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INSTITUTE OF TERRESTRIAL ECOLOGY

(NATURAL ENVIRONMENT RESEARCH COUNCIL)

WORLD WIDE FUND FOR NATURE/NERC CONTRACT

ITE PROJECT T08051h5/WWF GRANT 47/89

Final Report

REASSESSMENT OF THE STATUS AND FORTUNES OF PUFFINS ON THE ISLE OF MAY

M P HARRIS

Hill of Brathens
Banchory Research Station
Banchory
Kincardineshire
AB3 4BY

September 1989

C O N T E N T S

1 CONCLUSIONS AND RECOMMENDATIONS

2 INTRODUCTION

3 METHODS

- 3.1 Population count
- 3.2 Condition of adults
- 3.3 Breeding
- 3.4 Weight of chicks
- 3.5 Food and feeding of chicks
- 3.6 Proportion of immatures
- 3.7 Adult survival

4 RESULTS AND COMPARISONS WITH PAST DATA

- 4.1 Population
- 4.2 Condition of adults
- 4.3 Breeding
- 4.5 Proportion of immatures in the population
- 4.4 Adult survival

5 DISCUSSION

6 STUDIES IN BRITAIN AWAY FROM THE ISLE OF MAY

7 FUTURE WORK

8 ACKNOWLEDGEMENTS

9 REFERENCES

1 CONCLUSIONS AND RECOMMENDATIONS

1.1 The rapid increase of puffin numbers on the Isle of May and in northeast Britain has stopped. With hindsight it is obvious that the change commenced in 1982. The breeding population of the Isle of May has remained stable since 1985 but there are now many fewer immatures in the population than there were in the 1970s. There is a need for up-to-date estimates of amount of colony interchange and immature survival.

1.2 Breeding success has remained very high.

1.3 About 80% of the diet of chicks is sandeel. Adults have no difficulty in feeding young.

1.4 Fledging weight of chicks has declined and the effect of this on their post-fledging survival needs to be assessed.

1.5 About 50% of puffins hatched in the 1970's which survived to breed did so away from their natal colony.

1.6 Calculations suggest that the Isle of May population should be able to maintain itself.

1.7 Long-term studies are the only method of obtaining the data needed to assess the health of the British puffin population and of understanding what is happening to this and other seabirds in the Shetland Islands and elsewhere in the northern North Sea. Long-term studies are now out-of-favour and resources are not available to start new ones. Funding must be forthcoming to continue the few remaining which concentrate on the puffin.

2 INTRODUCTION

In the late 1960s it was realized that the numbers of puffins Fratercula arctica in Britain had declined and in 1973 NERC instigated a study into the status of the puffin and the reasons for its decline. The Isle of May, Firth of Forth (Figure 1) was chosen as a study site as the puffin population there was expanding rapidly. The project concluded that the decline in western Britain had been due to natural, probably oceanographic causes and that numbers had stabilised by the mid-1970s. In the early 1980s work on the Isle of May seabirds broadened and now ITE/NERC are carrying out a multi-species study of a seabird community. Although work on puffins continued it has been at a much lower intensity than previously.

In 1987 it became obvious that puffin numbers had stopped increasing, the adult survival rate appeared to have declined and there were fewer immature present than there once had been. This coincided with the finding that very few immature guillemots Uria aalge were recruiting into the Isle of May population (Harris & Wanless 1988) and reports that seabirds slightly further north were experiencing breeding failures (e.g. Heubeck 1988, Monaghan et al 1989). In early 1989 WWF placed a contract with ITE to reassess the status and fortunes of puffins on the Isle of May.

Figure 1. Position of the Isle of May. The arrows indicate the boundaries of the northeast British population.

The aims were to

1. Assess whether the numbers of puffins on the Isle of May were stable or declining.

2. If numbers were declining, determine whether this was due to decreased adult survival, and/or to insufficient recruitment of young birds.

3. Monitor the breeding output, and food and feeding of chicks.

4. Determine the proportion of immatures in the population.

5. Suggest priorities for future research on puffins in Britain.

3 METHODS

Fieldwork was carried out by M P Harris and a series of helpers 25-30 March and 10 April - 10 August 1989. The methods used were developed in the 1970s and details can be found in my relevent papers listed in the references. Only the barest outlines are given here. All results are directly comparable between years.

3.1 Population counts

The Isle of May is a relatively flat island and virtually all the nest-burrows are in flat areas where they can be counted. The population unit is a burrow showing signs of occupation; that is digging or with droppings in or in front of the entrance.

The numbers of burrows in 13 large permanently staked plots or quadrats were counted on 26 April; burrows in seven of these plots (Figure 2) have been counted annually each late April since 1973 and the total of these counts is used as an annual index of the size of the population. The other plots were positioned in later years to document future changes in low-density and recently colonised areas. A complete count of all burrows on the island was made by 4 people walking in narrow bands (marked by canes) across the island on 29-30 April.

Counts of burrows and estimates of the sizes of other colonies come from the records of the Seabird Group/Nature Conservancy

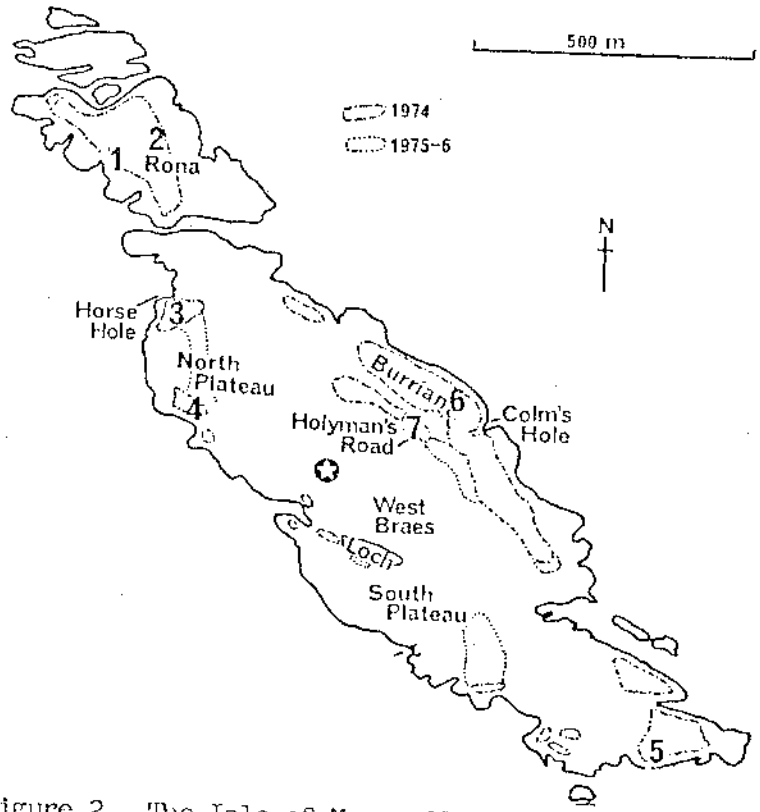

Figure 2. The Isle of May puffin colony. In 1989, puffins nested throughout the island. Numbers indicate the monitoring plots (see Table 1).

Council Seabird Colony Register (per C S Lloyd), The National Trust and personal records.

3.2 Condition of adults

Adults were weighed (to nearest g) after being caught in mist-nets set across the colony in March (3-4 weeks prior to laying) and in June and July (birds feeding chicks) or taken from burrows (incubating and brooding birds). The number of grooves on the bill of each bird were recorded as an indication of age (Harris 1981) as was the presence of traces of dark winter plumage on the face.

3.3 Breeding

Timing of breeding was measured by ageing chicks by bill measurements, where

bill length (mm) = 19.3 + 0.287 age (days) (Harris 1984),

and back-calculating to the hatching-date.

Breeding success was monitored in four separate parts of the island without removing adults by (a) feeling down marked burrows with a short stick to determine the presence or absence of an egg on 2-3 May (when most birds had laid) and, (b) rechecking those burrows where there had been an egg on 29 June (just prior to the main fledging time) for the presence or absence of a large chick. The clutch size is always one egg.

3.4 Weights of chicks

A series of chicks in burrows dispersed across the main colony were weighed every 4 days until near fledging when weighings were made daily. Peak weight attained (usually 7-10 days prior to fledging) and fledging weight were taken as indices of growth.

3.5 Food and feeding of chicks

Adult puffins carry loads of fish held in the bill back to their chicks. Food samples were obtained by mist-netting adults 14 June - 10 July and collecting, counting, weighing, identifying and measuring (total length) the fish in loads dropped by these birds. Nets were moved frequently so as to minimize disturbance. Annual mean values of the energy values of fish loads were calculated using published length-weight and length-energy values (Harris & Hislop 1978). On 16 June, the numbers of loads of fish taken to 42 numbered burrows in front of a permanent hide were recorded by a team of helpers taking 2 hr watches. Loads of fish lost to kleptoparasitic gulls were also noted.

3.6 Proportion of immatures

Puffins can confidently be assigned to one of three age groups based on the development of the beak; (a) adults which have probably bred (more than 2 bill grooves; Plate 1), (b) immatures

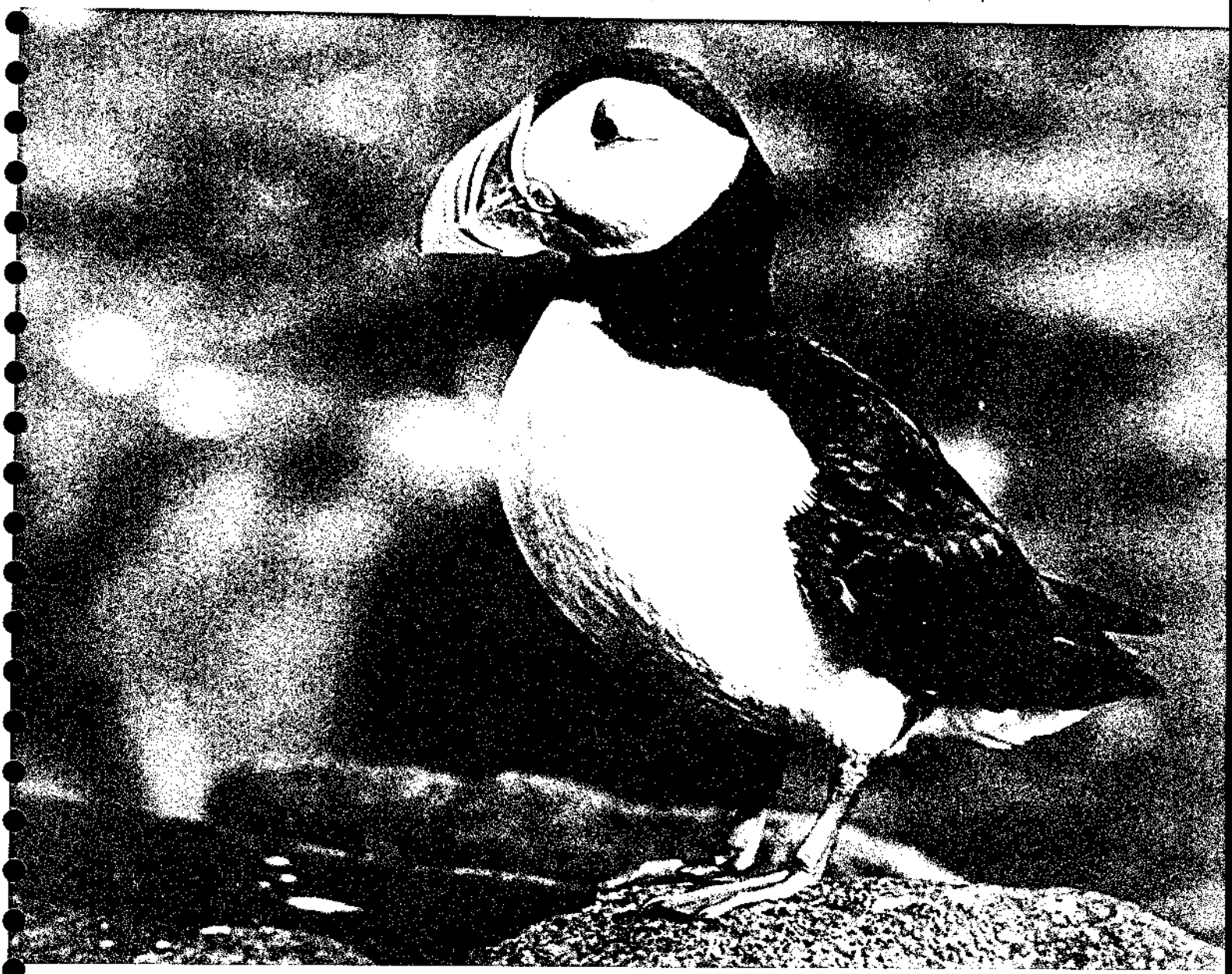

Plate 1. A breeding adult puffin with 3 well-developed bill grooves

(less than 2 grooves; Plate 2) and (c) intermediates (2 grooves) which are probably sexually mature but may not have bred (Harris 1984). Puffins were mist-netted during days when large numbers were ashore in July and had their number of bill grooves recorded. The proportion of individuals caught during the chick-rearing period up to 15 July with less than 2 grooves was taken as an index of the numbers of immatures present. Birds with one and half grooves or one and three-quarter grooves were considered to be 3-years-old (Harris 1981).

Between 5 and 10 July 1107 individual puffins were critically examined from hides using a 30-60x telescope to assess whether or not visual estimates could be used instead of mist-netting to obtain an index for the numbers of immatures present in a population; such a method would be much less time-consuming for the observer and less disruptive for the puffins than mist-netting.

Data collected during 1989 were compared with previous results which had been obtained using identical methods. For convenience these comparisons are made in the Results sections.

3.7 Adult survival

An estimate of the annual survival between 1988 and 1989 came from resightings of breeding puffins colour-ringed in previous years. An analysis of past resightings using a mark-recapture survival program based on a modified Jolly-Seber model was under taken by Dr S T Buckland.

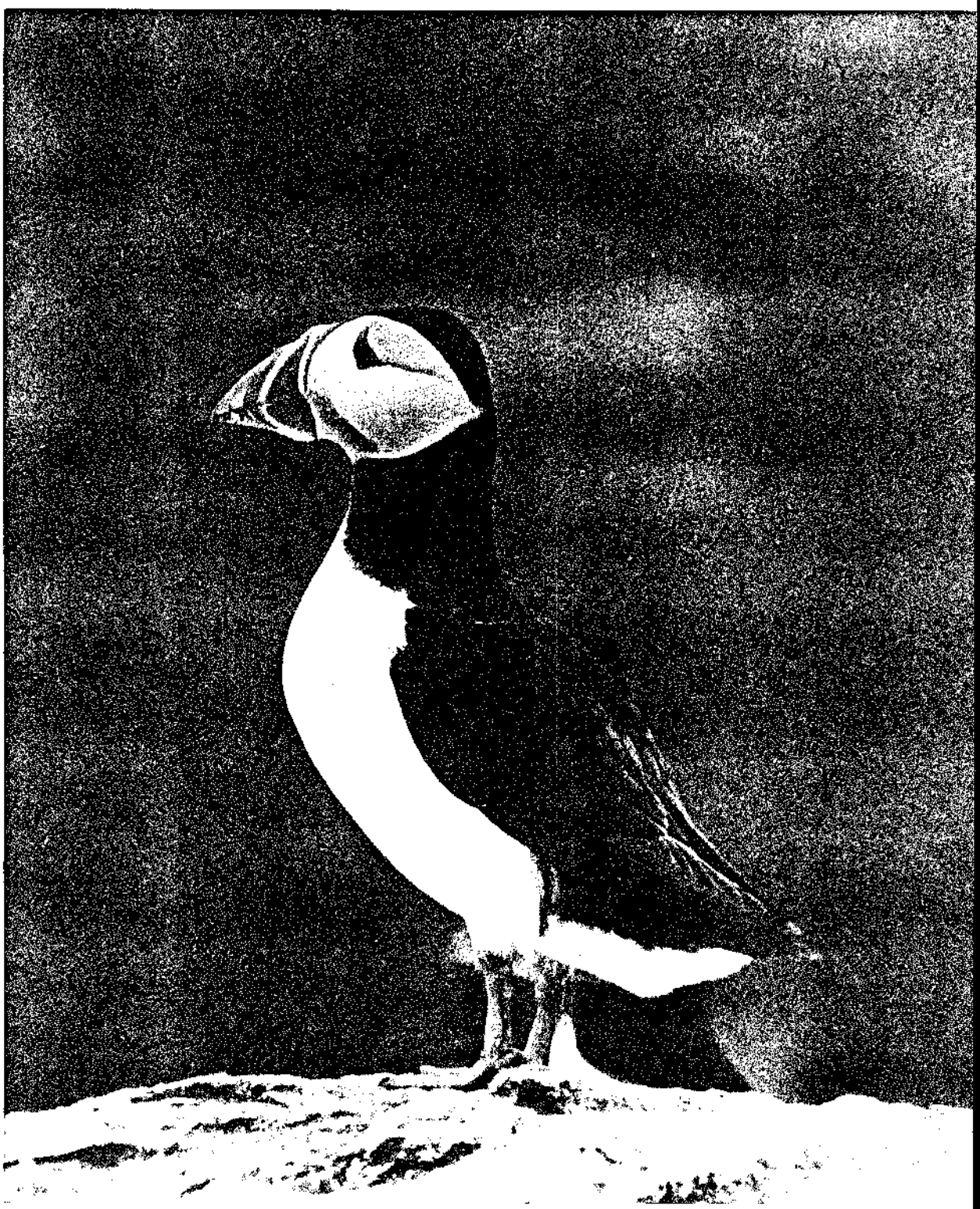

Plate 2. Immature puffin with a typical 'kinked' beak and well-defined bill grooves

4 RESULTS AND COMPARISONS WITH PAST DATA

4.1 Population

4.1.1 Monitoring counts on the Isle of May

The total number of burrows in the monitoring plots increased at 19% p.a. between 1973 and 1981; the rate of increase then slowed down (Figure 3). The 1989 monitoring count was slightly (7%) up on the 1988 count but still below the peak count of 1987 (Table 1). The population would now appear to be stable.

The monitoring plots were delimited in 1972 and, given the seven-fold increase in the numbers of burrows counted in them between 1973 and 1989, it is possible that there is now no room for more burrows. It is difficult to be objective about whether an area can or cannot hold any more puffin burrows, but superficially there appears to be room for more burrows in all plots. I divided each monitoring plot into 1 x 1 m sections measured the soil depth and assessed the proportion of it that was obviously unsuitable for puffins being rock or very shallow soil. I then plotted the density of burrows (on a log scale) in the 'available area' against year and, by inspection, determined when numbers in each plot stabilized. Examples are shown in Figure 4. Numbers in 6 plots stabalised between 1978 and 1984, 1 in 1984 and numbers in 1 were still

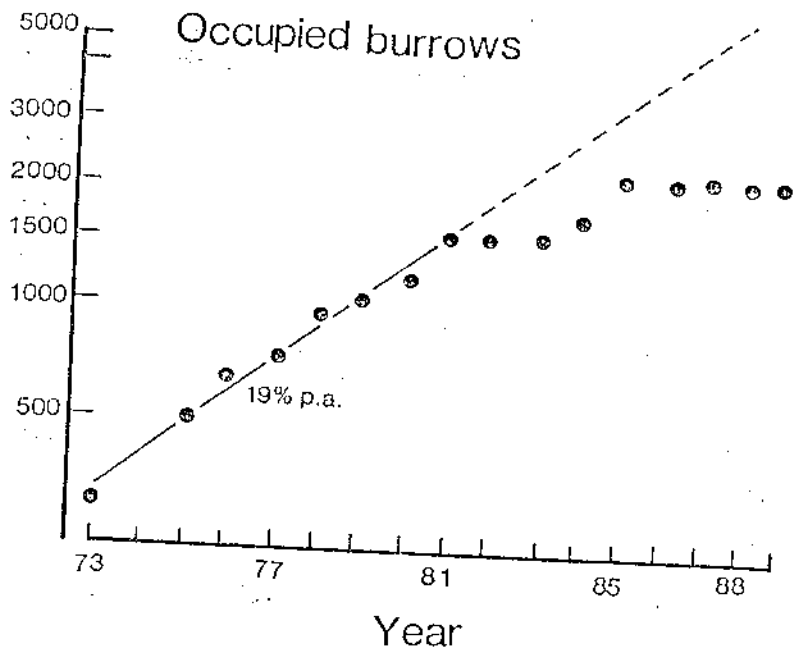

Figure 3. Counts of occupied puffin burrows in the monitoring plots on the Isle of May 1973-89.

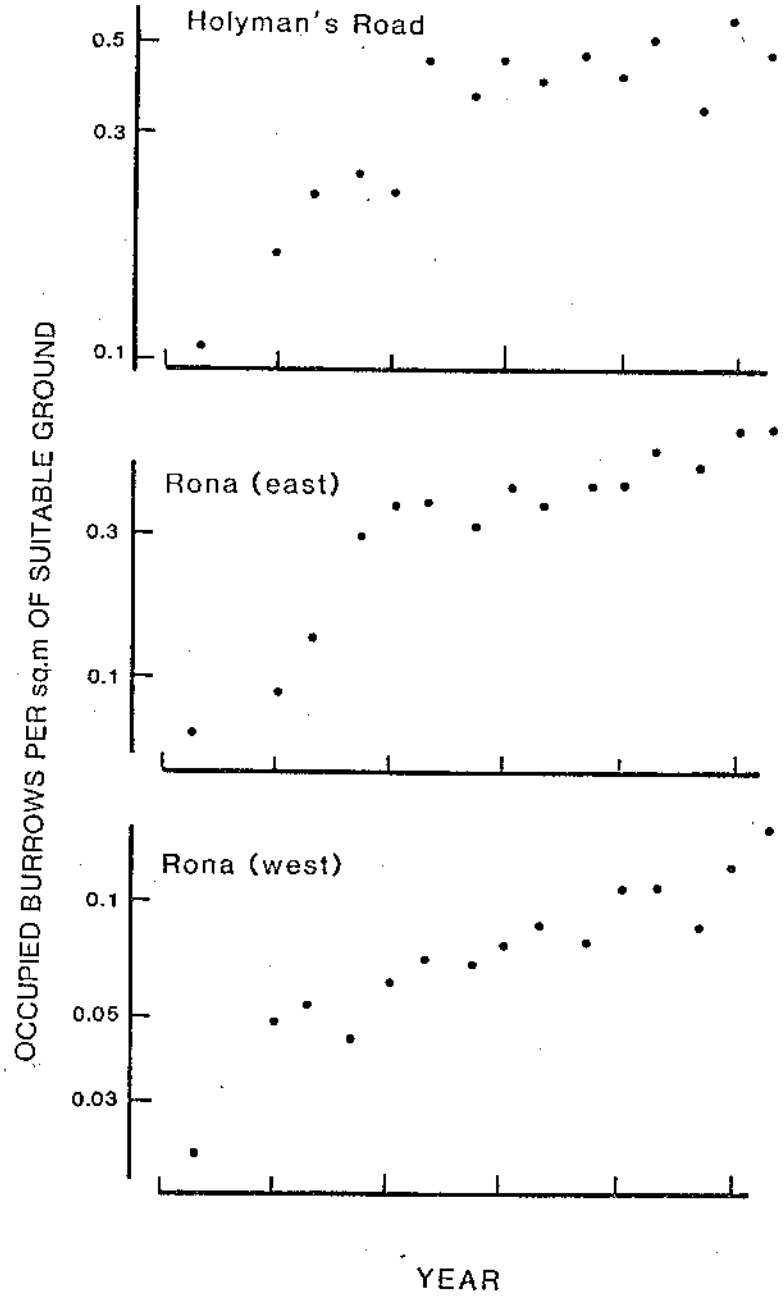

Figure 4. The density of occupied burrows (per m^2 of available habitat) in three monitoring plots on the Isle of May in relation to year. Note the log scale of y axis.

Table 1. Counts of occupied Puffin burrows in sample areas of the Isle of May over a ten-year period. All counts were made in late April by the same observer.

	PLOT	YEAR 1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	Area (m^2)
1	Rona (W)	27	34	36	33	46	46	37	54	65	103	800
2	Rona (E)	117	148	140	163	165	201	189	233	222	211	400
3	Horse Hole	324	400	416	430	609	633	600	663	550	656	2000
4	Bishop's Cove	155	177	159	155	163	203	172	198	205	79	1024
5	Lady's Bed	217	264	263	267	266	342	333	393	353	412	1450
6	Burrian	286	289	353	399	378	552	580	558	568	570	1200
7	Holyman's Road	130	146	144	152	141	165	113	190	150	229	396
	Monitoring total	1256	1458	1511	1599	1768	2142	2024	2289	2113	2260	7270

Note: Numbers refer to locations plotted in Figure 2.

increasing in 1989. The last plot used to have a high density of nesting gulls, most of which have been removed, and is close to a large concentration of puffins so may now be particularly attractive to new pairs.

4.1.2 Counts of the Isle of May population

The 1989 burrow count was 18,620 which compared with 12,211 in 1984 and 3064 in 1975 (Table 2). Although there had been a substantial increase since 1984 the mean rate was 9% p.a. compared with 17% p.a. 1975-84. There were, however, considerable differences within areas with the highest rate of increase (22% p.a.) 1984-89 being at South Plateau, a flattish inland area which had recently been colonized.

There was a highly significant correlation between the total island counts and the monitoring count for the four years (Figure 5) which suggests that the quadrats were representative of the whole colony.

4.1.3 Total British population

The total British and Irish population in 1984/88 was c. 600,000 occupied burrows with the majority (c.90%) being in Scotland (C S Lloyd pers. comm.). This was an increase of c. 20% since 1969/70. In part this increase could have been an artifact resulting from improved coverage of some of the large isolated colonies but the suggestion of an overall increase is supported by the results of regular monitoring

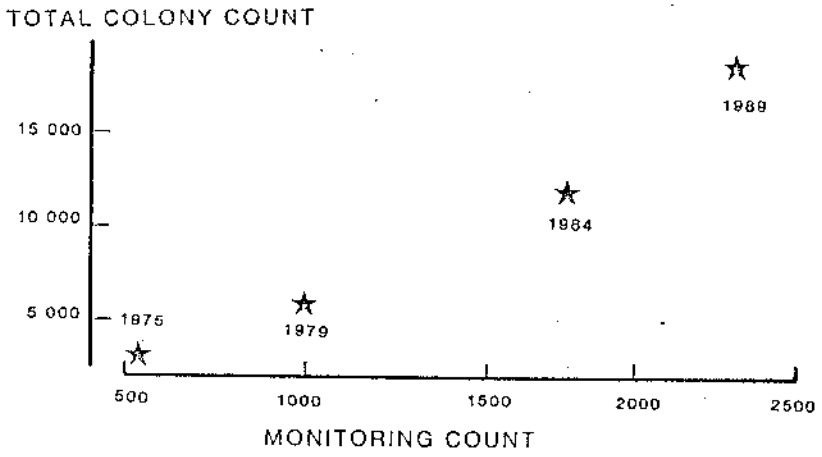

Figure 5. The relation between total population and monitoring counts (occupied burrows) in 1975, 1979, 1984 and 1989. The counts are significantly correlated ($r = 0.99$, $n = 4$, $P < 0.01$).

Table 2. Puffin census Isle of May 29-30 April 1989
Units = occupied burrows

Area	1975	1984	1989
Kirkhaven - Colm Hole	345	1518	2458
Colm Hole - Low Light			
Quadrat	144	378	570
Rest	968	2408	3522
TOTAL	1112	2786	4092
Holyman's Road (West side)			
South of Colm	40	561	1068
Northof Colm	63	347	517
Low Light - Tarbet	75	380	795
Rona			
East quadrat	34	165	211
Rest of east	422	2342	2731
North of Horn	43	106	112
West quadrats	19	46	80
Rest of west	31	77	103
TOTAL	549	2571	3237
North Ness	160	225	371
North Plateau			
Horse Hole quadrat	147	609	656
Bishop's Cove quadrat	76	163	79
North of Three Tarn	83	1193	1698
South of Three Tarn	0	82	125
TOTAL	306	2047	2558
Mill Door	10	c.100	101
South Plateau			
Cornerstone - Loch	23	35	259
Loch Side	c.10	c.100	c.150
Cornerstone - Pilgrims	0	70	135
TOTAL	33	205	544
South Horn	9	15	c.100
Maidens	5	2	? 0
Ardcarron	113	274	635
South Ness	244	1180	2152
GRANT TOTAL	3064	12211	18628

The 1989 count was made by S. Wanless, S. Holloway, R. Proctor and M.P. Harris

counts on Dun, St Kilda (one of Britain's largest colonies) which showed an increase of 18% between 1977 and 1987 (Harris and Rothery 1988). Numbers at the large colony at Hermaness, Shetland have remained fairly stable 1973-88 (A.R. Martin, pers. comm.). There have been proportionally large increases at some small southern colonies in England and Wales. Full details of the nationwide survey will be published by C S Lloyd et al..

In north-east Britain, the total numbers of pairs of puffins between Troup Head (Grampian) and Bempton (Humberside) (see Figure 1) was estimated at 10,000 in 1969, 17,000 in 1974, 24,000 in 1979 and 49,000 in 1984 which indicates a steady rate of increase of 10% p.a.. In 1989, the Farne Islands had c. 26,300 burrows (National Trust per P Hawkey) - an increase of 4.9% p.a. since the last count in 1984. Thus, in 1989 the two largest colonies in the area (Farnes Islands and Isle of May) had c. 45,000 burrows. There are few counts for other colonies to assess their recent fortunes, but taking a minimum total figure of 16,000 (no change since 1984) and a maximum of 25,000 (an increase at the Isle of May rate), the total north-east British population should be in the range 60,000-70,000, probably towards the lower end as no large as no large increases have been reported. The general increase in puffin numbers in the North Sea has now slowed down.

There is no reason to suppose that the population is threatened but it is important to determine what population parameters have changed and the possible causes.

4.2 Body condition of adults

There were no significant differences in the weights of prebreeding or breeding adults in 1989 and earlier years (Table 3) and the proportion of breeding adults retaining traces of winter plumage when they first returned in the spring was, at less than 1%, very low compared to 1988 (27%) (Table 4). The reason for the high 1988 figure is obscure.

Breeding adults in 1989 had significantly more bill grooves than those in 1970s (Table 5). Thus in 1988 over a half of breeding birds had 3 or more grooves which compared with only a quarter in 1974-80. Thus breeding adults in 1989 were, on average, older than similar birds in the 1970s.

4.3 Breeding

4.3.1 Timing.

The first fish seen being carried by an adult to a burrow in in 1989 was on 19 May and the median hatching date was 30 May which was well within the normal annual range (Table 6). Given an incubation period of 41 days, the earliest and median laying dates would have been about 8 April and 19 April. There

Table 3. Weights of breeding puffins on the Isle of May in 1989 compared to 1972-77.

Stage of breeding	Year	n	Mean weight (g) ±SE
Before breeding	1989	52	409.5 ±3.6
	1972-77	308	412.7 ±3.5
Incubating	1989	30	407.3 ±5.2
	1972-77	156	405.3 ±2.1
Feeding chick	1989	16	375.9 ±5.6
	1972-77	696	389.3 ±2.1

None of the differences between-years were significant.

Table 4. Proportions of puffins examined in late March-early April which showed traces of winter plumage.

Year	Date	Total examined	No. with trace of winter	% Winter
1973	9-11 April	160	0	0
1974	23 March-10 April	440	1	<1
1975	21 March-10 April	539	1	<1
1976	21-30 March	240	0	0
1977	30 March-10 April	345	0	0
1978	29 March-6 April	328	0	0
1979	1-11 April	107	2	2
1980	31 March-6 April	314	0	0
1981	3-11 April	704	6	<1
1982	27 March-10 April	885	10	1
1983	4-10 April	239	13	5
1984	2-5 April	171	2	1
1985	5 April	105	2	2
1988	27 March	287	77	27
1989	25-27 March	816	6	<1

Note: no observations were made in 1986 and 1987

Table 5. The number of bill grooves of puffins breeding on the Isle of May and in 1974–80. The percentage of the sample with various grooves are given in brackets.

		No. of bill grooves			
	Sample	2	2+	2±	3 or more
1989	77	6 (8)	16 (21)	14 (18)	41 (53)
1974–80	731	124 (17)	233 (32)	191 (26)	183 (25)

$X^2 = 28$, df = 3, $P < 0.001$

Table 6. Calculated annual median hatching dates of young puffins on the Isle of May.

	No.	Median	SD		No.	Median	SD
1973	187	28 May	13.9	1982	144	31 May	8.8
1974	193	11 June	11.4	1983	162	1 June	8.8
1975	282	3 June	10.8	1984	171	28 May	6.9
1976	145	7 June	10.3	1985	43	25 May	7.8
1977	444	4 June	8.5	1986	84	4 June	8.2
1978	436	3 June	8.8	1987	no information		
1979	612	5 June	6.7	1988	81	31 May	6.3
1980	506	31 May	7.7	1989	58	30 May	7.1
1981	485	28 May	8.0				

is a tendency for hatching to have become earlier since 1974, and between 1974 and 1989 the trend was highly significant (Figure 6). The importance of this trend and its cause are obscure. 1973 was a particularly early season and did not fit the pattern.

4.3.2 Success.

Breeding success in 1989 was 0.88 young fledged per burrow where an egg was recorded maintained the typically high breeding success of Isle of May puffins (Table 7).

4.3.3 Weight of chicks

The mean peak weights of 30 young was 320 g (SE 4.5) and the fledging weight of 28 was 279 g (SE 5.9). Although these weights were heavier than similar weights in 1988 (304, 264), they fit the gradual and significant decline in chick weights which has continued since the study started (Figure 7).

4.3.4 Food and feeding of chicks

Young were fed mainly small sandeels Ammodytes sp about 7 cm long - that is fish which had hatched early in 1989 (the 0-group of fishery biologists). The only other species to contribute significantly to the diet was herring Clupea harengus (Table 8). Sandeels made up 89% of the diet by weight, Clupeidae (herring and sprat Sprattus sprattus) 10% and other species 1%. In only 3 years (1973, 1983 and 1985) of the 17 years for which we have data have Clupeidae made up

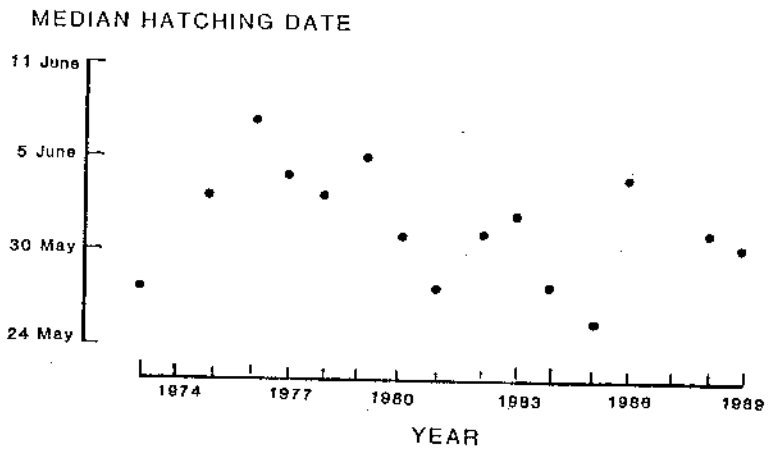

Figure 6. Median hatching date of puffins on the Isle of May 1973–89. The decline between 1974 and 1989 is significant ($r = 0.66$, $n = 15$, $P < 0.01$).

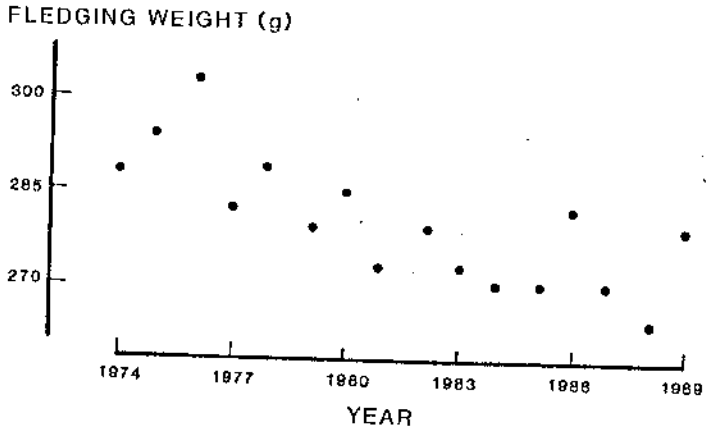

Figure 7. Mean fledging weights of puffins on the Isle of May 1974–89. The relationship, fledging weight (g) = 3494–1.62 year is significant ($n = 16$, $r = 0.75$, $P < 0.001$).

Table 7. Chick production of puffins on the Isle of May 1973-79

Year	Eggs followed	Young fledged/pair
1973	58	0.74
1977	51	0.73
1978	100	0.87
1979	139	0.90
1980	119	0.76
1981	35	0.89
1982	124	0.92
1983	168	0.79
1984	144	0.88
1985	166	0.79
1986	136	0.80
1987	176	0.93
1988	157	0.88
1989	164	0.88

Table 8. Food of young puffins on the Isle of May 1989

	Sample	Mean	S.E.
(a) Load weight (g)	101	9.3	0.36
(b) Fish/load	101	5.9	0.28
(c) Numbers and lengths of fish (mm)			
Sandeels *Ammodytes sp.*	598	78.6	0.46
Herring *Clupea harengus*	38	76.6	1.89
Rockling *Gaidropsarus/Ciliata*	21	34.5	0.84
Sprat *Sprattus sprattus*	1	120	
Unidentified flatfish	1	30	
Unidentified Gadidae	2	28, 29	

less of the diet (Figure 8).

The mean weight of a load of fish dropped by 101 adults was 9.3 g and the mean number of fish per load was 6 (Table 8). Both these were normal (Figure 9).

On 16 June, an all-day watch of 42 burrows each containing a single chick recorded a mean feeding rate of 5.67 ± SE 0.36 feeds/chick/day. This was the highest feeding rate recorded since 1977. Combining the above data gives a mean daily intake of a chick of 53 g of fish (equivalent to 345 kJ) which is the third highest recorded in 15 years of this study.

Gulls stole 11 (4.4%) of 249 loads brought to the area under observation. This is a relatively low rate of loss compared to some years, e.g. 13-19% of loads were lost during the period 1974-77.

4.4 Proportion of immatures in the population

4.4.1 Mist-net catches

Of the 396 Puffins mist-netted in the first half of July, 57 (14%) were immature (Table 9). Although this proportion was higher than the proportion in 1985-88 it was markedly lower than the peak level of up to 37% recorded in the late 1970s (Table 10). The proportion of immatures in the mist-net catches increased during the second half of July when it averaged 51% (204/398) (Table 9); this is normal and is caused by incresing numbers of immatures arriving at the colony and adults departing at end of the season.

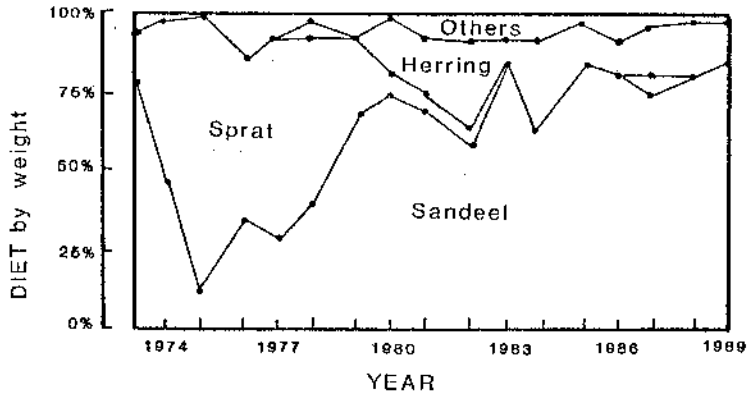

Figure 8. Diet of young puffins on the Isle of May 1973-89.

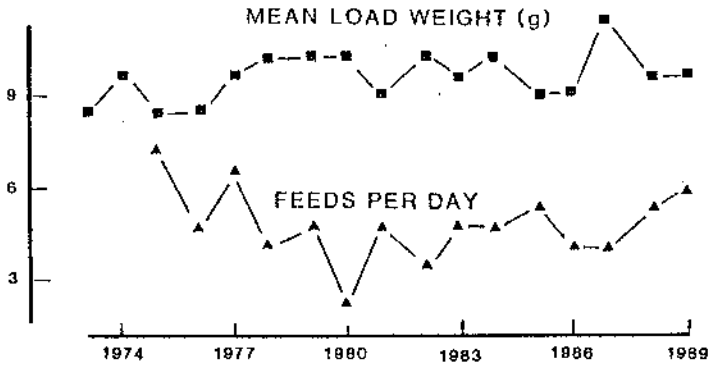

Figure 9. Mean feed weights and feeding frequency of young puffins on the Isle of May 1973-89.

Table 9. The number of bill grooves of Puffins mist-netted in July 1989

Date in July	Individuals with these numbers of bill grooves					
	0	less than 1	1	more than 1, less than 2	2	more than 2
3			1	9	8	110
5		4		7	3	47
7	1	5		16	16	78
10			1	7	7	46
12		1	1	4	7	17
Subtotal	1	10	3	43	41	298
16	3	3		19	17	20
18	9	12	16	53	22	70
20	5	11	7	19	4	16
22		1	1	12		24
23	1	10	2	11	5	5
25	3	4	1	4	7	4
Total	22	51	27	161	96	437

Table 10. Proportion of immature puffins (with less than 2 bill grooves) 1976–89

Year	Total birds handled up to 15 July	% immature
1976	676	12
1977	491	15
1978	739	28
1979	277	22
1980	380	37
1981	527	15
1982	753	15
1983	503	22
1984	502	14
1985	101	5
1986	317	10
1987	94	0
1988	47	0
1989	395	14

4.4.2 Sightings

There were few difficulties in separating puffins with less than 2 grooves from these with 2 grooves or more than 2 grooves using a telescope. However, the trace of any third groove was difficult to see. Therefore, I have combined the 2 and the more than 2 classes, because of (a) the practical difficulty, (b) some adults never have more than 2 grooves, and (c) they are all potential breeders. The proportion of immatures (less than 2 grooves) among the direct sightings and the mist-netted birds during the same period were not significantly different (Table 11).

4.4.3 Three-year-olds

Most 3-years-old puffins have one and half or one and three-quarter bill grooves and are probably capable of breeding the next year (though many may well not do so). Up to 12 July 40 such birds were caught (compared with 339 older birds); considering birds caught during the whole of July, there were 143 3-year-olds compared with 533 older birds.

Table 11. Comparison of bill grooves of samples of puffins a) viewed through a telescope and b) caught in mist-nets 5-10 July 1989.

	Bill grooves less than	Bill grooves 2 or more	Total
a) Direct sightings	168 (15%)	939 (85%)	1107
b) Mist-net catches	41 (17%)	197 (87%)	238

$X^2 = 0.63$, n.s.

4.5 Adult survival

Of 142 colour-ringed adults known to be alive in 1988, 121 (85.2%) were recorded in 1989. Comparable survival figures for 1986/7 and 1987/88 were 81.2% and 76.1%. These are, however, serious underestimates of survival as not all birds alive are recorded every year, some probably because they do not return, others because they are not seen. Estimates of survival improve in later years when some of the missing birds are found. For instance, in in 1989 I found 15 of 39 individuals which had been recorded in 1987 but not in 1988; these increased the annual survival for 1987-88 from 76 to 85%.

Annual survival in recent years has been much lower than it had been in the 1970s (Table 12). Unfortunately, this change in survival coincided with a change in my work pattern from full-time to part-time study of puffins. Thus the change could conceivably be an artifact due to a change in searching effort. However, the Jolly-Seber model for adult survival takes account of the variation in sighting effort and the preliminary results of this analysis confirm that there was indeed a marked reduction in adult survival rate after 1979, and suggests that survival is currently lower than previously (Table 13). As the model depends on sightings in subsequent years it cannot as yet give an estimate for survival for 1987-88 or 1988-89.

Table 12. Survival of breeding puffins on the Isle of May based solely on the number of colour-ring resightings.

	Overwinter survival	
	Alive in year	% alive in year
Year (n)	n	n+1
1973	130	94.6
1974	125	98.4
1975	132	94.7
1976	141	97.9
1977	281	95.0
1978	328	93.6
1979	286	95.0
1980	279	95.0
1981	294	86.1
1982	232	87.5
1983	179	86.0
1984	180	93.9
1985	166	89.8
1986	178	88.2
1987	163	85.0
1988	142	85.2+

+Possibly too low as some adults could still be alive and not all birds are recorded each year.

Table 13. Adult survival of puffins allowing for birds not being seen every year based on a modified Jolly-Seber model

Year	Calculated annual survival	95% Confidence interval
1972-73	93.0	82.7-100
1973-74	97.8	93.4-100
1974-75	98.6	95.5-100
1975-76	97.8	95.8-99.2
1976-77	97.2	95.0-99.2
1977-78	95.3	92.7-97.6
1978-79	97.1	94.8-98.9
1979-80	90.2	86.6-93.2
1980-81	92.5	88.8-95.7
1981-82	88.8	85.1-92.4
1984-85	96.0	91.9-99.7
1985-86	90.7	86.1-95.1
1986-87	91.0	85.9-96.0

5 DISCUSSION

5.1 Population

There is no doubt that the halcyon days for puffins in north-east Britain during which numbers increased about ten-fold in three decades are now past. The annual monitoring on the Isle of May indicates that the slowdown started between 1981 and 1982 and the breeding population has remained essentially stable since 1985.

5.2 Breeding

Since the early 1970s breeding success has been, and still is, very high. In the 1970s about 70% of mature adults were thought to breed each year (following Ashcroft 1979). However, with hindsight this is considered to be too low and the figure is now put at 90%. During the 1980s virtually all adults had burrows and probably bred each year.

5.3 Food of chicks

Isle of May puffins have access to at least 27 reasonably common small mid-water fish on which they could potentially feed their young but they concentrate on just 5 or 6 species (Harris & Hislop 1978). There has been a gradual change in the diet of young during the 1970s and 1980s. Sandeels have been the most important prey

throughout the period except for 1974-78 when sprats formed 50-86% of the diet (by weight). Sprats have a high energy density and the frequency in the diet is often much higher than expected compared to independent surveys of abundance which indicates that puffins are selecting them (Harris & Hislop 1978). During the 1980s the proportion of sprats declined and the proportion of herring increased (Figure 13), which reflects both the decline in the North Sea population of sprat and increase in the number of herring (Hislop & Harris 1985). Juvenile herring of the size brought in by puffins are not of particularly high energy value so it is unclear whether or not it would benefit puffins to select these fish to carry back to the chicks.

5.4 Chicks

There has been no suggestion that food has ever been short for chicks on the Isle of May since the study started in July 1972 and the adults seem capable of coping with losing up to 5-10% of the loads they bring ashore to kleptoparasitic gulls by simply returning to sea and finding more.

The gradual decline in the mean annual fledging weight between 1974 and 1989 (Figure 7) is one of the few changes in puffin biology noted which is statistically significant. This might be due to density dependence in that as colony size increased each pair

might have increasing difficulty in obtaining food for its chick (Gaston 1985, Furness & Birkhead 1984) but it is not possible to rule out that some other factor has changed gradually over the period. In some species of seabirds, e.g. Cape gannet Sula capensis and Manx shearwater Puffinus puffinus, young which are heavier at fledging have a higher survival rate than light young (Perrins, Harris & Britton 1973, Jarvis 1974). This relationship has yet to be demonstrated for any auk. An analysis of the retrap data for Isle of May puffins found no such effect (Harris & Rothery 1985) but the data referred to chicks reared in 1974-79 when conditions were obviously extremely good both for growth (mean fledging weight = 289 g) and for post-fledging survival (later). Conditions have changed as shown by a mean fledging weight 1980-89 of 274 g, so a reassessment of the effect of growth and/or weight on post-fledging survival is needed.

5.5 Immatures

5.5.1 Colony fidelity

Once a puffin has bred it rarely, if ever, moves to another colony, or to another part of the same colony, even when it cannot obtain a burrow. Immatures, however, often visit several colonies before settling down and many of these breed away from their natal colony (Harris 1983, Kress and Nettleship 1988).

Up to 1988, 335 (19%) of 1783 chicks colour-ringed on the Isle of May between 1973 and 1979 were resighted when they were 4 or more years old. Thirty-three (9.9%) of these were found at other colonies when they were old enough to breed and can be assumed to have emigrated (Figure 10). In a detailed, independent study large numbers of birds which were definitely breeding were checked during 3 seasons on the Isle of May and the Farne Islands, Northumberland (100 km away). Thirty-nine young which had been ringed on the Isle of May were found breeding, 30 at the natal colony and 9 on the Farne Islands - an emigration rate from the Isle of May to the Farne Islands of 23%. In a wider survey, only 11 (33%) of the 33 birds which had emigrated were seen on the Farne Islands whilst 21 (66%) were seen elsewhere. A more realistic estimate of emigration is given by 27 (i.e. 9 x 33/11) of 57 (i.e. 27 + 30) birds move to other colonies - an emigration rate of 47%. This figure is a minimum estimate since many British puffin colonies were not checked. However there are no grounds for suspecting that birds from the Isle of May emigrated preferentially to the colonies which were searched since the colonies covered a wide geographic area and range of sizes.

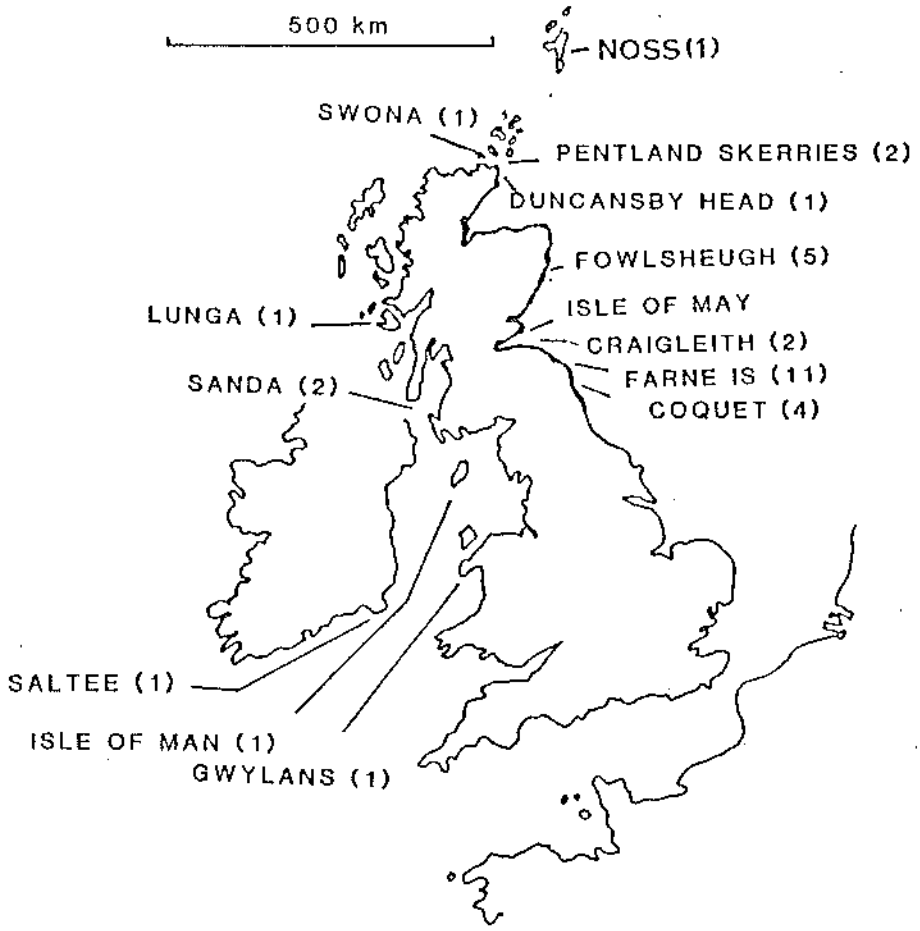

Figure 10. Locations of young puffins colour-ringed on the Isle of May as young in 1973-79 and seen elsewhere when four or more years old. The numbers in brackets refer to the number of individuals seen at the named colonies.

The Isle of May also received immigrants from other colonies including chicks ringed 1973-79 on the Farne Islands (40), Craigleith, Firth of Forth (4), Sule Skerry, Orkney (1) and Fair Isle, Shetland (1). It is difficult to assess the relative numbers of young emigrating out of and immigrating into the Isle of May, but clearly there used to be a considerable exchange of young birds between colonies in Britain. There is a need to assess whether this continues.

5.5.2 Survival to breeding age

The survival of chicks ringed in 1973-77 was high with up to 25% of some cohorts actually being seen back at the natal colony aged 5 years (the normal age of first breeding) and the calculated survival varied 26-33% (mean 28%) (details in Harris & Wanless in press). Survival of the 1978 cohort was noticably lower than other years, although (at 18%) the difference was not significant (Figure 11).

If the calculated emigration rate of 47% was typical, then 52% of young raised 1973-77 should have survived to breed. The comparable 1978 figure would be 33%. Large scale mist-netting of puffins stopped in 1984 by when the population became large and soil erosion prevented us entering some parts of the colony on a regular basis. Therefore we have no data for later cohorts. In 1989 we

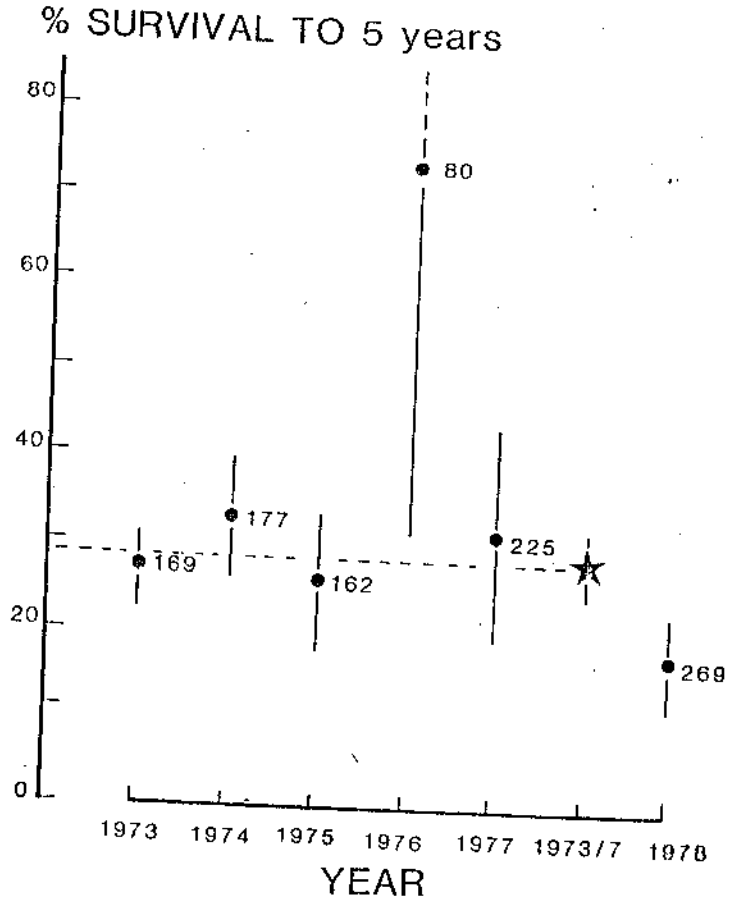

Figure 11. The survival to breeding age (±SE) of young puffins ringed on the Isle of May 1973-78. The numbers indicate sample sizes.

ringed chicks with numbered colour-bands in an attempt to obtain estimates of current chick survival by resighting rather than by recatching.

5.6 Adult survival

Like most other seabird species the puffin normally has a very high adult survival so that even a small increase in mortality will have serious consequences for the population. Survival rates for adult puffins of over 95% p.a. have been recorded in Newfoundland, Russia, Canada and Wales (Ashcroft 1979, Kress 1987, Hudson 1985) so the very high survivals recorded on the Isle of May up until 1979 can be regarded as typical. Some major change occurred between 1979 and 1980 and,apart from the winter of 1984-85, conditions have remained less good than they once were.

5.7 The population in 1990

It is possible to age immature puffins up to 3 year-old which are caught but it is difficult to use these figures to estimate the age structure of the population due to (a) differences in the time immatures of different ages spend at the colony, and (b) the different catchability of the different age classes. Although the proportion of immatures among the birds mist-netted was much lower than 10 years ago, it was higher than in more recent years (14%) (although in 1987 and 1988 few birds were examined).

The pertinent question is whether or not there are sufficient immatures to replace the adults dying; if not then the population must decline.

The adult survival rate cannot be predicted with any certainty but the best current estimate available, based on all birds sighted during the period 1984-89, is 92.5% (95% C.I. = 90.0 - 94.8). Assuming that (a) the proportion of 3-years-old determined by mist-netting is representative of the population, (b) the adult mortality remains at 7.5% p.a., (c) 3-year-olds also have a high survival, say 90% p.a., and (d) lack of burrows is not preventing some birds from breeding, we can calculate as follows:-

1. 18,600 pairs = 37200 adults x 7.5% mortality = 2790 adults dying between 1989 and 1990.
2. Using the ratio of 3-year-olds:adults found in (a) early July or (b) all of July, in 1989 there should have been
   either (a) 37200 x 40/339 = 4400 3-year-olds
   or (b) 37200 x 143/553 = 9980 3-year-olds
3. If 90% of these 3-year-olds survive, then 3950 or 8980 should be alive in 1990 to replace the 2790 adults dying.

There are many uncertainties in this rather simplistic calculation but the figures indicate that it is unlikely that the breeding population will decline in 1990.

6 STUDIES IN BRITAIN AWAY FROM THE ISLE OF MAY

Puffins are attractive birds and breed on cliffs and islands in some of the most spectacular scenery settings in Britain. It is, therefore, not surprising that the species has attracted the attention of ornithologists, both amateur and professional. However, as a study animal the species has considerable disadvantages -- (a) the colonies are often difficult or dangerous of access, (b) the nest is underground, (c) nesting birds are somewhat intolerant of disturbance, (d) adults are long-lived and have delayed maturity so that data on survival, age of first breeding, etc. which are essential to understanding the ecology of the species take many years to collect, and (e) the breeding season is protracted so that observers must spend many months in the field each year. Thus for some or all of these reasons most studies have been of rather limited duration or scope.

The following studies are currently being undertaken in Britain.

6.1 Skomer, Dyfed: Dr C M Perrins, University of Oxford

This was started in the early 1970s and currently collects data on adult survival rate, chick production, food and growth of chicks. It is supported by funds from the Nature Conservancy Council (NCC). It has also recorded a decline in adult survival in the 1980s.

6.2 Fair Isle, Shetland: Fair Isle Bird Observatory Trust

I collected data on the food of young during the 1970s and in 1986 (under contract from NCC) set up a scheme to monitor some aspects of puffin biology (Harris & Riddiford 1989). Data on adult survival, chick production, food, feeding rates and growth of chicks are now collected by FIBOT under a NCC contract.

6.3 Hermaness, Shetland: Dr A R Martin NERC Sea Mammal Research Unit, Cambridge

Food samples have been collected and general observations were made in 11 years between 1973 and 1988 with the financial support of NCC (Martin in press). In 1989 J McKee (funded by WWF) estimated breeding success and collected food samples at Hermaness (and also at Sumbrugh Head) (Richardson et al. 1989).

6.4 Foula: Dr R W Furness, University of Glasgow

Food samples have been collected over a period of years and general productivity assessed during the last few seasons (Furness 1989a).

6.5 Sule Skerry: D Budworth & A Blackburn

Information on numbers, food of chicks and weights of young have been collected sporadically since the mid 1970s. I have no recent information on this work.

6.6 Elsewhere

There is little scope for either the expansion of these studies or for starting new ones except on St Kilda. My own studies on Dun, St Kilda terminated in 1979 except for brief visits to count the numbers of burrows in fixed transects (Harris & Rothery 1988). St Kilda has the largest concentration of puffins in Britain, it is an NNR and has a resident summer warden; data on breeding success are easy to collect yet despite sustained I have failed to get NCC monitor puffin breeding success.

6.7 Abroad

Puffins in the Lofoten Islands have produced few young 1969-88 (Lid 1981, Anker-Nilssen 1987). Much effort has gone into studying the breeding success and food of the puffin on Røst but understanding the dynamics of this population, which is now declining has proved difficult due to lack of data on adult and immature survival. T. Anker-Nilssen has recently submitted a research proposal entitled "The feeding ecology, reproduction and population dynamics of Puffins breeding on Røst' to the Norwegian Research Council for Science and the Humanities to run for at least 4 years (1990-93). I have been asked to contribute towards the planning of this and to have the applicant on the Isle of May to standardize methodology.

7 FUTURE STUDY

The admittedly limited and fragmentary data suggests that (a) puffin numbers in Britain are now more-or-less stable, (b) annual adult survival rates of adults at the two colonies for which we have information has declined as perhaps has immature survival at one colony and (c) puffins in several colonies in Shetland have reared relatively few young in recent few years. A better understanding of the 'health' of the British puffin population needs information on the following topics.

7.1 Numbers of birds

This information is hard to obtain as most puffins nest in areas or habitats which make counting burrows difficult. There are also problems in ensuring that sample counts are representative of the population concerned. There is only limited scope for documenting population changes in detail.

7.2 Breeding success

Breeding success is straightforward to measure but only rarely do observers record whether failures to rear chicks are due to females not laying or to chicks or eggs being lost. The former suggests poor conditions in the late winter, the latter points to food shortage during the summer. There is no need for great precision

in the estimates of success unless post-fledging survival and emigration rates are also being documented.

7.3 Food of chicks

Food being brought to chicks is easily collected and gives a useful indication of whether or not puffins are managing to obtain the stable fodds of sandeel and clupeids or are (apparently) being forced to bring low energy value larval fish or gadoids, such as whiting Merlangius merlangus, to their chicks. Puffins can sometimes compensate for light loads or poor quality food by feeding the chicks more often, so feeding frequency also needs to be measured to determine the daily energy intake.

7.4 Adult survival

The survival rate of adult puffins is usually high so that adults have the potential of breeding 10-20 times. As noted in the Lofoten Islands many years of poor breeding success have to occur before there is a noticeable drop in breeding numbers. In contrast an increase in adult mortality has marked adverse effect on numbers. Adult survival can be measured accurately but requires sustained and substantial effort over a period of several to many years.

7.5 Immature survival and emigration rates

These are difficult to measure but, along with adult survival, are absolutely critical to understanding population demography.