THE BREEDING BIOLOGY OF THE MANX SHEARWATER

by

M. de L. Brooke

(Linacre College)

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University of Oxford,
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Edward Grey Institute,
Zoology Department,
South Parks Road,
Oxford.

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Abstract

Chapter 1 is purely introductory and gives a brief account of the taxonomic status of the subject of this thesis, the Manx Shearwater Puffinus puffinus. The main study area, Skokholm Island, Pembrokeshire is described and a general account of what is already known of the breeding biology of the Manx Shearwater is provided as a background to the more detailed studies described in the present work which was continued over five breeding seasons, 1973-1977.

In Chapter 2 I demonstrate that male and female Manx Shearwaters differed in the length of their bills and tarsi but not in wing length. However most of the chapter is concerned with the weights and measurements of shearwaters, most of which were of known age but unknown sex, caught at the colony by night. In 1973 and 1974 the weight of all age groups was highest in March and then declined to a minimum in June and July. Weight increased slightly in August. It was generally true that the older a bird was, the heavier it was in any particular month, and this effect appeared to hold good until the birds were 8-10 years old. Unlike weight, bill and wing length did not alter with age. The implications of these results are discussed in the light of current hypotheses concerning the delayed onset of breeding shown by many seabirds including the Manx Shearwater.

In the pre-laying period, covered by Chapter 3, both male and female Manx Shearwaters lost weight up until about two weeks before laying. Males lost weight more rapidly than females and this was related to the fact that males visited the burrow more regularly. In the two weeks prior to laying the male continued regularly to visit the burrow at night but the female was virtually absent from the colony; it appears that she may travel into the Bay of Biscay to feed during this period of absence. In the pre-laying period the weight of breeding birds was not different from the weight of birds which have bred formerly but which were not known to be breeding during the current season. However, breeding birds tended to be heavier than birds which started to breed in a future year. To test the possibility that young birds may be prevented from breeding by a shortage of burrows, artificial burrows were dug, and some were occupied by young birds, probably breeding for the first time. A burrow-blocking experiment was also carried out. The possibility that competition for burrows was greater in an area of higher as opposed to lower burrow density was investigated by comparing the pre-laying attendance pattern of breeders in the two areas. No difference was found.

Chapter 4 shows that the breeding success of newly-formed pairs was lower than that of established pairs, mostly because newly-formed pairs were less successful at incubation. The lower success of new pairs was not due to the new pairing per se but to the fact that such new pairs tended to include birds without previous breeding experience. Thus experienced birds may avoid the disadvantageous consequences (to breeding success) of forming a new pair if they mate with another experienced bird, and this they did. Divorce and change of breeding burrow were both more likely after a breeding failure than a success. Both the laying date and egg volume of individual female Manx Shearwaters varied little from year to year, once the first few years of breeding were passed. I am unable to reconcile this finding with Perrins' (1970) suggestion that the laying date of the female Manx Shearwater is determined by the difficulties she may encounter early in the season in building up sufficient food reserves to form the egg. Instead I propose that, although early laying would be advantageous from the point of view of chick survival (Perrins 1966), the shearwaters do not lay earlier because of the difficulties that would be encountered in successfully incubating

an early egg. Evidence supporting this idea is presented.

In each of the four study years the fledging weight of chicks declined as the season progressed, as described in Chapter 5. Various lines of evidence, including an egg-swapping experiment, support the view that this decline was mostly due to a deterioration of feeding conditions late in the season, rather than to a tendency for parents less proficient at rearing heavy young to breed later. It seems that date of fledging and weight at fledging may both influence the fledgling's chances of survival but I am unable to determine the relative importance of these two factors. Different pairs of shearwaters differed in their ability to feed chicks, but chick-feeding performance was not related to age or breeding experience.

Chapter 6 evaluates the parameters necessary for the construction of a life table. Of the chicks which fledge from Skokholm at least 25 % survive to breed on Skokholm, whilst adult survival is about 90 %. About 20 % of those adults known to be alive and to have bred previously do not breed in any one year. The age of first breeding, currently about six, has increased over the past ten or fifteen years. Among the birds which have been ringed as chicks on Skokholm and which bred there during the study period there was a 2:1 ratio of males to females. I suggest that about half the females fledging from Skokholm settle to breed in other colonies. The body measurements (used as an indicator of sex) and abundance of Skokholm-ringed birds on nearby Skomer Island support this hypothesis. The Manx Shearwater life table is therefore contructed to take account of immigration to and emigration from the Skokholm colony. Recruitment to the breeding population and loss by mortality are roughly equal.

Chapter 7 shows that the calls given by male and female Manx

Shearwaters were different. The response of other shearwaters to these calls was investigated by means of playback experiments. Females recognized the calls of their male mates but I am unable to show a selective response of males to the calls of their female mates. This difference is considered to be related to the different roles of the two sexes and to be associated with the fact that most calls heard from the ground were given by males whilst most calls uttered in flight were probably given by females. There is no evidence that nestlings can recognize the calls of their parents.

The value of colonial breeding is considered in the concluding Chapter 8. It seems that Manx Shearwaters in the dense Main Colony experienced a lower rate of predation, but they did not have greater reproductive success than those breeding in areas of lower burrow density elsewhere on the island. Although nesting habitat on Skokholm is not fully utilised there may be a limited supply of breeding burrows available. This would create competition for burrows which, together with competition for food, is suggested as an important influence on the breeding biology of the Manx Shearwater.

There are four appendices. The first shows that birds first caught in the colony at two years old were caught earlier in the year when three years old than those which were caught for the first time at three. Similarly, birds which have been caught when two or three years old were caught earlier in the year when four years old than those birds which were caught for the first time at four. These differences in time of return to the colony appear not to be associated with sex. Appendix 2 discusses the relationship between the body size of offspring and their parents. In the Manx Shearwater it appears that about three-quarters of the phenotypic variance of body size is due to genetic causes, and may therefore be inherited.

Appendix 3 describes a simple experiment designed to test the possibility that vision may be one sense used by Manx Shearwaters attempting to locate their breeding burrow. The result of the experiment was positive but more extensive tests would be required to assess the relative roles of vision and any other senses that may be employed in burrow location. Appendix 4 describes an unsuccessful visit to the Basque coast of northern Spain to assess the status of the Manx Shearwater in the south-east corner of the Bay of Biscay in the pre-laying period, late April. I tentatively suggest that it is only in exceptional circumstances that many shearwaters feed south of about 46° N.

Acknowledgements

My deepest thanks go to Chris Perrins whose ever-open door and mind were a great encouragement. His supervision was simply indispensable. Euan Dunn was quite as helpful during Chris' sabbatical year in Australia.

This study was completed while I was employed as warden of Skokholm Bird Observatory by the West Wales Naturalists' Trust and the Edward Grey Institute of the Zoology Department, Oxford. I am very grateful to these bodies for allowing me to complete these studies and providing logistic support. It is obvious that a long-term study, such as the Skokholm shearwater study, is dependent on the good will and co-operation of many people who may never even meet each other. I am thus very conscious of my debt to all who have toiled through long nights catching and ringing shearwaters on Skokholm over the past thirty years. No less am I grateful to those who helped me personally with fieldwork. These kind people include visitors to the island, members of the Edward Grey Institute, Ray and Jean Lawman and Viv Wood. Further thanks are due to the Skokholm lighthouse keepers who have always maintained a kindly interest in the antics of the Bird Observatory.

Before I knew anything at all about Manx Shearwaters Mike Harris and John Davis generously allowed me to tap their knowledge. Tim Birkhead, Nick Davies, Peter Evans, John Krebs, Ed Minot and Robert Prys-Jones all read various parts of this thesis and offered many helpful suggestions, whilst other members of the Edward Grey Institute made comments whose beneficial influence was greater than either they or I were aware at the time. Philip Bacon, Michael Bulmer and Mike Webber showed massive patience in answering my statistical queries.

I am very grateful to the Frank Chapman Memorial Fund and the

British Ornithologists' Union for supporting my visit to the Bay of Biscay, where I received great hospitality from the Basque people.

Finally let me thank Maggie who so kindly typed this thesis, and my parents who cheerfully let their son pursue his biological whims.

CHAPTER ONE

Introduction

Introduction

Taxonomic Introduction

The Manx Shearwater Puffinus puffinus belongs to a large group of marine birds, the Order Procellariiformes, an order which is divided into four families, the albatrosses Diomedeidae, the shearwaters, fulmars and gadfly petrels Procellariidae, the storm petrels Hydrobatidae and the diving petrels Pelecanoididae (Alexander 1954). The two largest groups of the Procellariidae are the gadfly petrels, genus Pterodroma, and the shearwaters, mostly genus Puffinus, and representatives of these two genera are found in all of the major marine zones recognized by Ashmole (1971) except the Arctic zone. The gadfly petrels predominantly live in the tropical and sub-tropical zones and cephalopods caught at the surface of the sea apparently form a large proportion of the diet of some species (Harris 1970a; Serventy, Serventy & Warham 1971; Imber 1973). In contrast shearwaters of the genus Puffinus are more highly adapted for an aquatic life (Kuroda 1954); highly compact plumage and high specific gravity are features which allow them to dive underwater in pursuit of prey, using wings and feet for underwater propulsion. The Manx Shearwater clearly shows the features recognized by Kuroda (loc. cit.) as being associated with such an aquatic way of life.

Puffinus puffinus has been divided into eight sub-species (Murphy 1952) which show both plumage and morphometric differences. The distribution of the eight sub-species is highly fragmented, covering the North Atlantic, the Mediterranean and parts of the Pacific Ocean, and their taxonomic relationships are probably complex and certainly in dispute (Bourne 1962; Vaurie 1965). The present study is devoted to the nominate race Puffinus puffinus puffinus which breeds on islands off the British, French and Irish coasts, and on Iceland, Bermuda, the Azores, Madeira, the Salvages and the Desertas (Murphy 1952).

The British and Irish population of the Manx Shearwater is centred on three areas, islands off south-west Ireland, the Hebrides and islands off south-west Wales, and the total British and Irish population is thought to number at least a quarter of a million pairs (Cramp, Bourne & Saunders 1974). Of this total a substantial number are found on the islands of Skokholm (35,000 pairs) and Skomer (95,000 pairs) off the Pembrokeshire coast (Perrins 1967; Corkhill 1973).

The Study Area

This study was carried out on Skokholm over four breeding seasons, 1973-1976, and supplementary observations were made on Skomer and in the south-east corner of the Bay of Biscay in the spring of 1977. Skokholm is an island of about 100 hectares lying some 3 km from the Pembrokeshire mainland (Figures 1.1 & 1.2). The island, uninhabited save for a manned lighthouse and a Bird Observatory operated during the summer months March to October, is largely composed of Old Red Sandstone and surrounded by cliffs up to 50 m in height. The cliffs provide nesting sites for a few shearwaters but the great majority nest on the relatively flat summit plateau over which they are well distributed avoiding only a moist central area, the Bog, where the sandstone is covered by boulder clay. Although the shearwaters are well distributed there are some areas of particular concentration, notably the Main Colony where, in about 7-8 ha. surrounding the lighthouse, there are 8-10,000 nesting pairs (Perrins 1967; Brooke 1973).

Although Skokholm is situated close to the entrance to the large oil-tanker terminal of Milford Haven there is no indication that the Manx Shearwater population is being adversely affected by oil pollution, and the species provides only a very small proportion of the corpses which are picked up during surveys of beached birds (Bourne & Bibby 1975).

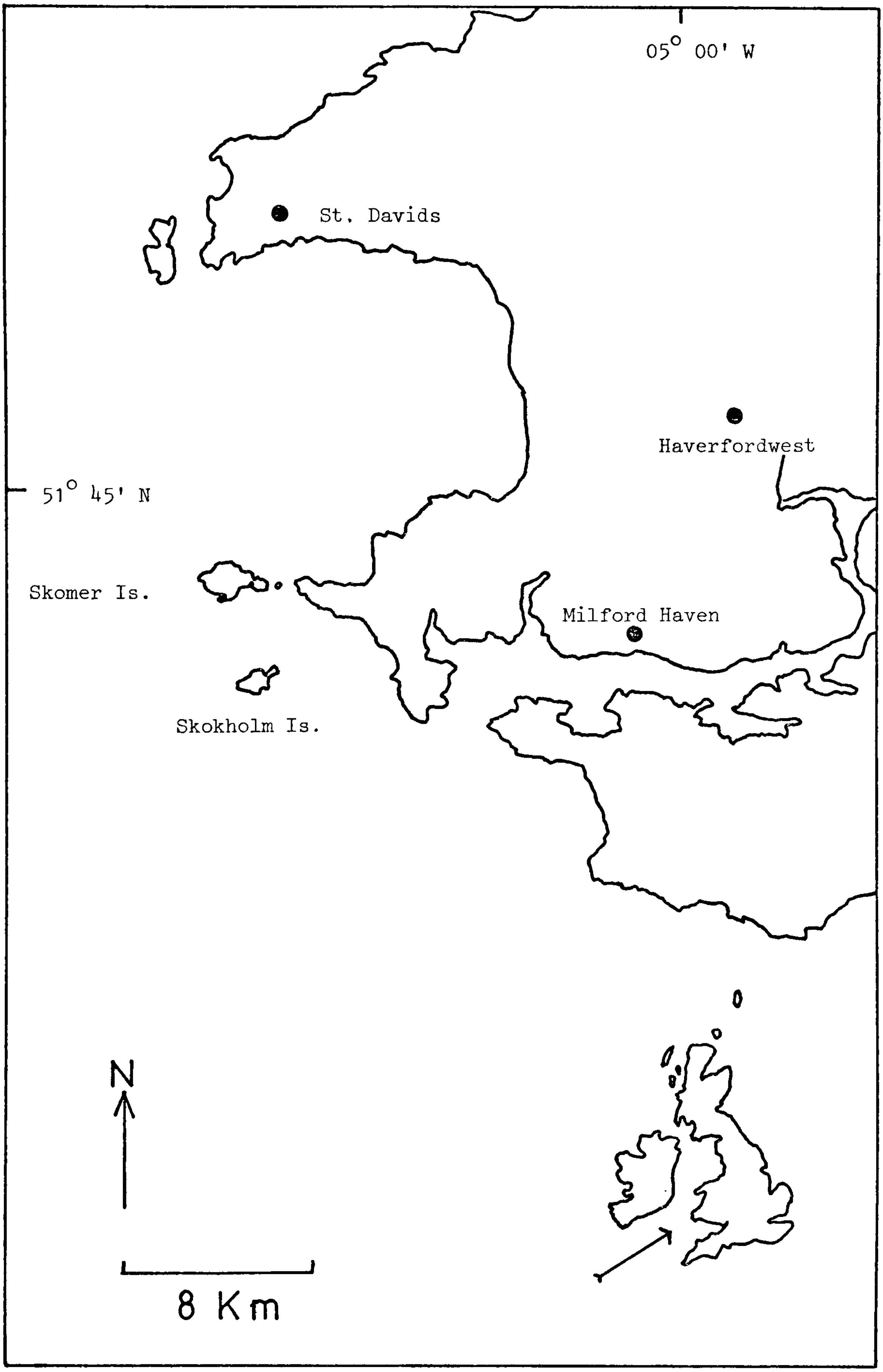
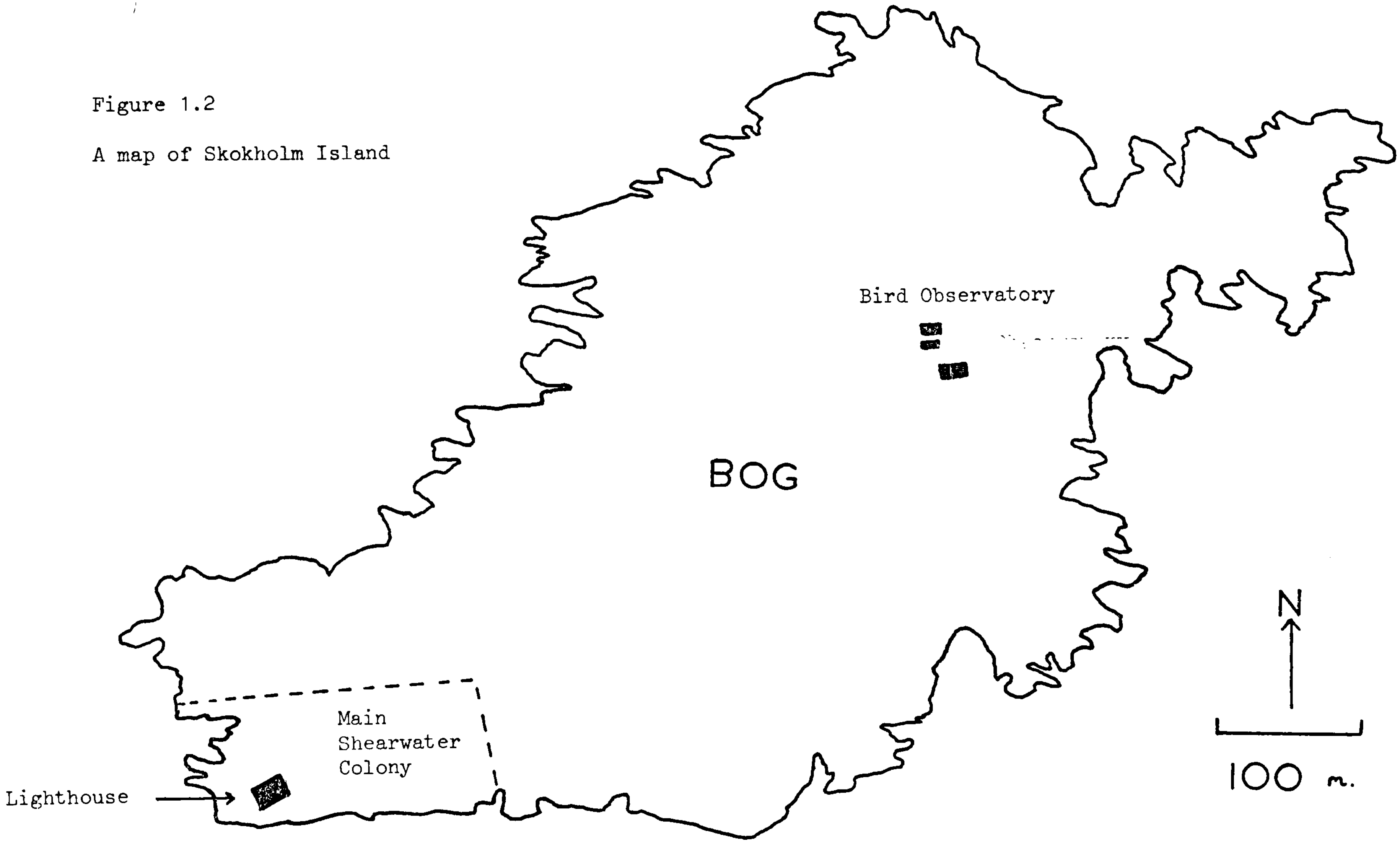


Figure 1.1 Map of south-west Wales, showing location of Skokholm Island

Figure 1.2

A map of Skokholm Island



History of Research on Skokholm

Little was known of the breeding biology of the Manx Shearwater before R. M. Lockley arrived on the island, as a tenant farmer, in 1927. His early publications (1930, 1931) provided basic information on incubation and fledging periods. Work was interrupted during World War II but resumed soon after, when the Bird Observatory re-opened in 1946, and concentrated on improving understanding of the extensive movements undertaken by shearwaters during the breeding season (Lockley 1953). Further detailed work on the breeding biology was stimulated by the liaison, in 1963, of the Bird Observatory and the Edward Grey Institute, Oxford, and this work has been reported by Harris (1966a & b) and by Perrins, Harris and Britton (1973).

A brief account of the breeding biology of the Manx Shearwater based on the research of Harris and Perrins, Harris and Britton will now be given. In its basic feature, a single egg followed by long incubation and fledging periods, the breeding biology of the Manx Shearwater is little different from that of other Procellariiformes (Lack 1968). The timing of breeding varies little from year to year, the peak of laying usually occurring around 10 May. The single egg, about 15% of the female's weight, is incubated by both sexes for about 50 days. The young is usually continuously guarded by one parent for the first week and thereafter is visited and fed only at night. A peak weight, about one and a half times the adult weight, is reached when the nestling is around 50 days old. The nestling is fed for another 10-15 days and is then deserted by the adults. After fasting for about eight days, during which time feather growth is completed, the young fledge when about 70 days old; the first young leave Skokholm in mid-August and the last in mid- or late October. They migrate south, very rapidly in some cases, to wintering grounds off the east coast of South America. Birds in the first year do not visit the breeding colony but at the age of two they return briefly in mid-summer. As they grow older they spend progressively longer periods at the colony during the breeding season until, by the age of five or six when breeding starts, they are presen at the colony throughout the breeding season.

Scope of the present study

The present study attempts to build on the foundation of knowledge provided by the earlier workers. Over the last 15 years some 86,000 fledgling shearwaters have been ringed on Skokholm, so that when these have returned to the island in later years of life, their age has been exactly known. Thus particular emphasis has been given to an examination of the effects of age and parental breeding experience on reproductive success and it has also been possible to analyse the weights of adults of different ages. Additional unexpected findings concerning the age of first breeding and the possible extent of female dispersal have also emerged from this study.

The completion of the study has depended entirely on the ease with which it is possible to catch shearwaters and to handle them with little fear that the reproductive cycle will be disturbed. Nevertheless the status of full-grown birds caught at the colony cannot be exactly known unless they are definitely breeding in study burrows or are ringed immature birds too young to be breeding. This is a drawback as is the inability to sex birds other than those which are (or have been) definitely members of a breeding pair in a study burrow (Serventy 1956).

While it is easy to catch Manx Shearwaters it is correspondingly difficult to make direct observations on their behaviour without the aid of special devices, since most activity takes place either at night, underground, or at sea. The only direct behavioural study I have attempted concerns the analysis of calls described in Chapter 7.

Methods

The methods used in this study are described in the appropriate chapter.

Unless otherwise mentioned statistical tests are those of Bailey (1959) for parametric data and Siegel (1956) for non-parametric data.

CHAPTER TWO

Weights and Measurements of the Manx Shearwater

Weights and Measurements of the Manx Shearwater

Introduction

Since 1960 large numbers of Manx Shearwater fledglings have been ringed each year on Skokholm Island. When these birds have returned to Skokholm in later years they have been of known age. In this chapter, I examine the weights and measurements of such shearwaters and consider the results in the light of current hypotheses concerning the age at which seabirds start to breed (e.g. Lack 1966). I also draw on data from birds of known sex breeding in study burrows.

Methods

There are no known means of accurately sexing Manx Shearwaters except immediately after laying when the cloaca of a breeding female is swollen and bluish (Serventy 1956). Her mate may then be assumed to be male. In March and April of 1974 and 1975 I measured 47 male and 47 female Manx Shearwaters breeding in study burrows. The wing was straightened and flattened to provide a maximum measurement to the nearest mm (Svensson 1970). The bill measurement taken was the length of the chord, measured along the dorsal mid-line, from the edge of the feathers at the base of the culmen to the most distant part of the curve of the hook. The tarsus length was the distance from the middle of the mid-tarsal joint to the distal end of the tarso-metatarsus (Dunnet & Anderson 1961). Bill and tarsus measurements were made with Vernier calipers to 0.5 mm. I took all measurements myself in order to reduce observer variation.

Most of the information in this chapter was obtained by catching birds at night when large numbers may be picked up from the ground by hand. Those that were ringed and of known age were measured and/or weighed. Birds caught in this way cannot be sexed nor is their breeding status known although it may be assumed that birds aged less than five are not breeding. A few five-year-olds may have been breeding but during the period of this study, 1973-1976, most shearwaters were not breeding until six and some may not have started breeding until eight or nine years old (Brooke 1973). During 1973 and 1974 birds caught at night were only weighed, whilst during 1975 and 1976 I measured wing and bill lengths respectively.

More than 80% of the birds captured at night were taken in the Main Colony (Perrins, Harris & Britton 1973) but, as the weights and measurements of birds in this colony did not differ from those measured elsewhere on the island, the results from all areas are lumped.

In 1975 and 1976 I collected the ringed tarsi of full-grown shearwaters which had been killed by gulls Larus spp. and also, in the autumn of 1976, the tarsi of predated fledglings. The tarsi were dried at room temperature for a minimum of one month. All flesh was then cleaned from the tarsi which were weighed and measured. The measurements taken were the maximum length and the thickness. The thickness was measured half-way along the length of the tarsus by taking two measurements at right angles to each other such that the smaller measurement was the minimum obtainable at that half-way point. Multiplication of these two measurements gives a crude index of the cross-sectional area of the tarsus, which will be termed the tarsus area index. For example, a tarsus where the two measurements were 3.3 mm and 2.0 mm would have a tarsus area index of 6.60.

Results

Sexual dimorphism in size

There is no significant difference in the wing length of breeding males and females but both the bills and tarsi of males are significantly longer than those of females (Table 2.1). Following Snedecor and Cochran (1967) it is possible to calculate a discriminant function for distinguishing male and

Table 2.1

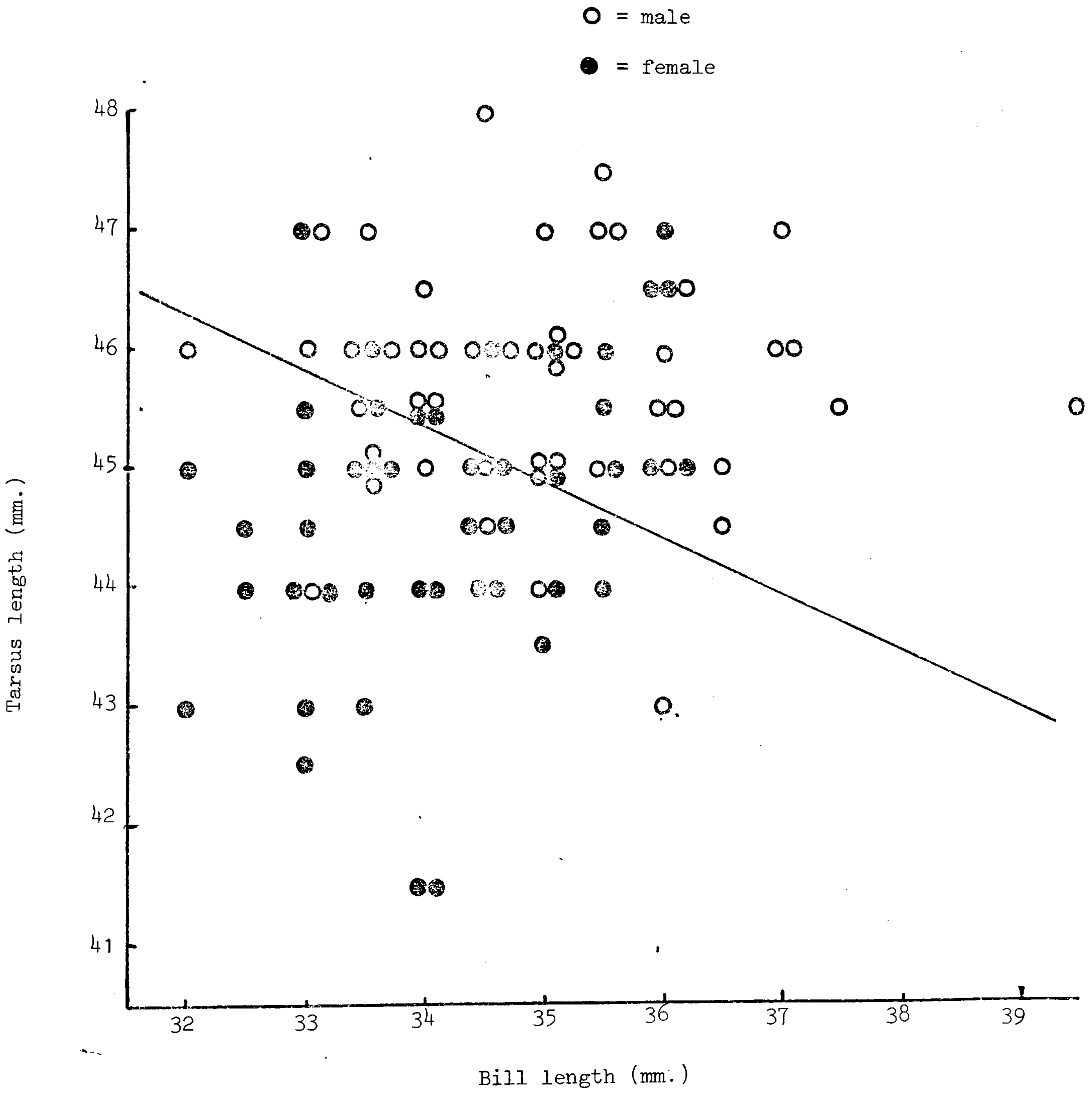
The mean wing, bill and tarsus lengths (± S.E.) of male and female Manx Shearwaters breeding on Skokholm. The sample size in all cases is 47 except for female tarsi where N = 46. All measurements in mm.

	Male	Female	p (t-test)
Wing length	240.1 ± 0.74	240.6 ± 0.64	N.S.
Bill length	34.95 ± 0.206	34.13 ± 0.165	$<$ 0.01
Tarsus length	45.73 ± 0.141	44.65 ± 0.182	$<$ 0.001

Figure 2.1

The tarsus and bill measurements of 47 male and 46 female Manx Shearwaters breeding on Skokholm. The line is the calculated discriminant function;

$$50.69 = 6.88\,(\text{Tarsus length} - 40) + 3.29\,(\text{Bill length} - 30)$$



female Manx Shearwaters using bill and tarsus measurements. Using this function alone 19.7% of shearwaters would theoretically be misclassified. In practice, of the 93 shearwaters where both bill and tarsus measurements were taken, 24 (15 females and nine males) or 25.8% are misclassified by the discriminant function (Figure 2.1). Where sexual dimorphism has been demonstrated in other Procellariiformes the male has usually been the larger sex, but he may be the smaller in some Hydrobatidae (Bourne 1964). It is not known if the differences in bill and tarsus length of male and female Manx Shearwaters are in any way related to differences in feeding niche (Selander 1966).

Weights

The mean monthly weights of different age classes of known-age Manx Shearwaters caught at night in 1973 and 1974 are shown in Figures 2.2-2.5. The data are tabulated in Table 2.2. Figures 2.2 and 2.4 show data from birds aged less than six years old while Figures 2.3 and 2.5 refer to birds that are six years old or older and which are therefore of breeding age, although not necessarily actually breeding.

The seasonal pattern of weight change during the two years is similar. Weights are highest during March and April, in the pre-laying period, and then decline steadily to reach a minimum in June and July when the greatest numbers of immature birds are visiting the colony and when breeding birds are feeding small chicks. During August there is a slight increase in weight. The same seasonal pattern is shown by birds of all age classes.

If Figures 2.2 and 2.3 and Figures 2.4 and 2.5 are compared it will be seen that the weights of birds younger than six overlap little with those that are six years old or older. Indeed it is generally true that the mean weights increase progressively with age. The two-year-olds, the youngest age class to visit the colony, are particularly clearly separated from all

Figure 2.2

Mean monthly weights of different age classes of known age Manx Shearwater on Skokholm in 1973. See Table 2.2 for sample sizes and standard deviations; samples of less than ten are shown in brackets. The horizontal line at a weight of 410 gm. is drawn to facilitate comparison with Figure 2.3

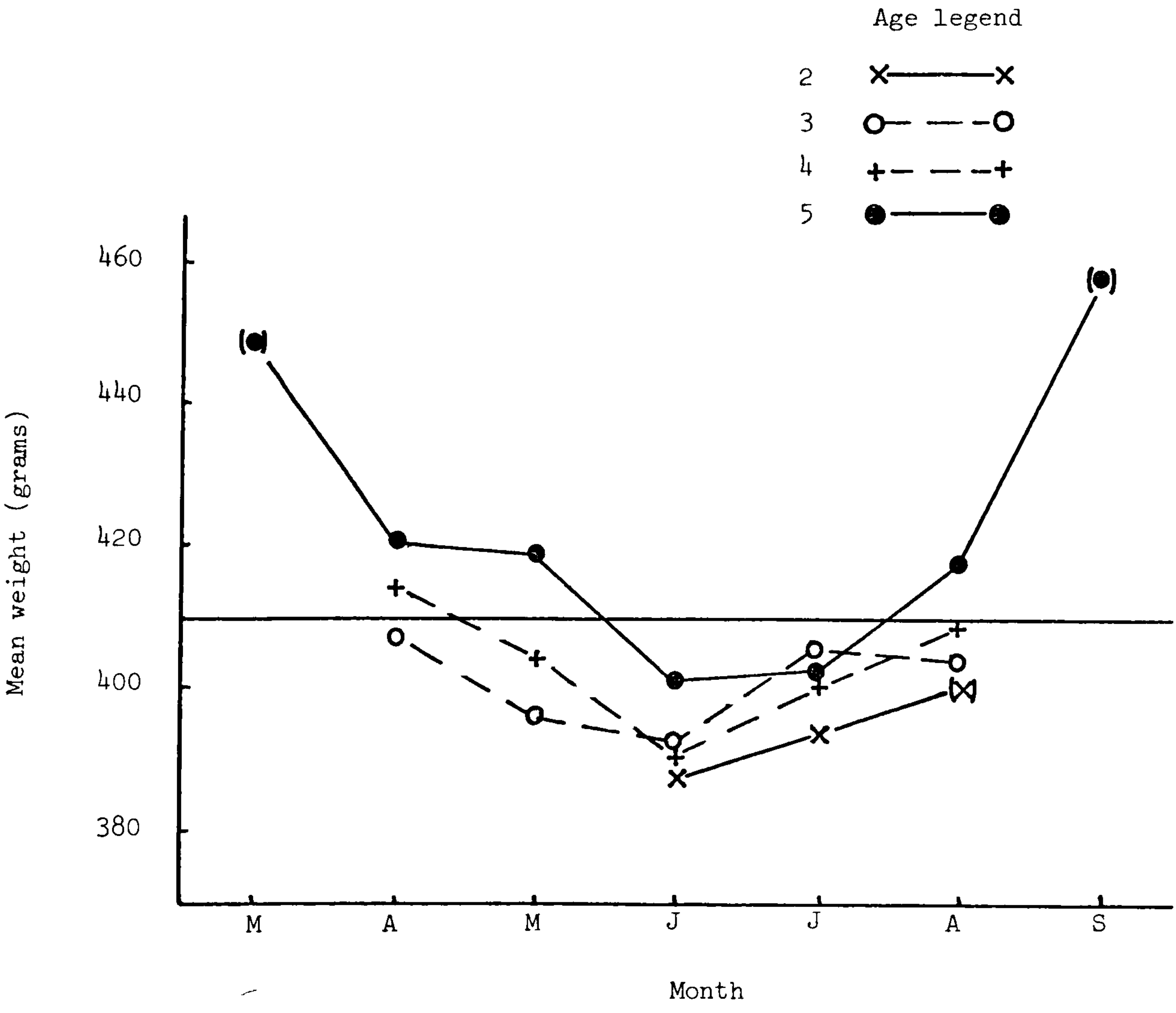


Figure 2.3

Mean monthly weights of different age classes of known age Manx Shearwaters on Skokholm in 1973. See Table 2.2 for sample sizes and standard deviations; samples of less than ten are shown in brackets. The horizontal line at a weight of 410 gm. is drawn to facilitate comparison with Figure 2.2.

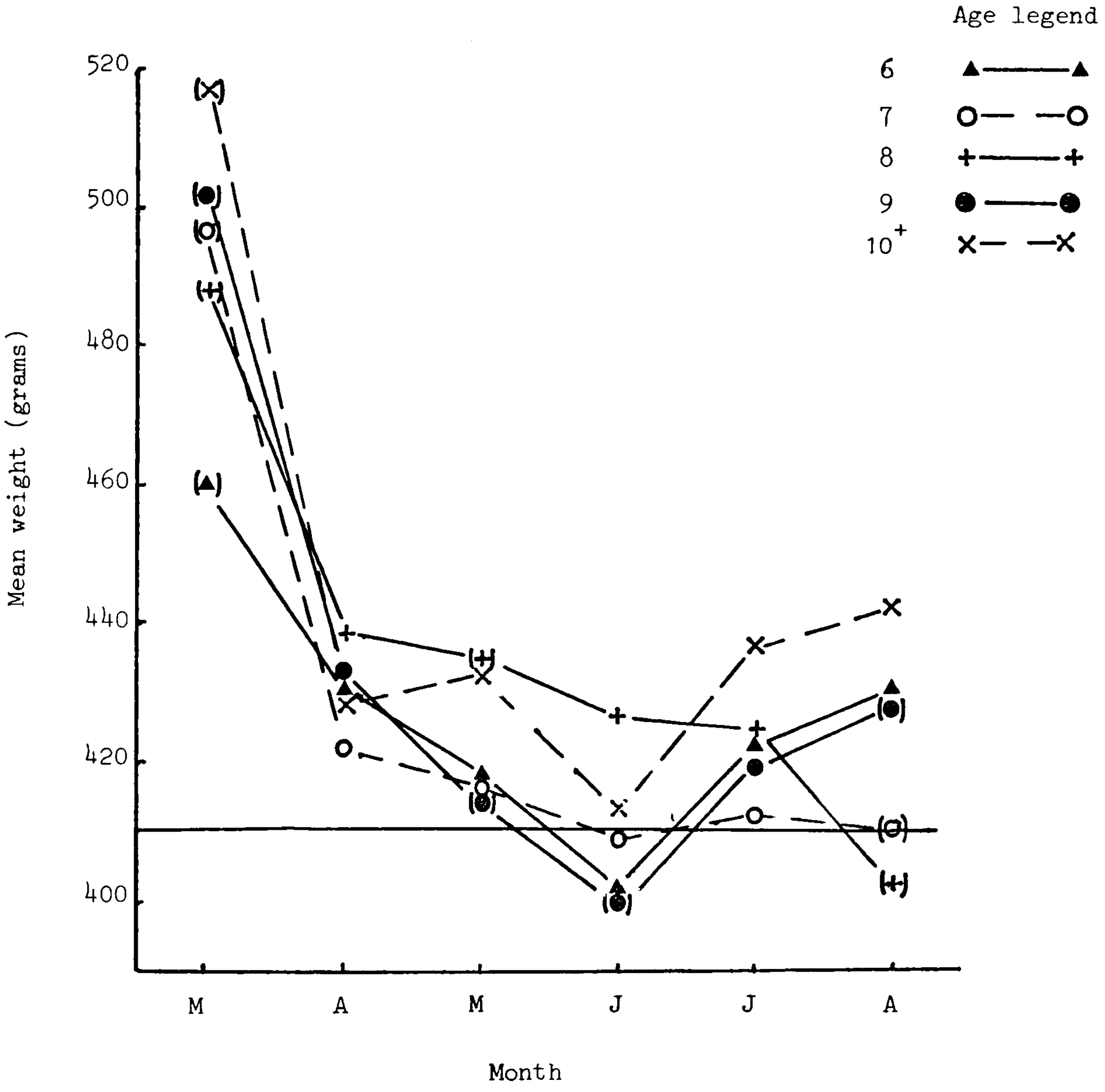


Figure 2.4

Mean monthly weights of different age classes of known age Manx Shearwater on Skokholm in 1974. See Table 2.2 for sample sizes and standard deviations; samples of less than ten are shown in brackets. The horizontal line at a weight of 410 gm. is drawn to facilitate comparison with Figure 2.5.

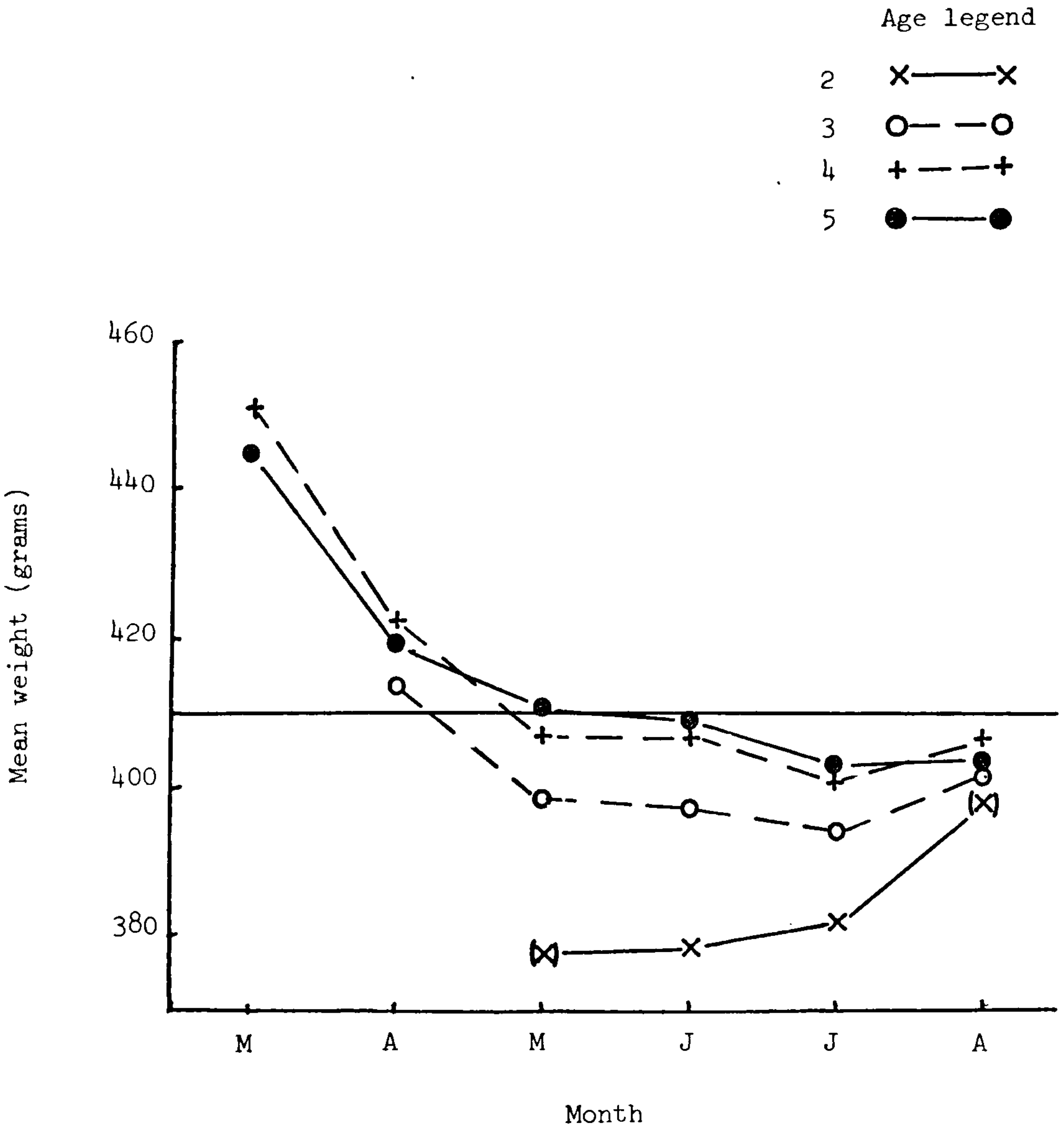


Figure 2.5

Mean monthly weights of different age classes of Manx Shearwater on Skokholm in 1974. See Table 2.2 for sample sizes and standard deviations. The horizontal line at a weight of 410 gm. is drawn to facilitate comparison with Figure 2.4.

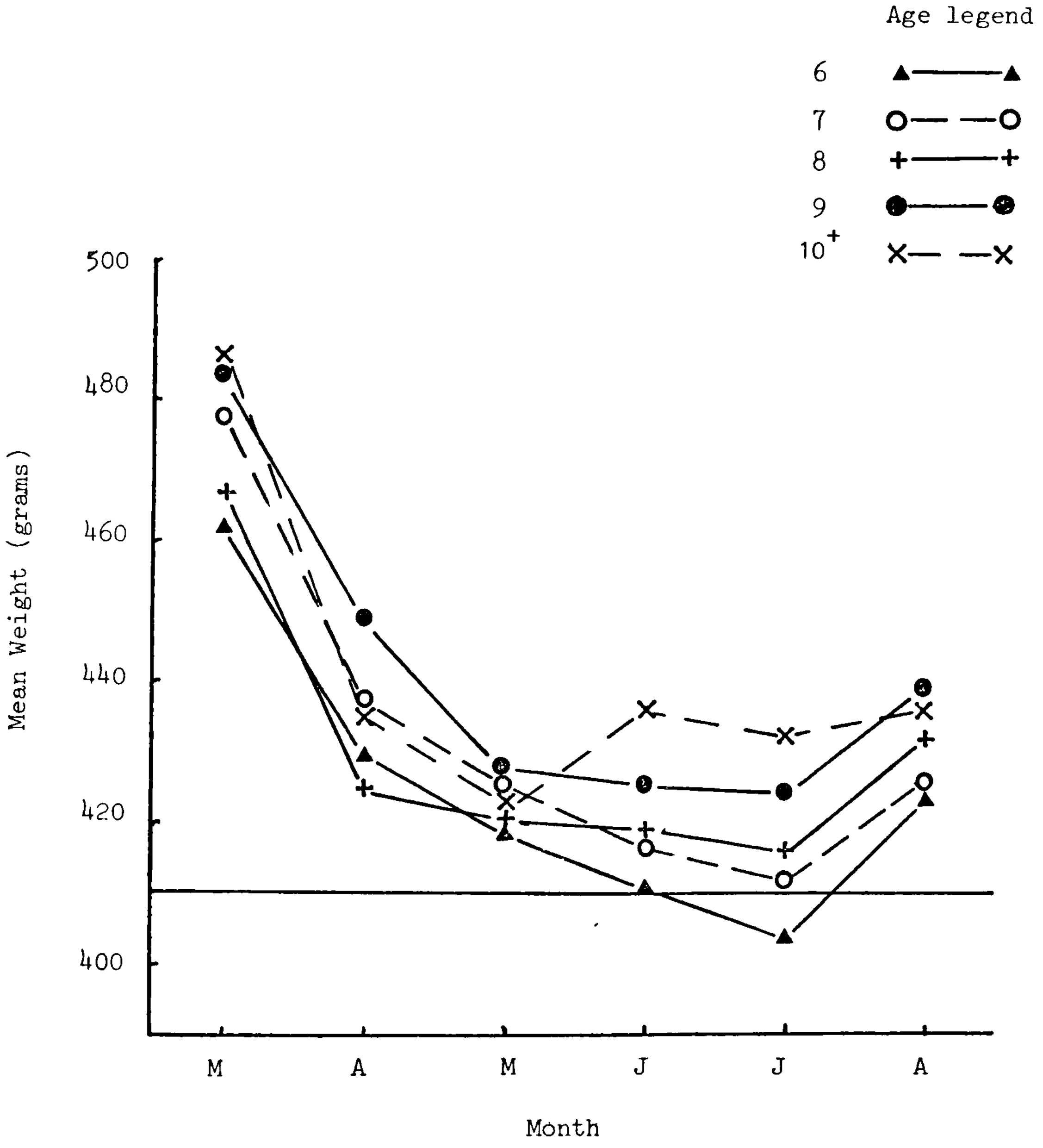


Table 2.2 The mean monthly weight in grams (± S.D.) of different age classes of known age Manx Shearwater on Skokholm in 1973 and 1974. Sample sizes are given in brackets below means.

<u>1973</u>

Age	March	April	May	June	July	August	Sept
2	-	-	-	387.7 ± 20.4 (33)	393.8 ± 24.0 (53)	400.0 ± 19.7 (5)	-
3	-	407.7 ± 20.3 (11)	396.2 ± 18.7 (29)	392.6 ± 22.5 (118)	405.2 ± 25.9 (153)	403.6 ± 25.7 (33)	-
4	-	414.0 ± 27.7 (36)	404.3 ± 27.8 (53)	391.0 ± 19.1 (120)	400.6 ± 24.4 (158)	408.5 ± 29.3 (43)	-
5	448.9 ± 25.5 (9)	421.0 ± 35.0 (55)	419.5 ± 27.3 (58)	401.7 ± 27.1 (99)	402.2 ± 27.1 (113)	417.4 ± 33.5 (35)	458.3 ± 40.4 (3)
6	460.0 ± 20.0 (3)	430.7 ± 43.2 (41)	418.4 ± 33.1 (32)	401.6 ± 28.4 (55)	422.6 ± 32.2 (64)	430.3 ± 19.4 (19)	520 (1)
7	497.2 ± 36.8 (9)	422.3 ± 42.2 (15)	416.4 ± 27.2 (18)	409.2 ± 23.0 (19)	412.8 ± 24.3 (27)	410.7 ± 21.2 (7)	520 (1)
8	488.8 ± 42.2 (8)	439.1 ± 38.0 (17)	435.6 ± 36.2 (9)	427.7 ± 32.5 (15)	422.8 ± 34.4 (32)	402.5 ± 59.2 (4)	-
9	502.0 ± 30.5 (3)	432.4 ± 32.0 (21)	415.0 ± 29.7 (4)	400.6 ± 38.7 (8)	419.4 ± 28.3 (24)	428.7 ± 43.5 (8)	-
10^+	517.9 ± 40.7 (9)	428.1 ± 30.9 (29)	434.0 ± 27.3 (27)	413.6 ± 32.2 (18)	437.2 ± 49.7 (34)	442.7 ± 29.3 (15)	-

Table 2.2 (cont.)

1974

Age	March	April	May	June	July	August
2	-	-	377.5 (2)	378.5 ± 21.0 (83)	381.4 ± 20.7 (113)	397.5 ± 24.4 (6)
3	450 (1)	413.9 ± 29.2 (13)	397.8 ± 18.9 (45)	396.6 ± 23.9 (200)	393.8 ± 19.4 (159)	401.5 ± 20.4 (53)
4	450.3 ± 33.8 (16)	422.5 ± 27.6 (78)	407.0 ± 24.4 (87)	407.6 ± 28.3 (269)	401.3 ± 24.9 (159)	405.8 ± 28.2 (85)
5	444.7 ± 25.7 (55)	419.4 ± 28.0 (89)	410.7 ± 30.4 (60)	408.0 ± 26.7 (178)	402.1 ± 28.0 (88)	401.8 ± 33.4 (54)
6	461.6 ± 36.1 (58)	429.0 ± 31.9 (73)	417.7 ± 26.9 (50)	410.9 ± 31.2 (140)	403.7 ± 33.6 (74)	423.7 ± 34.6 (46)
7	477.9 ± 33.4 (61)	437.6 ± 34.1 (47)	425.4 ± 37.5 (39)	416.0 ± 30.8 (96)	411.7 ± 25.6 (56)	424.2 ± 35.8 (41)
8	467.4 ± 29.7 (33)	424.6 ± 26.2 (26)	420.0 ± 31.5 (20)	419.3 ± 37.5 (44)	416.0 ± 29.1 (20)	432.1 ± 34.5 (14)
9	483.5 ± 35.2 (27)	448.9 ± 35.3 (28)	427.5 ± 31.6 (14)	425.2 ± 27.0 (29)	424.3 ± 27.3 (22)	439.1 ± 38.4 (23)
10^+	486.4 ± 40.6 (74)	436.2 ± 30.8 (46)	421.0 ± 31.7 (40)	436.1 ± 37.5 (66)	432.5 ± 35.5 (36)	436.1 ± 40.1 (49)

other age classes (Figures 2.2 and 2.4).

The increase in weight with age is illustrated further in Figure 2.6 where I plot the weighted means of the weights of different age classes of known age Manx Shearwaters in 1973 and 1974.

For each age class,

$$\text{Weighted mean} = \sum w_i \; \bar{y}_i$$

$$\text{and the variance of this mean} = \sum w_i^2 \,.\; \text{Variance } (\bar{y}_i)$$

where $\bar{y}_i$ is the mean weight of that age class in the ith month (April to August) and w_i is the weighting for the ith month.

$$\sum w_i = \sum N_i/_N = 1$$

where N_i is the total number of birds aged between 3 and 10^+ weighed in the ith month and N is the total number of birds in these age classes weighed in the months April to August inclusive. Two-year-olds are not included in this analysis since no two-year-olds were weighed in April (and very few in May) in either year. However, two-year-olds were significantly lighter than three-year-olds in July 1973 (t-test, $p < 0.01$) and June and July 1974 ($p < 0.001$). The weight of samples of older birds increases steadily until the birds are seven or eight years old (Figure 2.6). Thereafter, as the standard errors increase, the pattern becomes less clear.

Beyond the age of 10 sample sizes for individual year classes become very small. However, for the 1974 data, I compared the mean monthly weight of shearwaters aged 10-14 with those of known age that were at least 15 years old. In March, June and July the birds aged 10-14 were lighter whilst in April, May and August they were, on average, heavier than the birds aged at least 15; but none of these differences was significant. There may be no continuation of the increase in weight with age beyond about eight to ten years.

Figure 2.6

The weighted mean (± S.E.) of the weights of different age classes of Manx Shearwater weighed on Skokholm in the months, April to August, in 1973 and 1974. See text for further details.

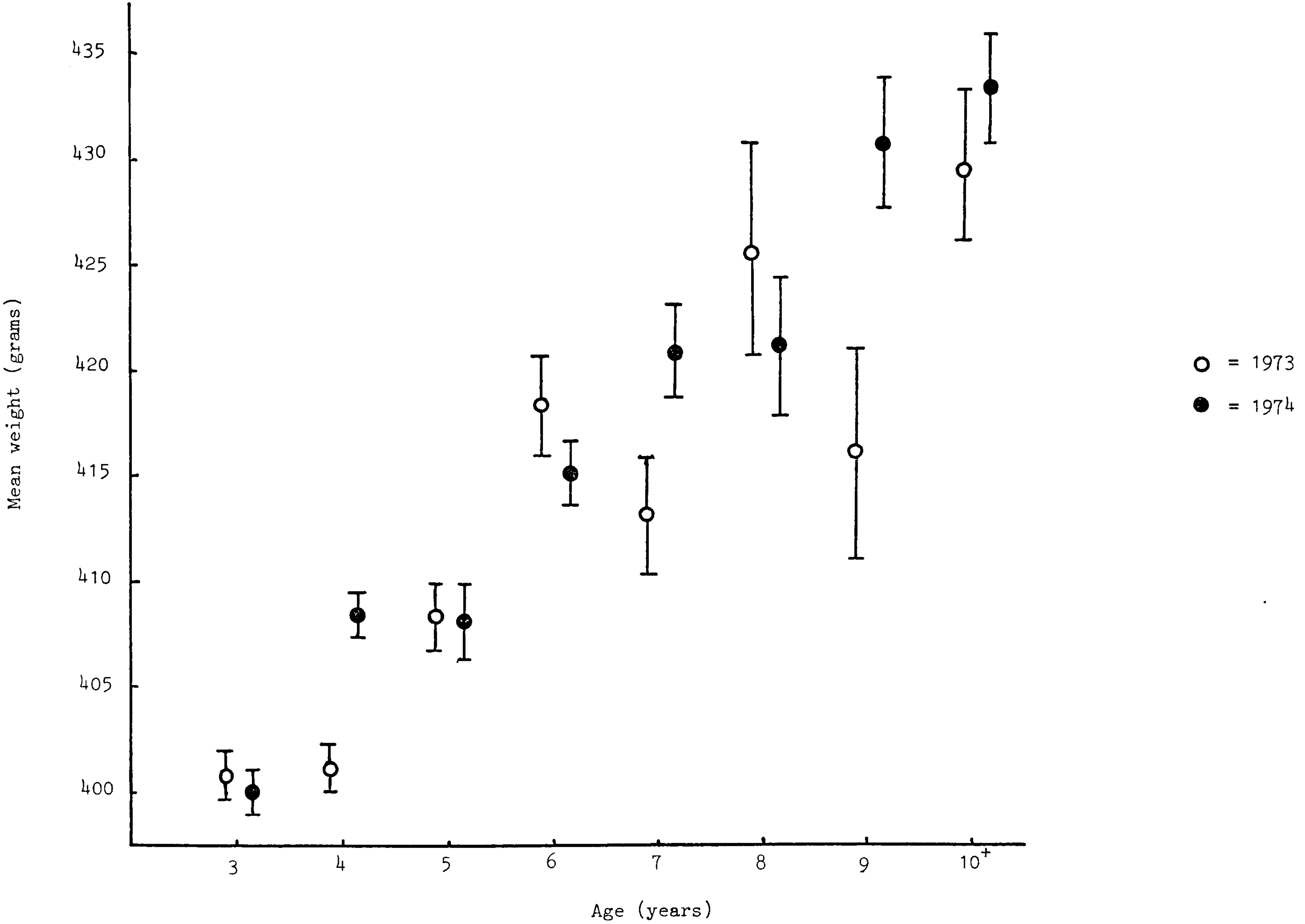

Mean weight (grams)
435
430
425
420
415
410
405
400
3
4
5
6
7
8
9
10+
Age (years)
○ = 1973
● = 1974

Figure 2.6 also allows a comparison between years. The only significant differences concern four-year-olds ($d = 4.56$, $p < 0.001$) and nine-year-olds ($d = 2.52$, $p < 0.05$), both of which were heavier in 1974. However, other age classes in the Figure show no particular tendency to be heavier in one year or the other and it is not obvious why four- and nine-year-olds should be distinct in this respect. The situation is made more puzzling by the two-year-olds, not shown in Figure 2.6, which were heavier in June (t-test, $p < 0.05$) and July 1973 ($p < 0.001$) than in the corresponding months of 1974.

During the period mid-June to the end of July immature Manx Shearwaters are visiting the colony in the greatest numbers (Perrins _et al_. 1973). If the lower weight of younger birds is because they experience greater difficulties in maintaining weight then they might have to spend more time away from the colony at the feeding grounds. This could be reflected in a lower frequency of capture at the colony. In Table 2.3 I compare the number of occasions on which individuals aged two, three and four were caught in the Main Colony in 1973 and 1974 in the period 15 June - 31 July. The analysis is restricted to birds both ringed as chicks and recaptured in the Main Colony (Perrins _et al_. 1973) since most ringing and recapture work was performed there. It is not possible to extend the analysis to five-year-olds since there is evidence (Perrins _et al_. 1973) that these birds become less available for capture, possibly because they are starting to spend more time underground. In both years two-year-olds were caught significantly less often than three- and four-year-olds, but there was no significant difference in the capture frequency of three- and four-year-olds.

If the lower weight of younger birds is related to the lower frequency of capture at the colony (Table 2.3) it might be predicted that, within an age class, the lighter birds would be caught less often than the heavier. Data I have analysed do not support this prediction. Possibly young

Table 2.3

The mean number of occasions individual Manx Shearwaters aged two, three and four were caught in the Main Colony in the period 15 June - 31 July during 1973 and 1974. Sample sizes in brackets.

			Age		
	2		3		4
1973	1.43 (149)	$p < 0.001$	2.05 (343)	N.S.	1.78 (300)
1974	1.33 (227)	$p < 0.05$	1.80 (245)	N.S.	2.05 (245)

Notes (i) Significance levels from X^2 tests.

(ii) In both 1973 and 1974 the number of captures of two-year-olds is less than the mean number of captures of four-year-olds (X^2 test, $p < 0.05$).

shearwaters do not visit the colony until they have reached a certain threshold weight, the level of this threshold increasing with age as feeding efficiency increases (see Discussion).

Wing length

During the period May-August 1975 the wing lengths of 863 different Manx Shearwaters of known age were measured (Figure 2.7). The mean wing length (± S.E.) of these birds was 241.8 ± 0.150 mm. In contrast to the weights discussed above there is no indication that wing length alters greatly with age, although two-year-old birds have a mean wing length (240.8 ± 0.397; N = 117) which is significantly shorter than the mean length (242.0 ± 0.160; N = 746) of all other age groups combined (t-test, $p < 0.01$). An increase in wing length between juveniles and second-year or adult plumage has been described by several authors (Metropolsky 1962, Stewart 1963, Pienkowski & Minton 1973). Pienkowski and Minton also showed that the wing length of the Knot <u>Calidris canutus</u> continues to increase after the second year but they were unable to clarify the exact relationship between wing length and age.

Bill length

During 1976 the bill lengths of 795 different Manx Shearwaters of known age were measured (Figure 2.8). There was no change in bill length with age. The mean bill length of every age class was greater than 34.54 (S.E. ± 0.138) mm which was the mean bill length of the sample of 94 breeding birds, containing equal numbers of males and females. The mean bill length of all 795 shearwaters of known age measured at night was 34.80 ± 0.045 mm which is greater than the value for breeding birds, but not quite significantly so (t-test, $0.05 < p < 0.1$). Nevertheless it seems possible that the samples of known age shearwaters captured by hand at night may contain an excess of

Figure 2.7

Mean wing length (± S.E.) of different age classes of Manx Shearwater on Skokholm in May - August 1975.

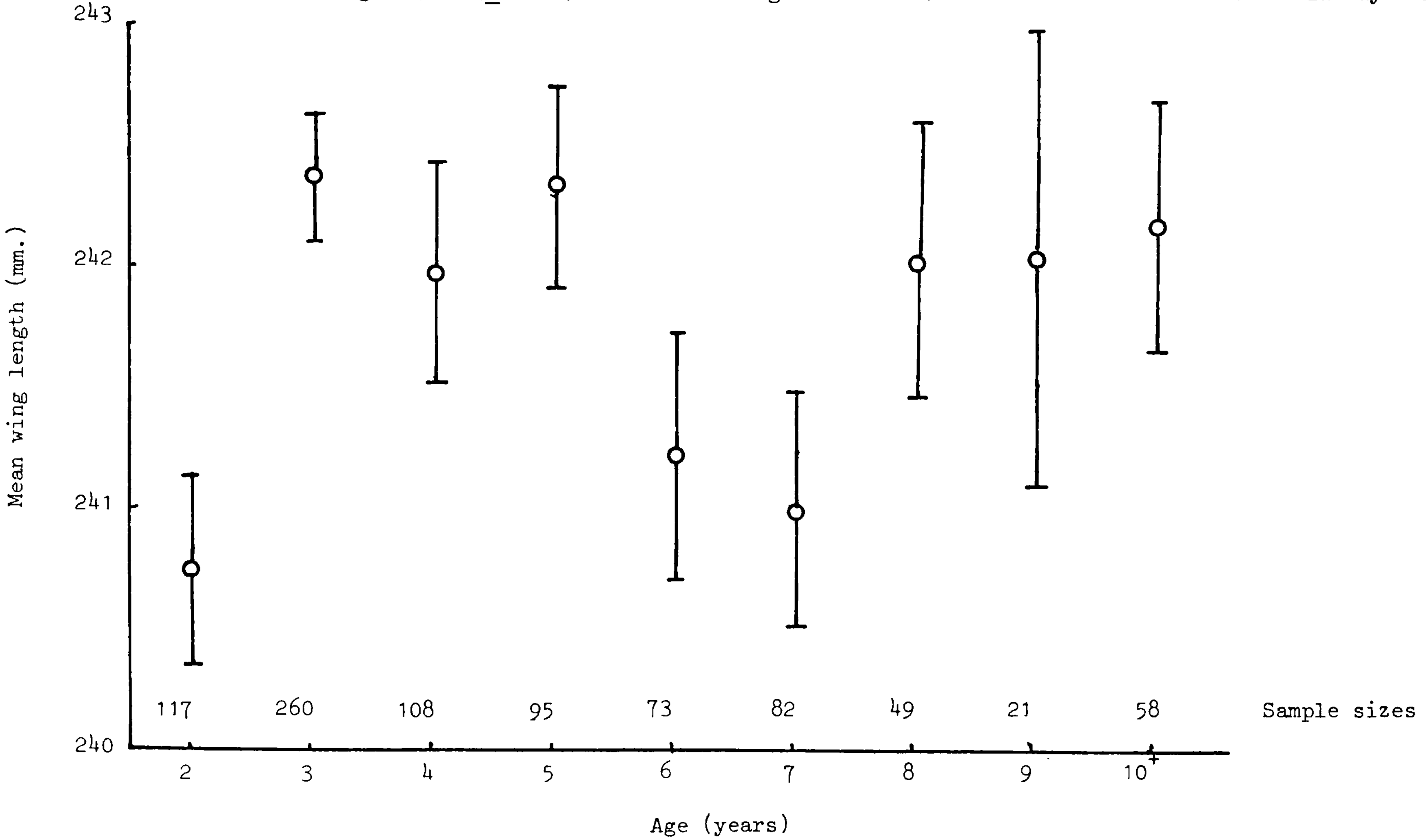
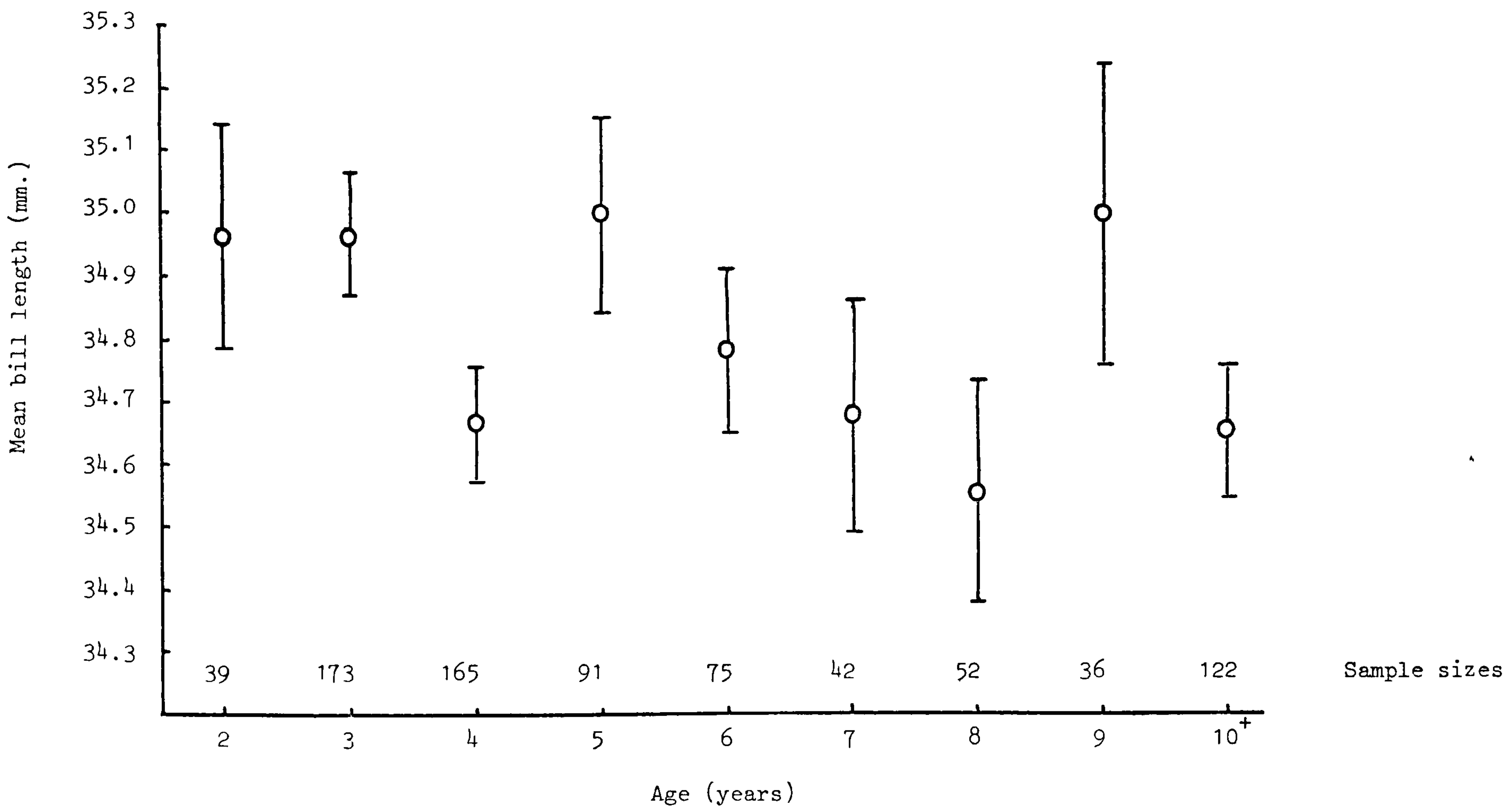


Figure 2.8

Mean bill length (± S.E.) of different age classes of Manx Shearwater on Skokholm in 1976.



males, either because males are, for some reason, easier to catch and/or because a higher proportion of male than female ringed shearwater fledglings return to Skokholm to be caught as birds of known age (see Chapter 6).

Tarsus measurements

In Table 2.4 I compare the tarsus measurements (length, weight and area index) of predated 1976 fledglings and predated ringed full-grown birds found dead during 1975 and 1976. All birds in the latter group were at least three years old. The tarsi of the full-grown birds were no longer but they were significantly heavier and broader in cross-sectional area than those of the fledglings.

Of the 49 ringed tarsi found and weighed, 34 came from shearwaters that had been ringed as fledglings. These birds were between three and 16 years old when they died and there was a significant correlation between age at death (in years) and tarsus weight ($r = 0.340$, $p = 0.05$), but not between age and tarsus area index. If one includes also birds which were ringed not as fledglings but when full-grown (and whose minimum age could therefore be established), then the mean tarsus weight (± S.E.) of 22 shearwaters killed when less than ten years old was 554.3 ± 11.13 mg and of 25 shearwaters killed when older than ten was 564.0 ± 9.52 mg; this difference is not significant.

Discussion

Changes in weight with age

As mentioned in the Methods section the actual breeding status of the Manx Shearwaters caught and weighed at night was usually not known, although birds less than six years old were almost certainly not breeding. It seems possible that the proportion of birds aged between six and ten that was breeding increased with age, since Brooke (1973) has shown that, in the Main Colony where most weights were taken, many birds start to breed at six years old but

Table 2.4

Mean tarsus measurements (± S.E.) of fledgling and full-grown Manx Shearwaters. Sample sizes are given in brackets below each measurement. See text for further details.

	Fledglings	Full-grown birds	p (t-test)
Length (mm.)	45.53 ± 0.136 (69)	45.85 ± 0.170 (50)	N.S.
Weight (mg.)	484.0 ± 5.33 (68)	558.3 ± 7.02 (49)	<0.001
Area index	6.784 ± 0.73 (69)	7.711 ± 0.09 (49)	<0.001

some probably do not start until eight or nine years old. If this is so, the proportion of non-breeders among the six-year-olds weighed (Figures 2.3 and 2.5) would be higher than the proportion among, say, the nine-year-olds. This effect would be accentuated if non-breeding birds, of whatever age, were more easily caught than breeding birds. If non-breeding birds were, at a given season, lighter than breeding birds of the same age, then the weight increase between the ages of six and ten (Figure 2.6) could be the result of the samples of older birds containing a higher proportion of breeders. This suggestion depends on the premise that non-breeding shearwaters are, at a given season, lighter than breeding birds of the same age. Only three weights of known-age shearwaters known definitely to be breeding were obtaine at night so this premise cannot be tested directly.

An indirect method of testing this point is by comparing the weights of birds, weighed by day in study burrows, that were either actively breeding in the current year or were known to have bred formerly but were not known to be breeding in the current year. The two groups of birds are presumed to be matched for age. The problem with such a comparison, in the present context, is that it is difficult to relate the weights of birds caught at night to the weights of birds taken from burrows; for example, shearwaters might be more easily caught at night when they are arriving to spend some days down their burrow than when they are leaving. In the following chapter I show there is no clear difference in the weight of breeders and former breeders in the pre-laying period of March and April. In 1975 data were also available for the first half of the incubation period, defined as 25 April - 30 May. It can be seen (Table 2.5) that, at this time, breeders are significantly heavier (t-test, $p < 0.001$ for males and females) when they arrive in a burrow than are former breeders. Knowing the number of days spent down the burrow by the incubating breeders and by the former breeders, and assuming a weight loss of 10 gm/day (Harris 1966a), the weights of the

Table 2.5

The mean weight (± S.E.) of Manx Shearwaters on the day they were first found in a study burrow in the period 25 April - 30 May 1975. Breeders were incubating at this time and consequently spent longer in the burrow than former breeders. The predicted mean weight on leaving the burrow assumes that weight is lost at the rate of 10 gm./ day when the bird is down a burrow (Harris 1966a). Sample sizes in brackets.

	Incubating breeders		Former breeders	
	Male	Female	Male	Female
Mean weight (gm.) at start of spell in burrow	486.7 ± 5.65 (32)	468.9 ± 5.87 (23)	431.6 ± 8.28 (16)	411.1 ± 4.56 (32)
Mean no. of days spent in burrow	7.84	6.17	1.50	1.63
Predicted mean weight on leaving burrow	408.3	407.2	416.6	394.8

two groups of birds when leaving the burrow may be predicted. The predicted weights do not differ significantly. It seems likely that the mean weight of a sample of breeders caught at night during incubation will exceed that of a sample of former breeders, and the extent of the difference will depend on the relative ease of capture of birds arriving at rather than leaving the burrow. Fisher (1967) has also shown that the weights of breeding Laysan Albatrosses Diomedea immutabilis were higher, at least during the incubation period, than the weights of birds which had bred formerly but were not currently breeding.

While weight changes between the ages of six and ten may reflect changes in the proportion of breeding birds, this cannot be so for the weight changes between ages two and five (Figures 2.2 and 2.4), and a different explanation is required. Lack (1966) suggested that the delayed onset of breeding observed among many birds, including the Manx Shearwater, occurs because to breed at too early an age would be dangerous for the individual and ineffective, since the bird would not have attained a level of proficiency, in the abilities required for reproduction, sufficient both to maintain itself and successfully to rear a chick (or chicks). Thus individuals which started to breed at younger than the normal age would leave fewer, not more young than those starting at the normal age. Lack (1966, p. 275) states that his view depends on two conditions. The first is that breeding should lower the survival chances of young adults. Fisher (1975a) has investigated the survival of Laysan Albatrosses in relation to their age of first breeding and found slight evidence that birds which initiated reproduction two years earlier or one or two years later than normal may not have survived as long as those which began breeding at the normal age. The second of Lack's conditions is that young parents should be less efficient at raising young than older parents. Such is indeed observed in many species including the Yellow-eyed Penguin Megadyptes antipodes (Richdale 1957), the Kittiwake Rissa tridactyla (Coulson & White 1958) and also the Manx Shearwater (Chapter 4). It is not, however, a necessary condition for Lack's view since younger birds could raise as many young as older birds but still benefit from delaying breeding if the first condition was met. This first condition implies that the birds which delay breeding should acquire, during the years of delay, some attributes which enable them to reduce the cost, to their own chances of survival, of reproduction. One such attribute could be increased feeding efficiency.

It is clearly very difficult to measure the feeding efficiency of a seabird but Orians (1969) and Dunn (1972) respectively have shown that immature Brown Pelicans Pelecanus occidentalis and first-year Sandwich Terns Sterna sandvicensis are less successful at catching fish than adults. The foraging efficiency of immature Little Blue Herons Florida caerulea, up to at at least nine months old, is lower than that of adults (Recher & Recher 1969). The prolonged post-fledging parental care observed in some terns (Ashmole & Tovar 1968, Dorward 1963) and boobies Sula spp. (Nelson 1966a) also implies that young birds are less successful at feeding than adults. However, none of these studies has shown that the feeding efficiency of immature birds increases year-by-year up until the age of first breeding. Such a demonstration is necessary if the lower feeding efficiency of young birds is to be considered responsible, either alone or in combination with other factors, for the delayed onset of breeding. The most satisfactory demonstration of this point is provided by Norton-Griffiths (1968) who found that young Oystercatchers Haematopus ostralegus, which do not start to breed until four or five years old (Harris 1967), take three years to become as efficient as adults at handling Edible Mussels Mytilus edulis. Also relevant is the observation that Adelie Penguins Pygoscelis adeliae raise more and heavier chicks as they increase in age from three to six, but previous breeding experience does not increase a bird's ability to raise heavier chicks (Ainley & Schlatter 1972). This suggests that the ability to raise heavier chicks is dependent on what is learned at sea and not the accumulated experience of interacting with mates, eggs and chicks during breeding.

The weight of Manx Shearwaters appears to increase year by year between the ages of two and six, the age of first breeding (Figure 2.6). It is not known whether the weight of a Manx Shearwater is related to its feeding efficiency but such a relationship seems likely on general grounds. Whilst the studies discussed in the previous paragraph showed that young birds are less efficient at foraging than older birds, there are also many studies which show that older birds are heavier. These include seabirds (Fisher 1967, Warham 1972, Ashcroft 1976), waders (Minton 1975) and landbirds, both passerine (Baldwin & Kendeigh 1938) and non-passerine (Murton, Westwood & Isaacson 1974, Redfield 1973). The work of Murton, Isaacson & Westwood (1971) related feeding efficiency and weight in the Woodpigeon Columba palumbus, where the socially dominant birds have a faster pecking rate and weighed more.

I conclude that the progressive increase in weight with age shown by immature Manx Shearwaters can be interpreted in support of Lack's (1966) hypothesis that at least one factor responsible for the delayed onset of breeding is that young birds are less efficient at foraging. The younger birds were also caught less frequently at the colony (Table 2.3) which could have been because it was necessary for them to spend more time at the fishing grounds.

In the absence of any detailed body analysis I do not know which components of the body increase in weight as the birds age. It is at least possible that the increase is partly due to an increase in skeletal weight since the tarsi of full-grown birds are heavier and thicker than those of fledglings (Table 2.4). They are not, however, longer and this agrees with the data presented in Figures 2.7 and 2.8, showing that there is no relationship between bill length, wing length and age.

Seasonal changes in weight

The pattern of weight change relative to the breeding cycle is fairly similar in the Manx Shearwater (Figures 2.2-2.5) and the Laysan Albatross (Fisher 1967). Fisher suggests that the decline in weight is due to the rigours of parental care, and the downward trend is reversed once the nestlings have passed their maximum weight, after which the parents feed them less often. He also proposed that juveniles may lose weight in parallel with breeding birds because of the activities of courtship and territory establishment. This explanation is unsatisfactory for the Manx Shearwater in at least three respects.

(i) Although there is a decline in the pre-laying period (Chapter 3), the weight of Manx Shearwaters known definitely to be breeding does not alter over the incubation period (Chapter 4).

(ii) The reversal of the downward trend occurs in late June or early July, at least a month before parent Manx Shearwaters reduce the rate at which they feed the chick.

(iii) It fails to explain why immature birds should increase in weight towards the end of the breeding season.

There is evidence that some Manx Shearwaters of breeding age may visit the southern half of the Bay of Biscay (c. 44°-45°N) in the pre-laying period (Perrins & Brooke 1976; see also Appendix 4) but during incubation the distribution of recoveries suggests that very few birds of breeding age travel south of 46°N. During the nestling stage the frequency with which chicks are fed has led Harris (1966a) to suggest that most breeding shearwaters are not feeding further than 300 km from Skokholm (51°42'N 5°16'W). Thus, during the chick stage, few breeding shearwaters are feeding south of 50°N.

Therefore, in the period March to July, the area where the breeding shearwaters from the Skokholm colony feed appears to move closer to the island. In August and September feeding conditions close to the island probably deteriorate since late chicks are lighter than those that fledge earlier (Perrins et al. 1973), suggesting that the parents of those late fledging chicks have experienced greater difficulties in feeding their young (see also Chapter 5).

A similar pattern of seasonal weight change is shown by birds of all age classes (Figures 2.2-2.5) and it will be noticed that weights decline steadily during the period March to June/July when other evidence cited above suggests the feeding areas are moving closer to Skokholm and quite likely improving. Weights start to increase as feeding conditions deteriorate at the end of the breeding season. An analagous situation is seen in many passerines and waders (Baldwin & Kendeigh 1938, Minton 1975) in which the weight is lowest during the breeding season and highest in mid-winter when the time available for feeding is at a minimum and feeding conditions may be especially unfavourable. Possibly the heavier winter weights represent 'insurance' against a time when conditions are so severe that a bird without additional reserves to draw on would die, and the negative correlation between winter weight and temperature is well documented (Haftorn 1951, Owen 1954, van Balen 1967). Applying similar thinking to the Manx Shearwater I would suggest that the birds must visit the colony carrying sufficient body (fat?) reserves to enable them to perform appropriate activities there and then to return to the feeding grounds. When the feeding grounds are more distant early in the season, these reserves must be correspondingly greater and the birds will be heavier. When feeding conditions may be deteriorating late in the season, the shearwaters start to increase in weight, possibly partly because of the deposition of pre-migratory fat, in preparation for the forthcoming rapid journey to the South Atlantic (Harris 1966a).

This explanation is in agreement with the fact that the youngest age groups, the two-, three- and four-year-olds visit the colony in greatest numbers in June and July (Perrins _et al_. 1973) when feeding conditions are possibly most favourable. At other times of year they may be unable to reach a high enough weight at the feeding grounds to enable them to fly from the feeding area to the colony and back, and this inability to reach a high weight may be related to the possibly lower feeding efficiency discussed in the previous section.

An implication of this explanation is that, since immature birds do visit the colony despite being of lower weight and having smaller reserves to utilise on the journey back to the feeding grounds, the advantages of such visiting must be substantial. The exact nature of these advantages remains a matter for speculation.

CHAPTER THREE

The Pre-laying Period

Introduction

At the beginning of the breeding season the earliest Manx Shearwaters visit the colony on Skokholm Island in late February or early March (Lockley 1942). Since laying does not begin until late April, with the peak occurring in early May (Harris 1966a), some birds are visiting the colony for a period of up to two months before laying. This chapter investigates the activities of the birds during this long pre-laying period during which time the pair-bond is (re-)established, a breeding burrow is prepared to receive the egg and mating occurs. In particular I examine weight changes, emphasize the contrasting role of the two sexes and consider evidence for the occurrence of competition for breeding burrows during the pre-laying period, which is the time of year when fighting at burrow entrances is most evident.

Methods

Data were gathered mainly during 1974 and 1975. In 1974 daily checks were maintained on two groups of burrows from 15 March until laying. One group, the Observatory burrows, was in the vicinity of the Skokholm Bird Observatory and contained about 40 burrows scattered at a fairly low density (see below). Many of the burrows in this area had been kept under observation since 1963 (Harris 1966a) and so the breeding histories of many of the adults breeding in these burrows during the study period were known. Three categories of bird are distinguished in the Observatory burrows:-

(i) Breeders, birds breeding during the current year.

(ii) Former breeders, birds which are known to have bred in the past but are not known to be breeding during the current year, although it is possible that they may be doing so either in one of the few burrows in the study area that could not be opened for inspection or beyond the limits of the study area.

(iii) Pre-breeders, birds not known to have bred in the past nor to be breeding during the current year but known to breed one or two years hence.

The second group, of about 20 burrows, was in the dense Main Colony where some 8,000-10,000 pairs breed in 7-8 ha. (Perrins 1967, Perrins, Harris & Britton 1973). The breeding histories of the birds in the Main burrows were not known but many were of known age, having been ringed as fledglings in earlier years. During the daily daytime checks on the Observatory and Main burrows the presence or absence of shearwaters was noted, and the individual identity of any birds present was established by ringing. Birds were weighed on the day they were first found down the burrow after a period of absence. Weight data in the Main Colony were only obtained from birds of known age.

The same daytime checking routine as was used in 1974 was followed in 1975 for the Observatory burrows, except that daytime checks commenced on 10 March instead of 15 March. The Main burrows were not checked in the pre-laying period of 1975. Additionally, in 1975, night-time checks were made on about 20 Observatory burrows. The checks were made every fourth night and were timed at 2200 and 0200 B.S.T. on the first night of checking, 2400 and 0400 on the second, 2200 and 0200 on the third and so on. The presence or absence of shearwaters and the identity of those present was recorded during the night-time checks. Since the two checks on any one night were four hours apart it would be possible for a shearwater to visit a burrow on one of the nights when I was checking burrows, and yet not be recorded.

A Manx Shearwater needs a burrow for breeding. There is therefore the possibility that the number of suitable burrows on Skokholm may be small enough to create competition for burrows. If competition for burrows were considerable then it is possible that some birds, otherwise capable of breeding, would be excluded from the breeding population. If additional artificial burrows were provided then such birds might well be enabled to breed. It might also be the case that the competition for burrows would be more severe in the dense Main Colony than elsewhere on the island, in which case artificial burrows would be occupied more rapidly in the Main Colony than elsewhere. To test these predictions I dug, between 20 and 24 March 1975, 30 burrows, each about 1.3 m. long, of which 15 were in the Main Colony and 15 elsewhere on the island, and recorded which were used for breeding in 1975 and 1976.

An indication of burrow density was obtained using a nearest neighbour method. For a random selection of 20 natural Observatory and 20 natural Main burrows the distance to the nearest occupied burrow in each of the four quadrants, north-east, south-east, south-west and north-west, was measured. The mean (± S.D.) of the 80 measurements for the 20 burrows in the Observatory and Main colonies was 9.30 ± 4.824 m. and 1.64 ± 1.033 m. respectively; this difference is significant (t-test, $p < 0.001$). For the artificial burrows the mean nearest neighbour distance (to any burrow, either natural or artificial) was 2.52 ± 1.207 m. for the 15 burrows in the Main Colony and 4.88 ± 2.309 m. for the 15 burrows elsewhere; this difference is also significant (t-test, $p < 0.001$). The nearest neighbour distance for the 15 artificial burrows in the Main Colony was significantly greater than the distance for the 20 natural burrows (t-test, $p < 0.001$) since the artificial burrows were necessarily dug in areas of relatively low burrow density where the ground was not already undermined by the presence of natural burrows.

Results

Weight changes during the pre-laying period

The weights of both male (N = 123) and female (N = 87) breeding Manx Shearwaters decline steadily during March and April as shown in Figures 3.1 and

Figure 3.1

The weight of male Manx Shearwaters on the day in March and April on which they were found, after a period of absence, in the burrow in which they subsequently bred in 1974. Data from Observatory burrows 1974.

The regression line is $y = 508.9 - 1.770x$ Day 0 = 10 March

N = 123
r = -0.507
$p < 0.001$

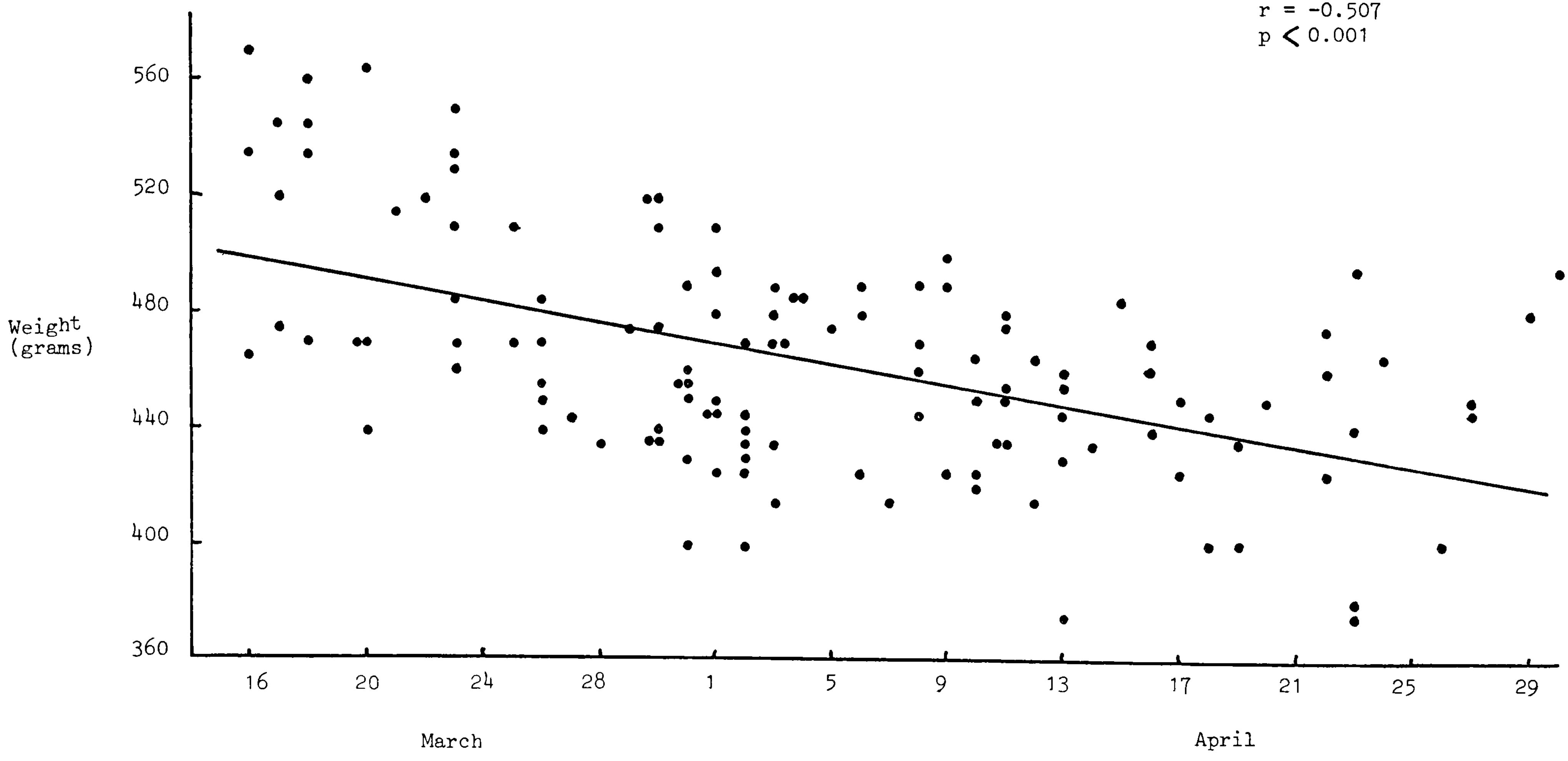


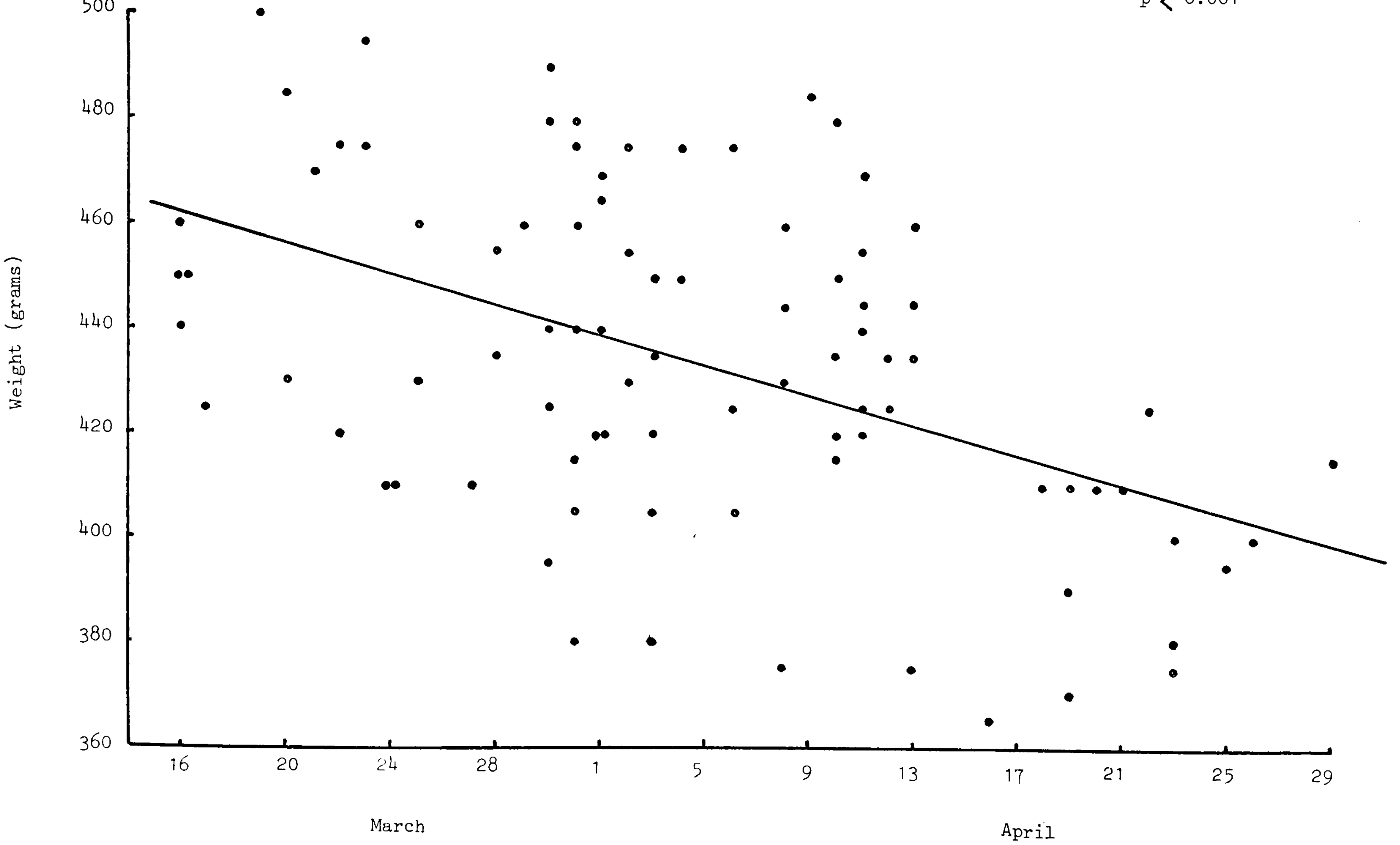
Figure 3.2 The weight of female Manx Shearwaters on the day in March and April on which they were found, after a period of absence, in the burrow in which they subsequently bred in 1974. Data from Observatory burrows 19

The regression line is $y = 470.5 - 1.412x$ Day 0 = 10 March

$N = 87$

$r = -0.466$

$p < 0.001$



3.2, where data from the Observatory burrows in 1974 are plotted. Data from 1975, where sample sizes were 91 for males and 73 for females, were essentially similar. In both 1974 and 1975 the decline in weight was better correlated, for both sexes, with calendar date than with stage of the breeding cycle (i.e. number of days before laying). There were no significant differences in the mean weight of males (± S.E.) in March and April in the two years (463.9 ± 3.55 gm. in 1974; 453.5 ± 4.05 gm. in 1975) nor in the slope of the regression (± S.E.) of weight on data (-1.770 ± 0.274 in 1974; -2.339 ± 0.241 in 1975). Likewise there were no significant differences in the mean weight of females (434.5 ± 3.46 gm. in 1974; 427.1 ± 4.07 gm. in 1975) nor in the slope of the regression of their weight on date (-1.412 ± 0.290 in 1974; -1.070 ± 0.301 in 1975). However, in both years the slope of the regression was greater for males than for females and, in 1975, the difference was significant ($d = 3.289$, $p < 0.01$). In other words males tend to lose weight at a somewhat faster rate than females in the pre-laying period in March and April.

There are no female weights available in the last ten days before laying, since the females are virtually absent from the colony during this time (Harris 1966a, and below). However, as shown in Figure 3.3, there is an indication that the weight of males tends to rise in the last ten days before laying. Since the median date of laying of the colony is about 10 May (Harris 1966a) the last ten days before laying fall, for most males, in early May and so this weight increase is not shown in Figure 3.1. During this period the males are infrequently seen in the burrow by day (Harris 1966a) and are thus able to feed at sea by day to build up food reserves in preparation for the first incubation stint. Earlier, in March and April, when a greater proportion of time is spent in the burrow, the weight declines as observed in Figure 3.1.

Figure 3.3

The mean weight of male Manx Shearwaters in relation to the number of days before laying. Data from Observatory burrows from 1974 (O) and 1975 (●). The birds were weighed on the day on which they were found, after a period of absence, in the burrow in which they subsequently bred. Points based on less than five weighings are shown in brackets.

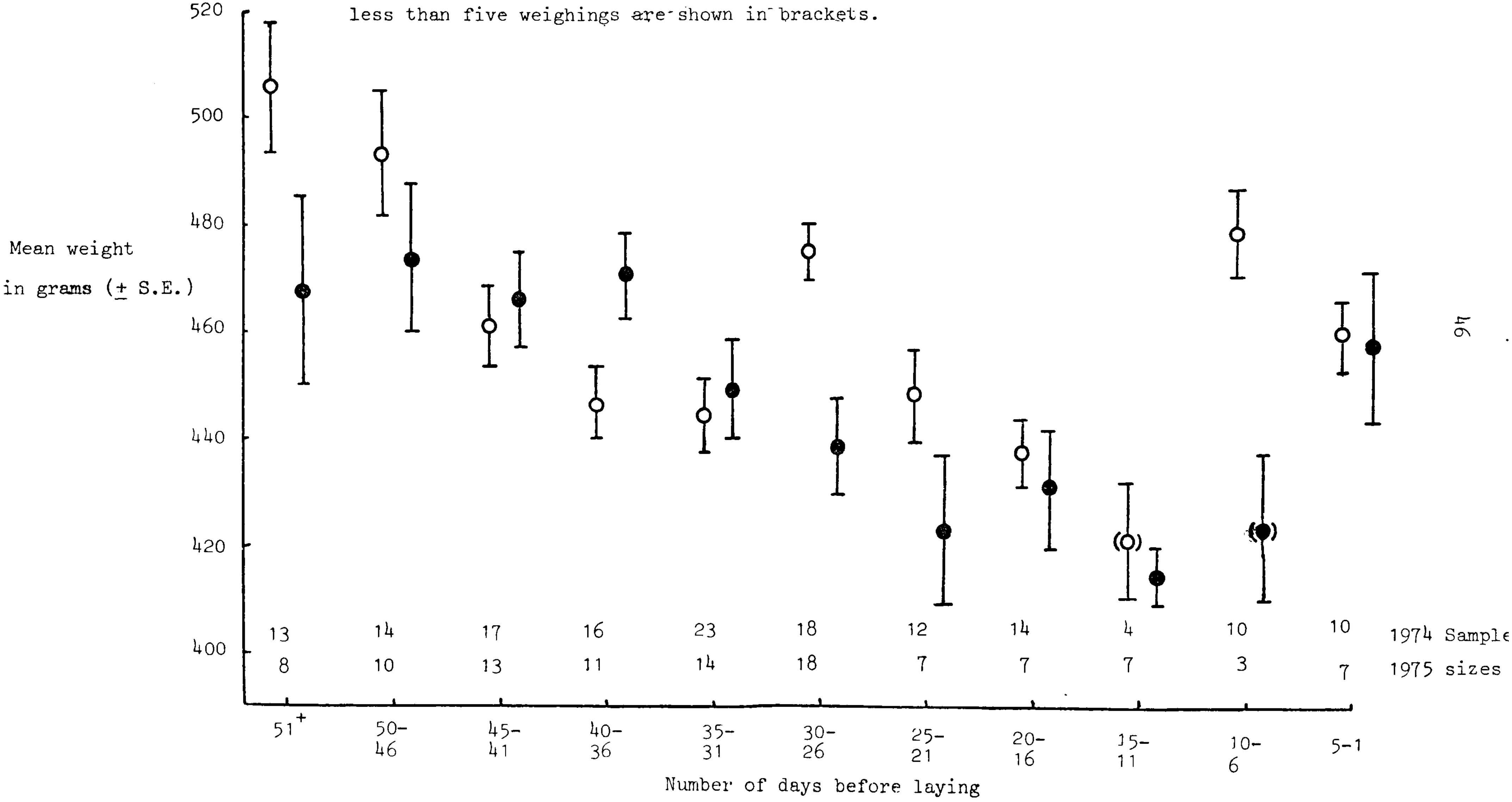


Table 3.1 gives the weight of breeders, former breeders and pre-breeders caught in the Observatory burrows in 1974 and 1975. No date corrections were made since there were no significant differences between the mean date of weighing of former breeders and breeders of either sex in either year, while the weight of pre-breeders was not correlated with date. The results are equivocal. Former breeders were lighter than breeders in 1974 but the reverse was true in 1975. Pre-breeders were consistently lighter than breeders but the difference was only significant for males in 1974. The non-breeding groups (former and pre-breeders) were heavier in 1975 than in 1974 and this difference was significant for males (former breeders, t-test, $p < 0.01$; pre-breeders, Mann-Witney U-test, $p < 0.05$). On the other hand breeders tended to be lighter in 1975.

Table 3.2 gives the mean weight in March and April 1974 of birds aged 7-9, 10-12 and those with at least six years previous breeding experience. Birds aged 7-12 were mostly taken for weighing from Main burrows whilst birds with at least six years previous breeding experience were individuals in Observatory burrows. Such individuals are probably at least 12 years old since during the study period, few shearwaters started to breed before the age of six (Brooke 1973). The mean dates of weighing of the groups are similar and the weights are therefore comparable. There is no significant indication that the weight of breeding birds varies with age. Likewise examination of both 1974 and 1975 data from breeding birds in the Observatory burrows revealed no relation between weight and previous breeding experience. These findings lend support to my contention, in Chapter 2, that the weight increase seen between the ages of six and ten in samples of birds caught at night is primarily due to the samples containing an increasing proportion of breeders.

The contrasting role of the sexes

Harris (1966a) has described the pattern of daytime burrow attendance of the Manx Shearwater during the pre-laying period. At about 30 days before

Table 3.1

The mean weight in grams (± S.E.) of Manx Shearwaters in the Observatory burrows in March and April, 1974 and 1975. Breeding birds were weighed on the day on which they were found, after a period of absence, in the burrow in which they later bred, former breeders and pre-breeders on the day they were first found in any burrow. Sample sizes in brackets. Using t-tests significant differences from the mean weight of breeders of the same sex in the same year are indicated thus : -

* $p < 0.05$

** $p < 0.01$

1974 data	Males	Females
Breeders	463.9 ± 3.55 (123)	434.5 ± 3.46 (87)
Former breeders	** 436.2 ± 7.84 (17)	420.0 ± 8.45 (12)
Pre-breeders	** 415.7 ± 8.05 (7)	430 (1)
1975 data		
Breeders	453.5 ± 4.05 (91)	427.1 ± 4.07 (73)
Former breeders	* 475.0 ± 7.53 (28)	430.0 ± 6.54 (21)
Pre-breeders	447.5 ± 9.64 (8)	420 (1)

Table 3.2

The mean weight in grams (± S.E.) of breeding Manx Shearwaters of various age groups in March and April, 1974. The birds were weighed on the day on which they were found, after a period of absence, in the burrow in which they later bred in 1974. Sample sizes are given in brackets below means. No differences within sexes are significant.

	Males	Females
Birds aged 7-9	456.4 ± 4.43 (32)	427.3 ± 8.29 (15)
Birds aged 10-12	459.4 ± 8.05 (25)	440.0 (2)
Birds with at least six years previous breeding experience	468.1 ± 4.50 (60)	439.0 ± 4.20 (53)

laying 20-25% of both males and females are to be found by day down the burrow in which they will later breed. This percentage declines as laying approaches and there is a tendency for the male to be present more often than the female.

In Table 3.3 I compare the total number of days spent down the burrow in the pre-laying period by the two sexes in 1974 and 1975 in the Observatory burrows. It will be remembered that daily pre-laying checks started on 15 March in 1974 and 10 March in 1975. In both years males spent significantly more days down the burrow than females and this is probably associated with the greater rate of decline in weight of males in March and April (Figures 3.1 & 3.2), since a male clearly cannot feed when down its burrow. Despite the fact that checks in the pre-laying period continued for five fewer days in 1974, the total number of days spent down the burrow by both sexes was greater in 1974, but for neither sex was the difference significant even if one excludes data from 10-14 March 1975. If the lesser number of days spent down the burrow in 1975 in any way reflects less favourable feeding conditions, requiring a re-allocation of time between feeding and burrow defence, then it is interesting that the mean weight of breeding males and females should have been somewhat lower in 1975. There was, however, no significant difference in laying dates in the two years (see Table 4.8).

The results of the checks at night carried out in 1975 are given in Table 3.4. Until 16 days before laying there was little difference in the frequency with which the two sexes were recorded, each being present on approximately 35% of nights. However, in the two weeks prior to laying, the female was not recorded at all but the male continued to be recorded in the burrow on about 30% of nights. During this time, when the female is forming the egg, there is evidence from recovery data that she may travel as far as the Bay of Biscay (Perrins & Brooke 1976; see also Appendix 4)

Table 3.3

The mean number of days (± S.E.) spent by breeding Manx Shearwaters down the breeding burrow in the pre-laying periods of 1974 and 1975.

	Males	Females	N	p (Wilcoxon Matched pairs test)
1974	8.00 ± 0.717	5.53 ± 0.437	40	< 0.001
1975	6.91 ± 0.791	4.97 ± 0.519	33	< 0.001

Table 3.4

The percentage of nights on which male and female Manx Shearwaters were recorded in the burrow in which they later bred. Data from the Observatory burrows in the pre-laying period of 1975. The number of observations is given in brackets after each percentage.

Days before laying	Male	Female
36+	36.2 (69)	24.6 (69)
31 - 35	45.9 (17)	50.0 (18)
26 - 30	27.8 (18)	16.7 (18)
21 - 25	33.3 (15)	26.7 (15)
16 - 20	35.3 (17)	41.1 (17)
11 - 15	20.0 (15)	0 (15)
6 - 10	38.1 (21)	0 (21)
0 - 5	27.3 (22)	0 (22)

but it seems unlikely that the male would travel further from the colony than the distance that can be flown during the daylight of one day, leaving one day for feeding, one day for the return journey and a visit to the burrow every third night. Assuming a flight speed of 45 km./hr. (Pennycuick 1969) and 12 hours of flying in a day the males could travel a maximum of about 550 km. from Skokholm, while the Bay of Biscay is about 800-1000 km. distant.

As mentioned in the Methods section my checking routine was such that it would be possible for the shearwater to visit a burrow on one of my checking nights, and yet not be recorded since I only made visits every four hours. There is, however, an independent method of determining male visiting frequency. This is by recording the mean number of days between laying and the first day the male is found incubating. Assuming that the male remains in the burrow from the first night that he returns and finds either his mate ready to lay or an egg, then the mean number of days can provide an estimate of the male visiting rate. Data were available from Observatory burrows in 1975 and 1976, when the mean number of days (± S.D.) was 1.11 ± 1.71 (N = 18) and 1.32 ± 1.70 (N = 22) respectively. These figures correspond to the male visiting on 31.1% of nights in 1975 and 27.5% in 1976. The male visiting rate derived from this analysis is thus similar to that presented in Table 3.4, and it seems likely that the male visits the burrow on about 30% of nights in the period immediately before laying.

Competition for burrows

Perrins _et_ _al_. (1973) considered where shearwaters that had been ringed as fledglings on Skokholm were recaptured in relation to their natal area. They found that more moved out of, than into, the Main Colony, possibly indicating either that some young were being forced to move away from this, their natal area, or that some were choosing to move from this dense area. I therefore examined data from the Observatory and Main burrows with a view to detecting differences in the pattern of pre-laying attendance that could be interpreted as indicating that birds in the Main Colony were spending more time visiting the burrow (and presumably less feeding) in order to defend the burrow against a greater number of potential intruders. No such differences could be detected, nor, as indicated in a previous section, were the younger breeders in the Main Colony lighter in weight than experienced breeders in the Observatory burrows. For example I examined the total number of days spent down the burrow by breeding birds in the period 40-21 days before laying, which is the period of peak daytime attendance (Harris 1966a). In this 20-day period the mean number of days (± S.E.) was, for males, 3.90 (± 0.373) in the 40 Observatory burrows and 3.62 (± 0.541) in the 21 Main burrows and, for females, 3.13 (± 0.291) in the Observatory burrows and 3.62 (± 0.541) in the Main burrows. No differences are significant.

Of the 30 artificial burrows dug in 1975 one, in the Main Colony, was used for breeding in 1975 and eight (five in the Main Colony and three elsewhere) were used in 1976. There was therefore no conclusive indication that burrows dug in the Main Colony were occupied more rapidly than those dug elsewhere. Of the 16 birds that bred in the artificial burrows (the pair that bred in the one occupied burrow in 1975 bred again in that burrow in 1976), six were already ringed. Of the three ringed birds breeding in the Main Colony there were two males aged six when first found breeding and one female aged five. Since few Manx Shearwaters start to breed before the age of six (Brooke 1973) it seems likely that these three ringed birds were breeding for the first time. This point may be reinforced by calculating the probability that a random selection (as opposed to a selection biassed in favour of young breeders) of two breeding ringed birds will contain two six-year-olds. This probability can be calculated knowing the proportion of ringed six-year-olds among the population of ringed breeding birds (see Table 6.5). This proportion is very roughly 10.4/90.0 and the probability is very approximately this value squared or 0.013. This probability would be lower still if full account were taken of the fledgling ringing effort in the two years from which the two six-year-olds survived. The five year old female was one of only two females found breeding at this age (or younger) during the study period, out of a total of 42 females of known age found breeding. It seems probable that the artificial burrows in the Main Colony were mostly occupied by younger birds breeding for the first time, and it may even have been the case that these shearwaters were enabled to breed at a younger age than would have been possible had they been obliged to compete with older birds for natural burrows. Of the three ringed birds which bred in artificial burrows elsewhere on the island, one was a seven year old female which may or may not have bred previously whilst the other two, a male and a female breeding together in the area of the Observatory burrows, were known to have been breeding in 1968 and 1963 respectively.

In the pre-laying period of 1974 I carried out a burrow-blocking experiment in the Main Colony from which it was hoped to learn if there was any critical period such that, if shearwater pairs were excluded from the burrow during this period, no breeding would occur in the burrow that year. All burrows used in the experiment were used for breeding in 1973. The experiment was not successful, partly because sample sizes were reduced by the birds' ability to dig round the blockage (stones) and re-enter the burrow despite my efforts at exclusion. Four experimental treatments were used:-

(a) Burrow blocked in October 1973 and blockage removed 30 March 1974. Eggs were laid in two of six burrows in this category.

(b) Burrow blocked October 1973 and blockage removed 10 April 1974. Eggs were laid in two of five burrows.

(c) Burrow blocked October 1973 and blockage removed 21 April 1974, at the start of the laying period. Eggs were laid in two of six burrows.

(d) Burrow open except for the period 30 March to 21 April 1974. An egg was laid in one of six burrows.

Of the seven experimental burrows where eggs were laid, five were used by the same pair as bred in these burrows in 1973, and there was no indication that the laying date had been affected by the experimental treatment. In the other two burrows the same female laid as in 1973, but the identity of the male was unknown in either 1973 or 1974. It seems possible that even under treatment (a) the blockage may have been removed too late to enable pairs which had not bred together before to move into and breed in the burrow made available by the experimental treatment. The fact that seven pairs did breed in the experimental burrows despite the considerable disruption to normal pre-laying attendance suggests that they were either unable to obtain another burrow in which to breed, or that they could obtain a burrow but only one of 'inferior quality'. This suggestion is highlighted by the persistence with which shearwaters dug round my blockage. In 16 of 17 cases where the birds rounded the blockage, eggs were laid in 1974.

Discussion

Since the weight of male and female Manx Shearwaters declines in March and April during the pre-laying period (Figures 3.1 & 3.2) it seems possible that feeding conditions are not particularly favourable at this time. A similar decline has been reported for a variety of seabird species (Richdale 1947, Fisher 1967, Scott 1970, Warham 1974) and it may well be a widespread phenomenon. On general grounds such a decline could be anticipated since, if conditions were sufficiently favourable to allow the birds to maintain weight while performing all the activities that must be fitted into the pre-laying period (courtship, nest-building, mating etc.), then they might also be sufficiently favourable to allow incubation and, as it appears advantageous for the Manx Shearwater to lay early (Perrins 1966), the birds would benefit from an appropriate advancement of laying date. As shown in Chapter 4 the breeding shearwaters do maintain weight during incubation.

Former breeders appear not to differ in weight from breeders in the pre-laying period (Table 3.1) although it must be remembered that birds classified as former breeders may include some which are breeding undetected. However, former breeders are lighter than breeders in the early part of the incubation period (Table 2.5) and Fisher's (1967) study of the Laysan Albatross also revealed that former breeders were lighter than breeders during the incubation period and Fisher thought it likely that they were also lighter in the pre-laying period. Carrick & Ingham (1967) found that when female Royal Penguins Eudyptes chrysolophus come ashore at Macquarie Island at the start of the breeding those weighing more than 4.8 kg. usually laid while those weighing less rarely did so. In the Royal Penguin weight does therefore appear to be associated with the likelihood of breeding. This in fact may also be the case in the Manx Shearwater since, although former breeders do not differ in weight from breeders, pre-breeding males are lighter than breeding males (Table 3.1). Possibly arrival at the colony at a certain weight is a necessary but not a sufficient condition for breeding in the Manx Shearwater and this agrees with there being no difference in the weights of breeding birds of different ages (Table 3.2). It is unfortunately impossible to determine whether pre-breeders are lighter because, in the absence of any 'intention' to breed, they have neither fed sufficiently nor undergone the necessary physiological changes to achieve a higher weight, or whether they have remained pre-breeders because they are lighter.

The more frequent attendance of the male Manx Shearwater at the breeding burrow (Tables 3.3 & 3.4) will facilitate fertilisation of the mate and reduce the opportunity of other males to mate with her. It is probably also important for the male to defend the burrow against intruders, for the burrow may be considered to be a Type C nesting territory (Hinde 1956), a small defended area around the nest. However, I have no detailed observations on the behaviour involved in burrow defence.

A pre-laying absence is a well-known feature of petrel biology. It has been recorded in shearwaters (Serventy 1967, Harris 1969b) and a variety of other Procellariiformes (Tickell 1962 & 1968, Dunnet, Anderson & Cormack 1963, Pinder 1966, Harris 1969a, Scott 1970). The absence may involve both sexes equally as in the Short-tailed Shearwater Puffinus tenuirostris (Serventy 1967) and the Fulmar Fulmarus glacialis (Dunnet et al. 1963), or it may be more marked in the female than in the male as is the case in the Manx Shearwater (Table 3.4), and notably also in the Dove Prion Pachyptila desolata (Tickell 1962) and the Cape Pigeon Daption capensis (Pinder 1966). Lack (1966) has argued that the pre-laying exodus enables the build-up of food reserves that will be required at the end of the period of absence, to enable the male to accomplish the first long incubation stint and the female to form an egg. Such an explanation seems satisfactory to explain the pre-laying departure of the Manx Shearwater and it carries the implication that food is not particularly abundant in the vicinity of the colony at this time. It does not necessarily imply that food is scarce everywhere; food may only be located at a considerable distance from the colony so that it would be energetically inefficient for the female to fly frequently between colony and feeding grounds. If food is not particularly abundant close to the colony it could be advantageous for the sexes to separate, in geographical terms, the location of their feeding sites, thereby increasing the area over which feeding occurs. Because of the male's role in burrow defence he must necessarily continue to feed relatively close to the colony while, as mentioned earlier, there is evidence that breeding females travel further afield, possibly as far as the Bay of Biscay in the pre-laying period (Perrins & Brooke 1976; see also Appendix 4). Thus intersexual competition for food could be reduced by a geographical separation of feeding sites, a separation made possible once the female has been inseminated early in the pre-laying period. Any reduction in competition for food at this time might promote the more rapid attainment of breeding condition by both sexes. I know of no species other than Procellariiformes where a geographical separation of feeding areas may serve to reduce intersexual competition for food during the breeding season. However, geographical separation of the sexes outside the breeding season is observed in certain migrant species (Deelder 1949, Dorst 1962) and it is worth noting that in these species also it is the male which migrates the shorter distance and so remains closer to the breeding grounds.

I have presented some evidence, from the provision of artificial burrows and the burrow-blocking experiment, that nest sites may be in sufficiently short supply to limit the Manx Shearwater breeding population. Direct evidence in support of this proposition could be gathered in two ways:

(i) By providing additional nest sites, ideally on a larger scale than I attempted, and observing whether birds, which would not otherwise have bred, were enabled to do so. The problem, in a shearwater study (see also Ashcroft 1976), is to demonstrate that birds breeding in the extra nest sites would not have bred elsewhere. However the young age of the ringed shearwaters breeding in the artificial Main burrows does at least suggest that they were breeding for the first time.

(ii) By removing breeding birds and observing whether their places in the breeding population were filled by birds that would not otherwise have bred. Harris (1970b) performed this experiment on the Oystercatcher on Skokholm. Territory-holding Oystercatchers were removed and their places were rapidly filled by birds from a non-breeding flock. The new occupants of the territories started to breed, demonstrating that their former membership of the non-breeding flock was not due to any physiological inability to breed. There are many other observations indicating that when territory holding birds are removed their places are rapidly filled (e.g. Orians 1961, Watson 1965, Krebs 1971, Manuwal 1974).

Competition for nest sites is vividly illustrated in other shearwater species such as the Great Shearwater *Puffinus gravis* (Rowan 1965), the Short-tailed Shearwater (Serventy 1967) and the Sooty Shearwater *P. griseus* (Richdale 1963) where large numbers of eggs are laid not in burrows but on the surface, there to be taken by predators. Eggs laid on the surface by Manx Shearwaters would be difficult to observe since, on Skokholm, gulls *Larus* spp. would rapidly eat the eggs before the observation could be made. During the study period approximately 620 eggs were laid in burrows that were closely checked during the laying period. In six of the burrows two eggs were laid by different females, and none of these 12 eggs was successfully hatched. That such competition for nest sites may act particularly against younger birds is shown by the work of Coulson (1971) on the Shag *Phalacrocorax aristotelis* and Serventy (1967) on the Short-tailed Shearwater. That competition for extensive territories (rather than nest sites) may also act against younger birds was shown by Krebs (1971) for the Great Tit *Parus major*.

The substantial length of the pre-laying period could itself result from the balance of two competing selective forces, the advantages of arriving at the colony as early as possible to obtain a burrow for the forthcoming breeding season and the disadvantages of leaving the feeding grounds and risking predation. In 1975 when my daily checks started on 10 March, before many burrows had been visited, the date when the male was first found in the burrow was closely correlated with laying date ($r_s = 0.616$, $N = 31$, $p < 0.01$) and the mean interval (± S.E.) between first arrival and laying was 45.4 ± 1.40 days ($N = 31$). In expanding populations of the Guillemot *Uria aalge* and Kittiwake on Fair Isle, Shetland, the date of arrival back at the colony at the start of the breeding season has become earlier as the colonies have grown (Dennis 1967) and competition for nesting space may have been increasing. The annual re-occupation of sites occurs later at smaller British Fulmar colonies than at larger ones (Fisher 1952). However the pre-laying period has also been suggested as a time when communal displays would be useful for assessing population density in order to limit the number of breeders in the forthcoming breeding season (Wynne-Edwards 1962).

CHAPTER FOUR

Some factors affecting the laying date, incubation and breeding success of the Manx Shearwater (*Puffinus puffinus* Brunnich)

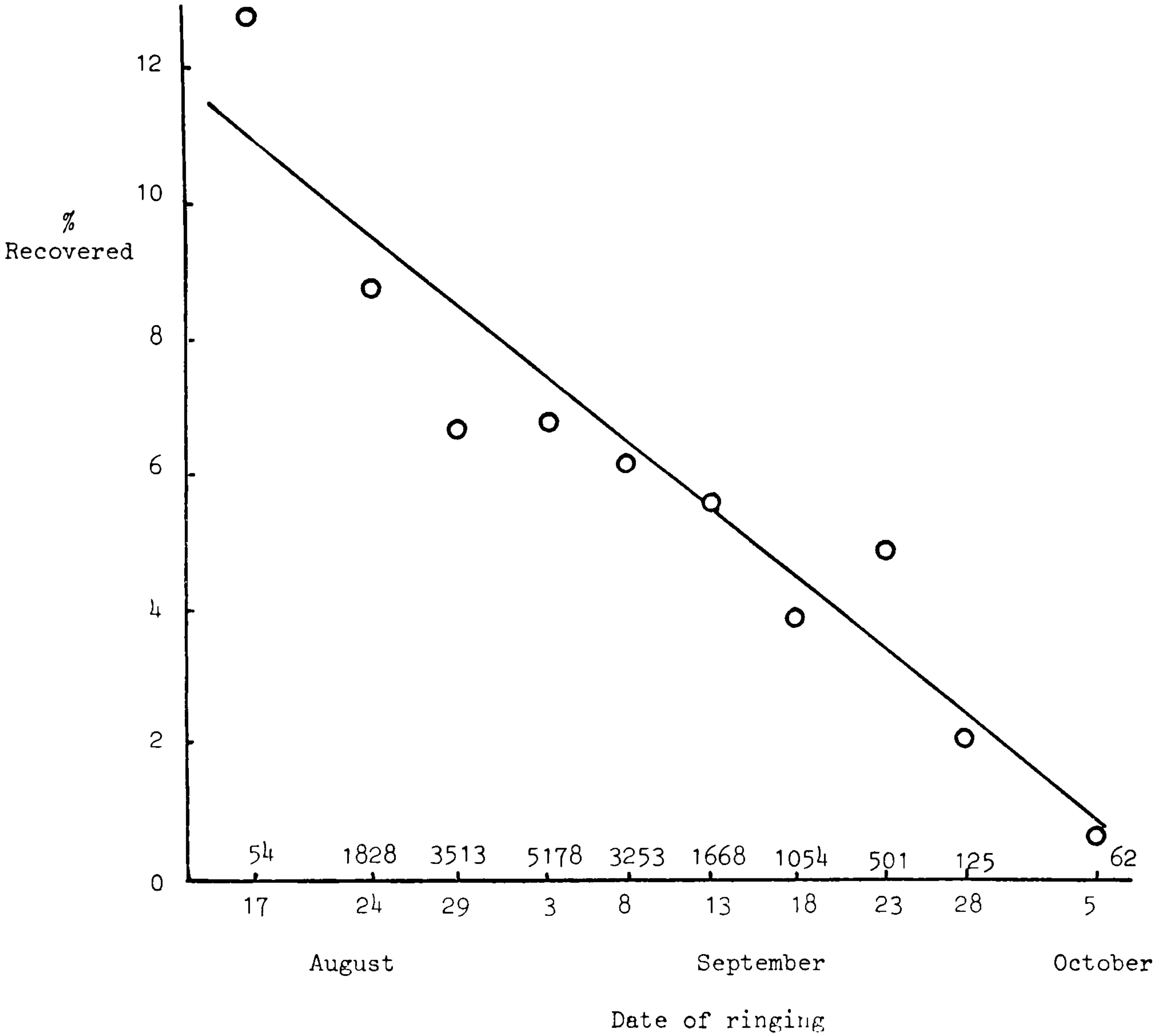
Some factors affecting the laying date, incubation and breeding success of the manx shearwater (Puffinus puffinus Brunnich).

Introduction

The manx shearwater (Puffinus puffinus) has been studied for many years on Skokholm Island, Pembrokeshire, Wales (Harris 1966a & b; Perrins, Harris & Britton 1973). These studies have provided considerable information on the breeding and population biology of this species and have formed the basis for the present study which attempts to examine in detail those factors which determine and influence the timing of laying. Particularly pertinent to this work is the observation that those young which are ringed and, it is assumed, fledged early in the season have a higher survival rate than those which fledge later (Figure 4.1, from Perrins 1966). In order to maximize its reproductive contribution to future generations an adult manx shearwater must first (and obviously) succeed in rearing chicks and second must attempt to rear those chicks as early as possible in the breeding season in order to increase the probability of their survival. Perrins (1970) has suggested a possible reason why manx shearwaters (and other species) do not lay earlier and so increase the probability of survival of their offspring. He proposed that, at the start of the breeding season, feeding conditions are unfavourable to the extent that females may have difficulty in obtaining sufficient food to produce the relatively large egg, about 15% of the female's body weight. Thus females are prevented from laying earlier and from rearing a chick at what would appear to be a more favourable time by a shortage of food. As the food supply improves during the laying period so, it is suggested, more and more females become able to produce an egg.

I consider this hypothesis in the light of information presented on the timing of laying in the manx shearwater and find it wanting. An

Figure 4.1 The percentage of young manx shearwaters recovered in relation to their date of ringing as fledglings (from Perrins, 1966).



alternative hypothesis based on the incubation period is proposed and considered.

Laying and breeding success

Methods

In the vicinity of the Bird Observatory buildings on Skokholm I maintained a detailed watch on a group of study burrows, to be termed the Observatory burrows, in each of four consecutive breeding seasons, 1973 to 1976. Some 70-80 eggs were laid in these burrows each year. The burrows were inspected daily during the laying, hatching and fledging periods so that precise information on the timing of breeding and breeding success could be gathered. Burrows in this study area have been under observation since 1963 (Harris 1966a) and so detailed records of the histories of many of the adults which bred in these burrows during the study period are available. Because the adults in these burrows were accustomed to human handling analysis of breeding success is restricted to these burrows. In the few instances where I considered my disturbance was responsible for a breeding failure then that burrow was excluded from the analysis of breeding success. Also restricted to the Observatory burrows is the analysis of the effect of mate change on laying date and of the incidence of divorce, the circumstance occurring when one or both members of a pair, which formerly bred together, breed with another partner during the next season that either of them breeds, although both members of the original pair are known to be alive during that season.

As far as possible all burrows in the study area were opened for inspection, but a few remained unopened because of the nature of the ground. It is also possible that birds previously breeding outside the study area moved to within it. With this caveat a 'new' breeder is a bird breeding for the first recorded time, in a burrow which has been regularly checked during the year preceding the first recorded breeding attempt. An 'experienced' breeder is a bird known to have made one or more previous breeding attempts. A 'new' pair is one where the two members of the pair are not known to have bred together in the previous year, provided that the burrow in which they are currently breeding was regularly inspected during the previous year. An 'established' pair is one where the two members of the pair are known to have bred together in the previous year.

Although much of the information presented in this paper was derived from the Observatory burrows these burrows were only occupied by a small number of birds which had been ringed as chicks and hence were of known age. To acquire a larger sample of known-age breeding birds I opened up for inspection burrows elsewhere on the island, particularly in the dense Main Colony (Perrins et al, 1973). A proportion of these burrows was opened during the incubation period in each season, 1973-1975, and so data concerning these burrows are available for fewer years than for the Observatory burrows. These burrows were checked daily during the laying periods of 1974-1976.

All birds breeding in study burrows were individually ringed and all were sexed by cloacal inspection (Serventy 1956) if handled in at least one season shortly after laying.

Results

Breeding success

The overall breeding success in Observatory burrows during the study period, measured as percentage of eggs laid producing fledged chicks, was 70.0% (Table 4.1), a figure very similar to that reported by Harris (1966a) and Perrins et al. (1973). Fledging success was consistently high and

Table 4.1

Breeding success of manx shearwaters in Observatory burrows, Skokholm.

Year	No. of eggs laid	No. of eggs hatched	% Hatching success (A)	No. of chicks hatched	No. of chicks fledged	% Fledging success (B)	Breeding success (A x B)
1973	68*	55	80.9	66	61**	92.4	74.7
1974	79	54	68.3	56	56	100.0	68.3
1975	69	44	63.8	45	44**	97.8	62.4
1976	72	57	79.2	57	54	94.7	75.0
Totals	288	210	72.9	224	215	96.0	70.0

* Includes one egg which was a re-lay, the first egg having been lost within a week of laying.

** In 1973 and 1975 there were four and five chicks respectively showing symptoms of the disease, puffinosis (Harris 1965a). These nevertheless left the burrow alive and are considered to have fledged successfully.

variations in overall breeding success were mostly due to variations in hatching success which was lowest in 1975 and highest in 1973, but the variations were not so great as to suggest significant differences between years (X^2 test, $p > 0.05$).

Breeding success of established pairs was higher than that of new pairs (Table 4.2). There is no significant difference in the fledging success of the two groups but the hatching success of new pairs is significantly lower than that of established pairs. It is also possible to consider the hatching success of three mutually exclusive categories of new pairs.

(a) Those where both members of the pair have previous breeding experience.

(b) Those where one member of the pair is a new breeder and the other an experienced breeder.

(c) Those where both members are new breeders.

This comparison is made in Table 4.3. Where both members of the pair have previous breeding experience (Category a), hatching success is significantly higher (X^2 test, $p < 0.01$) than where one or both members of the pair are new breeders (Categories b and c). In fact the hatching success of Category (a) new pairs (86.2%) is higher than that of established pairs (79.1%) but not significantly so. There is no significant difference in the hatching success of new pairs belonging to Categories (b) and (c). Within Category (b) new pairs there is no indication that hatching failure is more likely according to whether the new breeder is a male or a female.

There are insufficient data to compare the hatching success of pairs in their second season of breeding together with those which have bred together for more than two years. There were, however, 19 pairs which bred together in 1972 and in every one of the four following study years. They were therefore classified as 'established' throughout the study period. The hatching success of these pairs was 63/73 or 86.3% - the number of eggs laid does not equal 76 because three hatching failures were certainly due

Table 4.2 The breeding success of new and established pairs of manx shearwaters on Skokholm.

	Established pairs				New pairs			
Year	No. of eggs laid	% Hatching success	% Fledging success	% Breeding success	No. of eggs laid	% Hatching success	% Fledging success	% Breeding success
1973	44	81.8	97.2	77.3	17	88.2	93.8	82.7
1974	59	72.9	100.0	72.9	16	62.5	100.0	62.5
1975	49	69.4	97.0	67.4	14	50.0	100.0	50.0
1976	39	97.4	97.4	94.8	30	63.3	89.5	56.7
Weighted means		79.1	98.0	77.5		66.2	94.3	62.5

The hatching success of established pairs is higher than that of new pairs
($X^2 = 4.86$, 1 d.f., $p < 0.05$)

Table 4.3

Hatching success of three categories of new pair of manx shearwater on Skokholm. Data from 1973 - 1976. See text for detailed definition of the three separate categories.

Category of pair	No. of eggs laid	No. of eggs hatched	% Hatching success
(a) Experienced x Experienced	29	25	86.2
(b) Experienced x New	25	15	60.0
(c) New x New	20	11	55.0

to my disturbance. The hatching success of other established pairs, excluding these 19 pairs, was 88/118 or 74.5% which is lower than the hatching success of 86.3% of the 19 pairs, but the difference is not quite significant (X^2 test, $0.05 < p < 0.10$).

I have been unable to detect any significant seasonal trends in breeding success.

If a pair fails to rear a chick in one season this might be because the breeding burrow is in some way unsuitable. It might therefore be advantageous to move to a different burrow the following season. Table 4.4 indicates that pairs are more likely to move burrow following breeding failure than following breeding success. Eviction by other pairs was probably not responsible for the change of burrow since in none of the ten instances of change was the vacated burrow used for breeding by another pair in the season following its use by the original pair. Ashcroft (1976) reported that puffins (Fratercula arctica Brehm) were more likely to move after breeding failure than after success but in this species the difference was not significant.

A breeding failure could also be due to an inability of the two members of the pair properly to co-ordinate their activities (Coulson 1972). If this were so then there could be mutual advantages in divorce, which would allow each member of the pair to mate with another, possibly more suitable, partner and it would be predicted that divorce would be more frequent after breeding failure than success. This is observed (Table 4.5). A similar result has been observed for the kittiwake (Rissa tridactyla L.) (Coulson 1972) and the red-billed gull (Larus novaehollandiae Forster) (Mills 1973). Additionally in the kittiwake, where the frequency of divorce is higher than in the manx shearwater, the probability of divorce is higher after two years of breeding failure than after one. No such effect can be detected in the shearwater.

Table 4.4

The number of occasions on which unchanged manx shearwater pairs on Skokholm moved burrow between consecutive seasons according to their breeding success. Data from Observatory burrows, 1973 - 1976.

	Fledged chick in year N - 1	Did not fledge chick in year N - 1
Breeding in same burrow in year N	121	19
Breeding in another burrow in year N	3	7

Fisher Exact Test, $p < 0.001$

Table 4.5

The incidence of divorce in manx shearwater pairs on Skokholm.

Data from Observatory burrows, 1973 -1976.

	Number of pairs which fledge a chick	Number of pairs which do not fledge a chick
Continue to breed together	131	27
Divorce	7	10

X^2 test, $p < 0.001$

There are disadvantages to divorce including the possibility of failing to find a new mate and breed for one or more seasons; of 34 divorced birds, only 16 are known to have bred in the season following their last breeding attempt in the pre-divorce pairing. Another risk of divorce is the higher probability of hatching failure in the new pairs into which the divorcees will enter than in established pairs (Table 4.2). However both divorcees and other experienced breeders seeking a new mate can apparently achieve as high a hatching success in a new pair as is achieved by established pairs, if they mate with another experienced breeder (Category a, Table 4.3). On the other hand there is no evidence that the hatching success of a new breeder is significantly affected by whether its first breeding attempt is made with another new breeder or with an experienced breeder (Categories b and c, Table 4.3). There is therefore selection on experienced breeders to mate with other experienced breeders when forming a new pair, and Table 4.6 indicates that there is a higher frequency of experienced breeder/experienced breeder combinations in new pairs than would be expected by chance. Coulson (1966) has also reported that, when new Kittiwake pairs are formed, birds with similar breeding experience tend to mate together. It would be expected, on the basis of Table 4.6, that there would also be a tendency for birds of similar age to mate together, a result observed in the red-billed gull (Mills 1973) and the arctic tern (<u>Sterna paradisea</u> Pontoppidan) (Coulson & Horobin 1976). I have few data on this point but they are nevertheless suggestive (Table 4.7).

Laying

Laying Dates

The timing of breeding of the manx shearwater varies little from year to year (Table 4.8). Such constancy of timing is a feature of other migrant shearwater species such as the great shearwater (<u>Puffinus gravis</u> O'Reilly)

Table 4.6

The observed frequency with which the three different combinations of new breeder and experienced breeder occur when new manx shearwater pairs are formed on Skokholm. Data from Observatory burrows, 1973 - 1976. Expected frequencies are generated assuming random pairings between 65 new breeders and 89 experienced breeders.

	New breeder x New breeder	New breeder x Experienced breeder	Experienced breeder x Experienced breeder
Observed	20	25	32
Expected	13.7	37.6	25.7

X^2 test, $p < 0.05$

Table 4.7

The year when breeding manx shearwaters on Skokholm were ringed as chicks if their mate was also ringed as a chick.

Number of pairs

Year when male was ringed as chick		1968	67	66	65	64	63	62	61
	1965		1	(1)					
	66			1	1				(1)
	67		(1)						1
	68	(1)	1						
	69			1					

Year when female was ringed as chick

Note: The four figures in brackets refer to pairs that were not sexed.

Table 4.8

The timing of laying of the manx shearwater in the Observatory burrows in six different years on Skokholm. Data for 1963 - 1964 from (Harris 1966a) and for 1973 - 1976 from this study. Of 15 between-year comparisons available only one, that between 1973 and 1976, is significant at the 5 % level (Median test).

Year	Median laying date	Sample size
1963	10 May	63
1964	9 May	66
1973	10 May	68
1974	9 May	80
1975	9 May	71
1976	8 May	73

on Tristan da Cunha (Rowan 1952), the sooty shearwater (Puffinus griseus Gmelin) on islands off New Zealand (Richdale 1963) and the short-tailed shearwater (Puffinus tenuirostris Temminck) in Australia (Serventy 1963). In the latter species the mean date of laying appears to have varied by no more than four or five days over the last 120 years.

The manx shearwater differs from these species in having a more extended laying period. In the present study 94.5% of 292 eggs were laid in the one month period 26 April-25 May but the earliest and latest eggs were laid about 20 April and 20 June respectively. In contrast 85% of the eggs of the short-tailed shearwater are laid within three days of the mean date of laying.

Such constancy of timing could arise if either the population as a whole laid at the same time each year whilst individual birds were not consistently early or late with respect to the population or, alternatively, the population laid at the same time each year and, additionally, individual birds were consistently early or late. These two alternatives are distinguished in Table 4.9, a table of analysis of variance. The within-pair variance is seen to be significantly less ($p < 0.001$) than the between-pair variance and I conclude that individual pairs tend to breed at a constant time relative to the population as a whole.

Data from new pairs were excluded from Table 4.9 since, as detailed in Table 4.10, new pairs which breed together the following season advance their laying date by a mean of 5.6 days in that following season. This is significantly different (t-test, $p < 0.001$) from the advance of only 0.6 days shown by established pairs. In fact this advance of 0.6 days is not significantly different from zero. When a female moves from an established pair to breed with another male in the following season her laying date is delayed by a mean of 1.7 (S.E. $\pm$ 3.63) days, but the sample size (10) is small

Table 4.9

A table of Analysis of Variance of the laying date (20 April = 0) of unchanged manx shearwater pairs breeding in the Observatory burrows, Skokholm, in the period 1973 -1976. Data from pairs breeding together for the first time are excluded.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Between-pairs	5369.8	57	94.2	5.82
Within-pairs	1795.9	111	16.2	

$p < 0.001$

Table 4.10

Change in laying date of unchanged manx shearwater pairs breeeding in consecutive years in the Observatory burrows, Skokholm. Year N is 1973, 1974 and 1975.

Status of pair in year N		Change of laying date in days (± S.E.) between year N and year N + 1. (+ is equivalent to earlier in year N +1)	Sample size
Established		+ 0.6 ± 0.54	106
New	Female is experienced	+ 7.0 ± 2.25	15
	Female is new breeder	+ 3.6 ± 1.20	11
	Total for new pairs	+ 5.6 ± 1.41	26

A feature of Table 4.10 is that there is no significant difference in the advance of laying date shown by new pairs the following season according to whether the female breeding in that new pair is an experienced or a new breeder. This suggests that the influence of the pair bond on the timing of breeding is generally more important than the influence of age or breeding experience. Nevertheless there is a slight but significant tendency for older birds to lay at an earlier date (Figure 4.2). There are insufficient data for known-age females older than ten years old to determine the age beyond which there is no further advance in laying date. It may be about ten years old for the mean date of laying of 49 eggs laid in the Observatory burrows by females in established pairs with at least ten years previous breeding experience was 7.6 May (S.E. $\pm$ 0.96 days). This mean date may be compared with the regression line shown in Figure 4.2, and is the date of laying of ten year old females.

Egg size

Not only the laying date but also the egg volume of the manx shearwater show little variation from year to year (Table 4.11). Harris (1969c) failed to find any correlation between laying date and egg size in the manx shearwater. In the present study there was a tendency for egg size to decline through the laying period and the correlation coefficients (sample sizes in brackets) between egg volume index and laying date were as follows:- 1973, $r = -0.387$ (69); 1974, $r = -0.134$ (78); 1975, $r = -0.211$ (69); 1976, $r = -0.029$ (72). Only in 1973 was the correlation significant ($p < 0.01$). The regression coefficient in 1973 was significantly different from that in 1976 (t-test, $p < 0.05$) but no other differences were significant. If only established pairs are considered, thereby eliminating from the regression equations new breeders and birds whose laying dates are possibly affected by being in a new pair, then there is little indication of a systematic correlation between laying date and egg size (1973, $r = -0.316$ (45);

Figure 4.2

The laying date of known-age female manx shearwaters on Skokholm, 1973 - 1976. Only females breeding in established pairs are plotted. Lines join laying dates of the same individual in different years. The regression line is as shown but it is unlikely to be linear. N = 31. $r = -0.399$, $p < 0.05$

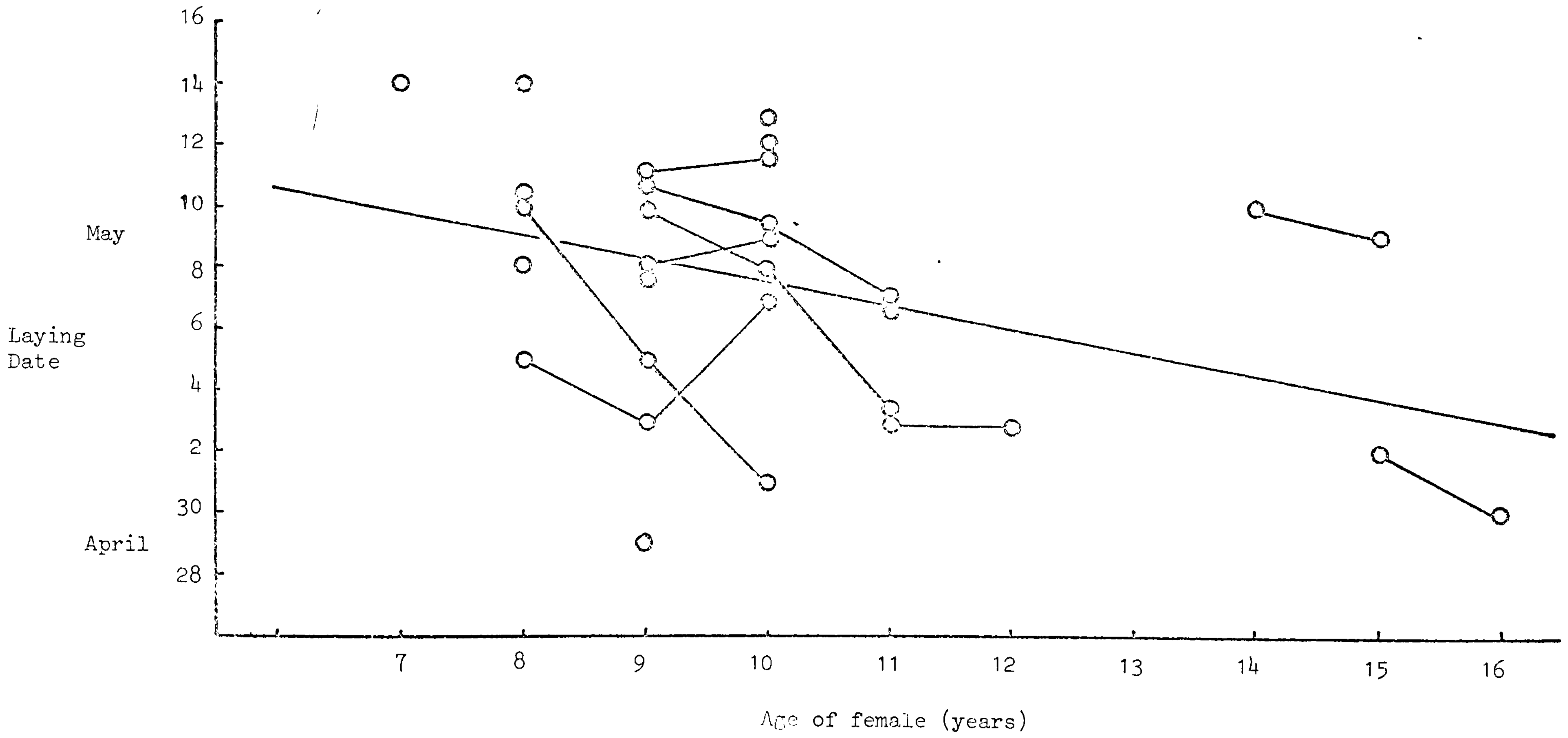


Table 4.11

The mean volume index of manx shearwater eggs laid in the Observatory burrows on Skokholm, 1973 - 1976. Egg volume index is (length in cm.) x (breadth in cm.)^2. No differences between years are significant.

Year	Mean egg volume index (± S.E.)	Sample size
1973	102.7 ± 0.81	83
1974	100.7 ± 0.85	85
1975	102.8 ± 0.78	72
1976	102.3 ± 0.86	76

Table 4.12

A table of Analysis of Variance of the egg volume index of individual female manx shearwaters breeding in the Observatory burrows, Skokholm, in the period 1973 - 1976. Data from new breeders are excluded.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Between-birds	9076	72	126.1	6.37
Within-birds	3125	158	19.8	

$p < 0.001$

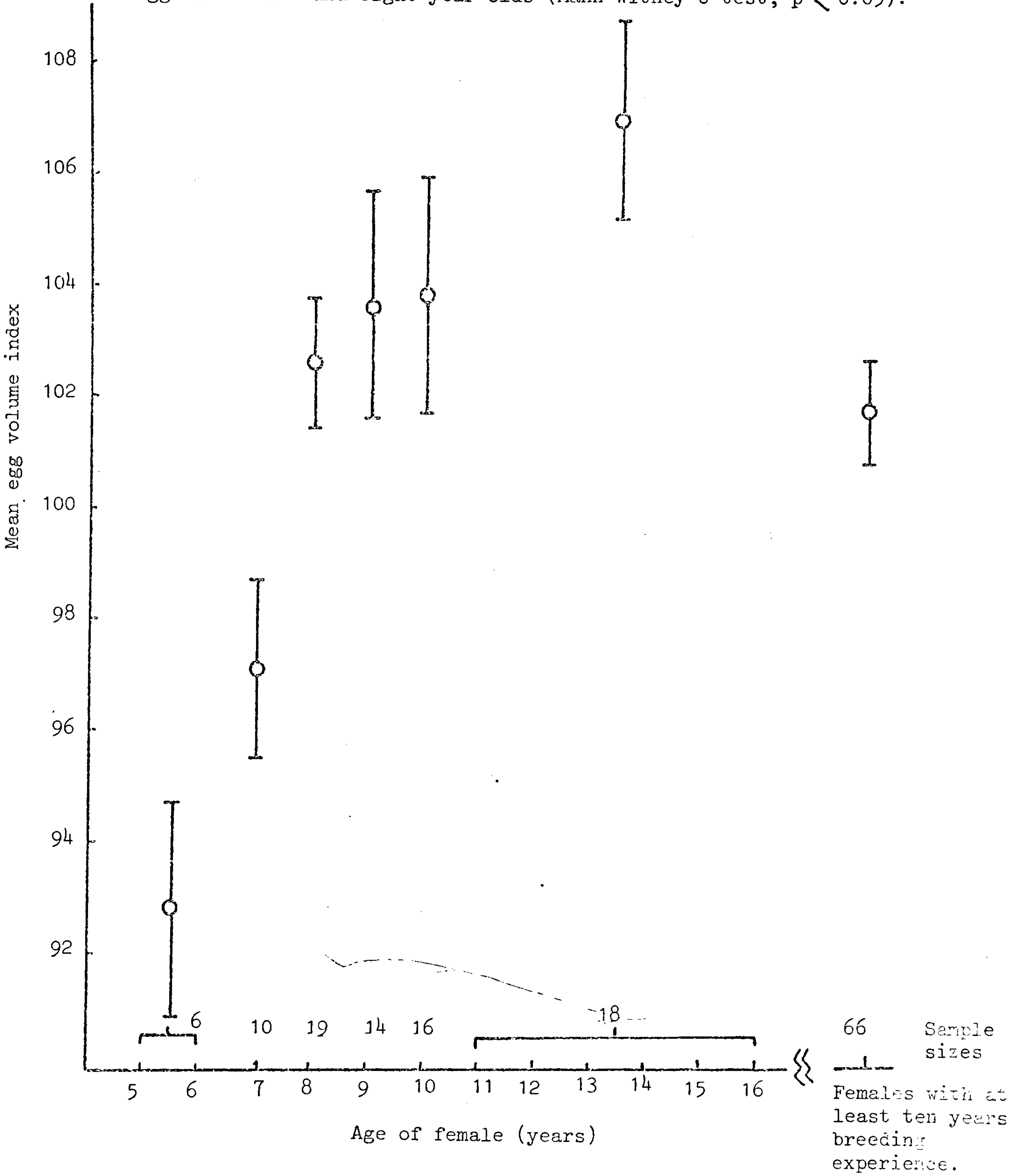
1974, $r = -0.180$ (61); 1975, $r = -0.151$ (53); 1976, $r = 0.219$ (41)), although the correlation in 1973 was still significant ($p < 0.05$). Again the regression coefficient in 1973 was significantly different from that in 1976 (t test, $p < 0.05$) but no other differences were significant. Because there are significant differences between the regression coefficients in different years and also because the observations in different years are not independent, since individual females lay a similar-sized egg (Table 4.12, below) on a similar date (Table 4.9) in different years, it is not legitimate to produce a combined regression of egg volume on laying date for all four years.

The constant egg volume observed in Table 4.11 could arise if the population as a whole laid eggs of similar size each year whilst individual birds did not lay consistently small or large eggs or, alternatively, if the population laid similar-sized eggs each year and, additionally, individual birds laid consistently small or large eggs. These two alternatives are distinguished in Table 4.12, a table of analysis of variance. The within-bird variance is seen to be significantly less ($p < 0.001$) than the between-bird variance and I conclude that individual females tend to lay an egg of similar size in different years.

Data from new breeders were excluded from Table 4.12 since, as shown in Figure 4.3, young birds tend to lay smaller eggs than do older birds. Egg volume increase quite sharply between the ages of six and eight, and more slowly thereafter. The laying of smaller eggs by younger females is a well-known phenomenon amongst seabirds. In species which lay only a single egg it has been reported in the gannet (<u>Sula bassana</u> L.) (Nelson 1966b) and the razorbill (<u>Alca torda</u> L.) (Lloyd 1976). A similar trend of increasing clutch volume (as opposed to single egg volume) with age is seen in species which lay multi-egg clutches, for example the kittiwake (Coulson 1963a), the herring gull (<u>Larus argentatus</u> Pontoppidan) (Davis 1975) and the shag

Figure 4.3

The mean egg volume index (± S.E.) of known-age female manx shearwaters breeding on Skokholm, 1973 - 1976. The egg volume of females with at least ten years breeding experience is also shown. The only significant difference between adjacent points representing known-age birds is that between the eggs of seven- and eight-year-olds (Mann-Witney U-test, $p < 0.05$).



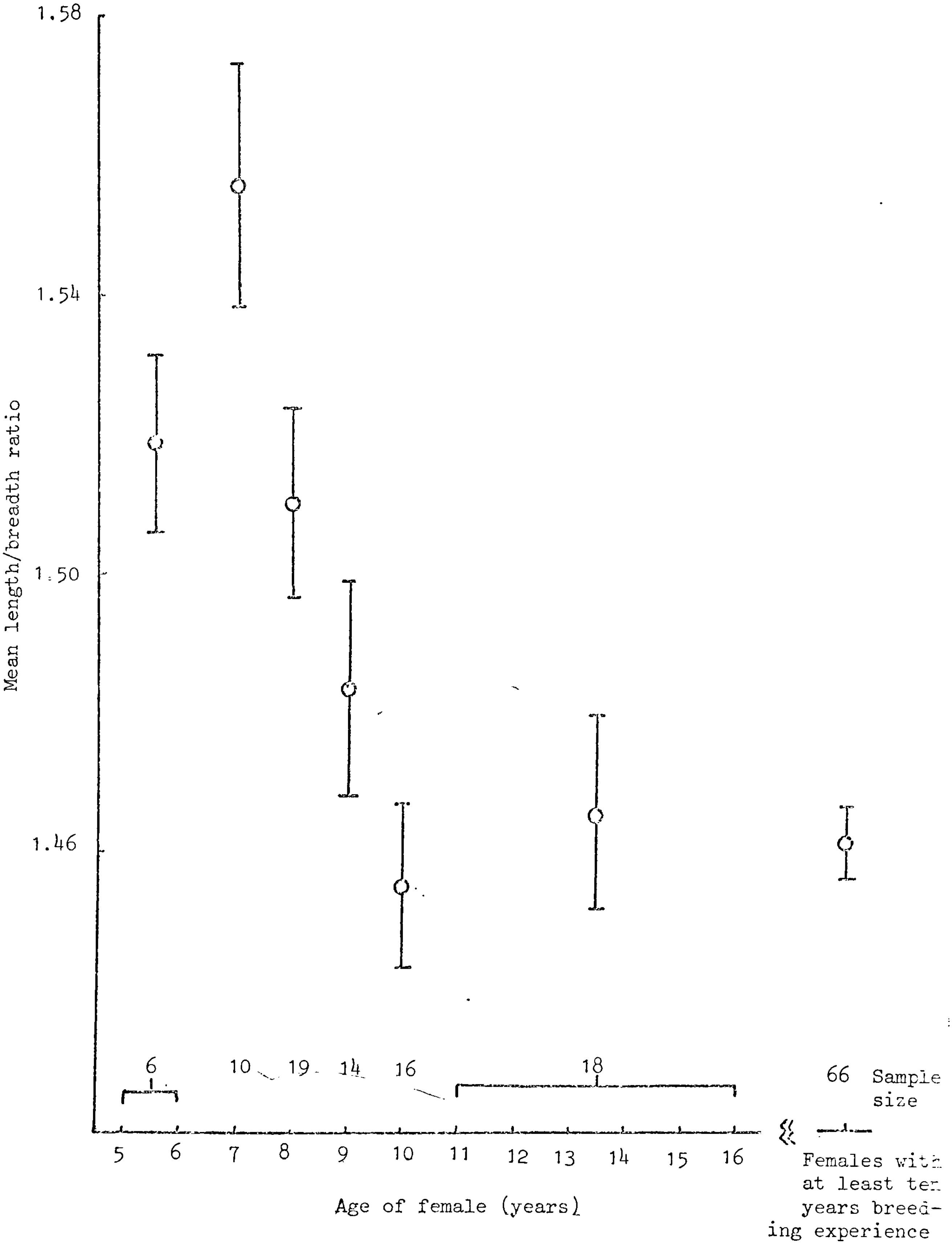
(Phalacrocorax aristotelis L.) (Coulson, Potts & Horobin 1969). The value of an increased egg volume in terms of increasing the probability of survival of the young which hatch from that egg has been demonstrated for the herring gull (Parsons 1970; Davis 1975), the common tern (Sterna hirundo L.) (Nisbet 1973) and great tits (Parus major L.) belonging to late clutches (Schifferli 1973). Using multiple regression techniques I have been able to eliminate the effect of laying date but unable to detect any residual influence of egg volume on the manx shearwater's fledging weight, the importance of which has been demonstrated by Perrins et al. (1973). Nor is there any association between egg volume and hatching or fledging success.

The mean egg volume index of females aged 10-16 years is 105.5 (S.E. ± 1.40) which is significantly greater (t test, $p < 0.05$) than the mean volume index of females with at least ten previous years breeding experience (101.8 ± 0.94). The latter group of females are all at least 15 years old and some may be considerably older since they have been breeding in the Observatory study burrows since 1963 (see Methods and Harris 1966a). A decline in egg size in females aged more than about ten years old was observed in the herring gull by Davis (1975) who attributed the decline to the improved chick-rearing ability of such experienced adults. This ability may enable the adults to compensate for any disadvantages of hatching a smaller chick from the smaller egg and indeed possibly to benefit themselves from the reduction in the amount of resources devoted to egg formation. Great tits aged four and over do not show a reduced clutch volume (Perrins & Moss 1974) but a lower hatching rate leads to reduced reproductive success and this is also associated with increased adult mortality. The reduced egg volume of the experienced manx shearwater is not associated with reduced (or improved) reproductive success but the average life-span of the species is about ten years from the age of first breeding (Perrins et al. 1973) so it might be anticipated that any senility

Figure 4.4

The mean length/breadth ratio of the eggs of known-age female manx shearwaters breeding on Skokholm, 1973 - 1976. The mean length/breadth ratio of females with at least ten years previous breeding experience is also shown.

Note: No differences between adjacent points are significantly different but the mean length/breadth ratio for birds aged 5 - 9, 1.5139 (S.E. ± 0.0107) is significantly different (t-test, $p < 0.001$) from the mean ratio for birds aged 10 - 16, 1.4500 (S.E. ± 0.0117).


1.58
1.54
1.50
1.46
Mean length/breadth ratio
6
10
19
14
16
18
66
Sample size
5
6
7
8
9
10
11
12
13
14
15
16
Age of female (years)
Females with at least ten years breeding experience

effects, if they exist and influence reproductive success at all, would not become prominent until after many, perhaps 20, years of breeding. The study has not continued long enough to allow a considered judgement on this matter.

The length/breadth ratio of the egg laid by the female manx shearwater declines up to age of about ten and thereafter changes little (Figure 4.4). The tendency for older females to lay more spherical eggs has been reported, for example, from the kittiwake (Coulson 1963a), the yellow-eyed penguin (Megadyptes antipodes Hombron & Jacquinot) (Richdale 1957) and Buller's mollymawk (Diomedea bulleri Rothschild) (Richdale & Warham 1973). It is also known from the domestic hen (Gallus gallus L.) (Romanoff & Romanoff 1949) where it is presumed that the shape of the egg is determined by the general physiological condition of the reproductive system and particularly by the muscular tone of the oviduct.

Discussion of Breeding Success and Laying Date

The higher breeding success of established pairs (Table 4.2) is a well-known phenomenon amongst long-lived seabirds and is presumably an important reason why mate constancy is the rule in such species. It has been observed in (and this list is by no means exhaustive) the kittiwake (Coulson 1966), the gannet (Nelson 1966b) and the arctic skua (Stercorarius parasiticus L.) (Davis 1976). In some species such as the arctic skua the lower breeding success of newly formed pairs is partly due to the fact that new pairs breed later in the season when conditions may be less favourable since there is seasonal decline in breeding success even among established pairs (O'Donald, Wedd & Davis 1974). However, in the manx shearwater, the lower success of new pairs is not related to any seasonal decline in breeding success and appears to be related principally to the lower hatching success of new pairs and particularly those containing new breeders (Table 4.3). The difficulties to be overcome by new pairs attempting to hatch the egg are also illustrated by the fact that the mean incubation period of 48 new pairs which succeeded in hatching the egg was 52.4 (S.E. ± 0.62) days which is significantly longer (t test, $p < 0.001$) than the 50.6 (S.E. ± 0.20) days taken by 145 established pairs. The average incubation period of yellow-eyed penguins breeding for the first or second time is also greater than that of older breeders (Richdale 1957).

Experienced breeders can apparently reduce the cost to breeding success of forming a new pair by mating with another experienced breeder (Table 4.3) and this they frequently do (Table 4.6). However there probably remains a cost in terms of delayed breeding (Table 4.10 and text) and hence reduced survival probability of any chick reared (Perrins 1966). Coulson (1966) suggested that kittiwakes with similar breeding experience tend to mate together when new pairs are formed because birds with considerable breeding experience return to the colony in February, less experienced birds in March and early April and new breeding birds in April and early May. Thus, if pairs are formed fairly soon after return to the colony, birds will tend to mate with a partner of similar breeding experience to themselves.

In 1974 and 1975 I started daily checks on some of the Observatory burrows on 15 March and 10 March respectively, about two months before the median date of laying. The mean dates of the first daytime capture of males and females in the burrow in which they later bred are given in Table 4.13. There is evidence that males with greater breeding experience are caught earlier than those with limited experience but the effect does not hold for females. Since more experienced females do not appear to return earlier to the colony Coulson's explanation for the kittiwake data cannot be supported for the manx shearwater.

Table 4.13

The mean date of the first daytime capture of manx shearwaters down the Observatory burrow in which they later bred. Sample sizes in brackets.

	Birds with: -	0 - 2 years of previous breeding experience		At least 5 years of previous breeding experience
Males	1974	1 April (7)	N.S.	22 March (20)
	1975	1 April (7)	$p < 0.05$ (Mann-Witney U-test)	23 March (16)
Females	1974	1 April (6)	N.S.	31 March (26)
	1975	27 March (4)	N.S.	27 March (21)

I have no definite evidence concerning the behavioural mechanisms which enable an experienced manx shearwater to select and mate with another experienced breeder. Since the species is monogamous and since both sexes benefit equally from the selection there is no immediate reason to suppose that the selection is principally the concern of one sex or the other and that sexual selection, in the sense of Darwin (1890), is involved. Nevertheless, in the pre-laying period, the male spends more time visiting the breeding burrow (Harris 1966a; Perrins & Brooke 1976) which may mean that the experienced female has more time available to search actively for an experienced male with which to mate. In the polymorphic arctic skua on Fair Isle, Shetland, dark plumaged males are selected by some females when new pairs are formed (O'Donald, Davis & Broad 1974) and, in this instance, the dark plumage provides both a means and a reason for the selection since, in new pairs, the breeding success of pairs with dark males is higher than those with pale males. The experienced female shearwater has a reason for selecting an experienced male, but I do not know the means by which she does this.

As discussed in the introduction there is an advantage to the manx shearwater in breeding as early as possible in the season since chicks fledging early are more likely to survive (Perrins 1966). There is no evidence that birds which breed early experience a higher mortality which could offset their reproductive advantage, and accordingly Perrins (1970) suggested that, early in the season, females may have difficulty in obtaining sufficient food to produce an egg, and are thereby prevented from laying earlier. The suggestion leads to several predictions which can be tested against the data presented for the manx shearwater and against data from other species where there is also a seasonal decline in reproductive output. Prominent among such other species is the great tit studied by Perrins (1965)

If food limited the formation of egg(s), then it would be expected that there would be variations between years in the timing of laying according to whether food was more or less abundant. Variation in the timing of laying is seen in the great tit (Perrins 1965) and there is evidence that the onset of laying in Audubon's shearwater (Puffinus lherminieri Ridgway) is determined by an irregular improvement in feeding conditions (Harris 1969b). However there is little variation in the timing of laying of the manx shearwater (Table 4.8).

It may be argued that, if the laying date of the manx shearwater varies little between years, feeding conditions could instead be reflected in changes in egg volume. In years when feeding conditions are poor the female might lay on a similar date to normal but produce a smaller egg, reflecting the greater difficulty she has had in building up food reserves. In fact Tables 4.11 & 12 indicate that manx shearwaters laid a similar-sized egg in each of the study years.

In the great tit smaller females lay earlier than larger females (Jones 1973; Garnett 1976). It is suggested that this occurs because smaller females need a smaller absolute amount of food for maintenance and so, when feeding conditions begin to improve at the start of the breeding season, the situation where sufficient food is available both for maintenance and for the formation of an egg is reached earlier for smaller females than for larger females. The observation is therefore in accord with Perrins' (1970) hypothesis. The laying date of 39 manx shearwater females in established pairs in 1974 (the year when I made most measurements of body size) did not significantly correlate with wing length ($r = 0.162$, $p > 0.1$) nor with bill length ($r = -0.119$, $p > 0.1$).

Lack (1966) suggested that the delayed onset of breeding showed by the manx shearwater could be the result of the long period of time required to achieve a level of feeding proficiency sufficient to enable the adult to feed both itself and a chick. Unless the bird actually delays breeding until it reaches a peak or approaches very close to an asymptotic level of feeding proficiency it would be expected on this hypothesis that, if the difficulties in obtaining food were responsible for delaying laying, the laying date of females would advance as they became older. This is observed in the manx shearwater (Figure 4.2). Some advance of laying date with age is seen in other seabird species such as the laysan albatross (Diomedea immutablis Rothschild) (Fisher 1969), the kittiwake (Coulson 1966), the herring gull (Davis 1975) and the shag (Coulson et al. 1969), and also the great tit (Perrins 1965), but in the yellow-eyed penguin the laying date becomes later with age once the first two years of breeding are passed (Richdale 1957).

From the foregoing discussion I conclude that the timing of laying of the female manx shearwater is not determined primarily by the difficulties she may experience in building up the food reserves necessary to form an egg but these difficulties may have some importance as evidenced by the advancement of laying date and increase in egg size with age. If food for egg formation is not considered the primary determinant of laying date the question as to why the manx shearwater does not breed earlier remains, and I now propose an alternative hypothesis.

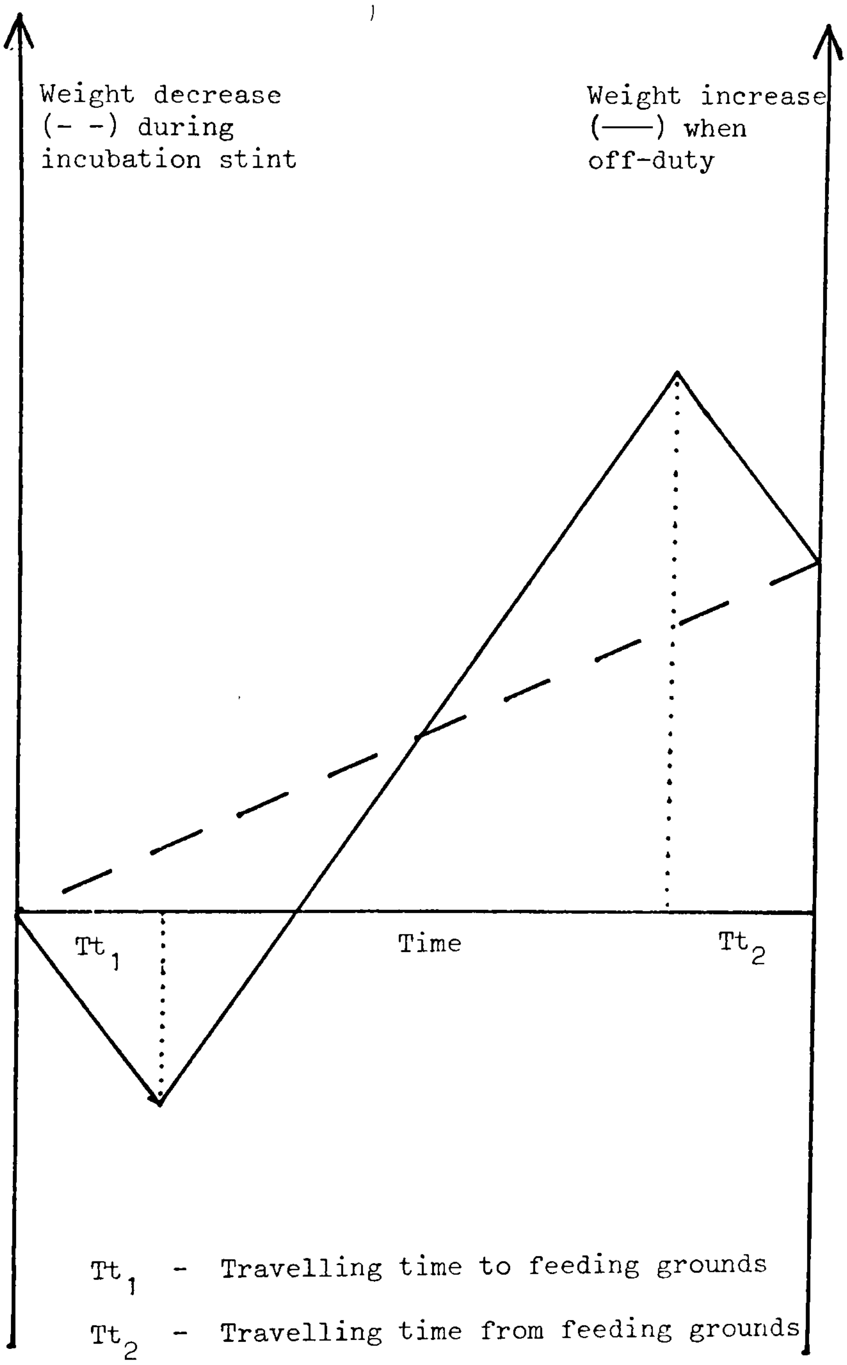
Since the manx shearwater only lays one egg per season it is evidently important to lay that egg at a time of year when the egg may first be hatched successfully, and the nestling then reared. If the egg is laid too early to allow successful incubation then the opportunity of breeding successfully that year is effectively lost since relaying only occurs very rarely (Harris 1966a; once out of 77 eggs lost in the Observatory burrows in the study period) and, in any case, any chick fledging from a replacement egg will fledge late with a correspondingly low chance of survival. I therefore suggest that the manx shearwater delays laying until such time as there is a high probability that any egg laid can be successfully incubated by the two parents. Successful incubation demands more or less constant attendance by the two parents since an unattended egg, though it may be resistant to chilling (Matthews 1954), is frequently damaged when other shearwaters visit the burrow by night (personal observation).

The incubation schedule of the manx shearwater has been summarised by Harris (1966a), and the problem facing a pair of incubating shearwaters is depicted in Figure 4.5. If the members of the pair are not to lose weight during the 50-day incubation period, then the net rate of weight increase of the off-duty parent, including the time spent travelling to and from the feeding grounds, must equal the rate at which the incubating parent loses weight in the breeding burrow. If feeding conditions are poor or the feeding grounds distant then the above requirement cannot be met and, it is suggested, the manx shearwater delays laying. As either feeding conditions improve and/or the feeding grounds move closer to the colony so incubation becomes possible. If the improvement continues during the incubation period then the off-duty parent can recoup the weight loss of the last incubation stint more rapidly and either return to relieve the partner after a shorter period or return to the burrow at a higher weight. Evidence that the duration of incubation stints decreases as the season progresses is offered below.

Perrins' (1970) hypothesis has the merit that the factor, food, which limits the onset of laying can also serve to initiate laying. In other words the proximate and ultimate factors determining the timing of laying are the same. In the present hypothesis incubation is proposed as the ultimate factor. In view of the year-to-year constancy of laying both of individuals and of the population (Tables 4.8 & 4.9) a possible proximate

Figure 4.5

A simple graphical illustration of the weight changes a manx shearwater undergoes during incubation, assuming that weight is not lost over the whole incubation period.



factor would be light, the importance of which in inducing sexual development has long been known (Rowan 1938). However Marshall and Serventy (1959) carried out experiments on the short-tailed shearwater which, like the manx shearwater, shows a constant laying date and found that sexual development appeared to be controlled by an internal rhythm and, within the time limits of the experiment, did not respond to artificial changes in the light regime. In the absence of experimental evidence I suggest that the observed constancy of laying date of the manx shearwater is largely the result of control by some unidentified factor which shows very exact annual periodicity and which may be exogenous or endogenous (Gwinner 1975). Clearly the control mechanism must be responsive to changes in the pair-bond status of the female and, given the advantages of laying early, it must enable the female to lay a little earlier as she ages, gains breeding experience and possibly becomes able to maintain incubation from an earlier date. Thus there is a small advance of laying date with age (Figure 4.2) and this tendency is compatible both with my hypothesis and that of Perrins. The constancy of egg size, once the female has passed the first few years of laying during which time anatomical changes may be important, is simply taken to be a characteristic of the individual female (Romanoff & Romanoff 1949), a characteristic on which no strong selective forces are known to be acting in the manx shearwater.

By emphasising the possible difficulties of incubation early in the season this hypothesis suggests that the delay of laying date experienced by females when they form a new pair may not simply be a disadvantageous consequence of pair formation. The delay may actually serve to increase the chance that the new pair, whose incubation activities may not be as well co-ordinated as those of an established pair, will succeed in hatching the egg because, by delaying laying, incubation is carried out at a more favourable time.

Incubation Period

I now consider evidence concerning a seasonal change in feeding conditions such as might serve to facilitate incubation.

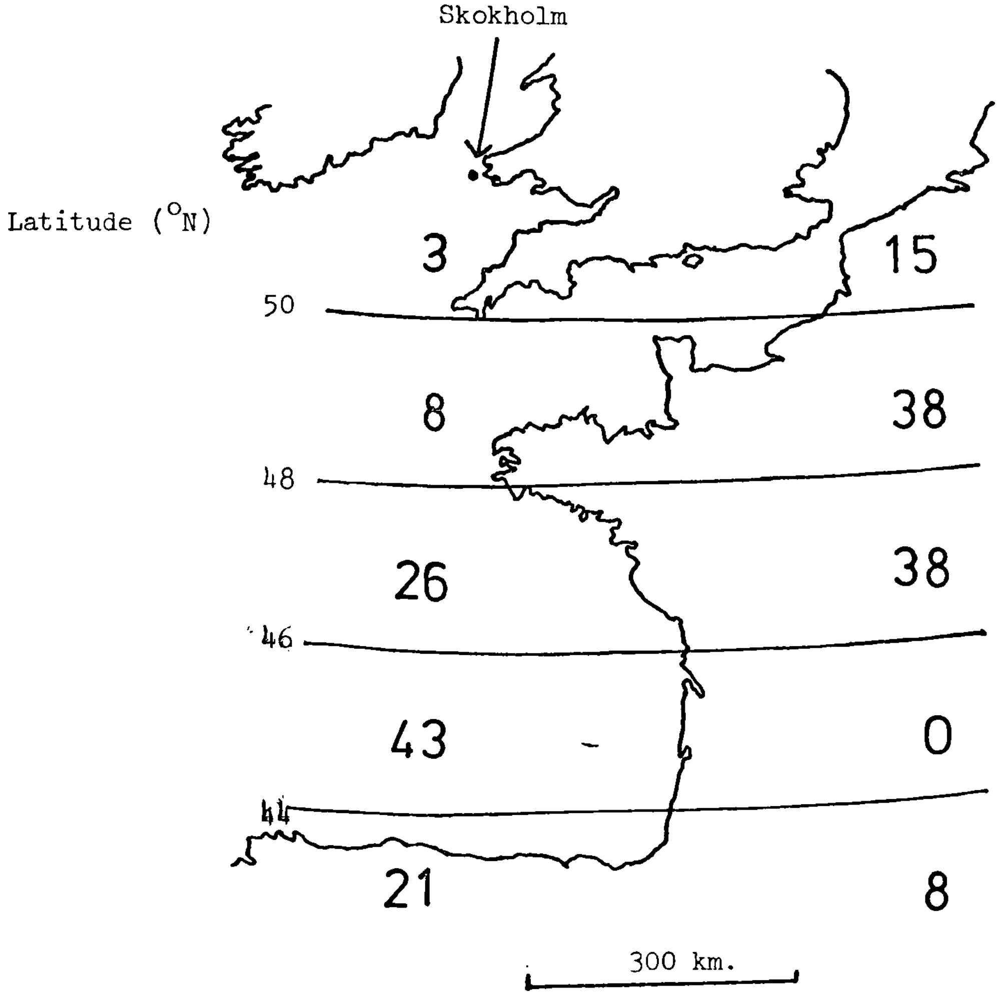
There are no data available concerning the rate at which shearwaters can catch fish and the rate at which they increase in weight at the fishing grounds. However there is evidence that shearwaters of breeding age are recovered closer to Skokholm during the incubation period than during the pre-laying period (Perrins & Brooke 1976), as is illustrated in Figure 4.6. During the nestling period, roughly July and August, they may be feeding even closer to Skokholm; Harris (1966a) has suggested within a radius of 300 km.

If the feeding grounds are moving closer to Skokholm during the incubation period, thereby reducing the travelling time (Figure 4.5), then this could result in a tendency for the length of incubation stints to decrease during the incubation period. There appears to be a direct relationship between the length of the incubation shift and the feeding distance in the sooty tern (Sterna fuscata L.) (Brown 1975). I collected data on the length of incubation stints from 16 Observatory burrows in 1975 and from 23 burrows in 1976. There were no significant differences in the lengths of incubation stints in the two years and therefore data from 1975 and 1976 are amalgamated in Table 4.14. Data from stints interrupted by hatching are excluded. It is seen that stints commenced before 31 May (approximately the middle of the incubation period) tend to be longer for both males and females than stints started after 30 May. I also examined incubation data from 1963 and 1964 kindly supplied by Dr. M. P. Harris and the same tendency was observed in these years, but it was then not significant.

It is important for my argument that the reduced duration of incubation stints should not be accompanied by any reduction in the weight of breeding

Figure 4.6 (after Perrins and Brooke, 1976)

Latitude of recovery of adult manx shearwaters, in at least their sixth year of life, recovered at sea.



Left-hand column of figures; percentage of 80 birds recovered in each of the five latitudinal bands between 1 April and 10 May.

Right-hand column of figures; percentage of 13 birds recovered in each of the five latitudinal bands between 11 May and 30 June, a period roughly corresponding to the incubation period.

Table 4.14

The mean length in days (± S.E.) of incubation stints of the manx shearwater on Skokholm in 1975 and 1976. Sample sizes in brackets.

	Incubation stint commenced	
	Before 31 May	After 30 May
Males	7.58 ± 0.23 (73)	6.88 ± 0.29 (51)
	t-test, $p < 0.1$	
Females	6.29 ± 0.24 (55)	5.42 ± 0.23 (60)
	t-test, $p < 0.02$	

adults since, if there was such a reduction, this could indicate that the shorter incubation stints result not from any improvement in feeding conditions but from a tendency of the breeding birds to return to relieve the mate in the burrow before they themselves have fully made up the weight loss experienced during the last incubation stint. Table 4.15 indicates that there is no seasonal reduction in the weight at which breeding adults return to the burrow to begin incubation stints.

There is thus circumstantial evidence that feeding conditions, in so far as they affect breeding adults, improve during the incubation period. If this improvement started during the pre-laying period and was necessary to raise feeding conditions to a level which allowed adults to sustain incubation for about 50 days, then it becomes possible to suggest that the manx shearwater is unable to lay its egg at the optimum time for rearing a chick because it would experience difficulties in successfully incubating the egg laid early enough to produce that chick.

Table 4.15

The mean weight of manx shearwaters in grams (± S.E.) at the start of incubation stints. Sample sizes in brackets. In neither 1975 or 1976 is there a significant difference between the mean weight at the start of stints begun before 31 May and the mean weight at the start of stints begun after 30 May.

		Incubation stint commenced	
		Before 31 May	After 30 May
Males	1975	486.7 ± 5.65 (32)	481.0 ± 5.07 (36)
	1976	472.8 ± 4.78 (44)	472.5 ± 4.11 (38)
Females	1975	468.9 ± 5.87 (23)	472.9 ± 5.44 (34)
	1976	460.1 ± 4.54 (32)	459.8 ± 4.69 (37)

CHAPTER FIVE

Factors affecting the weight and survival of nestlings

Factors affecting the weight and survival of nestlings

Introduction

It is known (Perrins 1966) that the date at which young Manx Shearwaters fledge influences the probability that they will survive to return to the natal colony, Skokholm Island. Usually it is the case that those young fledging early in the season are more likely to survive than those fledging later. During the years 1965, 1966 and 1967 some 10,000 young Manx Shearwaters were caught immediately prior to fledging, ringed and weighed (Perrins, Harris & Britton 1973). In each year the weight of the fledglings declined during the fledging period although the rate of decline varied between years. The probability of survival of the fledglings was not only related to their date of ringing but was also influenced by their weight at ringing. Survival of the heavier birds was higher than the lighter ones.

In this chapter I attempt to examine the factors influencing the weight of fledglings and, in particular, try to determine whether the lower weight of the late-fledging young is due to poorer feeding conditions late in the season or to a tendency for adult shearwaters less proficient at rearing heavy young to breed later.

The work of Perrins (1966) and Perrins _et al_.(1973) leaves unanswered one question. Do the early fledging young generally have a higher survival simply because they are, on average, of higher weight, or are there seasonal factors acting independently of weight to affect the chances of survival of the young? I analyse the survival and weight data gathered from 1965, 1966 and 1967 fledglings but am unable satisfactorily to answer this question.

Methods

In the vicinity of the Observatory buildings on Skokholm I maintained a detailed watch on a group of study burrows, termed the Observatory burrows, in each of four breeding seasons, 1973 to 1976. About 45-55 chicks were reared in these burrows each year. The burrows were inspected daily in the hatching period, so that the hatching date is known, and also daily from when the chick was 35 days old until it fledged when about 70 days old. During the latter period the chick was weighed daily (at the same time each day) so that the peak weight, which occurs between days 39 and 61 (Harris 1966a), was known as was the 60-day weight, the fledging weight, the age when last fed and the age at fledging.

Many of the Observatory burrows have been under observation since 1963 (Harris 1966a) and so detailed records of the histories of many of the adults breeding in these burrows are available. As far as possible all burrows in the area where the Observatory burrows were situated were opened for inspection, but a few remained unopened because of the nature of the ground. It is also possible that birds previously breeding outside the study area moved to within it. With this caveat a bird is considered to be making its first breeding attempt when it is breeding for the first recorded time, in a burrow that has been regularly checked during the year preceding that first recorded attempt.

Although much information in this chapter was derived from the Observatory burrows these burrows were only occupied by a small number of birds which had been ringed as chicks and hence were of known age. To acquire a larger sample of known-age breeding birds I opened for inspection burrows in the Main Colony and elsewhere on the island. These burrows will be referred to as Main and Elsewhere respectively (Perrins _et_ _al_. 1973). A proportion of these burrows was opened in each season, 1973-1975, so that data on chick weights from these burrows are available for a maximum of four years. The routine of burrow checking and chick weighing for these burrows was identical to that maintained for the Observatory burrows. In general the only Main and Elsewhere burrows that were studied in detail were those where one, or in a a few cases both, parents had been ringed as chicks. The pattern of chick growth in these burrows might therefore not have been representative of the growth of all chicks, and so analysis of the effect of hatching date on chick weight was restricted to chicks in the Observatory burrows whose parents, it is thought, represented a random sample of the population.

In an experimental attempt to determine whether the low weight of late fledging young is due to poorer feeding conditions late in the season or to a tendency for adult shearwaters less proficient at rearing heavy young to breed later, I swapped eggs between early and late laying pairs. The rationale for such an experiment is as follows. If, for instance, early-laying pairs, now with a late-hatching egg and late-fledging chick, rear a heavy chick and the late-laying pairs, now with an early-fledging chick, rear a light chick, then parental factors are probably more important than seasonal factors, or vice versa. This experiment was conducted in the Main Colony in 1974 and 1975. For the purpose of deciding how to re-allocate the eggs during the swapping experiment the experimental burrows were split into two equal groups, according to whether the egg was laid before or after the median laying date. Burrows from each group were paired at random, by drawing from a hat, and eggs were then swapped between the pairs of burrows. 14 pairs of eggs were swapped in 1974, and the mean difference (± S.D.) in the laying date of the two eggs of the pair was 12.6 (± 8.43) days. 18 pairs of eggs were swapped in 1975 and the mean difference was then 10.7 (± 5.88) days. Experimental chicks were weighed at five-day intervals. Unchanged Manx Shearwater pairs which raised an experimental chick in 1974 were not used in the 1975 experiment. However, when pairs which had raised an experimental chick in either 1974 or 1975 raised their own chick in either 1975 or 1976 respectively, the growth of this chick was also monitored, by weighings at five-days interval, thus effectively providing a between-year control of the within-year swapping experiment.

In discussing survival in relation to fledging weight and date of fledging I consider a bird to have survived if it was known to be alive on 1 January following the year in which it was hatched, either because it yielded a ringing recovery after this date or, as in over 90% of instances, because it was recaptured alive on Skokholm. Obviously some birds may have survived without being recaptured, particularly if they moved from their natal area to an area of the island where little recapture work was done (see also Chapter 6). However analysis of data from chicks ringed in the Main Colony in 1968 and 1969 showed no relation between date of ringing as a fledgling and probability that surviving fledglings would be recaptured outside the Main Colony. Following Perrins et al. (1973) the analysis of survival in relation to fledging weight and date was restricted to birds ringed in the Main Colony.

Results

Seasonal influences on the weight of chicks

The mean weight of chicks when fledging from the Observatory burrows is given in Table 5.1. Chicks showing visible symptoms of puffinosis (Harris 1965a) are excluded from the Table, which also indicates significant differences between years. In each year there was a negative correlation between hatching date and fledging weight and the correlation was significant ($p < 0.01$) in all years except 1976. The correlation coefficients were as follows (sample sizes in brackets): 1973, r = -0.415 (53); 1974, r = -0.393 (56). r = -0.469 (39); 1976, r = -0.200 (53). Data for 1973, the study year when the seasonal decline in fledging weight was most marked, are plotted in Figure 5.1. The slopes of the regression of fledging weight on hatching date

Table 5.1

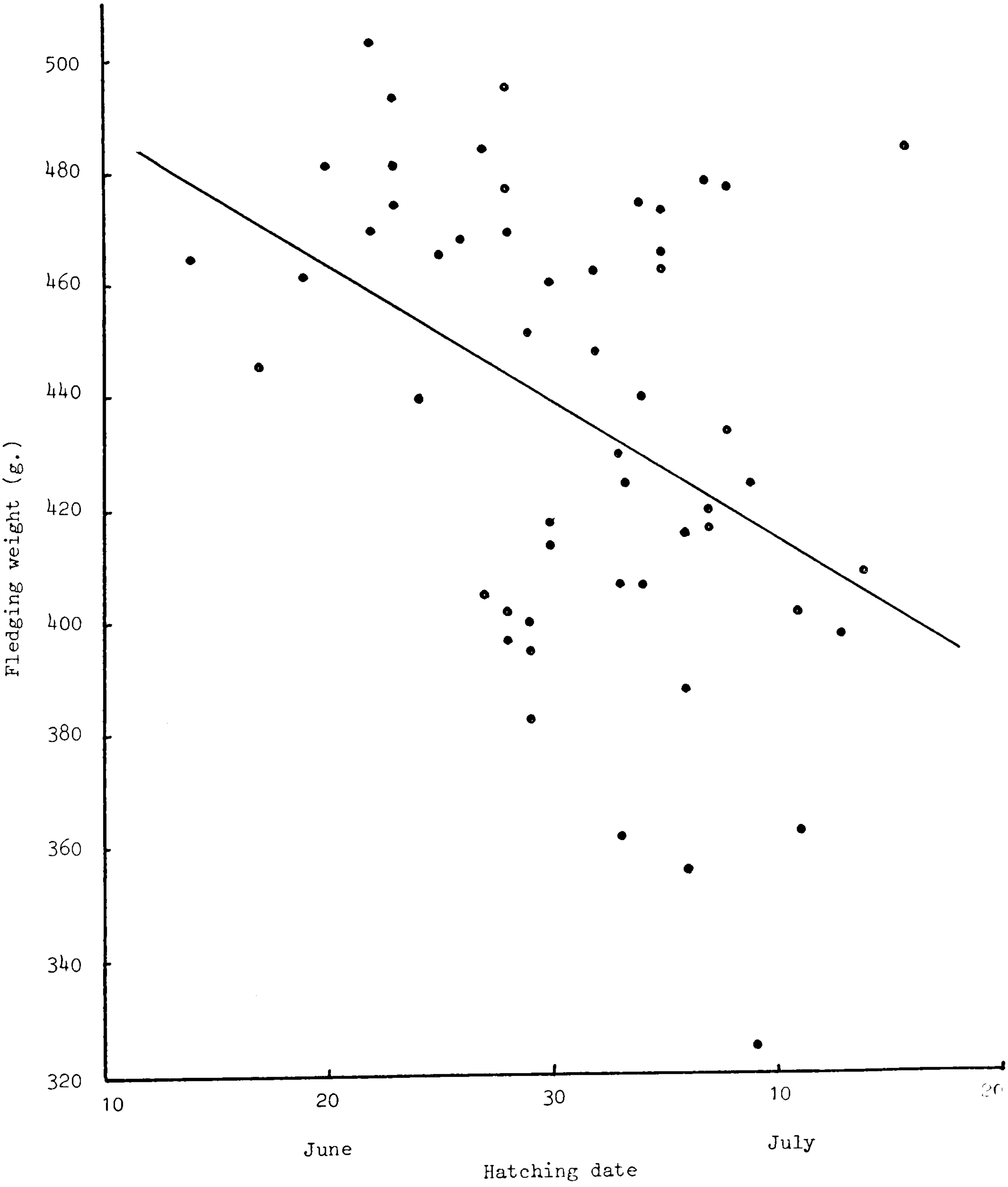
The mean weight of Manx Shearwater chicks when fledging from the Observatory burrows on Skokholm, 1973 - 1976.

Year	Mean Weight (gm.)	S.E.	Sample Size
1973	438.2	5.38	57
1974	455.2	5.69	57
1975	427.1	5.09	41
1976	444.7	5.52	54

Significant differences (t-tests); 1973 v 1974, $p < 0.05$
1974 v 1975, $p < 0.001$
1975 v 1976, $p < 0.05$

Figure 5.1

The relation between fledging weight and hatching date for Manx Shearwaters hatched in the Observatory burrows in 1973. The regression line is: - $y = 488.6 - 2.439\,x$ N = 53



for the four years are given in Table 5.2, again excluding puffinosed chicks. There are no significant differences in the slope in different years. However, since it is assumed that chicks in the Observatory burrows are reared by a random selection of breeding adults, the fact that there are marked differences between years in the rate of decline of fledging weight could be taken as suggestive prima facie evidence that environmental as opposed to parental factors are at least partly responsible for that decline.

The seasonal decline in fledgling weight was not due to any change in the age at fledging. Combining all four study years the mean age (± S.D.) at fledging of 99 chicks which hatched on or before 28 June was 71.1 (± 2.89) days. The mean age of 102 chicks which hatched after 28 June was 71.2 (± 2.75) days.

Whilst, as mentioned above, there was usually a significant negative correlation between hatching date and fledging weight, in none of the four study years was there a significant correlation between hatching date and peak weight. Such a correlation might be expected if there was a tendency for adult shearwaters more proficient at rearing heavy young to breed earlier. The peak weight is usually reached when the chick is about 50 days old (Harris 1966a), some 10-15 days before the last feed and 20 days before fledging. Since fledging weight but not peak weight is negatively correlated with hatching date it seems possible that the seasonal decline in fledging weight is particularly due to difficulties the parents may have in feeding the chick in the last 20 days before fledging, especially if the chick fledges late in the season. Two lines of evidence support this possibility, as discussed below.

(i) The chick usually receives its last feed about 8.5 days before fledging (Harris 1966a, this study) but the duration of the starvation period can vary between 1 and 23 days (this study), and is positively

Table 5.2

The slope (gm./day) of the linear regression of fledging weight on hatching date for Manx Shearwater chicks fledging from the Observatory burrows on Skokholm, 1973 - 1976.

Year	Slope	S.E.	Sample Size
1973	- 2.44	0.749	53
1974	- 1.57	0.501	56
1975	- 1.72	0.533	39
1976	- 0.96	0.659	53

correlated with hatching date ($r = 0.249$, $p < 0.02$) as shown in Figure 5.2. What is, in effect, the same result may be expressed by saying that the number of days between hatching and the last feed is negatively correlated with hatching date ($r = -0.257$, $N = 204$, $p < 0.01$). In both these correlations data from all four years have been lumped together since the day when the chick receives its last feed is influenced by the state of the moon (adults visit the burrow less frequently during bright nights around full moon), and the phase of the moon at the mean fledging date is different in different years. The parents of late chicks therefore feed the chick for a lesser number of days and this is to the detriment of the chick's survival chances, since it fledges at a lower weight. Presumably the adults improve their own survival chances by deserting the chick earlier. Harris (1966a) has suggested that the pattern of growth of the young shearwater and the existence of a starvation period allow the adults to leave the breeding area rapidly at the end of the breeding season, when feeding conditions may be deteriorating, and commence migration earlier than would be the case if they had to feed the young until fledging.

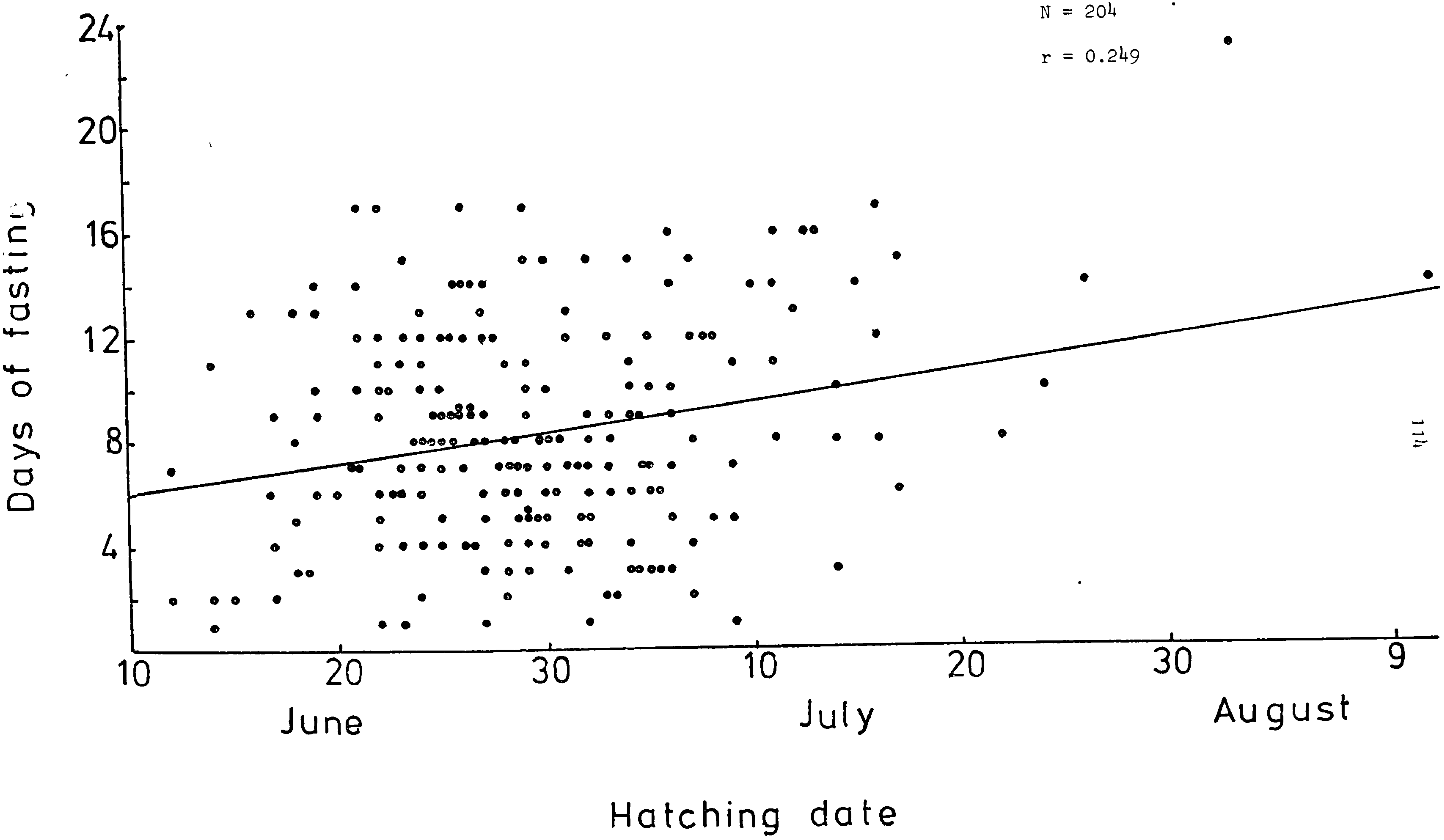
(ii) If adults desert late chicks at a younger age because feeding conditions are then deteriorating, this could be also reflected in the late chick receiving fewer feeds in the last ten days before desertion. To investigate this I correlated the number of feeds received in the ten days before the last feed and the date of the last feed. Because the day-to-day weight loss of a young shearwater which is not fed overnight depends on a number of factors such as the size of the last feed, the number of days which have elapsed since the last feed and the age of the chick (Scott 1970), I arbitrarily decided to consider that a chick had been fed if it gained weight or if it lost not more than ten grams between weighings. Combining all four years there was a significant correlation ($r = -0.286$, $N = 207$, $p < 0.01$) between the number of feeds received in the ten days before the last feed and

Figure 5.2

The duration of the starvation period of Manx Shearwater nestlings in Observatory burrows on Skokholm plotted against hatching date. Data from 1973 - 1976 combined. The regression line : $y = 0.119x + 6.017$

$N = 204$

$r = 0.249$



and the date of the last feed (Figure 5.3). There is no evidence that those chicks which receive fewer feeds receive more food at each feed, since the weight change of the chick in the ten days before the last feed is well correlated with the number of feeds received in that ten day period ($r = 0.563$, $N = 203$, $p < 0.001$).

Parental influences on chick weight

Since individual pairs tend to lay at the same time each year (Chapter 4) and since there is a tendency in all years for later chicks to fledge at a lower weight, it would be expected that individual pairs would tend to fledge their chicks at a similar weight, relative to the mean fledging weight, in different years. However, given the regression of fledging weight on hatching date for a particular year, it is possible to predict the fledging weight of a chick hatching on a particular date and then determine the magnitude and sign of the deviation from the prediction shown by any one chick. If unchanged individual pairs show consistent differences in their ability to feed chicks then the within-pair variation in the deviation of the chick's fledging weight from the prediction should be less than the between-pair variation. This is the case as shown in Table 5.3. Thus, after correcting for date, individual pairs tend to fledge chicks at a weight which is consistently greater or less than expected on the basis of the chick's hatching date. There are insufficient data available to determine whether this result is in any way due to the fact that individual pairs typically breed in the same burrow in different years (Table 4.4).

Since the breeding histories of many of the adults breeding in the Observatory burrows are known, it is possible to assess the influence of adult breeding experience on chick fledging weight, as is done in Table 5.4. There is no detectable relationship between the breeding experience of adults and the fledging weight of the chicks they rear.

Figure 5.3

The number of feeds received by Manx Shearwater chicks in the Observatory burrows in the ten days before the last feed plotted against the date of the last feed. Data from 1973 - 1976 combined.

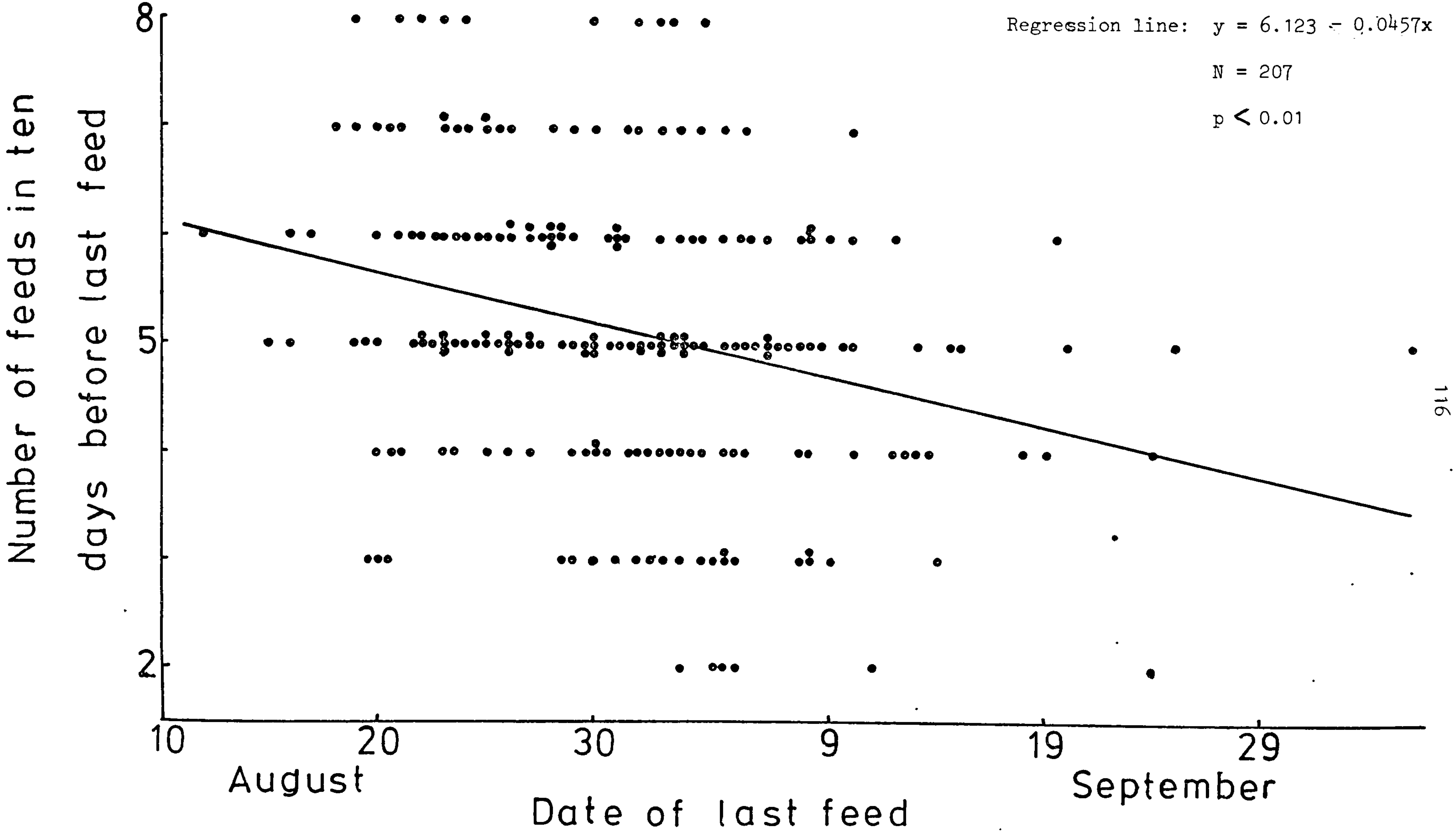


Table 5.3

A table of analysis of variance of the deviation, from the regression of fledging weight on hatching date, of the fledging weights of chicks raised by 53 unchanged Manx Shearwater pairs which fledged a chick in the Observatory burrows in more than one year during the study period, 1973 - 1976.

Source of variation	Sum of squares	Degrees of freedom	Mean square	F-ratio
Between pairs	75177	52	1445.7	1.528
Within pairs	84191	89	946.0	

$p < 0.05$

Table 5.4

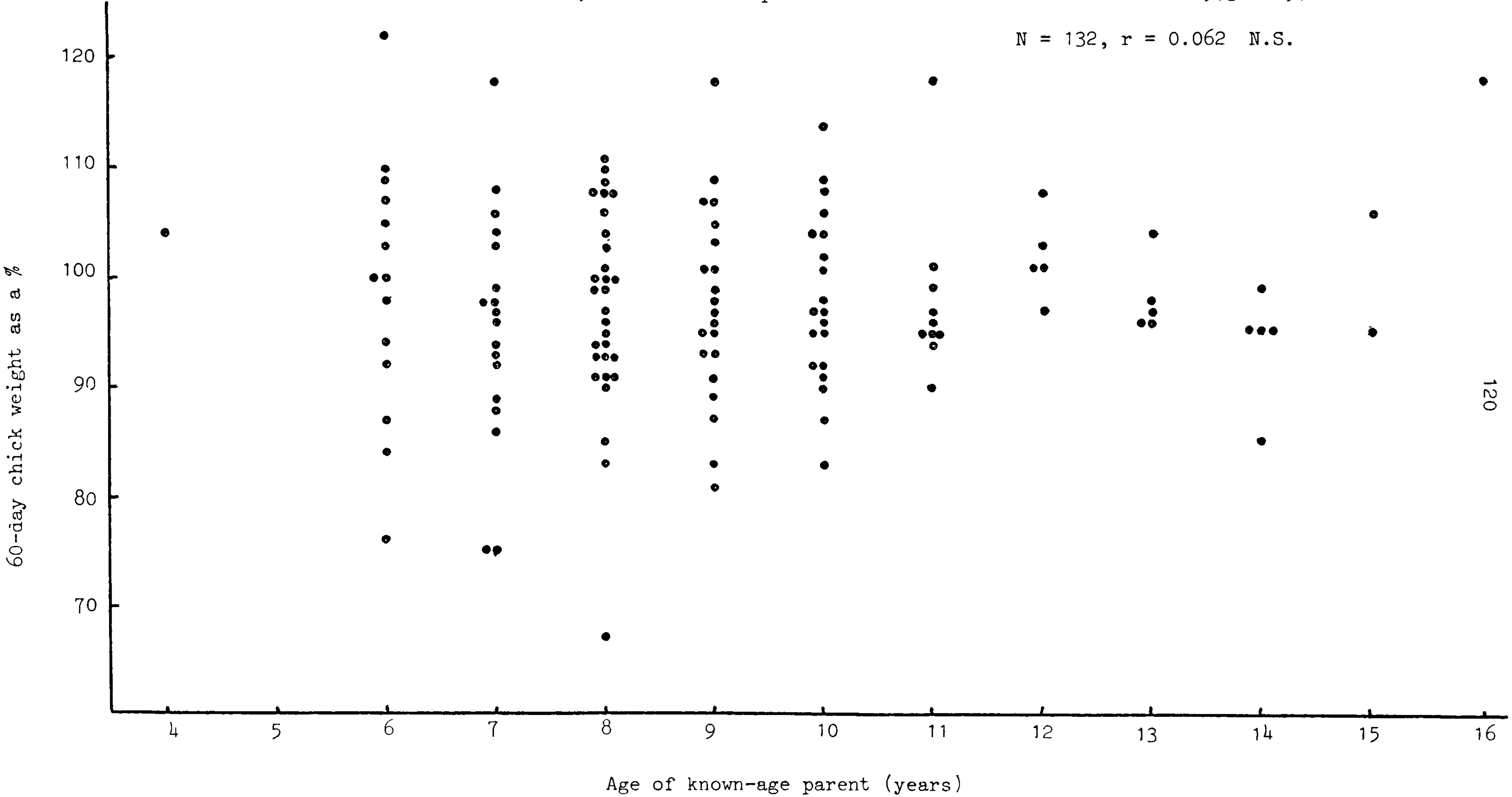
The mean fledging weights (gm.) of Manx Shearwater chicks reared by adults of differing breeding experience in the Observatory burrows, Skokholm. Sample sizes in brackets. None of the means of the three columns are significantly different.

Both parents have made x previous breeding attempts	x =	0 - 1	2 - 4	5^+
1973		398.5 (2)	418.5 (2)	439.3 (22)
1974		467.6 (5)	441.0 (2)	456.1 (23)
1975		425.0 (3)	404 (1)	436.6 (17)
1976		453.3 (10)	425.8 (5)	445.2 (20)
	Means ± S.E.	447.2 ± 8.38	425.2 ± 8.14	444.9 ± 4.94

This matter can also be investigated by comparing the weights of chicks reared by parents of known age, most of which were breeding in Main and Elsewhere burrows. There is a problem in making such a comparison. The mean age (± S.E.) at fledging of chicks reared in the Observatory burrows was 71.2 ± 0.20 days (N = 201) which is significantly greater (t-test, $p < 0.001$) than the mean age, 68.0 ± 0.33 days (N = 124), at which chicks from Main and Elsewhere burrows departed from the burrow. The age at peak weight for the two groups was 51.3 ± 0.34 (N = 211) and 51.7 ± 0.51 (N = 100) days respectively, which is not significantly different. The early departure of the Main and Elsewhere chicks probably does not represent earlier fledging and faster development but instead results from the fact that chicks in these areas were disturbed, when they emerged from the burrows to exercise in the few nights prior to fledging, by the nocturnal chick ringing activities that were carried out in the areas where the Main and Elsewhere burrows were situated but not where the Observatory burrows were situated. After the disturbance the Main and Elsewhere chicks probably returned to a burrow other than their own before actually leaving the island one or more nights later. Accordingly to compare the weights of chicks reared by parents of known age I have used 60-day weight. 60-day weight is positively correlated with fledging weight in chicks reared in the Observatory burrows ($p < 0.001$ in 1973, 1974 and 1976; $p < 0.05$ in 1975). Since there are significant annual variations in fledging weight (Table 5.1) and also in 60-day weight, the 60-day weight of chicks with one or two parents of known age is experessed as a percentage of the mean 60-day weight of all chicks reared in Observatory burrows during the appropriate year. The results are shown in Figure 5.4. It must be emphasised that, in the great majority of cases, the age of only one parent was known and there was no information at all on the age or breeding experience of the other parent. However, had there been a marked effect of parental age on 60-day chick weight, this would probably have been

Figure 5.4

The 60-day weight of Manx Shearwater chicks, with one or two parents of known age, expressed as a percentage of the mean 60-day weight of all chicks reared in the Observatory burrows in the appropriate year. Where both parents are of known age, the chick is plotted twice, once for each parent. Data from all areas and from 1973 - 1976.



detected despite the masking effect of the parent of unknown age. The fact that parental age appears not to influence 60-day chick weight agrees with the observation (Table 5.4) that parental breeding experience does not affect chick fledging weight. Nor is there any significant relationship between parental age and chick weight if male and female parents are considered separately.

Egg-swapping experiment

In the previous two sections I have implicated environmental factors as being partly responsible for the seasonal decline in fledging weight and also shown that, after correcting for date, individual pairs tend to fledge chicks at a weight which is consistently greater or less than expected. No tendency for adult Manx Shearwaters more proficient at rearing heavy young to breed earlier in the season has yet been demonstrated.

The egg-swapping experiment was carried out in the Main Colony and, for the reasons explained above, it was not legitimate to analyse the fledging weight of the experimental chicks reared from eggs which had been swapped between burrows. 60-day weight was used instead.

The slopes of the regression of 60-day weight of experimental chicks on hatching date are given in Table 5.5, as are the slopes of the control provided by the regression of 60-day weight on hatching date of chicks in the Observatory burrows. In neither year is there a significant difference between the slope of the regression for experimental and control chicks. However, in 1974, the 60-day weight of the experimental chicks shows a significant negative correlation with hatching date. The early chicks, now being raised by late-laying pairs, are heavier than the late chicks, and this suggests that the seasonal decline in 60-day weight may be more due to deteriorating environmental conditions than to any tendency for adult shearwaters more proficient at rearing heavy young to breed early. This

Table 5.5

Egg-swapping experiment. The slope of the regression of 60-day weight on hatching date (gm./day) for: -

(a) Swapped experimental chicks in the Main Colony

(b) Control chicks in the Observatory burrows

	Year	Slope	S.E.	N	p
(a)	1974	-5.709	2.261	18	< 0.05
	1975	+1.489	2.033	13	N.S.
(b)	1974	-0.974	0.733	56	N.S.
	1975	-1.763	0.909	44	N.S.

suggestion was not confirmed by the 1975 data.

Ten unchanged pairs which had raised experimental chicks in 1974 raised their own natural chicks in 1975. A further six pairs which had raised experimental chicks in 1975 raised their own chicks in 1976. I corrected the 60-day weight of all 32 chicks, both experimental and natural, to a percentage of the mean 60-day weight of all chicks in the Observatory burrows in the appropriate year, whether 1974, 1975 or 1976. It was now possible to investigate how the percentage

$$\frac{\text{Corrected 60-day weight of natural chick}}{\text{Corrected 60-day weight of experimental chick raised previous year}} \times 100$$

was related to the difference, in days, of the hatching date of the two chicks. The results are plotted in Figure 5.5, and it is seen that where the natural chick hatches at an earlier date than the experimental chicks hatched the previous year it tends to be heavier at 60 days old, and vice versa.

Since the difference in hatching date of the two chicks, raised by the same parents, is correlated with the ratio of their 60-day weights, this indicates that seasonally variable factors are involved in determining that weight. Combining this with the evidence of the previous sections it seems likely that the seasonal decline in fledging weight seen in all four study years was mostly due to a deterioration of feeding conditions late in the season rather than to any tendency for adult shearwaters more proficient at feeding chicks to breed early in the season. But my failure to substantiate this latter possibility does not mean it can be wholly excluded.

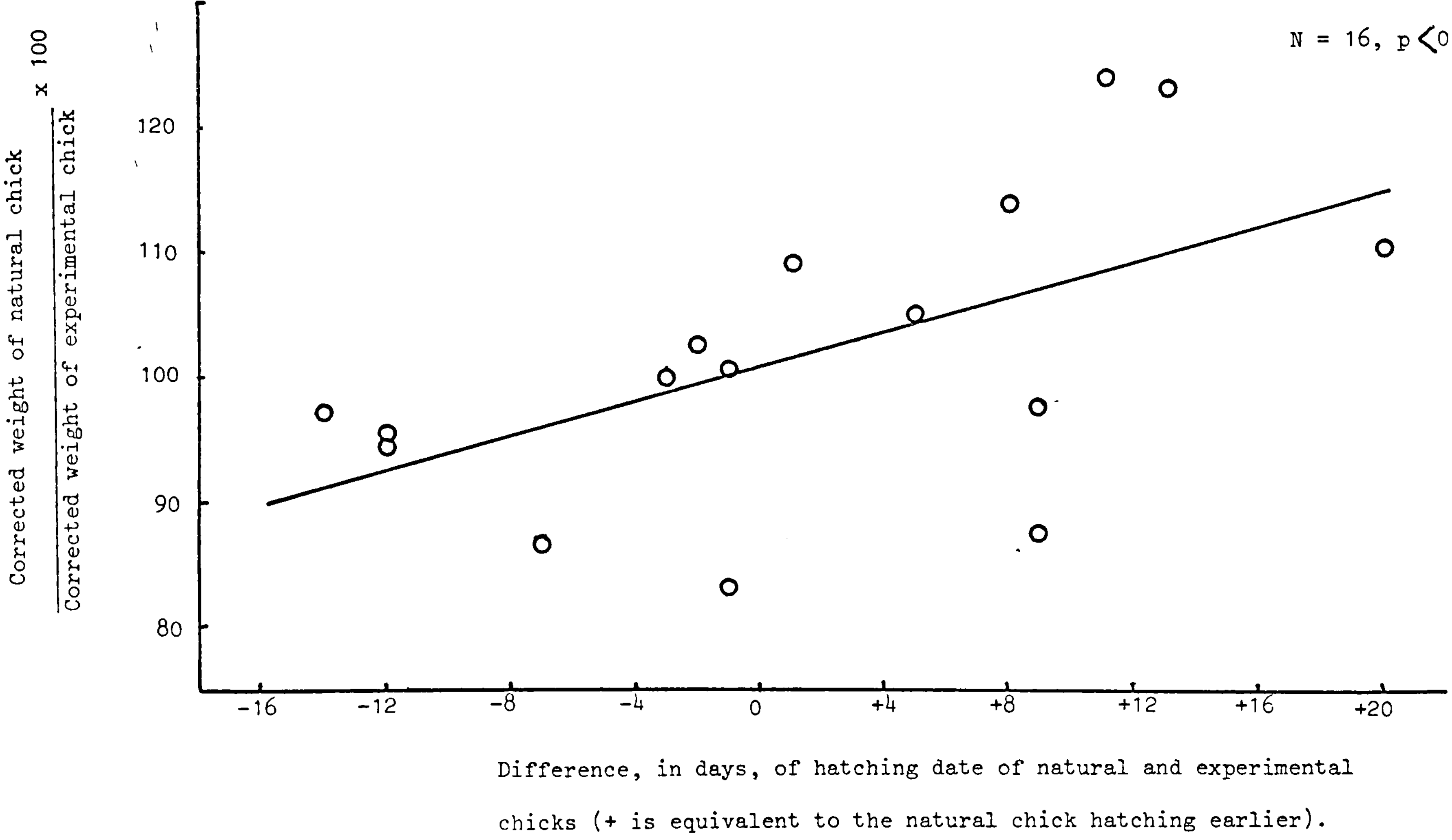
Survival of fledglings

In Figure 5.6 I plot the percentage survival of fledglings ringed in the Main Colony against the date of ringing which is very closely related to the date of fledging. The years analysed are 1964-1969, which covers the

Figure 5.5

The egg-swapping experiment. The relationship between the corrected 60-day weight of the natural chick, the corrected 60-day weight of the experimental chick reared the previous year and the difference in hatching date of the two chicks. See text for further details. The regression line : $y = 101.18 + 0.706x$

$N = 16$, $p < 0.05$



period during which the greatest effort was put into the ringing of shearwater fledglings. In all years except 1967 there was a tendency for the survival of those fledglings ringed late in the season to be lower than those ringed earlier, as summarised in Table 5.6. The survival figures for 1967 are apparently influenced by the relatively high survival of those chicks ringed between 2 and 7 September. Thus the conclusion reached by Perrins (1966) stands and it is usually the case that the earliest ringed fledglings have the highest rate of survival. However there is considerable annual variation in the change of survival with date of ringing, as was also reported by Perrins.

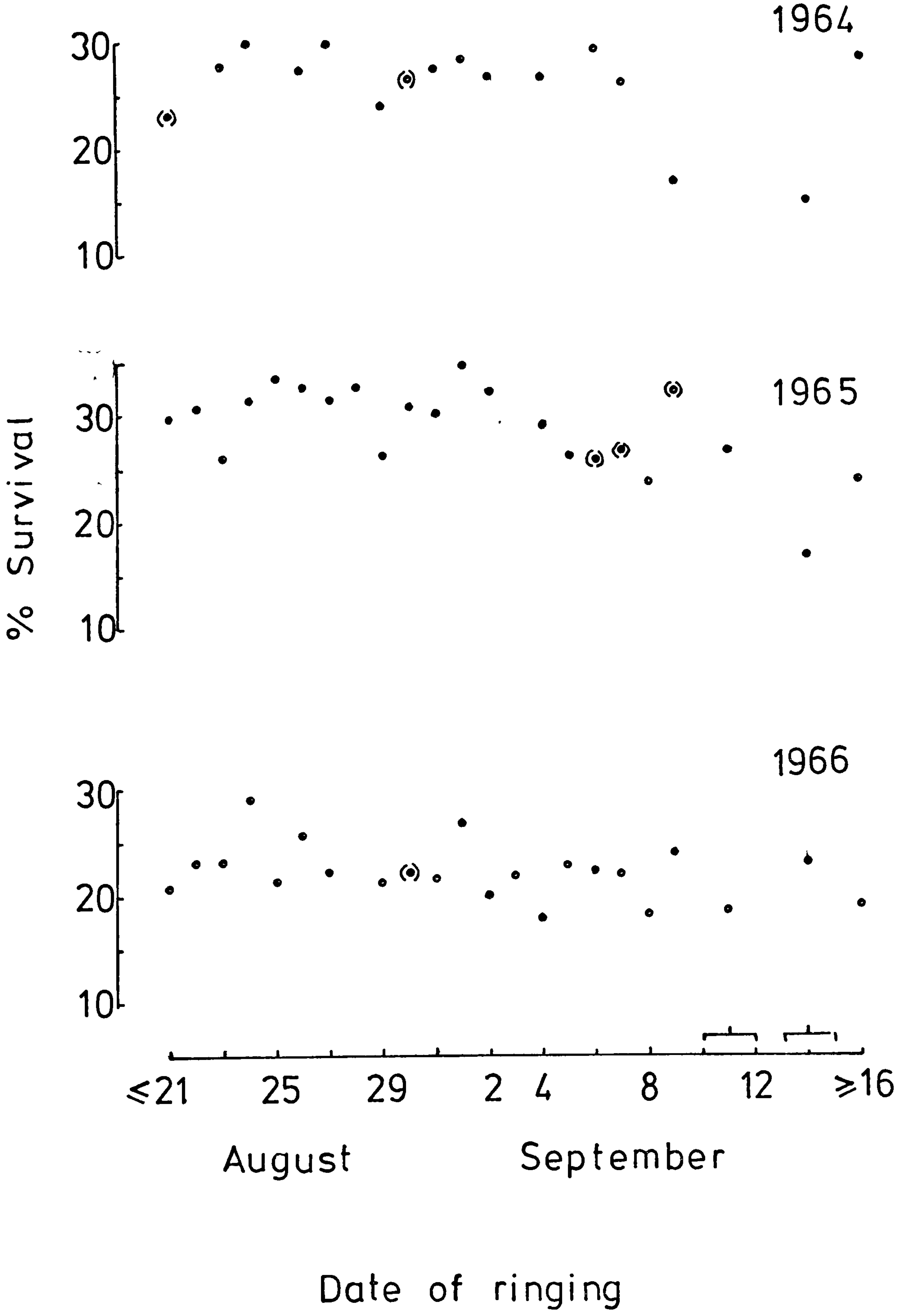
As mentioned previously large numbers of fledglings were weighed in 1965, 1966 and 1967. Since the survival of the 1965 and 1966 fledglings was not significantly related to date of ringing, it is impossible to answer the question posed in the Introduction, namely do the early fledging young generally have a higher survival simply because they are, on average, of higher weight, or are there seasonal factors acting independently of weight to affect the survival chances of the young? Any attempt to answer this question using weight and survival data from 1967 must be treated with great caution as the survival pattern of 1967 fledglings was atypical (Figure 5.6).

Suppose that when conditions for survival are severe the survival of light fledglings is reduced by a greater amount than is the survival of heavy fledglings; then the mean weight of those fledglings which survive will be related to the severity of the conditions. In Figure 5.7 I plot the mean weight of those chicks which are known to have survived against the date of ringing and weighing. In each year the mean weight of the chicks which survive alters little over the span of the fledging period. There is a slight indication that the mean weight of chicks surviving from those ringed in

Figure 5.6

The percentage survival of Manx Shearwater fledglings ringed in the Main Colony, Skokholm, plotted against date of ringing. When less than 50 fledglings were ringed on the date concerned the point is shown in brackets. See also Table 5.6.

Figure 5.6


1964
1965
1966
% Survival
30
20
10
30
20
10
30
20
10
≤21
25
29
2
4
8
12
≥16
August
September
Date of ringing

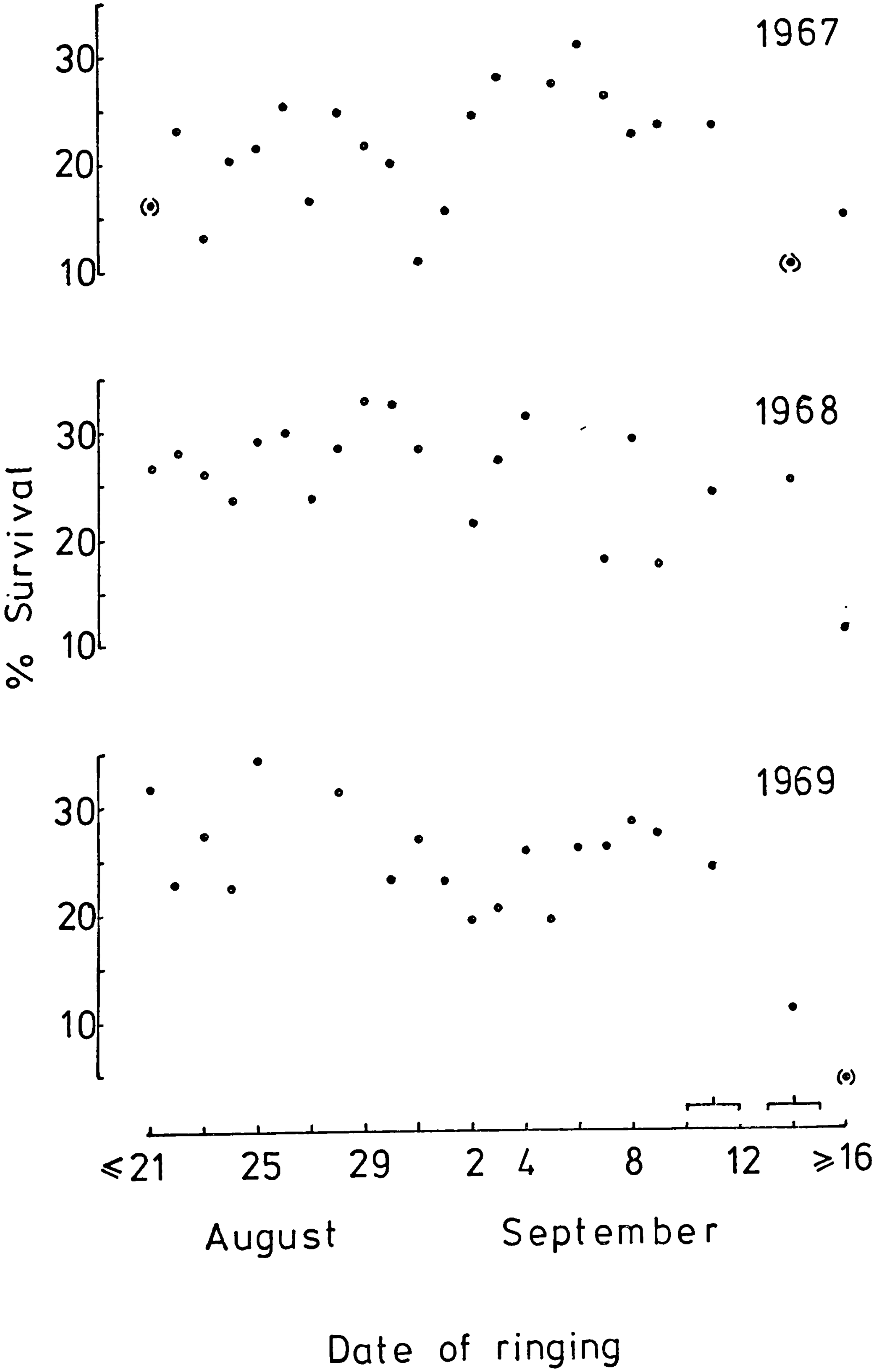

1967
1968
1969
% Survival
30
20
10
≤21
25
29
2
4
8
12
≥16
August
September
Date of ringing

Table 5.6

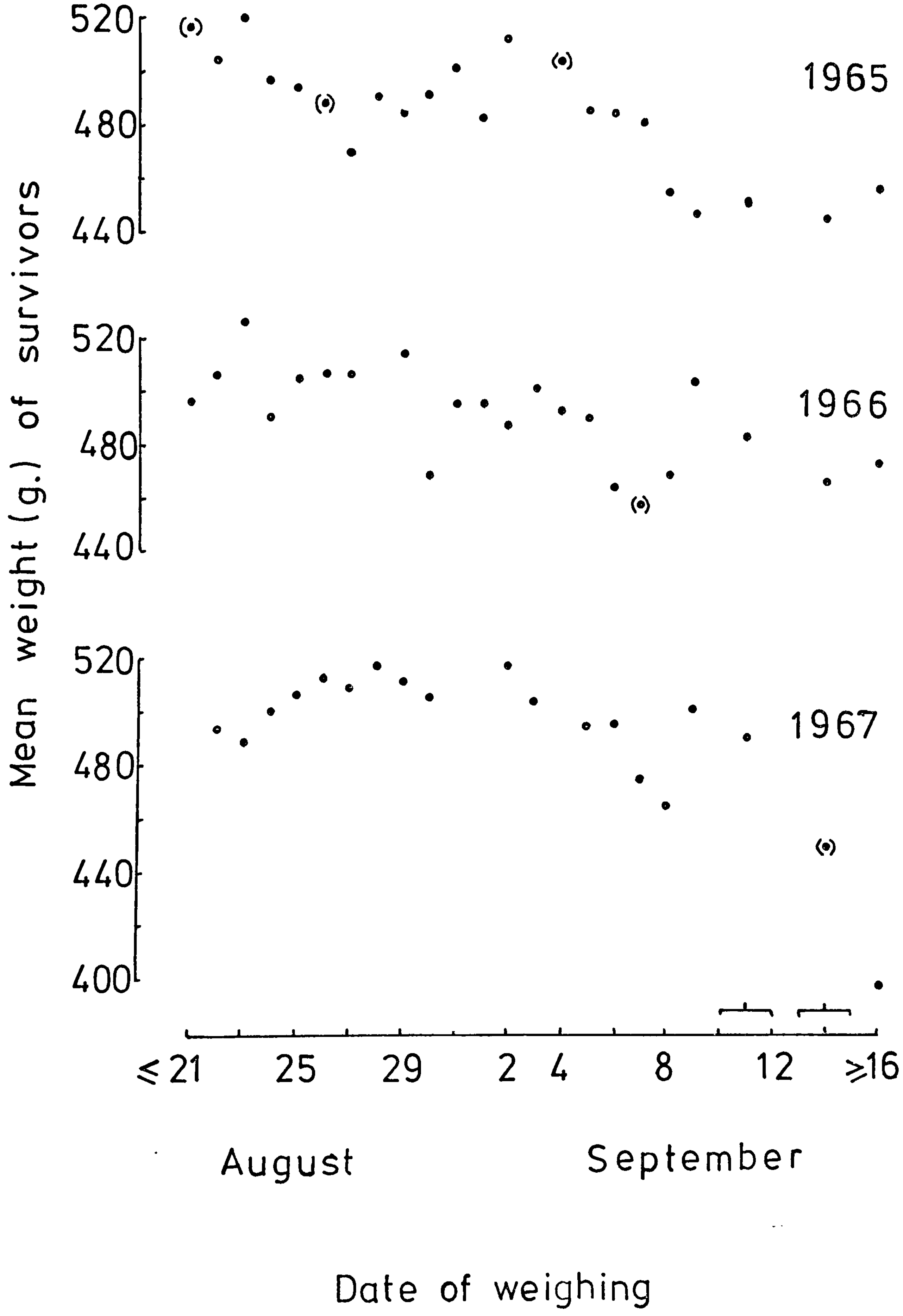
The percentage survival of Manx Shearwater fledglings ringed in the Main Colony, divided according to the date of ringing. The number of birds ringed in each period is given in brackets after the survival figure.

Ringed:-	Before 1 September	After 31 August	p (χ^2 test)
Year of ringing			
1964	27.2 (1437)	26.4 (1196)	N.S.
1965	30.7 (2363)	27.9 (1375)	N.S.
1966	22.7 (1173)	21.4 (2468)	N.S.
1967	21.2 (2345)	24.6 (1819)	< 0.01
1968	28.5 (2096)	23.7 (1509)	< 0.001
1969	28.3 (1040)	23.2 (2357)	< 0.01

Figure 5.7

The mean weight of Manx Shearwater fledglings that are known to have survived in relation to date of weighing (= date of ringing). The analysis was done 5 February 1975 and was restricted to fledglings weighed in the Main Colony, Skokholm. Each point usually represents between 20 and 50, and never more than 100 surviving birds. Where the point represents less than 10 birds it is shown in brackets. The total number of known survivors from each of the three year classes was 474 from 1965, 593 from 1966 and 680 from 1967.

Figure 5.7


Mean weight (g.) of survivors
520
480
440
1965
520
480
440
1966
520
480
440
400
1967
≤21
25
29
2
4
8
12
≥16
August
September
Date of weighing

September was lower than the mean weight of those ringed in August. Had this effect occurred in 1967 only it could have been interpreted as reflecting less severe conditions allowing a greater overall survival and a proportionately greater survival of chicks of relatively low weight. As it occurs in all three years, between which there are differences in the seasonal trend in survival (Table 5.6), it seems more likely that the small seasonal decline in the mean weight of surviving chicks is due to a bias resulting from the fact that late catches will contain a higher proportion of departing young than early catches which will contain a higher proportion of young that, having only recently been deserted, are heavier and still a few days away from departure.

I now consider the percentage survival of young ringed in the Main Colony in 1967 at a high weight, arbitrarily defined as greater than 500 gm. The percentage surviving was 22.8 (of 879 fledglings ringed) if they were ringed in August and 30.5 (455 ringed) if they were ringed in September (X^2 test, $p < 0.01$). Thus the percentage of heavy young which survive increases as the overall survival increases (Table 5.6). This suggests that, although a chick of high weight has a greater chance of survival (Perrins _et al_. 1973), the possession of the fat deposits associated with high weight is not fully able to compensate for those seasonal factors which influence the survival chances of chicks of all weights. There is no knowing whether this very tentative suggestion also applies to a typical year (unlike 1967) when the probability of survival of fledglings decreases later in the season.

Discussion

In a number of seabird species experienced older birds are known to be able to raise more chicks from the eggs they hatch than are younger birds. These include the Herring Gull (Davis 1973) and the Gannet (Nelson 1966b).

In the Gannet most chick losses from the nests of younger breeding birds occur in the first few days after hatching; after this initial period younger birds are as successful at raising chicks as older birds. Richdale (1957) has found that Yellow-eyed Penguins which first breed at two years old are less successful at rearing chicks than older birds but those penguins which first breed at three years old are not less successful. Coulson & White (1958) reported that Kittiwakes breeding for the first time were as well able to feed broods of one as older birds but they could not feed broods of two as successfully as older birds. In Table 4.2 I showed that inexperienced Manx Shearwater pairs have a lower hatching success but the fledging success of these pairs was not significantly lower than that of experienced pairs. This study has also failed to reveal any effect of parental age or breeding experience on the fledging weight of chicks (Figure 5.4 and Table 5.4). Thus either inexperienced breeders have delayed breeding until they have reached a given level of competence and are, in fact, just as capable of catching food and delivering it to their young as experienced breeders, or they need to put more effort into the feeding of young. This latter possibility might be tested if data on weight changes during the nestling period were available for both experienced and inexperienced breeders, but they are not. In general it is disadvantageous for individual birds with a high life expectancy significantly to jeopardize their own chances of survival for the sake of improving the chances of survival of one offspring reared early in the reproductive period (Stearns 1976) and, on these grounds, it seems more likely that inexperienced breeders are as well able to feed their young as experienced breeders. That breeding Manx Shearwaters do not reduce weight, and presumably also their survival chances, in circumstances where feeding the chick is more than usually difficult is also illustrated by Harris' (1966a) observation that the weight of parents feeding experimentally provided twins was not lower than the weight of control parents.

Little is known of changes in the size of the Skokholm Manx Shearwater population in recent years. The limited evidence available suggests that the population may have increased during the first two-thirds of this century, along with a number of other British seabird species such as certain gulls Larus spp. (Harris 1970c), the Fulmar (Fisher 1966), the Kittiwake (Coulson 1963b) and the Gannet (Nelson 1966b). Lockley (1930) mentioned that, according to local history, the numbers of shearwaters on Skokholm were steadily on the increase; their numbers could have been reduced by the nineteenth century habit of collecting many birds for bait in lobster pots. In 1930 Lockley estimated the population at 10,000 birds; later (1942) he amended the estimate to 10,000 pairs. Harris (1966a) and Perrins (1967), using two different methods, estimated a breeding population of 35,000 pairs. If there has been a population increase then there presumably was an ample food supply during the breeding season in the years of population increase and there is no reason to suppose that this food supply is now declining. However Brooke (1973) has presented evidence that the age of first breeding has increased over the last 10-15 years. Possibly this is due to increased competition for nest sites consequent upon the increased population size, resulting in the exclusion of younger birds from the breeding population. If this were so, then, by the time those younger birds commence breeding, they may have lived longer than the number of years required to reach peak feeding efficiency (see also Chapter 2 and Lack 1966), with the result that they are able to feed their first chick was well as older birds feed later chicks.

Competition for nest sites is vividly illustrated in other shearwater species such as the Great Shearwater (Rowan 1952), the Short-tailed Shearwater (Serventy 1967) and the Sooty Shearwater (Richdale 1963) where large numbers of eggs are laid, not in burrows, but on the surface. That such competition for nest sites may act particularly against younger birds is shown by Serventy's observation that the eggs laid on the surface were generally narrower than those laid in burrows and narrow eggs are generally laid by younger females, although not necessarily those in their first year of breeding. A comparable result was provided by Coulson (1971) working on the Farne Islands where Shags breeding for the first time are normally excluded from better nesting sites by older birds. Following a population crash in 1968 the younger birds were able to move into the better nesting sites and this was an important factor in improving their breeding success. If younger Manx Shearwaters are prevented from breeding by competition for burrows with older birds then, if artificial burrows are provided, these should mostly be occupied by younger birds and I have presented some evidence (Chapter 3) that this occurs.

Perrins _et al_. (1973) have discussed the role of fat deposits carried by the fledging young shearwater and concluded that the fat stores laid down by heavy young give them a greater chance of migrating a long distance without feeding, possibly even as far as the winter quarters off Brazil. The fat stores thereby enhance the survival chances of the heavy young. I have presented evidence that late in the season adults experience increasing difficulties in feeding young as shown, for instance, by the lower fledging weight (Table 5.2) and longer starvation period (Figure 5.2). These observations could be interpreted in support of the conclusion of Perrins _et al_. (1973) for the fat stores carried by high weight young may serve to shield them from the environmental influences which create difficulties for those adults still feeding young late in the season. One way the fat stores could serve to shield the young is by enabling them to fly beyond the area to which the late-breeding adults are restricted. The adults are restricted by the requirement to continue feeding the chick. Unlike some other petrels (Ashmole & Ashmole 1967), the Manx Shearwater is not known to have any digestive adaptations which would enable it to feed the chick with oil, rather than fish, the advantage of oil being that it provides more calories per unit weight so that feeding adults can continue to forage either for a longer period or further afield before they attain the maximum load that can be carried back to the chick.

The demonstration (Table 5.3) that individual pairs tend to fledge a chick at a weight which is consistently greater or less than expected on the basis of the chick's hatching date implies that different pairs differ in their ability to feed a chick. There are insufficient data to determine whether this ability is related to any other important parameter, such as mortality. However similar differences in quality are known in other bird species and, given individual variation, they are not unexpected (see Perrins & Moss 1975). Coulson (1968) has shown that Kittiwakes breeding in the centre of a colony not only have higher breeding success but also experience lower mortality outside the breeding season. Murton, Isaacson & Westwood (1971) have shown that Woodpigeons Columba palumbus of different status in the feeding flocks have different chances of subsequent survival, survival being higher for the birds feeding in the centre of the flocks than for those feeding at the front. Perrins (1971) found that the survival rate measured from a breeding study population of the Swift Apus apus was higher than the rate obtained from the recoveries of birds ringed throughout Britain under the national ringing scheme. He suggested that a breeding population may only contain the 'cream' of the species whilst birds ringed by the national scheme will also include birds of lower quality, and higher mortality rate.

CHAPTER SIX

Population Biology

Population Biology

Introduction

An attempt to construct a life table for a bird species requires a knowledge of several parameters, including the nesting success, the mortality between fledging and the onset of breeding, the mortality of breeding adults and the proportion of adults which do not breed in any one year. The attempt may be complicated by annual variations in mortality and by age-specific variations in nesting success or adult mortality. It is also necessary to know whether the population under consideration is closed or subject to immigration or emigration. Perrins, Harris & Britton (1973) presented a simple life table for the Manx Shearwater on Skokholm Island, Pembrokeshire. During a four year study, 1973-1976, of the Manx Shearwater, also on Skokholm, I gathered data on several of the parameters necessary for the construction of a life table, and found that the life table of Perrins _et_ _al_. (1973) requires some modification.

I. Survival rate of young birds

In the period 1960-1975 between 2,000 and 10,000 Manx Shearwater fledglings were ringed each year on Skokholm and many of these birds have been retrapped on the island in later years. In theory it should be possible to calculate survival rates for different year classes from these numerous retraps. In practice it has proved impossible for reasons which have been discussed by Perrins _et_ _al_. (1973). In an attempt to overcome the problems, particularly those resulting from the birds becoming shy of being trapped, Perrins _et_ _al_. used a simple capture-recapture technique to estimate the number of birds in any year class alive at any time. In their method a single recapture each year was all that was scored. I repeated their method to estimate the survival of chicks from the 1967-1971 year classes, based on the results of trapping in 1973 and 1974 (Table 6.1). Following Perrins et al., Table 6.1 is based on chicks ringed in the Main Colony only, since this is where most ringing and recapture work has been carried out. Since some birds do not return to the Main Colony but to elsewhere on the island and since recapture rates are different in the other areas, two lines are given for each year, (i) for those birds recaptured in the Main Colony and (ii) for those recaptured elsewhere

The survival estimates made in Table 6.1 agree reasonably closely with those made by Perrins et al. (Table 6.2), except that there is a marked difference in the survival of those fledglings born in 1967. It seems unlikely that this cohort would have experienced an approximately 70% mortality between 1969 and 1973, but I have no satisfactory explanation of these divergent survival estimates.

The survival estimates will be too low if some birds consistently evade capture and are never caught at all. That such a bias exists to a significant extent is suggested by Table 6.3, in which I compare the number of occasions on which birds of the 1969 year class which were ringed and recaught in the Main Colony were captured in 1973 with the number of occasions on which they were captured in 1972. Birds recaptured frequently in 1973 are those which were recaptured more frequently in 1972 and likewise those captured only once in 1973 tended to be those not caught at all in 1972. Extending the argument one might infer that birds not caught at all in 1973 were also not caught at all in 1972. Orians & Leslie (1958) also found that some birds were turning up in recapture samples more, and others less, frequently than expected. If such an effect exists, it will make the survival estimates presented too low since only a part of the population can be sampled, and this will be true whether the effect is due to individual birds having intrinsically different catchabilities or to uneven sampling over the study area.

Table 6.1 Recaptures of young Manx Shearwaters and estimates of survival. See text for further details

Natal year	Number of fledglings ringed	Total recaptured 1973	Total recaptured 1974	No. of individuals caught 1973 & 1974	Estimated to be alive	% survival based on estimate
1967	4342	(i) 255 (ii) 19	179 6	89 2	513) 57) 570	13.1
1968	3605	(i) 339 (ii) 49	224 15	131 3	580) 245) 825	22.9
1969	3397	(i) 389 (ii) 45	242 20	156 8	603) 113) 716	21.1
1970	2567	(i) 408 (ii) 23	329 20	201 7	668) 66) 734	28.6
1971	2477	(i) 153 (ii) 8	283 13	79 3	548) 35) 583	23.5

Table 6.2

A comparison of survival estimates of young Manx Shearwaters. Data for survival to 1969 from Perrins *et al*. (1973) and for survival to 1973 from this study.

Natal year	Survival estimate for fledglings surviving to 1969	Survival estimate for fledglings surviving to 1973
1964	19.0	-
1965	23.1	-
1966	22.6	-
1967	42.3	13.1
1968	-	22.9
1969	-	21.1
1970	-	28.6
1971	-	23.5
Means	26.7	21.8

Table 6.3

Recaptures in the Main Colony in 1972 and 1973 of Manx Shearwaters ringed as fledglings in 1969. Figures underlined are those where the observed total exceeds the expected total, assuming there was no association between the number of times an individual bird was recaptured in the two years.

		Number of occasions captured in 1972				
		0	1	2	3^+	Totals
Number of occasions captured in 1973	1	$\underline{117}$	$\underline{48}$	16	11	192
	2	42	$\underline{26}$	$\underline{13}$	13	94
	3	16	$\underline{13}$	5	$\underline{14}$	48
	4^+	19	13	$\underline{11}$	$\underline{25}$	68
Totals		194	100	45	63	402

X^2 test, $p < 0.001$

The survival estimates given in Table 6.2 may be too low and an estimate of survival of 25% to the age of first breeding, about six years old (Harris 1966b and Section II), is probably minimal. Comparable data for other Procellariformes were given by Serventy (1967) for the Short-tailed Shearwater and by Harris (1973) for the Waved Albatross Diomedea irrorata where 38% and 65% respectively of ringed fledglings were actually recaptured on the breeding grounds. Approximately 55% of Laysan Albatrosses survive from fledging to the onset of reproduction (Fisher 1975b). In the British Storm Petrel Hydrobates pelagicus Scott (1970) estimated that 40% of fledged chicks survived to breeding age.

All the above figures are only valid estimates of survival, rather than of return rates to the colony, if there is no emigration of survivors from the colony. After considering the age of first breeding I present data in Section III of this chapter suggesting that there is a significant amount of emigration from the Manx Shearwater colony on Skokholm, and this might be a reason why the survival estimate for the Manx Shearwater appears to be rather lower than in the other species mentioned. As shown later, I estimate that roughly 50% of females may emigrate. If it is assumed that no males emigrate, then the survival estimate is only three-quarters of the true figure, and the survival estimate should be increased by one-third.

II. Age of first breeding

In May and June 1973 I opened some 200 shearwater burrows in the Main Colony on Skokholm and found 51 breeding birds of known age incubating eggs. The age distribution of these birds was different from what would have been expected on the basis of earlier studies.

Harris (1966b) reported a similar study. In 1964 and 1965 he opened a large number of burrows both in Main Colony and elsewhere on the island and found 18 breeding birds of known age. There was no apparent difference in the age of breeding birds in the Main Colony and elsewhere on the island. Details of these birds and others found by previous workers are given in Table 6.4.

Table 6.4 (after Harris 1966b)

Age of Manx Shearwaters when first found breeding on Skokholm.

Year of retrap	Age in years						
	3	4	5	6	7	8	9^+
1953			1				
1956			1				
1960			1	2	1		
1964		1	2	4	2	1	
1965	1		3	1	2	1	1
Totals	1	1	8	7	5	2	1

Ideally these figures should be corrected to take account of the different number of shearwater chicks ringed each year. However this is not possible if the distribution of ringing effort between the various sub-colonies does not match the distribution of effort spent searching for ringed birds in burrows. A further complication is that, before 1958, chicks were ringed with aluminium rings which, as Harris (1964) has shown, may be lost due to abrasion and corrosion before the birds start to breed. Since 1958 rings made of a more resistant alloy, monel, have been used.

Harris also examined the gonads of seven birds of known age during the laying period. None of the females (three aged four, one five) showed any signs of breeding, although the three males (two aged four, one three) may have been capable of breeding as free spermatozoa were seen in sections of the testes.

Further studies, mostly between 1963 and 1969, are summarised by Perrins _et al_. (1973). Manx Shearwaters, ringed as young, were first found breeding at three years (1), four years (4), five years (14) and six years old (12), although the possibility that the birds have bred undiscovered for one or more years is not ignored. Adding the above data to deductions made from the age distribution of birds caught at night on the surface, they concluded that during the 1960's the majority of shearwaters were not breeding until at least five years old but that virtually all were breeding by their sixth year.

Table 6.5 gives the age distribution of birds, ringed as chicks, found breeding in the Main Colony in 1973. The actual number of birds in each age class is corrected to the total expected if exactly 5,000 had been ringed in the Main Colony each year; since 1963 the number ringed in this colony each year has usually been between 3,000 and 5,000. This correction makes two assumptions, neither of which may be strictly met. Firstly that all cohorts have returned with equal fidelity to their natal area. Perrins _et al_. (1973)

Table 6.5

Age of Manx Shearwaters, ringed as young, found breeding in the Main Colony, Skokholm, during 1973. See text for further details.

	Age in years								
Number of birds	6	7	8	9	10	11	12	13	14
Actual	9	6	12	11	5	2	3	2	1
Corrected	10.4	8.2	15.7	20.7	14.2	6.8	*	6.2	7.8

* It is not possible to correct the total for 12 year old birds, ringed in 1961, since the number of chicks ringed in the Main Colony in that year is unknown.

showed that about 14% of birds were retrapped away from their natal sub-colony (see also Section III). Secondly, that all cohorts have experienced equal mortality between fledging and first breeding; this is unlikely to be the case.

These data from 1973 suggest that few, if any, birds were breeding when younger than six years and that some were not breeding for the first time until eight or nine years old. The corrected figures for ten year old and older age classes decline as would be expected.

In 1974 I inspected approximately 200 burrows outside the Main Colony in areas where the density of burrows is generally lower than in the Main Colony. Table 6.6 gives the age distribution of 43 birds, ringed as chicks, found breeding outside the Main Colony in 1974. Again the actual number of birds in each age class is corrected to the total expected if exactly 5,000 had been ringed outside the Main Colony each year. This correction is extremely crude for not only are the two assumptions above not necessarily met but also there was little correspondence between the distribution of chick-ringing effort amongst the various sub-colonies outside the Main Colony and the distribution of my effort in 1974 when I was inspecting breeding burrows. Nevertheless the conclusion reached from the 1973 data stands. Few five year old Manx Shearwaters breed, many start breeding when six years old but some may not begin to breed until about eight years old.

I further examined data from closely observed study burrows, restricting the analysis to birds which had been ringed as chicks and which I could be fairly confident were breeding for the first time, since they were breeding for the first recorded time, in a burrow which was regularly checked during the year preceding the first recorded breeding attempt. The mean age of first breeding of such new breeders is 6.2 years (N = 11) for those ringed as chicks before 1967 and 7.1 years (N = 10) for those ringed as chicks after

Table 6.6

Age of Manx Shearwaters, ringed as young, found breeding in colonies other than the Main Colony, Skokholm, during 1974. See text for further details.

	Age in years									
Number of birds	5	6	7	8	9	10	11	12	13	14
Actual	1	10	9	8	5	6	3	0	0	1
Corrected	1.1	10.1	7.2	7.9	4.7	9.7	6.2	-	-	8.3

1966. The difference is not quite significant (Mann-Witney U-test, one-tailed, $0.05 < p < 0.1$).

The mean age of first breeding of such new breeders was 6.8 if they were male (N = 14) and 7.0 if they were female (N = 5). Another slender indication that males begin breeding at a slightly younger age than females is provided by the observation that, of 25 birds that were ringed as chicks and found breeding at six years old or younger, 19 were males and only six were females. This compares with a ratio of 82 males to 42 females amongst all birds that were ringed as chicks and found breeding during the study period (see Section III for a detailed discussion of this unequal sex ratio). Small sexual differences in the age of first breeding have been recorded in some other Procellariiformes. In the Fulmar and the Laysan Albatross males begin breeding at a slightly younger age than females (Dunnet 1975; van Ryzin & Fisher 1976) while, in the Short-tailed Shearwater, females commence breeding at a younger age than males (Serventy 1967).

It has become accepted as an axiom of population biology that animals will start breeding at a younger age when conditions are favourable than when they are unfavourable, and competition for some limited resource required by breeders is more intense (Gadgil & Bossert 1970). Two alternative hypotheses for this postulate are offered by Lack (1966) and Wynne-Edwards (1962). Lack suggested that the delayed onset of breeding observed amongst many birds occurs because to breed at too early an age would be dangerous for the individual and ineffective, since the bird would not yet have attained a level of proficiency in the abilities required for reproduction sufficient both to maintain itself and successfully to rear a chick (or chicks). Thus, on average, individuals which started to breed at younger than the normal age would leave fewer not more young than those starting at the normal age. If conditions for breeding improved, for whatever reasons, then the level of proficiency required would presumably be lower and it might become worthwhile for the younger bird to attempt breeding. In contrast Wynne-Edwards proposed that the onset of breeding is delayed by group selection in order to reduce the number of young reared by the population and so prevent over-exploitation of the available resources. If the level of available resources relative to the population level increased over the long term, then such selection would presumably act to reduce the age of first breeding.

There is better evidence for mammals than for birds that the age of first breeding is indeed responsive to changes in the level of available resources relative to the population level. In the 1930's the age at sexual maturity of the Southern Fin Whale *Balaenoptera physalus* was ten or eleven years but, following a period of over-fishing and population decline, it is at present only six years (Lockyer 1972). Carrick, Csordas & Ingham (1962) reported a study of the Southern Elephant Seal *Mirounga leonina* at South Georgia where large numbers are killed by sealers and at Macquarie Island where the population is dense and not culled. At South Georgia nearly all the cows have their first pups when three years old whereas at Macquarie their average age at first breeding is six. In populations of small mammals showing cyclical fluctuations the age at sexual maturity generally increases when the populations are at peak levels (Krebs & Myers 1974).

There is less evidence for changes in the age of first breeding in birds. Valverde (1960) found a tendency for sub-adult Imperial Eagles *Aquila heliaca* to breed more commonly during a period of low population density. Although most Grey Herons *Ardea cinerea* do not breed until at least two years old, Milstein, Presst & Bell (1970) suggested that it is breeding by yearlings which allows colonies to make spectacular increases, which presumably happens when conditions are more favourable than usual. These examples have all concerned a reduced age of first breeding when conditions are relatively favourable. There is no important logical difference between this situation and that where the age of first breeding increases because competition for some limited resource has become more intense.

If there has been an increase in the age of first breeding of the Manx Shearwater in the past 10-15 years then it is possible that the population was formerly expanding and that this expansion is now slowing down, or has already ceased. As the population expansion has slowed and the birds are again (almost) fully exploiting a limiting resource, competition for that resource (e.g. food, nesting burrows) may have increased and resulted in the exclusion of younger birds from the breeding population. I now consider evidence for a past increase in the Skokholm Manx Shearwater population.

A number of British seabird populations are known to have increased substantially during the first two-thirds of this century; these include certain gulls Larus spp. (Harris 1970c), Fulmar (Fisher 1966), Kittiwake (Coulson 1963b) and Gannet (Nelson 1966b). Unfortunately the difficulties of censussing a nocturnal burrowing species such as the Manx Shearwater are such that the number of breeding pairs on Skokholm is poorly documented. Lockley (1930) mentioned that, according to local history, numbers were steadily on the increase; their numbers could have been reduced during the nineteenth century by the habit of collecting large numbers for use as lobster pot bait. In 1930 Lockley estimated the population at 10,000 birds; later (1942) he amended this estimate to 10,000 pairs. Harris (1966a) and Perrins (1967) used two different methods and both estimated a population of about 35,000 breeding pairs. In 1973 I followed Perrins' method for the Main Colony (Brooke 1973) and estimated a breeding population of 10,600 pairs, an increase of 13% over Perrins' 1967 figure of 9,400 pairs. Such an increase is probably within the limits of likely experimental error. Nevertheless the colony may have increased slightly in the period 1967-1973, and almost certainly did not decline. Had there been a decline, this could have indicated that the apparently greater age of first breeding was either due to greater competition for burrows caused by a reduction in the number of burrows suitable for breeding, or to greater competition for food because of a reduced food supply during the breeding season.

III. The dispersal of female Manx Shearwaters

During this study a total of 178 Manx Shearwaters which had been ringed as chicks on Skokholm were found breeding and, of this total, 124 were sexed by cloacal inspection (Serventy 1956) either during the season when they were first found breeding or during a subsequent season or, in a few cases, simply by sexing the mate with which they bred. 54 birds were therefore not sexed because the burrows in which they were breeding were opened too late in the season to allow accurate sexing by cloacal inspection and neither the bird nor its mate was found breeding in another season. Of the 124 shearwaters which were sexed 82 were males and 42 were females. Thus the proportion of males (± S.E.) was 0.66 ± 0.04 and of females 0.34 ± 0.04. The ratio of males to females is significantly different from 50:50 (Binomial test, $p < 0.001$).

About half the Manx Shearwater chicks ringed on Skokholm are ringed in the dense Main Colony of about 7-8 ha where some 10,000 pairs nest (Perrins 1967; Brooke 1973). A majority (61%) of the sexed shearwaters which had been ringed as chicks and which I found breeding were breeding in the Main Colony. Since more birds move out of the Main Colony than into it (Perrins _et_ _al_. 1973), it is possible that the unequal sex ratio could have arisen from a sex-related tendency to move into or out of the Main Colony. This is not a sufficient explanation since the proportion of males among the shearwaters ringed as chicks was 0.67 ± 0.05 amongst those breeding in the Main Colony and 0.65 ± 0.07 elsewhere on the island.

Only three of the breeding shearwaters ringed as chicks were more than 15 years old which is approximately the predicted median age of a breeding shearwater (Perrins _et_ _al_. 1973). If males began to breed at a very much younger age than females this could explain the deviation of the sex ratio from 50:50. There is no sign that this was occurring to a significant extent (see also Section II). 1975 was the year when I had the largest number (80) of breeding Manx Shearwaters which had been ringed as chicks under observation The mean age (± S.E.) of the 60 males was 9.27 ± 0.321 years and of the 20 females was 9.70 ± 0.505 years; the difference is not significant.

The relative scarcity of females amongst the breeding Manx Shearwaters which had been ringed as chicks could arise in several ways.

(i) More males could have been captured and ringed. Most shearwater chicks are caught for ringing as they depart from their natal burrow immediately prior to fledging. There is no reason to suppose that male fledglings are more readily caught than females and I know of no evidence for any wild bird population that the ratio of male eggs to female eggs differs at laying significantly from 50:50. As Fisher (1930) has pointed out natural selection will favour parents which make an equal investment in offspring of the two sexes. In the case of the Manx Shearwater this would result in the production of fledglings with a 50:50 sex ratio since the sexes are of closely similar size, unless nesting failures fell particularly on eggs or young of one sex or the other. The breeding success of the Manx Shearwater is fairly high with a hatching success around 78% and a fledging success around 89% (Perrins <u>et al</u>, 1975; Chapter 4). The few failures during the nestling period are mostly due to accidents and I have no evidence concerning the sex of eggs that fail to hatch. Once parental care ends differential mortality between the sexes has no effect on the optimum sex ratio at birth (Leigh 1970).

I conclude from this discussion that there is no reason to suppose that more male than female Manx Shearwaters have been ringed as fledglings, but this possibility cannot be excluded. It does however seem very unlikely that the ratio of male to female fledglings at ringing was 2:1.

(ii) Differential mortality between the sexes could produce the observed inequality in one of two ways. Firstly, if males experienced a greater adult mortality and started to breed at a younger age then, since the birds ringed as chicks are younger than the predicted median age of a breeding shearwater (see above), males would predominate among breeding birds ringed as chicks and would, on average, be younger than the females. This possibility has been excluded above. The second alternative, greater female mortality, would only produce the observed inequality if many females from other colonies moved to Skokholm to breed to maintain the necessary 50:50 sex ratio amongst breeding pairs. However, among breeding adult Manx Shearwaters, there are no significant differences in mortality between the two sexes (see Section IV); if there is a difference it may be males which experience the higher mortality. There are no known means of sexing fledgling Manx Shearwaters but, since adults of the two sexes do not differ in mortality, it would be surprising if immature shearwaters experienced greatly different mortalities. The overall sex ratio (including non-breeders) of the Skokholm Manx Shearwater population is unknown and therefore cannot shed further light on this problem.

(iii) Females could leave the natal colony in significantly larger numbers than males. The predominance of males amongst the breeding shearwaters ringed as chicks would then arise if unringed females from other colonies moved to Skokholm to breed. It would not arise if there was no such compensatory immigration. Harris (1972) considered available Manx Shearwater recoveries and concluded that, although immature shearwaters may sometimes visit other colonies, the number which settle to breed in other than the natal colony is very small. The extent of female emigration required to produce the observed ratio of approximately two males to one female among the breeding Manx Shearwaters which have been ringed as chicks will now be discussed since, at first sight, it is not easy to reconcile Harris' conclusion and the suggestion of extensive female emigration.

Some 25,000 Manx Shearwater chicks fledge from Skokholm each year (Perrins 1967). If it is assumed that only females emigrate then one quarter of these chicks may be potential female emigrants, leaving three-quarters (now with a ratio of two males to one female) as birds which will, if they survive, return to the natal colony, Skokholm. Of the 6,000 potential female emigrants about 33% (i.e. 25% x $^{4}/_{3}$) may survive to breeding age. In the ten-year period 1961-1970, 63,000 Manx Shearwater chicks were ringed on Skokholm, approximately 25% of the total number of chicks produced in that period. Thus, on average, there may be about 500 ringed birds from each year which both survive to breeding age and emigrate. Since the life expectancy of breeding Manx Shearwaters is about ten years (Perrins *et al*. 1973) a maximum of about 5,000 Skokholm-ringed female shearwaters could be alive and breeding in other colonies in any one year. However two further factors make it likely that this total is an over-estimate. The first is that the rate of chick-ringing in the period before 1961 was not as high as in the period 1961-1970. Since the life expectancy of a breeding Manx Shearwater is about ten years, about half of the shearwaters breeding in 1976 would have fledged before 1961, when the intensity of chick ringing was actually very much lower; hence fewer ringed chicks from each year class. The second factor concerns ring loss. Nearly all shearwaters ringed before 1958, when a new more durable alloy was introduced, would have lost their rings by 1976 (Harris 1964; personal observation), as would a proportion of those ringed subsequently. It might be realistic to suggest that no more than 2,500 Skokholm-ringed Manx Shearwaters of breeding age were alive in other colonies in 1976.

It is likely that a large proportion, say three-quarters, or 1,875, of any Skokholm emigrants would settle in the large colony on Skomer Island, only 4 km. from Skokholm. There are 190,000 breeding adult Manx Shearwaters on Skomer (Corkhill 1973) and possibly another 40,000 birds of breeding age not actually breeding in any one year (see Section V). The frequency of

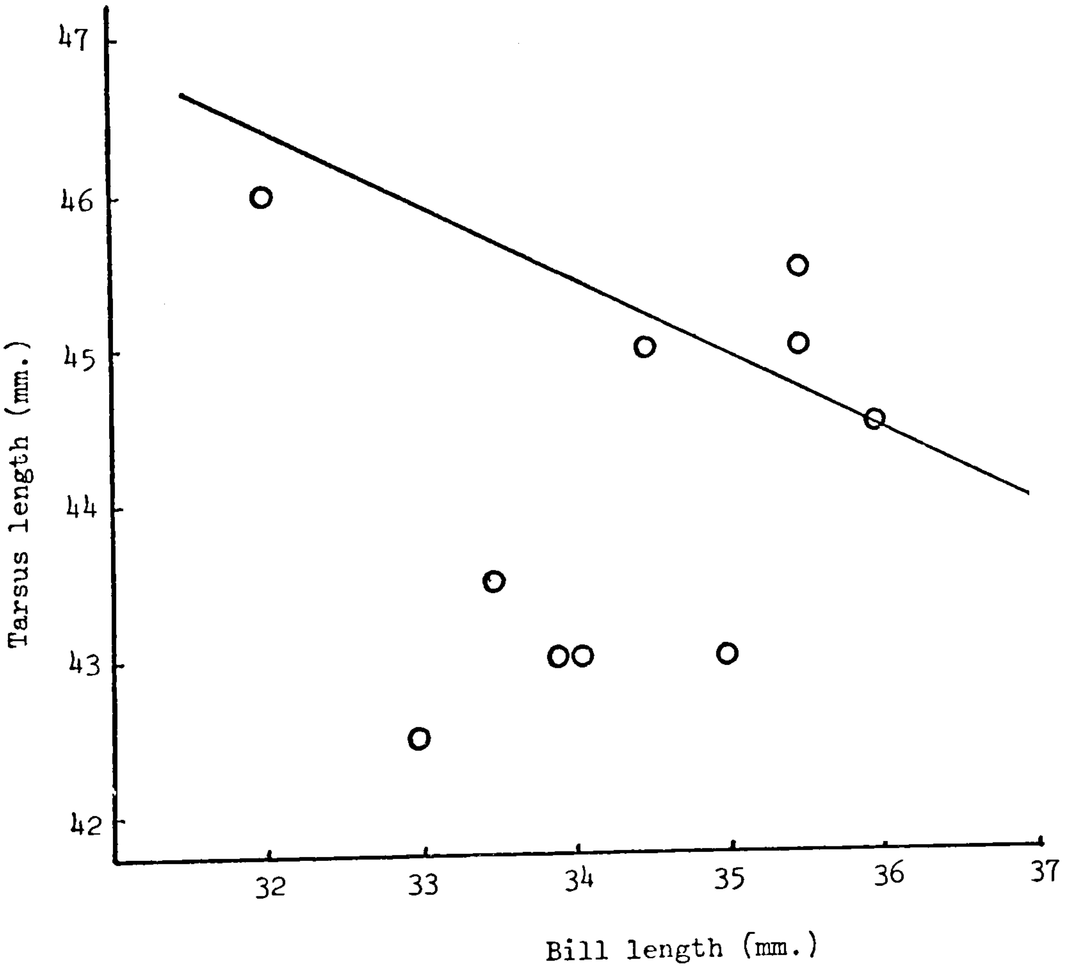
1,875 Skokholm-ringed birds in this total Skomer population of 230,000 adult shearwaters would be 1 in 123. The frequency of Skokholm-ringed shearwaters at other Irish Sea colonies (Harris 1972) would almost certainly be even lower. Thus the degree of emigration required to produce the observed preponderence of males amongst the shearwaters which have been ringed as chicks on Skokholm and later breed there is not so great as to raise the frequency of Skokholm-ringed birds among the breeding adults of other colonies above levels that could only be detected by very intensive effort, particularly by opening up large numbers of breeding burrows. This time-consuming task has not been undertaken at other colonies, and since relatively few fledglings have been ringed at other colonies, any immigration into the Skokholm population would probably also pass undetected.

In March 1977 I visited Skomer Island to catch Manx Shearwaters. During March virtually all birds caught by hand at night on Skokholm are of breeding age (Perrins _et_ _al_. 1973; personal observation), and this is presumably also true on Skomer. On Skomer an on-going catching strategy was followed so that it is unlikely that any birds were handled more than once. Of 850 birds handled, 14 carried Skomer rings and seven Skokholm rings, and none of the ringed birds was caught more than once. The seven Skokholm birds had all been ringed as fledglings between 1958 and 1972 and the frequency of these birds in the Skomer population was 7 in 850 or 1 in 121 (c.f. prediction in previous paragraph).

A second visit was made to Skomer in June 1977. Over the two visits a total of ten birds that were of breeding age (six or older) and that had been ringed as chicks on Skokholm were caught. The bill and tarsus measurements of these birds are shown in Figure 6.1. The figure also shows the discriminant function derived in Chapter 2 from shearwaters of known sex. The discriminant Y is given by

Figure 6.1

The bill and tarsus measurements of ten Skokholm-ringed Manx Shearwaters of breeding age caught on Skomer in March and June 1977. The diagonal line is the calculated discriminant function separating males and females on Skokholm (see Figure 2.1), males falling above the line and females below.



$$Y = 3.292 \times 10^{-3} \times X_1 + 6.877 \times 10^{-3} \times X_2 - 5.0689 \times 10^{-2}$$

where X_1 = (Bill-length - 30) mm

X_2 = (Tarsus length - 40) mm

The mean value of Y for the sample of Skokholm birds, containing an almost 50:50 sex ratio (47 males, 46 females) is, by definition, zero. The standard deviation is 1.0438×10^{-2}. The mean value of Y (± S.D.) for the ten Skokholm-ringed birds caught on Skomer was $-0.8344 \times 10^{-2} \pm 0.9924 \times 10^{-2}$. The two samples are significantly different (t-test, one-tailed, $p < 0.02$) and the direction of the difference is in accord with the suggestion that most of the emigrants on Skomer were female.

It is worth mentioning at this point that, in addition to the ten birds of breeding age, six birds that were aged four or five and that had been ringed as chicks on Skokholm were also caught on Skomer. These 16 emigrants had thus been ringed in the period 1958-1973 during which time the number of chicks ringed in the Main Colony was 40,315 and in other areas on Skokholm was 41,330. However 15 of the emigrants had been ringed in the Main Colony and the ringing location of the sixteenth had not been recorded. This finding suggests that more birds move out of the Main Colony than into it, as was also reported by Perrins _et_ _al_. (1973) for movements within Skokholm.

If female shearwaters leave the natal colony to breed elsewhere more frequently than males, it would also be expected that, within Skokholm, female would show less fidelity to the natal colony. This is the case as shown in Table 6.7. 85% of males breed within 150 m of the site where they were ringed as chicks but only 49% of the females do so.

I conclude that about half the female Manx Shearwaters reared on Skokholm emigrate and, if they survive, breed elsewhere. It seems unlikely that many males emigrate. In no other Procellariiform yet studied has

Table 6.7

The distance between the site where Manx Shearwaters were ringed as chicks and the site where they were found breeding on Skokholm in 1973 - 1976.

	Distance (m.)				
	0 - 150	150 - 300	300 - 600	600 - 1200	Total
Females	20	2	6	13	41
Males	68	6	5	1	80

$X^2 = 27.20$, 2 d.f., $p < 0.001$

Note: The distance between the two most widely separated shearwater burrows on Skokholm is about 1700 m.

extensive inter-colony dispersal been demonstrated. However, in other colonial seabirds greater male fidelity to the natal area has been shown for the Red-billed Gull (Mills 1973) and the Herring Gull (Chabryzk & Coulson 1976). It is also seen in a migrant passerine, the Pied Flycatcher *Ficedula hypoleuca* (Berndt & Sternberg 1969) and a resident passerine, the Blackbird *Turdus merula* (Greenwood & Harvey 1976). Greenwood and Harvey suggest a reason for this phenomenon. When the male plays a more important role than the female in securing a breeding territory he maximises his chances of obtaining a territory by returning to the natal area, where suitable breeding territories already exist and where he is familiar with spatial and temporal variations in resource availability. The female benefits from dispersal since she thereby avoids any deleterious effects (to her offspring) of inbreeding which would result if she was as faithful to the natal area as her male relatives. By dispersal she is also able to exercise a choice of breeding area and of mate when eventually she does settle to breed. I find this explanation broadly satisfactory for the Manx Shearwater since it is the male who spends more time visiting the breeding burrow in the pre-laying period (Harris 1966a; Perrins & Brooke 1976). Burrow visiting by the male Manx Shearwater is probably equivalent in function to territorial defence (see also Chapter 8).

IV Adult Survival

Annual adult survival of the Manx Shearwater has been reported as 96% by Harris (1966b) and as 90.2% by Perrins *et al*. (1973). The annual survival of the Manx Shearwater is determined by recording the absolute recapture rate in subsequent seasons of adults breeding in study burrows. As far as possible all adults alive are recaptured. If some adults which are alive evade capture, then the survival estimates will be too low. In particular adults might evade capture by moving to breed outside the area where the study burrows are located. The average annual survival during this study was 87.7% (Table 6.8), the figures for males and females being 87.2% and 90.3% respectively. The overall average survival is not a mean of the figure for males and females since included in the overall survival figure is a number of birds which had bred previously but were not then sexed and which were not known to have bred during the study period. It is possible that part of the reason for the apparent failure to breed of such birds was that the burrows they occupied were on the fringes of the study area. If this were so then it would be more likely that such birds, although still alive, would evade capture and therefore provide a higher apparent mortality. It is not feasible to distinguish this possibility from the alternative, that birds without burrows actually suffer higher mortality (Perrins 1971).

Since the number of missing adults is small it is possible to calculate a correction factor only for birds seen in 1975 but not in 1976. In the latter year 37 adults known to be alive in 1975 were not seen. In the present study period it happened that 37% (29 out of 78 cases) of the birds not seen in any one year were recaught in subsequent seasons. If this correction is applied to 1976 then the 1975-76 survival is raised to 88.1%. If the correction is also applied to males and females then the average survival for these two sexes in the period 1972-1976 becomes 89.5% and 91.5% respectively and the average survival of all birds in this period is 89.1%. This compares closely with an average survival figure of 90.2% published by Perrins _et_ _al_. (1973). My figure is lower principally on account of the relatively poor survival in 1975-76. It appears (Table 6.8) that mortality bore particularly heavily on males. In 1975 hatching success was relatively low (Table 4.1) and failure of the male to return to incubate appeared to be responsible for seven out of 25 hatching failures. In other years failure of the male to return to incubate was apparently responsible for seven out of 53 hatching failures. Although these survival figures do not

Table 6.8

Survival of breeding Manx Shearwaters from one season to the next. See text for further explanation.

Year		Number of breeding birds caught during year	Number known to have survived to next season	% minimum survival
1972	Males	90	82	91.1
	Females	85	78	91.8
	Total (including birds not sexed)	188	167	88.8
1973	Males	90	83	92.2
	Females	92	83	90.2
	Total	185	166	89.7
1974	Males	97	87	89.7
	Females	93	86	92.5
	Total	192	175	91.1
1975	Males	95	72	75.8
	Females	98	85	86.7
	Total	195	158	81.0
Averages	Male			87.2
	Female			90.3
	Total			87.7

demonstrate any significant difference between males and females it is worth noting that, of 85 birds known to be alive at least ten years after their first recorded breeding attempt, 46 were female, 36 were male and three were not sexed. The difference is also compatible with the observation that males may begin to breed at a slightly younger age than females (Section III).

Botkin and Miller (1974) considered available longevity records for a number of long-lived species and pointed out that the maximum life-spans actually achieved by birds were often less than would be predicted on the basis of the observed annual mortality and the assumption of age-independent mortality. Coulson and Wooller (1976) have shown that the annual mortality of the Kittiwake increases with age, and Webber (1975) found that the annual mortality of the Great Tit increased rapidly after the birds reached four years old. In the Laysan Albatross there is a complex relationship between breeding experience and mortality (Fisher 1975b). In Table 6.9 I compare the survival of birds that are known to be breeding and are in their tenth or subsequent year of breeding with the survival of 'new' breeders. A 'new' breeder is one breeding for the first recorded time in a burrow which has been regularly checked during the year preceding the first recorded breeding attempt. Survival of the experienced breeders is lower than that of new breeders but not significantly so.

Even if there were age-dependent differences in survival this would not invalidate the use of a simple survival figure in life-table calculations, provided that the birds from which that survival figure was derived comprised a random sample of the total population of all breeding birds. This condition was met in the present study.

Table 6.9

Survival of Manx Shearwaters according to whether they were 'new' breeders or birds in their tenth or subsequent year of breeding. Data extracted from study burrow records for the years 1964 - 1976 inclusive.

	Number caught during year	Number known to have survived to next season	% minimum survival
New breeders	121	114	94.2
Experienced breeders	150	138	92.0

X^2 test, N.S.

V The incidence of non-breeding among adults known to have bred previously

In each year a proportion of the Manx Shearwaters, which had bred in a previous year in study burrows, were not known to be breeding, although they were known to be alive. Combining all four study years, between which there were no known significant differences, the proportion of previous breeders not known to be breeding was 206 out of 730 cases, or 28.2%. The proportion for males was 24.4% (85 out of 348 cases) and for females 27.3% (98 out of 359 cases); this difference is not significant. The figure for both males and females is lower than that for all birds combined since a number of birds which bred in study burrows before, but not during, the study period were not sexed. All birds breeding in the relevant study burrows in this study were sexed, and there would therefore be a strong tendency for the birds which had bred previously but did not breed in a study burrow in any of the four study years to include a relatively high proportion of unsexed birds.

The proportion of previous breeders not known to be breeding did not differ in the three separate areas where study burrows were located. One of these areas, the Knoll, was bounded on all sides by a 40 m strip of ground in which there were no shearwater burrows. Moreover burrows in the Knoll colony were easily opened for inspection so that, in this colony, I could be confident that few, if any, breeding attempts were missed. The proportion of previous breeders which were not known to breed was no lower in this area than in the other two areas. Nevertheless it remains highly likely that some previous breeders which were not known to breed did in fact do so beyond the limits of the study areas. In the life table below I assume that 20% of all Manx Shearwaters which have bred previously and are alive in a particular year fail to breed in that year. Ashcroft (1976) reported that 10-30% of adult Puffins did not breed in any one year. A roughly similar incidence of non-

My examiners pointed out that the term 'life table' should not be used to describe my attempt to balance recruitment to and loss from the breeding population. Instead life table is correctly applied to a description of mortality versus age, and there is no simple single term which could be substituted in the present context.

breeding was found in the Waved and Laysan Albatrosses (Harris 1973; Fisher 1976). In these two albatrosses non-breeding was particularly likely after the loss of the mate but there was no evidence that non-breeding occurred because the birds needed a periodic 'rest'.

VI A Life Table for the Manx Shearwater

Recruitment to the breeding population

Nesting success - 70% (Table 4.1).

Of 70 fledglings a minimum of 25% may survive to return to the colony at breeding age (Section I) and a further 8% are lost to the colony by emigration (Section III). If immigration at least balances emigration, which is not unlikely since the nearby Skomer colony is about three times as large as the Skokholm colony (Corkhill 1973; Perrins 1967), then:-

Each 100 breeding pairs produce 33% of 70 or 23.1 birds which will be recruited to the breeding population each year.

Loss to the breeding population

With a 10% annual adult mortality in a stable population (Section IV), 100 breeding pairs contain 180 birds with previous breeding experience and 20 new breeders. 20% of shearwaters which have bred previously and are alive do not breed in any one year (Section V). Therefore 180 actively breeding adults represent 225 adults with previous breeding experience. Thus:-

Each 100 breeding pairs represent 245 breeding adults from which 24.5 breeders are lost each year.

Conclusion

This life table might imply a declining population, for which there is no evidence (Section II). It seems probable that the estimate (25%) of the proportion of fledglings which survive to return to the colony may be somewhat low (Section I), although other adjustments to the life table could

CHAPTER SEVEN

Inter-sexual vocal differences and individual vocal recognition in the Manx Shearwater (*Puffinus puffinus*)

Inter-sexual differences and individual vocal recognition in the Manx Shearwater (*Puffinus puffinus*)

Introduction

The large colony of manx shearwaters (*Puffinus puffinus*) on Skokholm Island, Pembrokeshire, Wales, has been the subject of several studies (Harris 1966a & b; Perrins, Harris & Britton 1973), all of which have been principally concerned with population biology. This emphasis on population biology has arisen because it is easy to catch and mark individual birds, both breeders and non-breeders. However, because all departures from and arrivals at the colony take place under cover of darkness and because breeding birds are temporarily disturbed if inspected inside their nesting burrow, there have been no detailed behavioural studies.

Any long-lived colonial bird which retains the same mate year after year, as does the manx shearwater (Harris 1966a), needs some mechanism by which the pair can re-establish contact at the start of the new breeding season. If considerable site fidelity is shown by both male and female, as happens in many seabirds including the manx shearwater, this alone will facilitate re-establishment of the pair-bond and if the bird can individually recognize the mate of the previous year this would also be of value, particularly when a change of nest site occurs. In a nocturnal species like the manx shearwater the value of visual displays in the maintenance of the pair-bond may well be less than in species active at the colony by day, and it is possible that vocal signals will assume a correspondingly greater significance in this respect. As Beer (1970) has pointed out, good evidence for individual recognition of voice in birds comes from colonial species or species living in thick vegetation, both circumstances where the use of the omnidirectional characteristics of sound transmission and reception would allow for the more ready detection of individuals than would the use of vision.

A non-breeding bird also needs a mechanism whereby it may attract or recognize a potential partner of the opposite sex. If this cannot easily be achieved by visual display, because of darkness, vocal and olfactory signals (Bang & Cobb 1968; Grubb 1974) provide possible alternative mechanisms.

There is a great deal of calling in a manx shearwater colony at night and in 1976 I attempted a preliminary analysis of its significance.

Inter-sexual vocal differences

Method of obtaining recordings

I obtained recordings at night of twenty different males and eighteen different females using a Phillips 2205 Cassette Recorder. The birds were sexed by cloacal inspection (Serventy 1956). All birds bred in 1976 except one male which bred in 1975 but was not known to have bred in 1976, and all birds were alone in their own nesting burrow when recorded, except for one male which was recorded when alone in a burrow close to its own nesting burrow.

Because of the need to obtain recordings from birds of known status it was possible to record the voices of only three spontaneously calling males. The other seventeen males were stimulated to call when I played back to them the recording of male A (one of the three spontaneously calling males) and the stimulated call was then recorded. If necessary for the acquisition of a longer or clearer recording the last few seconds of the recently-recorded call of the male in question were played back to him. This invariably re-stimulated calling which was then recorded. Recordings of males were made in the pre-laying period or, in two cases only, during incubation.

No spontaneously calling females were recorded. Female B was recorded when she called in response to a playback of her mate, male A. The other seventeen females were stimulated to call when I played back the recorded call of female B and the stimulated call was then recorded. If necessary for the acquisition of a longer or clearer recording the last few seconds of the recently-recorded call of the female concerned were played back to her. This re-stimulated calling which was then recorded. All recordings of females were made during incubation.

If shearwaters have repertoires of calls akin to the song repertoires of passerine birds (Hartshorne 1973) and if matching occurs (Lemon 1968) then my recording technique will provide a biassed sample of the calls of any one shearwater. This possibility is unlikely to account fully either for the differences found in the calls of the two sexes or for the outcome of the playback experiments described below.

Results

The duration of the recordings obtained varied between 14 and 68 seconds, including periods of silence, but most recordings lasted 20-40 seconds. Both male and female calls showed a similar pattern, a series of repeated units, each lasting about 1-1.5 seconds followed by a terminal 'gurgle'. The repeated units in the calls of eighteen males and eleven females, chosen at random, were analysed on a Kay Sound Spectrograph. The units of the male call show a combination of clear notes which, to my ear, have a ringing vibrant quality, and harsher sounds which contain notes with frequencies spread throughout the 0-2 Khz band, as illustrated in Figures 7.1-7.4. Female calls lack the clear notes and consist entirely of the harsher sounds. This difference was sufficiently marked to enable me subsequently to assign spontaneously-calling birds to one sex or the other with considerable confidence and I conclude that males and females sound different.

Figures 7.1 - 7.4

Each figure shows, on the upper line, sound spectrographs of the calls of two male Manx Shearwaters and, on the lower, the calls of two female Manx Shearwaters. 16 different birds are shown altogether.

Figure 7.1

Figure 7.2

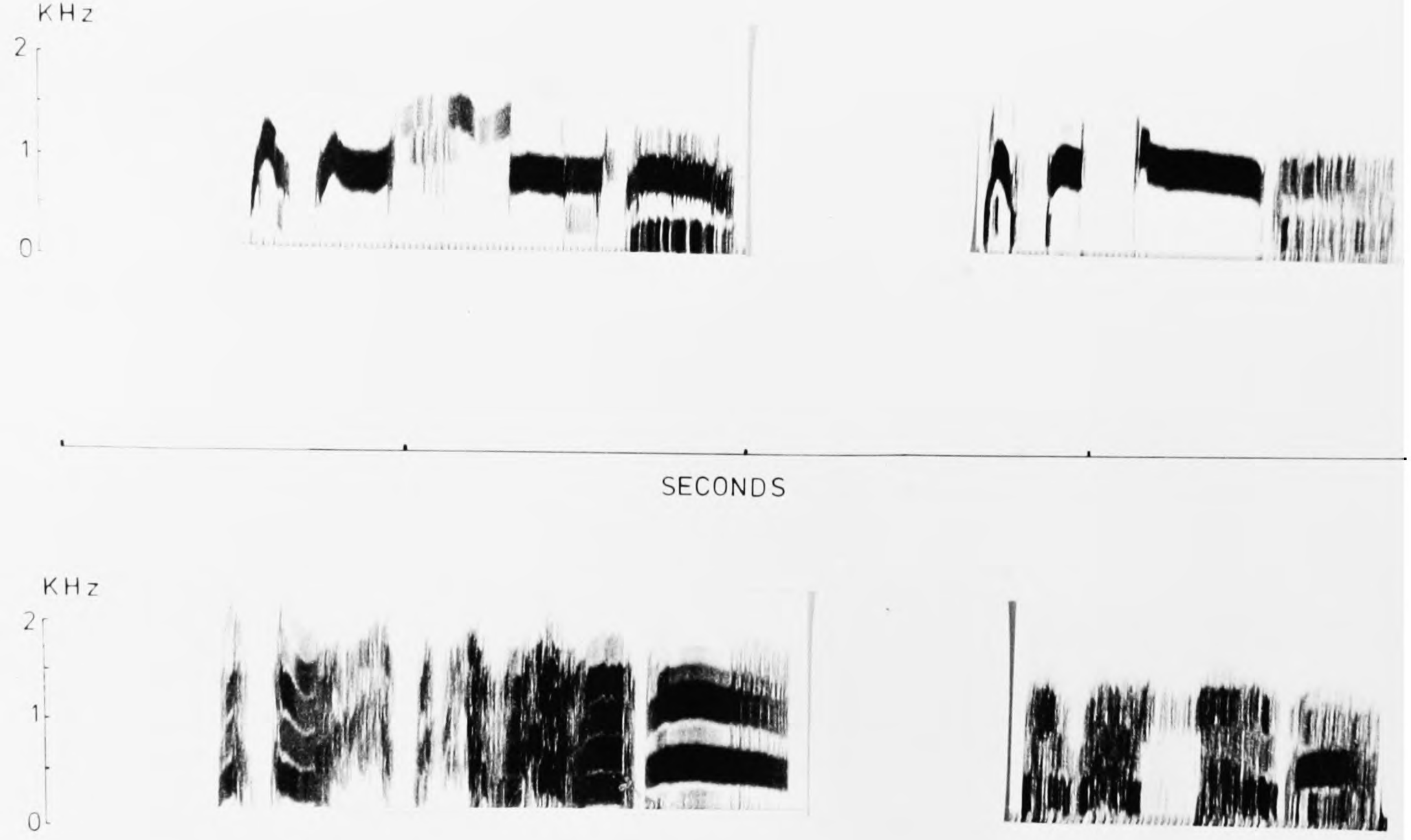


Figure 7.3

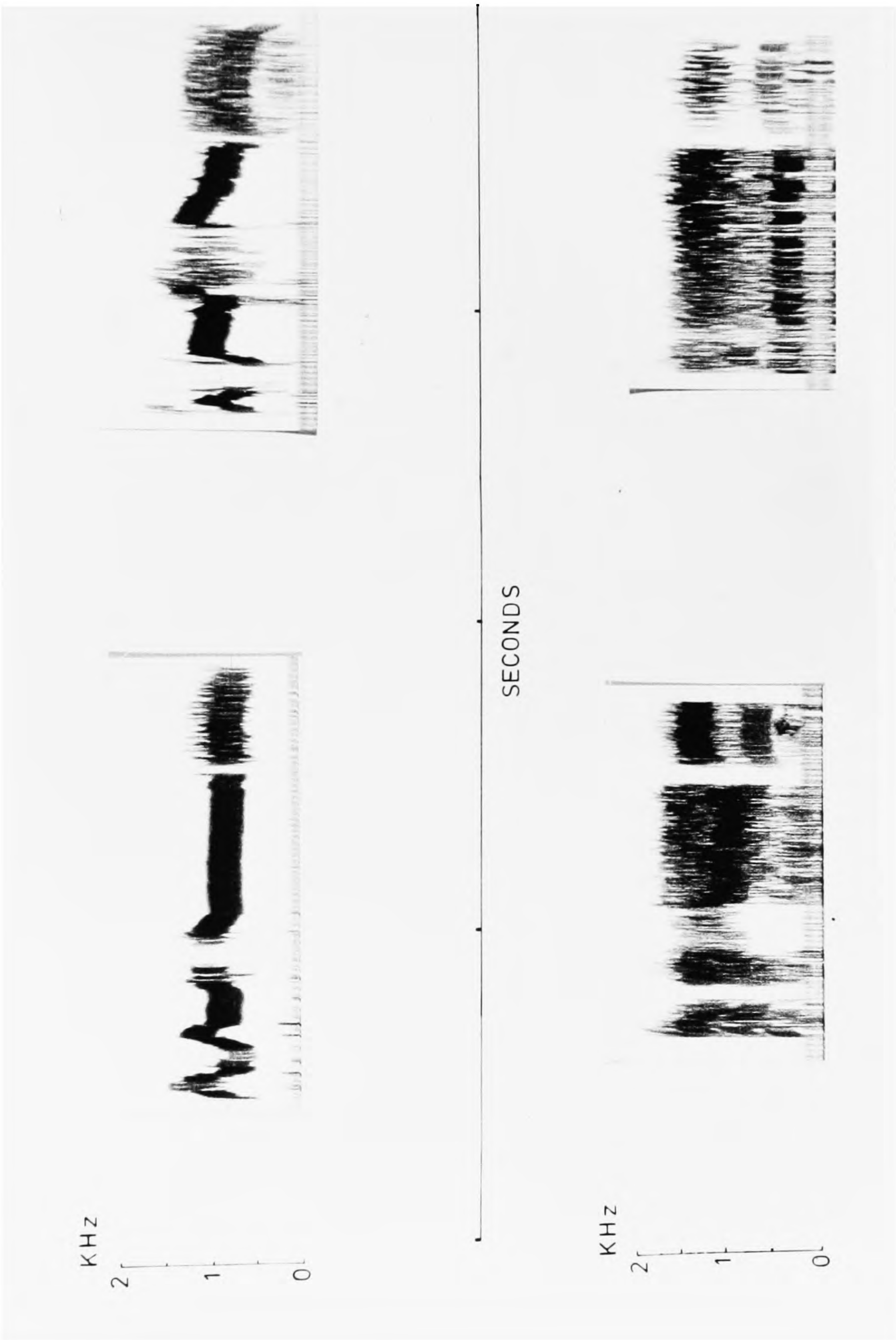
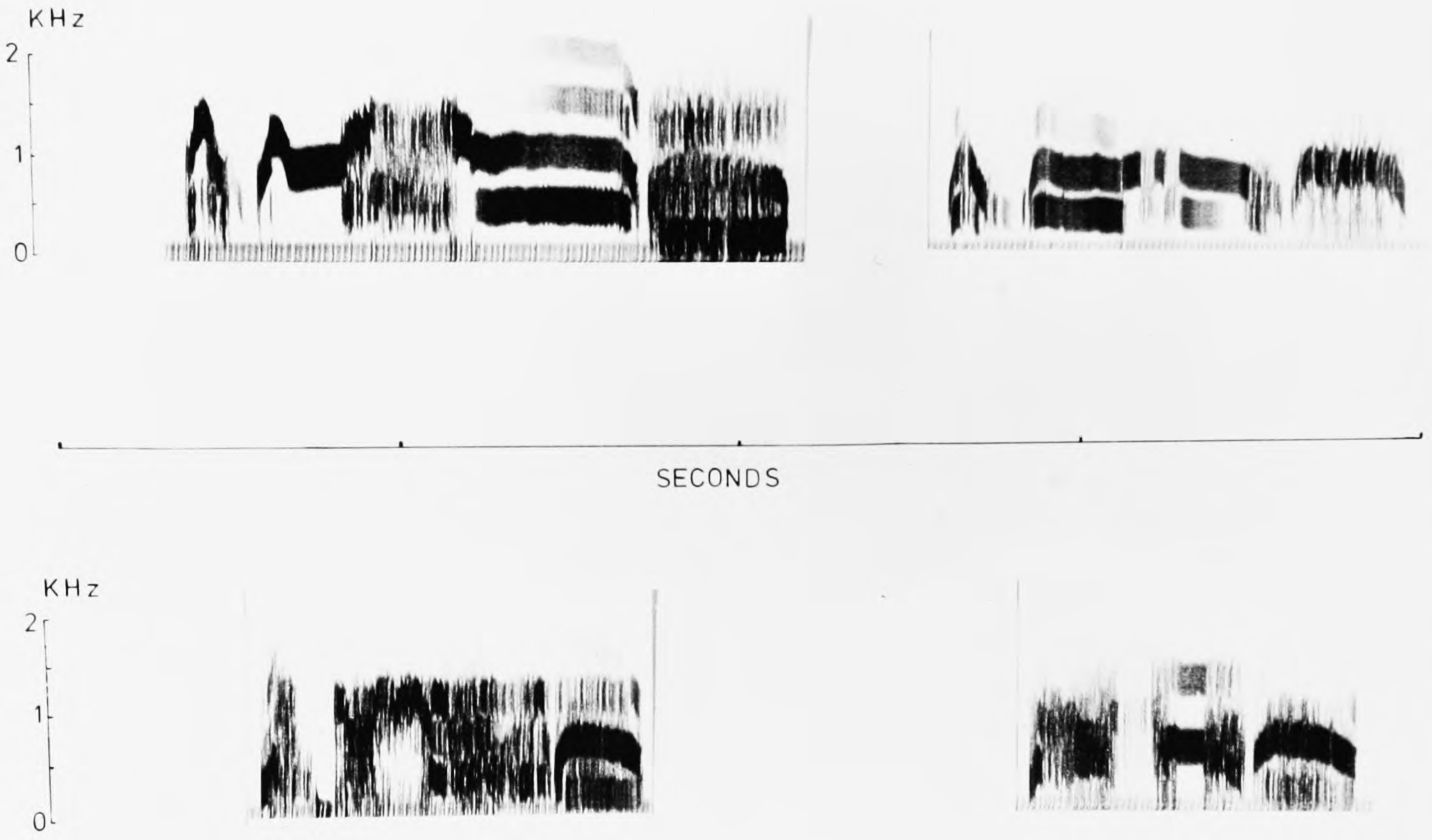


Figure 7.4



I asked three colleagues who were familiar with spectrographs but had not participated in this work independently to sort the twenty-nine spectrographs (eighteen male and eleven female) into two groups, without specifying the number that should occur in each group. Two people achieved the correct separation of eighteen males and eleven females; the third person grouped eight female spectographs together but incorrectly assigned the other three to the male group.

The responses of the manx shearwater to the playback of recorded calls.

Playback methods

Playback tests were carried out at night on adult shearwaters incubating alone in their nesting burrows. No bird experienced more than one playback per night and no single recording was played to a particular incubating adult more than twice. In each playback test the recording was played through once only and I noted whether or not the incubating bird called in response to the recorded calls. No attempt was made to measure other possible response parameters such as movement along the burrow towards the source of the sound. Although the recordings were variable in duration this probably did not affect the results obtained since, if a vocal response was given, it would usually commence a few seconds after the start of playback.

Results

Tables 7.1 and 7.2 show that males nearly always responded to male recordings but females never did unless they were the mates of the recorded male, in which case they responded on about half the occasions.

If female calls were played to an incubating adult then that adult would nearly always respond if it was a female but was significantly less

Table 7.1

The frequency of response of incubating adult Manx Shearwaters to the playback of male calls.

	Responds	Does not respond
Male	23	2
Female (other than mate of recorded male)	0	26

Males are more likely to respond to male calls than are females (X^2 test, $p < 0.001$).

Table 7.2

The frequency of respone of incubating female Manx Shearwaters to the playback of male calls.

	Responds	Does not respond
Mate	13	11
Non-mate	0	26

A mate is more likely to respond to a male's call than a non-mate (X^2 test, $p < 0.001$).

likely to respond if it was a male (Table 7.3). In contrast to the selective response of the female to the call of her own mate described above there was no significant indication that a male was more likely to respond to the call of his own mate than to the call of another female (Table 7.4). I have been unable to identify any features of a female call which make it more likely that a male will respond to it, nor any features of the incubating male which might have predisposed him to respond to a female call.

Acoustic basis for individual recognition of males by their female mates.

Methods

The ability of females to respond selectively to the calls of their mates implies that, for males, the within-bird variation in calls is less than the between-bird variation. To investigate this further I selected ten males whose call had drawn a response from their mates and obtained recordings on three further nights from nine of these males and on two further nights from the tenth male. The method of obtaining these further recordings was similar to that used to obtain the original recordings. The males, which were incubating alone in their nesting burrow, were stimulated to call by playback of male A, and the stimulated call was then recorded. If necessary the last few seconds of the recently-recorded call were played back to re-stimulate calling.

Results

Figures 7.5-7.9 show sound spectrographs from a random selection of five of the ten males. Each figure shows, in the top left, the spectrograph of a unit occurring in the original recording used in the playback experiment whilst the other three spectrographs are from recordings made on three further nights. No attempt was made to select similar sounding units for

Table 7.3

The frequency of response of incubating adult Manx Shearwaters to the playback of female calls.

	Responds	Does not respond
Female	34	2
Male (other than mate of recorded female)	14	25

Females are more likely to respond to female calls than are males (X^2 test, $p < 0.001$).

Table 7.4

The frequency of response of incubating male manx shearwaters to the play-back of female calls.

	Responds	Does not respond
Mate	12	14
Non-mate	14	25

A male is not significantly more likely to respond to the call of his mate than to the call of another female (X^2 test, N.S.).

Figures 7.5 - 7.9

Each figure shows the call of a single male Manx Shearwater given on four different nights.

Figure 7.5

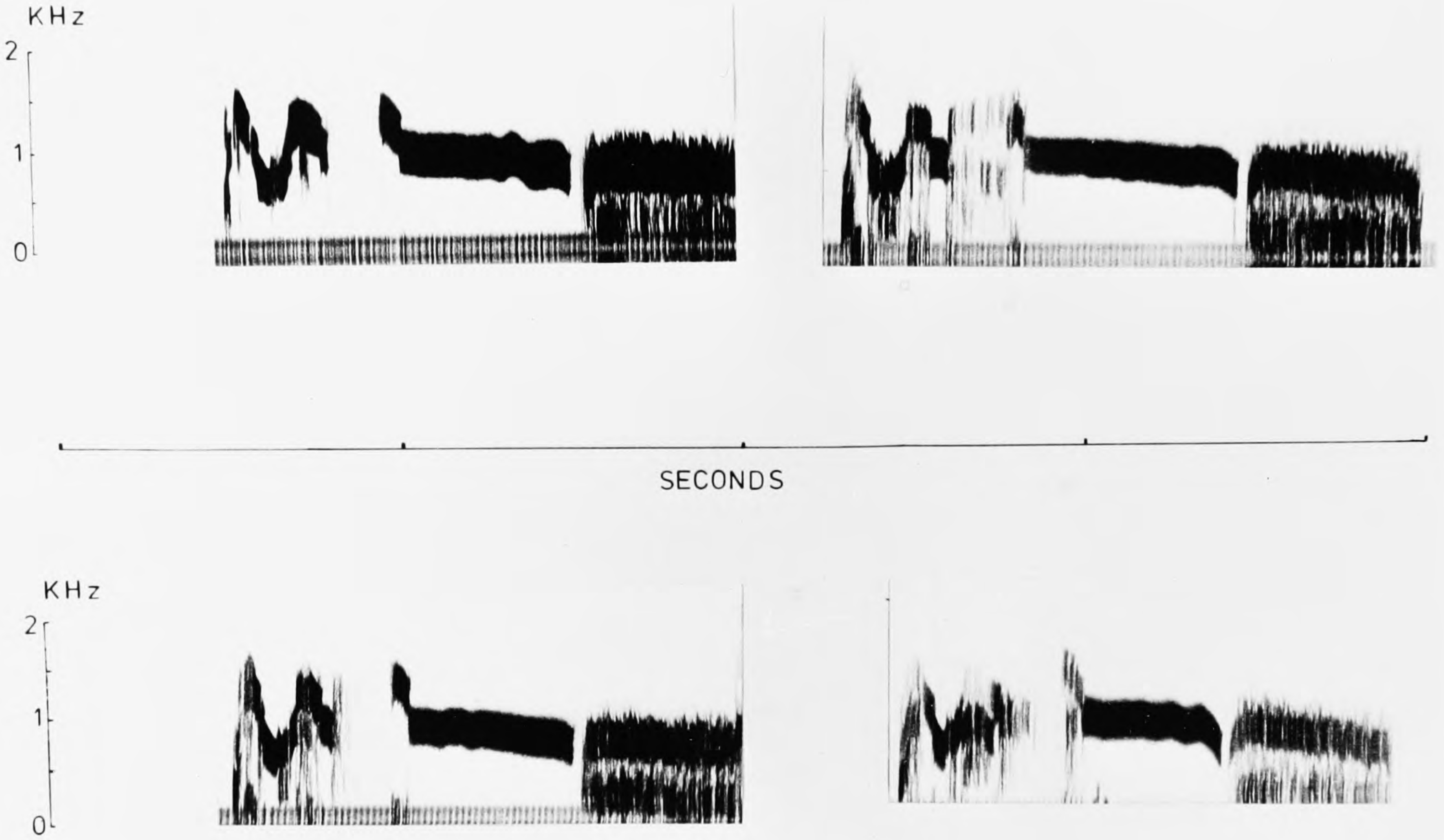


Figure 7.6

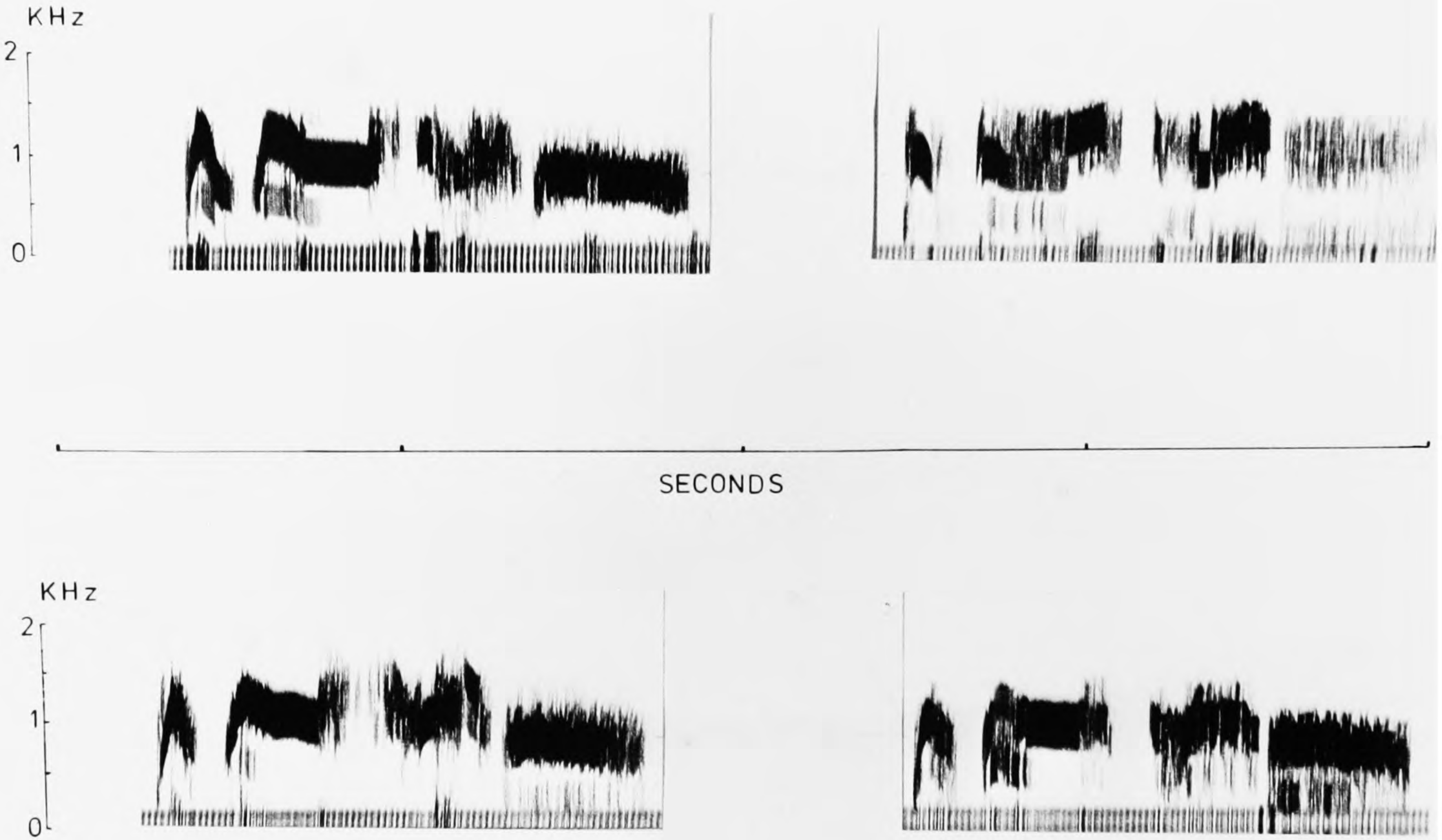


Figure 7.7

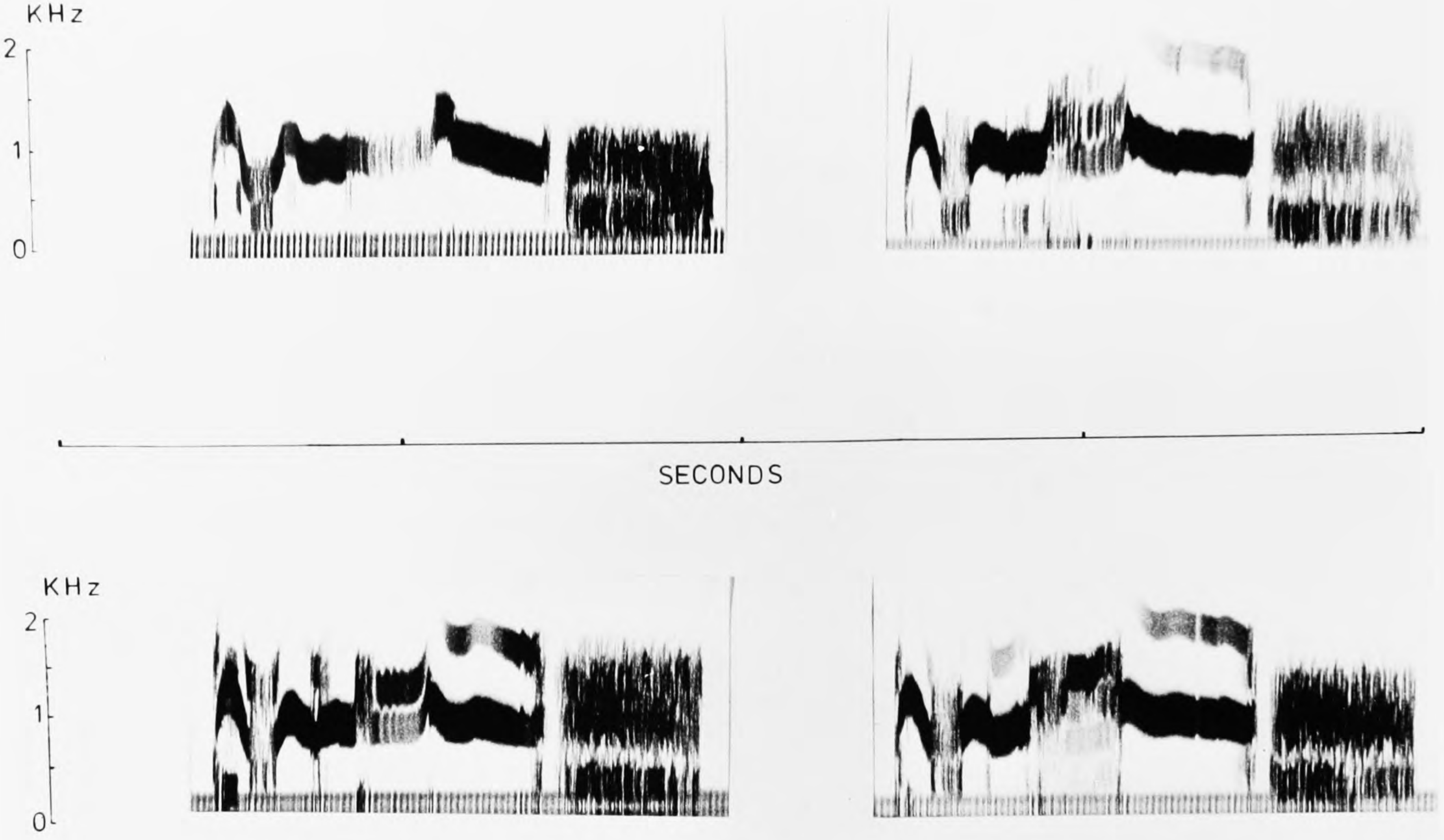


Figure 7.8

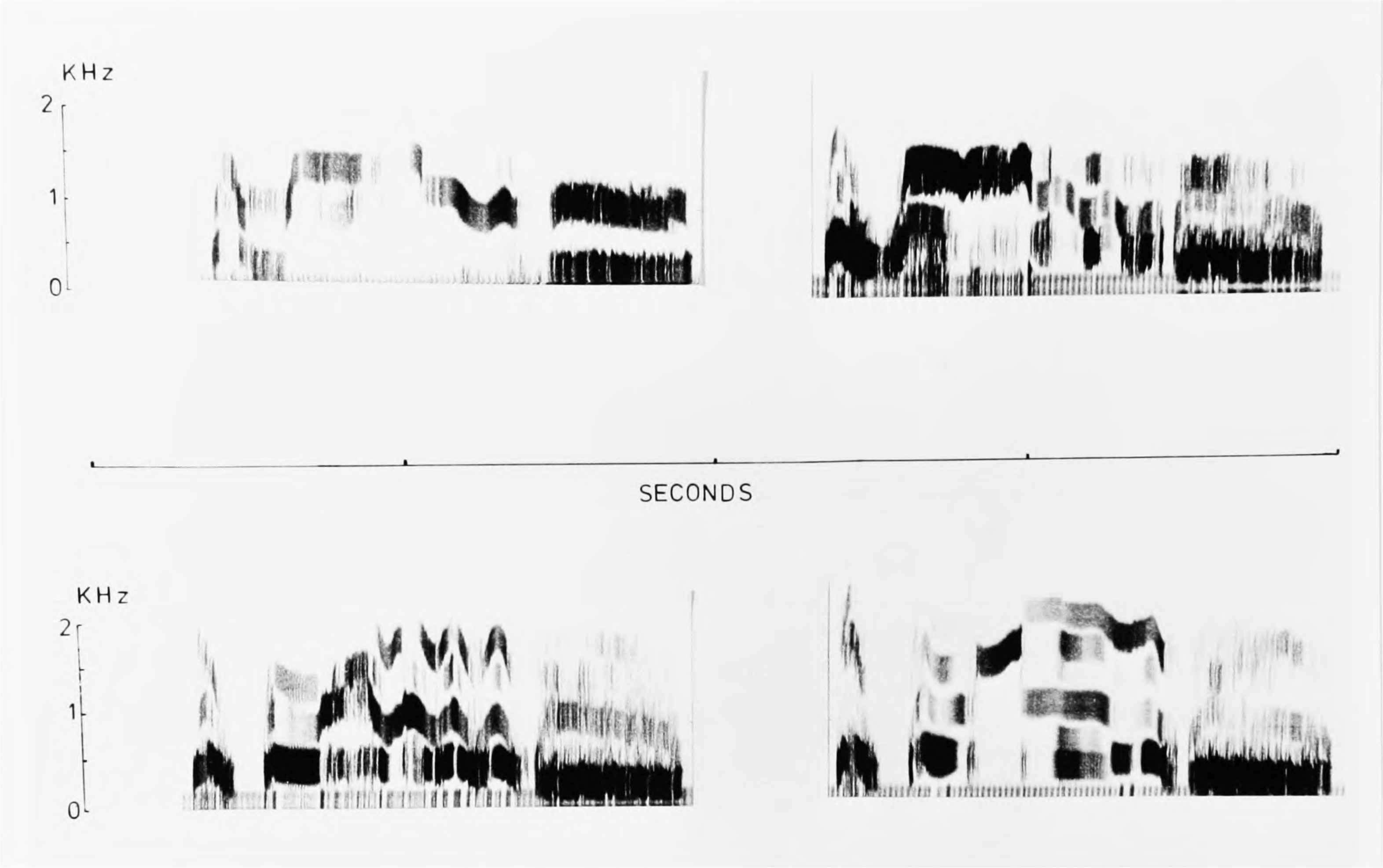
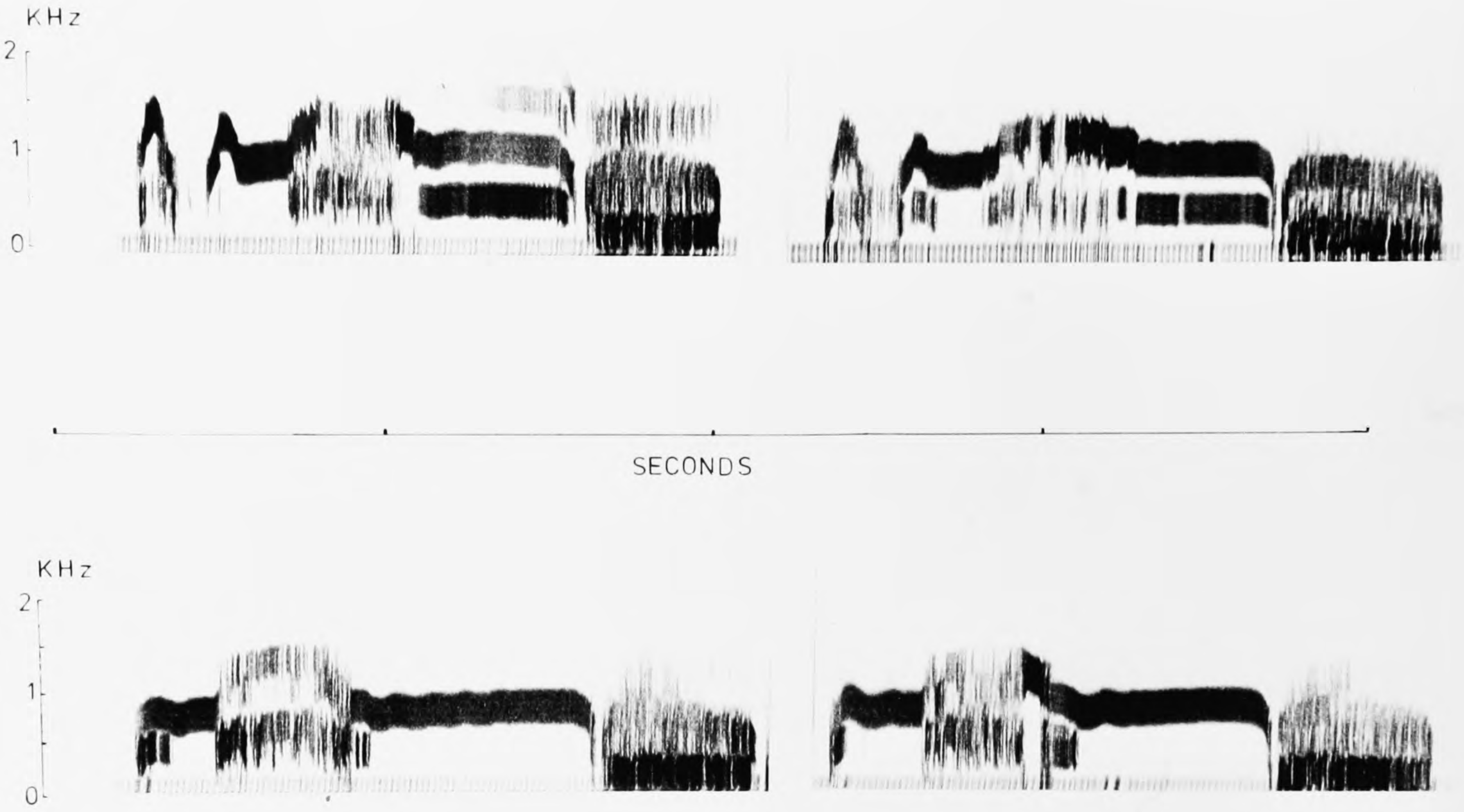


Figure 7.9



spectral analysis. Nevertheless visual inspection strongly suggests that the calls of males have a sufficient number of individually distinct characteristics to provide a basis for their recognition by females, but it is not known which characteristics are actually utilised by females (Hutchison, Stevenson & Thorpe 1968; White, White & Thorpe 1970).

From the ten males used in this study I had obtained a total of thirty-nine spectrographs. One spectrograph from each male was then displayed and I asked three colleagues to match the remaining twenty-nine spectrographs to one of the displayed spectrographs. The spectrograph to be matched was proffered to the colleague who was given 30 seconds for the matching before the spectrograph was removed and the next one provided. Using this testing method each person should have achieved an average 2.9 correct matchings if matching was random. In fact the number of correct matchings was 13, 17 and 20 respectively ($p < 0.001$ in all three cases). Spectrographs of male manx shearwater calls can be successfully matched by human subjects but it is worth noting that the matching is not as successful as the discrimination of male and female calls and this parallels the results obtained from the shearwaters themselves (Tables 7.1-7.3).

Time did not allow me to obtain further recordings of females and therefore it is not known whether the calls of different females are individually distinct, despite the lack of evidence that males selectively respond to the calls of their mates (Table 7.4).

Response of nestlings to the calls of adults

Early in the night, probably before the nestlings had been fed, recorded calls of male and female manx shearwaters were played to unattended nestlings aged between thirty and sixty days using the playback methods described above. The vocal response elicited in some cases was a soft cheeping similar to that heard when an adult is feeding a nestling. There was no evidence of selective vocal responsiveness to the parents' calls nor was there any significant difference in the frequency of response to adult males and females (Table 7.5). The sex of the nestlings was not known.

Sex ratio of manx shearwaters calling on the ground and when flying

On three consecutive nights 29-31 July 1976 I spent about an hour walking slowly and without light through the shearwater colony, following a different route each night and recording the number of individuals of each sex calling on the ground within 10 m of my route. I did not attempt to differentiate birds calling on the surface and from within burrows. On each night about twice as many male calls as female calls were heard (Table 7.6). A small number of calls were not assigned to one sex or the other, usually because these calls were muted and brief.

On three consecutive nights 25-27 July 1976 I walked for about a mile through the Skokholm shearwater colony recording the number of individuals which flew close enough to be discerned in the darkness as flying birds and which were giving either 'male-type' or 'female-type' calls. I refer to these calls as male-type and female-type because I can provide no formal demonstration that they were indeed given by males and females respectively. However the difference between the types of calls was similar to that heard from birds of known sex on the ground and spectrographic analysis of a small number of recordings made of calling flying birds confirmed this difference. On each night about three times as many female-type calls as male-type calls were heard (Table 7.7).

Although I do not have precise data to establish the point I have the strong impression that this dichotomy exists throughout the breeding

Table 7.5

The frequency of response of nestling manx shearwaters to the playback of adult calls.

	Responds	Does not respond
Male parent	4	9
Female parent	4	12
Total parent	8	21
Male non-parent	2	11
Female non-parent	5	9
Total non-parent	7	20

There is no significant difference between the frequency of response to parents and non-parents, or to males and females.

Table 7.6

Number of male and female Manx Shearwaters heard calling on the ground.

Date	Male	Female	Sex uncertain
29 July	36	20	5
30 July	12	5	-
31 July	14	6	1
Totals	62	31	6

Binomial test: Female $<$ Male

$p < 0.001$

Table 7.7

Number of 'male-type' and 'female-type' calls heard from Manx Shearwaters flying over the colony at night

Date	Male-type	Female-type	Sex uncertain
25 July	8	29	-
26 July	11	36	-
27 July	9	34	1
Totals	28	99	1

Binomial test: Male-type $<$ Female-type

$p < 0.001$

season and that male calls are always the more frequent among calls given on the ground whilst female-type calls always predominate amongst calls given by flying shearwaters.

Discussion

If ecological constraints on the manx shearwater, such as predation by gulls (Larus spp.), restrict activity at the colony to the hours of darkness then the usefulness of visual displays in sexual advertisement is reduced. Vocal signals may come to fulfil this role instead and this may be the reason for the sexual differences in the calls of the manx shearwater. Other shearwaters for which sexual differences in call have been suggested, but not demonstrated, are Cory's shearwater (Calonectris diomedea) (Roux & Jouanin 1968) and sooty shearwater (Puffinus griseus) (J. Warham, pers. comm.). Jouanin & Gill (1967) have also suggested a sexual difference in the calls of Barau's petrel (Pterodroma baraui). A disadvantage of using vocal signals for sexual advertisement is that they are less suitable for directing at one specified individual than are visual signals.

Why do males respond to the playback of male calls and females to the playback of female calls (Tables 7.1 & 7.3)? If the role of passerine territorial song given by males is to discourage the intrusion of conspecifics (Krebs 1977) and/or to attract females (Armstrong 1963) then the call of the male manx shearwater may fulfil the same function. The greatest threat to the status of a breeding male would be his replacement by an intruding male and it would be advantageous to the burrow-occupying male to discourage by calling any male that was about to intrude. Using the same argument a female's role as the occupant of a particular breeding burrow is most threatened by the intrusion of another female and the responsiveness of females to the calls of other females

(Table 7.3) may serve to inhibit such intrusion. A similar explanation could be given for Penney's (1968) observation that most fights between territorial Adelie penguins (Pygoscelis adeliae) at the beginning of the breeding season occur between members of the same sex (see also Tinbergen 1939; Lack 1941).

While a bird's principal concern must be with its own status as a burrow-occupant, there are also advantages in retaining the same mate in successive years (Chapter 4) and these advantages (earlier laying and the production of a heavier chick with a greater probability of survival) accrue equally to both sexes. The ability of females to recognize the calls of their mates (Table 7.2) and the lack of evidence that males selectively respond to the calls of their mates (Table 7.4) therefore requires explanation. There is no a priori reason for supposing that the parental investment (Trivers 1972) of the two sexes is markedly different. During the pre-laying period when the female is building up food reserves with which to make the egg, the male continues to visit the nesting burrow (Perrins & Brooke 1976) and subsequently the labour of incubation and chick-rearing is, so far as is known, approximately equally shared (Harris 1966a). This contrasts with the situation in, for example, ducks (Lack 1974) and some orthopterans (Mayr 1963) where the male's investment is smaller than that of the female and consequently mate selection is primarily the concern of the female since she has more to lose by misplacing her investment.

In the case of the manx shearwater I suggest that the ability of females to recognize the calls of their mates (Table 7.2) and the fact that males apparently do not selectively respond to the calls of their mates (Table 7.4) may be related to the different role of the sexes. The male of a breeding pair has the more important role in burrow defence in the pre-laying period (Harris 1966a; Perrins & Brooke 1976) and therefore it will commonly be the case that, as the female arrives at the colony from the sea, she will be attempting to locate the male with which she mated the previous year and which will already be on the ground occupying a burrow. It would expedite location and re-establishment of the pair bond if she could recognize his call, particularly as unchanged pairs may move some distance, up to 30 m in this study, between breeding burrows in successive years. The ability of a male to recognize the call of a particular female would seem less useful since, once the female has located and come into contact with a male beside or inside a burrow, there is the possibility of using other non-vocal recognition signals. This difference in the role of the two sexes only exists in the pre-laying period but not subsequently (see above). However there is evidence that, among birds without known previous breeding experience, males are more often caught than females (Table 7.8) which suggests, since to be caught a bird must be on the ground, that males spend more time on the ground than females. Thus I propose that it is valuable for a female to be able to recognize the call of an established or a potential mate given from a burrow, but that the reverse is not necessarily true if the male can use other recognition signals once a female has physically located him.

It follows from this hypothesis that male calls should be more frequent than female calls amongst calls given on the ground. This is observed (Table 7.6). Since a female call frequently draws a vocal response from a male (Tables 7.3 & 7.4), the value to a female of calling in the air (Table 7.7) might be to increase the likelihood that she will hear, amongst birds calling on the ground, the voice of either an established or a potential mate.

An implication of these ideas, that calling is primarily concerned with burrow-ownership and the establishment of the pair bond is that, after

Table 7.8

Number of manx shearwaters, without known previous breeding experience, that were breeding for the first time in year N + 1 and were : -

	Caught in colony in year N	Not caught
Males	22	4
Females	14	13

Males are more frequently caught than females (X^2 test, $p < 0.05$).

mid-May when most birds have settled disputes over burrow-ownership and begun incubation (Harris 1966a), most calling is due to non-breeding birds. There is no evidence on this point since there are no ready means of determining the status of spontaneously calling birds, whether flying or on the ground. However the activity of breeders is not greatly affected by the state of the moon (Harris 1966a) but the number of non-breeding birds visiting the colony is substantially greater during dark new moon periods (Harris 1966b), when the amount of calling is also substantially greater.

The possible use of calling as means of burrow location has been a matter for previous speculation (Lockley 1969) and the ability of the female to recognize the male's call would potentially provide her at least with the opportunity to home in on the nesting burrow if the male was calling from within it. Further experimentation would be necessary to establish whether this actually occurs. However the calling of the mate from within the burrow cannot be the only mechanism used for burrow location since both parents can locate the burrow to feed the unattended nestling, which does not call. I have also closely observed one incubation change-over, when the male relieved the female, and, in this instance, the female did not call at all before the male entered the burrow. Other senses which might be used in burrow location include olfaction (Grubb 1974) and vision (Appendix 3).

The chick apparently does not respond selectively to the parents' calls (Table 7.5). This is not unexpected since the immobile nestling can take no active steps to move towards its parents and solicit food. It must merely wait inside the burrow for the arrival of the parents and would not obviously benefit from the ability to recognize its parents' calls. This situation contrasts with that facing the nidifugous young of the common tern (Sterna hirundo) (Stevenson et al. 1970) or Adelie penguin (Penney 1963). Young of both these species recognize the calls of their own parents. Nor does it appear that the manx shearwater parent can individually recognize its own chick, but this inability does not result in the parent providing food for unrelated offspring if it is only in exceptional circumstances that the nestling in a bird's burrow is other than its own. In August 1976 I swopped two half-grown nestlings, both about 35 days old and of similar weight, between burrows some 120 m apart. Both continued to be fed and to grow normally. The ability of the parent to recognize its own chick becomes important only when the topographical location of the chick ceases to provide accurate information about its parentage (Davies & Carrick 1962; Tschanz 1968) or when there is a prolonged period of post-fledging parental care (Ashmole & Tovar 1968).

This study did not attempt to investigate vocal differences between different areas of the Skokholm manx shearwater colony. No such differences were immediately apparent nor are the calls of the manx shearwaters I have also heard on Skomer Island, Pembrokeshire and St. Kilda, Outer Hebrides strikingly different from those of Skokholm birds. Through the kindness of Peter G. H. Evans I was able to make a sound spectrograph of a male from the Puffin Island colony, Co. Kerry. His call was not obviously different from that of Skokholm males.

CHAPTER EIGHT

Colonial breeding and its influence on the breeding biology of the Manx Shearwater

Part I

The significance of colonial breeding

This final chapter reviews some influences on the breeding biology of the Manx Shearwater revealed by the present study. Many of these influences naturally stem from the fact that the bird must necessarily breed close to the sea at sites which are fairly secure from ground predators, since the Manx Shearwater's morphology renders it relatively helpless on land. It is only to be expected therefore that Manx Shearwaters should mostly breed on offshore islands and this will inevitably lead to some aggregation of nest sites. Also promoting aggregation of nest sites will be any advantages which accrue to a bird which returns to its own natal area to breed, rather than spending time and energy searching for a better area, if such exists. It is less clear why, within areas of fairly uniform breeding habitat such as Skokholm, nest sites should be clumped (Perrins 1967) and why there should be marked differences in burrow density in different areas (Chapter 2).

There are two principal hypotheses concerning the value of colonial breeding. The first is that colonial breeding evolved as an anti-predator strategy (Patterson 1965, Lack 1968), and the second that colonial species are more efficiently able to exploit patchily distributed food supplies (Crook 1965, Ward & Zahavi 1973, Krebs 1974). Both might be present advantages of colonial breeding for the Manx Shearwater, although the present advantages may not accurately reflect those selective forces which initially promoted colonial breeding.

There is some evidence that predation on adult Manx Shearwaters is lower within than outside the Main Colony. In the seven years 1970-1976 (records do not extend further back because of an unfortunate loss of data), 203 shearwaters aged at least five years old were found dead on Skokholm.

All were assumed to have been killed by gulls unless there was a clear indication that this was not the case. Birds ringed when full-grown were assumed to have been killed where ringed since full-grown birds rarely move within the island (Harris 1966b). Birds ringed as pulli were only scored if they had been recaptured alive in a later year and were then assumed to have been killed at the place of recapture. In 1973 and 1975 I opened up breeding burrows in the Main Colony and in 1974 burrows elsewhere on the island. This allowed an estimate of the proportion of ringed birds amongst the breeding adults of the two areas to be made whence, knowing the breeding population of the two areas, the total number of ringed birds may be calculated, and the expected frequency of birds from within and without the Main Colony in the 203 predated birds may be determined. The relevant calculations are made in Table 8.1, and it appears that adults from the Main Colony experience a lower rate of predation.

The Main Colony has several features which may contribute to the lower rate of predation. For instance it is some distance from any of the large Skokholm gulleries and the terrain is particularly exposed which allows grounded shearwaters to take flight more rapidly, at least when a moderate wind is blowing. It is therefore difficult to know whether the Main Colony is dense because of these favourable features which may reduce predation, or whether the greater density of nesting birds per se contributes to the lower predation rate, possibly because any predator would find it very difficult to approach undetected (Pulliam 1973, Page & Whitacre 1975). It is not known if the lower predation rate of adults in the Main Colony means that these adults have a higher survival, since adult survival (Chapter 6) was determined from study burrows outside the Main Colony.

Predation on young birds is of two types. Around dawn in July and August a few Herring Gulls and Lesser Black-backed Gulls _Larus fuscus_ walk through the colony inspecting burrows and catching any chicks which have

Table 8.1

A comparison of the rate of predation of adult Manx Shearwaters within and outside the Main Colony.

	Within Main Colony	Outside Main Colony
No. of birds found incubating	455	197
No. of ringed birds	176	37
% of ringed birds	38.7	18.8
No. of breeding adults (Perrins 1967; Brooke 1973)	20,000	50,000
No. of ringed adults available to be predated	7736	9391
Expected number of ringed birds in a total of 203 predated birds	91.7	111.3
Observed number	70	133

$X^2 = 8.94$, 1 d.f., $p < 0.01$

remained too close to the burrow entrance. This activity has only been observed in the Main Colony where the density of burrows is presumably high enough to make it energetically profitable for the gulls; but the total number of chicks captured is probably small. Larger numbers are taken during the fledgling period; the number of freshly predated fledglings found on Skokholm in the four years, 1973-1976, was 473, 238, 366, and 359 respectively. It would, however, be difficult to relate fledgling predation to burrow density because of two further variables.

(i) Distance of the burrow from the cliff edge. Since fledglings can rarely take flight from the centre of the island chicks leaving burrows far from the sea have a longer overland journey, and presumably higher risk of predation, than chicks leaving burrows on the cliff edge.

(ii) Puffinosis (Harris 1965a). This disease is restricted to where shearwater burrows are found in stands of bracken Pteridium aquilinum. Afflicted chicks are more likely to be predated than healthy ones.

Since the Main Colony is close to the cliff edge and does not suffer from puffinosis chicks fledging from this colony may experience lower predation than those fledging from burrows elsewhere on the island but, as with adult predation, it is uncertain to what extent (if any) this is due to the high density of the colony and to what extent small differences in habitat and colony location are sufficient to reduce predation.

The investigation of whether colonial breeding promotes the efficient exploitation of food by the Manx Shearwater may only be achieved indirectly, by comparing reproductive success in areas of different breeding burrow density. I have no satisfactory measure of breeding success (% of eggs laid producing fledged young) in the Main Colony since the adults, being unaccustomed to handling, were prone to desert, so that observed breeding success was lower than in the Observatory burrows. In 1974 the median laying date of 47 eggs in Main burrows, unbiassed by selection for birds of known age, was 8 May. The median laying date of 80 eggs in Observatory burrows was 9 May (Table 4.8); the difference is not significant (median test). The significance of laying date lies in its relation to fledging date and hence fledging weight (Chapter 5) and subsequent survival probability (Perrins, Harris & Britton 1973). Not only were the laying dates of eggs in the Main and Observatory burrows little different but also the 60-day weights of chicks reared in these two colonies were not significantly different (Table 8.2). There is thus no indication that the greater burrow density of the Main Colony was related to greater reproductive success, as might have been predicted if the aggregation of nests increased the efficiency of exploitation of food resources. One might suggest that the entire Skokholm colony acts as an 'information-centre' (Ward & Zahavi 1973) for food exploitation so that differences in reproductive success would only be found if one could compare the Skokholm colony with another of quite different size.

In conclusion, general ecological constraints may lead to the Manx Shearwater forming loose colonies. This may in itself serve to reduce predation if the number of shearwaters is sufficient to 'swamp' those predators active in the vicinity of the colony. Within the colony, burrows may be clumped where predation is lower (Table 8.1). The lower predation may be more due to local habitat features than to the higher density of nesting birds. There is certainly no observation suggesting that shearwaters actively co-operate to resist predators as does the Black-headed Gull <u>Larus ridibundus</u> (Kruuk 1964), but it remains possible that a dense group of nesting shearwaters is more likely to detect any approaching predator (Pulliam 1973).

Table 8.2

The mean 60-day weight in grams (± S.E.) of Manx Shearwater chicks raised in the Main and Observatory burrows, Skokholm, in the years 1973 - 1976. Sample sizes in brackets. Within years, no differences between the Main and Observatory means are significant (t-tests).

Year	Main	Observatory
1973	549.6 ± 6.35 (40)	546.8 ± 6.59 (58)
1974	558.1 ± 11.75 (21)	584.7 ± 7.77 (56)
1975	526.6 ± 9.57 (32)	538.3 ± 7.97 (44)
1976	550.7 ± 12.59 (16)	555.9 ± 7.45 (53)

Note: Chicks reared by adults which were not their own parents, as a result of the egg-swapping experiment carried out in the Main Colony in 1974 and 1975 (see Chapter 5), are not included in the Table.

Part II

The influence of colonial breeding on the breeding biology of the Manx Shearwater

The fact of clumping of nest sites has implications for other aspects of the Manx Shearwater's breeding biology. It may increase competition for those sites if it is advantageous for an individual, attempting to join the breeding population, to delay breeding until it can occupy a vacant burrow in the centre of the clump (Coulson 1968), rather than attempt to breed in a burrow on the fringes of the clump or to dig its own new burrow in the centre, where the ground may be physically unable to contain many more burrows. In any case the digging of a new burrow (Skokholm Manx Shearwaters do dig burrows, unlike those studied on Skomer (Ashcroft 1976)) does not necessarily take a shorter time than the delay involved in securing ownership of a burrow that is already dug. This point is important since it emphasizes the fact that, although further nesting habitat is available, nesting sites are not available. Not until a Manx Shearwater is about five years old does it spend the entire breeding season at the colony (Perrins _et al_. 1973). If the chance that a five-year-old will breed in its sixth year is roughly the same whether it spends the fifth year searching for an unoccupied burrow or digging a new burrow, then there will be considerable competition for burrows and very few suitable burrows will be unoccupied, as is the case on Skokholm. Thus I suggest that competition for nesting burrows arises partly because of the aggregation of nest sites but mostly because available burrows are in limited supply. This contrasts with the situation of open-nesting seabirds where the breeding success in high density areas may be demonstrably higher (Patterson 1965, Spurr 1975) and the competition for nest sites is primarily due to the clumping of occupied nest sites, not to the lack of other suitable sites nearby (Nelson 1966b, Birkhead 1976).

If competition for the available nest sites is important various predictions may be made, some of which have been fulfilled by this study. In Chapter 3 I showed that artificial burrows are occupied by birds which may be breeding for the first time, and hence might have been unable to breed but for the provision of the artificial burrows. I was unable (Chapter 3) to show any difference in the pre-laying attendance of birds in the Main and Observatory Colonies. This could imply that competition for burrows is primarily a consequence of a general shortage of burrows and is not especially severe in the Main Colony. Against this may be set the observation that more birds move out of the Main Colony than into it (Perrins _et al_. 1973) and that all the emigrants trapped on Skomer had been ringed as fledglings in the Main Colony (Chapter 6).

It seems that the Manx Shearwater may take several years to reach a peak of feeding efficiency (Chapter 2). If competition for food and/or burrows prevents birds from breeding until or beyond the age when a peak of feeding efficiency has been reached, then it would be expected that inexperienced breeders would not be lighter in the pre-laying period than experienced breeders (Chapter 3). They would also be as well able to feed a chick as experienced breeders (Chapter 5), on the assumption that the ability to feed a chick is primarily dependent on the parent's ability to catch food at sea. On the other hand, inexperienced birds are less successful at hatching the eggs they lay (Chapter 4) and presumably many of the abilities required for successful incubation cannot be improved until the first breeding attempt.

While competition for nesting burrows may limit the breeding population in any one year, the overall population level seems more likely to be determined, in the long term, by the food supply, given that areas of suitable nesting habitat do remain available for use on Skokholm. In the case of the Manx Shearwater there is no knowing whether the food supply during or outside the breeding season is the critical controlling factor (Ashmole 1963). Available evidence, discussed in Chapter 6, indicated that the population has increased during this century, but it is uncertain whether this was due to an increasing food supply or to a former reduction in the shearwater population, by man's activities (Lockley 1930), below a level that could be sustained by a roughly constant food supply. Whichever is the case, the increased age of first breeding (Chapter 6) would result if competition for food during the breeding season increased as the population once more approached a limit determined by the food supply, or if the increase in the shearwater population resulted in increasing competition for nesting burrows.

This discussion has been hampered by the problems involved in distinguishing the relative importance of competition for food and nesting burrows. My provision of artificial burrows has lent support to the idea that competition for nesting burrows may be of importance. It would not be desirable to reduce substantially the number of nesting burrows, to test whether this would further increase the age of first breeding. It is also difficult to assess the importance of competition for food since the monitoring and experimental manipulation of the food supply of a seabird is rarely a practical possibility.

However, the problems of feeding may particularly influence immature birds which are of lower weight (Chapter 2), visit the colony for a shorter period of the breeding season (Perrins _et al_. 1973) and visit the colony less frequently in the middle of the breeding season (Table 2.3). Birds younger than five may be unable to gain sufficient weight at the feeding grounds to allow them to visit the colony at the beginning and end of the breeding season, when feeding conditions may be most unfavourable (Chapters 2 & 5). Only when birds reach an age of about five or more do they visit the colony throughout the breeding season.

Male Manx Shearwaters are more likely to be caught at the colony in the year preceding their first breeding attempt, commonly at six years old, than are females (Table 7.8) and they also visit the burrow more frequently in the pre-laying period (Chapter 3). This sexual difference may be considered to be related to the fact that females have a greater energetic investment (the egg) to offer with each act of mating (Wilson 1975). If females only mate with males occupying a breeding burrow, without which a chick cannot be reared from the egg, then the behaviour involved in burrow occupation will become particularly developed in males. Once developed this behavioural dichotomy carries the advantage that the female may be absent from the colony in the immediate pre-laying period (Table 3.4) and so presumably form an egg more rapidly. Meanwhile the male continues to visit the burrow to prevent its occupation by other birds and to take the first incubation shift. It is this dichotomy which I also consider to be responsible for the sexual differences in calls and in responsiveness to calls described in Chapter 7.

Once the role of burrow defence has fallen to the male, there will be selection for males to attempt to occupy a burrow as early in life as possible, provided that they do not thereby decrease their chances of surviving to breeding age. Why is it that males generally occupy a burrow close to where they themselves were reared (Table 6.7)? There are two possible related reasons.

(i) By returning to his natal sub-colony a male can ensure that he occupies a burrow in habitat that proved adequate for rearing chicks in the past, since he himself was raised there. Moreover, his own genes, received from his parents, are likely to be those that will promote successful breeding in that area. An objection might be raised to this idea. Although the natal sub-colony contains adequate nest sites, it is possible that other colonies would contain better sites, so that the male would benefit by moving to these sites. Presumably this does not happen because any selection of another better site carries the risk of mistaken choice. If this risk is not outweighed by the potential advantages then the conservative option, return to the natal sub-colony, will be selected for. There is the further point that the earlier in his life a male begins to visit a sub-colony, the sooner he may be able to establish himself as the occupant of a particular burrow. Since the sub-colony where he himself was reared contains adequate nest sites it may be advantageous to begin visiting this colony rather than spend time, and conceivably delay the start of breeding, searching for a more favourable sub-colony.

(ii) By returning to his natal sub-colony a male can ensure that he occupies a burrow with related males nesting nearby. This could reduce conflict for burrows (Clutton-Brock & Harvey 1976), but only if older males can recognize their now-mature offspring reared several years previously. Such recognition seems extremely improbable in the Manx Shearwater.

If the risks are not too great, dispersal may benefit the female since she thereby avoids any deleterious effects (to her offspring) of inbreeding if she was as faithful to the natal area as her male relatives. By dispersal she is also able to exercise a choice of breeding area and of mate when eventually she does settle to breed (Greenwood & Harvey 1976). The useful exercise of this choice may be partly dependent on the immature female having more time available than the male, who is concerned to a greater degree with burrow occupation. Time to make the choice also results if the female takes several years to reach the minimum level of feeding efficiency required for successful breeding (Chapter 2).

I cannot test these ideas since there are insufficient data, for males, to relate degree of dispersal from the natal colony to either age of first breeding or reproductive success. The limited data available for females suggests no relationship between degree of dispersal and reproductive success. No such relationship would be expected if the distance a female dispersed was the result of her own choice.

Conclusion

This thesis has established a number of facts concerning the breeding biology of the Manx Shearwater with tolerable certainty. The story has been developed by inference but answers to many questions cannot yet be given.

'Ask, and it will be given you; seek and you will find.'

(Matthew 7.7)

Such is the optimism which propels biologists.

Appendix 1

Date of return to the colony of immature Manx Shearwaters of different ages

Perrins, Harris and Britton (1973) have shown that many two-year-old Manx Shearwaters return to the Skokholm colony during the new moon periods of June and July, but few earlier. More three-year-olds and even more four-year-olds return in March and April but there is still a pronounced peak in these two age classes between May and July. A similar tendency, for the youngest birds to visit the colony just in the middle of the breeding season and the older immature age-groups to visit for a longer period each year, has been recorded in other seabirds, for example the Razorbill (Lloyd 1976), the Puffin (Ashcroft 1976), the Sooty Shearwater (Richdale 1963), the Laysan Albatross (Fisher and Fisher 1969) and the Fiordland Crested Penguin *Eudyptes pachyrhynchus* (Warham 1974).

I examined retrap records for 1973 and 1974, the two years during this study when most nocturnal trapping of shearwaters was carried out. The analysis of records was restricted to birds ringed as fledglings in the Main Colony (Perrins *et al*. 1973) and later recaptured there since this colony is where most ringing and recapture work has been concentrated. The analysis revealed that those birds captured at two years old were likely to be captured earlier in the following year, when they were three years old, than those which had not been caught when two years old. Similarly birds that had been caught when two or three years old were caught earlier in the following year when they were four years old than those which had not been caught before reaching the age of four (Tables A1, 1 & 2). The analysis cannot be continued to consider five-year-olds since, as Perrins *et al*. (1973) have shown, these birds become less available for capture, possibly because they are starting to spend more time underground.

Table A1.1

Mean date of first capture (± S.E. in days) of three year old Manx Shearwaters, separated according to whether or not they had been caught the previous year as two-year-olds. Sample sizes are given in brackets below means. Significance levels determined by t-tests.

Birds aged three in : -	Caught as two-year-old		Not caught
1973	8 June (± 2.6) (82)		24 June (± 1.4) (319)
		$p < 0.001$	
1974	11 June (± 3.2) (78)		28 June (± 1.8) (206)
		$p < 0.001$	

Table A1.2

Mean date of first capture (± S.E. in days) of four year old Manx Shearwaters, separated according to whether or not they had been caught as two- or three-year-olds. Sample sizes are given in brackets below means. Significance levels determined by t-tests.

Birds aged four in : -	Caught as two- or three-year-old		Not caught
1973	30 May (± 2.1) (199)	$p < 0.001$	12 June (± 2.7) (170)
1974	30 May (± 2.7) (200)	$p < 0.002$	15 June (± 3.4) (129)

It is possible that the observed differences in the time of first capture arise because individual birds differ in the ease with which they are captured, for which there is some evidence (Chapter 6). Thus, for example, those birds caught when two years old might be the individuals more easily caught and therefore they would tend to be the birds first caught when three years old. This possibility can be tested by working out the mean date of first capture of those four-year-olds which were caught when two years old but not when three years old. This group of four-year-olds would presumably tend to include those particularly skilled at evading capture, since they were not caught when three years old. The mean date of first capture of these four-year-olds was 28 May (N=9) in 1973 and 31 May (N=6) in 1974; in both cases the date is closer to that for the four-year-olds which were caught when two or three years old than for the four-year-olds which were first caught when aged four (Table A1.2), and it is this latter group of four-year-olds which would contain the higher proportion of birds skilled at avoiding capture if differential catchability was responsible for the observed results. I conclude that the differences in date of first capture (Tables A1.1 and 2) reflect differences in the time of return to the colony.

Since many of the birds aged two, three and four had been weighed in 1973 and 1974, it was possible to compare the weights of birds first caught in the colony at two, three or four years old. No significant differences emerged, nor does the date of fledging of those birds that survive to return to the colony influence the age at which they will be first caught.

If males are more frequently caught in the year preceding breeding (Table 7.8) then they may also return to the colony at a younger age than females. If this were the case then, since males have a longer bill than females (Table 2.1), it would be predicted that birds first caught at two years old would, on average, have longer bills than those first caught at three. Similarly the mean bill length of those first caught at three could be greater than that of birds first caught at four. The mean bill lengths (± S.E.) of those 1972 fledglings that were first caught in the Main Colony at age two (N=83), three (N=171), and four (N=86) were 34.83 (± 0.138) 34.68 (± 0.090) and 34.81 (± 0.132) mm respectively. No differences were significant. The 1972 fledglings showed the same pattern of return to the colony (Table A1.3) as was seen in Tables A1.1 & 2.

The possibility of a sexual difference in the age of first return to the colony can be also examined by comparing the proportion of sexed known-age breeding birds (of various age classes) that were first caught when aged two, three or four. No significant differences between the sexes were detected. For example, of the 76 birds which were breeding in the Main Colony and which had been ringed as chicks, 20 out of 51 males and 6 out of 25 females were caught at night when two or three years old. The difference between males and females is not significant.

Since Manx Shearwaters visit the colony for about four summers before starting breeding (Perrins et al. 1973) and, in doing so, leave the feeding grounds and expose themselves to the risk of predation (Harris 1965b) this activity must confer some benefit which compensates for the energetic cost of flying between colony and feeding grounds and for the risk of predation. This benefit to the immature bird could accrue through an increase in future reproductive potential, or possibly through the capacity of the colony to assist as an 'information centre' facilitating the location of feeding grounds (Ward & Zahavi 1973, Krebs 1974). Whichever is the case the degree of benefit could well be dependent on the age of the bird and there would be selection acting on a bird to begin visiting the colony as soon as a point

Table A1.3

Mean date of first capture (± S.E. in days) of Manx Shearwaters ringed as fledglings in 1972 in

(i) 1975, separated according to whether or not they had been caught as two-year-olds

(ii) 1976, separated according to whether or not they had been caught as two- or three-year-olds.

Sample sizes are given in brackets below means. Significance levels determined by t-tests.

Date of first capture in : -	Caught as two-year-old		Not caught
(i) 1975	17 June (± 2.2) (92)		1 July (± 1.5) (262)
		$p < 0.001$	
	Caught as two- or three-year-old		Not caught
(ii) 1976	6 June (± 2.8) (138)		16 June (± 3.4) (97)
		$p < 0.05$	

in its life was reached when the benefit exceeded the cost. In general it would seem that the benefit/cost ratio increases with age, since older birds spend more time visiting the colony, and that for immature birds it is highest in mid-summer, the period when the greatest number of such birds visit the colony, and lower in April and May when longer flights between colony and feeding grounds may be required (Perrins and Brooke 1976). Thus those individual birds for which the benefit/cost ratio exceeded one in their second year would tend to be the birds for which the benefit/cost ratio exceeded one for the greatest amount of time during their third summer. On these very general grounds it might be predicted that those birds which visited the colony in their second year would be the birds to appear first in the third year, as is indeed observed. But I have been unable to discover any specific parameters by which birds which start to visit the colony at different ages may be distinguished, nor are there any data available to relate age of first visiting to age of first breeding, reproductive success or mortality.

Appendix 2 The heritability of body size

It is obviously true, at least at an interspecific level, that animals tend to be the same size as their parents and it is a reasonable hypothesis that body size is controlled partly by genetic and partly by environmental factors. The only study known to me of the genetical control of body size in a wild bird population is that of Garnett (1976) who studied the Great Tit and found that approximately three-quarters of the phenotypic variance of body size (measured by tarsus length) was due to genetic causes and one quarter was due to environmental causes. He was also able to identify some selective forces acting on body size. Larger individuals were shown to be at a selective advantage in the immediate post-fledging period when most juvenile mortality occurs and they were also dominant at winter feeding stations, whilst smaller females laid at an earlier date and therefore tended to rear more fledglings.

In the Manx Shearwater males have slightly longer bills and tarsi than females but there are no wing length differences between the two sexes (Chapter 2). These sexual differences in body size might be associated with slight differences in feeding niche and in reducing intersexual competition (Selander 1966). However there has been no detailed work to identify the selective forces acting on shearwater body size, although these presumably exist and differ between the eight races which differ in body size (Murphy 1952).

That part of the phenotypic variance in body size which is due to genetic causes may be inherited. One estimate of heritability is obtained from the slope of the regression of mean offspring value on mid-parent value where the value refers to some parametric measure (Falconer 1960). This estimate was convenient to use during the present study since I had mid-parent values for the wing, bill and tarsus measurements of 35 Manx

Shearwater pairs which raised chicks to fledging in one or more of the four study years, 1973-1976. Wing, bill and tarsus measurements for these chicks were also available, but data from chicks showing symptoms of puffinosis (Harris 1965a) were excluded. The mean number of measured young raised per pair was 2.49 (wing measurements), 1.88 (bill) and 1.90 (tarsus), but the mean offspring values were not weighted according to the number of offspring raised by each pair. The wing length was taken the day before fledging whilst bill and tarsus measurements were taken at 60 days old, some ten days before fledging. The measurement techniques used were those described in Chapter 2.

The relationships between offspring value and mid-parent value for wing, bill and tarsus measurements are shown in Figures A2.1, 2 & 3, and the values of heritability obtained using these three measurements are given in Table A2.1. None of the three estimates is significantly different. As in the Great Tit studied by Garnett (1976) it appears that approximately three-quarters of the phenotypic variance of body size was due to genetic causes. However there was no significant correlation between chick body size and fledging weight and it is the latter which is known to influence significantly the probability of post-fledging survival (Perrins, Harris & Britton 1973).

Figure A2.1

Mean offspring value plotted against mid-parent value for the wing measurements of 35 Manx Shearwater pairs which raised young in the period, 1973 - 1976. $r = 0.392$ $p < 0.05$

Regression equation: $y = 0.658x + 77.69$

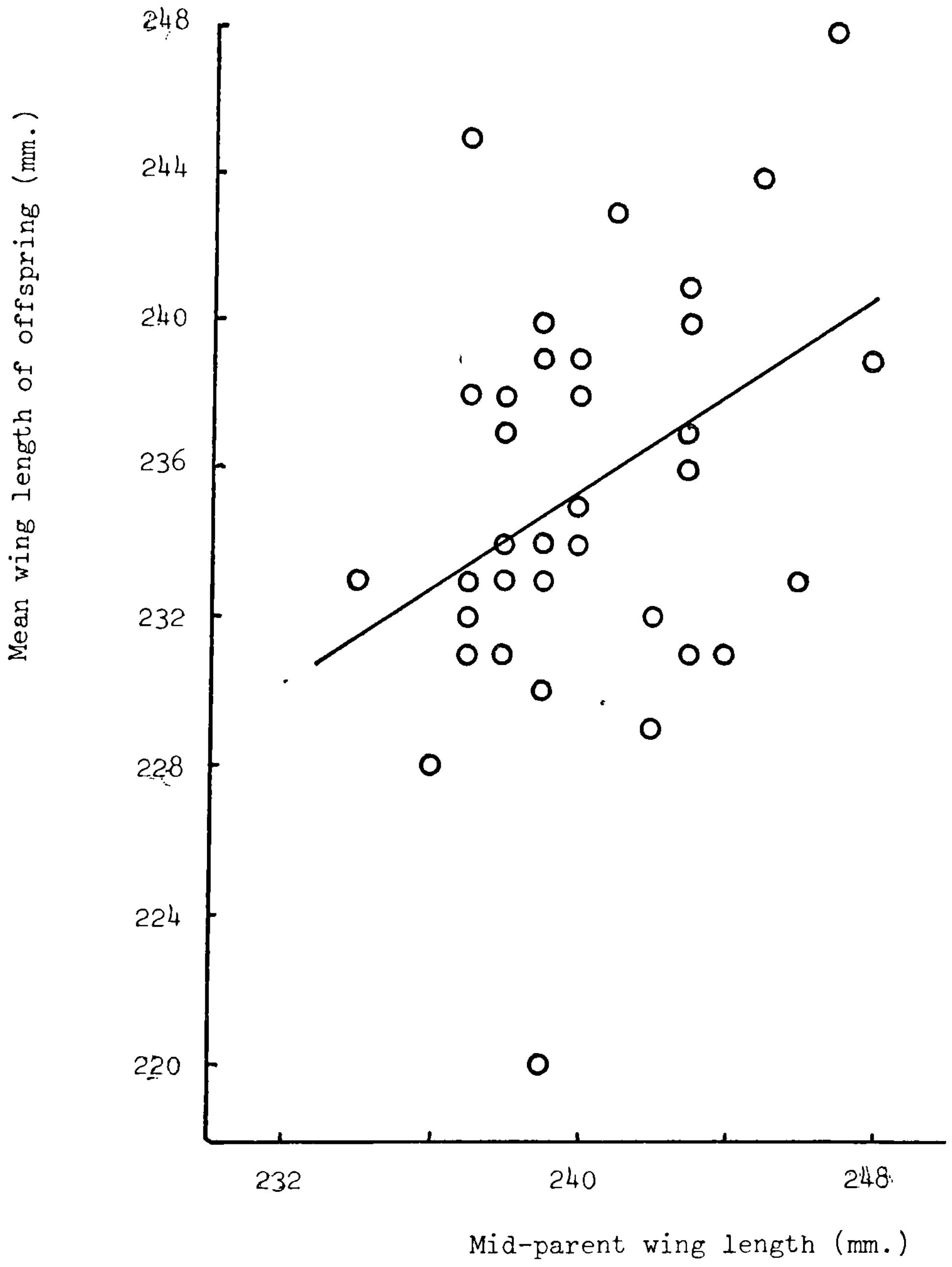


Figure A2.2

Mean offspring value plotted against mid-parent value for the bill measurements of 33 Manx Shearwater pairs which raised young in the period, 1974 - 1976. $r = 0.474$ $p < 0.01$

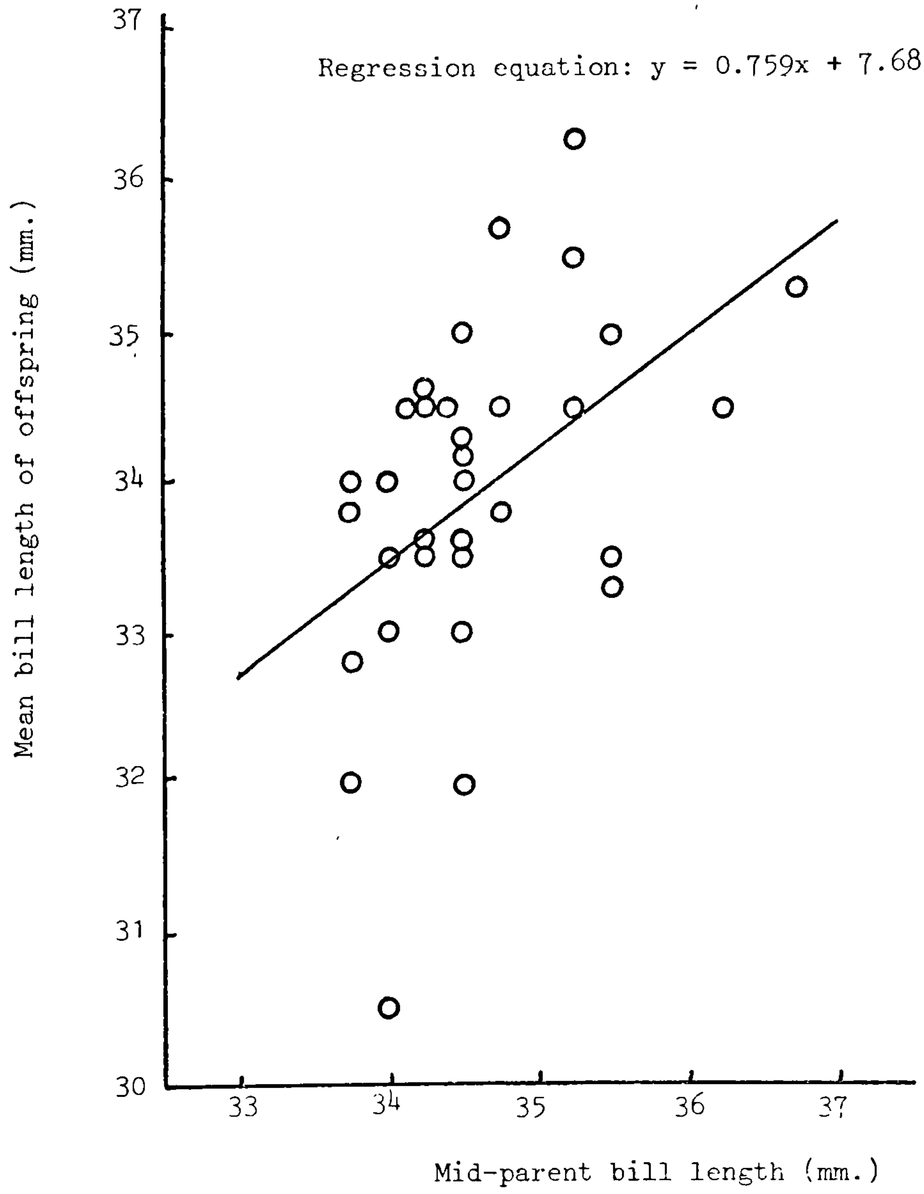


Figure A2.3

Mean offspring value plotted against mid-parent value for the tarsus measurements of 32 Manx Shearwater pairs which raised young in the period, 1974 - 1976. $r = 0.649$ $p < 0.001$

Regression equation: $y = 0.920x + 3.41$

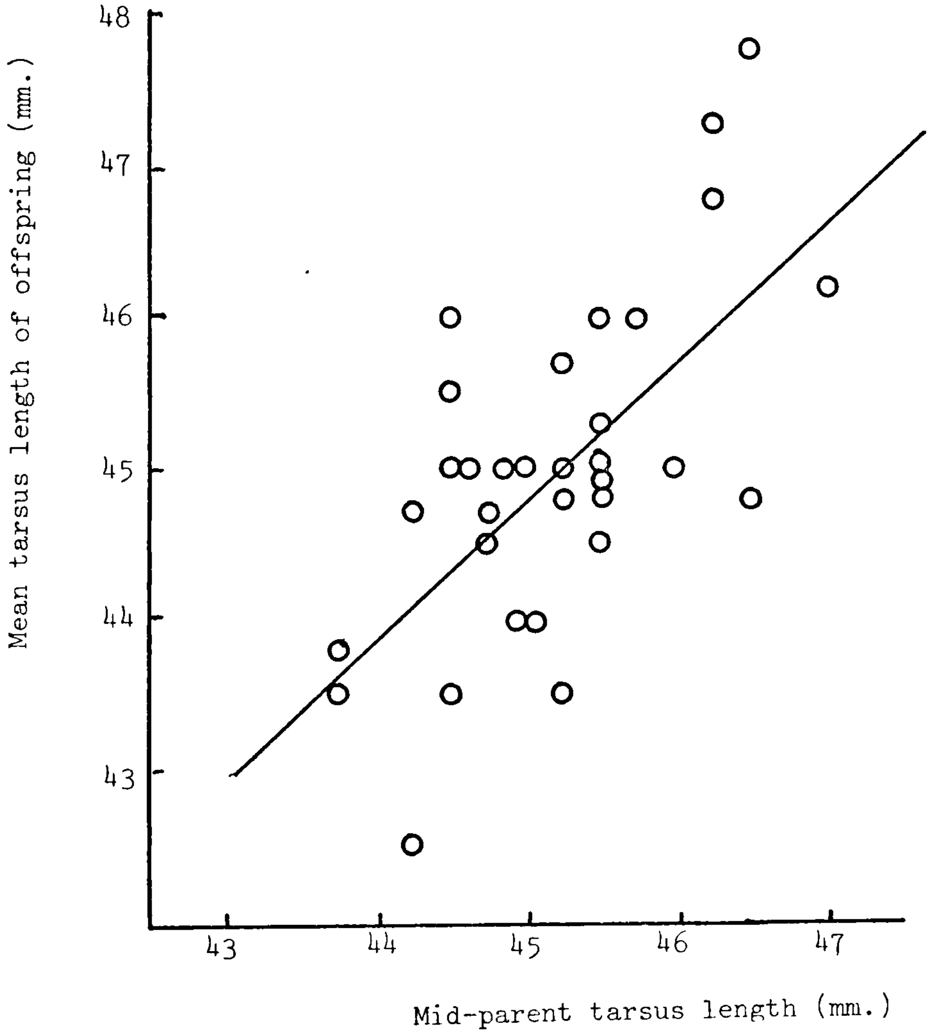


Table A2.1

The heritability of body-size in the Manx Shearwater as estimated by the slope of the regression of mean offspring value on mid-parent value for three body measurements, wing, bill and tarsus length.

Measurement	Heritability (=slope) ± S.E.	Sample size	P
Wing	0.658 ± 0.269	35	< 0.05
Bill	0.759 ± 0.253	33	< 0.01
Tarsus	0.920 ± 0.197	32	< 0.001

Appendix 3

A visual basis for burrow location by the Manx Shearwater?

Since the Manx Shearwater Puffinus puffinus only flies in from the sea to its nesting burrow during the hours of darkness, the mechanism it uses to locate the burrow has long been a matter of interest (Lockley 1942). Not only is the colony in darkness when the bird arrives but also the burrow is one amongst many dug in ground that may be lacking in oustanding features that could be used as 'landmarks'. Moreover on Skokholm Island, Pembrokeshire, the density of burrows may be as high as 0.5 burrows/m^2 so that it is essential for the shearwater to be able to locate its own burrow to within a metre or less.

This note describes a simple experiment carried out on Skokholm designed to test the possibility that vision may be at least one of the senses used in burrow location; the experiment does not exclude the possibility that other senses may also be important. Even on the darkest moonless nights there is some residual light on an offshore island like Skokholm so that it would not be impossible for the shearwater to see the location of its own burrow and the use of sight would be facilitated by the habit of circling the colony in the air before actually landing on the ground.

Lockley (1969) has suggested that the calls given by Manx Shearwaters when flying over the colony have an echolocatory function, but there is no evidence to support this suggestion. Other animals known to use echolocation, such as bats (Griffin 1958), cetaceans (Schevill 1964), Collocalia swiftlets (Medway 1967) and oilbirds Steatornis caripensis (Griffin 1953), all produce a pattern of discrete pulses of sound, quite unlike the audible calls of the Manx Shearwater. Another possibility, involving calling, is that the partner flying in from the sea may recognize the call its mate gives from within the burrow, and hence locate the burrow. I have evidence (Chapter 7) that females can recognize the calls of their male mates and this mechanism of burrow location is potentially available to females. However, females frequently enter the burrow to feed the silent chick without the male being already there and another mechanism is required on such occasions.

Grubb (1974) has shown that Leach's Petrels Oceanodroma leucorrhoa may use olfaction to navigate to their own nesting burrows and it does seem possible that most Procellariiformes have a useful olfactory sense (Bang & Cobb 1968). I have no direct evidence concerning the use of olfaction in Manx Shearwaters and would merely observe that Manx Shearwaters do not have, as far as the human nose is concerned, the characteristic musky odour of Leach's Petrels.

Methods

The principle of the method is similar to that employed by Tinbergen (1932) in his study of digger wasps Philanthus triangulum. It is to provide a conspicuous visual clue to the location of the burrow, allow the bird to become accustomed to the presence of the clue, move the clue and then observe whether the ability to locate the burrow is impaired.

Experimental burrows

Between 20th March and 19th April 1976, in the pre-laying period, I placed cardboard boxes over the entrances of 17 shearwater burrows. The cardboard boxes were painted with white emulsion paint, held in position by stones and were all of the same dimensions, 45 x 30 x 12 cm. A hole, 10 x 10 cm was cut in one side of the box and the shearwater had to pass through this hole in order to enter its burrow.

After the birds had laid I was able to establish, with certainty, the identity of the two members of each pair; they were then individually ringed. Incubation was chosen as the period for the experimental tests since the sequence of events occuring during the night of an incubation change-over is well-defined. One partner flies in from the sea, enters the burrow and relieves the sitting mate which then departs, usually the same night, for the feeding grounds. In the experimental test the white box was moved from its position over the burrow entrance and replaced by another white box of identical dimensions to control for any odour cues associated with the white box used during the training period. Strictly speaking this control only excludes those odour cues acquired by the white box during the training period; it does not exclude odour cues that may be associated in general with white boxes. The new white box was then placed, not over the burrow entrance, but about 60 cm to one side or the other so that the box no longer overlapped the burrow entrance at all. The actual burrow entrance was obscured, but not blocked, with scraps of local vegetation and a circular sod was removed from the ground covered by the displaced white box to provide a crude imitation of a burrow entrance, at least when observed from outside the entrance to the white box. Inside the displaced white box was placed a simple trap which was nearly invisible from outside the box. A test was considered to have occurred when a bird returned to incubate. If it entered the breeding burrow, then there was no indication that the ability to locate the burrow had been reduced but if it entered the white box and was trapped this could be such an indication provided that the frequency of such entries was greater than that occurring under the control treatment (see below).

No bird was tested more than once and no experimental test occurred until at least a month had passed since the white box was first placed over the burrow in the pre-laying period.

Control burrows

It is possible that shearwaters could enter the white boxes during the experimental tests for reasons other than a reduction in their ability to locate their burrow; for instance to escape predation by gulls. This possibility was controlled for as follows. In the pre-laying period white boxes were placed beside 17 shearwater burrows, in a position similar to that occupied by the experimental white boxes during the experimental tests. The date in the pre-laying period when white boxes were first placed over or beside experimental and control burrows was matched. The procedure then followed at the control burrows was exactly as described for experimental burrows except that, when a test was made, the white box now containing a trap was in the same position as during the training period, and also the white box used in the control test was the same one as had been in position throughout the training period.

Results and conclusions

Eggs were laid in 14 experimental and 11 control burrows and I was able to test 28 experimental and 21 control birds. At incubation change-overs 20 experimental birds entered the breeding burrow and eight were trapped in the displaced white boxes whilst all 21 control birds entered the breeding burrow (Fisher Exact Test $p \doteqdot 0.007$). In three of the 20 instances where the experimental birds entered the burrow, the trap inside the white box had been sprung and there were indications that a bird had forced its way out of the trap. The probability that the experimental birds would enter the white box or the breeding burrow was not related to the phase of the moon which suggests that this probability was not greatly influenced by how dark the night of the experimental test was.

In 1975 I performed a pilot experiment along the lines described above but without control burrows. Of 14 experimental birds tested, ten entered the breeding burrow and four were trapped in the displaced white boxes, the same proportion as were trapped in the 1976 experiment. No birds tested in 1975 were also tested in 1976.

Although, in the 1976 experimental tests, only eight birds out of 28 failed to locate their own burrow, various factors could be acting to mitigate the effects of the displacement of the experimental visual cue, the white box. The terrain surrounding the burrow and any nearby visually prominent features were in no way altered. Any odour cues associated with the burrow or the ground immediately in front of the burrow entrance would still be available to facilitate burrow location. So too would any cues, vocal or otherwise, given by the member of the pair awaiting relief down the burrow. Any proprioceptive cues would also still be available (Wells 1968) to facilitate correct burrow location.

I conclude that the displacement of a visually prominent cue can impair the ability of a Manx Shearwater to locate its own burrow. This suggests that vision may play a role in burrow location but more exhaustive tests would be required to assess the relative roles of vision and any other senses that may be employed.

Appendix 4. A visit to the Basque coasts of France and Spain in April 1977

The purpose of the visit

Since before World War II there have been frequent reports of Manx Shearwaters Puffinus puffinus ringed on Skokholm Island, Pembrokeshire, being recovered at sea and dead on the shore in the south-east corner of the Bay of Biscay, the so-called 'Basque Triangle'. The breeding status of these shearwaters has been uncertain since very few of those recovered have belonged to closely observed study burrows. By acquiring birds caught by fishermen, since this is the most common means of recovery, the first question I hoped to answer was:- What proportion of the birds visiting the south-east of the Bay of Biscay are breeders, as opposed to non-breeders?

Perrins and Brooke (1976) analysed Biscayan recoveries at sea of birds at least six years old and therefore of breeding age. They found that recoveries after May 10, the median laying date of the Skokholm colony, were, on average, further north than recoveries in the pre-laying period (see Figure 4.6). Since the pattern of pre-laying attendance of males (Table 3.4) precluded their travelling so far from the colony as females would have time to do, it was conjectured that most breeding birds which went to the south-east of the Bay of Biscay, say south of 46°N, were females. By timing my visit at the end of the pre-laying period, late April, I hoped that dissection of captured shearwaters would enable me to confirm (or refute) this idea.

To answer these questions, a minimum sample of some twenty birds would be required for autopsy. The number of recoveries received suggested that this total would not be beyond achievement, given that the present study did not require ringed birds. In the event I was unable to acquire a single Manx Shearwater and the reasons for this will now be outlined.

The fishing industry in north-east Spain

While in Spain for the period 10 April - 4 May, I visited and made enquiries in the following fishing ports, Bermeo, Lequeitio, Ondarroa, Motrico, Pasajes San Pedro and Fuenterrabia, and also St. Jean de Luz in France. Two types of large fishing vessel operate out of these ports. The trawlers are mostly based in Ondarroa and Pasajes and, given the narrow width of the continental shelf off Spain itself, mostly fish off the French coast from Bordeaux (c. 45° 30' N) northwards towards Grand Sole and Ireland. These trawlers, working throughout the year, are commonly at sea for eight or ten days at a time. The more numerous fishing smacks are somewhat smaller, about 30 m long, carry a crew of about 15 and have an annual fishing cycle approximately as follows:-

(a) December-March. Line fishing for hake *Merluccius vulgaris* and bream *Pagellus* spp., and also netting of mackerel *Scomber scombrus* and sardines *Sardina pilchardus*.

(b) Seine netting for anchovies *Engraulis encrasicholus* from late March until the end of May or early June.

(c) Followed by tunny (*Sarda sarda* and *Thunnus* spp.) fishing, on trolled hooks, until the middle of September, when they move south towards the Canaries until the end of the year.

During my visit the anchovy fishing was at its height. The actual netting is done by night and, if conditions are favourable as appeared to be the case during my visit, the boats can depart one afternoon, fish through the night and return to port to discharge the catch the following day. Only in adverse conditions do they need to travel further north, towards Bordeaux, in pursuit of fish.

The distribution of Manx Shearwaters at sea

The following notes are a composite picture built from discussions with a hundred or more fishermen. There was effective unanimity in the story told.

Since the anchovy boats were fishing close to the Spanish coast, and it was Manx Shearwaters caught well to the south that were required, I directed my enquiries to these boats for about the first ten days. The fishermen on these boats are mostly Basques and the Spanish name for the Manx Shearwater, '*Pardela pichoneta*', is not well known. Instead 'martinas' is used but this refers to shearwaters in general and it became apparent that the fishermen were really only familiar with the Great *Puffinus gravis* and Sooty Shearwaters *P. griseus* (and possibly also Cory's Shearwater *Colonectris diomedea*) which appeared in the tunny fishing season. There was complete agreement that very few shearwaters were to be seen at all close to the Spanish coast during April and only a few, mostly older, Spanish fishermen appeared to distinguish Manx from Great Shearwater, both species being black-backed and white-bellied. Other names given to the Manx Shearwater were 'Zapatillo' (Bermeo) and 'Gabaixa' (Ondarroa). The French fishermen of St. Jean de Luz appeared more familiar with the Manx Shearwater as a distinct species and commented that it was mostly to be found in local waters in April (as expected from the recovery data) moving northwards later in the year. However they confirmed that the Manx Shearwater was scarce; one might see an occasional group of perhaps five birds. Some of the anchovy fishermen who distinguished Manx Shearwaters suggested they had become less common in recent years but I received no intimation that 1977 was a year of particular scarcity.

As it became apparent that the anchovy boats would be unable to provide an adequate sample of shearwaters, I turned to the trawlers, spending about a week requesting help from the skippers as they departed from Ondarroa and the following week meeting all returning boats which might be bringing shearwaters back to port. It was hoped to obtain birds that, if not caught close to the Basque coast, were at least caught at the south of the Manx Shearwater's April distribution.

It was immediately obvious that the trawler skippers, particularly those fishing north of La Rochelle (c. 46°N), were very much more familiar with the Manx Shearwater than were the anchovy fishermen. The trawler skippers effectively confirmed the story so far received in that they said that there were very few Manx Shearwaters to be seen south of about 46-47°N, some even saying that substantial numbers were not encountered until about 49°N.

The trawlers did not return to Ondarroa with any dead Manx Shearwaters while I was in Spain, although, shortly after my departure, the 'Golgoi-Iparra' arrived with two pigeons which had been reported over the radio as shearwaters! It was not practicable to go to sea with a trawler given the length of the trip involved and the uncertainty as to where the southernmost Manx Shearwaters were to be captured.

The circumstances of capture at sea of Manx Shearwaters

Although it may rarely happen that shearwaters become entangled in nets, shearwaters of all species are generally captured on line and hook baited with liver, ham, a lump of fat etc. This practise is prohibited in France which is presumably the reason why most recoveries at sea in recent years have been received from Spanish fishermen.

A number of people commented that the birds are more readily caught in rough weather. There appear to be three possible reasons for this.

(i) Because the birds are blown from their normal feeding areas to the exploited fishing grounds.

(ii) Because the available birds are easier to catch, possibly because they are more hungry.

(iii) Because the crew cannot fish in rough weather and therefore has more time available for peripheral activities such as bird-catching. The sea in the southern half of the Bay of Biscay was mostly fairly calm during my visit to Spain.

If the Manx Shearwaters are mostly caught in rather particular circumstances, this could be the reason for the fact that recoveries have been received in batches, up to 14 ringed individuals having been taken on one fishing trip (Perrins & Brooke 1976).

Conclusions

It is not easy to reconcile the distribution of recoveries with the fishermen's observations that there are relatively few Manx Shearwaters in the southern half of the Bay of Biscay. Various explanations may be considered.

(i) The feeding areas of the birds may have moved northwards in recent years. This would accord with those fishermen's comments that Manx Shearwaters had declined in recent years. However, the distribution of recoveries, both at sea and on the shore, in different years lends no support to this idea.

(ii) There are rather few recoveries between about 43° 30'N and 45° 00'N (see Perrins & Brooke 1976). The recoveries off the Spanish coast, which is at about 43° 20'N, are therefore relatively close to the coast. Unless recovery localities at sea have been extensively misreported (which seems unlikely since the latitudinal pattern of recovery of birds recovered at sea and on the shore is similar), it may be that it is only rather unusual weather conditions which cause the birds to come south of the usual southern boundary of their distribution at about 46°N. Possibly these conditions are most frequent in March and April and are such that the birds near the Spanish coast are enfeebled so that they are more likely to be blown onto the shore or to be caught by fishermen.

Given the frequency with which males visit the burrow in the pre-laying period (Chapter 3), they would probably not have time to travel as far from Skokholm as 46°N, and the possibility that females fly much further from the colony at this time remains open.

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