, although of course their real breeding status is not recognizable until all the eggs have been laid. Their behavior is comparable to that of the breeding males; they stay ashore in the daytime; and some of them build nests and sit on them, a feature which extends well into the incubation stage. What love-habits they are able to practice towards a female on the few occasions when they get a chance, have pair-formation value. Eventually, at some period, before a successful breeding season, these love-habits culminate in the winning of a mate.

These males also perform love-habits with social value, as when in the company of juveniles, of other males with a comparable status, and of unattached two-year-old females on what appears to be a social basis. Coition I do not think can possibly take place in any of these temporary associations with other females which are of that group giving no evidence of an urge to "keep company."

As for males which have not bred and two-year-old males, they are generally not noticed until the incubation period begins. Exceptions seem to be males which have been in the colony for some years, like 692 and B15 (Chapter VII). On the whole, the love-habit behavior of these two groups throughout the yearly cycle resembles that of the old unmated breeding males.

Birds Apparently Indifferent to Sex.—This group includes a few of the two-year-old females, many of the two-year-old males, and some of the older males which have never bred. The young females seem to have no attachment for any male, apparently because the urge to form a pair has not awakened within them; it should be remembered that if the urge appears there are plenty of males available. Since each one of several of these females is found in different colonies within the space of a few weeks, they apparently are unattached to males. The possibility that they have several attachments is unlikely. Love-habits which they perform have only social significance. Of course, unemployed males do attempt love-habits with pair-formation value with these females. Often the males appear to be succeeding, but if the two individuals concerned are seen again, they appear to be acting like total strangers to each other. Obviously the female's response has been of a social nature.

Many of the young males, too, do not seem to have acquired the mating urge and behave much in the same way as the females just mentioned, except that they are not approached by any of the latter with pair-formation intent. Their love-habits are entirely social.

Finally, in this group, are some birds, apparently all males, whose behavior is still puzzling me. They are what I call "confirmed bachelors," apparently not at all interested in becoming mated. Is it possible that they lack the urge? They make no nest and are not attached to any particular spot in the colony. To my knowledge, they have not made any advance of pair-formation value to a female penguin. All this is in great contrast to the behavior of such a male as 692. They are definitely a small group, their behavior towards other penguins being purely of a social nature.

Birds Which Have Lost Eggs or Chicks.—For some ten days or so, birds which have lost eggs or chicks carry on with the normal behavior expected under these circumstances before reverting to pre-egg behavior. This is followed by the typical spasmodic behavior of the winter until the molt, when both birds, if still in the colony, normally molt together at their previous nest site, indicating that the union is still intact.

Love-habits that take place within these mated pairs are known to have family value, since if both members of the pair are in the colony in the following spring, they will usually be found still mated. When the winter stage has been reached and individuals of a mated pair are ashore alone, there is a tendency for each to seek the company of other birds.

In the morning on the way to the sea these birds which have lost eggs or chicks will meet the several types of unemployed birds, all of which show no hurry to enter the water and may not do so until 8 a.m., in contrast to breeding birds which leave at approximately 5 a.m. In the meantime, all these unemployed birds form little groups. Similarly, in the afternoon when these birds return, long before the breeders do, they once more group up for some hours before proceeding to their camps.

It is under such circumstances that love-habits are given free expression. Many of these habits have purely social value even when opposite sexes are involved. Such occasions afford the chance for the foundation of the future mating of two birds, although not necessarily in the succeeding season. For every foundation that is initiated, there are also many other affairs that come to naught. It can be readily understood that the birds get to know each other and affinities are formed.

All, including the breeding birds which have to pass through the unemployed group, become involved in love-habits. Reference has already been made to the actions of the unemployed males 692 and 104 towards the breeding female 115 (Chapter II). A further incident is as follows: On 2 March, 16 days before her last chick entered the water and when she had lost her mate, 115 had another experience. She landed at 4 p.m. and halfway home met the unemployed old breeding male 117, which greeted her with "sheepish looks," then some "excited shakes," and finally "half trumpets." As 115 walked on, apparently indifferent to these approaches, he indulged in a "full trumpet" and followed her for approximately 20 meters before giving up the affair.

The foregoing three incidents with the males 692, 104, and 117 clearly indicate that a breeding female is apparently not interested in love-habits with pair-formation value when she has chicks, even if her mate is lost. All birds concerned were well known to each other, and the love-habits, from the males' point of view, definitely had pair-formation value.

Summary.—Love-habits with pair-formation value among unemployed birds may take place at all times of the year and in the breeding season these love-habits are confined only to the unemployed birds. Approaches may be directed towards breeding birds but response is lacking. Love-habits with social value occur among all types of birds at all times of the year. Those with family value are restricted to breeding birds in the breeding season and to mated pairs outside the breeding season, including birds which have lost eggs or chicks.

TRUMPETING AMONG YELLOW-EYED PENGUINS*

Family Value.—Among breeding birds, in the period of incubation and in the chick stage in particular, the "full trumpet" has family value, being restricted almost entirely to activities with-

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*See also Chapter II.

in the family group which includes the chicks (Chapter IX). In the other stages of the annual cycle it still has family value when confined to the mated pair, but when members of a mated pair join in the "general chorus" that occurs from time to time, the behavior then has social value.

Pair-formation Value.—When the "full trumpet" takes place between two birds which are "keeping company" and in conjunction with mutual love-habits one may say that the behavior has pair-formation value. This is true even though it is known that but few of such pairs will ever become mated.

Social Value.—Pending further research, all other uses of the "full trumpet" as a love-habit are classed as having social value. One outstanding feature of the "full trumpet" is its far greater prevalence among unemployed birds than among breeding birds.

The first condition under which the "full trumpet" is used with social value is observed among isolated penguins, in the incubation and early chick stages. As far as I have been able to ascertain, these isolated penguins are all males. When working in the daytime among incubating birds sitting quietly on their eggs, a person is frequently interrupted by a "full trumpet" from somewhere in the bushes. One call may be given or it may be repeated several times. Never, to my knowledge, has an incubating bird responded.

If the bird is located, it will turn out to be a single unemployed male which has never mated and may be two years old or more. I have never known an old unmated breeding bird to behave in this way. That, however, may be due to paucity of observation, but I do not think so.

If the observer does not betray his presence he may see the penguin he is watching give a violent "shake" and then break into a "full trumpet"; oblivious to all around him, the bird can be caught easily in this trance. If the observer is still out of sight, he may see the bird run several meters through the shrubs with arched back and beak pointed to the ground before once more "shaking" and "trumpeting." The affair often takes place in an area but little frequented by penguins, one often well back beyond the normal limit.

One of these birds has no companion with it and has not been "keeping company" with any other bird, and, further, I do not think that it has done so in a previous season. Even if the ceremony had pair-formation significance, it occurs too late to result in the formation of a mated pair. As already indicated, the presence of a female has nothing whatever to do with the performance. The subsequent history of many of these birds I have been able to trace for several years. Many appear in different colonies and mate with resident females on whom the trumpeting could have had no influence; others again have remained unmated.

After considering the facts for a long time, I can offer for this trumpeting by isolated males only the explanation that the affair is a substitute activity. As we know from the dissection of B15, the gonads of these males have been enlarged, and as the behavior gradually ceases with the advance of the chick stage, it would seem that the birds, which are usually relatively young, have been unable to satisfy the urge to form a pair. They have stayed ashore in the daytime in response to this urge, the satisfaction of which has been thwarted, a fact which is expressed in substitute activity —in this case a combination of the "excited shake" and the "full trumpet."

The second condition under which the "full trumpet" occurs with social value is somewhat different and involves two or more solitary males which are ashore in the daytime. During the pre-egg stage, mated males, if alone, will take part, but after this stage the practice concerns only the various types of unemployed birds, but not those which are "keeping company." The active birds are spaced well apart out of sight of each other, either at a nest or camp site, from where they take the stage in turn. The following example will give a good idea of what happens.

At 1:30 p.m. of 14 September 1940, I arrived at a colony to hear three birds trumpeting at each other; it was the pre-egg stage. Two of the birds, 69 and 74, both old breeding males, were at this date already mated. The third was 675, a three-year-old unemployed male which did not secure a mate till 1943 and then in a neighboring colony. In 1941, 675 was observed trumpeting alone under conditions just described above, but in the new colony.

At 2:45 p.m., 73, the female mate of 74, appeared over the bank from the sea, and steered a course straight for 74. Knowing the birds and being aware of their previous history, I knew that 73 was cognizant of the whereabouts of her mate, so that the trumpeting was not for her benefit. Nor can I see that it was in the nature of a challenge, as is the case with Red Deer, for 675 was not a contestant for 73 against 74. The mated pair was already established. Further still, the calls were not an advertisement of territory as they are with many birds. Bird 69 was mated and was a considerable distance from the place where he nested. It is possible that 675 began trumpeting as an isolated male penguin under conditions described above and that the other two males, acting on the power of suggestion, took up the theme.

The third condition involves all types of birds, including juveniles, and is commonly heard in the evening after the birds return from the sea, and in the morning before they enter the water. One bird seems to set the others off and it is not long before there is a chorus of cries coming from all directions. I cannot see that this behavior has anything to do with pair-formation; it concerns the colony as a whole. The Yellow-eyed Penguin does like to know if there are other birds present. The usual method is to emit little single note calls, but the bird also employs the "full trumpet."

Breeding birds, when alone at the nest, either at the pre-egg stage or in charge of an egg or chick in the early stages, do not, within my experience, take part in these "full trumpet" exhibitions. When the chicks are older the attendant parent will take part. For example, in one instance, Z12 was standing on a rock some meters from his chicks; it was 5:57 a.m. and forty-six minutes after the female had entered the water. Suddenly, he delivered a "full trumpet" which was answered by the unemployed male 692 not far below. Later, as he continued his calls, Z14, another unemployed male, replied. This behavior of Z12 I am not able to understand, especially as the "full trumpets" were interspersed with "excited shakes." Finally, when trumpeting occurs within the family group or between a pair "keeping company," although this does not have social value, it may begin a series of "full trumpets" by other birds, which are then acting socially.

SEGREGATION

There is no evidence whatsoever of segregation in the Yellow-eyed Penguin either between the sexes or among the several types of birds in a community. As already stated, this species is "fond of company," and the only occasion when there is any objection to the presence of another bird is when there is a potential threat to "property rights." The following is a good example of this intra-specific tolerance among three distinct parties of birds each of which was independent of the others.

At 1 p.m. on 25 November 1939, the male 74 was sitting on eggs, the chick in one of which was pipping. Lying down ten feet away was X10, whose excreta were yellowish, indicating he had been at least one day ashore. Bird X10 was a three-year-old male which bred for the first time in 1941. Now, if these birds had been unbanded, the assumption, by a casual observer, would have been that they were mated. The partner of 74 was 73, which was absent in the daytime according to the custom with the Yellow-eyed Penguin.

But that is not the whole story. At right angles to the line between 74 and X10 and only four meters away from 74, was another bird, also lying down, whose excreta were yellow. She was M11, an unemployed two-year-old female which had no connection with either 74 or X10. This grouping of penguins with no matrimonial relations is a common feature of a Yellow-eyed Penguin colony, and it is not correct to say without banding evidence that the mate of an incubating bird is, under such circumstances, "standing in the scrub nearby."

UNEMPLOYED BIRDS IN OTHER SPECIES

In the literature, little direct reference is made to the unemployed members of the other species of penguins, but from the discussion of love-habits and pair-formation behavior in Chapter III, it seems certain that, as in the Yellow-eyed Penguin, unemployed birds are an important group in the other species.

As for segregation, I can find nothing which definitely indicates that it exists. Falla (1937: 65-66) suggests that in the Adélie Penguin there might be segregation of the sexes immediately before the molt, but his figures are an insufficient basis for conclusions and are the reversal of Gillespie's observations on the King Penguin (1932: 73). Further, it is apparent in many places in the literature, especially in the works of Bagshawe (1938) and of Gillespie (1932: 59, 73, 101), that other penguins are also "fond of company," that all types of birds mix freely, and that there is no segregation.

DISCUSSION OF UNEMPLOYMENT IN BIRDS

Causes and Incidence of Unemployment.—The phenomenon of unemployed birds in any species has not received the attention usually accorded breeding members. This is due partly to insufficient banding, coupled with the subsequent, more difficult work required in tracing the unemployed, and partly to the lack of an appreciation of their importance. A further differentiation which is rarely considered is the one between the true non-breeding birds and birds which, because of loss of their eggs or chicks, are apparently non-breeding at the time of observation. It is a common fault for observers who make brief visits to colonies of penguins and petrels to assume that egg-laying is still in progress. The mistake is made because the observers note birds occupying or working at nest sites, without realizing that these are unemployed birds and without knowing that the breeding birds already have all laid their eggs for that season.

There are three main causes of unemployment among birds. The first is impotence because of immaturity, and applies to each of the sexes. In many species of birds when the breeding season arrives all individuals are potential breeders, but in other species one or more seasons must elapse before it is possible for the individuals to breed. Penguins belong to the latter class; most species of penguins spend at least one year as juveniles, and cannot breed until almost three years old. Petrels probably have an even more protracted pre-breeding period. (See Chapter VI.) Gannets and some gulls do not breed until several years of age.

The second cause is a preponderance of one sex, usually the male, over the other, as was described in Chapter V for the House Wren, the English Robin, the Yellow-eyed Penguin, and the Royal Albatross. Further records are provided by the Song Sparrow (Nice, 1937: 86) and ducks (Hochbaum, 1944: 53). The percentage of these unemployed males is considerable, amounting, according to my own observations on the Yellow-eyed Penguin and the Royal Albatross, to nearly 50 per cent of all potential breeding males.

The third cause of unemployment is loss of eggs or young; the loss varies considerably from year to year. In the worst season in my records 53 per cent of breeding Yellow-eyed Penguins became unemployed. No comparable records are available for petrels. In birds which, in one season, re-nest if a loss occurs, this type of unemployment will not be present to any extent, except perhaps towards the end of the season when it is too late for the birds to begin another nest or when a series of losses has occurred in quick succession, as Nice (1939: 112-118) described in Bell Vireos, *Vireo bellii* Audubon. Among birds such as penguins and petrels, which have a long and restricted breeding season, a second nesting is not usually attempted. Although it is not the case with any petrels and penguins within my experience, there are records, as for example by Murphy (1936), of re-laying shortly after newly laid eggs have been removed.

With the three factors just mentioned in mind, one can readily understand that the percentage of unemployed in any population could be considerable, even exceeding that of the breeding birds.

This is true of penguins and petrels. For example, a perusal of Table 39 will indicate that in the year 1938-39, of the 88 penguins recorded, 18.2 per cent were non-breeding and 43.2 per cent lost either eggs or chicks, so that 61.4 per cent of the adult population became unemployed that season.

In the three burrowing petrels, Sooty Shearwater (1942b: 95, 1944b: 103), White-faced Storm Petrel (1943b: 105-106), and Fairy Prion (1944c: 172-173), evidence is produced of a high percentage of unemployed birds. It was not possible to decide, however, to which class they belonged and in what proportion they were present. A comparable state of affairs is indicated by Campbell (1933: 87) and Fleming (1939: 406) for the White-faced Storm Petrel, by Roberts (1940b: 158) for Wilson's Petrel, by Lockley (1932: 207-208) for the British Storm Petrel, *Hydrobates pelagicus* (Linnaeus), by Gross (1935: 387) and Ainslee and Atkinson (1937: 237-238) for Leach's Petrel, *Oceanodroma leucorhoa leucorhoa* (Vieillot), and by Wood Jones (1937: 188) for the Fairy Prion.

Wynne-Edwards (1939) and Murphy (1936: 664) have noted a large percentage in pelagic birds. Lockley (1942: 113) states that by July, 40 or 50 per cent of Manx Shearwaters have failed to hatch chicks. Salmon and Lockley (1933: 144-145) on Grassholm observed 4,750 gannet nests occupied and approximately 1,500 unemployed birds. Finally, Fisher and Waterston (1941: 217, 252) record the hatching of 20,000 young Fulmars when 10,000 non-breeders were present. Later, they indicated that successful breeders varied in the different colonies from 23.6 to more than 75 per cent.

In conclusion, Wynne-Edwards (1939: 127) would seem to be correct in saying that there is more non-breeding in petrels than in penguins, gannets, gulls, and various Alcidae. Kendeigh and Baldwin (1937: 120) estimate non-breeding House Wrens as one-third of the total birds present at any one time.

Intermittent Breeding and the Molt.—Intermittent breeding apparently occurs frequently in many Arctic species (Bertram, Lack, and Roberts, 1934: 824-830), and Wynne-Edwards (1939) thinks it to be common in the Fulmar, of which, he states, one in three breeds each year. He gives three reasons for his views. On 26 July when breeding Fulmars would be feeding young, he found 400 miles away from the nearest known breeding grounds, birds that, judging by their worn claws, could have been breeding. These old birds were in the molt, and therefore were not attending chicks. Finally, in the 16 of these birds dissected, breeding organs were small, as if the birds had not bred for a season.

Lockley (1942: 112) disagrees with these views. He points out that Manx Shearwaters feed more than 400 miles away while attending young, that breeding organs would be small in any case, and finally that birds which had lost their eggs would molt at the same time as the true non-breeders and therefore be indistinguishable. My own experience with other species of petrels causes me to agree with Lockley, who concludes (p. 115) that "intermittent breeding among the smaller sea-birds is not yet proved." As evidence Lockley points out (p. 114) that one of his shearwaters did not miss breeding in ten years and that others returned year after year until they disappeared. He had the same experience with the British Storm Petrel (*op. cit.*: 111).

A reference to Table 24 will indicate that breeding in successive seasons obtains in the Diving Petrel, the Fairy Prion, and the White-faced Storm Petrel. Whether individual Sooty Shearwaters breed in successive seasons is not clear from Table 24. Records were not made until after the chicks were hatched, and even though some pairs were found together again in a succeeding season in an empty burrow I could not ascertain whether breeding was intermittent or whether the birds had merely lost their eggs at an earlier date in that season. Incubation lasts eight weeks, and many eggs do get buried or scraped out of burrows before incubation is completed.

Possibly, however, this species is an intermittent breeder. The young are taken annually as food by the Maoris, and there is considerable variation in their catches. This variation could be caused by intermittent breeding, but, of course, it could also be caused by the loss by the breeding birds of either eggs or young chicks.

In surveying the Royal Albatross for ten consecutive years, I noted that four mated pairs which had previously reared chicks returned and apparently did not produce eggs. Possibly, the eggs were removed. If the eggs were not removed, the observation suggests that there may be intermittent breeding among large petrels.

In summary, I am in agreement with Lockley that the smaller petrels do not breed intermittently, although I recognize that the Royal Albatross and possibly the Sooty Shearwater may do so. Finally, there is no direct evidence of intermittent breeding in the Fulmar. As for the Yellow-eyed Penguin, once breeding age is attained members breed every year provided they acquire a mate. The same statement seems to apply to the Little Blue, the Erect-crested, and the King Penguins. It is, therefore, probably safe to assume that intermittent breeding does not occur among penguins.

From the discussion on intermittent breeding arises the question of the time of molting by the unemployed birds. Wynne-Edwards postulates (1939: 131): "If reproduction be inhibited, due to immaturity of the gonads or other cause, and the physiological succession leading up to this climax is not set in motion, it seems likely enough that the cycle should proceed directly to the next series of events of which the post-nuptial moult is usually the most important."

This postulate of Wynne-Edwards seems to apply to the molt in penguins and petrels whether individuals are true non-breeders or birds which have lost eggs or chicks. In the Yellow-eyed Penguin, breeding birds which have reared chicks are, on the average, the last to molt. All other birds, including those which have lost eggs or chicks, molt at the same average time at an earlier date.

In all six petrels which I have watched, the unemployed, including non-breeders and breeding birds which have lost eggs or chicks, gradually leave the breeding area as the chicks begin to grow (Richdale, 1942b: 98, 1943a: 31, 1943b: 105, 1944a: 206, 1944b: 103, 1944c: 172, and unpublished work on the Royal Albatross). Presumably these birds leave the breeding area because of the approach of the next phase in the annual cycle—the molt. This view is supported by the fact that several weeks after the conclusion of the breeding season the Broad-billed Prion returns to its breeding ground and will be found to have commenced molting (1944a: 206-210).

Similarly, Lockley (1942: 112), as already noted, states that Manx Shearwaters which have lost eggs molt early. Finally, Fisher and Waterston (1941: 255) indicate clearly that Fulmars at non-breeding stations leave early in the season. This resembles closely what happens in my six species of petrels.

Effect of Unemployed Birds on Breeding Biology.—Wynne-Edwards (1939: 131) raises another interesting point about non-breeders. He shows how among Kittiwakes, *Rissa tridactyla tridactyla* (Linnaeus), the whole population repairs to the breeding ground; in Gannets only some of the immature birds do so; in Fulmars it is much the same except that no non-breeding bird builds a nest; and finally, in Pomatorhine Skuas, *Stercorarius pomarinus* (Temminck), probably all of the immature remain in the winter quarters. In the Yellow-eyed Penguin, the whole population, including juveniles, occupies the breeding area, but I do not know what happens in the other species of penguins.

For petrels, not much information relative to non-breeders is available, such information being difficult to obtain. In the Diving Petrel, I have recovered young in their colony of hatching when they were almost two years old, which indicates that at least in this species all immature birds do not remain at sea. I have not recovered other young of any other species.* In the Royal Albatross, I have recovered unemployed males of breeding age year after year, and I have also recovered in successive years, unemployed birds of unknown sex in the Sooty Shearwater.

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*In the 1947-48 season and since the above was written I have, for the first time, discovered the return of young Royal Albatrosses to the colony where they were hatched. There were two; one was nearly six and the other nearly eight years old. Each appeared to be a female and neither had apparently bred.

Unemployed members, especially of breeding age, seem to be present in many communities of birds in the breeding season, always near the nesting birds. As Kendeigh (1941: 46) states for the House Wren, some individuals make no attempt to nest at all, in others the urge to do so occurs in sudden temporary and unsuccessful splurges, and yet others maintain territory throughout the season but do not mate. It is remarkable how closely this pattern is followed by the Yellow-eyed Penguin, and comparable behavior appears to obtain in the petrels watched.

In regard to the incidence of love-habits among unemployed birds, it has already been shown that, in the Yellow-eyed Penguin the incidence is high when breeding members of the community are preoccupied with reproductive duties. This results in birds becoming acquainted with each other, the development of affinities, and, in some cases, the formation of a mated pair.

In the Royal Albatross, there is one important difference in that the love-habits of a section of the unemployed birds are more intense than in other groups. When on shore a community of this species, which occupies the same area, may be divided into three divisions—the mated birds, those "keeping company," and those without any attachments. The second group consists of birds which have paired up for the first time, although some of them may not actually breed until eighteen months later. They remain as distinct entities in the same way as do breeding birds, and they endeavor to keep aloof from the more excitable activities of the third group. The love-habits of this second group are identical with those of the mated pairs whether the latter are breeding that particular season or not.

The third group is composed of unemployed birds which have formed no attachments. Their behavior, however, seems to indicate that the primary aim of each in being ashore is to form an alliance with another bird of the opposite sex. Birds of this group seem to perform the most intense ceremonies. For example, the elaborate wing-waving, neck-stretching and whining or "dance," as figured by Matthews (1929: pl. 49), I have never seen performed other than by unattached unemployed birds, and, as far as I can ascertain from the meager evidence available in the literature, the same remarks apply to all the Diomedeidae, with the possible exception of the genus *Phoebetria.*

Unemployed individuals of the smaller petrels perform love-habits, especially at night, in the breeding season for other birds. This is evident from my own studies, including unpublished results on the Mottled Petrel, and those of other workers such as Lockley (1932 and 1942), Darling (1938: 94-95), and Fisher and Waterston (1941: 251). Such behavior continues until the breeding area is vacated late in the season. It has been noticed also that pairs of these species may "keep company" in the burrows and that in a subsequent season they may be mated.

In conclusion, the presence of potentially breeding birds on the breeding grounds in any avian community coupled with their love-habit activity, constitutes a menace, with pair-formation significance, to the breeding birds. But the resultant competition, as already noted (Chapter V), is an aid to mating efficiency which not only is helpful to the individual but also is of general advantage to the species in its struggle for existence. Kendeigh (1941: 45) sums up the position thus: "The presence of the non-breeding, but potentially breeding population seems to have an effect on territorial behavior of nesting birds and to cause them to be continually on the alert in the defense of their possession."

SUMMARY

The term "unemployed" is used to describe all penguins which, at the time an observation was made, were without eggs or chicks when other birds were so employed. The unemployed group in a Yellow-eyed Penguin population may be divided into twelve distinct classes, exclusive of juveniles. Love-habits with pair-formation value occur among unemployed penguins at all times of the year, and in the breeding season are confined to them. Love-habits with social value occur among all types of birds at all times of the year. The phenomenon of "trumpeting" is considered according to the three values given to love-habits in this paper. "Trumpeting" is far more prevalent among unemployed birds and has largely social value. "Trumpeting" with social value may occur in three main ways—by isolated unemployed males probably as a substitute activity, by unemployed and breeding males when the latter are alone, and by all types of birds as a "general chorus." There is no evidence of segregation in penguins. Unemployed penguins are tolerated by breeding birds as long as "property rights" are not infringed. The causes of unemployment among all species of birds are non-attainment of breeding age, an unbalanced sex ratio, and loss of mate, eggs, or young at breeding period. The percentage of unemployed birds in any bird community may be considerable. This is particularly true of penguins and petrels. Intermittent breeding does not appear to occur in the smaller petrels or in penguins. It may obtain in the Royal Albatross and the Sooty Shearwater. Unemployed petrels and penguins molt in advance of breeding birds that have reared chicks. In some species of birds the immature accompany the breeding birds to the nesting area, in others only some immature do so, whereas in still others none does so. Love-habits in the breeding season occur among the unemployed of many species of birds and probably have a beneficial effect on the mating efficiency of the species.

Chapter VIII

Incubation

Incubation in the Yellow-eyed Penguin, including spans of incubation by sexes, "change of guard," parental responsibility by sexes, general behavior, love-habits. Incubation in other species of penguins. Discussion of incubation in birds. Summary.

INCUBATION, AS INDICATED by the hatching of the chicks in the majority of instances on the same day, usually begins after the second egg is laid, although by no means always. The average period of incubation is 42 days with extremes of 40 and 50 days. The earliest laying date in the ten years of observation was 11 September and the latest 15 October. The earliest hatching was 28 October and the latest 26 November. These dates cover the period under discussion. Family life has begun, and pair-formation and coitional influences no longer dominate behavior for breeding birds.

INCUBATION IN THE YELLOW-EYED PENGUIN

Spans of Incubation by Sexes.—It has already been noted that from a time immediately before the laying of the first egg and in the period of egg deposition the male is not so much in evidence in the daytime as he had been earlier in the pre-egg stage. The male is usually back at night, however, and is sometimes alone in the daytime with the single egg. Soon after the second egg is laid the male takes charge.

At each of 19 nests which I visited daily, the male took charge of the eggs 24 hours at the most after the second egg was laid. The shortest period, to my knowledge, was seven hours. Table 36 shows that from 72 visits to nests after dark the male was present 57 times, either alone or with the female, in the period of oviposition. This makes it clear that even if the female were alone in the daytime when the second egg appears the male will usually

Table 45

Incubation Spans by Sexes

	Days in span	1	2	3	4	5	Total
Number of times	♂	21	17	10	0	0	48
	♀	24	10	5	3	2	44

be present that night. From what I know of the change-of-guard behavior the female would stand up for the "welcome" ceremony, and it would not be long before the change-over would occur. Failing the return of the male on the evening of the day the second egg was laid, it would be rare for him not to return fairly early next day. In summary, it may be concluded that the male in the first hour or two after the second egg is laid takes the first turn at incubation.

In working out the span that each sex incubates at one stretch, it is essential to visit the nest twice daily. If the nest is visited only once, change of guard may occur twice without the observer's knowing it.

Table 45 was compiled from visits made only once per day and its accuracy is to be judged accordingly. The table indicates, however, that the sexes do not change guard every night in the period of incubation and that the length of time varies from one to five days, with a strong tendency towards the shorter intervals. The bird off duty does not return to the colony until it is ready to change guard.

To test out more satisfactorily what really happens I carried

Table 46

A Survey of Incubation Spans by Sexes

	20 October	21 October		22 October		23 October
Nest	9 p.m.	11 a.m.	9 p.m.	11 a.m.	9 p.m.	11 a.m.
A	♀	♀	B ♂	♂	♂	♂
B	B ♀	♀	B ♂	♂	B ♀	♀
C	♂	♂	♂	♂	B ♀	♀
D	♂	♂	♂	♂	♂	♂
E	♀	♀	♀	♀	♀	♀

N.B. *B* means both present, and ♂ or ♀ indicates sex incubating.

out a short survey between 20 and 23 October 1939, visiting each of five nests twice daily (Table 46). The nests were so spaced that a thorough search of the colony would reveal a mate possibly not at the nest. The search revealed that when both birds were ashore they were both at the nest and that further still, when this was so, the bird which had returned that day was always on the eggs. This confirms my idea that when a bird comes home it immediately changes guard, so that its mate is the next to go to sea. Though Table 46 does not show it, should a bird return when at least about three hours of daylight remain, the relieved bird will enter the water that day, staying away all night; otherwise it waits until the following morning to enter the water.

A bird does not come home in the evening, sit on the eggs at night, and then leave for the sea again in the morning without giving its partner a chance to acquire food. But this procedure does occur immediately before the eggs appear and in the period of egg deposition, when the male is frequently at sea fishing. He comes back at night, although not necessarily every night, sits on the empty nest or single egg, and yields his place to the female in the morning before going off to sea again. Earlier in the season the roles may be reversed (Table 25). It will be observed that the female does return on some evenings, keeps the male company, and goes off to sea again in the morning, leaving the male behind.

Change of Guard. (See also Chapter IX.)—In the evenings during the incubation period and often at any time of the day when the chicks are being fed, as the birds change guard a colony of Yellow-eyed Penguins resounds with cries of the birds as the absent partners return to the nest. To find out what happens at these times, I watched all day at a nest.

At 4 p.m. the male eventually appeared some 90 meters away, and after frequently stopping to preen and peer around, he arrived within two meters of the nest at 5:08 p.m., although he was not visible to the female on the nest. As he took a step forward, the female saw him and immediately broke into an "open-yell"; the male ran up quickly with arched back and beak to the ground;

and both put their heads together to perform a most intense "welcome" ceremony (fig. 12). As the first burst of noise gradually subsided, the heads were lowered, and several of the less intense love-habits were performed. The "welcome," followed by the other love-habits, was repeated three times. After the last "welcome" the female resumed her position on the nest; she then rose and gradually sidled off the nest. Meanwhile, the male gradually stepped on to the nest as the bulk of the female's body was removed, and straddled the eggs, at the same time putting them in place with his beak.

A few days later I waited again; this time it was the female which was at sea. When she arrived the usual "welcome" occurred, after which the female edged in alongside the male, endeavoring to hurry him off the nest. When half off he hesitated and seemed loath to go, and so to expedite matters she pecked his tail. The male shot forward immediately.

The arrival of the absent bird at the nest is apparently a sufficient stimulus to set off the "welcome" ceremony automatically. When weighing penguins I have handled both members of a mated pair at the nest at all stages of the annual cycle. The first is always released in such a way that it returns to the nest. When the second is similarly treated and arrives alongside its mate the "welcome," varying in quality according to the individuality of the birds, is performed. If the bird is timid, only a little "throb" instead of the full "welcome" is given. The situation demands something, and this "throb" is probably in the nature of a substitute activity.

A good example illustrating this automatic force occurred once when I was sitting in full view some three meters from a timid, incubating male. At 6:30 p.m. when the female hove in sight, the male, instead of giving vent to an "open-yell," as was his habit, emitted only a little "throb." The female, not at all timid, ignored me. As she reached the nest only a half-hearted "welcome" took place and once only. Owing to my presence the male would not budge from the nest. The female quickly pushed her head and neck underneath him so that she felt the eggs. Gradually she managed to push him far enough up so that she had the whole of her body under him as she took her position on the eggs. It was evident that it was her turn to incubate. The two birds remained in these positions all the time I was present.

A close watch has been kept many times as a bird returning from fishing reached the nest. I am forced to the conclusion that the bird on the nest recognizes its mate on sight or, if the incoming bird should call prior to this, then the bird on the nest recognizes its mate's voice. It immediately responds with one of the love-habits already enumerated. With some birds the "open-yell" is used, and with others the most exciting love-habit of all, the "full trumpet." The variation is considerable.

I have seen nothing which indicates that the incubating bird tends to treat the incoming bird as a potential enemy until a certain signal of identification is given. I feel sure of this point. Many times in ten years I have watched the incoming bird; it always knew its mate instantly on sight or hearing.

If, however, the incubating bird hears another approach, it cannot be sure from footsteps or comparable noise whether such a bird, when out of sight, is its mate or not. It does not adopt an aggressive attitude pending verification, but utters a little single throaty call of inquiry. If by call of response, or by appearing in view, the bird proves to be a strange penguin, then the incubating bird adopts a threatening attitude.

This call of inquiry is common at all stages of the annual cycle. As just noted, the call has family value, but when the call concerns penguins which are unmated it has social value and is merely the announcement of presence to an unknown bird which it hears moving in the vegetation. Time and again my movements have been the cause of this inquiry call.

Is the Male the More Responsible Parent?—The task of incubation is shared equally. To determine this, I noted the sex of the bird which was on the eggs for 889 inspections in a period of eight years. The female was present 460 times and the male 429 times. The count was made in the period from the day the second egg was laid to the day the first chick was free from the shell. As I arrived at some nests not long after the second egg appeared, an undue bias may possibly have been given to the records for females.

In the period of hatching there is no particular sex in charge. Sometimes the male is on at the beginning and sometimes the female, and before hatching is complete, guard has usually changed. As a rule, both eggs hatch on the same day, but I have known odd eggs to hatch as long as two days apart. Therefore, in these instances, as the hatching time for one egg is two days, the total hatching period will last four days. Hence it may easily be understood why change of guard occurs in the period of hatching. Occasionally, however, one sex is in charge for the entire period. The foregoing remarks are supported by 80 visits to nests when the chicks were hatching. The male was in charge 34 and the female 46 times.

In summary, there is nothing in the foregoing evidence to signify that either sex is the more responsible parent. Both are equal in this respect on the average, but there are individual differences.

General Behavior.—After the laying of the second egg, neither sex seems to have a strong inclination to sit constantly. Frequently birds are noticed standing up over the eggs or may be seen sitting on them with a portion of the eggs visible. Variation in this early feature of the incubation period probably is a big factor in the variation in length of the incubation period.

An interesting event occurred long after dark (9 p.m.) on 27 September 1939. Approaching quietly from around a corner, I switched on the electric torch to discover the female standing erect 30 centimeters from the nest while the male was two meters away preening himself. The egg was reposing in the middle of the nest open to the sky, for this nest was above the scrub line. The male, quickly sensing that all was not normal, rushed to the nest, straddled the egg, ran his beak around it, and tucked the egg under him.

With well over a thousand records, I have never seen an egg in the daytime exposed in this fashion. A bird was always in a position to cover the egg instantly should danger threaten. It would seem that hereditary enemies of the Yellow-eyed Penguin, probably the Skua chiefly, although none exists on the Otago Peninsula, move around in the daytime and that these penguins are aware that night time is relatively safe.

The behavior of the male needs explanation. From his position he could not see the egg, but he was obviously aware it was uncovered; in addition, the light of the torch would have dazzled him. It was not reaction to the egg being uncovered that caused him to act but rather reaction, I think, to his recognizing the egg was in danger. A comparable bit of behavior was that of the male 28 (Chapter II) when he saw me; in this case his chick was in possible danger.

In general, the Yellow-eyed Penguin does seem to respond to the stimulus of seeing eggs uncovered. For example, at nests in thick undergrowth I have sometimes lifted a bird off the nest for observational purposes, to find that soon after, the second bird has slid on to the nest. I was not aware of the latter's presence, for it had fled on hearing my approach. A comparable situation exists when young chicks are present—seemingly a response to a visual stimulus, but in view of the incident at night just mentioned, one wonders if that is the correct interpretation. Some of the birds which have fled certainly could not see the eggs. What is it that brings them back on the nest? It is difficult to say with any degree of confidence.

Out of the 292 nests observed in the four main colonies, only two with eggs have been deserted. At each nest the male was a two-year-old and the females three and four years old respectively. Oddly enough, the nests occupied by the different mated pairs were in exactly the same place in successive years. Both females were of the non-timid type and became aggressive when approached. The first desertion occurred in 1943.

On 2 October B23 was covering two eggs and had W35 alongside her. On 10 October the eggs were cold, with no bird attending. Seven days later, B23 was again on the eggs, and on 23 October she was still incubating, but she must have been off for food in the meantime. That night at 7 o'clock, I discovered W35 in another colony a mile away where he was trumpeting and alone, in circumstances frequently observed for unemployed males at the incubation. This informed me that he had deserted B23 and I did not see him again. Female B23 was forced to desert the eggs, but in 1945 she was still in the colony breeding.

The second desertion occurred in 1944. On 6 October the female W45 was incubating two eggs, but on 14 October they were cold and deserted. On 28 October W49, the male, was lying down three meters from the nest and the eggs were cold. Both birds were again present in 1945. As the male in each case was the faulty partner and a two-year-old, the only explanation I can offer is that the males had not reached the stage when they could take the responsibility of incubating. It may be remembered that some two-year-old females produce eggs and that some do not.

Love-habits.—An important point to remember about the incubating birds is that a member of a mated pair sees very little of its partner at the time of incubation, probably less than at any other period of the annual cycle, with the possible exception of the winter. This means that the majority of the love-habits occur in the change-of-guard ceremonies, and, to a lesser degree, in the early morning before the departure of the sea-going partner, on the few occasions when the two birds are together for the night. Further, since breeding birds have very little opportunity for other than family duties, their love-habits naturally have little else than family value.

On their way to and from their nests, however, incubating birds will meet other breeding birds and also unemployed members. Occasionally, in passing these neighbors, minor love-habits will be performed, the significance of which, as far as the breeding bird is concerned, is rarely more than social.

As for love-habits with pair-formation value, I have no record of any instances of "flirtation" once the two eggs have been laid and before the advent of the molt, so that the pair-bond is evidently all-important. Of course, advances will be made to breeding birds by the unemployed members of the community (Chapters II and VII) but without any reciprocity.

INCUBATION IN OTHER SPECIES OF PENGUINS

Spans of Incubation by Sexes.—Evidence of the time the male first takes charge of the egg or eggs after they are laid is somewhat meager and tends to be conflicting. Bagshawe (1938: 266-269) made hourly observations on a mated pair of Gentoo Penguins for some days, before and after the eggs appeared. The second egg was laid between 10 p.m. and 11 p.m., and the male took charge approximately seven hours later. It should be noted, however, that the male was absent when the second egg was laid and did not return until rather less than two hours before the change-over. Had he been present when the second egg appeared doubtless this would have occurred earlier. A similarly quick change of guard is effected in the King Penguin (Gillespie, 1932: 102, 107).

Distinctly different is Levick's record (1915: 67) of a female Adélie Penguin which was not relieved by the male for 14 days after egg deposition. Bagshawe (1938: 288) challenges this and points out that relief could have occurred in the night. Murphy (1936: 449) records a comparable instance concerning the Magellan Penguin, in which the female is said to incubate for eight to ten days after the eggs are laid.

In regard to the two other species I have studied, no information is available concerning the Little Blue Penguin; in the Erect-crested Penguin (1941b: 38), the second egg was laid between 4:30 p.m. on 22 October and 2:30 p.m. on 23 October when the female was in charge. At 5:30 p.m. next day, the male was incubating, with the female close by. It may be seen that the change-over occurred within 49 hours at the most. As these birds changed positions on the nest frequently, at all periods of the 24 hours, it probably was not the male's first turn on the egg.

Somewhere in the literature, at least one worker has stated for most of the species of penguins that the sexes take turns in incubating. By analogy, this is probably true of those not mentioned and is in keeping with the general rule that birds which lack sexual dimorphism in plumage, and which have mutual love-habits, incubate alternately.

Information relative to the length of the alternate spans which the sexes use is somewhat scanty. For a third of the species there is nothing available at all, and for many of the remainder the data are incomplete and conflicting. The last factor is probably due to considerable variation not only among members of the same species but also among the several species of the different genera.

In the King Penguin, Gillespie (1932: 109) records the spans as varying from 12 hours to ten days, and Murphy (1936: 349) quotes one observer who states that the change is every 24 hours and another who says that it is every two days. Since these two have failed to note any variation, their observations could not have been very critical.

In the Gentoo Penguin, Murphy (*op. cit.*: 374) explains that the relief is at irregular intervals, varying over many days, where ice conditions are a hindrance. At South Georgia, three or four days are common lengths of time. Bagshawe (1938: 269), in his hourly check over the first nine days after the second egg was laid, noted that the male's span varied from 12 to 31 hours and the female's from six to 24. In the Adélie Penguin, Levick (1915: 66) says that the sexes remain absent from "about 7 to 10 days." In the single case he gives, the male was on guard 13 days and the female 13 and four days before the chick hatched.

In the Little Blue Penguin, Hursthouse (1939: 15) gives the times as 18, 12, 5, 1, and 2 days respectively but points out that the first record may have been inaccurate. In the succeeding year (1940: 121) the longest record by each sex was six days. For the White-flippered Penguin, O'Brien (1940: 314) indicates a somewhat different procedure. He asserts that the females sit mostly in the daytime, and the males at night between 1 a.m. and 3:45 a.m.

In the African Penguin, Roberts (1940a: 222) was informed that captive birds ranged from 12 hours to three and one-half days incubating at a stretch, and Kearton (Murphy, 1936: 459) states that the change is every 12 hours. For the Magellan Penguin, Murphy's observers (*op. cit.*: 449) note a variation from six hours to ten days.

Concerning the genus *Eudyptes*, there appears to be variation peculiar to the genus and requiring further investigation. Roberts (1940a: 222) carried out a ten-day watch at 19 nests of the Rockhopper Penguin and found that the spans extended from three to more than ten days. Presumably the partner not incubating was at sea, although Roberts does not actually say so.

The behavior of the single pair of Erect-crested Penguins which I observed was different from that of the aforementioned Rockhopper Penguin (1941b: 37-43). From the laying of the first egg on 21 October up to 30 October at least, neither partner had entered the sea, which meant that the male had fasted 27 days and the female 25 days since arrival from their winter quarters at

TABLE 47

Alternate Spans on Egg by the Sexes in a Mated Pair of Erect-crested Penguins, 15 to 28 December 1939

Sex	Hours on egg	Hours bird at sea
♀	5: 15	
♂	8: 25	
♀	3: 25	
♂	6: 35	
♀	5: 45	
♂	15: 15	♀ 11: 35
♀	15: 40	
♂	0: 08	
♀	0: 12	
♂	33: 15	♀ 13: 05
♀	19: 57	♂ 9: 02
♂	0: 08	
♀	0: 15	
♂	13: 05	
♀	1: 30	
♂	8: 45	♀ 8: 45
♀	2: 15	
♂	13: 50	♀ 12: 40
♀	8: 40	
♂	3: 35	
♀	1: 20	
♂	0: 05	
♀	10: 00	♂ 9: 30
♂	26: 25	♀ 12: 40
♀	4: 45	
♂	6: 25	
♀	3: 58	♂ 3: 58
♂	0: 02	
♀	1: 10	
♂	28: 15	♀ 9: 20
♀	10: 55	
♂	13: 20	♀ 9: 25
♀	14: 45	
♂	0: 20	both leave for sea together

sea. Between 21 October and 13 November I visited the nest 17 times and found the female in charge on 14 occasions and the male on three. On each visit both birds were present. Their behavior was puzzling but was clarified between 15 December and 28 December, when I camped and slept alongside the nest and recorded all their movements. Details of the spans of each sex on the egg are given in Table 47.

Table 47 has been drawn up from my paper on the Erect-crested Penguin (*op. cit.*: 42) and gives the dates and times of the various events. The spans on the egg by the male varied from two minutes to 33 hours and 15 minutes, and by the female from 12 minutes to 19 hours and 57 minutes. The total time spent on the egg in the period under review was 177 hours and 53 minutes for the male, and 109 hours and 57 minutes for the female. The excess by the male was partly due to the greater amount of time spent at sea by the female, 77½ hours in seven days, as against 22½ hours in three days by the male. The range varied from 8 hours and 45 minutes to 13 hours and 5 minutes for the female, and from 3 hours and 58 minutes to 9 hours and 30 minutes for the male.

Neither bird was absent for a single night, a procedure which was apparently exceptional, according to evidence in my paper. Change of guard usually occurred when the sea-going bird returned to the nest and then subsequently at irregular intervals at any time in the day and night. The change-over generally took place at least once in the night.

A further interesting episode in the story of this mated pair was observed (1941b: 41). From some time between 26 November to 2 December and 20 December, making a period of at least 19 days, the male did not enter the water. He was at the nest all the time but took turns with the female at incubation.

It is difficult to determine to what extent other species of *Eudyptes* behave like the Erect-crested Penguin. From Roberts' observations just noted, the inference seems to be that one sex has long spells on the nest, with the other absent at sea. A comparable situation seems to exist in the Drooping-crested Penguin, as far as

I could ascertain from my meager observations on the species. One individual, which I had marked for three days, was alone for that period, and it appeared that most of the other incubating birds were also by themselves. Another feature which impressed me was the fact that I failed to see a single bird enter or leave the sea, a fact seeming to indicate that change of guard came either at long intervals or late in the day.

Concerning fasting in the period of incubation there are the observations of Matthews (1929: 589) on the Macaroni Penguin while the bird is off duty. His visit was on 25 November, when egg-laying was well advanced and when, he was convinced, the birds were in pairs. This behavior would seem to correspond with that of the Erect-crested Penguin.

In conclusion, it would appear that in most species, individuals of a mated pair when incubating see but little of each other. When one is incubating, the other is usually at sea; relief from duty seems to carry also the right to acquire some food before once more taking a turn at the nest. In the Erect-crested Penguin, if my mated pair is typical, the procedure seems to be different. The Macaroni Penguin, judging by the observations of Matthews cited above, may behave in this respect like the Erect-crested Penguin.

Change of Guard.—It seems to be a general rule that guard is changed in the other species as soon as the sea-going bird returns to the nest. This is noted in the Gentoo Penguin by Bagshawe (1938: 270), in the Little Blue Penguin by Hursthouse (1939: 15), in the White-flippered Penguin by O'Brien (1940: 314), and in the Erect-crested Penguin by me (1941b: 42). In the last-named, however, it may occur at other times when both birds have been present for some time. As in the Yellow-eyed Penguin, the stimulus is apparently the appearance of the mate after its absence. It is interesting to note that I have observed one of a pair of Erect-crested Penguins leave the egg but the second bird fail to respond either because it was not looking or because it was busy preening itself; the sight of the exposed egg quickly brought the first bird back on to it (1941b: 50). This would suggest that in the Erect-crested Penguin the signal for the change-over is some visual sign by the incubating partner. As against this, relief is often effected in the dark.

The literature is not clear regarding behavior during the relief ceremony. In the Erect-crested Penguin, it may be highly emotional or there may be no accessory action whatsoever. Highly emotional behavior is more frequently the rule. The "full trumpet" may be used, as in the Gentoo Penguin (Bagshawe, 1938: 270) or the "ecstatic," as in the Adélie Penguin (Wilson, 1907: 48; Levick, 1914: 90). The lesser love-habits as noted in the King Penguin by Gillespie (1932: 102), the Gentoo Penguin by Murphy (1936: 374), and the African Penguin by Kearton (Murphy, 1936: 459), are common. In the Little Blue Penguin the change occurs in the burrow to the accompaniment of weird expiratory and inspiratory sounds (my observations) and in the White-flippered Penguin a "croaking wail" is heard from the burrow (O'-Brien, 1940: 314).

In regard to the question of recognition of a mate, Bagshawe (1938: 216, 255, 277) thinks that in the Gentoo and Ringed Penguins this is effected on sight and certainly on hearing. According to my own observations (1941b), recognition of a mate by sight and hearing is definitely true of the Erect-crested Penguin. Moreover, in the Erect-crested Penguin, as in the Yellow-eyed Penguin, there was no sign of any hostile reaction on the part of an incubating bird towards a home-coming partner preliminary to recognition, as is thought to occur in the Gentoo Penguin (Roberts, 1940a: 214).

Is the Male the More Responsible Parent?—In the section on the Yellow-eyed Penguin considerable evidence has been produced to make it clear that in the periods of incubation and hatching neither sex is the more responsible parent.

Several published observations indicate that this statement is true of the other species. For example, Bagshawe (1938: 269) shows that in the Gentoo Penguin a male incubated for 111 hours and the female for 99 hours from the laying of the second egg. Levick's "watch-bill" (1914: 91-93) indicates practically equal times for both sexes in the Adélie Penguin. Comparable behavior has been observed in the Little Blue Penguin (Hursthouse, 1939: 15, and 1940: 121). Finally, in my own observations on the Erect-crested Penguin (Table 47), the male shows an advantage of 68 hours in 14 days, but this is probably due to individuality.

Those who claim that the male is the more responsible parent are Gillespie (1932: 110, 125) and Falla (1937: 79-81). The former has apparently based his views on his King Penguin, "Charles," which was certainly more diligent than his mate, but I suggest that this is an individual characteristic. As for Falla, he does not bring forward any direct evidence to support his contention. More than casual visits to colonies are required to form trustworthy conclusions on the proportion of time spent by each parent in incubation.

Murphy (1936: 397, 431) suggests that in the Adélie and Rockhopper Penguins the female is the better parent. In addition, Levick (1915: 69) states that "the hen [Adélie] is very much more efficient and reliable than the cock." It is obvious that far more detailed investigations are required in order to resolve these differences of opinion.

General Behavior.—It seems likely that the disinclination to sit tightly shown by the Yellow-eyed Penguin after the eggs are laid obtains also in the other species. This view is strengthened by published variations in time of incubation as summarized by Roberts (1940a: 223). Certainly my mated pair of Erect-crested Penguins was somewhat remiss in sitting on the egg in the early stages.

Apparently all penguins which lay two eggs and which at least nest on the surface of the ground, keep the first egg covered in some degree before the appearance of the second. It seems to be universally agreed that there is a difference of from two to five days between the laying of the two eggs, varying somewhat in the different species. In spite of this, in some species the two eggs hatch either on the same day or with only one day in between. This is the rule with the Yellow-eyed Penguin (1941a: 274), with the Little Blue Penguin (1940: 186), with the White-flippered Penguin (O'Brien, 1940: 315), and apparently with some Gentoo Penguins (Falla, 1937: 59). I can find no further information.

The Gentoo Penguin sometimes begins incubation as soon as the first egg is laid; Bagshawe (1938: 199) records that two eggs laid three days apart also hatched three days apart. Bagshawe is supported by Murphy (1936: 377) and by Matthews (1929: 586). The behavior of the Ringed Penguin is slightly different, for incubation begins at a midway point. Two sets of eggs laid four days apart hatched with two days in between, and a third set laid at a three-day interval hatched with only one day between (Bagshawe, 1938: 273). According to Wilson (1907: 49), in the Adélie Penguin there is a big difference in the size of the two chicks, with a difference of possibly three days in age.

A probable explanation of the difference in the commencement of incubation between species of the genus *Pygoscelis* and species higher up the phyletic scale is the influence of their habitat. In colder regions the lower temperatures would probably have an adverse effect on the first egg if it were not thoroughly covered before the advent of the second.

Love-habits.—There is but little literature on the value of love-habits in breeding penguins other than in the Yellow-eyed Penguin. Doubtless all three of the values described earlier exist in the love-habits of the other species. Behavior studied from this point of view would be a fruitful line of research. Noteworthy, however, is the greater prevalence of love-habits with family value among Erect-crested Penguins than among Yellow-eyed Penguins. Members of mated pairs of the former species, according to my observations, spend a large portion of their time together ashore in the period of incubation. This statement may apply also to the Macaroni Penguin (Matthews, 1929: 589).

DISCUSSION OF INCUBATION IN BIRDS

General Remarks.—An excellent analysis of incubation behavior has been published by Nice (1943: 219-225). Briefly, it seems that in the majority of birds both sexes incubate. Although there are exceptions, this is usually the procedure where both sexes have similar plumage; penguins and petrels, within my experience, adopt this method. In species which exhibit sexual dimorphism, usually the less brightly colored partner incubates. Where both are conspicuously colored, the nest is often in a cavity and the task of incubation is usually divided.

When both sexes incubate, the periods on the eggs may be as short as seven minutes, as in the Lesser White-throat, *Sylvia communis* Latham (Nice, *op. cit.*: 220), or as long as 18 days as in the Laysan Albatross, *Diomedea immutabilis* Rothschild (Hadden, 1941: 210). Lengthy records, from my own observations, are Buller's Mollymawk, *Diomedea bulleri* Rothschild, up to 24 days,* the Royal Albatross (1942a: 253) up to 14 days, and the Sooty Shearwater (1942b: 100 and 1944b: 100) up to 13 days. My shortest record is one of two minutes by the Erect-crested Penguin (Table 47). Generally speaking, however, penguins have long periods on the eggs but probably not as long as petrels. With the Diving Petrel it is interesting to note that the change-over occurs nightly (1945b: 43).

In regard to the lapse of time before the male takes his first turn on the eggs, Noble, Wurm, and Schmidt (1938: 27) indicate that in the Black-crowned Night Heron the male soon takes charge once he sees the egg; seeing the egg greatly stimulates him. I have observed comparable behavior by a male Royal Albatross which happened to be present when the egg was laid. With difficulty I persuaded the female to rise. As soon as she did so, the male spied

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*On the Snares Island Expedition from 9 January to 26 February 1948 I was able to work out, in considerable detail, the spans of incubation by each sex in Buller's Mollymawk. The first span by the female after the egg was laid, from 60 records, produced a mean of 5.92 days and a range of 0 to 24 days. Sixteen subsequent spans by the female gave a mean of 10.76 days and a range from 5 to 20 days. For the male, 39 spans on the egg gave a mean of 10.81 days and a range of 6 to 21 days. In addition, a female had been incubating for 23 days unfinished on the day we left the island.

the egg, put his beak under the female, ran it over the egg, and then approached as if to change guard, but the female sat down again. When I returned nearly five hours later the male was on the egg and alone. In most cases the male takes charge within 24 hours. Previously, it has been noted that comparable behavior occurs in penguins.

In cases where both sexes incubate, there is generally some ceremony between the two partners before guard is changed. This has been noted in many species—for example, in herons by Huxley (1924b: 156-160), in the Black-crowned Night Heron by Allen and Mangels (1940: 21), and in terns by Palmer (1941: 79). Many have recorded it in penguins. It also occurs in the Royal Albatross but does not follow an elaborate pattern. Judging by the weird cries that issue from the burrows of smaller petrels, they have a relief ceremony.

Behavior which I have observed at change of guard in the Yellow-eyed and Erect-crested Penguins seems to occur under three different sets of circumstances. In the first place, it may be seen as a preliminary to nest relief in incubation or when chicks are being guarded. Secondly, the same actions are performed outside the incubation and guard stages whenever two mated birds meet whether at the nest or not. If at the nest site, the birds do not necessarily change places on the nest. Finally, when two birds have been occupying a nest site, whether eggs or chicks are present or not, a long silence may be broken by behavior identical to that used immediately before change of guard. Comparable behavior occurs in the Royal Albatross and apparently in other species with a relief ceremony (Huxley, 1924b: 157).

It would seem, then, that the "welcome" ceremony has two functions. First of all it probably has greeting value when two birds meet after an absence. Secondly, it probably has bond-holding significance as explained in Chapter III, a function which obtains at all seasons. The "welcome" ceremony is claimed by some writers to have recognition significance. The ceremony, however, often takes place with undiminished ardor subsequent to the recognition, by the bird on the nest, of its mate by voice when still out of sight. The recognition hypothesis would, therefore, seem to be ruled out.

In Chapter IV it was shown conclusively that in the Yellow-eyed Penguin the incubation period is one of recuperation for both sexes. This view is supported by Nice for female Song Sparrows (1937: 26-27). Further proof is afforded by the fact that out of 292 matings not one nest has been lost in incubation because of the decease of a parent bird. A few adults have disappeared in the chick stage and a few more in the molt, but the great majority vanish in winter. These remarks concerning the incubation period are contrary to established opinion and require further investigation in other birds. It is interesting to note that in ducks the evidence of Hochbaum (1944: 150) points to a pattern comparable to that in the Yellow-eyed Penguin; most deaths occur after family responsibilities are over for the year.

Coition after Eggs Are Laid.—In the literature, the performance of coition by breeding birds after the eggs are laid and even in the period when chicks are being fed, is reported at fairly frequent intervals. Coition would seem to be more prevalent among land species but even so is probably abnormal and exceptional. The male possibly remains potent after the female has passed through her period of receptivity (Tinbergen, 1939c: 35) and can therefore accommodate the female should aberrant behavior arise on her part. It is more usual, however, for coition to cease either after the first egg is laid or when the clutch is completed.

On coming to families like penguins and petrels, one thing that has impressed me regarding the claims that coition occurs among breeding birds after the eggs are laid, is that the observations were not made on individuals which were being studied as thoroughly as the Old World Warblers (Sylviidae), the Snow Bunting, the Song Sparrow, and the House Wren have been studied. It seems to me that many of the observed acts of coition were not by breeding birds at all but by the unemployed members of the community.

Two essentials in an endeavor to unravel this and other problems are, as I have said earlier, to have the birds under observation marked, and to know, if possible, something about their previous and subsequent history. Coition among breeding penguins and petrels after the eggs are laid is rare for two reasons. In the first place, evidence has been produced (Chapter VI) that the urge normally ceases just before the first egg is laid. Cessation of the urge to copulate is especially characteristic of the female, as it is also in the female of breeding Royal Albatrosses (Chapter VI).

Secondly, coition fails to occur because of lack of opportunity. For example, in the Yellow-eyed Penguin, as already indicated, members of the mated pair see but little of each other in incubation, although they are together a little more once the chicks have hatched. This would appear to be true in many of the other species. In the Erect-crested Penguin, according to the single mated pair I watched, the birds were together at the nest in incubation for long periods but, although the love-habits employed were intense, I did not see any attempted coition.

Among petrels there is less opportunity for coition than among penguins. As shown a little further back, change of guard may be infrequent and at long intervals. When the chicks arrive, in albatrosses parents may remain with them for as long as six weeks, but in the smaller petrels the brooding usually ceases within a day or two after hatching. Once again the opportunity for coition is lacking. Never, in all my visits, which number nearly 500, to my Royal Albatross colony, have I seen anything that resembled coition among the breeding birds, all of which were securely banded.

In summary, I am forced to the conclusion on the evidence available that coition among breeding birds at the incubation and the chick stages may occur at rare intervals in penguins. (See Chapter VI.) In petrels, and particularly in albatrosses, it is hard to believe that it takes place at all.

Among unemployed penguins and petrels, however, the situation is entirely different; there is evidence that while the breeding birds are busy with reproductive duties the unemployed indulge in coition. In the Yellow-eyed Penguin, I have not actually witnessed the act, but by analogy from the other species one may believe that it occurs, particularly among those unemployed pairs which occupy a camp or nest site at the pre-egg, incubation, or chick stages. The gonads of the male at least, judging by those of B15, are in the right condition.

In the other species of penguins, coition obviously does occur among the unemployed both at the pre-egg and post-egg stages of the breeding cycle. Bagshawe (1938: 249-263) says of the Gentoo Penguin that coition is frequent at the pre-egg period in birds which do not produce eggs.

In the post-egg period, Bagshawe (*op. cit.*: 283) observed coition between two Ringed Penguins on 10 January, 42 days after the first eggs had been laid, and presumably when all had long since been deposited. If so, the two birds concerned were unemployed. Falla (1937: 91) on 3 December saw many acts of coition at empty nests by Rockhopper Penguins, by which date he considered that most of the eggs were laid. If this is correct, some of the birds performing coition were probably unemployed "keeping company." A further record of coition at a later date is that between two King Penguins (Gillespie, 1919: 314). Finally, in unemployed Erect-crested Penguins, I saw attempted coition several times after the egg was ejected and also in the molt (1941b: 35, 49).

As for petrels, I have seen attempted coition among unemployed Sooty Shearwaters towards the end of the incubation period. It is with the Royal Albatross, however, that my most important observations in this connection have been made, for coition among unemployed birds has been noted many times whilst the breeding birds were sitting quietly on their eggs, but never among breeding birds. These facts, and the knowledge that inferences in the literature that breeding birds have been seen copulating are not supported by banding experience, have made me sceptical of these claims. Once banding is adopted, I suggest that observations relative to coition at the incubation and chick stages will be comparable to mine on the Royal Albatross.

SUMMARY

Male Yellow-eyed Penguins soon take charge of the eggs once the clutch is complete. This is true of other species of penguins and also of the Royal Albatross. The span of the sexes on the eggs in penguins varies considerably from a few minutes to at least 10 days. Exact data for a 14-day survey are given for the Erect-crested Penguin. Penguins and petrels tend to have long spans. There is a record of 24 days for the Buller's Mollymawk. In the Yellow-eyed Penguin a change-of-guard ceremony always occurs when the sea-going bird returns to its mate on the nest. This is true even if the latter has already recognized the former by sight or hearing. Comparable behavior seems to occur in other penguins. In the Erect-crested Penguin, however, change takes place at times other than when a partner has just returned from the sea. In mutually-behaving birds like penguins, behavior noted at change of guard may be observed, as a preliminary to nest relief, when two mated birds meet at times other than at the incubation and guard stages, and at spasmodic intervals when the two partners are together, whether it is the breeding season or not. The "welcome" ceremony, therefore, seems to have two functions—greeting value and bond-holding significance. Neither sex in penguins or petrels is the more responsible parent. Out of 889 inspections in the Yellow-eyed Penguin, the female was incubating 460 times and the male 429. Love-habits among breeding penguins in incubation have family value. They will mix with the unemployed birds on a social basis. The incubation period is one of recuperation in many species of birds. Weight increases prove this in the Yellow-eyed Penguin. Coition in species like penguins and petrels, once the eggs are laid, is rare among breeding birds. This is due to two reasons. The urge normally ceases immediately before the eggs are laid, and after that, the opportunity is lacking. Coition does occur, however, among unemployed birds when breeding birds are busy with eggs and young.

Chapter IX

Chick Stage

The chick stage in the Yellow-eyed Penguin, including guard stage, from end of guard stage to loss of the male, from loss of male to departure of chicks. The chick stage in other species of penguins. Discussion of the chick stage in birds. Summary.

BETWEEN 15 DECEMBER 1939 and 5 February 1940, I camped within a few meters of the nest of the male Z12 and his mate 115. From an observation tent it was possible to watch proceedings without being seen by the penguins. In the whole of that time the camp was not left unattended. Further, from 19 November, when the chicks hatched, until 14 December I was present nearly every day for varying periods. Finally, from 6 February to 18 March, when the last chick departed, I camped again from each Friday afternoon until Sunday evening. As a result, the behavior of these two adults and their two chicks was recorded in great detail. Only data dealing with the love-habit behavior of the parents will be considered here.

Since individual penguins behave so differently, it is not claimed that the behavior of Z12 and 115 is characteristic of the species. Where pertinent, the observations made on other Yellow-eyed Penguin parents will be utilized. Birds Z12 and 115 were each banded on opposite legs with scarlet celluloid rings, so that, with a telescope, I was able to recognize them as they entered and left the water fully 180 meters away.

CHICK STAGE IN THE YELLOW-EYED PENGUIN

Guard Stage

Share of Sexes in Guarding Chicks.—November is the month in which the hatching of the chicks of the Yellow-eyed Penguin occurs. Occasionally they hatch at the end of October; I have no record so late as December. For the first 25 days after hatching I have been unable to study the movements of the parents in the same detail as subsequently, but enough has been observed to indicate that their behavior does change abruptly. Following the time of the more lengthy and irregular absences of one, and then the other, parent in the incubation period, each parent now spends at least a portion of each day at the nest.

For the first day or two the general rule is for the parent, which goes fishing, to return fairly early. Both birds remain together all night, and the second one enters the water on the following morning. This procedure is soon modified and in some cases is never even adopted. Table 48, although compiled from the time when the chicks were 26 days old, demonstrates exactly what happens from after the first few days.

TABLE 48

Movements of 115 and Z12 from 15 December to 2 January
(Chicks hatched on 19 November)

Date 1939	Sex at 8 a.m.	Returning bird	Food given WB	Food given R	Outgoing bird	Its return p.m.	Food given WB	Food given R
			grams				grams	
16 Dec.	♂	♀ 2:01 p.m.	284	397	♂	—		
17 Dec.	♀	♂ 11:30 a.m.	369	284	♀	7:35	0	85
18 Dec.	♀	♂ 5:00 p.m.	369	312	—			
19 Dec.	♂	♀ 3:30 p.m.	340	284	♂			
20 Dec.	♀	♂ 12:45 p.m.	255	227	♀	8:35	198	113
21 Dec.	♂	♀ 4:21 p.m.	284	312	♂	—		
22 Dec.	♀	♂ 10:21 a.m.	227	142	♀	8:10	198	340
23 Dec.	♂	♀ 5:43 p.m.	340	397	—			
24 Dec.	♀	♂ 4:10 p.m.	198	227	♀	—		
25 Dec.	♂	♀ 2:38 p.m.	482	454	♂	—		
26 Dec.	♀	♂ 3:05 p.m.	482	454	♀	8:25	170	312
27 Dec.	♀	♂ 6:15 p.m.	454	312	♀	—		
28 Dec.	♂	♀ 2:25 p.m.	397	454	♂ *	7:47	198	198
29 Dec.	♀	♂ 12:05 p.m.	227	284	♀	7:15	142	142
30 Dec.	♀	♂ 5:30 p.m.	340	312	♀			
31 Dec.	both	♀ 5:00 p.m.	369	482				
	gone	♂ 7:45 p.m.	198	198				
1 Jan.	♀	♂ 7:00 p.m.	340	340	—			
2 Jan.	♂	♀ 3:30 p.m.	255	170	♂ **	6:40	142	227

* ♂ departs at 2 p.m. before ♀ returns.
** ♂ departs at noon before ♀ returns.
N.B. *WB* and *R* refer to chicks.

Leisure time ashore is not a feature of the guard stage. Practically all the daylight hours are spent at sea by one of the parents. Of the 18 days under consideration (Table 48), only on three occasions did it happen that each bird was not in the sea for part of the day. One bird absented itself from the colony all night on seven occasions, and on nights when both were present at the nest, the return of the sea-going bird did not occur until rather late in the afternoon.

When a bird enters the sea shortly after daylight following a night ashore it will return that afternoon fairly early. The second bird will then leave for the sea immediately and, if relief has not been too late, will return that night, otherwise it will not come back until the following morning; the earliest arrival, according to my records, is 9:30 a.m. If, on the other hand, a bird is relieved rather late, it remains at the nest for the night. The latest hours at which a relieved bird left were 5:30 p.m. and 6:15 p.m. at a time when darkness fell at 9 p.m. On both these occasions the bird remained away all night. The earliest hour at which a relieved bird elected to remain for the night was 5 p.m.

It will be noted from Table 48 that, as a rule, the adults took turns in going for food and that no case is on record where one bird came home, fed the chicks, and departed immediately for the sea again out of turn. But there were three instances, two by the female and one by the male, where the bird which was last home the night before went off to sea again in the morning out of turn.

Table 49 records the number of hours by the sexes spent in fishing from 17 December to 2 January. For the purpose of the table it has been assumed that the bird absent overnight was not fishing at least between 9 p.m. and 5 a.m., these periods not being included in the calculations. The fishing times range from 6¾ to 16¼ hours, with a total of 143½ hours for the male, and from 5¼ to 15½, with a total of 124½ hours for the female. The greatest actual absence from the nest was 24¼ hours for the male and 23½ for the female, a great contrast to the range of one to five days in the incubation period.

Share of Sexes in Feeding Chicks.—By weighing the chicks four times daily at 8 a.m., noon, 4 p.m., and 8 p.m., I was able to work out the quantity of food received from each parent. Table 50 shows that between 15 December and 2 January each parent fed the chicks 13 times, and that each gave practically the same amount. On eight occasions a second meal was given in a day, but it was always smaller in quantity. Not once did an incoming parent fail to feed the chicks. The table shows clearly that two parents, at the guard stage, have no difficulty in feeding their offspring.

From the data in Table 49 there does not seem to be any corre-

Table 49

Relation between Time Absent and Amount of Food Given

Date 1939	Sex	Time absent hours	Part of day absent	Amount of food given grams
17 December	♂	14½	over night	652
	♀	8	during day	85
18 December	♂	12	during day	680
19 December	♀	10½	during day	624
20 December	♂	13¼	over night	482
	♀	7¾	during day	312
21 December	♀	11½	during day	595
22 December	♂	10	over night	369
	♀	9¾	during day	595
23 December	♀	12¾	during day	737
24 December	♂	11¼	during day	425
25 December	♀	13½	over night	936
26 December	♂	16¼	over night	936
	♀	5¼	during day	482
27 December	♂	11¼	during day	765
28 December	♀	12¼	over night	851
	♂	6	during day	397
29 December	♂	7	during day	510
	♀	7¼	during day	284
30 December	♂	10½	during day	652
31 December	♀	15½	over night	851
	♂	12¾	during day	397
1 January	♂	12	during day	680
2 January	♀	10½	during day	425
	♂	6¾	during day	369

N.B. When the parent was absent all night, the time between 9 p.m. and 5 p.m. is not included.

lation between the length of time a bird is absent and the quantity of food given to the chicks. The majority of the short absences involve a small amount, but this is because, in most instances, the chicks had already been fed that day.

In conclusion, all data and observations indicate that the chicks were fed once daily and sometimes twice.

Return to and Departure from Nest.—The following is a typical account of what happens when a bird, this time the male, returns home in the guard stage. The procedure is not always the same and differs also with individual mated pairs. The incoming bird may land any time between 9:30 a.m. (my earliest record) and 8:35 p.m. (dusk), although the evening arrival does not often occur after 8 p.m.

The bird lands, hops, and walks some meters quickly over the rocks out of reach of any extra large waves, and there it spends some ten minutes preening itself. Then it commences the journey uphill to the nest 180 meters away. The bird is never in a hurry, and frequent are the halts for peering around, further preening, or a session of panting, especially acute on hot days. While stationary the bird usually holds the flippers out from the body. Male Z12 generally spent approximately forty minutes in reaching the nest, but I have known him to take one hour. When within a few meters of the nest and when still out of sight of the female, he seems to hesitate considerably in going forward. The female behaves differently, going straight to the nest without hesitation.

As the male appears in sight, the female usually gives a quick look straight at her partner and breaks into an "open-yell," whereupon the male walks up to her quickly. Close beside her he performs a "half-trumpet." Together they then give several "half

TABLE 50

Food Received by Chicks, 15 December to 2 January

	First meal of day		Second meal of day		
Sex	Number of meals	Amount grams	Number of meals	Amount grams	Total grams
♀	8	5691	5	1700	7391
♂	10	6155	3	1161	7316

trumpets," which end in the adoption of the "sheepish look." Resuming an erect posture and facing each other, both birds indulge in the full "welcome." This is repeated a number of times before gradually subsiding into "half trumpets," "throbs," and "sheepish looks." The male then looks behind the female, which walks away from the nest. He thereupon straddles the chicks, runs his beak over them, and then sits down on them. Meanwhile, the female has moved away a meter or two for preening before finally lying down for a sleep. As this is going on, the male is poking the chicks to make them interested in food.

The outgoing bird generally leaves shortly after the change of guard just described. When it stays at the nest all night there is additional behavior. To find out what happens at the departure ceremony I crept into the observation tent before daylight on 23 December.

At 4:15 a.m., the male was lying down close by and, as the female had returned at 8:10 p.m. the night before, it appeared to be his turn to go to sea; the female was lying down a little farther off. By 4:40 a.m. each had given a few "shakes" and "half trumpets." The female then went up to the male and both indulged in a few quiet "shakes," after which the female went slowly along the track to the sea, and the male took up a position on a suitable rock to watch her go. At 5:11 a.m., she flopped into the water. I have never been able to determine how they decide which is to go fishing for the day, for, if night intervenes, it is not always in turn (Table 48).

General Behavior.—For the first two weeks the chicks are continuously brooded by one of the parents in turn. After this, the chicks gradually begin to display independence until the fourth week, when they are too large to be covered. At this stage, one of the parents remains alongside in the daytime. At night, the parent on guard, if the second bird is present, usually retires some meters from the nest in order to keep the second bird company. Under these circumstances, the chicks follow and sprawl close by. The positions thus taken up shortly after dark are usually maintained until well after daylight, when one of the parents goes off to sea.

In the behavior of the adults in the guard stage there is considerable difference according to the individual parent. In the period of incubation those parents which remain on the eggs at the approach of a human being as a rule just sit stolidly without defiance. When the chicks are being guarded, most parents will show some degree of aggression towards an observer. Those that flee will soon come back, especially if a chick is made to squeak. Exceptional parents will actually attack.

Space does not permit the presentation of many examples illustrating the foregoing behavior. An interesting one was observed at 3:35 p.m. on 13 November 1937, ~~when~~ I was weighing two six-day-old chicks, in the presence of the female 75. She had usually fled at the egg stage, but on this occasion retreated to a position immediately outside the nest. At this moment, the male 67 arrived. He must have sensed there was something abnormal, for I heard him crashing through the nettle in a great hurry. Arriving at the nest, he gave one short "welcome" to the female, which did not respond, and then made a swift attack at me, at the same time keeping up a chuh! chuh! sort of noise well down in the throat. As soon as I showed him the chick, he became greatly agitated and advanced farther towards me. When I put the chick on the ground outside the nest, he covered it immediately and let it rest on his foot. All the time he continued the chuh! chuh! noise. Occasionally, the female gave a "half trumpet." The male did not sit flat on the chick but rose and fell as it moved under him; later the chick was put back in the nest by the male.

Two important points arise from this example, which is by no means peculiar. First, even though the male was disturbed, he could not help giving one short "welcome" as he reached the nest. Secondly, he was able to recognize his young and helpless chick out of the nest either by sight or sound or both, and he was able to brood it outside the nest.

A comparable situation occurred with the female 115 (1941a:

275) some days after her eggs had been stolen. She was brooding on the empty nest when I showed her two other penguin eggs. Her behavior indicated that she knew what they were. As I placed them on the ground before her, she made no attempt to give me the usual peck, but quickly running her beak round them she guided them into position under her. The Yellow-eyed Penguin is apparently not fixed to the egg or young-in-nest situation as rigidly as are some other birds.

The female 75 did not respond to the chick-out-of-nest situation as the male did, nor will all penguins respond to eggs-out-of-nest as 115 did. Here is the essence of faulty deductions about penguins. It would not be correct to assume that the situation is beyond them. They are probably aware of the situation, but another factor, in this case fear, inhibits action. Both 67 and 115 were aggressive types. Hence, in the interpretation of the behavior of penguins care should be taken not to mistake a bird's stolidity for lack of awareness.

In case a reader should think that the foregoing account of 67 and 75 supports the theory of the responsibility of the male parent, it is necessary to give an outline of my experience with the male Z12 and the female 115. The latter's reactions to my weighing her chicks were to endeavor to interpose herself between me and her offspring; when this maneuver failed, she would come up to the weighing cloth stretched on the ground, and "open-yell" at me as I adjusted the balance. Sometimes she pecked my hand. Some weeks later, she ceased the yelling and protective attitude, and merely came up and watched proceedings. As the chicks became almost fully-fledged, she ceased even this practice, simply remaining where she happened to be. The male on the other hand never ventured to approach me unless the female was advancing in front of him, from which position he "open-yelled" at me. If alone he would retreat some distance and leave the chicks to themselves.

Love-habits.—The résumé of love-habits at the incubation stage given in Chapter VIII also applies among breeding birds with young chicks, and need not be repeated here. The following observations are useful, however, as they give some idea of behavior which probably strengthens the pair-bond and also of the factors which probably tend to keep the mated pairs intact from season to season.

As I watched Z12 and his family day after day I could not help noticing that Z12 behaved towards 115 and the chicks in a way that was closely akin to affection. The visual and auditory stimuli of the family on his behavior were most marked. The female also had her way of showing concern over the chicks when danger threatened, and the stimulus of chicks pleading for food exerted a stronger influence on her than the stimulus caused by the attentions of an overzealous mate.

The following isolated incident, although not exactly typical of many, for the behavior of Z12 varied considerably, will help to illustrate the male's apparent affection for the female. At 3:05 p.m. on 23 December, change of guard occurred and the female left for the sea immediately. More than five hours later, the male saw her returning when she was some ten meters away, and gave forth an unusually vociferous "open-yell." Perhaps he had not expected her that night—that is to say, if he had any means of assessing such a state of affairs. He was certainly excited over something. Without any reciprocation of welcome, the female approached the chicks to feed them. The male advanced towards her with bent head, with neck curved, and bill pointing to the ground. He then attempted the "arms act." The female, however, made no response, continuing to feed the chicks, and it was not until she had finished, that she commenced to respond to the male with "half trumpets." The effect on the male was to cause him to give a "full trumpet."

Whenever a bird at home is incubating eggs or brooding chicks in the nest, as far as I can ascertain, the "welcome" ceremony is always performed before anything else happens. In the foregoing case the chicks, aged 34 days, were some meters out in front of the nest, and the male was standing on the empty nest.

The female under these circumstances met the pleading chicks first and fed them; the stimulus of nest-plus-mate was lacking. The reason for the male's reversion to an act of the pre-egg stage—the only one I have ever witnessed—can probably be explained as substitute activity. Psychologically, he apparently expected the "welcome" ceremony in response to his "open-yell." This, coupled with his observed "affection" for the female, created in him a sense of frustration, causing him to perform the "arms act," which is a preliminary to coition. His "full trumpet," given when the female did respond, may probably be regarded as a substitute activity as well.

Another incident shows the concern of Z12 for the female. On 25 January the female stayed ashore all day and, late in the afternoon, took up a position on the long grass some 40 meters from the nest where she was completely hidden. At 7:55 p.m., the male arrived and gave a "full trumpet." The chicks rushed out and were fed. After this, further calls could not induce the female to betray her whereabouts. The behavior of the male indicated plainly that he was aware she should be somewhere in the vicinity. At midnight, the female was still hidden, but at eight o'clock next morning both were gone.

At 5:40 p.m. that day, during heavy rain, the female returned, fed the chicks, and took up her position as she had the night before. The male returned at 7:05 p.m. and after a careful look around gave a "full trumpet." This time, the hidden female replied. The effect on the male was immediate. He gave a quick look in the direction of the call, stood up on his toes, and uttered one of the most vigorous "full trumpets" I have ever heard (fig. 13). By 7:13 p.m., the chicks were fed, and the male hurried along to the female; then intensive love-habits were performed. All night they stayed together, leaving the chicks some distance away unguarded. Next morning both parents entered a very rough sea. From this expedition Z12 never returned.

End of Guard Stage.—In the study of the guard stage, one important aim was to discover the method of termination. This was revealed by the behavior adopted by Z12 and 115, and I have no reason to think that other mated pairs behave differently, although allowance has to be made for those individual differences so prevalent in penguin behavior.

After daylight on 28 December, when the chicks were 39 days old, 115 entered the water. At 2 p.m., Z12 became unusually restless and began wandering towards the sea. Going down the slope at 2:15 p.m., he shortly afterwards disappeared in the waves. Meanwhile, at 2:25 p.m., 115 arrived, but as she always used a different route she did not meet her restless mate. At 7:43 p.m., the male gave a "full trumpet" from five meters below the nest and caused the female, which was lying down, to look around, but that was all. Four minutes later he gave several "full trumpets" and "shakes" without eliciting any response from the female, which rose and walked away two meters. This apparently casual behavior was in strong contrast to the "welcome" ceremonies that occur at the nest. The chicks then appeared and occupied the male's attention.

Next day, the female was alone in charge until 12:05 p.m., when the male returned, leaving the female free for an excursion to the sea, from which she returned at 7:15 p.m. On 30 December the male left at 4:30 a.m., returning at 5:30 p.m. to free the female, which stayed away all night. Next day, the male left early and the chicks were alone all day for the first time until 5 p.m., when the female returned. The male did not appear until 7:42 p.m., and this time both birds went through their elaborate "welcome" ceremony. It seems that unless the female has been absent for some time she is not interested in "welcomes."

On 1 and 2 January a parent stayed ashore all day but, on 3 January, both departed in the morning for the first time, thus marking the end of the guard stage. It will be observed that the process is a gradual one.

It is not until towards the end of the first six weeks, when the parents are about to leave the chicks unguarded in the daytime, that the chicks, on seeing a parent arrive, commence calling for food; they plead for more after the feeding is finished. This may be one of the signals that urge both parents to fish by day. It cannot be that the parents are beginning to feel personal hunger through insufficient intake of food, for the amount of food given by both parents together, at this stage, is no greater and is frequently less than that transferred by 115 in the last month when she was feeding the chicks alone. Another interesting point is

TABLE 51

Return of Parents—3 to 26 January

Date	First bird home	Time p.m.	Food given		Second bird home	Time p.m.	Food given	
			WB	R			WB	R
			grams				grams	
3 January	♂	4:05	198	284	♀	4:55	227	170
4 January	♀	6:31	368	482	♂	8:13	142	57
5 January	♀	7:10	170	680	♂	home all day		
6 January	♂	2:58	227	255	♀	4:15	284	57
7 January	♂	6:45	312	425	♀	8:15	340	142
8 January	♂	7:20	482	652*	♀	7:24		
9 January	♀	6:20	369	425	♂	7:30	142	170
10 January	♀	6:44	425	482	♂	7:05	0	170
11 January	♀	6:33	284	369*	♂	6:50		
12 January	♂	6:15	198	255	♀	7:15	142	198
13 January	♂	5:55	510	595	♀	6:15	85	0
14 January	♂	5:45	397	369	♀	home all day		
15 January	♂	5:30	340	482	♀	6:15	113	85
16 January	♂	5:50	454	482	♀	6:18	57	0
17 January	♂	6:40	425	510	♀	10:50	340	142
18 January	♂	6:45	284	425	♀	home all day		
19 January	♂	4:50	369	397	♀	6:10	57	0
20 January	♂	4:51	255	255	♀	home all day		
21 January	♀	7:30	369	369	♂	8:30	284	397
22 January	♀	5:45	539	567*	♂	5:50		
23 January	♂	6:54	227	567	♀	7:45	227	113
24 January	♂	5:35	255	369	♀	8:30	284	57
25 January	♂	7:55	369	284	♀	home all day		
26 January	♀	5:40	198	113	♂	7:05	255	340

* Food given by each parent is not separated.
N.B. *WB* and *R* refer to chicks.

that parents with only one chick to feed leave their progeny unguarded at the same period as those with two, even though the single chick could well be fed by one parent fishing each day.

From End of Guard Stage to Loss of Male

Share of Sexes in Guarding Chicks.—Just as there was a distinct change in the behavior of the parents when the eggs hatched, so there was a further change when it was no longer necessary to guard the chicks by day. In the 24 days which followed the end of the guard stage, both birds were at the nest each night. Night absences ceased. As a rule, both birds entered the water shortly after daybreak, and did not return until the afternoon. The female stayed ashore all day on four occasions and the male on one only; the chicks were fed at least once daily. A third change in behavior was the procedure when a bird came home. Not once did it return from the sea and re-enter the water on the same day, even though the male on one occasion came back to the nest as early as 2:58 p.m.

Out of 19 days when both entered the sea, the male came home first twelve times, and the female came home first seven times. The arrival time for the first bird varied from 2:58 p.m. to 7:30 p.m., and for the second from 4:15 p.m. to 10:50 p.m. (after dark). Table 51 gives further details.

In Table 52, the times when both parents return from fishing are given in class intervals of 30 minutes. There are 43 records. Twenty-nine (67.25 per cent) occur between 5:30 p.m. and 7:30

TABLE 52

Times of Arrival when Both Parents Go Fishing

Time	Number	Time	Number
Before 3:00 p.m.	1	Before 7:30 p.m.	8
Before 3:30 p.m.	—	Before 8:00 p.m.	2
Before 4:00 p.m.	—	Before 8:30 p.m.	4
Before 4:30 p.m.	2	Before 9:00 p.m.	—
Before 5:00 p.m.	3	Before 9:30 p.m.	—
Before 5:30 p.m.	1	Before 10:00 p.m.	—
Before 6:00 p.m.	8	Before 10:30 p.m.	—
Before 6:30 p.m.	5	Before 11:00 p.m.	1
Before 7:00 p.m.	8		

p.m. That means that the birds require most of the day for fishing, and the times extend still further as the chicks grow older, a procedure which, with few, if any, exceptions applies as well to other families of Yellow-eyed Penguins. If a visit is paid to a colony in the guard stage, there are comings and goings all day, but in the next period, the colony seems lifeless until well after midday, when the earliest birds begin to arrive.

Although left unguarded by day, the chicks are closely watched by one of the parents at night. I thought at first that this task of sentry was the duty of the last bird home but later found that to be incorrect. On one occasion, the male reached the nest a few minutes prior to the female, but before he delivered his supply of food the female fed the chicks and retired some meters. The male then took his turn and was left with the chicks for the night. The same procedure was repeated a day or so later, when both parents arrived simultaneously. The second bird to feed took charge of the chicks. The bird off duty may be found any distance up to 30 meters from the nest lying down asleep. Any alarm call from the chicks will bring it hurrying to their aid.

Share of Sexes in Feeding Chicks.—It will be remembered that, at the guard stage, both parents feed the chicks equally, and that the process takes place shortly after change of guard except in the very early stages, when the parents have to stimulate their offspring to partake of food. Further, the chicks are not fed at night at the guard stage or if they are I have not observed such feeding. Subsequent events are a little different and not so clearly defined.

Table 53 reveals that in 20 meals which could be measured, the male delivered 12,731 grams of food, as against 7,570 grams in 17

TABLE 53

Food Received by Chicks, 3 to 26 January

First bird home	Number of times	Amount of food grams	Second bird home	Number of times	Amount of food grams
Male	15	10,774	Male	5	1,957
Female	6	4,450	Female	11	3,120

meals for the female. An adequate number of observations probably would show that the female delivered approximately as much food as did the male. On three occasions the parents delivered food more or less together, so that I could not separate the deliveries.

The first bird home, whether male or female, nearly always gives a much greater quantity of food than the second (Table 51); by the time the second bird feeds the young their keen hunger has been appeased. Since the male was home first more frequently than was the female, it was logical that he should part with more food. The female, however, was at sea longer, but there was no evidence to show that she had not caught as much fish; she may have caught more than the male.

I soon discovered, however, that the chicks were, at the post-guard stage, sometimes fed in the night and shortly after daylight, by the bird which was last home, and in this instance it was more often the female. Between 8 p.m. and 8 a.m. the chicks were not weighed so that I could not measure this quantity, but the 8 a.m. weights on many occasions indicated plainly what was taking place. After that I investigated.

At 4 a.m. on 9 January I observed the chicks worrying the female for food. They did not receive any and, as their weights at 8 a.m. showed a normal drop, they had not received any in the night. That day the male came home at 7:30 p.m., after the female, but he did not feed the chicks until 9 p.m. On the night of 10 January I heard the chicks pleading for food, and the 8 a.m. weights showed that the parents had obliged. At this date, the chicks began following the parents all over the place begging for food, so that night feeding became much more common. Again on 13 January the female arrived home after the male did and she gave up only 85 grams, which is readily understood, since the male had a little earlier fed 1106 grams. Once again next morning, the scales indicated that feeding had occurred in the night. The new period thus inaugurated a supplementary system of feeding.

Return to and Departure from the Nest.—Z12 and 115 now appeared to become very casual in their behavior towards each other when leaving the nest in the morning and when they happened to reach land more or less together. In the morning, when both started off for the sea at or approximately at the same time they did not journey together, although one or both might be escorted to the water by unemployed penguins. On 8 January Z12 landed almost immediately after the female, but the latter did not wait for him. Instead, she proceeded over the rocks and up the main track until she came to her side track leading to the nest. The male followed some distance behind and at the junction took his side track, beating the female to the nest by four minutes. Two days later, I saw them land together with three others, and the same procedure was followed, except that this time, the female arrived at the nest twenty-one minutes ahead of the male.

Whatever the reason for this apparently indifferent behavior, it is not that they failed to recognize each other on the beach. Plenty of evidence is available to show that birds know each other away from the nest; for example, 721, 61, 60, and 70 (Appendix I) all knew each other on the beach. The same applies to 20 and 18 (Chapter III), and in addition 20 knew 18 again when she returned to her colony some miles away.

At this period, the "full trumpet" was employed, more frequently by the male, in ways unexpected by the observer. I incline to the opinion that these trumpets served as substitute activities caused by some unusual situation. On other occasions, there was much trumpeting by unemployed birds from several different points in the colony, one bird setting off the others. Even Z12 on one of these occasions, when the female was absent, joined in the "general chorus" (Chapter VII). As far as I could tell the behavior then had social value.

On 3 January, the first day on which both parents entered the sea together, the male returned at 4:05 p.m. Fifty minutes later the female appeared, and when fully ten meters from the nest and still out of sight she trumpeted. This was most unusual behavior for her, and I cannot explain it. The male, of course, recognized her voice. On another occasion when she returned after dark, she trumpeted when a long way from the nest. The male was always likely to trumpet if the chicks were not visible when he arrived. I have already mentioned his response to the hidden female on 26 January.

On 17 January the female did not come home until 10:50 p.m., unusually late indeed. All the intensive love-habits were used that night and were kept up for a considerable time. Both birds employed the "full trumpet" frequently; the whole pandemonium was interspersed with the pleading calls of the chicks. The latter, of course, were usually responsible for the breakdown of the homecoming ceremonies of the parents.

Love-habits.—Regarding love-habits at the post-guard stage, it is difficult to give a definite pattern, as they are so variable, but the male is still the more demonstrative. The clear-cut "welcome" ceremony, followed immediately by the orthodox change of guard, is absent, for the chicks are no longer in a fixed spot. When the mated pair meet near the nest the "welcome" ceremony does take place, but there are many occasions when it is not used.

Another feature noted, once the chicks left the nest, was the frequent use of the "salute" by the male, both when he returned to find the female had preceded him and also when the female returned after he had arrived first. Not once did I see the female "salute," but she would respond with the "gawky" attitude (fig. 5), with flippers pushed out in front, the neck stretched up fully in a vertical direction, and with the beak at right angles.

After the loss of Z12 on 27 January, the love-habits of the female were rigidly confined to her family. About this time, too, penguin chicks in general have grown large and powerful, so that their constant, persistent, and vigorous pleadings for food monopolize the attention of their parents. The result is that the adults are seemingly unable to take much notice of each other, and love-habits between them are less in evidence. In spite of this distraction, however, there are some periods of great excitement.

From Loss of Male to Departure of Chicks

From 27 January to 18 March, when the second chick departed for the sea, the female was left alone to rear her two chicks. One chick soon became dominant and received most of the available food supply. The other I kept alive by hand feeding it with mussels (*Mytilus edulis*).

Reactions of Female.—For the ten days that followed the loss of the male, the female appeared to behave in a rather abnormal way. The quantity of food she delivered was small (Table 54), a fact that may have been due to the exceptionally bad spell of weather in these ten days. Moreover, her daily comings and goings became irregular. On 1 February she did not come home at all, the first time since the end of the guard stage that a parent had been absent all night, and this, at a time when the chicks could ill afford to be deprived of food. She returned late on 2 February (7:50 p.m.). Early on 3 February she left the chicks, ostensibly for the sea, but on reaching the halfway mark remained there until after daylight on 4 February before entering the water. Her return was delayed until, as late as 6:30 p.m. on 5 February, and then she gave only 284 grams to one chick and nothing at all to the other. For the first five days in February she fed the chicks only twice.

My continuous records were then broken. On 9 February she was again absent all night. After this, however, she probably did not "transgress" again as the meals delivered became substantial (Table 54). Her subsequent "diligence" is proved by the fact that the dominant chick became the biggest I have ever handled, even though the female was a small adult.

Even her family love-habit behavior altered. On 27 January she guarded the chicks at night as usual. Next day, she returned late (7:50 p.m.) and when 50 meters from the chicks and still out of sight she gave a "full trumpet," a most unusual performance for her. Two nights later she repeated the behavior, only on this occasion she took a long time to make up her mind to proceed any farther. On 31 January she gave a short single note call and then sat down on the ground without bothering to look for the chicks. This apparent indifference was unusual for her. The dominant chick recognized his mother's voice but took ten and one-half minutes to find her.

The foregoing are the facts as observed; their interpretation is not easy. It does seem, however, that the female was aware of the absence of the male. Although she appeared so indifferent at times to his love-habits, the loss of the stimulus of these would seem to have caused her behavior to change.

Feeding the Chicks.—By 10 February the female seemed to have recovered from her "lapse." That day, although it was exceptionally rough, she arrived home at the relatively early hour of 4:30 p.m. and delivered 1021 grams of food. A comparison of the amount of food delivered before and after 10 February is illuminating (Table 54). From 27 January to 9 February she im-

TABLE 54

Return of Female, 27 January to 10 March

Date	Time p.m.	Food given WB	R
		grams	
27 January	8:15	284	198
28 January	8:00	369	113
29 January	7:20	454	57
30 January	6:30	510	57
31 January	7:00	539	0
1 February	did not return		
2 February	7:50	539	284
3 February	ashore all day		
4 February	did not return		
5 February	6:30	284	0
7 February	4:30	unknown	
9 February	did not return		
10 February	4:30	851	170
11 February	not back by 8 p.m.		
16 February	4:30	unknown	
17 February	4:25	794	142
18 February	8:00	879	0
19 February	8:15	539	0
20 February	8:00	unknown	
21 February	8:00	unknown	
23 February	3:30	unknown	
24 February	3:00	794	227
25 February	8:30	unknown	
29 February	after 6:30	unknown	
1 March	7:00	unknown	
2 March	5:00	652	397
3 March	unknown	unknown	
8 March	8:10	85	1077
9 March	9:45	gone	624
10 March	unknown	unknown	

parted 3688 grams in seven days. After that, and up until 9 March 7231 grams were received by the chicks on the eight days I was able to measure the food. The amount of food given to chicks in their last month ashore is therefore considerable, and there is no reason to suppose that the delivery of 115 exceeded the normal. *It is obvious that one parent cannot feed two chicks successfully.*

An interesting point was noted in the behavior of the female when feeding the chicks. For example, on the date mentioned above, 10 February, she was immediately besieged by the dominant chick, which soon received 851 grams. The second chick was lying down several meters away making no attempt to plead. Though it was still pleading, the female pushed aside her clamorous offspring and advanced towards the weakling. On reaching him, she gave several excited "open-yells" and though sorely depleted of food managed to regurgitate 170 grams to this chick, which had had practically nothing in the previous eight days.

Once again, how should this unusual act be interpreted? In general, feeding is in response to the pleadings of the chicks or, at least, it so appears. As a rule, when one chick receives a ration he sits back momentarily, allowing the second chick his opportunity. In the foregoing instance, without the stimulus of pleading, the parent fed the silent chick and, furthermore, had to advance a little distance to do so. I had noticed also this characteristic of the female at the guard stage. Even though a chick which had received several turns was still in the best position to receive food and was pleading vigorously, I have seen the female brush it aside and feed the other; I have even seen her strike the first chick with her flipper so that she could feed the second and less fortunate one.

In summary, it would seem that this female at least was not entirely an automaton. She did seem to possess some power of discrimination when feeding and did not blindly follow the stimulus of the pleadings of the chicks. A position somewhat comparable to the foregoing arises when the chicks attempt to obtain food from adults which are not their parents; in these instances the chicks are refused.

Arrival Times of Female.—The general tendency borne out in Table 55 when compared with Table 52 is that adults which are feeding young towards the end of the season tend to arrive home unusually late in the evening. This was fully supported by visits to other colonies. Two factors account for their tardiness. The first is that with the approach of winter, fishing hours become restricted and secondly, at this stage, the chicks require a greater amount of food. These conditions can be met under only normal circumstances by staying at sea as long as possible.

The birds, however, do sometimes return early. For example, on 23 and 24 February, 115 reached her chicks at 3:30 p.m. and 3:00 p.m. respectively. On these two days a large flock of Sooty Shearwaters was fishing close in shore and small fish in thousands lined the edge of the rocky coastline. Apparently, 115 was fishing underneath the Shearwaters, for obviously she had not traveled far for food on those two days.

Is There a Starvation Period?—The literature disagrees somewhat regarding the existence of a starvation period at the end of the chick's life ashore. I was anxious to find out something concerning this. At 8:10 p.m. on 8 March the female fed 1077 grams to the weak chick, which for the first time secured the best position in which to be fed, and only 85 grams to the strong chick. This brought the latter's weight to 6068 grams, which is exceptionally

TABLE 55

Times of Arrival When Only the Female Went Fishing

Time	Number	Time	Number
Up to 3:00 p.m.	1	Up to 7:00 p.m.	3
Up to 3:30 p.m.	1	Up to 7:30 p.m.	1
Up to 4:00 p.m.	—	Up to 8:00 p.m.	5
Up to 4:30 p.m.	4	Up to 8:30 p.m.	4
Up to 5:00 p.m.	1	Up to 9:00 p.m.	1
Up to 5:30 p.m.	—	Up to 9:30 p.m.	—
Up to 6:00 p.m.	—	Up to 10:00 p.m.	1
Up to 6:30 p.m.	2		

heavy and certainly not the weight of a chick passing through a starvation period. Next morning before 7:30 a.m., this chick had entered the water. The female continued to feed the second chick for another ten days when it departed.

To gain additional evidence on this point, I weighed two other chicks at a nearby colony at 10 a.m. and again at 8 p.m. The chicks departed on consecutive days and each was fed the night before. It will be seen, therefore, that the chicks of the Yellow-eyed Penguin are usually fed to the end of the period ashore.

CHICK STAGE IN OTHER SPECIES OF PENGUINS

Guard Stage

Share of Sexes in Guarding and Feeding Chicks.—In all species of penguins where this part of penguin behavior has been investigated, it has been found that the sexes take turns in looking after the offspring. It would seem, too, that in those species which are known to have irregular and long spans at incubation, the behavior changes abruptly to regular, short spans of absence and, as a result, the chicks are fed at frequent intervals.

For example, Levick's "watch-bill" (1914: 91-93) makes it clear that in the Adélie Penguin the parents changed guard and fed the chicks on an average of approximately every 30.6 hours, with a range of from 14 to 40 hours. Observations lasted for the first 19 days after hatching. In the Little Blue Penguin records show that, in the early stages, the young chick may be fed in the daytime by the guarding parent as well as at night (1940: 188). After that it is fed nightly by the parents in turn (*op. cit.*: 189, 195). As the Little Blue Penguin is nocturnal when on land, there is no change of guard until after dark. Hursthouse (1939: 16-17) also noted this nightly change. In the African Penguin according to Kearton (Murphy, 1936: 459), the change and feeding are frequent, occurring every three hours.

A departure from the ritual described above seems to obtain in the Emperor Penguin. Wilson (1907: 12, 14) thinks that the chicks are common property and are brooded and fed by a number of different adults. This community behavior in the Emperor Penguin is apparently evident again in additional species which adopt the "crèche" system at the post-guard stage.

General Behavior.—As in the Yellow-eyed Penguin, all penguin chicks are brooded for a time by the sexes in turn. This period varies considerably among the species, for some develop slowly and the others more quickly. For example, the Little Blue Penguin completes the chick stage in exactly half the time it takes the Yellow-eyed Penguin. There is a corresponding difference between the two species of the genus *Aptenodytes.*

Interesting behavior was observed in the Gentoo Penguin by Murphy (1936: 374). When a brooding parent was forced from the nestlings, it lingered nearby and trumpeted until the disturbance had passed. The trumpeting seemed to me to be substitute behavior caused by the thwarting of its brooding inclinations. It could not be interpreted as a threat towards the aggressor.

End of Guard Stage.—Most writers at least imply that there is a guard stage in the other species, but few give any precise details of its method and the date of its termination. It is probably a gradual affair as in the Yellow-eyed Penguin. This stage I have recorded in detail for the Little Blue Penguin (1940: 193) and am supported by the earlier record of Hursthouse (1939: 16-17). It is worthy of note that the two single chicks I was watching were both left alone by day on the twenty-eighth day and that two chicks in the same burrow were left on the twenty-seventh and a second pair on the forty-first day. This would seem to indicate that, as in the Yellow-eyed Penguin, it is not really the need to supply a greater quantity of food that sends off both parents to sea in the daytime. The foregoing observations on the Little Blue Penguin were made at the same time and in the same detail as were the affairs of Z12 and 115.

Post-guard Stage

Share of Sexes in Guarding and Feeding Chicks.—As in the Yellow-eyed Penguin, there is a distinct change in the behavior of the parents once the guard stage is completed. In general, there are two different types of reaction; one is communistic and the other individualistic.

In the communistic system two species, the King and the Emperor Penguins, seem to group in large numbers. For the former this is stated by Roberts (1940a: 223-224, pl. IV), who provides illustrations to support his statement. The whole colony is included in one group. For the Emperor Penguin, the position seems to be much the same. Mawson (1915: opp. p. 114) gives a picture of a large group of young sprinkled with a few adults, taken on Haswell Island. The chicks were at the peak of the downy stage (*op. cit.*: 116-117).

In the Gentoo and Adélie Penguins, the other two species which are definitely communistic, the procedure is a little different. The groups are much smaller, being of approximately 20 or 30 individuals, and are known as crèches. This is noted for the Gentoo Penguin by Matthews (1929:587), Murphy (1936: 379), Falla (1937: 58), Bagshawe (1938: 223), although no exact numbers are given. In the Adélie Penguin, the information is more precise (Wilson, 1907: 49; Gain, 1914: 29; Levick, 1914: 96; Murphy, 1936: 398), and two of the writers give photographs amply portraying the phenomenon (Wilson, opp. p. 40; Gain, pl. IV). It is obvious, too, that the chicks, as in the Emperor Penguin, are huddled together at the peak of the downy stage.

In the individualistic type, families of all other species concerning which there is information seem to remain to the end as an isolated group. Of the Ringed Penguin, for example, Murphy (1936: 412) states definitely that it is not communistic but remains as a family group. Roberts (1940a: 223), however, seems to imply that it does form groups. Another doubtful case is the Rockhopper Penguin. Murphy (1936: 424) quotes Beck, who states that when two-thirds grown the chicks of the Rockhopper Penguin leave the nest and group in bands of 12 to 20.*

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*The Snares Island Crested Penguin, according to my observations made between 9 January and 26 February 1948, remains as an isolated family group. When I arrived, the fledglings were on the verge of entering the sea.

In the Yellow-eyed Penguin, where sufficient nests lead to a common track from the sea, a group of a dozen or so chicks may be seen. This is not a crèche. The chicks are together merely because of their penchant for company, and for the same reason there may be an adult with them. The latter need not necessarily be a parent of one of the chicks but may be an unemployed bird. When the parents do return they feed only their own chicks and usually the family proceeds to its own particular camp spot farther away from the sea. It is just possible that Beck's observations on the Rockhopper Penguin show a behavior comparable to that of the Yellow-eyed Penguin. As this species nests much more closely than the Yellow-eyed Penguin, the grouping of chicks would be greatly facilitated.

The burrow-nesting genus *Eudyptula* is different again from the foregoing species. The family remains strictly as an isolated and individualistic unit until broken up by the departure of the chicks. Desire for company is not characteristic of this species. This is apparent in the Little Blue Penguin from my own observations (1940) and also those of Hursthouse (1939). The same remark seems applicable to the White-flippered Penguin (O'Brien, 1940). The position in the genus *Spheniscus* is difficult to assess, so few records being available, but Murphy (1936, opp. p. 431) gives a picture of two fledgling Magellan Penguin chicks in a burrow, so that possibly the behavior is the same as in the genus *Eudyptula.*

In summary, it appears that the King and Emperor Penguins group themselves into large mobs; that the Gentoo and Adélie Penguins occur in groups of much smaller numbers; that the other surface breeders are individualistic but may come together to satisfy the desire for company; and that the burrow-nesting species, with the matter uncertain for the genus *Spheniscus*, are rigidly individualistic.

One point that has impressed me in the endeavors to interpret the relations between adults and young in crèches is that the observations published are made on unmarked birds of both age groups.

Without banding, how is it possible to know whether or not the adults feed their own chicks? Then arises the question of the status of the adult which are in the crèches. These adults may be unemployed birds or parents or a mixture of both.

Mawson (1915: 116) notes that adult Emperor Penguins were seen to join the group of young under observation but that feeding was not seen. Could these adults have been unemployed? Matthews (1929: 587) watched adult Gentoo Penguins return to a group of chicks which started to pester the newcomer. The latter was usually reluctant to part with food at first, but finally did so to one or two chicks and then left again. Could not this hesitant behavior be attributed to the possibility that the chicks pestering it were strange young and that the adult was taking time to find the legitimate offspring? Yellow-eyed Penguin chicks will worry parents other than their own.

In the communistic system, as reported for the genus *Aptenodytes*, it may be that the adults feed any chick which pleads vigorously enough. It is also reported that these adults far outnumber the chicks. If so, it is unlikely that even the weakest chicks would be left unfed and eventually starve. By weak chicks I mean healthy ones low down in the dominance scale, and not those constitutionally unsound. The latter succumb in any case.

Regarding the small crèches, as employed by the Gentoo and Adélie Penguins, Murphy thinks (1936: 398) that the parents keep to their own little groups. This assumption is probably correct and is consistent with comparable behavior which I have observed in the species of penguins and petrels that I have watched and that adhere to their own particular neighborhood in their colony. If this is so, it would be an easy matter for parents to find their own chicks and for the latter to recognize their parents in a small group. Murphy (*loc. cit.*) and Gain (1914: 29) infer the opposite, stating that the parents feed the chicks without distinction. Yellow-eyed Penguin chicks know their own parents by voice and hearing and *vice versa*, and this characteristic applies in a group. Why cannot penguins with small crèches do the same thing? I am convinced that only banding can finally answer this question.

Another problem arises from these small crèches. There is no suggestion, as in the genus *Aptenodytes*, that the adults far outnumber the young and therefore insure that the less dominant chicks would not starve to death. Rather it seems that parents and chicks are more or less in equal numbers. If this is so, the dominant chicks under a system of communistic feeding would receive most of the food, and many of the less dominant, which would survive under the system of feeding adopted by the Yellow-eyed Penguin, would succumb. But is this what happens? If not, then the parents must surely recognize their own chicks on the crèche and feed them to the exclusion of others. That many chicks do not survive is well known, but this seems to be due either to constitutional weakness or to loss of one or both parents.

Is There a Starvation Period?—In the Yellow-eyed Penguin, there is generally no starvation period at the end of the chick's life ashore. The direct evidence supplied is supported by the presence of large splashes of white excreta which may be observed at the stances of fully-fledged chicks in every colony where I have worked. Few direct data are available concerning the other species. My own observations on the Little Blue Penguin (1940: 195-197) indicate that chicks may not be fed for a period of one night up to several days before departure. Hursthouse (1939: 16 and 1940: 122), working by direct observation on a pair of chicks in two succeeding years, records that feeding occurred up to the evening before they left. All normal chicks are usually fed after all the down has disappeared. Among the Snares Island Penguins it was a common sight to see adults feeding young entirely free of down. I did not have any of the birds banded, but even so, the evidence seems to indicate the absence of a starvation period in this species.

Murphy (1936: 377, 380) states that young Gentoo Penguins are fed long after the completion of their molt and Bagshawe (1938: 223) says the same thing. In the Adélie Penguin, Levick (1914: 112) saw fully-fledged chicks clamoring for food; although he did not see the actual feeding, the observation is significant. Finally, in the Ringed Penguin, Murphy (*op. cit.*: 412) remarks that the young "are dependent upon their own parents until the end of their upbringing."

In opposition to the above evidence is an opinion by Falla (1937: 50) that chicks of the King Penguin "are evidently not fed after they commence to moult their down." This view does not appear tenable. In penguin chicks, the feathers grow rapidly after the down begins to molt, and it is not likely that the chicks would require less food in the period when the feathers are growing. In conclusion, it would appear from the data available, if one allows for individual differences, that the normal young of penguins are fed until they enter the water.

DISCUSSION OF THE CHICK STAGE IN BIRDS

Part Played by Sexes in Feeding Young.—As far as I can ascertain from the literature, in most species of penguins while the chicks are being brooded or guarded, each sex feeds the young at least once every second day. This means that the chicks are fed daily by the incoming bird shortly after it changes guard on the nest.

The petrels are somewhat different. The Royal Albatross guards its chick for a period varying from four to six weeks (1942a: 258) but does not change guard daily (p. 257). For at least the first 22 days, however, one parent, even though it has not been relieved for as long as five days, may feed the chick daily (pp. 255-257). After that the chick may miss a meal for an odd day or so.

At the guard stage, the young of the Diving Petrel are fed nightly by each sex in turn, and for the first ten days from hatching may receive a meal in the daytime, on the average, one-third of the times when parents are guarding them (1945b: 46-48). The last day on which a chick was found guarded was the fifteenth (*op. cit.*: 48).

The procedure in the White-faced Storm Petrel, Fairy Prion, and Sooty Shearwater is different. In all three species, from shortly after hatching, the chick is left alone in the daytime. In the short initial period, however, when the chick is brooded, it may be fed by the parent in charge (1943b: 112, 1944c: 41, and 1945c: 50).

In the Little Pied Cormorant, *Phalacrocorax melanoleucos* (Vieillot), the Stewart Island Cormorant, and the Spotted Shag, *Stictocarbo punctatus* (Sparrman), which I have watched, the young are fed by both sexes alternately not long after the incoming parent has changed guard. The intervals range from 40 minutes to two hours.

After brooding and guarding in the daytime has ceased, young penguins in general are fed daily by each parent. In the Royal Albatross, the chick is usually fed by each parent in turn (1939: 484-485), but there are exceptions, and, further, sometimes both adults arrive together. Further still, the meals are not delivered daily, the longest period of fast recorded being 4¼ days (*op. cit.*: 476).

As for the Diving Petrel chick, it rarely misses its nightly meal, given usually by both parents but sometimes by only one (1945b: 47). The other three petrels mentioned, and, in addition, the Broad-billed Prion are not fed nightly. The two Prions may miss from one to four nights (1944a: 193, and 1944c: 44-45), the White-faced Storm Petrel may miss up to five nights (1943b: 218-219), and the Sooty Shearwater may miss up to ten nights, eight and nine being common (1945c: 52).

In the cormorants mentioned, once the parents begin to fish simultaneously the intervals between meals tend to lengthen, but each parent still gives several daily. An excellent account of an eight-day watch at a nest of Big Black Shags, *Phalacrocorax carbo* (Linnaeus), with four young at the post-guard stage, is that by Williams (1945: 35-36). The young were fed 64 times, 31 by the male and 33 by the female. Generally, the sexes fed in turn; the male, however, on one occasion returned out of order, the female on four occasions. The mean interval between the meals was one hour and 29 minutes, with a range of from five minutes to four hours and 10 minutes. The standard deviation was 0.99 hours, ±.12.

These remarks from personal observations on the species named conclude the evidence of the part played by the sexes in feeding their young. What happens in other species of birds may be learned from the extensive literature. Nice (1943: 234-236) gives a good summary.

Recognition by Parents and Young.—From the foregoing discussion arises the question of recognition of the young by the parents and vice versa. Tinbergen (1939c: 40) gives three ways of orientation by the parents of the Snow Bunting: "... first, the old bird remembered quite well the exact place where it had fed a certain young the last time, and alighted just there the next time, even in those cases where the young in the meantime had moved to another place; second, in all those cases when it evidently searched for the hidden young, it was directed to it by a single call, and appeared to localize the sound much better than we could; third, in similar cases the adults looked around and were able to discover the young by sight. ..."

This is exactly what happens in the Yellow-eyed Penguin. A parent will return to a spot where he expects to find the chicks. If they have moved he searches for them or may possibly call out. The chicks immediately recognize their parent's voice and he recognizes theirs when they reply. Both parties recognize each other on sight. I have often held a pair of chicks in the observation tent as a parent approached. When the chicks have responded to his call, he has come right up to the tent immediately.

A chick of the Royal Albatross can recognize a parent flying overhead (1939: pl. 61, fig. 2) and, further, a parent can recognize its young 26 meters away from the nest (p. 480), although the parent would not feed the young in that spot. For the burrowing petrels, there is no evidence to indicate that parents and young recognize each other outside the burrow. Within my experience, all feeding occurs inside the burrow. In the Little Blue Penguin, however, chicks will wait for parents outside the burrow and will be fed there, as I observed on the island of Whero, near Stewart Island. The chicks were almost fully fledged.

Nice (1943: 239-242) gives an excellent summary of recognition within the family group. "So long as the parents respond to what is in the nest, there is no need for personal recognition." Once the young begin to leave the nest, parents recognize their own young and probably each individual of the family. This latter point seems to be corroborated by the behavior of the Yellow-eyed Penguin female 115 in pushing aside her vigorous and clamorous chick in order to feed the second one, which had been thoroughly dominated and was making no attempt to plead for food.

In a previous section it has been shown that chicks of the Yellow-eyed Penguin will solicit adults, other than their parents, for food and that, within my experience, they are refused. What happens in other species, especially those in which the young collect in groups, is not certain. Parent cormorants (Stewart Island Shag) landing near a group of chicks will be immediately assailed by several of the nearest youngsters. The adults brush aside these aspirants, wait, shift from one point to another, and search for what I have assumed to be their own chicks. Feeding then takes place.

End of Guard Stage.—It has already been indicated that in the Yellow-eyed and Little Blue Penguins, the leaving of the chicks by the parents in the daytime at the end of the guard stage is not a sudden affair. The several families display considerable variation, and there is also a difference between the sexes themselves. In petrels, within my experience, a comparable situation obtains.

For the Royal Albatross (1942a: 257-258), the male was the first to abandon the chick. After that he found the absent female at sea and returned with her to the nest two days later. The female then guarded the chick for another five days before finally leaving it. This example amply demonstrates the indefinite behavior at the period of transition to the post-guard stage.

This indecisive behavior is clearly indicated in nine families of Diving Petrel which I watched carefully (1945b: 48). In one striking case the first parent deserted its chick on the eighth day after it hatched, but the second bird did not do so until the seventeenth day, although it missed its turn on the thirteenth day. Evidence of a comparable pattern in other petrels is published in my papers on the White-faced Storm Petrel (1943b: 114), on the Fairy Prion (1944c: 41), and on the Sooty Shearwater (1945c: 50). For other petrels, the characteristic has been recorded by Roberts (1940b: 167) for Wilson's Petrel; by Gross (1935: 391) and Ainslee and Atkinson (1937: 239) for Leach's Petrel; and by Lockley (1932: 210 and 1942: 37, 38, 73) for the British Storm Petrel and the Manx Shearwater respectively.

The Starvation Hypothesis.—The notion that a starvation period of some length comes at the end of the period ashore in penguins and petrels has gained much credence in some quarters, but this notion is not substantiated by any of my observations. It has already been shown that a starvation period does not appear to occur in penguins.

The two large albatrosses were thought to abandon their chicks several months before the chicks flew. My observations on the Royal Albatross, however, indicate that not only are chicks fed to the last but that a parent may return to feed its chick after the latter has actually left the breeding area (1939: 482-485, and 1942a: 260).

In the Diving Petrel, it is exceptional for the chicks to be left unfed the night before the chicks leave the burrow (1943a: 44, and 1945b: 47). In the two Prions observed, a short starvation period tends to occur at the end of the chick stage, although a fair proportion of chicks, approximately 20 per cent, are fed on the last night (1944a: 200, and 1944c: 167). In the White-faced Storm Petrel, the starvation period tends to be slightly longer than in the Prions, but even so, 13 per cent of the chicks are fed on the last night (1943b: 339).

Finally, concerning the Sooty Shearwater I have not yet carried out sufficient observations. Lockley for the Manx Shearwater (1930: 204-214, 1931: 204, and 1942: 85) records a short fast period before departure. The same rule may be applicable in the Sooty

Shearwater. On the other hand, I have found food in the stomachs of fledglings killed by the mutton-birders when the fledglings were out of the burrows. It is evident, therefore, that the fast period is short, not long as suggested by Cockayne (1909: 38).

SUMMARY

The chick phase in penguins is divided into the guard and the post-guard stages. At the guard stage, the sexes share equally the watching and feeding of the young. In the Yellow-eyed Penguin, the chicks are fed at least once daily. One parent is frequently absent all night. Most of the daylight hours are used in fishing. This is probably true of the other species of penguins as well. Petrels tend to have a different pattern. They do not always feed the chick daily. Cormorants feed several times a day. The end of the guard stage is a gradual affair in both penguins and petrels. In penguins it is not affected by the number of chicks guarded. At the post-guard stage, both sexes in the Yellow-eyed Penguin fish simultaneously and return to the nest towards the end of the day. Both feed the chicks. Absences at night cease. Petrels, at this stage, feed the chicks at intervals from one to ten days. Cormorants feed several times daily. If a penguin parent is lost, the surviving bird can feed only one chick. In penguins, family life at the post-guard stage may be either communistic or individualistic. In the former type, the young may congregate in large mobs, as in the genus *Aptenodytes*, or into smaller groups, as in the Adélie and Gentoo Penguins. Other species appear individualistic. Some chicks, as in the Yellow-eyed Penguin, group up for company's sake but are fed as a family unit. Others, as in the Little Blue Penguin, remain isolated all the time. It is suggested that chicks in crèches may be fed by their own parents. Parent penguins and young recognize each other by sight and hearing. This is true also of the Royal Albatross. A starvation period is not usual at the end of the penguin chick's time ashore. This is true also of some petrels, but others have a short starvation period.

Chapter X

The Molt

The molt in the Yellow-eyed Penguin, including general behavior, weight in relation to molt, love-habits, unemployed birds. The molt in other species of penguins. Summary.

WITH THE ARRIVAL of the molting period the annual breeding season for the Yellow-eyed Penguin draws to a close and, for breeding birds, the process is generally delayed only long enough to enable them to "fatten up" preparatory to molting. The actual dates of the molt fall between the end of January and the end of June. A few stragglers and, I think, birds in ill-health are still shedding the last of their feathers in June. The peak months, for all types of birds, are February and March.

My own observations on the molt were restricted to five years, from 1937 to 1941. Included in this period is the season of 1938-39, in which occurred abnormal mortality among adults and chicks and which had a marked influence on the year 1939-40. In the Yellow-eyed Penguin, the duration of the molt is usually 24 days and is counted from the time when the birds first stay ashore. If one of a mated pair finishes its molt before its mate, there is a tendency for the bird which finishes its molt first to remain a little longer than it otherwise would. Published records of the length of the molt contain some conflicting statements, due to the failure to begin counting the commencement of the molting period from a uniform date. When about to molt, penguins signify the event by staying ashore and ceasing to feed. Penguins do not feed again till they enter the water after the completion of their molt. This would seem to be the best point from which to work out the duration of the period of molt, the one which I have used.

THE MOLT IN THE YELLOW-EYED PENGUIN

General Behavior.—One of the first indications of the molt period is the sudden appearance about the colony of large extra areas of white excreta, due to accelerated feeding by the birds, giving the impression that many more penguins than usual are visiting the place. As I have not carried out a detailed survey of the movements of individuals at the brief pre-molt stage, I am not sure of their behavior, but there is evidence that the penguins revert to the procedure adopted in the winter; that is, they occupy spasmodically the old nest site or its vicinity.

Breeding birds, and for that matter resident unemployed members, return, as a rule, to their own particular colony for the annual lie-up to molt, even though there are occasional records of the process having been performed elsewhere. If the molt of each member of a mated pair coincides or overlaps, as it usually does, the birds molt together. Of the 240 breeding birds under observation, 181, or 75.5 per cent, were recorded as molting in their own colony. Twenty-six, or 11 per cent, were not found in their molt but were seen subsequently, and 33, or 13.5 per cent, were never seen again. As it is known that five of the last group succumbed, probably a fair number of the others met a similar fate.

Data relative to the departure of the chicks in relation to the molt of the parents indicate that neither sex of the adults molts before the other. Forty-seven males began to molt, on the average, 23.3 days after the chicks departed, with a range of one to 51 days, and 45 females averaged 22.6 days, with a range of four to 58 days.

Of 66 mated pairs whose molting dates were observed, in 21 pairs the males molted first, in 24 it was the female, and in 21 I could not ascertain which sex was first. The evidence shows that no one sex molts before the other.

Another interesting point is the influence of the female on the molt of the male. There is no definite example to quote, but it seems that a male mated to a late-laying female would molt late, but if, in the next season, he were mated to an early-laying female he would probably molt earlier. If this were not so, a male mated to an early-laying female one year and to a late-layer the next year would be liable to commence his molt before the departure of the chicks, but this has not happened within my experience. There are records (Chapter VI) of males mating with early females one season and late females in another, but I do not have the relative molt data.

There are, however, records of molting dates of males mated to late females and also records of the same males when unemployed. For example, in 1940 and in 1941, the male 74 was mated to the unusually late female 73 and began his molt on 14 April and 10 April respectively. These dates are unusually late. In 1938 and in 1939, when unemployed he molted on 26 February and on 12 March respectively. The latter date is on a par with 26 February, since in 1939 all molting dates were much retarded. The dates for the unemployed bird are average and indicate plainly the influence of the female on his April molts of 1940 and 1941.

Weight in Relation to Molt.—The greater average weight of the male is maintained in the molt, when neither sex puts on more relative weight than the other. The males average approximately one pound heavier at the beginning, a lead which is naturally reduced to 0.5 pounds as the molt is completed. The heaviest breeding bird that I ever weighed was a male which tipped the scales at 19½ pounds. His mate commenced to molt at 17 pounds. Some of the females were also exceptionally heavy, two of them weighing as much as 18½ pounds each; unfortunately I did not find their mates. One of these females, a small bird, entered the water when her molt was finished, weighing 10½ pounds, which is exceptionally heavy, especially in view of the fact that on the day after she laid her second egg she was down as low as 9¾ pounds.

Table 56 gives the weekly fluctuations in weight of 25 male and 25 female breeding penguins from the first to the twenty-second day, immediately before they entered the water. All the weights were taken from birds beginning their molt in February and in March. Late breeders usually did not commence until April and, in the few birds available, it was found that their weight was on a par with that of the earlier-molting birds. A long-deferred molt usually indicated bad health and possibly non-recovery from the molt. One hundred per cent of the males and 80 per cent of the females indicated in Table 56 began their molt when the birds were 16 or more pounds in weight.

Love-habits.—If undisturbed a bird will remain approximately two and a half weeks after which, if alone, it tends to wander until it finds company. It is then that love-habits with social significance will take place. For example, the young female 603, when passing through her first molt into adult plumage finished up in the company of two fully-fledged chicks which had not left the neighborhood of their nest site. Unemployed birds almost fully-molted may be found in the company of breeding birds which are alone and without their mates no matter at what stage the breeding birds are in; obviously, the unemployed have sought company. Birds with traces of the old feathers and other birds which had entirely new feathers and which had not entered the water since beginning the molt may be found in little groups on the main tracks or near the landing ground. The predominant behavior of all these birds has social value.

I have never actually witnessed the arrival of one member of a mated pair at its nest site when its mate has preceded it and is already partly molted. It is difficult to believe, however, that anything other than the full "welcome" ceremony would take place at this meeting. Certainly among mated pairs, love-habits do

Table 56

Weekly Molting Weights in Pounds of Mated Penguins

Sex	Number	1st day	8th day	15th day	22nd day
Male	25	17.57	15.03	12.25	9.63
Range		(19½-16)	(16½-13½)	(13½-11)	(10¾-8½)
Female	25	16.60	14.32	11.62	9.16
Range		(18½-14½)	(15¾-12½)	(13-10)	(10½-8)

occur for, at spasmodic intervals while molting, these birds may indulge in "sheepish looks," "shakes," "throbs," and "half trumpets," and, less frequently, in the "full trumpet" and "welcome." All this behavior has family value. Finally, love-habits with pair-formation value will also take place. As indicated in Chapter III, these may subsequently result in a mated pair, but, on the other hand, they may not.

The Unemployed Birds.—Discussion of the molt in unemployed birds has been excluded from the chapter on unemployed birds because this subject of molt seems more appropriately treated here. The main difference between unemployed and breeding birds in the molting period is, generally speaking, the difference in the time of that event, as indicated by Table 57, which deals with 283 adult penguins of all types. It may be observed that the peak of molting for the unemployed is considerably earlier than for the breeding birds. Parents which have lost either eggs or chicks molt at the same time as those groups which did not nest at all, so that birds which are feeding chicks are obviously pre-

TABLE 57

Weekly Totals of Molting Adult Penguins
(1937 to 1941)

Week ending	Non-nesting	Parents which lost nest	Successful parents	Total
28 January	1	1		2
4 February	2	3		5
11 February	9	4		13
18 February	23	10		33
25 February	13	16	17	46
4 March	12	5	19	36
11 March	15	6	29	50
18 March	5	4	23	32
25 March	8		19	27
1 April	4		6	10
8 April	1		3	4
15 April	2		4	6
22 April	4	2	3	9
29 April	4	1		5
6 May	2			2
13 May	2	1		3
Total	107	53	123	283

vented by some physiological factor from molting earlier than they do.

THE MOLT IN OTHER SPECIES OF PENGUINS

General Behavior.—Although only a little information is available, it is obvious from the literature that all penguins "fatten up" before the molt, a fact which is recorded by Gillespie (1932: 71) for the King Penguin. As regards behavior, between the time of departure of the young and the beginning of the molt, it appears that some of the species at least spend all the time at sea. This seems to apply particularly to the genus *Eudyptes*, and is recorded by Murphy (1936: 431) for the Rockhopper Penguin, by Falla (1937: 111) for the Royal Penguin, and by me for the Erect-crested Penguin (1941b: 46-47). A female of the last species which had lost its eggs fasted ashore for 15 days with her mate prior to 9 February, after which she did not appear again till 24 March, when she began her molt. In the Little Blue Penguin, after the young had left from three burrows, I placed sticks across the mouths of the burrows. No entry was made until the parents returned to molt (1940: 204). Apparently this species also stays away from its burrow in the period of preparation for the molt.

As in the Yellow-eyed Penguin, breeding birds probably return to the nesting place to molt, and both members of the mated pair tend to molt together. This is noted in the Gentoo Penguin by Bagshawe (1938: 224), in the Erect-crested and Little Blue Penguins by me (1941b: 34-35, and 1940: 203-204), in the White-flippered Penguin by O'Brien (1940: 318), and in the Magellan Penguin by Murphy (1936: 449-450). It is worthy of note that my mated pair of Erect-crested Penguins began the molt on the same nesting rock and used the nest site as a pivot for all activities. As the feathers began to fall, the two birds adjourned to crevices among the rocks, apparently to keep out of the wind.

From the foregoing references and from other literature, there is nothing to indicate that one particular sex molts ahead of the other. Another point concerning which no direct information is available is the influence of the female on the molt of the male, but if mated to a late-laying female a male probably will not molt before the chicks have departed. The general rule is for the parents to delay their molt until the chicks have set out, but there are exceptions (Bagshawe, 1938: 224; Kearton in Murphy, 1936: 459).

Weight in Relation to Molt.—From the limited amount of data available, it would seem that the variations in weight among the sexes are comparable to those in the Yellow-eyed Penguin. O'Brien (1940: 318) states that outside the molting period, White-flippered Penguins average 907 grams for males and 765 grams for females, and that, before the molt, the weights are 1644 grams and 1247 grams respectively. It is interesting to note that during the National Antarctic Expedition the heaviest Emperor Penguin, weighed in November not long after the molt commenced, was 40,824 grams and proved to be a female. Molting weights from my own studies of the Little Blue and Rockhopper Penguins have already been published (1940: 202-203). One individual of the first species began to molt weighing 1410 grams and finished 15 days later weighing 857 grams. Comparable figures for a Rockhopper Penguin, which completed its molt after three weeks, were 2,551 and 1,403 grams.

Love-habits.—The generally accepted view seems to be that penguins are very inert in the molt and uninterested in the ordinary affairs of life, but there is evidence that this is not correct. For example, Bagshawe (1938: 224) states that "while the old birds are moulting the male will still sometimes bring stones to his mate for their nest," and further, that after some have finished the molt many build nests for their spouses. Presumably these are birds which have cast off all their feathers and have not entered the water. All these remarks refer to the Gentoo Penguin, but Bagshawe also has something more significant to say concerning the Ringed Penguin (*op. cit.*: 279). It is this: "Even when moulting they show great affection for each other and still continue the waving of their heads together and screeching."

In support of the foregoing are my own observations on the Erect-crested Penguin (1941b: 34-35), which have also been recorded on a movie film. In the molt this mated pair carried out all their elaborate love-habits with as much vigor as in those other long periods of fast that occurred in the other phases of their annual cycle. The bouts were exceeded in vociferousness only when the mated pair were united after an absence.

From what we know of the Yellow-eyed Penguin and of the three species just mentioned, it would appear that love-habits occur in many of the other species in the period of molt. If they do occur then, it is reasonable to suppose that love-habits of all three of the values, which I have postulated, take place. Subsequently, mated pairs probably result.

The Unemployed Birds.—Owing to the fact that so few penguins have been marked in the wild state, but little study has been made of the distinction between breeding and unemployed birds in the molting condition. There is evidence in several places in the literature that when the chicks are still downy there are adults molting. Is it not possible that some of these are unemployed members and not parents at all? My own single record of a banded Little Blue Penguin parent which had lost its chick indicates that unemployed parents in this species molt early (1940: 204).

SUMMARY

The molt extends from the time when the birds stay ashore until they re-enter the water. This period lasts 24 days in the Yellow-eyed Penguin and 14 days in the Little Blue Penguin. In the Yellow-eyed, Erect-crested, and Little Blue Penguins, the birds usually molt at the nest site with their own mates. No particular sex molts first. Unemployed Yellow-eyed Penguins, on the average, molt before breeding birds. This is true in the other species. Migratory penguins appear to spend at sea the time between the departure of the chicks and the molt. Sedentary birds appear to spend part of the time ashore. The heaviest-molting Yellow-eyed Penguin was a male weighing 19½ pounds. Females are lighter on the average. Love-habits take place in penguins in the period of molt. Affinities are formed and a mated pair may result.

APPENDIX I

LOVE-HABITS OF ♀ 70 AND ♂ ♂ 60, 61, AND 721 IN WINTER OF 1939

	Mate of each bird in							
	1936-37	1937-38	1938-39	1939-40	1940-41	1941-42	1942-43	1943-44
♀ 70	A	721	61	61	dead			
♂ 60	—	—	B	U*	676	676	676	lost
♂ 61	GW	GW	70	70	U*	U*	lost	
♂ 721	C	70	63	U*	U*	U*	B16	B16

*Unemployed.

Before 9 July 1939, I had paid only four visits to the colony after the molt, but it was not until this day that I realized that ♂ 61 was concerned about something, his restless behavior giving me the impression that he was looking for a mate. After approaching two other penguins, he suddenly with rapid hops and jumps chases ♂ 60 over the rocks till the latter enters the water. Bird 61 follows, making "full trumpet" calls whenever he is on the surface. Ten minutes later he lands and "salutes" ♀ 18, which ignores the approach. When ♂ 721 lands in twenty minutes' time, 61 immediately goes up to him, "salutes," and 721 replies with a little "throb" before walking away. Another bird lands, which 61 also "salutes" without receiving any response. Bird ♀ 70 did not appear at all that evening.

15 July—4:20 p.m.: ♀ 76 and ♂ 61 land with four others. Bird 61 is soon on "mutual-preening" terms with 76. At 4:30 p.m. ♂ 60 lands and quickly takes an interest in 76 by chasing her over the stones, but later, after she returns to 61, 60 "salutes" her, only to be promptly pecked away by 61. The latter soon leaves 76 for another bird, but 60 makes no further approaches towards 76.

16 July—3:55 p.m.: ♂ 61 lands with four others, followed five minutes later by ♀ 70, which 61 immediately "salutes." She takes no apparent notice, but in a very short time they are "mutual-preening." At 4:10 p.m. ♀ 76 and ♂ 60 land. Bird 61 immediately attempts to chase 60 off the premises. The latter evading him, however, "salutes" 70, and thereupon 61 chases him again before returning to 70. At 4:18 p.m. 61 and 70 ascend the path from the beach for some yards, with 60 following. Once more he is chased away by 61. Birds 70 and 61 carry out "mutual-preening" operations for some time. Meanwhile, 60 "salutes" ♀ 29, but, receiving not the slightest response, tries another bird. By 4:35 p.m., 61 has left 70 for his nest in the bush, but the latter returns to the beach to see 60 once more "salute" 29 with the same results as before. Bird 60 then tries 70, which also remains indifferent. At 4:40 p.m., ♂ 721 lands, and soon "salutes" 70, rousing 60 to act likewise. A few minutes later, 721 rushes 70, and pushes himself against her as she moves off down the path. Bird 60 also comes in with a "salute." Soon after this, 721 also disappears up the path, leaving 70

and 60, back to back, some six feet away. After 15 minutes in this position 60 turns, "salutes" 70, and is rewarded by a few minutes of "mutual-preening."

21 July—4:20 p.m.: ♂ 61 and ♀ 70 land simultaneously. They keep together, preening themselves until at 4:44 p.m. bird 61 for no apparent reason re-enters the water. Bird ♂ 60 lands at 4:53 p.m. and immediately without a "salute" stays with 70. At 4:58 p.m. 61 returns and after a few minutes "salutes" 70, which commences "mutual-preening" with him. Just as 61 leaves 70 by herself in order to preen with another bird, ♂ 721 lands at 5:05 p.m. At 5:20 p.m. both 60 and 721 commence "saluting" and bustling 70. This causes 61 to give a "full trumpet," the first I had heard on shore in these observations, and to join the trio; then the three males persistently harass 70. Eventually, first 60 and then 721 depart to try other birds, while 61 remains with 70.

23 July—5:03 p.m.: ♀ 70 arrives first. Nine minutes later ♂ 60 appears and with the stage all to himself approaches 70, which flees as he follows. After some yards she stops and "salutes," 60 doing likewise as he catches up with her. Then she runs away again with 60 in pursuit, and they stop with a distance of six feet between them. Bird 70 again moves off, with 60 following. Meanwhile, ♂ 721 has landed and joins in with a "salute," as 70 happens to pass him. By the time 70 begins to ascend the path with 721 close behind, it is 5:25 p.m. When he reaches her she "salutes" with her back to him as she did to 60. Bird 721, continuing on the path until he is twelve feet past her, suddenly turns, rushes up to her, and "salutes" in splendid style, but 70 appears to take no notice. All the same I believe from experience with other birds, especially ♀ 115 and ♂ Z12, that there is some response in such cases, though imperceptible to the human eye. Meanwhile, 60 has been trying out another bird. At 5:27 p.m., 721 once more approaches 70 just as a strange bird, sex unknown, is performing a "shake" in front of her. At this juncture the scene is complicated, as 60 suddenly rushes in and "salutes" 70, chases 721 off, and stops three feet beyond 70, both being back to back for two minutes, before he once more approaches her. At this moment 721 returns to attempt to "salute" 70, but 60 deliberately stands in the way. By going round 60, 721 is able to reach 70, which walks down the path where she is approached by an unknown bird, which is immediately attacked by 721, quickly aided by 60. The stranger gives an "open-yell" and flees. The advent of darkness now prevents further watching. ♂ 61 did not appear at all this day.

6 August: Not one actor in the drama appeared, though there were nine other penguins on shore.

16 August—4:20 p.m.: ♂ 721 and ♀ 70 land together. Till 4:56 they remain together, indulging only in a little "mutual-preening." Now 721 "salutes," followed by another quiet period till 5:02 p.m., when 721 touches 70's breast and "salutes" again. Bird 70 does not turn away and they begin

"mutual-preening." At 5:10 p.m. 721 goes slowly off to his nest, leaving 70 on the path. ♂ 60 and ♂ 61 do not appear.

17 and 18 August: Only ♀ 70 comes home.

19 August—5:19 p.m.: ♂ 60 lands; at 5:28 p.m. ♂ 721; and at 5:30 p.m. ♀ 70, which stands by herself. Nine minutes later 721, which is standing among a group of birds, leaves their company and moves towards 70, which begins to walk away, but stops and continues her preening as 721 halts a yard from her. In this scene the human observer would have declared that 70, which was busy preening, was unaware of 721's presence in the assembly of birds, but the fact that she moves off as soon as he shifts indicates that she knew he was there. At 5:42 p.m. 721 goes over to ♀ 29 and engages in a "mutual-preen"; at 5:47 p.m. 60 "salutes" 29 without result; 721 does likewise without gaining a response; and at 5:55 p.m. 721 returns to 70, which "mutual-preens" with him.

20 August—4:03 p.m.: ♂ 721 and ♂ 61 land with others, while ♂ 60 returns at 4:10 p.m. At 4:23 p.m. 61 gives a "full trumpet," for which there appears no obvious reason, and which is apparently addressed to nobody in particular. Fourteen minutes later he repeats the performance, and at 4:46 p.m. he leaves the beach and the other birds, and makes for the track. Soon after ♀ 70 lands at 4:50 p.m., 721 begins a "full trumpet" in front of ♂ 760, a two-year-old, and then "têtes" at him, possibly with the idea of driving him away, but he is not interested in 70 in any case. Then 721 "mutual-preens" with 70, staying with her until 5:18 p.m., when he ascends the bank to the track where 61 has been all this time. When in 70's company, 721, at 5:12 p.m., had given a "full trumpet"; at 5:25 p.m. he gives a "half trumpet." Ten minutes later, 70 joins the birds on the track. As 61 approaches her, 721 asserts himself, rushes in and appears to dominate the female, whereupon 61 withdraws from the contest, leaving 721 and 70 together, while he with a few "shakes" goes up to and preens with another bird. The two pairs remain together till 5:45 p.m., when 61 again approaches and is met by a threatened peck from 721, while 70 remains unmoved. At 5:47 p.m. 721 moves off and tries several other birds, leaving 61 and 70 together. By 5:50 p.m. 70 allows 61 to preen her, a privilege which has been vouchsafed to 721 some time before. Then darkness prohibits any further observation. Bird 60 seems to have fallen out of the contest for a few days.

21 August: Only ♂ 721 and ♂ 60 arrive and indulge in a little "mutual-preening" with other birds.

22 August—4:07 p.m.: ♂ 60 lands, and at 5:13 p.m. ♂ 721, both behaving much as they had done the night before. At 5:07 p.m. ♀ 676 had landed and by 5:30 p.m. 60 is "mutual-preening" with her, continuing to do so until dark, while 721 appears to reflect an attitude of complete detachment.

23 August—5:05 p.m.: ♀ 70, ♂ 60, and ♂ 721 land together, and all stand about busy with their toilet till 5:17 p.m., when 721 approaches 70,

which, evidently aware of his intentions, hops off two yards, and "salutes." A minute later 721 rushes past her to the track. At 5:22 p.m. 721 "salutes" her again, but she moves off and loses herself in a crowd of birds, thus ending the affair for the night.

24 August—4:35 p.m.: ♂ 60 lands and is soon "throbbing," "shaking," and "half trumpeting" with a strange bird. At 4:53 p.m. ♂ 61 appears after an absence of some nights, and when ♀ 70 lands at 5:03 p.m. immediately advances towards her across the stones for five yards, but she makes no response. At this moment 60 suddenly appears, causing 70 to hurry away over the rocks with the two males in hot pursuit. At the base of the track 70 stops, while 61 passes her, ascends the track, and emits a "full trumpet." All is quiet for ten minutes until the arrival at 5:17 p.m. of ♂ 721, which immediately races across the rocks to "salute" 70. Bird 60 does likewise, and 70 ascends the track where 61 had been for some time. Both 61 and 721 rush past her for three feet and "salute" together. Then 721 turns, and pushes his breast up against hers, and though she does not move at the moment she soon turns her back on him as 61 gives a little "half trumpet." At 5:30 p.m., after 70 has been standing six feet from the group for a while, 60 rushes up and "salutes," closely followed by 721 and then 61, and for a time the three continue to importune her. At 5:33 p.m., 60 gives a "full trumpet," 721 rushes past 70 and "salutes," while a little later 61 comes up with the back arched, head down, and with water dripping from the end of his bill. By 5:37 p.m. all finish up standing in a row, in the order of 70, 721, 61, and then 60. At 5:38 p.m. 60 makes friends with another bird, staying in its company for a few minutes. At 5:45 p.m. 61 "trumpets," and soon repeats the call. Bird 60 comes up and gives a "shake," while 721 again pushes his breast up against 70's, the latter acquiescing in the treatment. A little way off 61 and 60 "tête" at each other and 60 gives a "full trumpet." At 5:48 p.m. 721 proceeds up the track, 61 and 60 have another "tête," just as 70 also begins to ascend the track, closely followed first by 61 and then 60. The three males continue on to their respective nests, where they spend the night alone, 70 returning to the base of the track and staying near the other birds not in the "drama."

25 August—5:03 p.m.: ♂ 721, ♀ 70, and ♂ 60 land with others. Ten minutes later 60 approaches 70 just as 721 commences a "shake." Bird 70 moves off towards the base of the track, the others following, while 721 comes up close to 70, and the pair go through "mutual-preening" operations for some time. At 5:30 p.m. 70 slowly climbs the bank to the base of the track, reaching it at 5:35 p.m., with 721 and 60 close behind. Bird 60 "salutes" 70, which moves off and is then followed and "saluted" by 721, but no activity follows. At 5:40 p.m. 721 "throbs" slightly at ♀ 676, which is close by, but she moves off. The next minute 721 adopts the "sheepish look," causing 70 to "mutual-preen" with him. By this date it appeared to me that 721 was the favored suitor, for she was more frequently in his company, and

seemed to respond to him better, especially in connection with what seemed to be an attempt at the "arms act." Till the fall of darkness at 6:00 p.m., 70 and 721 stay together preening, and occasionally 721 gives a "shake," to which the female always replies with a preen. At 5:55 p.m., 60, after remaining inactive since 5:35 p.m., suddenly rushes over and "salutes" ♀ 18, and though receiving no response he stays with her.

26 August—3:30 p.m.: ♂ 60 and ♀ 76 land, followed by ♂ 721 at 3:37 p.m. Twenty minutes later 60 gives four "shakes" by himself for no apparent reason, and from then till dark does much "mutual-preening" with a strange bird. ♀ 70 and ♂ 61 do not come home.

27 August—4:09 p.m.: ♂ 721 lands and very quickly goes over and "salutes" ♀ 76, which just continues to preen herself. At 5:33 p.m. ♂ 60 and ♂ 61 land, closely followed by ♀ 70 at 5:34 p.m. All is quiet till 5:45 p.m., when 61 "trumpets" after a "tête" at 60, which approaches and "salutes" 70, and is rewarded by a "mutual-preen." Bird 721 and then 61 do the "full trumpet," while 60 gives a quiet "shake." Within the next two minutes, 721 gives three "trumpets," which are followed by several silent "half trumpets" from 61. On my departure at dark (6 p.m.), 70 is standing in her indifferent attitude, with flippers stretched out, head and neck pushed back in her shoulders, and eyes shut.

28 August—4:12 p.m.: ♂ 61 lands, and seven minutes later goes through several "shakes" all on his own, which seems unusual, for the only other bird in the vicinity is a stranger which is some distance away. At 4:38 p.m. ♂ 721 arrives, while 61 has gone down close to the water's edge. ♂ 60 comes in at 6:00 p.m. but the non-appearance of ♀ 70 this evening causes everything to be quiet.

29 August—6:39 a.m.: ♂ 721 and ♂ 61 walk down together from their nests in a most friendly fashion and enter the water. Meanwhile, ♂ 60 has been at his nest with a two-year-old female, which enters the water at 7:55 a.m., but 60 stays ashore all day. At 4:21 p.m. 61 lands, squeals twice, and three minutes later re-enters the water, not to return that night. This seems strange behavior. Bird 721 lands at 4:34 p.m. and ♀ 70 at 4:54 p.m., but the former makes no sign that he is aware of her presence, until 5:06 p.m., when he goes up to her. Up till 5:40 p.m. 721 "salutes" 70 several times, with apparently no effect, but at the last attempt 70 walks around him and also "salutes." After that they remain together and "mutual-preen."

30 August—4:34 p.m.: ♂ 61 lands, and at 5:06 p.m. ♂ 721. Four minutes later 61 goes over to 721 and "full trumpets" in front of him. He then repeats this call, causing 721 to leave and go to the base of the track. There is no further activity and at 6:05 p.m. both males go off to their nests.

31 August: ♂ 61 remains ashore all day. At 5:03 p.m., ♂ 721 arrives, ♀ 71 appearing at 5:51 p.m. At 6:00 p.m. 70 ascends to the base of the track, to be immediately approached and "saluted" by 721 for the first time this evening. Bird 70 then walks round him and likewise "salutes."

By this time it is dark. This more active behavior by 70 helped to make me believe that she had accepted 721.

1 September—5:08 p.m.: ♂ 61 lands, followed by ♂ 721 at 5:18 p.m. With the non-appearance of ♀ 70 there is no activity at all, and both go to their nests.

2 September—5:06 p.m.: ♂ 721 and ♂ 61 land together with another bird. At 5:30 p.m., 61 "trumpets" three times after answering calls from the water, but 721 remains immobile. The two birds retire to their nests at 5:39 p.m., 721 "trumpeting" from his nest at 6:00 p.m., but 61 is silent. This was the first time I had heard the "trumpet" call from the nest that season.

3 September—4:26 p.m.: ♀ 70, ♂ 721, and ♂ 61 all land together at 4:26 p.m., and except for 721 are soon on the base of the track. At 4:50 p.m. 61 approaches 70, "salutes" her, and they both "kiss-preen." Bird 721, without any love-habits at all, ascends the track to his nest at 4:55 p.m. Bird 61 soon follows, but suddenly rushes back to 70, "salutes" her, and they "kiss-preen" again as water drips from 61's bill. "Mutual-preening" continues till 5:05 p.m., when 61 gives several violent bouts of "shaking," but 70 takes no notice and is half asleep. At 5:11 p.m. he gives a "full trumpet," followed by more "shakes," but 70 is still immobile. A vigorous "half trumpet" rouses 70 from her lethargy, and she "mutual-preens" for some minutes. The kind of behavior described after 5:05 p.m. continued till 6:00 p.m., when I left. It was the first time I had seen 61 in the company of 70 for so long, and both birds evidently spent the night on the track together, for the mark I made at the nest of 61 was found next day not to have been disturbed.

4 September (this was the last night on which I was able to watch the landing, and it is unfortunate that the closing scenes of the "drama" remained unobserved) 4:48 p.m.: ♀ 70 and ♂ 721 land together, and at 5:03 p.m. 721 turns, faces 70, and is about to "salute" when she walks away. He is, however, soon successful in some "mutual-preening" and at 5:10 p.m. makes his first "salute." This is repeated twice and they "mutual-preen" till 5:20 p.m., when they rest. At 5:27 p.m. 721 "salutes" again and finishes with a "shake." For the remainder of the evening 721 pays great attention to 70, which responds to his "salutes" and "shakes," some of which are vigorous, only by occasional preens.

16 September: Twelve days now elapse before my return to the colony, and in this period a union has apparently been solemnized, the contracting parties being not ♀ 70 and ♂ 721 as I had expected, but 70 and ♂ 61. I found the pair firmly established at their old nesting site where they were to rear a family in 1939-40. That day 721 was occupying a very good nest, while ♂ 60 was absent.

On 19 September 721 only was present, and two days later both were absent. On 23 September, however, 721 had the two-year-old female 676, a daughter of the female 29, with him at his nest, but 60 was absent. At 6:30

p.m. on 25 September, 721 and 676 were together, while 60 had a juvenile with him, but I do not for a moment think that this was a case of "keeping company." It is more than likely that the juvenile, as is the custom with juveniles, followed 60 to his nest. Next day, at 4:00 p.m., I found 60 with 676, at another spot, between the nest of 721 and 60. Bird 60 was not again seen in this part of the colony, but 721 and 676 were observed several times up till 7 October, merely wandering about together. Several times in the winter 676 had been standing about on the rocks, but I had not seen 721 pay any attention to her, though 60 had made her acquaintance at this stage.

Appendix II

Behavior of ♂ ♂ 143 and 20 and ♀ 18 in Winter of 1939

	Annual Mates of Important Individuals						
Bird	1937-38	1938-39	1939-40	1940-41	1941-42	1942-43	1943-44
1 ♂	5	35	18	18	18	U*	U*
15 ♂	18	18	U*	U*	636	636	636
18 ♀	15	15	1	1	1	20	20
20 ♂	35	5	U*	U*	U*	18	18

* Unemployed.

22 April 1939—Midday: ♂ ♂ 143 and 20, and ♀ 18 were indulging in love-habits at Colony B and had stayed ashore all day. The old mate of 20 had been found dead six days earlier; 18 had been mated to ♂ 15 for the season just passed; and 143 was a young bird ready to breed for the first time. All three had not long completed their molt. Birds 20 and 18 were the chief actors, whereas 143 was the odd member of the trio.

Later, the foregoing three birds were frequent visitors at Colony W, where I also watched ♂ ♂ 60, 61 and 721, and ♀ 70. Bird 143 took no further part in proceedings, but 20 continued to pay attention to 18, with whom he always "kept company" for the night. Bird 18 was last seen at this colony on 29 August and bird 20 on 31 August. I naturally expected to find these two mated at their own colony. Great was my astonishment, then, to discover that 18 had mated with ♂ 1, at the old spot where I had seen the trio on 22 April previously. This particular spot happened to be about 230 meters away from the main Colony B, and how 1 mated with 18 was not discovered. Here the newly mated pair reared a family in the succeeding three years. (For subsequent events see Chapter III.)

After the events of 22 April, birds 20 and 18 were first seen at Colony W on 9 July though no doubt they had been there previously. Bird 143 was first seen on 16 August and paid five visits, to my knowledge. Bird 20 was there fourteen times, and 18, ten times, when I was present.

Up till 22 August birds 18 and 20 were on the rocks three and seven times respectively, and though I had not noticed any mutual behavior it may have happened, for I was, of course, very much preoccupied with the "drama" of ♀ 70 and the three males. Bird 18, however, had been "saluted" several times at her first two appearances. Here follow some observations on the behavior of the two birds.

22 August—4:45 p.m.: Bird 20 lands, followed at 5:07 p.m. by 18. At 5:22 p.m. they "mutual-preen" and then 20 adopts the "sheepish look." After some preliminary "throbs" they both perform the "half trumpet" and the "excited shake" in unison. These emotional exchanges soon cease and the pair stand together as if nothing had happened. At 5:24 p.m., 18 adopts the "sheepish look," which quickly develops into a "shake." Bird 20 "shakes" also, and then both break into a "half trumpet" which lasts some time. At 5:26 p.m. they stand apparently indifferent before once more breaking into "throbs," "shakes," and "half trumpets," ending with a "mutual-preen" which ceases at 5:29 p.m. Bird 18 "throbs" slightly as 20 moves away three feet, and stops facing her. Both now indulge in self-preening, and it appears that the excitement has spent itself. At 5:31 p.m. 18 "throbs" and "shakes" with a strange bird, causing 20 to come up close to her, the three standing silently till 5:34 p.m., when 18 and 20 once more commence their "throbs" and "half trumpets," but a minute later "mutual-preen." This latter activity continues till 5:36 p.m., and at 5:37 p.m. 18 leans over and preens the breast of 20, causing him to "throb" slightly, and then to preen her till 5:40 p.m., when he turns his back on 18. The latter then bends over to preen the tail of 20, which action makes him jump and move off three feet. Bird 18 goes up close to him, causing 20 to adopt the "sheepish look." They "mutual-preen" till 5:43 p.m., when 18 jumps up on to a high rock alongside, and 20 follows, adopting the "sheepish look," and "mutual-preening" occurs. At 5:45 p.m., 18 moves further on, 20 following with the "sheepish look" and with head bowed. Two minutes later the same thing happens, but as it is a wet, dark night I can follow them no longer. It will be noted that 18 initiated a number of the scenes, and that she usually responded to the attentions of 20, behavior in marked contrast to that exhibited by ♀ 70.

24 August—5:18 p.m.: Bird 18 lands last. Soon forsaking the other birds, she and 20 ascend to a position well up the bank, and here perform all the love-habits mentioned before. This behavior is maintained for the remaining nights they are together. Male 721 had "saluted" 18 when she landed on 24 August, but she had taken no notice, and when ♂ 143 appeared on 26 August, he took no notice of 18 and 20.

APPENDIX III

BEHAVIOR OF ♀ 29 IN WINTER OF 1939

On 8 July I first noticed ♀ 29, a resident of Colony B, at Colony W. She appeared on thirteen of my visits, and except for one or two "mutual-preens," avoided attempts at mutual love-habits. At first, I thought she was remaining faithful to her old mate, 26, but when she did return to her old colony, I found her mated to 21. The previous season's mates of both 21 and 29 had not returned.

On 8 July ♀ 29 lands with several others and remains separated from the other birds, busily preening herself. On 15 July she behaves in a similar manner. The next night ♂ 60 "salutes" her on two occasions, but she takes no notice. For the following two nights no bird approaches her, but on 17 August, 2B (sex unknown) is allowed a little "mutual-preen" at 3:56 p.m. This is repeated twice, but at 4:23 p.m. when 2B tries a fourth time, he is repulsed with a "tête," thus ending the affair, and 29 remains aloof for the rest of the night. Male 721 on 19 August is permitted a preen at 5:42 p.m., and then, at 5:47 p.m., 60 follows 721, and each gives a "salute" without eliciting a response. The next night 29 stays alone, but on 21 August 29 approaches 721 and a "mutual-preen" results. I do not think this was a display of initiative on the part of 29; rather would it seem that she was moving over the rocks and met 721 on the way. Some ten minutes later, when 721 again approached her for a preen, she turned away. During all her appearances for the remaining three nights she assumed a strictly neutral role.

APPENDIX IV

MALE 37 ACQUIRES A NEW MATE

On 29 January 1940, ♀ 6 was found dead, but her mate 37 managed to rear the two chicks. In April, shortly after his molt had been completed, the copious excreta at his former nest, with a few fresh, green fern leaves therein, indicated plainly that he was not alone. My next visit to the colony was at 11 a.m. on 29 June. Bird 37 was found alone at "Big Ver." nest, approximately five meters away. Judging by the quantity of nesting material, and the flattened nature of the stance, two birds, at least, had been there. At my next two visits on 6 July and 20 July, bird 37 arrived at 2:45 p.m. and 4:25 p.m. respectively, immediately entering the bushes. Further signs at the nest, from time to time, showed that activity was still progressing. At noon, on 15 September 37 was found at "Big Ver." with ♀ 8, with whom he subsequently reared a chick. Now, for the three previous seasons, 8 was mated to ♂ 28, first at the "Fern," and later at "Below Fern." Bird 28 was, this same day, found mated, only four yards below "Big Ver." with the ♀ 25, which had been absent from the colony in 1939-40, but in 1938-39 had been mated to ♂ 7, at "Big Ver."

Birds are not usually found ashore, during the day, in the month of June, except in the case of bad weather. On 29 June, ♂ 37 was the only bird ashore, a fact which, in conjunction with the evidence of action round the nest, clearly showed that love-habits had been taking place. Seeing that ♂ 28 deserted his 1939-40 site, and nested so close to 37 and 8, it may be that he was the odd member of one of those trios. When ♀ 25 returned to the colony, I knew from the behavior of other birds that she would go to the nesting site of the 1938-39 season. Finding it occupied she would remain in the vicinity, and in so doing would be discovered by 28. For a nest, this mated pair had only a scoop in the sand, without any nesting material, and the position was a very exposed one, which is unusual in this part of the colony. These features made me think that their mating was a hurried affair. The first intimation I had of their presence came when I found them together on 15 September.

It is perhaps interesting to continue the story of the above four birds into the 1941-42 season. In March 1941, ♀ 8 was ashore with a badly injured foot resulting in the molt overtaking her before she could put on weight. In September 1941, I found ♂ 37 and ♀ 25 mated midway between the "Fern" and "Big Ver." nests, while ♂ 28 had made a nest in exactly the same place as the previous season. Bird 8 did not return and must be presumed dead, and 28 remained unmated. Bird 37, therefore, has twice separated the latter from his mate. In 1946-47, 37 and 25 were still mated.

A case similar to the foregoing is that of ♀ 19 and ♂ 32, which in 1938-39 nested in a cave some 180 meters from the colony. In 1939-40, ♂ 14, which had evidently lost his mate, was found mated in the main colony, at the "Cliff" nest, with 19. Bird 32 built and occupied a nest approximately five meters below, but failed to secure a mate. Here again it would appear that, as 32 was found close to 19 and 14, and so far removed from the cave, he must have been a member of still another trio. It can scarcely be regarded as accidental that the males 28 and 32 were both so far away from their old nests and in close proximity to the new nests of their previous season's mates.

APPENDIX V

MATRIMONIAL AFFAIRS OF ♂ ♂ 69, 72, and 74, AND ♀ ♀ 65, 73, AND 75 IN 1940-41 SEASON

Annual Nesting Arrangements

Nest	1936 -37		1937 -38		1938 -39		1939 -40		1940 -41		1941 -42		1942 -43		1943 -44		1944 -45	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Hollow	A	65	72	65	72	65	72	65	72	65	72	73						
No. 9	72	B																
Big Net.	67	75	67	75	66	75	66	75					72	73	72	73	72	940
Fuchsia									69	75	720	75						
Big Log													720	75	720	75	720	B23
Mueh.	66	73	66	73	67	73	74	73										
Log			74	C									74	B23	W35	B23		
Fence					74*				74	73	74*							
Cave					69	68												
No nest							69*				69*							

* Unmated.

N.B. Any bird which is not further mentioned disappeared from the colony the following season.

The foregoing has been made out to give a clear picture of the nesting arrangements, each year that I have known them, of the six birds under consideration in this section. In the latter half of the winter of 1940, I had noticed that eighteen meters from the old nest of 65 and 72, a new nesting site was apparently in preparation, and I was somewhat puzzled by this. On 15 August I discovered 74 and 65 together, outside the latter's nest of two seasons before, going through all the various love-habit actions, which seemed to indicate that they had mated. Their excreta showed that they had been ashore all day. This event, together with the new camp just mentioned, suggested that 65 had not been in 72's company recently. As 74 had abandoned 73's nesting site, I began to wonder what had happened there, for I knew that both 73 and 72 were still in the colony.

On 26 August and 27 August I found 72 alone, at the new camp, under the log, at 10 a.m. and at 9 p.m. Next day at 10 a.m. 72 and 75 were together at this new camp, and according to all previous observations, had formed a fresh partnership. Obviously these birds had been "keeping company" for some time. On the morning of 29 August 72 and 75 were together at the former nesting site of 72 in 1936-37. The previous night I had seen 69 on the landing ground, but that was all I had seen of the other members of the group.

I did not visit the colony again till 1:30 p.m. on 14 September, when I found that 72 and 65 had mated at their previous site, that 74 and 73 had done likewise at the previous site of 74 two seasons before, and that 69 was alone not far above the landing ground. Bird 75 could not be found. I did not locate her until 23 November, when, after a long search, she was found in a most unusual place with two chicks, but it was not till a few weeks later that I discovered that 69 was her new mate.

After the chicks had been disposed of, in March 1941, matrimonial complications seemed to be setting in again. I had always been under the impression that the alliance of 73 with 74, in 1939-40, was made only because she had no other choice (1941a: 272). Her exceptionally late laying date that year seemed to support my contention. Her second egg was laid in 1937-38 on 2 October, in 1938-39 on 1 October, in 1940-41 on 7 October, but in 1939-40, it did not apear till 15 October, which was six days later than the latest laid by any other bird in the eight years under observation, since 1936-37. In the succeeding three seasons, the dates were 30 September, 10 October, and 5 October respectively.

In the period of molt in 1941, 73 again showed that there was an affinity between herself and ♂ 72. On 28 March 1941, 72 was found alone in the same place where he had been wtih ♀ 75 the previous August, and was beginning his molt. This shift from the nesting site seemed to portend that something new was taking place. On 4 April he was still alone in the same spot. On 13 April, the time of my next visit, he was back at his nest, with 73 as his companion. The state of the female's feathers indicated that she had arrived for molting about 6 April. The normal behavior of a bird about to molt is to return to its old nest and its old partner. How did 73 find 72? It is quite likely that 73 may have proceeded to the nest of 72, for we know, of course, that she was no stranger to that part of the colony. But I should say that 73 found 72 by the use of calls. She may have called either from the water, or just after landing, or more likely after she had climbed the cliff. In either case, 72 would recognize her and reply—further calls on the part of each bird would bring about reunion. These conclusions are not mere conjecture but are based on close observation.

Now, on 20 April 74 was at his old nest alone, molting, having arrived about six days before. Birds 72 and 73, the former fully molted, were still together. When 74 reached his home he would call out in the usual manner, but no response would be forthcoming from 73, which could not help hearing him.

On 26 April both 72 and 73, having completed their molt, had entered the sea, but 74 was still at his nest. Later that afternoon 73 landed, and wandered up the track to the colony. When I investigated, two hours later, I found 74 still alone, while 73 was alone at the nest of 72. She had made her choice even though 72 did not come home that night, and it appeared probable that 72 and 73 would mate in 1941-42. Meanwhile 65, which I had found at her nest on each of the previous four seasons, did not appear in 1941. She did not return, and 72 and 73 reared a family in each of the three succeeding seasons.

APPENDIX VI

BEHAVIOR OF ♀ 70 AND ♂ 61 SEVEN DAYS BEFORE FIRST EGG APPEARED

The behavior of this mated pair was observed on 16 September 1939, and is actually a continuation of the events given in Appendix I.

2:35 p.m.: 61 touches 70, which is lying down on the nest, and causes her to give a series of "shakes" with beak almost touching the edge of the nest. This continues for ten minutes, the only action by the male being gently to touch the female, which responds with a few silent "shakes." In between each bout the female has a little sleep.

2:45 p.m.: 70 half rises and scratches her neck with her foot, while the male nibbles her head, and then bends down to touch the ground at her feet. This stimulus is sufficient to induce another series of "shakes." Till 3:10 p.m., the female sleeps, with occasional breaks for a self-preen. The male, however, is fully awake, and while continuing to nibble 70 in different places, occasionally peers around, as if to make sure that no intruder is coming.

3:10 p.m.: 61 turns his back to 70 and "mouths" a stick, an action that causes 70, though half asleep, to "shake" vigorously, and to "mouth" the straw on the edge of the nest. This occurs twice in the next three minutes. There is a period of little activity till 3:30 p.m., when the female appears wide awake and a bout of "mutual-preening," broken for short rests, lasts till 3:50 p.m., when the female settles down again on the nest and goes to sleep. The male remains awake, and occasionally preens himself.

4:20 p.m.: The female rises, shuffles quietly in front of the male, and off the nest, the male immediately taking her place. He starts to delve into the straw and rearrange it, then, sitting down on it, begins using his feet to shape it. Meanwhile the female is busy preening herself. This continues till 4:30 p.m., when the male for the first time since I have been watching gives a slight "shake." Three minutes later he repeats the action when the female happens to touch him with her foot as she tries to scratch herself. Now that he is on the nest, the male adopts the somnolent attitude, and the female continues preening herself.

4:39 p.m.: The female for the first time bends down and nibbles the side of the male's neck, causing him to "shake" vigorously.

4:42 p.m.: The female moves round, the male rises, and the female picks up a stick to add to the nest. She then proceeds to preen her mate a little. The male responds to all this by a number of "shakes." There is quietness until 4:53 p.m.

4:53 p.m.: The female suddenly turns and with her back to the male, inserts her head under a log for a straw, causing the male to "shake" immediately, although he must have had difficulty in seeing what she was doing. After a further ten minutes of waiting without any activity, I left the mated pair to continue their love-habits unobserved.

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