387

The Behavioural Ecology of the Whooper Swan
(*Cygnus cygnus cygnus*)

Mark Andrew Brazil

Thesis submitted for the degree of
Doctor of Philosophy

Department of Psychology,
University of Stirling.

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The Wild Swans at Coole

The trees are in their autumn beauty,
The woodland paths are dry,
Under the October twilight the water
Mirrors a still sky;
Upon the brimming water among the stones
Are nine-and-fifty swans.

The nineteenth autumn has come upon me
Since I first made my count;
I saw, before I had well finished,
All suddenly mount
And scatter wheeling in great broken rings
Upon their clamorous wings.

I have looked upon those brilliant creatures,
And now my heart is sore.
All's changed since I, hearing at twilight,
The first time on this shore,
The bell-beat of their wings above my head,
Trod with a lighter tread.

Unwearied still, lover by lover,
They paddle in the cold
Companionable streams or climb the air;
Their hearts have not grown old;
Passion or conquest, wander where they will,
Attend upon them still.

But now they drift on the still water,
Mysterious, beautiful;
Among what rushes will they build,
By what lake's edge or pool
Delight men's eyes when I awake some day
To find they have flown away?

W.B. Yeats
1865-1939

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CONTENTS

LIST OF TABLES

LIST OF FIGURES

Abstract

The behaviour and ecology of Whooper Swans (*Cygnus cygnus*) were studied on the wintering grounds in Scotland and the summering grounds in Iceland, with a view to extending our general knowledge of the biology of this little studied species.

Comparisons are drawn between feeding behaviour shown in terrestrial, freshwater and marine habitats. In Central Scotland Whooper Swans were found to feed mainly on agricultural land and to actively select stubble fields, where they fed on waste grain, from their arrival in autumn until mid-winter. They then changed to feeding on grass from mid-winter until their departure in the spring. They were found to have adopted an activity pattern similar to that of geese, i.e. they were diurnal and flew each morning and evening between a roost-site and a feeding site. The daily activity cycle of feeding varies between habitats, but the differences are not fully explained by functional requirements.

The factors affecting the timing of morning and evening flights are discussed. The length of the feeding day increased with daylength and the level of feeding per hour increased so that more time was spent feeding in the spring than at any time during the winter. Although Whooper Swans were found to compensate to some extent for the shortness of winter days by departing to the roost later relative to sunset, it is suggested that it is in the spring when their energetic requirements are highest; they need to store enough energy for migration and breeding and/or moult.

The percentage of birds head-up was found to decline curvi-linearly with increasing flock size while the percentage feeding increased.

Since there was no apparent relationship between peck rate and flock size, birds in larger flocks gain from increased food intake. A seasonal change in flock size was noted in Central Scotland with larger flocks occurring more frequently between autumn arrival and mid-winter than from mid-winter to spring departure. Although other factors may be involved as well, it is suggested that the advantages of flocking to Whooper Swans may vary depending on whether the food is patchily distributed (waste grain), or relatively uniformly distributed (grass).

Differences in the amount of time allocated to feeding and vigilance were analyzed according to age and breeding status, and seasonal changes are discussed.

The breeding success of the Whooper Swan, measured using the percentage of cygnets and the mean brood size, was found to vary greatly from year to year. Measurements of mean brood size in Iceland during summer were found to correspond well with those in Scotland the following winter. A particularly poor breeding season in 1979, a year with a very late spring, was noted both in Iceland and on the wintering grounds in Scotland.

Whooper Swans are monogamous and territorial. The female does most of the nest building and all of the incubation, while the male remains on the territory, usually either vigilant or feeding. The range of behaviours exhibited by males and females during the incubation and fledging are described and the time allocated to them is analyzed. Displays between adjacent territory holders are described for the first time. These displays were found to be commoner during the fledging period than during incubation. Females were also observed to take part in defence against intruders and it is suggested that an important role of the Whooper Swan's territory is to provide a safe feeding area for the family after hatching.

Behavioural co-operation between mates helped to maintain a high degree of protection for the nest and cygnets. Cygnets maintained closer proximity to each other than to their parents and tended to associate with a single parent; usually the female. As cygnets aged, distances between them and from them to their parents increased and their parents spent more time feeding and less time vigilant.

The behaviour of non-breeding birds is also described and it is suggested that non-breeders tend to moult in a separate flock from failed breeders. Moult and migration are also discussed in order to provide as full a picture as possible of the Whooper Swan's year.

CHAPTER ONE: INTRODUCTION

The Whooper Swan (*Cygnus cygnus*) is one of seven species of swans in the genera *Cygnus* and *Coscoroba*, found in North and South America, Eurasia and Australasia. The taxonomy of swans is still controversial, although the northern swans have generally been considered four distinct species (see Boyd 1972). Delacour and Mayr (1945) considered them to be two polytypic species while Johnsgard (1974), on the other hand, took the more radical view that they were a single polytypic species. I follow Wetmore and Parkes (in Palmer) and Palmer (1976) in considering that the Whooper and Trumpeter Swans (*Cygnus buccinator*) are not conspecific. The Whooper Swan is monotypic and ranges widely from Iceland and Fennoscandia, across arctic Russia to Kamchatka, Koryakskiy Khrebet and the Aleutian Islands. It breeds generally in the boreal zone, its range being virtually contiguous with its more northerly, tundra-breeding relative, the Bewick's Swan (*Cygnus columbianus bewickii*).

The Whooper Swan winters in Britain, West Europe (especially in the Baltic) east to the Black and Caspian seas and in Korea, Japan and eastern China. The size of the population breeding in Iceland and wintering in Britain is about 6700 (Brazil and Kirk in prep.), that wintering in north-west Europe is about 14000, those of the Black and Caspian sea regions total about 25000 (Ogilvie 1972; Atkinson-Willes in press) and in Japan there are on average 13000. In Korea there are 2000-3000 swans roughly 60% of which are Whooper Swans (Won in press). The numbers using large areas of the species range are not known, (for example eastern China) but the total world population is not less than 60000 and is probably between that figure and 100000.

In spite of its wide distribution, its conspicuousness and beauty and its appearance in the folk-lore and mythology of many regions, the species has been remarkably little studied. Very little has been published on the species other than brief descriptive accounts, the most widely known of which probably being those of Venables and Venables (1950) and Airey (1955), on the Whooper Swans of Shetland and the Lake District respectively. The paperby Boyd and Eltringham (1962) on the status and distribution of the Whooper Swan in the British Isles could perhaps be regarded as a turning point in our developing knowledge of the species, since for the first time information on the population size, distribution and composition were collated.

The first detailed field studies of the species were those by Hewson (1964, 1973) and Henty (1977). The former concerned mainly with flock composition and the latter with diurnal movements. Apart from these few papers on the species in its winter haunts, there are three very important papers by Haapanen, Helminen and Suomalainen (1973a, b, 1977), which present the results of the only previous major study of the species and provide almost all that is currently known of the species on its breeding grounds. The last of these three papers discusses the summer behaviour of wild breeding birds from incubation through to fledging and as the only paper on these topics in this species, it alone forms the background to the work done on breeding biology and behaviour during this study.

The few previous papers on the Whooper Swan had left vast areas of the species' ecology and behaviour unstudied, for example none had covered migration or moult. Very little was known about daily or seasonal movements, feeding ecology or flocking and less still was known of the increased use of agricultural land on feeding behaviour. No data were available on the ecology of non-breeding birds and very little information was available from the Icelandic population.

Prior to the period of this study, Whooper Swans in the Stirling area had shown an interesting pattern of movement, several small flocks utilizing several fields during a single day. Initially this study was planned as a detailed examination of this situation and of the factors affecting habitat selection.

Preliminary observations soon revealed, however, that for reasons unknown, the pattern of usage of the area by Whooper Swans had changed to a more regular system with a single flock in the area utilizing a single field often for several days, thus virtually eliminating the phenomenon to be studied.

Preliminary reading revealed that the species was poorly known, thus the focus of the study was shifted and broadened to provide a wider description of the behaviour and ecology of the species. The breadth of the project was again increased when visits to the breeding grounds in Iceland were made possible in 1978, 1979 and 1980 and further by the opportunity to visit Japan in 1980. Increasing the breadth of the study inevitably reduced its depth, although a general theme of interest in feeding behaviour and ecology runs most central to the thesis. Extra studies such as that of geographical variation in bill patterns (Brazil in press) and morphology, and of migration and movements (Brazil unpublished) have been retained separately.

In view of the initial change in direction of this study, a primarily descriptive approach has been taken to the annual cycle of events in the Whooper Swans year, from winter in Britain, to migration, breeding and moulting in Iceland in order to extend as much as possible our understanding of the species as a whole. It remains for more detailed studies to be made of specific aspects of the biology of the Whooper Swan

This broad approach has a different focus of interest from much of the more recent work in behavioural-ecology, especially that on waterfowl where, for example, fine details of social behaviour (e.g. Scott, D.K. 1980 a,b,c,d) and feeding ecology (see Owen 1980) are typically being studied. Such detailed studies, however, are obviously only possible because of the wider knowledge of the species in question. It is hoped that this short study will at least provide the general background for future interest and study of the Whooper Swan.

The aims of this study were to examine:

1) daily and seasonal movements and the factors affecting habitat selection (extending the work of Henty (1977).
2) feeding ecology and behaviour.
3) how the species' behaviour may have changed in association with its increased usage of agricultural land.
4) the composition of winter flocks as a means of assessing annual variation in reproductive success (see also Boyd and Eltringham 1962; Hewson 1964).
5) the general breeding biology and behaviour of the species in Iceland (see Haapanen et al 1973a,b, 1977).
6) to extend the work done in Finland (Haapanen et al) by studying the behaviour of non-breeding birds for comparison with breeders and by looking in much greater detail at aspects of the behaviour of both

parents and cygnets.

7) details of the primary moult using captive birds and birds caught for ringing.

This study has relied on an observational rather than an experimental approach and since, unfortunately, marked individuals were not available until the very end of this study, has dealt with 'average', rather than known individuals. As with other studies in behavioural-ecology, the dominant concern has been with behaviour as an ecological factor affecting the distribution and/or abundance of individuals (see Krebs 1972), for example habitat selection, the sharing of time amongst different behaviours, group or flock composition and dynamics, territoriality and parental care and with the interactive effect between such factors and environmental factors such as habitat availability and climate.

CHAPTER TWO· HABITAT USE

2.1 Introduction

The aim of this chapter is to provide information on the study area, on the availability of suitable habitat and the use of that habitat by Whooper Swans. Since this study is primarily concerned with terrestrially feeding swans, the history of the development of this habit and its effects on the behaviour of the swans are discussed. The movement of swans around the study area is outlined and discussed with reference to the changes which have occurred since the study by Henty (1977).

2.2 Description of the Scottish Study Areas

Previous data collected by Henty (1977) and my own initial observations indicated that a relatively small study area, at no great distance from the University of Stirling, could be watched profitably and conveniently. The minimum requirement was that the area(s) chosen should enclose both foraging and roosting sites used for much of the winter.

Two study areas were chosen, one to the east (circa 60 km^2) and one to the west (circa 25 km^2) of Stirling (see Fig. 2.1). Both were situated in flat farmland with a mixture of arable and ley fields. The area to the east of Stirling is traversed by the tidal river Forth and the area to the west by its two tributaries, the rivers Forth and Teith. Busy roads connect small towns and there are, associated with these, many power lines and telephone wires. There is also much fishing and shooting centred on the rivers. Agriculture depends mainly on winter wheat, barley and sheep. Other cereals, root crops and livestock are much less common.

Fig. 2.1 Map of the study areas east and west of Stirling

The area to the east of Stirling lies between the A91 to the north and the A905 to the south and extends to Abbey Craig in the west and Alva and Alloa in the east. The area to the west of Stirling lies between the A84 and the A811, as far west as the B8075 and extends to Stirling in the east.

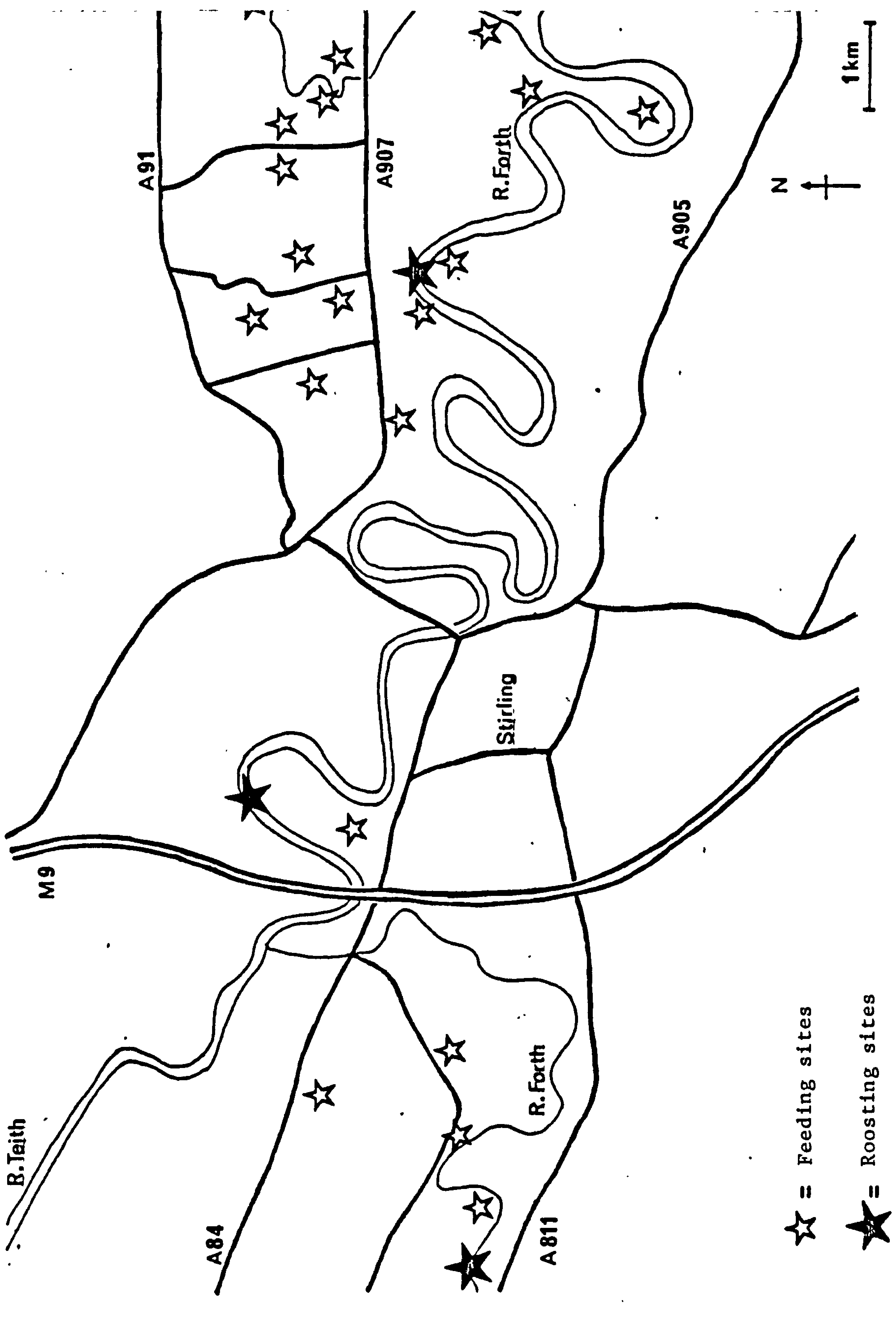


Fig. 2.1 Map of the study areas east and west of Stirling

2.3 Habitat Availability

A habitat survey was made of the two study areas in winter 1978-79 using a road transect method. The roads forming the perimeter of each area were used as the transects and were recorded in October and December 1978 and January and April 1979. The field types adjacent to both sides of the road were recorded every 0.16 km. It was assumed that the transect samples were representative of the study areas, and they were not obviously inconsistent with general impressions. The aim was to examine the availability to Whooper Swans of two main habitats: stubble and grass. Thus only crude distinctions were made between crop types. The frequencies of plough, 'root' crops, stubbles, grass and hay were recorded (see table 2.1). Fields of undersown stubble were classified as stubble if their general appearance was brown and if grass covered only a small proportion of the surface; they were classified as grass if their general appearance was green and if a large proportion of the surface area was comprised of grass. Hay includes only uncut crops; cut hay was classified with grass.

Each year ploughing reduced the availability of stubbles as winter proceeded. Ploughing occurred later in the cold winter of 1978-79 than in 1979-80. While the availability of grass decreased only slightly between October and April, stubble decreased in both areas by over 50%. There was, however, always more stubble available to the west of Stirling than to the east.

Table 2.1

The proportions of samples of three crop types within the study areas during winter 1978-1979.

Eastern Area

	October	December	January	April
Grass	45.9%	45.9%	Snow cover	39.8%
Stubble	15.3%	10.2%	"	4.0%
Hay	7.1%	7.1%	"	7.1%

n= 98

Western Area

	October	December	January	April
Grass	42.2%	43.6%	Snow cover	39.4%
Stubble	24.3%	20.2%	"	10.1%
Hay	14.7%	14.7%	"	9.2%

n= 218

2.4 Habitat Selection

The swans did not use crop types in the study area in proportion to their availability. From October until December over 40% of both areas was grass, whereas stubble at its maximum in October only contributed 24.3% of the western area and 15.3% of the eastern area (table 2.1). The swans, however, used predominantly stubble fields until January or February, then used grass fields.

In 1977-78, 'autumn' use of stubble overlapped with 'spring' use of grass in January and February. There were, however, 151.5 bird days (b.d.) on stubble in January and 65 b.d. on grass. In February the situation was reversed, with 71 b.d. recorded from grass and only 31 b.d. from stubble. Birds were not recorded on stubble after February (table 2.2). In 1978-79, use of stubble and grass overlapped in December and February. In December, 284 b.d. were recorded from stubble and 317 b.d. from grass. No birds were recorded on grass in January 1979, but in February 412.5 b.d. were recorded from grass and only 69 b.d. from stubble. Again, no birds were recorded on stubble after February. In 1979-80, no overlap in use occurred at all. Birds last used stubble in December and first used grass in January.

The availability of grass declines only slightly during the winter as ploughing occurs (table 2.1). New grass, such as winter wheat and the early spring growth of leys is of greater nutritional value than old grass, which becomes less palatable as it gets longer (Ogilvie 1978). In autumn, grass is presumably a poorer food source than grain, which is higher in carbohydrates. Later in the winter there were fewer areas providing grain for food than grass, which begins to increase in protein content as the growing season recommences. 'Root' crops were not common in the study

Table 2.2

Habitat use within the study areas (percentage of bird days)

	1977-78				1978-79			1979-80		
	Stubble	Grass	Flood water	Total bird days	Stubble	Grass	Total bird days	Stubble	Grass	Total bird days
October	0	0	0	0	100	0	6	100	0	63
November	99.7	0	0.3	673.5	100	0	1372	100	0	1339.5
December	100	0	0	532	47.3	52.7	601	100	0	54
January	55.6	26.2	17.3	261.75	100	0	174	0	100	303.5
February	9.8	22.4	74.4	317	14.3	85.7	481.5	0	100	46
March	0	100	0	207.25	0	100	43	No observations		
April	0	100	0	85.75	0	100	356.75		"	
May	0	0	0	0	0	100	14		"	
Total bird days	1385.5	429	262.5		1905	1143.25		1456.5	349.5	

area and the use of them by swans was rare and confined to potatoes. In other areas of Scotland, and in the Fens, potatoes are an important food (Kear 1963).

For part of winter 1977-1978 an area of the eastern study area close to the river Forth was flooded. The area was visited by swans in November 1977, but in January and February it was used consistently as a feeding ground. In February, more bird days were spent there than at either stubble or grass (table 2.2).

My observations showed that in Central Scotland Whooper Swans fed on waste grain in stubble fields from late October until late January or early February, when they switched to feeding on grass. There seemed to be a number of possible reasons for this: decreasing seed densities, loss of stubble area, and renewed growth of grasses. The situation, however, was more complex than this, since for the most part, when the swans were feeding from stubble fields they used the area east of Stirling and roosted on the tidal Forth near Manor Neuk, whereas when they changed to foraging on grass, they moved to the area west of Stirling and roosted on the Forth near Kildean (Fig. 2.1). The reasons for this move are not known. A similar preference for stubbles in the autumn and grass in the spring has been observed in Aberdeenshire and the Dumfries area (J. Kirk pers. comm.).

Feare et al (1974) found that in stubble fields used by Rooks (Corvus frugilegus), grain density declined rapidly from September until November and thereafter more slowly until March. This is likely to be a general pattern for stubble fields since grain is used by many species as winter food. Murton (1965) found that as stubble fields became exhausted between November and early January Wood Pigeons (Columba palumbas) moved to Clovers (Trifolium sp.) and Sprouts (Brassica sp.). Although stubble fields are available for use by swans throughout the whole winter, the grain density is likely to fall too low for swans to feed satisfactorily, hence the switch to grass.

2.5 The historical development of field feeding and its influence on behaviour

Field-feeding by Whooper Swans and other northern swans is a recent phenomenon, and since the majority of observations discussed in Chapters Three, Four and Five were of swans feeding on land, this section is included here to provide the necessary background. Traditionally swans spend the winter on open fresh-water, marshes or shallow tidal areas. They have apparently only begun to feed on agricultural land in Britain since the hard winters of the 1940's (Owen and Kear 1972). The first report of this behaviour appears to be that of Anderson (1944) who saw Whooper Swans in Scotland feeding on grass fields up to three miles from the nearest loch, after flooding had subsided. Floyd (1946), on the other hand, noted that Whooper Swans were never seen at any distance from water although he had seen up to twenty-five Bewick's Swans grazing on stubble fields after the harvest.

Whooper Swans have only flown to fields specifically to feed on potatoes since the 1930's and 1940's and, as with the Mallard (Anas platyrhynchos), Pink-footed (Anser brachyrhynchus) and Greylag Geese (Anser anser) which began the habit earlier, it was probably due entirely to changes in farming practices (Kear 1963; Pilcher and Kear 1966). Use of stubble and grass may have developed from flights to potato fields, from the use of flooded stubbles or pastures, or as a response to severe conditions; in southern Sweden, for example, Whooper Swans regularly feed on croplands during cold periods (Nilsson 1979) and in the Fens Bewick's Swans moved to agricultural land after the freezing of deep and extensive floods. In the latter case it is known that the habit has continued and become more widespread (Cadbury 1975; Scott 1980a).

Whistling Swans (*Cygnus columbianus columbianus*) have made a similar move to feeding on agricultural land; Gunn (1973) reported that they had only begun making daily flights to corn fields in the previous five years. Nagel (1965) regarded feeding in dry corn stubble by Whistling Swans as unusual, "an atypical response to the prolonged winter freeze of 1964 in Utah". Tate and Tate (1966), however, regarded instances of field feeding as part of the normal feeding pattern for Whistling Swans in central California. Trumpeter Swans were found by McKelvey (1979) to have increased at estuaries surrounded by agricultural land. He believed the higher concentrations to be a response to (a) the increased attractiveness of agricultural land for food, since more pastures had been planted with fast-growing grasses high in nutrient content and thus with higher food values than estuarine foods; and (b) the proximity of water, since the swans were still dependent on the estuaries at night and during snow (McKelvey in press).

It is apparent from what little information there is on field-feeding by swans that it is not only recent, but also variable, in occurrence, from region to region. The recent change in behaviour is not confined just to swans, it has occurred also in Brent Geese (*Branta bernicla*) and Greater Snow Geese (*Anser caerulescens*) (see Ogilvie 1978).

It is only to be expected that, where swans have changed from feeding from water to field-feeding, other aspects of their behaviour will also have changed, or new aspects become evident. Field-feeders, unlike aquatic feeders, must contend with having to fly daily between roost site and foraging site, an event which may be influenced by many factors (see 4.3.1 and 4.3.2). Their feeding strategies might have to be adapted to different foods and their activity patterns to different aspects of disturbance.

Whooper Swans using agricultural land have adopted a similar daily activity pattern to that traditionally shown by geese; they commute between night-time roosts and day-time foraging sites and feed intensively in the morning and afternoon, resting at mid-day. The same has been reported of the Bewick's Swan in the Fens where fenland feeding was only first recorded in 1970 (Owen and Cadbury 1975). Unlike geese (Ogilvie 1978), Whooper Swans have not been recorded feeding on land by moonlight.

The development of field-feeding by Whooper Swans has brought them, not unexpectedly, into conflict with farmers. Such conflict may lead to changes in human attitudes towards swans and in turn this could lead to further changes in the behaviour of the birds. Grazing of agricultural land by waterfowl inevitably leads to accusations of damage caused directly by grazing pressure, from puddling, burning or competition with stock, and indirectly by causing stock to avoid areas previously used by waterfowl. Crop damage caused by Whooper Swans has already been reported from Iceland (Kear 1964; Harrison 1967).

Several experimental studies have been made to examine the effects of goose-grazing on grass crops and the findings apply equally well to Whooper Swans. Geese and swans usually arrive after most crops have been harvested. Therefore they could cause damage only when competing directly with livestock for grazing, when eating unharvested 'root' crops or where they remain late in the spring. However, Kear (1970a) showed that loss of winter foliage due to grazing was not detrimental to harvest yields of silage grass, winter wheat or spring barley, but lowered silage yields occurred if grass was grazed in May. Wright and Isaacson (1978) considered that the effect of goose grazing on yields depended on the stage of growth of the crops, grazing intensity, soil type and weather and that grazing does little harm and may even be beneficial, as long as the meristem remains undamaged. Clark and Jarvis (1978) showed that, of ten fields grazed by geese, yields differed significantly between grazed and ungrazed plots on only two fields. In both cases yields were greater in grazed than ungrazed plots. Some manurial effect of the droppings may have been involved here. Patton and Frame (1981) on the other hand reported appreciable economic loss where geese grazed improved grassland, because of the need to supply alternative food to stock.

Marriott (1973) showed experimentally that, contrary to reports, the application of droppings increased yields of rye grass and clover, except for trials in which small applications were used. Moreover, sheep were not seen to avoid areas used by geese, nor was 'burning' observed. The only conclusive damage, other than by late spring grazing, was retardation of crop growth by puddling, caused by tight concentrations of waterfowl feeding in wet conditions on heavy soils (see Wright and Isaacson 1978).

It is apparent from these experimental studies that the Whooper Swan cannot really be regarded as an agricultural pest, occurring as it does in most areas in much smaller concentrations than do geese. Convincing the farmer of this, however, is another matter. To him any loss of grazing is significant. Disturbance by farmers or their dogs was an important factor leading to much of the movement between fields during this study and may have also contributed to the complete absence of swans at times. Should the species increase in numbers, interactions with farmers would probably increase and disturbance by them could well lead to another shift in habitat selection or in feeding rhythm.

2.6 Winter Movements

Henty (1977) suggested that swan flocks utilizing the area east of Stirling split up more often than the present study has shown. He observed small flocks in the area simultaneously and these moved regularly between fields and sometimes used separate roost sites (as inferred from the direction of their departure at dusk). Since 1977 the pattern of movement by the swans has changed and so far no explanation has been found for this. It has been rare to find swans other than in a single flock and, although flocks have changed size and even disappeared for varying lengths of time, any flock present has tended to use a single field over a period of several days and also a single roost site.

Selection of feeding fields has also changed. Whereas from 1974 to 1976 it occurred on several occasions during a day, if the flocks were moving about, during the present study, selection occurred only once each day, as the birds left the roost site in the morning. Whooper Swans leaving a roost site must climb above tree and power-line height before flying out to the fields. From this height (about 30 m) they are able to see the fields available to them, as well as where earlier birds have landed. The appearance of fields varies greatly from the air and geese and swans in flight may be capable of recognising good feeding fields.

Abandonment of previously favoured fields may be due to disturbance or reduced food density. Where birds have been disturbed, they have always moved to another field of the same type.

Winter movements, distribution and habitat use are all affected by severe weather. Bannerman (1957) stated that the numbers of Whooper Swans vary "from year to year according to weather conditions", he considered the species to be "a very regular hard weather visitor, not only to Scotland, but also to many English counties", and the Outer Hebrides as their "chief wintering place". This is no longer the case, since they are now much more common on the Scottish mainland (Boyd and Eltringham 1962; Brazil and Kirk in prep.). Although many Whooper Swans use fresh-water habitats on the mainland, the increase in numbers there since Bannerman's (1957) account may be related in part to the development and increase in the use of fields for feeding.

Severe weather in early winter probably causes late migration from Iceland and movements south within Scotland or from Scotland to England or Ireland. It is suspected that hard-weather movements of swans occur between Europe and Britain, although there is no firm evidence. Prolonged freezing reduces the area of freshwater available to swans, while snow cover prevents them from using fields for grazing; for example, the cold weather of much of January and March 1979 drove birds from the study area. Shorter cold periods may be the cause of absences of just a few days. The weather in January 1979 was severe throughout Scotland (figures from the Parkhead weather station at the University of Stirling showed a mean maximum of only 3.6°C and a mean minimum of -3.8°C for the month) and most inland waters were frozen for several weeks. Swans became scarce in central areas while larger numbers were reported in the south west. A sighting of 19 Whooper Swans flying south west out to sea near Portpatrick, Wigtown, on 4th January 1979 (G. Sheppard pers. comm.) supports the theory that movement to Ireland occurs in hard weather.

2.7 Conclusion

Results of surveys of habitat availability and use by Whooper Swans showed that they fed from stubble fields from October until late January or early February and from grass fields from then on. Although the availability of stubble fields also declined during the winter, the extent of the change in use was much greater than the relative change in availability of the habitat, suggesting that active selection of field types occurred.

The switch in use of field types was presumed to occur because of the relative quality of grain and grass as food sources at different seasons, the availability of grain and the changing energy requirements of the birds themselves. Whooper Swans have, apparently as a result of feeding terrestrially, developed a feeding regime and commuting system which closely resembles that of geese.

The pattern of daily movement around the study areas has changed since the only previous study (see Henty 1977). Birds have recently tended to remain in a single flock, for both feeding and roosting, rather than in several. Selection of feeding fields occurred only once each day, during morning flight, unless the flock was disturbed during the day. Severe weather appears to affect the distribution of Whooper Swans and disrupts the pattern of daily movements.

In retrospect, Stirlingshire has not proved to be an ideal area for the study of Whooper Swans. Between the previous study, from 1974 to 1976 (Henty 1977) and the beginning of the present study, in 1977, the pattern of field use and movement of swans in the area changed markedly. Observations made over the last three winters suggest that the area is used by medium sized flocks passing through on their way south, or by flocks resident for short periods when conditions elsewhere have caused them to move in. Use of the area in late winter and spring seems to be erratic, with smaller flocks; and swans are sometimes absent from the area for prolonged periods.

CHAPTER THREE: THE COMPOSITION OF WINTER FLOCKS

3.1 Introduction

In this chapter, the flocks making use of the study areas in Central Scotland are described. The relative use of different localities within the study areas is examined and the variation in numbers of cygnets and the size of broods within the flocks are all discussed in detail. Breeding success, as indicated by the percentage of cygnets in flocks in this study, is discussed in relation to national figures.

3.2 The Distribution and Size of Flocks

Data was collected from the study areas during the period 31st October 1977 until 7th February 1980. For the purposes of this study the term 'flock' was used for all numbers of birds including single individuals. Each flock was given an identification number, which was retained if the flock remained the same size during consecutive observation periods even if it had moved to a different locality; a new number was given if the flock had changed in size or structure.

This method was used to facilitate the calculation of use in bird days for different localities and for different years. Without marked individuals it was impossible to assess how long individuals remained in the flocks. A fairly high rate of turnover of birds is suggested by the almost daily changes in flock size. Birds may either pass through or be absent for short periods before returning. Inevitably, flocks are not independent and many birds may be recorded on more than one occasion. Thus calculated indices, such as mean flock size, may be biased; relative comparisons between years depend on assuming that biases are effectively constant. A further consideration is that if statistical probabilities are calculated from raw data then probability values are inflated because of a lack of independence in the data units. It will be seen that in later sections (3.3.1 and 3.3.2) it was practical to isolate certain units of data thought to be reasonably independent, in order to make useful comparisons with other studies. In this section, however, since the only comparisons to be made were relative ones and in view of the difficult nature of the data, no such selection has been made.

During this study 191 flocks were recorded from the study areas, totalling 6932 bird days (b.d.): 2078 b.d. were recorded in winter 1977-78, 3048 b.d. in winter 1978-79 and 1806 b.d. in winter 1979-80. The intensity of observations varied between years, hence there is no implication that the number of birds which used the areas was directly proportional to the number of bird days recorded. The higher figure for winter 1978-79 did represent a real increase in bird presence since the difference between the intensity of observation in winters 1977-78 and 1978-79 was not great. Without individually marked birds it was not possible to know whether the increase in bird days was due to more birds passing through the area or to more individuals staying for longer periods. Observation intensity and bird days were reduced in winter 1979-80 owing to my absence from the area from mid-February until April, whilst conducting field-work in Japan. Sixty-four field days were recorded in winter 1977-78, 73 in winter 1978-79 and 59 in 1979-80. The first two are minimum figures since not all days when swans were not found were recorded in the first two winters.

Twenty-eight localities were used by swans within the study areas. Nine of these received more than 250 b.d. use each, while the remaining

19 each received less than 100 b.d. use. Of the nine most frequented localities, three were used in only one winter, two were used in two winters and four were used in all three winters. Thus different localities were used to greatly differing degrees by the swans from winter to winter.

Flocks using the study area ranged in size from 1 - 134. The mean flock size for all 28 localities varied little between years (34.7 ± 26.6 winter 1; 36.3 ± 33.5 winter 2; 36.6 ± 27.1 winter 3). If the nine heavily used localities are considered separately, however, then the mean flock sizes for the three winters are 40.1 ± 27.1, 40.0 ± 35.2 and 39.9 ± 27.3; while for the remaining less used localities they are 18.1 ± 16.0, 18.3 ± 13.6 and 13.5 ± 5.7 respectively. Thus localities receiving greater use held larger flocks than those less heavily used, rather than holding similar sized or smaller flocks for longer.

A cumulative frequency distribution was plotted to give an indication of the relative importance of flocks of different sizes (see fig. 3.1), 75% of all flocks in Central Scotland (the study area and the immediate vicinity) were of less than 60 birds, but 75% of all birds were in flocks of larger than 37 birds. The only comparable study, although based on a much larger sample, is that of Boyd and Eltringham (1962). They reported smaller flock sizes on the whole; most flocks were of less than 10 birds and only 5% of flocks contained more than 50 birds.

It is apparent from the present study that large or small flocks did not occur at random throughout the winter (see fig. 3.2). Large flocks, especially those of over 40 birds, were commoner between October and the end of the year. Before 31st December 75% of birds were in flocks of

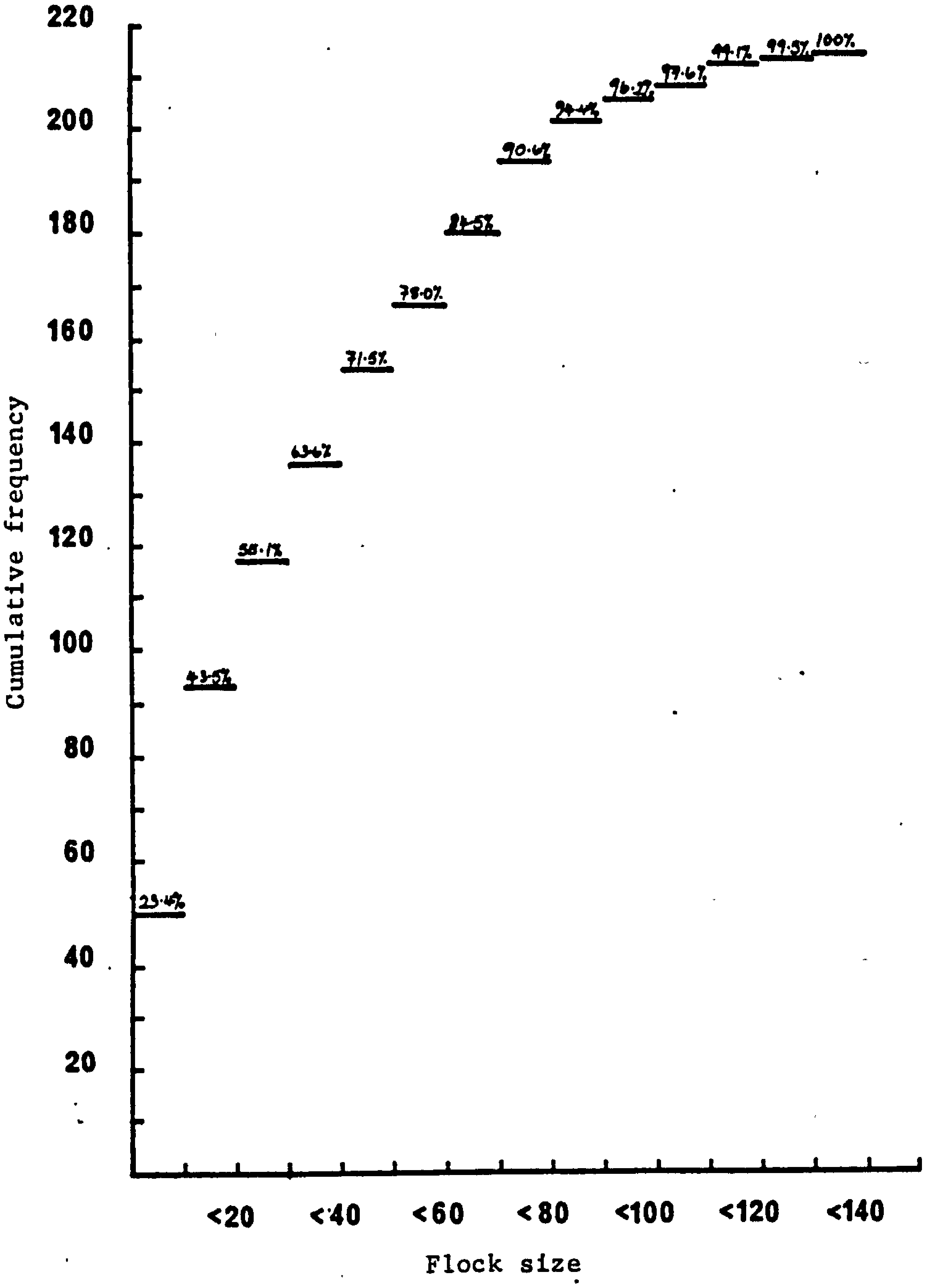


Fig. 3.1. A cumulative frequency distribution of Whooper Swan flock sizes in Central Scotland; 1977-80

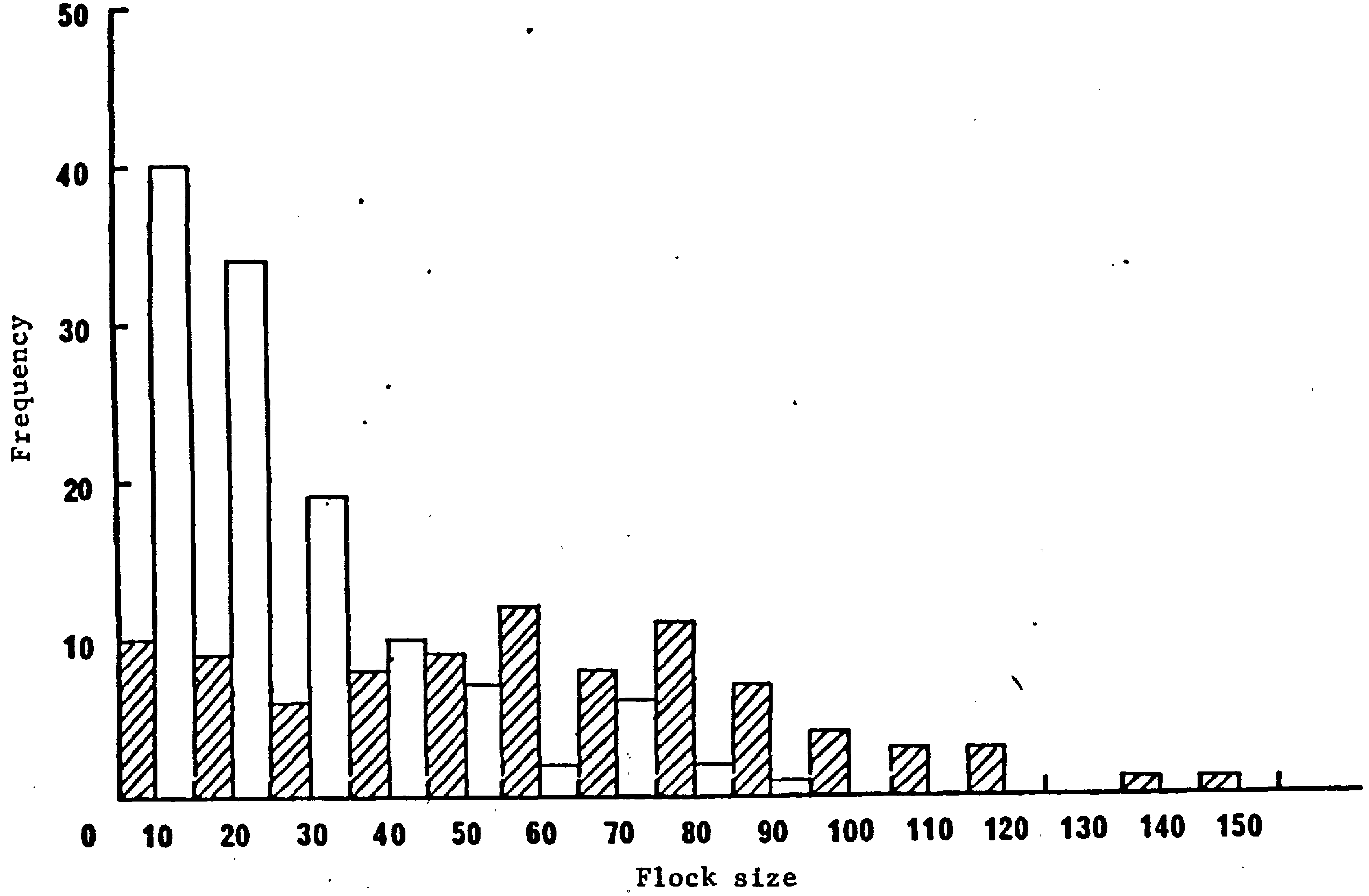


Fig. 3.2. A frequency distribution of Whooper Swan flock sizes in Central Scotland; 1977-80. (Shaded columns represent flocks before 1st January; unshaded columns represent flocks after 1st January).

greater than or equal to 52,(similarly, Boyd and Eltringham (1962) found that in October and November large groups contained nearly half of the swans recorded). In contrast, small flocks, especially those of less than 30 birds; were commoner between the beginning of the year and spring migration. From January onwards 75% of birds were in flocks of greater than or equal to 19. Similarly, Thompson and Lyons (1964) found that small flocks, isolated pairs or family groups, of Whistling Swans were commoner in spring in Wisconsin.

The more common occurrence of small flocks of Whooper Swans in the latter half of the winter in this study may well represent family parties leaving larger flocks and moving north independently and perhaps earlier than those birds which will not breed. Sightings of apparently intact family groups in Iceland in spring 1979 support this view (pers. obs.).

3.3 The Structure of Flocks

During this study the largest stable unit was the family, composed of a pair with up to five cygnets. There was no indication that young of previous years were associating with their parents and younger siblings on the fields, although this has been shown to be of common occurrence in the Bewick's Swan (see Scott 1980 c.). It is possible, of course, that observations of unmarked birds at long range would preclude such observations anyway, thus it still remains a possibility in the Whooper Swan.

Flocks using the study areas were different from those visiting provisioned refuges such as those of The Wildfowl Trust at Welney and Caerlaverock, in that they seemed to be particularly unstable, often changing dramatically in size or structure overnight, and with a rapid turnover of individuals. In many respects they are best described as aggregations (Wilson 1975). It will be seen later, however, (section 5.6) that belonging to one of these 'flocks' does appear to confer certain advantages which may be a result of either the physical nature of the flock, or of co-operative behaviour. They should therefore perhaps be regarded as social groups rather than as aggregations (see Morse 1977).

The number of swans using, or passing through, the Stirling area is only a small proportion of the Scottish wintering population, which is currently estimated at about 4100 (Brazil and Kirk in prep.). The proportion of cygnets present in these flocks does not necessarily indicate the general level of breeding success for the whole population. Since there appears to be some traditional pattern to the use of areas by Whooper Swans, changes in brood size and in the ratio of cygnets to adults from year to year in a particular area are of interest and reflect relative changes in reproductive success. Nothing is known about the catchment area for any particular wintering site. It is not known, for instance, whether discrete breeding populations winter as discrete units, although it is now known that moulting flocks of non-breeders become widely dispersed during the winter (Brazil unpublished).

The proportion of cygnets present and, where possible, brood sizes were recorded, in order to study the annual variation in breeding success. It was assumed, in the absence of evidence to the contrary, that the swans utilising Central Scotland were a representative sample of the whole population. Certainly the very bad breeding season of 1979 (pers. obs.) was reflected from within the study area the following winter, and data from other years agrees well with reports from other areas (see Bell 1979).

Two hundred and thirteen flocks were recorded from Central Scotland, including the previously defined study area and the immediate vicinity, between 31st October 1977 and 7th February 1980. Of these, 118 flocks contained cygnets, and the number of cygnets was accurately determined for 110 of them.

3.3.1 The Percentage of Cygnets in Flocks

The percentage of cygnets was recorded for each flock where the number of cygnets could be accurately determined (n=110). In order to be able to make comparisons with previous studies a mean percentage of cygnets was calculated for each winter. There are problems, however, when making such calculations.

Swan flocks are very mobile during the winter, the number of birds they contain changes erratically and whole flocks may leave an area. It is not possible to calculate the total number of adults or cygnets present during a winter without marked individuals and hence a truly accurate percentage of cygnets cannot be obtained. For practical and political reasons Whooper Swans were not individually marked during this study.

In order to understand the biases involved when calculating the proportion of the flocks which were comprised of cygnets three ways of analysing the data were used. The most obvious ways of looking at the data seemed to be to calculate the percentage of cygnets from:

1) All flocks which contained cygnets. This method suffers the possibility of two types of bias, firstly multiple recording of cygnets may occur and secondly the proportion of cygnets will be further inflated by discarding those flocks which contained no cygnets. This method was

expected to produce a maximum mean percentage, that is a ceiling figure for comparison with other methods.

2) All flocks which were recorded. The inclusion of all those flocks without cygnets should lower the percentage recorded and produce a minimum mean percentage. This method also suffers from inflation due to the multiple recording of cygnets, although as in the previous case, multiple recording of adults will also occur.

3) All those flocks which were thought to be independent. In this case such discrete units were identified where a major change had occurred in the flock; where cygnets were absent followed by a new arrival, or where cygnets were present in two different flocks on the same day. This method was expected to produce an intermediate mean percentage and to go furthest in reducing the biases inherent in methods 1) and 2).

Method 1) was discarded because it clearly exaggerated the total output of cygnets from the adult plumaged population and, because flocks were comprised of a mixture of non-breeding and breeding swans, it could not estimate the proportion of cygnets produced by the breeding population either.

Having thus discarded method 1) the results from methods 2) and 3) were in fact very similar (see table 3.1). Either of these two methods was felt to give a reasonable representation of the annual variation in cygnet production during this study. Method 3), however, was felt to be the least biased and was therefore used for comparison with national figures (fig. 3.3).

The production of young by arctic and other high latitude birds can vary dramatically between years. Often several reasonably successful

Table 3.1

The percentage of cygnets calculated by three different methods

Method	1977-78	1978-79	1979-80
One	17.64%	23.87%	5.48%
Two	12.25%	10.57%	2.58%
Three	13.05%	12.67%	3.75%

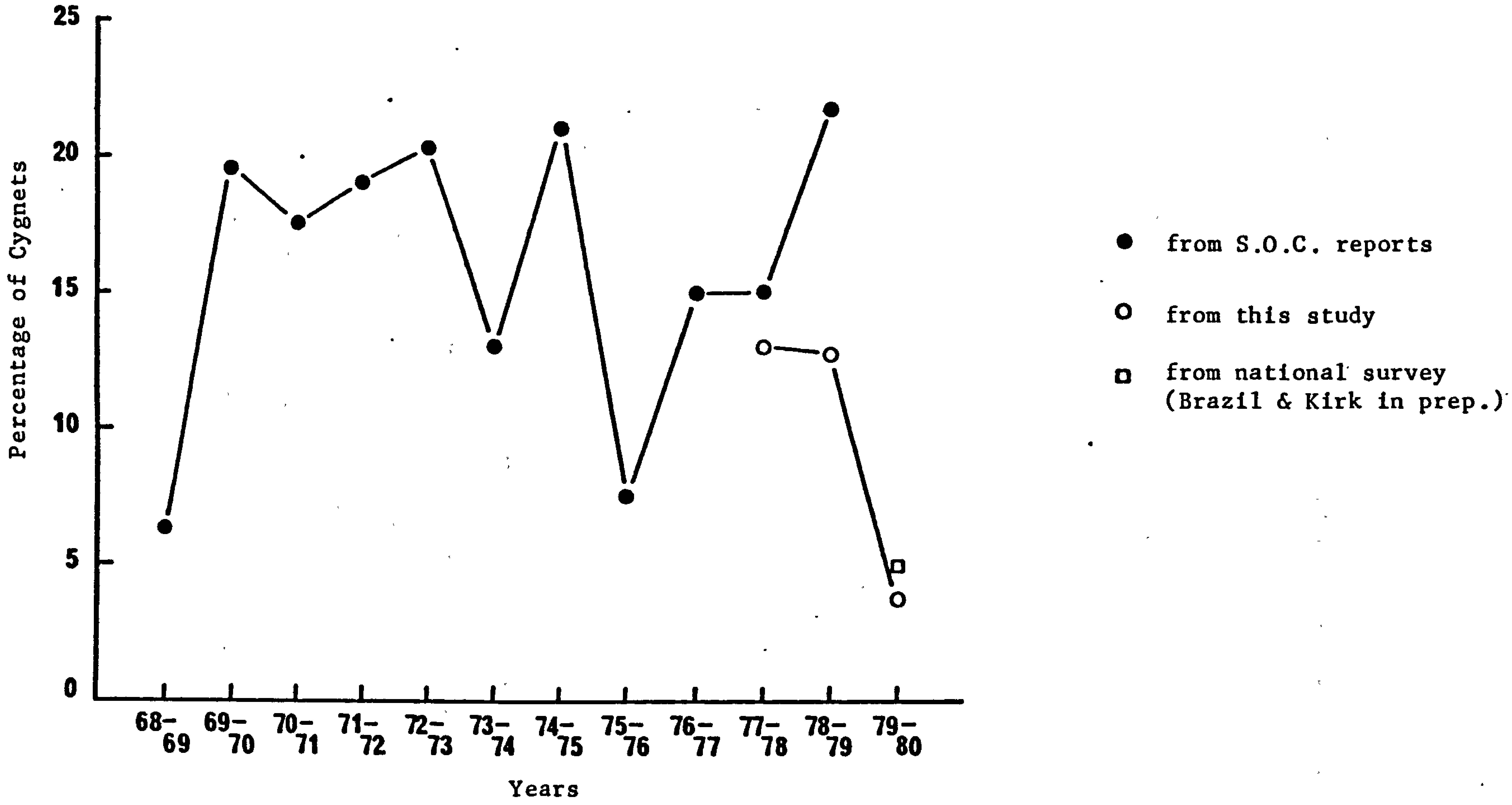


Fig. 3.3. The percentage of cygnets present in Scotland from 1968-1980.

breeding seasons occur consecutively, followed by a year of almost complete failure. Detailed studies of the population dynamics of the Whooper Swan have not yet been made, but existing estimates of breeding success (see fig. 3 .3) suggest that they follow the same pattern. The mean percentage of cygnets in most winters ranges from 13% to 21.6%. Only infrequently is the percentage much higher or lower.

Using the independent units method, the mean percentage of cygnets was 13.0 in 1977-78, 12.7 in 1978-79 and 3.7 in 1979-80. The extremely low figure for the last winter is very similar to the figure of circa 5.12% obtained from a national census during the same winter (Brazil and Kirk in prep.).

3.3.2 The Percentage of Cygnets in Relation to Flock Size

Hewson (1964) found a tendency for more cygnets to occur in small flocks than in larger ones, the mean percentage of cygnets in flocks of fewer than 20 birds was 26.4 and that in larger flocks was 15.1%, while Airey (1955) had suggested that family parties are coherent units and that they tend to stay away from the bigger flocks. The results of this study are similar to those of Hewson (1964), the percentage of cygnets in small flocks (less than 20 birds) being greater than that in larger flocks (11.8% and 5.6% respectively). These percentages have been calculated from the total number of cygnets and total number of birds occurring in flocks of less than or equal to 20, and greater than 20. The flocks used in this analysis were those acceptable for method 3) (see 3.3.1.). As can be seen, however, from fig. 3.4 variation in the distribution of cygnets occurred from year to year. In 1977-78 the pattern was particularly clear, but it was not apparent in 1978-1979 or in 1979-1980.

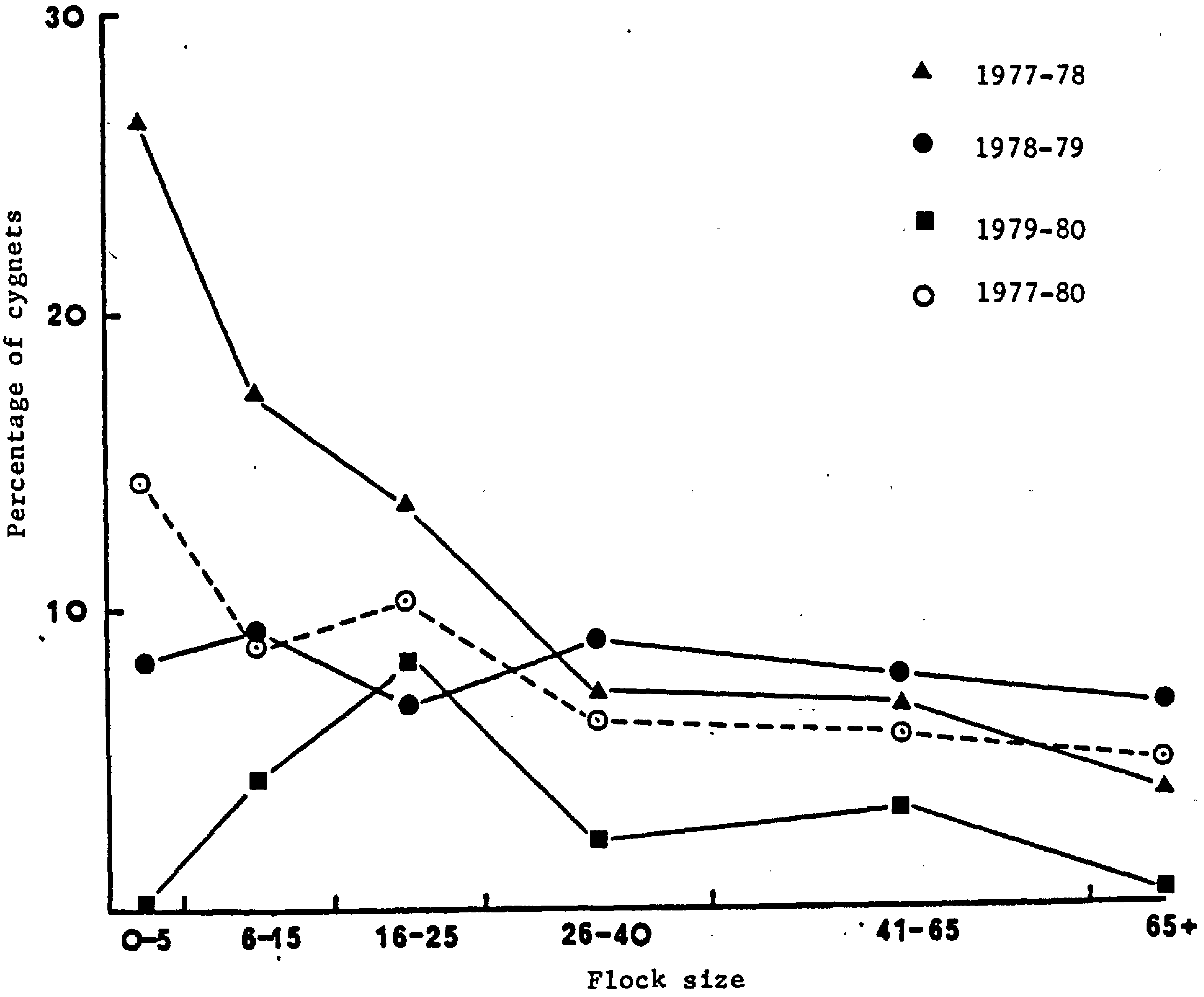


Fig. 3.4. The percentage of cygnets in relation to flock size; 1977-80.

Although in general there was enough data each year to make the individual points in fig. 3.4 fairly reliable, one critical point (for the smallest flock size in 1979-80) was based on only a single record, hence it seemed reasonable to examine all years together. The percentage of cygnets and flock size were negatively correlated over all three years combined (n=6, s=-13, p=0.0166. Kendal Rank Correlation, two tailed test). However, since a Concordance test had revealed that the results from each of the three years were not similar, further analysis was done. The data from winter 1977-78 differed most from that of the other two winters, so data from winters 1978-79 and 1979-80 were combined and separate correlation analyses were done on the years 1977-78 and 1978-80. In 1977-78, the percentage of cygnets and flock size were highly, negatively, correlated (n=6, s=-15, p=0.0028, two tailed), but not so in 1978-80 (n=6, s=-9, p=0.136, two tailed) (see fig. 3.4). The interpretation of these results is somewhat difficult. Certainly the winter of 1979-80 was exceptional in that the proportion of cygnets was extremely low, similarly winter 1978-79 was different from winter 1977-78 in that in 1977-78 of the 31 flocks included in the analysis only 38.7% did not contain cygnets, whereas in 1978-79 58.8% of 51 flocks did not contain cygnets.

From this short study it is not possible to conclude which of the first two years was the most typical, however, the significant effect in 1977-78 resembles that of Hewson (1964) and no year showed the reverse trend.

The percentage of cygnets in small flocks is much more variable than that in large flocks, because small flocks may be composed of either just families (high percentage of cygnets), just non-breeders (no cygnets) or a mixture. Large flocks, on the other hand, are a more representative sample of the population, only a small proportion of which breed. Consequently the proportion of cygnets in large flocks is unlikely to be great unless there are factors affecting the distribution of the birds, such that families choose to join large flocks. This is perhaps not implausible, although apparently not the case, since if individuals in large flocks incur any advantages in terms of more effective feeding or predator detection, then parents might be expected to make an effort to join them so that they and their offspring would benefit from these advantages. There might be some disadvantages for families in large flocks; they might suffer increased feeding competition, for example (see Scott 1980 a.).

The proportion of cygnets present within flocks varies during the winter, and cygnets are scarce amongst early arrivals in September and October (see Boyd and Eltringham 1962). This is almost certainly due to families leaving independently and later for the wintering area than non-breeders (see Bell 1979), which in turn is due to the lengthy fledging period of the cygnets. The same phenomenon also occurs in some geese, for example the Brant (see Barry 1962). By remaining longer on the breeding grounds, cygnets are better developed when they migrate and may therefore be better able to survive the journey (see Hansen et al 1971).

3.3.3. Brood Sizes

Brood size is, of course, limited by clutch size, the factors affecting which will be discussed in section 8.3. A total of 186 broods were counted from 50 flocks during this study. Parents without cygnets are indistinguishable from adults which have not bred. Thus all broods of zero are missed. Consequently it is not possible to calculate the proportion of adults which have bred, nor is it possible to calculate an absolute mean brood size.

The calculation of brood size suffers similar problems to those mentioned in section 3.3.1. It cannot be known whether broods of the same size seen on different occasions are identical or not, consequently a single brood might be over or under represented in the data. As in section 3.3.1 three methods of approach seemed reasonable, each biased in a slightly different way. Method one assumed that all observations of broods made on different dates were independent; where two separate counts were made at the same locality on the same day, the maximum number of broods was used. Method two, the opposite extreme, assumed that no observations of broods were independent, except when recorded together at the same locality, or at separate localities on the same day when there was little likelihood of them having moved from one to the other. Method three, an intermediate assessment, relied on isolating separate units of data which were almost certainly independent. This was basically the same as method two with the addition that where there had been a discontinuity in the presence of swans in the study area, broods before and after the discontinuity were regarded as independent.

Using the methods outlined above, three separate estimates of mean brood size were obtained for each winter. It was expected that mean brood sizes calculated by these different methods would be markedly different, but the differences proved to be very small (see table 3.2).

As in section 3.3.1 method three was felt to eliminate the most bias

Table 3.2

Estimates of mean brood size

Method	1977-78	1978-79	1979-80
One	1.7	2.4	1.1
Two	2.0	2.5	1.4
Three	2.1	2.5	1.3

and was therefore felt to provide the most useful result. Since the different methods used subsets of the same data, it was not possible to compare results obtained by the different methods, however the results were consistent; within year variation was much less than that between years.

The reduction in mean brood size from 2.5 in 1978-1979 to 1.3 in 1979-1980 clearly reflects the very poor breeding season of 1979 as did the exceptionally low percentage of cygnets recorded from this study (3.7%) and from the national survey (5.12%; Brazil and Kirk in prep.) during winter 1979-80.

The most frequent brood size was two in winters 1977-78 and 1978-79 (see fig. 3.5), although larger broods were commoner in 1978-79. A similar observation for north-east Scotland was made by Bell (1979). A chi-squared analysis showed that there was a highly significant difference between years in the frequency of different brood sizes (χ^2=17.82, 4d.f. p=<0.01).

Boyd and Eltringham (1962) suggested that poor breeding success was as likely to be due to failure to hatch or rear any young as to reduced brood size. The results from this study, however, suggest that the reduction in percentage of cygnets in 1979-80 was due to higher mortality of cygnets and/or to a general reduction in clutch size; not due entirely to failure by one sector of the population and normal breeding success by another, which would result in a reduced proportion of cygnets in the population, but normal brood sizes.

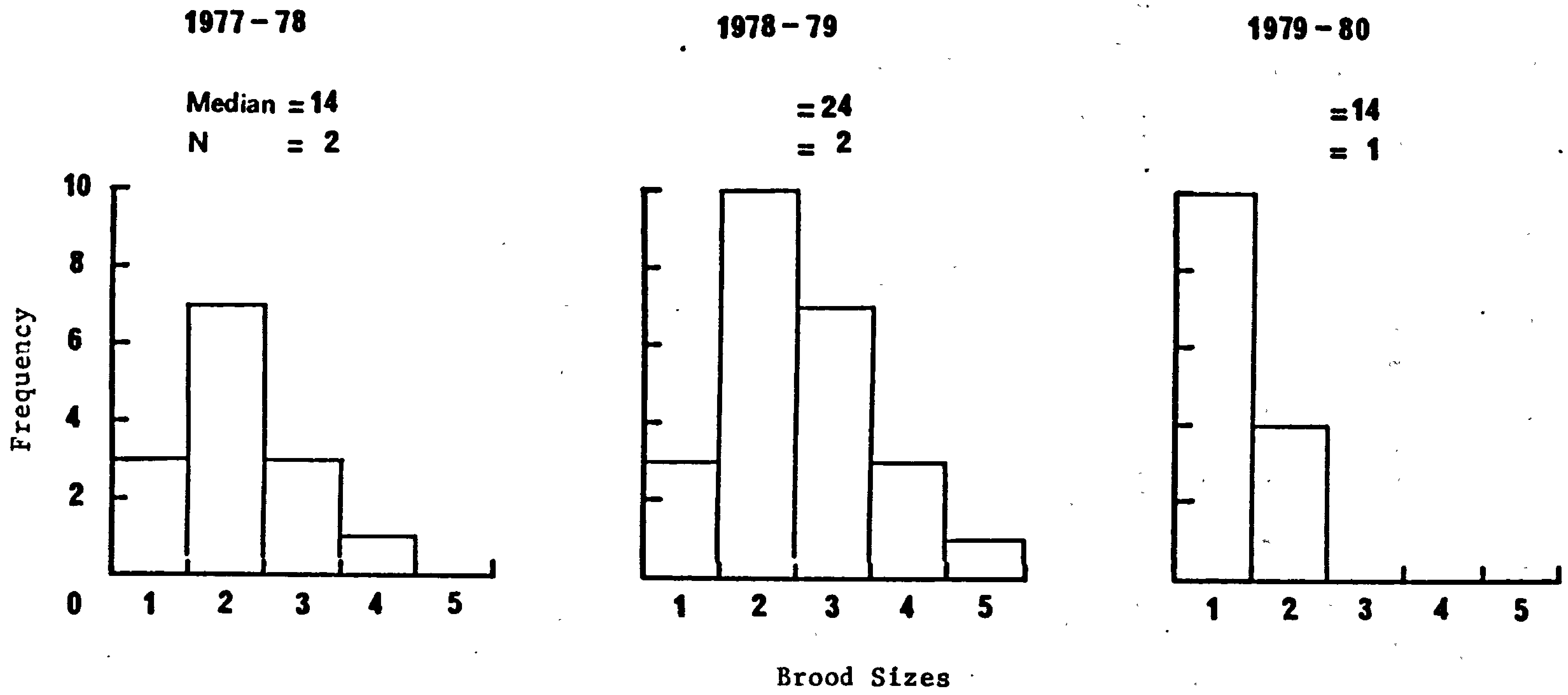


Fig. 3.5. The frequency of different brood sizes; 1977-80

The poor breeding success of 1979 was due to a very late spring in Iceland. Highland breeding areas remained frozen too late into the summer for many pairs to breed at all, and many lowland pairs lost eggs or whole clutches. Those young which did hatch were about three weeks later than in the previous year (pers. obs.). Smaller broods may have been a result of smaller clutches due to reabsorption of eggs by females forced to delay laying. It is a frequent phenomenon in waterfowl that clutch sizes are smaller in late seasons (similarly reduction of clutch size with time occurs in passerines) and the most acceptable view seems to be that this is related to the amount of reserves carried and their rate of depletion (see Newton 1977; Owen 1980).

Although not enough datawere available from this study to examine the possibility of variation in brood size month by month during the winter, the simplest expectation would be for mean brood size to decline slowly during the winter due to cygnet mortality. This explanation, invoked by Boyd and Eltringham (1962) to explain a decline in the percentage of cygnets present in early winter after initial autumn arrivals, fails to take into account the arrival of adults (without young) in early winter. It seems most likely that some non, failed or late breeders remain behind in Iceland and quite a large number probably winter there. Severe winter weather in Iceland would force more to migrate south after the peak arrivals in October and November. The arrival of more adults would, by dilution, reduce the percentage of cygnets recorded. It is also likely that the autumn and spring migrations are the times of greatest risk for cygnets, not the intervening period. Of the two, autumn migration probably represents the time of greatest risk, since at that time the cygnets are smallest.

My scanty data do not show any clear seasonal variation in brood size and no clear picture emerges from other studies, probably due to the differences in the timing of movements of families and other adults and possible observational artefacts involving the overlooking of faster maturing cygnets in spring.

3.4 Conclusion

6932 bird days were recorded during the study. Use of the study areas was very uneven with nine localities heavily used (more than 250 b.d. each) and 19 less so (less than 100 b.d. each) and the use of localities varied greatly from year to year. The mean flock sizes for all localities, or for heavily and less well used localities separately, remained similar in each of the three winters of the study. Localities were well used because larger flocks occurred there, not because flocks stayed there longer. Large flocks were commoner in autumn and early winter and small flocks were commoner in late winter and spring. The percentage of cygnets in flocks was similar in the first two winters at approximately 13%, but in 1979-80 it was very much less at 3.75%; this reflected the very poor breeding season of 1979 in Iceland. There was a significant difference in the frequency of different brood sizes between years and mean brood size fell from 2.5 to 1.3 during the same period. The percentage of cygnets declined significantly as flock size increased when data from all three winters were combined.

CHAPTER 4: FEEDING ROUTINES IN TERRESTRIAL AND AQUATIC HABITATS

4.1 Introduction

An increase has been noted in the use of agricultural land by swans, since the hard winters of the 1940's (Owen and Kear 1972), especially by the Whooper Swan. Such a shift from the use of aquatic habitats might be expected to have a marked effect on the species' behaviour.

The aim of this chapter is to:

1) examine the daily flight pattern associated with the use of agricultural land, i.e. commuting between a roost-site and a foraging site.
2) examine the daily activity patterns of birds feeding terrestrially for comparison with those feeding aquatically.

4.2 Daily Movements: Arrival and Departure Times

The movement of animals from a night-time roosting or sleeping site to a day-time foraging area is a common phenomenon especially among birds. The factors affecting the timing of arrival at, and departure from the roost are many and varied. Light intensity, season, daylength and weather factors such as heavy cloud, fog and frost are all important.

A relationship between roost flights and light intensity has been found for Wood Ducks (_Aix sponsa_) (Hein and Haugen 1966), Starlings and Grackles (_Sturnidae_ and _Icteridae_) (Nice 1935), Herons (_Ardeidae_) (Seibert 1951) and Cattle Egrets (_Bubulcus ibis_) (Siegfried 1971). Where light intensity is the controlling factor, weather factors such as cloud and mist are expected to delay morning flight and advance evening flight (e.g. Hein and Haugen 1966). Seibert (1951) found that Herons left the roost at a lower light intensity than that at which they arrived, while Seigfried (1971) suggested that a specific light intensity threshold for roosting is modified by environmental constraints and physiological needs. Longer periods of darkness in mid-winter lead to a greater hunger in visually feeding birds, which in turn is likely to cause earlier departure in relation to light intensity. Hein and Haugen (1966), found that there was least change in the start of evening flight, while the end of morning flight and the duration of evening flight changed most. They also found that on dark or foggy days morning flights were delayed and evening flights were prolonged (because the starts of the latter were well advanced while the ends were only a little earlier). In general, it appears that conditions of poor visibility lead to adjustments in flight times such that the illumination at flight times resembles that on clear days.

In the present study arrival and departure time data were collected to test two alternative, although not necessarily mutually exclusive, hypotheses:

1) Daylength and Temperature Hypothesis

During the period of shortest days, birds endure longer periods of darkness and lower temperatures and hence have lower morning energy stores. Reduced daylength leaves less time available for feeding. Assuming that time spent at the foraging grounds is positively correlated with energy requirements, it was predicted that during mid-winter birds would arrive earlier at and depart later from the foraging area and time spent feeding would be increased relative to daylength.

2) Safety Hypothesis

Terrestrially feeding swans are primarily visual feeders. During flights between roosting sites and foraging areas they are at risk from objects along their flight path, such as telephone and power lines and trees. Collisions were found to be the cause of between 33% and 44% of all swan casualities in studies by Ogilvie (1967) and Owen and Cadbury (1975). Thus it is very dangerous for diurnal species to fly at low altitude when it is dark. Activity on the foraging grounds during darkness would also be expected to add to the risk of attack from ground predators. Because of the increased risk of mortality from activity during darkness, it was predicted that swans should arrive and depart at a specific light intensity which would allow them to fly safely between roost and foraging sites.

4.2.1 Methods

Whooper Swans grazing on fields were watched up to and including their departure to the roost on several evenings between 7th November and 6th February 1980. Similarly, between 9th November 1978 and 24th January 1980, they were watched as they arrived at the feeding grounds from the roost. The time of arrival or departure for each sub-flock and the light reading (zenith) at arrival or departure time was recorded using a standard Weston photographic light meter. This was later calibrated against a 40x Optometer to convert light meter readings into foot candles. Light readings were also taken at regular intervals in the 30 min. preceding arrival or departure. Times (G.M.T.) were converted into minutes before or after local sunrise or sunset (Glasgow minus two mins.). A 50% departure time was used (following Henty 1977). The 50% arrival or departure time, was the time by which half of the flock had arrived or left the foraging grounds. Davis (1956) showed this to be the endpoint least influenced by chance variation. Data were available for 41 evenings for days ranging in length from seven hours to 15½ hours, and 18 mornings for days ranging in length from seven hours to 13 hours (daylength is the period between sunrise and sunset).

4.2.2. Results

Arrivals were evenly distributed throughout the period from 60 min. before local sunrise to 10 min. afterwards. Departures were normally distributed, occurring in the period from sunset until 90 min. afterwards. Peak departures occurred between 31 and 40 min. after sunset (see fig. 4.1). Thus there was a distinct difference in the overall pattern of arrivals and departures.

If arrivals and departures are re-examined with respect to daylength, an effect which was masked by the previous analysis becomes apparent. There was a tendency (although not significant) for arrivals to occur earlier on short days and later on long days ($r=-0.387$, $p>0.1$. Pearson Correlation; see fig. 4.2). Departures occurred later after sunset on short days and earlier on long days ($r=-0.5$, $p<0.01$, own data; $r=-0.58$, $p<0.001$, including data from Henty; see fig. 4.3). The few data points for very long spring days (over 12 hr.) have been left out of this analysis (see fig. 4.2 and 4.3). Thus in fig. 4.1 departures soon after sunset were contributed by long days and delayed departures were contributed by short days; there was no standard departure time which applied to all seasons.

This study has shown a strong relationship between departure time and

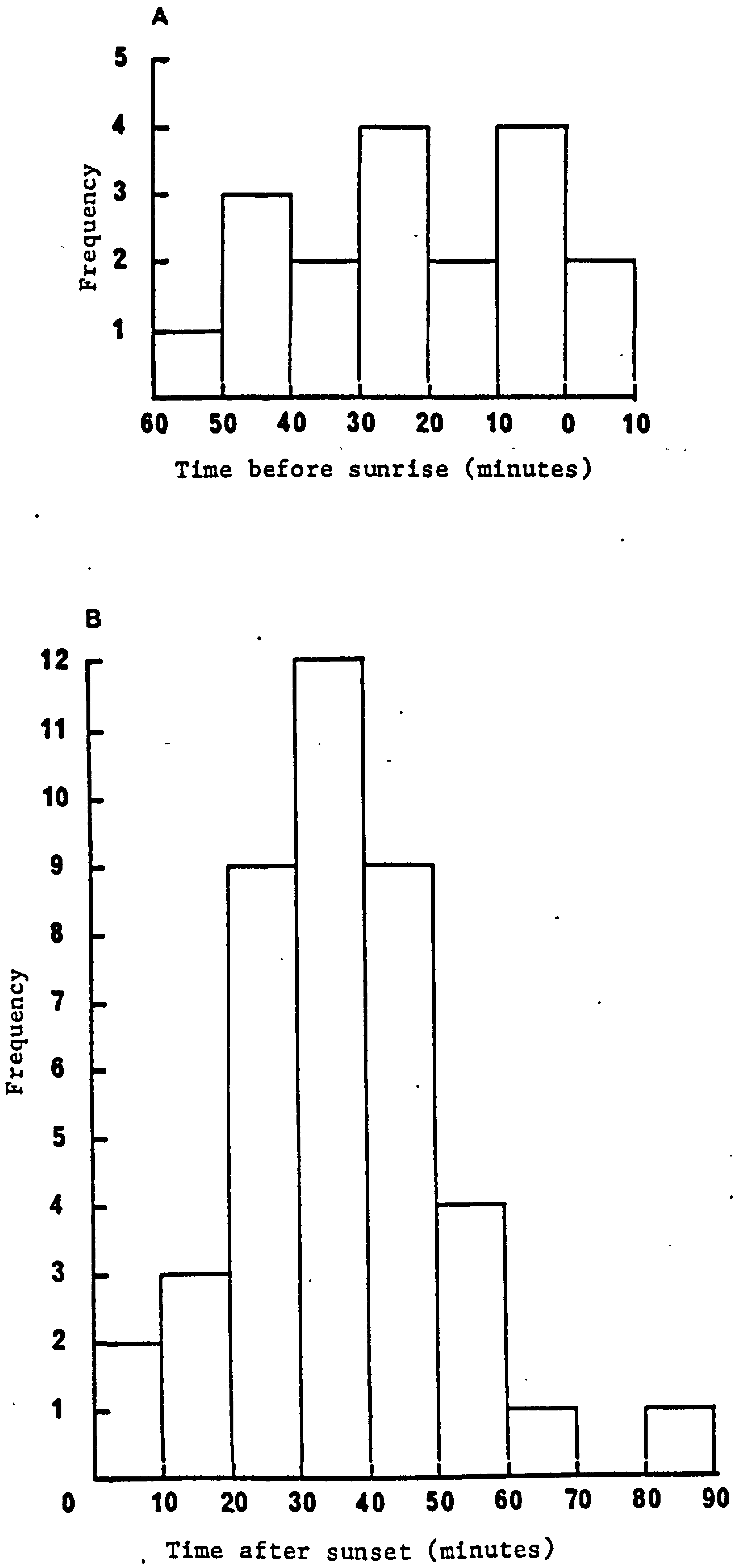


Fig. 4.1. Arrivals at the feeding grounds (A), and departures to the roost (B) in relation to sunrise and sunset.

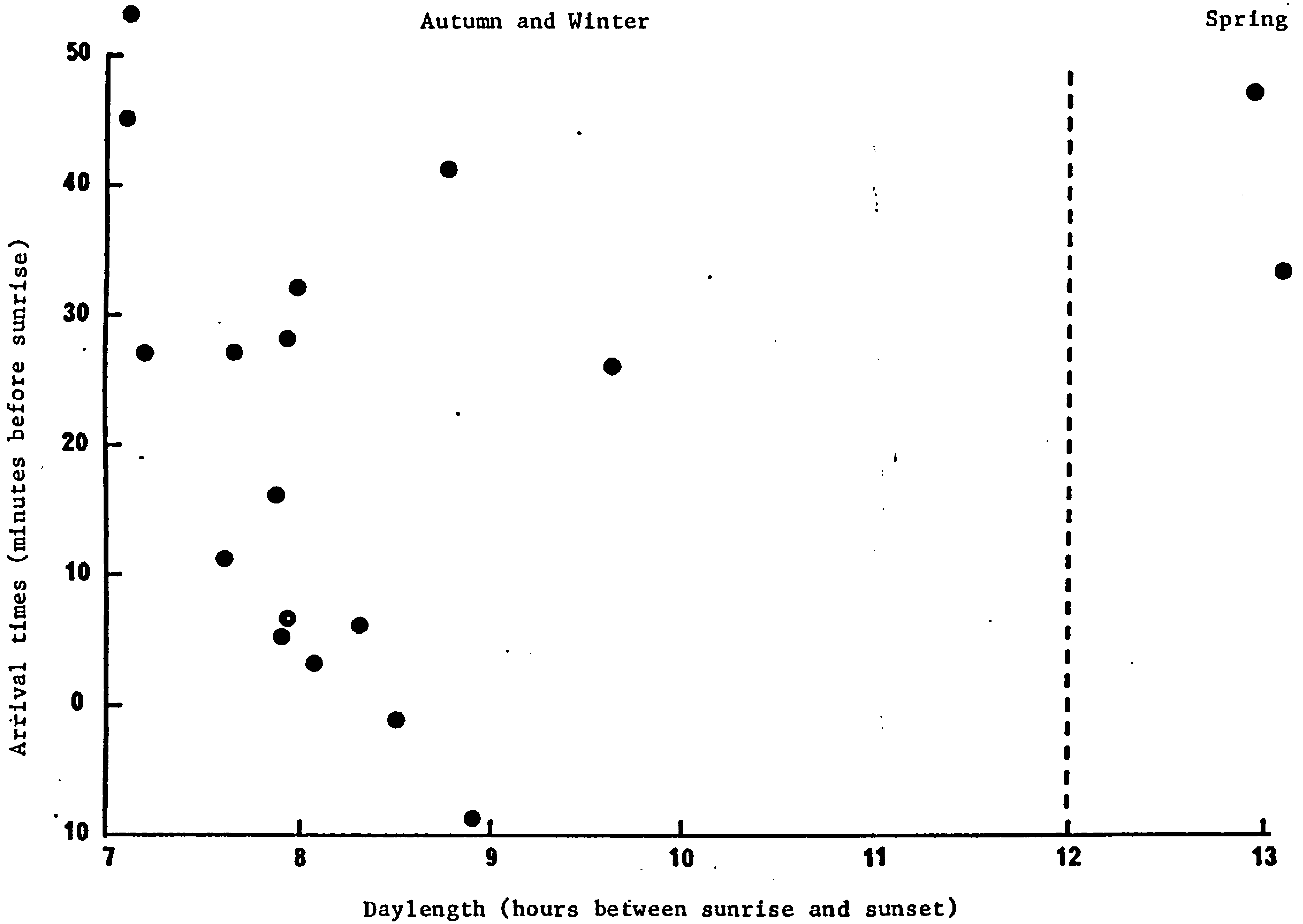


Fig. 4.2. Arrival times of Whooper Swans at the feeding grounds in relation to daylength (n=16, r=-0.387, p<0.1)

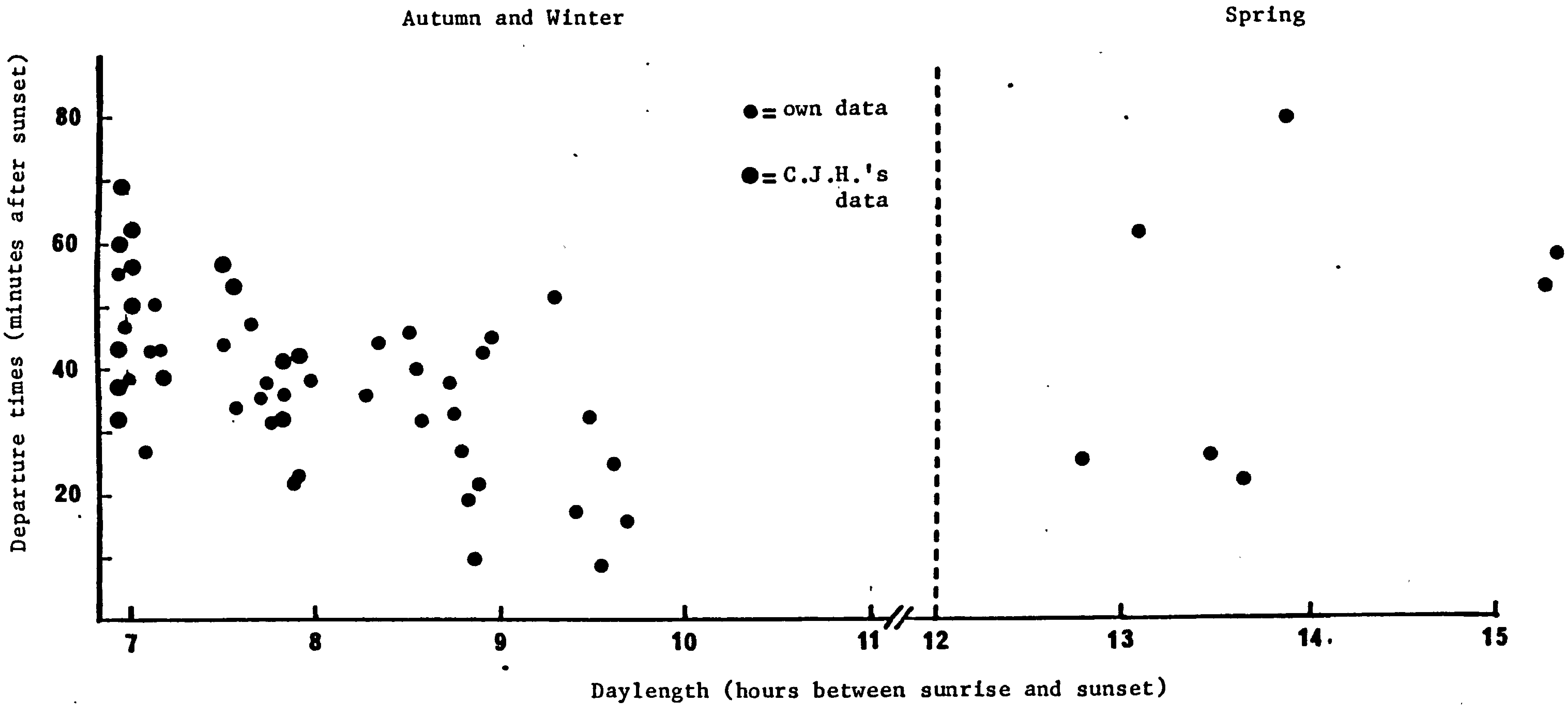


Fig. 4.3. Departure times of Whooper Swans to the roost in relation to daylength. (n=34, r=-0.50, p<0.01; n=49 (including C.J.H.'s data), r=-0.584, p<0.001).

light intensity for a series of evenings with different light conditions (fig. 4.4). The frequency of departures increased markedly with falling light intensities. Few departures occurred at light readings above three or four on the Weston meter (0.1-0.3 f.c.). The majority occurred at light readings of less than two (<0.1 f.c.). Broadly speaking illumination was directly correlated with the time of day, such that birds leaving the fields earlier did so at higher light intensities than those leaving later the same evening. Daily variation in weather conditions, however, can lead to marked variability in light intensity at a given time relative to sunrise or sunset. Consequently, birds leaving at the same time relative to sunset on different days could be leaving at very different light levels.

The results suggest that arrivals were spread over a wide range of light levels whereas departures tended to be concentrated in the lower section of the same range (fig. 4.4). Since duller days tend to be associated with short winter days rather than longer spring days, in mid-winter swans might be expected to leave earlier relative to sunset if they tend to depart at a constant light, i.e. simple seasonal effect. If light readings at the 50% departure times are compared with daylength, however, it is clear that departures at low light levels occurred in mid-winter and those at higher levels occurred towards spring (fig. 4.5). Thus swans left the fields later, relative to sunset, in mid-winter than in spring.

The data also suggested a tendency for birds to arrive at lower light levels in mid-winter than in late winter, i.e. they arrived earlier with respect to sunrise in mid-winter (fig. 4.6). The sample, however,

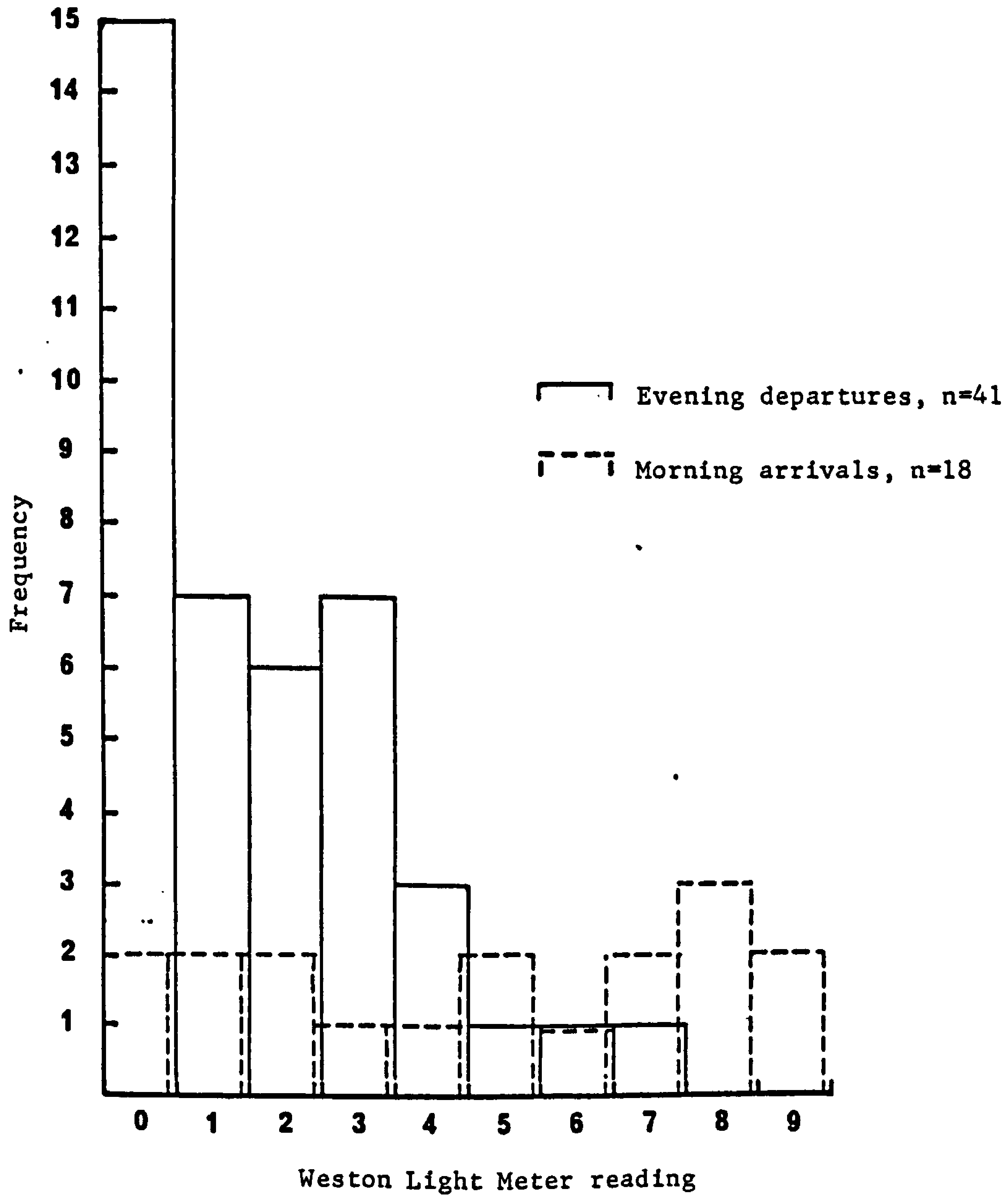


Fig. 4.4. Departures to the roost and Arrivals at the feeding grounds in relation to light intensity.

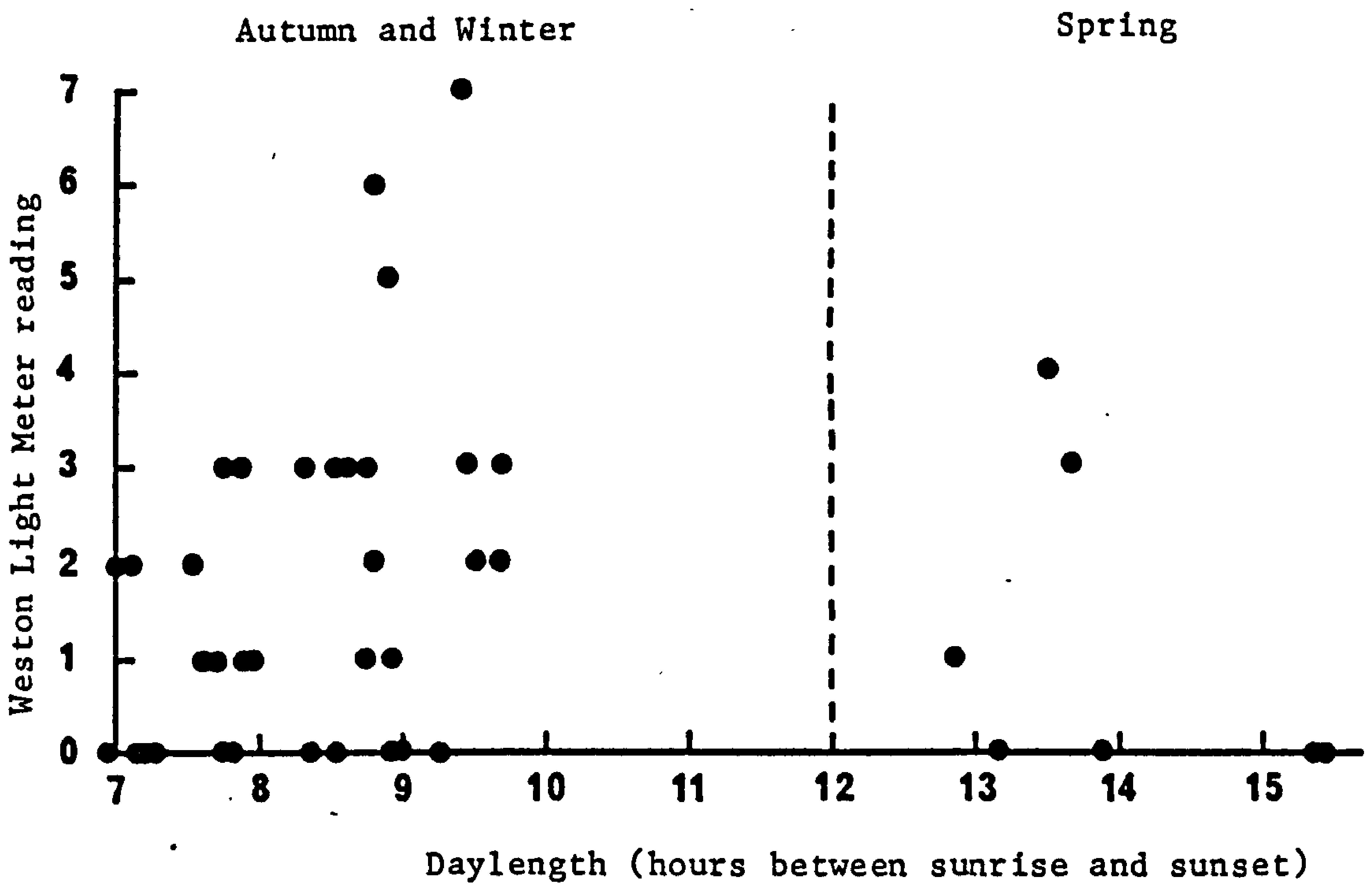


Fig. 4.5. Light intensity at Departure, in relation to daylength. (n=34, r=0·44, p=<0·02)

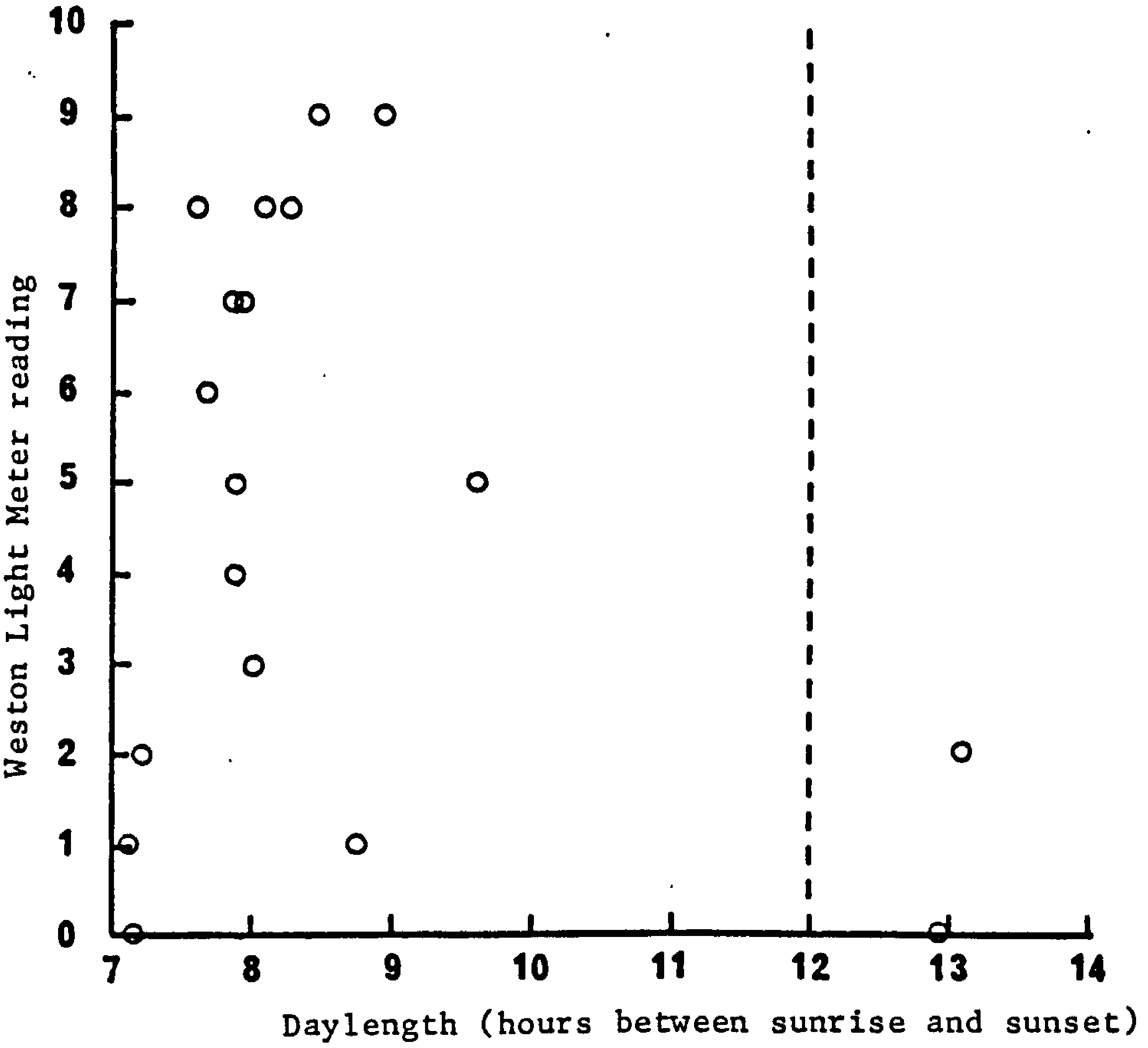


Fig. 4.6. Light intensity on Arrival, in relation to daylength. (n=16, r=0·39, p=>0·1)

was small (n=16) and variable, the regression was not significant, although it was in the expected direction.

4.2.3 The effect of cloud-cover

Departure times were found to be correlated with daylength and light intensity at departure. It was also expected that low temperatures would necessitate the birds feeding for longer to make up for greater energy losses. Neither the present study, however, nor that of Henty (1977) support this idea (see 4.3), although a more general seasonal pattern is apparent. There remains great variability in the data as yet to be explained. Although light intensity at a given time is correlated with daylength, greater variation between days can occur owing to the presence or absence of a cloud layer.

Brief descriptive notes were made of weather conditions during each observation period. These included 'percentage cloud cover', based on a visual estimate. This was rather a crude method, thus the data are presented in broad categories (fig. 4.7). For the period of the winter when daylength was less than 12 hr. there was a significant negative correlation between departure time and percentage cloud cover. Early departures were associated with heavy cloud cover ($r=0.368$, $p<0.05$, $n=31$), as expected from the association of departure times with light intensity.

Both daylength and hence light intensity at a given time under standard conditions are predictable cyclical variables. Cloud-cover, on the other hand, is unpredictable. If the swans responded only to daylength a smaller scatter would be expected in the data. Unpredictable variables such as cloud cover are contributing to this scatter.

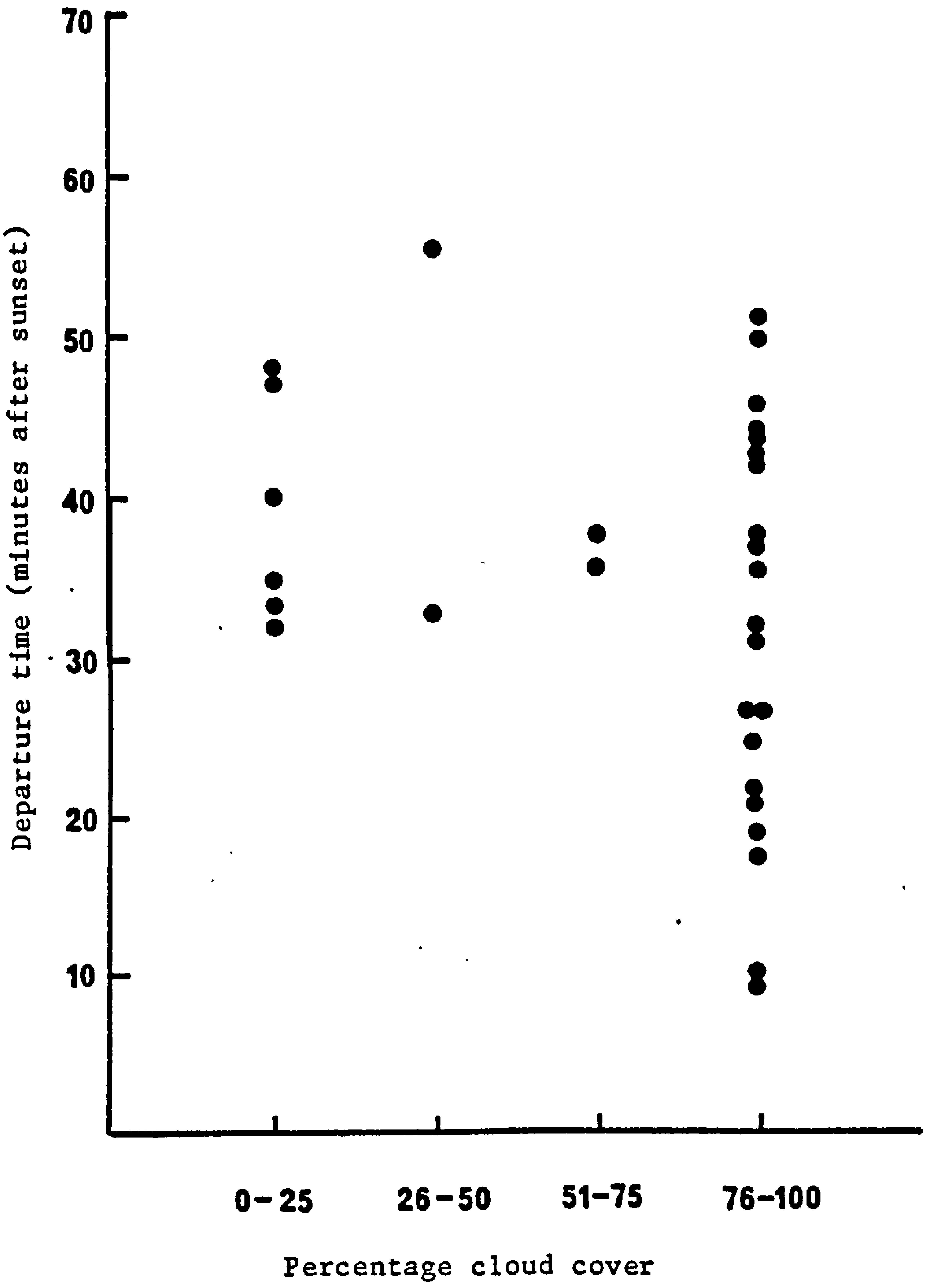


Fig. 4.7. Departure time in relation to cloud cover ($n=31$, $r=-0.369$, $p<0.05$)

4.2.4 The effect of temperature

If temperature acts upon birds such that low temperatures lead to increased heat loss and hence higher rates of energy consumption, and if the length of time spent feeding is directly related to energy requirements, then a simple prediction might be that on days following nights of low temperature birds should arrive earlier and/or depart later from the fields, thus extending their feeding time and therefore potentially increasing their energy intake.

Weather records were obtained from Parkhead weather station at the University of Stirling; temperatures (maxima and minima) were recorded at 0900 hr. No correlation was found between departure time and either maximum or minimum temperatures (fig. 4.8), but a positive correlation was found between arrival time and both maximum and minimum temperatures (fig.4.9) (Max. $r=0.605$, $p=<0.05$ all data; $r=0.647$, $p<0.01$ excluding data from longest days. Min. $r=0.639$, $p<0.01$ all data; and $r=0.642$, $p<0.01$). Contrary to expectations, based on simple energetic grounds, birds arrived later, not earlier, on mornings following cold nights.

Air temperature varies rapidly from day to day, but since at night the swans roosted on the river Forth, the night time water temperature might have been expected to be more important than air temperature, because heat exchange with water is more rapid than with air and because the swans have their legs and feet in direct contact with the water. Water temperatures were in fact more stable than air temperatures; they changed slowly over long periods (days), falling with decreasing day length. Freezing point was rarely reached, but temperatures were slow to rise again in the spring. The micro-climate at an aquatic roost site, partially

Fig. 4.8. The relationship between night-time temperatures (maxima and minima) and departure time the following day.

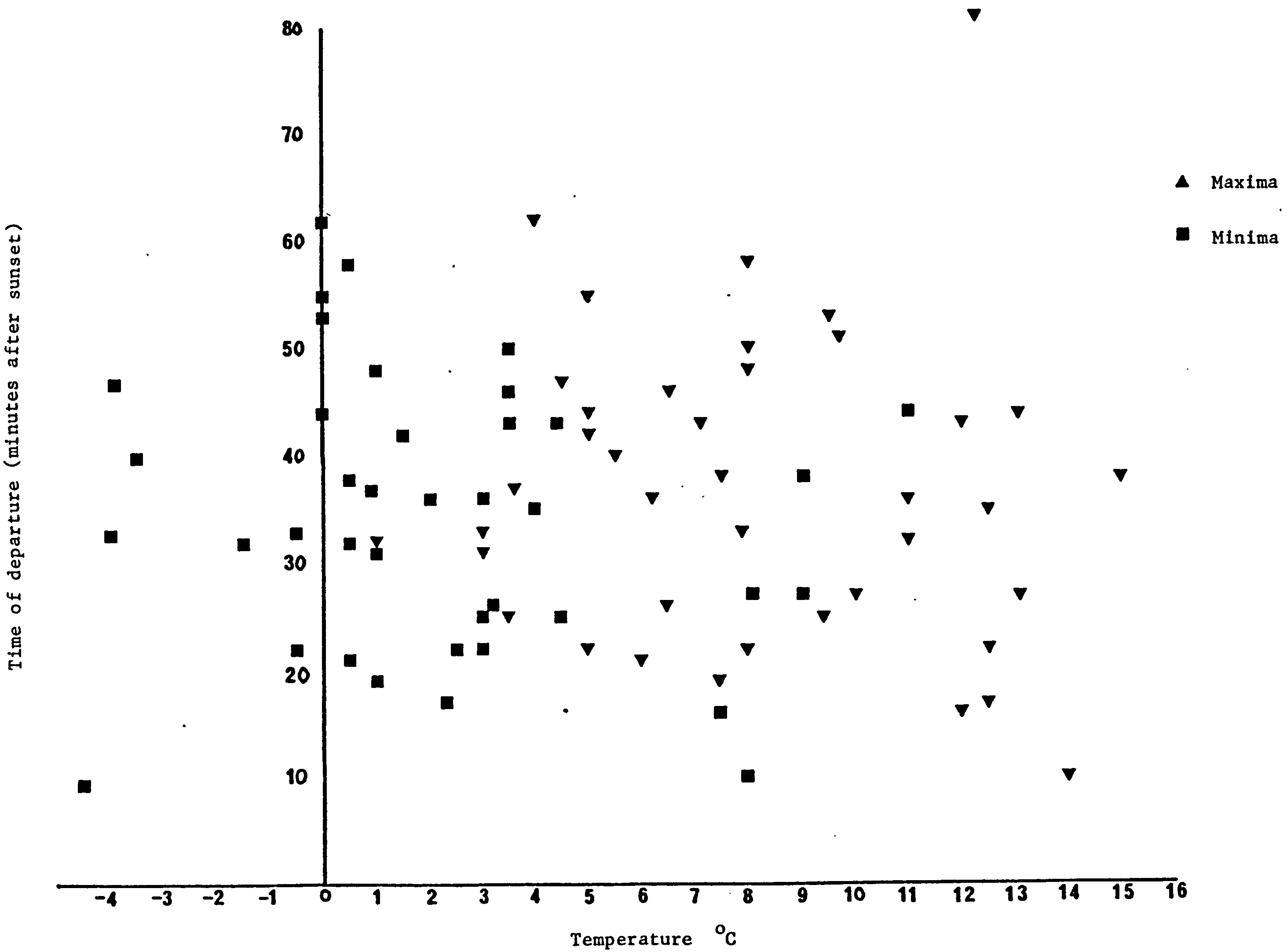
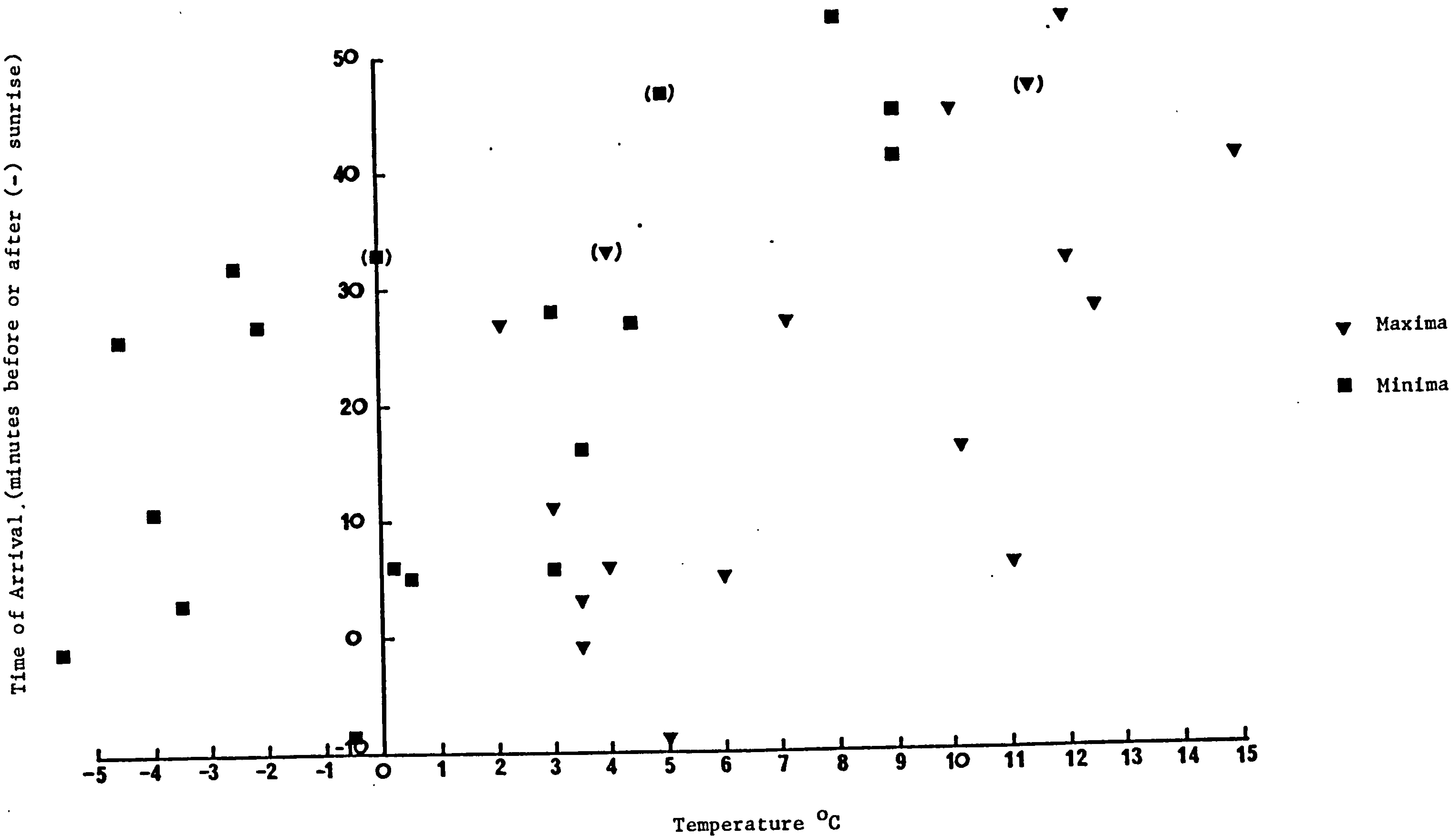

Time of departure (minutes after sunset)
80
70
60
50
40
30
20
10
-4
-3
-2
-1
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
Temperature °C
▲ Maxima
■ Minima

Fig. 4.9. The relationship between night-time temperatures (maxima and minima) and arrival time the following day. Points in brackets are for days of longer than 12 hr. and have been excluded from the analysis.
Maxima; $n=15$, $r=0.647$, $p<0.01$.
Minima; $n=16$, $r=0.642$, $p<0.01$.


Time of Arrival.(minutes before or after (-) sunrise)
50
40
30
20
10
0
-10
-5
-4
-3
-2
-1
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Temperature °C
▼ Maxima
■ Minima

sheltered by banks and vegetation is likely to be more favourable than surrounding areas and would reduce the impact of the local climate.

Data made available by the Forth River Purification Board, for Drip Bridge (just up-river from Stirling) showed that temperature ranges were small and mean temperatures varied little from year to year (table 4.1). Only in 1979, a year with a very prolonged cold winter, did the water temperature reach zero. It seems, therefore, that fluctuations in water temperature were even less likely to account for large day to day variations in arrival or departure times, than air temperatures.

The factors affecting roosting flights are discussed in section 4.4.

4.3 Time budgets

Time or Activity budgets have provided much of the basic material for this study, as they have for those of so many other species, ranging from other waterfowl; for example, Harlequin (Histrionicus histrionicus), (Bengston 1972); Pintail (Anas acuta), (Krapu 1974); Gadwall (Anas strepera), (Dwyer 1975); waders, e.g. Curlew Sandpipers (Calidris ferruginea), (Puttick 1979); passerines, e.g. Sunbirds (Nectariinidae), (Gill and Wolf 1978); Starlings (Tinbergen 1977); to mammals, e.g. Gibbons (Hylobates lar), (Carpenter 1940); Mink (Mustella vison), (Dunstone 1978); and insects, e.g. Honeybees (Apidae) and Harvester Ants (Myrmicinae), (Wilson 1971). Time budgets, especially those measured in energetic terms, are of interest not only in themselves, but also because they contrain "the forms and priorities of social behaviour" (Wilson 1975).

4.3.1 Methods

To examine the pattern of behaviour shown by field feeding Whooper

Table 4.1

Water Temperatures from Drip Bridge, Stirling

Year	Mean °C	Range
1975	10.8	4.8-18.5
1976	10.9	2.4-23.0
1978	11.0	6.0-19.0
1979	7.4	0.0-15.0

Data from Forth River Purification Board

Swans in Central Scotland, monthly activity budgets were compiled for the winter of 1977-78 and supplementary day budgets were compiled for later months.

Scans were made every 15 min. and the proportion of the flock engaged in each of four mutually exclusive behavioural categories was recorded. These behaviours were: feeding, preening, roosting and head-up. The category 'feeding' includes birds obviously pecking and those between pecks, i.e. with the neck below the horizontal line of the body and the head close to the ground (see 5.2 for full description). 'Preening' covers all comfort movements, including wing flapping and defaecation. 'Roosting', includes birds standing or sitting, with their eyes open or closed, the head usually rests on the back, tucked into the feathers. Sometimes, especially when the birds are facing into a strong wind, the neck is curved such that the head lies almost horizontally on the lower neck, pointing forwards. 'Head-up', includes birds both standing or sitting where the head and neck are raised above the level of the body. Head-up is in fact a continuum of positions which are not as readily separated as they are in Geese, e.g. into Head-up and Extreme Head-up (Lazarus and Inglis 1977). Subjectively, however, head-up was used by birds which were generally observant of their environment, while extreme head-up occurred when a specific stimulus had been perceived, and was directed towards that stimulus, e.g. disturbance or birds joining or leaving the flock. The major disturbing factors in this study were the same as those found by Airey (1955): people, dogs and shooting.

Since the behavioural categories recorded were mutually exclusive, the behaviour of flock members could easily be assigned during scans.

Several scans were averaged to obtain the mean proportion of the flock engaged in each behaviour and hence the proportion of time spent in each behaviour.

Time budgets were also examined in November 1978 and February 1979 in order to check that the same general pattern of activity was occurring, i.e. that the pattern was not unique to the winter of 1977-78. The same methods were used, but instead of data from several days being combined, results were compiled from a continuous dawn to dusk watch.

For comparison, some data were collected from birds using a flooded area in Central Scotland and from a bay in northern Japan. For the discussion of time budgets in a tidal area (section 4.4.2c), however, data have been combined into two hour blocks, not one hour as in all other sections, and these were based on scans made every 30 min. not every 15 min.

4.3.2. Results

4.3.2.1 Terrestrial

Of the four major activities observed while birds were on the foraging grounds, feeding took 61.6% to 75.3%, head-up 14.5% to 16.5%, roosting 4.1% to 18.8% and preening 1.7% to 4.4% of time (ranges are for winter months, calculated per hour of daylight; see table 4.2). The amount of time spent feeding each day increased during the winter from November to March. In November the cumulative time spent feeding by an average bird over an eight to nine hour day was 6.4 hr. and by March it was 9.8 hr. over a 12 to 13 hr. day (table 4.3).

Table 4.2

The time budget of Whooper Swans in the Stirling area, in winter 1977-78

	on land			on water	on land
Behaviour	November	December	January/ February	January/ February	March
Feeding (mean percentage per hour of daylight)	70.8	72.7	61.6	31.5	75.3
(mean percentage per hour)	26.5	27.3	28.2	14.4	40.8
Preening	2.1	1.7	3.7	8.7	4.4
	0.8	0.7	1.7	4.0	2.6
Roosting	12.7	9.0	18.8	29.6	4.1
	67.3	65.9	62.7	67.8	47.9
Head-up	14.5	16.5	16.1	30.0	16.1
	5.4	6.2	7.4	13.7	8.7
Number of Observations.	n= 75	79	120	106	144

Table 4.3

Cumulative time spent feeding (in hours) on land, in 1977-78

Time of day	Month			
	November	December	January/ February	March
06-0700				0.9
07-0800			0.3	1.7
08-0900	0.7	0.8	0.9	2.5
09-1000	1.4	1.7	1.6	3.2
10-1100	2.3	2.5	2.4	3.9
11-1200	3.1	3.1	2.7	4.6
12-1300	3.4	3.7	3.2	5.4
13-1400	4.0	4.3	3.8	6.2
14-1500	4.8	5.2	4.6	7.0
15-1600	5.6	6.1	5.5	7.7
16-1700	6.4	6.5	6.3	8.5
17-1800			6.8	9.1
18-1900				9.8

There was a marked feeding rhythm from November to February with high morning and afternoon peaks (figs. 4.10 to 4.12), by March this pattern had changed somewhat, with birds feeding at a higher rate for a longer time each day (fig. 4.13). The mid-day lull in feeding, marked in other months, had almost disappeared by this time. In December (see fig. 4.11) the mid-day feeding lull was not as marked as in November, January or February.

Roosting during the day was closely linked with feeding in that it peaked during the feeding lull and otherwise occurred at a very low level. Head-up and preening were linked in the same way but less markedly so. Head-up did occur throughout the day, but with a noticeable increase occurring usually at the beginning and towards the end of the day. Preening occupied least time and occurred throughout the day.

The same general pattern occurred in November 1978 and February 1979 (see figs. 4.14 and 4.15). In February the birds again spent longer on the fields than during November.

4.3.2.2. Freshwater

From 17th January until 8th February 1978, the study flock was on deeply flooded meadows by the river Forth, near Cambus. The area coincided with the direction in which birds had occasionally been seen flying to roost earlier in the winter. Between 8th and 15th February the retaining bank was breached and the meadows were drained. The flock then resumed its use of fields in other parts of the study area.

The swans on water steadily increased their feeding until about

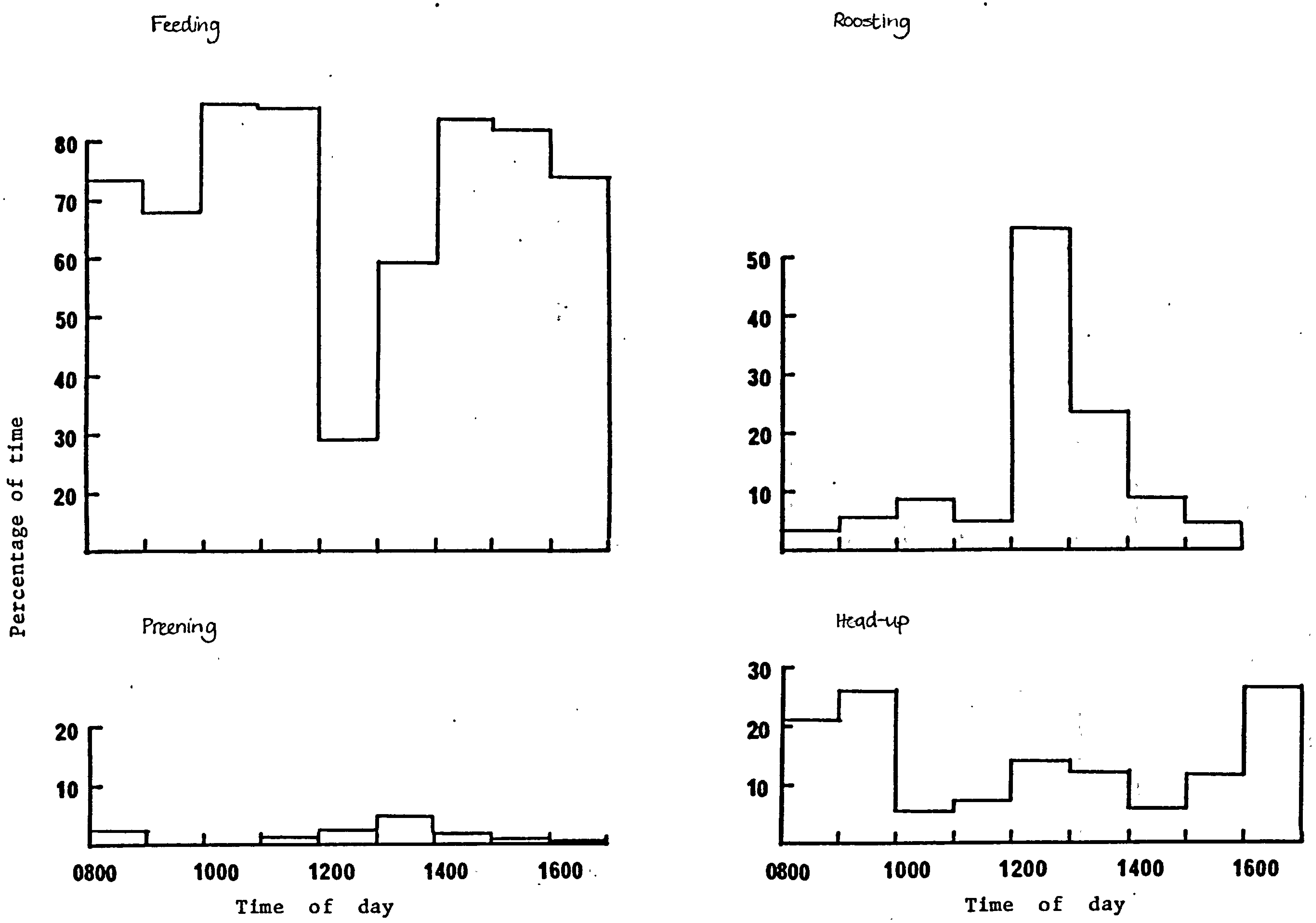


Fig. 4.10. Time budgets, November 1977

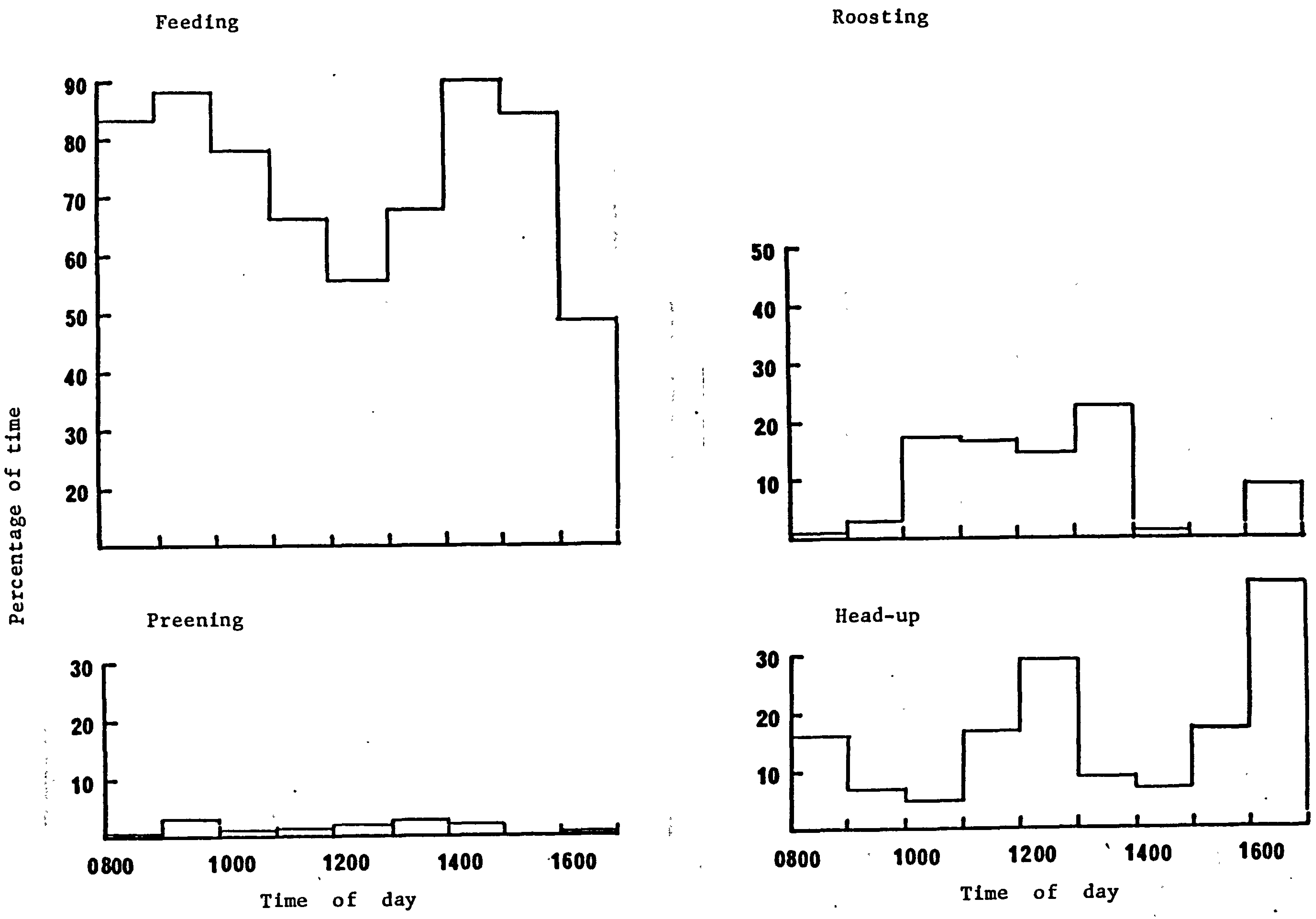


Fig. 4.11. Time budget; December 1977

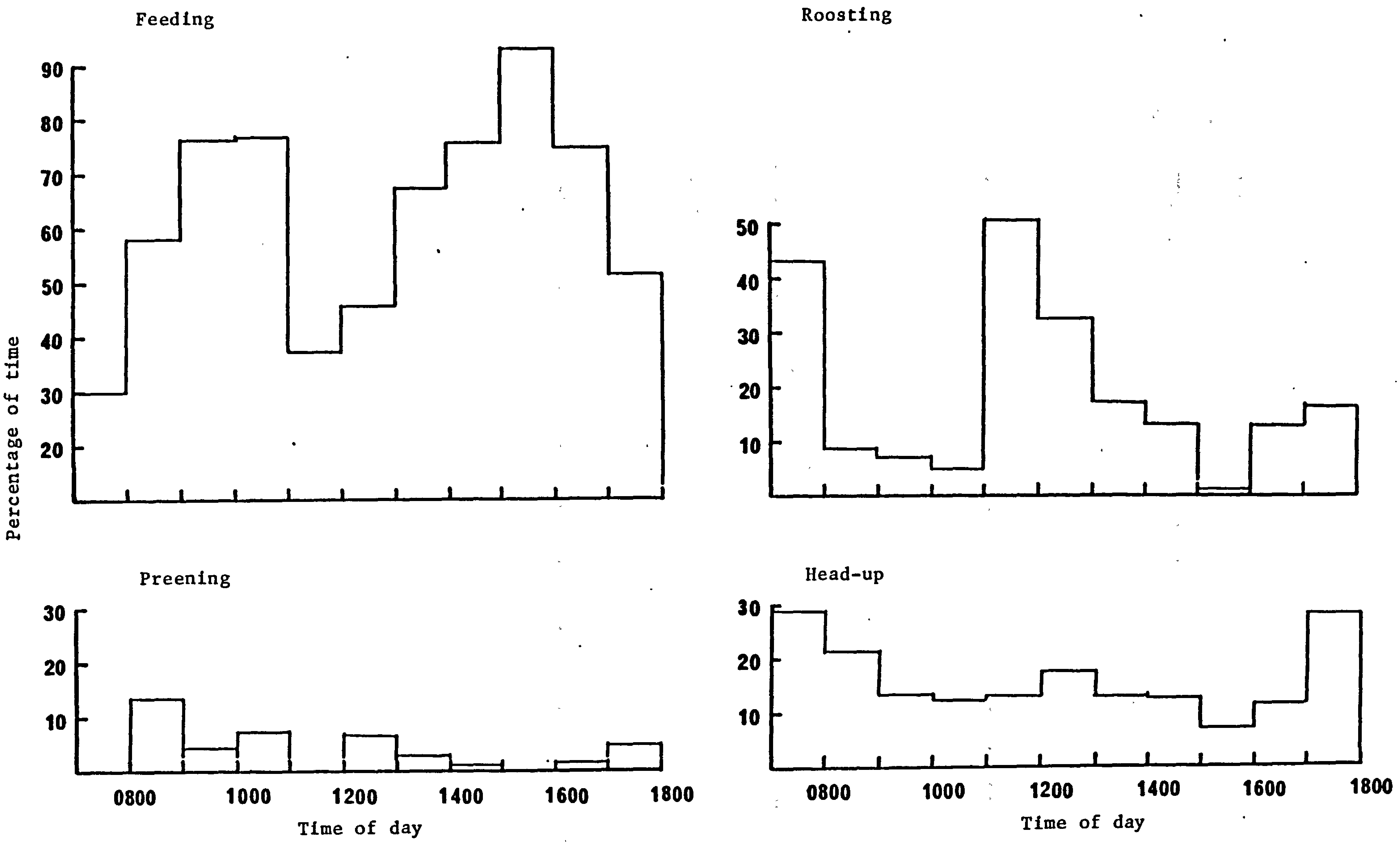


Fig. 4.12. Time budget; January & February 1978

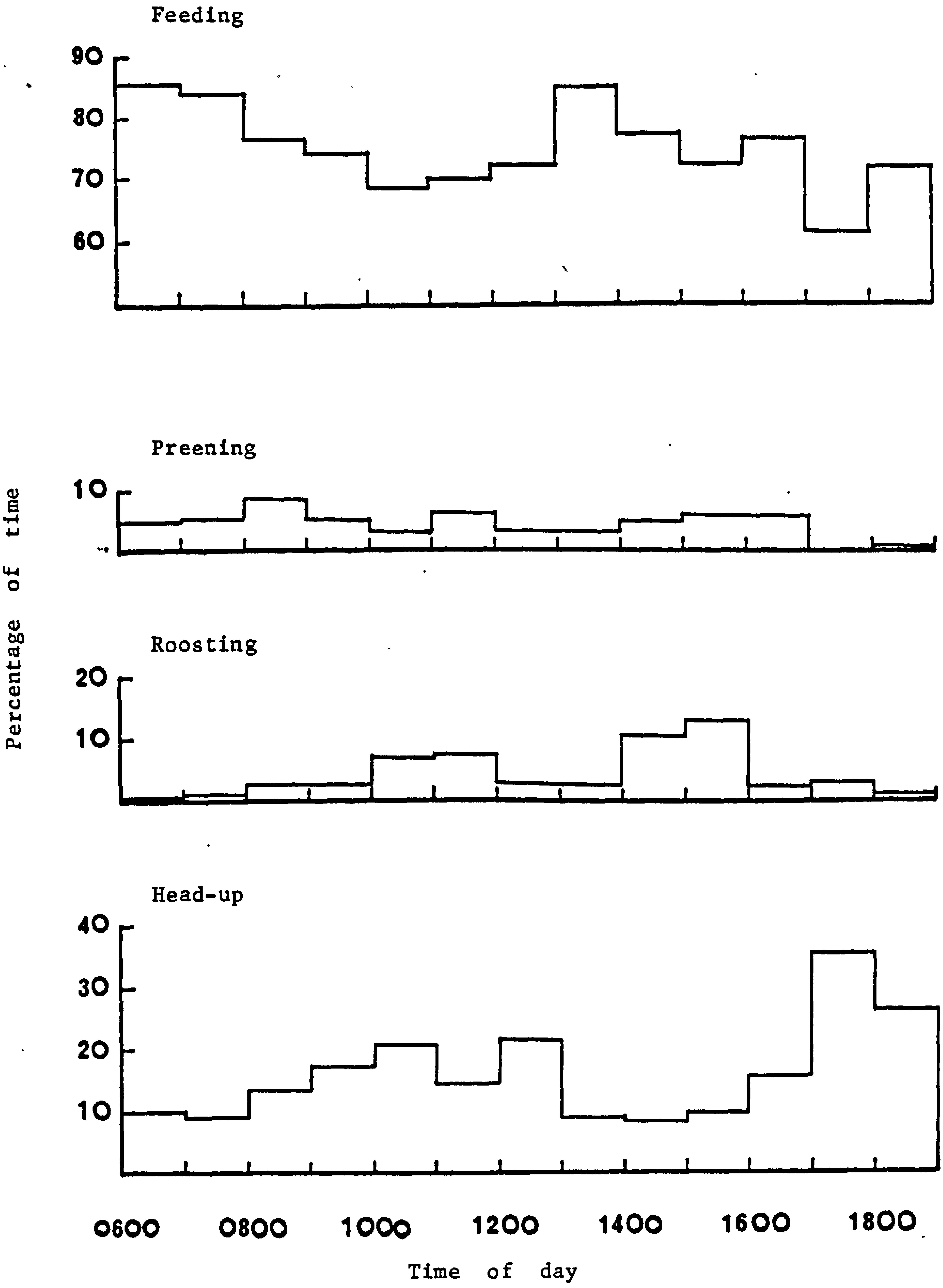


Fig. 4.13. Time budget; March 1978

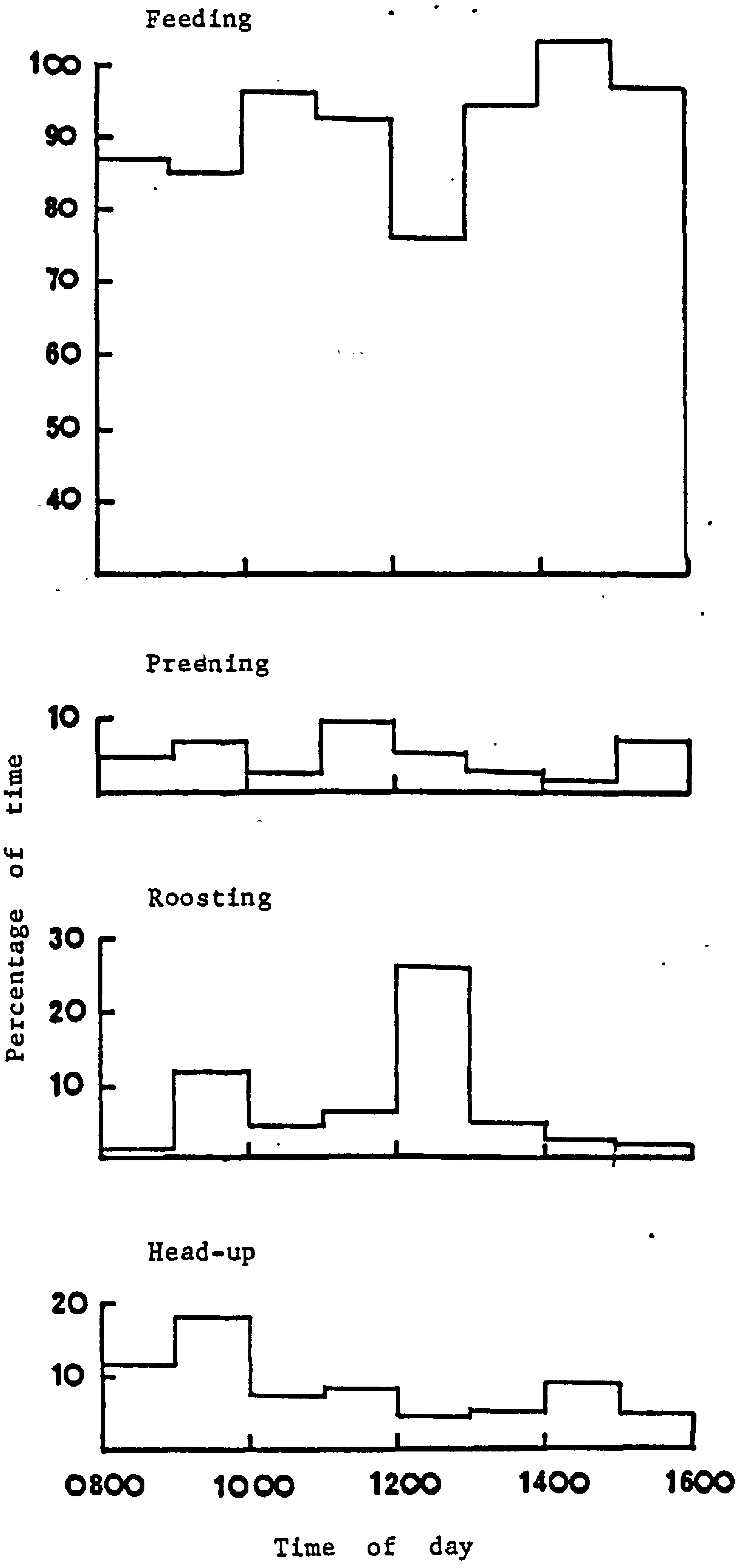


Fig. 4.14. Time budget, 22nd November 1978

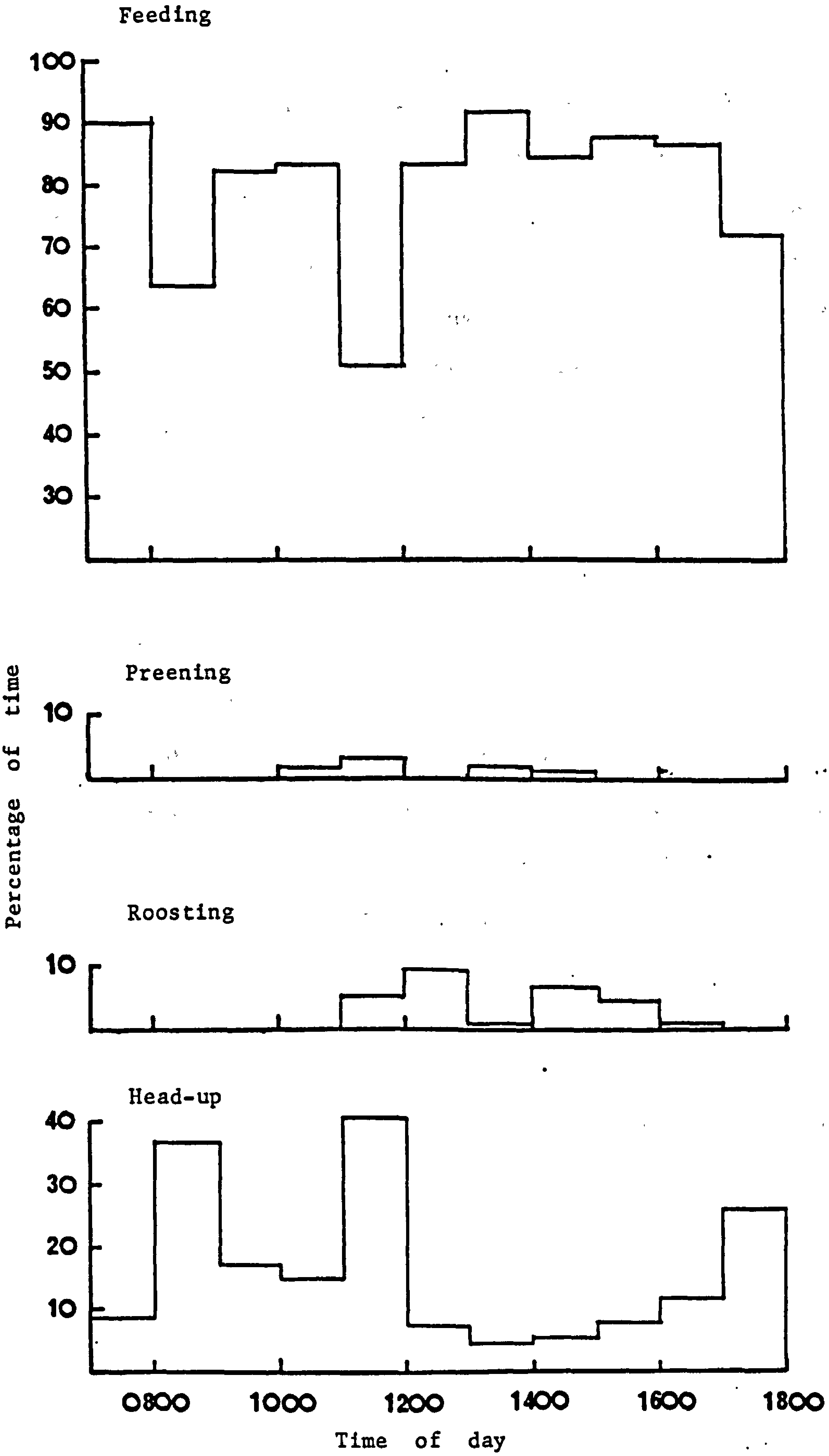


Fig. 4.15. Time budget, 16th February 1979

1400 hr., which was between seven and eight hours after sunrise. This activity pattern was very different from that noted for terrestrially feeding swans (section 4.3.2.1), but similar to behaviour observed amongst swans at the Fens (Owen and Cadbury 1975). At Cambus, roosting was the dominant activity in the morning, preening reached its maximum (18%) at between 1100 and 1200 hr., while head-up occurred throughout the daylight period at between 18 and 47% (see fig. 4.16).

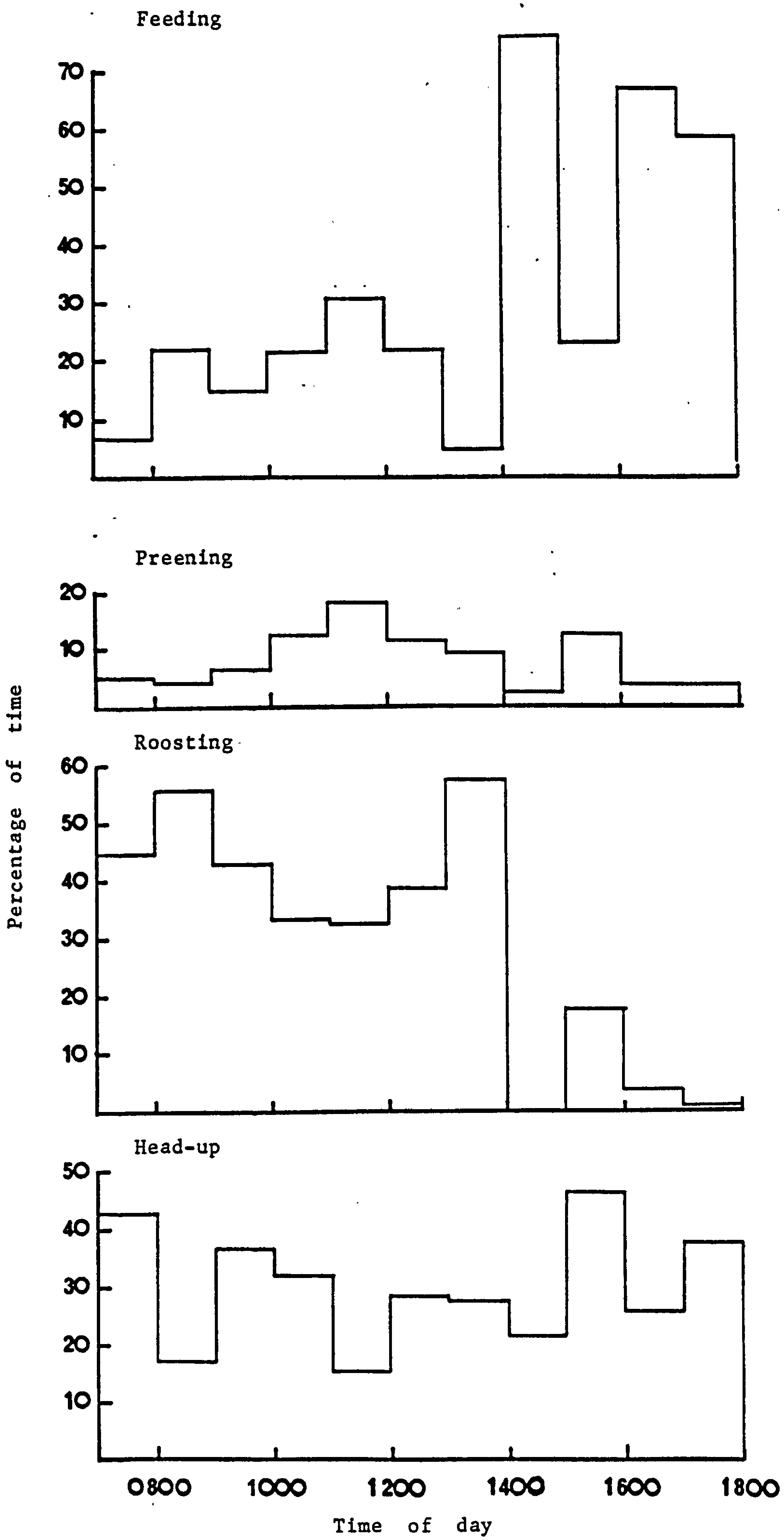
4.3.2.3 Tidal

Whooper Swans were studied between 2nd and 7th March 1980 at Mutsu bay, northern Honshu, Japan. They were found to use two distinct areas, either the northern shore-line of the bay or the shore-line and point area of a peninsular about one kilometre to the south (see fig. 4.17). The groups using these two areas were not isolated, nor were they completely separate from other groups in the Ominato area. On the other hand birds were consistent in using these two areas.

Data from all dates were combined into two hour blocks and expressed in relation to time or tide (e.g. figs. 4.18 and 4.19). Roosting was the dominant behaviour at the point and feeding the second most important, whereas head-up and preening were much commoner at the north-shore, feeding took up less than 20% of time and roosting rarely occurred. Birds from the north-shore moved to the point to roost.

At the point, feeding tended to peak during the middle of the day if the data are grouped according to time, or towards low tide if grouped according to tide. Conversely, roosting occurred more in the mornings and afternoons and possibly showed an increase over high tides. At the

Fig. 4.16. Time budget; January and February 1978 (on water).


Feeding
70
60
50
40
30
20
10
Preening
20
10
Roosting
60
50
40
30
20
10
Head-up
50
40
30
20
10
Percentage of time
0800
1000
1200
1400
1600
1800
Time of day

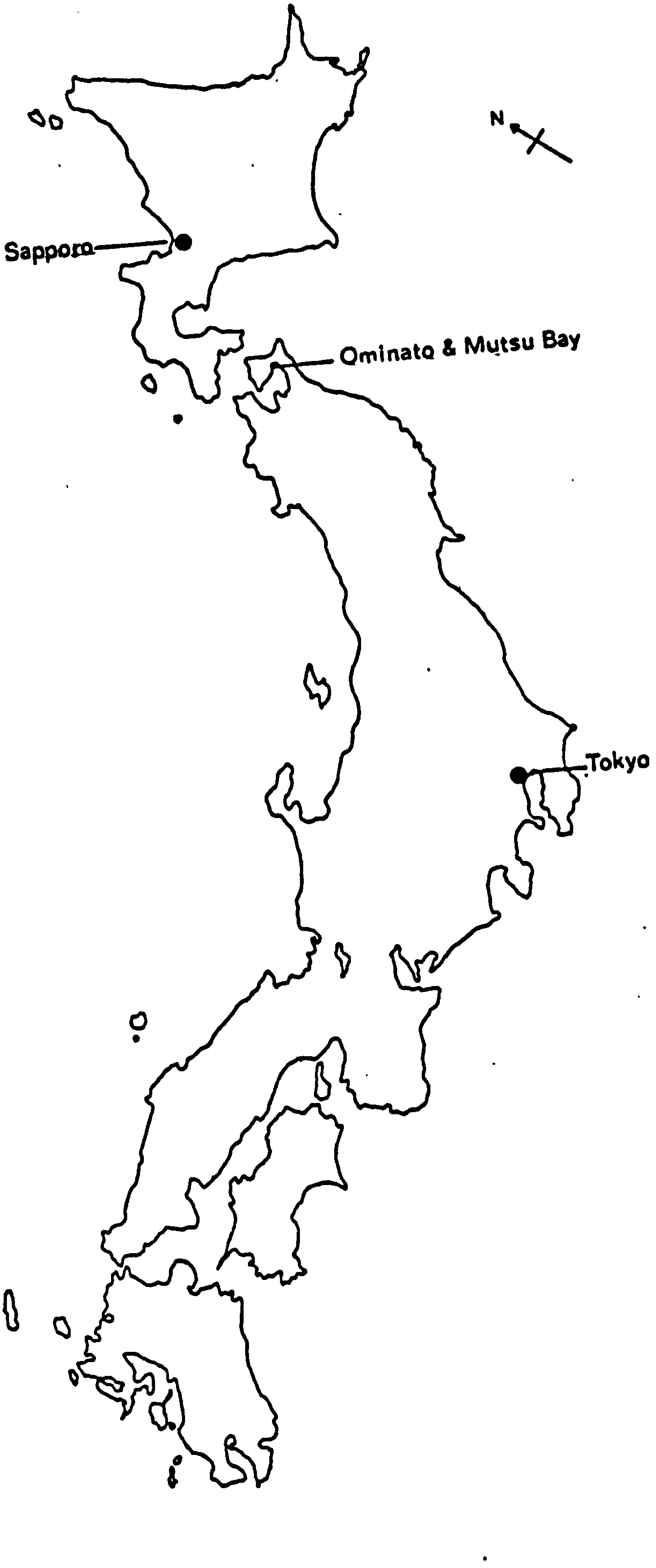
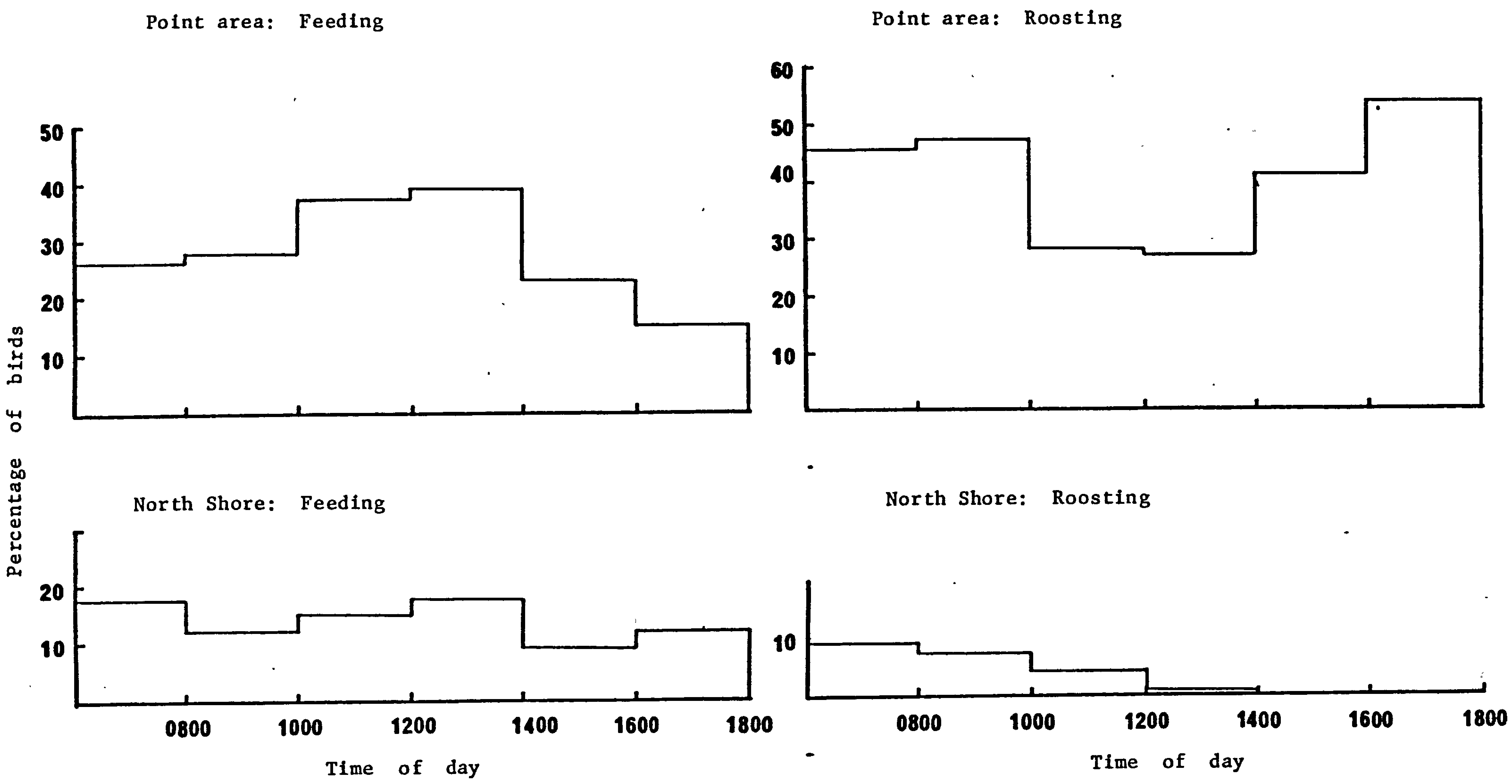


Fig. 4.17. Map of Japan


Point area: Feeding

Point area: Roosting

North Shore: Feeding

North Shore: Roosting

Fig. 4.18. Time budget of Whooper Swans at Mutsu Bay, Japan, 1980 in relation to the time of day.

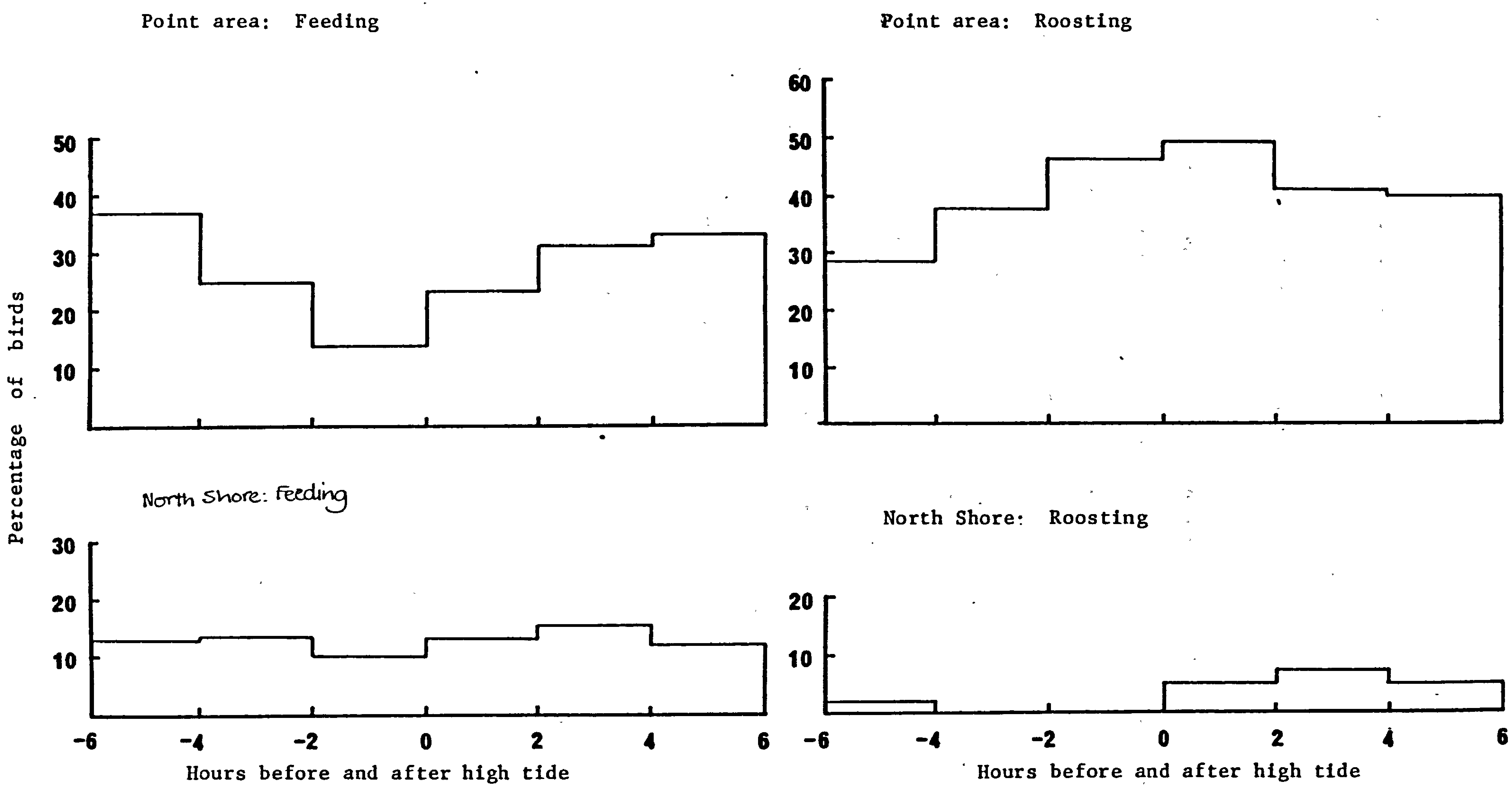


Fig. 4.19. Time budget of Whooper Swans at Mutsu Bay, Japan, 1980 in relation to the tide.

north-shore feeding occurred throughout the day at the same level, regardless of the state of the tide. Roosting, however, decreased from dawn onwards, and increased after high tide.

During the observation period the numbers using the point increased ($r=0.492$, $p=0.001$) and the numbers using the north-shore declined ($r=0.287$, $p=0.02$) and there was a significant negative correlation between numbers at these two localities ($r=-0.451$, $p=0.001$). The level of roosting at the point increased as numbers increased ($r=0.342$, $p=0.002$) and decreased as numbers increased at the north shore ($r=-0.412$, $p=0.001$). Feeding, conversely, decreased as numbers increased at the point ($r=-0.379$, $p=0.001$) and increased as numbers increased at the north shore ($r=0.392$, $p=0.001$). The data thus supported the subjective impression that birds moved to the point to roost. Since feeding and roosting are mutually exclusive these complementary results were to be expected.

There is not enought data available over a large enough change in tidal state to make conclusive statements about the feeding rhythm, however, certain results are apparent. On a rising tide, feeding at the point and preening at the north-shore decreased with time ($r=-0.494$, $p=0.009$ and $r=-0.551$, $p=0.005$ respectively) while head-up at the north-shore increased with time ($r=0.478$, $p=0.011$). On a falling tide head-up, roosting and preening, at the north shore, were correlated with time and tide (see table 4.4). The result of using Kendalls partial rank correlation was to raise the r values of both variables (see table 4.5) suggesting that Time and Tide were counter-active in their effect on behaviour.

Table 4.4

The correlation of behaviour with time or state of tide

Behaviour	Correlated Variable	r	significance
Head-up	Time	0.532	0.001
	Tide	-0.251	0.029
Roosting	Time	-0.412	0.001
	Tide	0.397	0.001
Preening	Time	-0.588	0.001
	Tide	0.340	0.004

Table 4.5

Partial correlation of behaviour with time and state of tide

Behaviour	Correlated Variable	Variable held Constant	r
Head-up	Tide	Time	-0.296
	Time	Tide	0.557
Roosting	Tide	Time	0.432
	Time	Tide	-0.453
Preening	Tide	Time	0.414
	Time	Tide	-0.622

It is clearly obvious that the feeding pattern in this tidal environment is not at all like the patterns shows by swans on non-tidal waters (see Cadbury 1975; this study 4.3.2.2) or on land (this study 4.3.2.1). It shows neither an increase in feeding during the day to an afternoon plateau, nor a clear-cut pattern of morning and afternoon peaks and a mid-day lull, in fact feeding at the point tended to peak during the middle of the day.

4.4 Discussion

Feeding on agricultural land by Whooper Swans has developed over the last 50 years. In association with this change from aquatic habitats their daily pattern of activity now involves commuting between a night-time roost site and a day-time foraging site. They have to obtain enough energy for basal metabolism, thermoregulation, foraging, daily flights, fat deposition and, in the case of cygnets, for growth. Certain energy requirements are affected by the season, for example, in mid-winter low temperatures and wind serve to increase heat loss. Consequently, energy expenditure must be increased if a constant body temperature is to be maintained. Extreme weather conditions, prolonged snow, frost or flooding may force swans to move to a different area, thus increasing flight costs.

The factors affecting the daily movements were examined in order to test two hypotheses. The first suggested that short days and low temp eratures would lead to higher energy demands and hence more time spent feeding, consequently the swans would arrive earlier at the foraging grounds and/or depart later for the roost. The second suggested that, owing to the dangers associated with being on land during darkness, the swans would always arrive after it was light and leave before it was dark, the result being that time spent feeding would be limited simply by day-length. Whooper Swans are highly visual animals and do not usually feed or fly after dark. The most pertinent stimulus to them, therefore, is probably light intensity.

Before discussing the results, it is important to note that the circumstances of observation at arrival and departure are different. Measurements of light intensity at departure times were made at the site where the birds would perceive and respond to such a stimulus, however, measurements at arrival times differed because they were made when the birds reached the foraging area. Assuming the same mechanism to be at work, the swans responded to a stimulus perceived whilst still at the roost, which caused them to leave for the foraging area, thus there was a delay, equal to the flight time, between departure from the roost and the measurement of arrival at the feeding grounds. Even though this flight time was short (about three to five minutes) and varied from day to day and from sub-group to sub-group, it often occurred when light levels were changing most rapidly. Since observation of the birds on the foraging grounds was the prime objective, light intensity was measured at arrival times at these areas, rather than at departure times from the roost site.

Arrivals were evenly distributed with respect to sunrise and suggested no tendency for movements to occur at a fixed time; departures on the other hand suggested a tendency for movements to occur at a fixed time in relation to sunset. The latter agrees with hypothesis two and suggests a seasonal change in roost flight times whereas the former does not. Departures also occurred later on short days than on longer days and arrivals tended to occur earlier on short days. Both, again supporting a seasonal pattern in roosting flights. Early departures were associated with heavy cloud cover, which tends to reduce light intensity.

Seasonal variation in roosting behaviour has been reported from many studies, Hinde (1952) for example, found a marked seasonal change in roosting in relation to sunset in the Great Tit (*Parus major*), Blue Tit (*Parus caeruleus*) and Great Spotted Woodpecker (*Dendrocopus major*). Some waterfowl have also been shown to exhibit this relationship. Hein (1961), for example, found both light intensity and season to be important for the Wood Duck; morning flight began when illumination reached one foot candle in August, whereas in November it began at illumination levels of less than a quarter of a foot candle. Evening flights were similarly affected; birds arrived at the roost between 70 and two foot candles in August and between four and one quarter foot candles by late October. Martin (1957), found that flight times of the Wood Duck were linked with sunset and sunrise, that is they were seasonally variable with respect to clock time. Morning flights began about half-an-hour before sunrise and evening arrivals were concentrated mostly between 15 and 30 min. after sunset. Siegfried et al (1977) found marked seasonal variation in arrival time at the roost by the African Black Duck (*Anas sparsa*) and Davis (1956) found that the roosting time of Starlings (*Sturnus vulgaris*) was half-an-hour before sunset in summer. He found no correlation between the 50% arrival time and light intensity, temperature, wind or cloud cover, although both observers involved were subjectively convinced that birds roosted earlier on dark days. Brodie (1980) found that roosting in Starlings became later relative to sunset as mid-winter approached and that roosting occurred earlier on days of poor visibility; i.e. results very similar to those of the present study.

It seems likely that for temperate zone species, experiencing a shifting photoperiod, a seasonal response would be the most basic. Seasonal photo-periods have long been shown to be important in controlling cyclical changes such as song, gonadal growth and hence breeding, migration, hibernation and even thermal tolerance (e.g. Hoar 1956; Roberts 1964).

Departures occurred later on short days and more often at lower light intensities; this is in fact two ways of stating that on the short days of mid-winter swans stayed longer on the fields relative to sunset than in spring. This clearly contradicts the second hypothesis and agrees with the first. It suggests that in mid-winter Whooper Swans are under some energetic stress and need to feed for longer. The fact that departure times were found to be earlier on nights with heavy cloud (section 4.2.3) (see Davis 1956; Brodie 1980) supports the earlier suggestion that light intensity was the major stimulus affecting diurnal movements.

It would be reasonable to delay departure because extra feeding time was required, yet on many evenings the last few minutes, often 10 or more, were not spent feeding. Waves of head-up tended to spread through the flock, while wing-flapping (a flight intention movement, possibly also functioning to build up temperature in the wing muscles for more efficient flight) became more frequent. Some birds often began head-bobbing and calling, and frequently, small groups of them walked about through the flock. They sometimes fed again briefly, but eventually all the members of the flock would stop preening and raise their heads; finally departure occurred. Where sub-groups departed separately it was usually the birds which had recently been head-bobbing that left first. During the time that this occurred visibility often became poor. It is possible, contrary to the assumption of hypothesis one, that for much of the winter the swans are not under extreme energetic stress and can afford to spend time on the foraging grounds not feeding.

Temperature, a factor which was expected to play a major role in determining food requirements, foraging time and hence arrivals and departures, did not affect departures and affected arrivals in a way contrary to expectations. Low temperatures and frosts are likely to be correlated with clear skies, higher light levels and hence earlier departures from the roost, but instead arrivals at the feeding grounds occurred later at low temperatures. Temperature has been shown to be a fundamental influence in the timing and magnitude of morning flight in some geese (Raveling et al 1972; Ogilvie 1978). Their results were consistent with those of the present study, whereas Owen (1980) considered morning flights by geese to be related to light intensity and the conditions of the feeding grounds. Low temperatures appear to over-ride a commuting system linked primarily to light intensity. It could be that on cold mornings, especially if frosts are involved, the energetic cost of warming up food for processing is too great to be worth the cost of flying to the fields. Wood Pigeons, for example, fed first on tall Brassica plants which were at a higher temperature than Trifolium, then moved to Trifolium later as the temperature rose (Kenward and Sibly 1977). For species which have no readily available alternative food supplies inactivity might be the most adaptive response to severe cold, functioning to conserve energy (e.g. Markgren 1963; Raveling et al 1972). In less severe conditions activity might be postponed until air temperatures rise.

Since lower temperatures are commoner in mid-winter, while the days are still very short, any effect of temperature should magnify the effect of daylength. This clearly did not occur (see figs. 4.3 and 4.8). It seems that any tendency for earlier arrival on short days was counterbalanced by later arrivals on colder days, many of which would also be short days. Departure times seemed to be independent of temperature. Neither hypothesis adequately explains such results.

Light intensity is clearly an important proximal stimulus for commuting flights, but its effect varies with season and daylength. The obvious seasonal change is in the available feeding time. Low temperatures act contrary to this change, since they tend to cause later arrivals on short days where available feeding time is already limited. It appears that any increased cost of thermo-regulation is outweighed by some effect on feeding effectiveness. Consequently the effect of temperature is more complex than was envisaged in hypothesis one.

Wind might also affect the daily movements since coupled with low temperatures it could increase energy lossess. The micro-climatic advantages of a riverine roost have been noted earlier (section 4.2.4), but birds could still be affected by winds parallel to the river. Wind velocity has been shown by many studies to affect heat loss directly and hence energy uptake and requirements (e.g. Gesseman 1972). Behavioural adaptations such as roosting in flocks are, however, known to aid thermo-regulation by decreasing wind speed (e.g. in waders, Whitlock 1979) and presumably birds could easily shelter from the wind by moving round a bend in the river. It seems unlikely therefore that wind speed could help to explain the daily variation in arrival or departure times.

Henty (1977) found "no noticeable effect of frost during the preceding 24 hr. although continued hard weather disrupted the whole commuting system". If the swans were already under energetic stress, cold weather would be expected to exacerbate this. The effects of low night-time temperatures, the critical period at high latitudes for many species (Kendeigh 1961), can be ameliorated behaviourally in several ways. Some species seek dense vegetation (Frazier and Nolan 1959; Swann 1975) or roost communally, e.g. Wrens (Troglodytes Troglodytes)(Armstrong 1955), Treecreepers (Certhia familiaris) (Lohrl 1955), or as in the case of Dippers (Cinclus cinclus) (Shaw 1979), in groups and in shelter under bridges.

In spite of the apparent lack of effect of temperature or wind-speed on the Whooper Swan, there was a marked effect on the commuting system caused by prolonged cold periods. Birds left the area entirely if snow cover was complete, during long periods of low temperatures, frosts or after severe flooding. For example, all birds left the study area in the latter half of January 1979 during a prolonged cold spell, while during the same period of 1978 all the birds moved to a flooded area close to the river Forth. Rather than being energetically constrained Whooper Swans may just be prone to catastrophic changes in food availability such as it being frozen or covered by frost or snow.

Whooper Swans tended to arrive earlier at feeding fields and depart later from them on short mid-winter days than on the longer days of autumn or late winter and spring. However, on the very long days of spring (longer than 12 hr.) they also arrived very early and left very late, even though daylength has increased in spring (see figs. 4.2 and 4.3). Hence the feeding day was almost doubled in spring. In conjunction with the time budget data available from the spring (fig. 4.13), this result suggests that the time of greatest nutritional requirement was prior to the spring migration, not during the short days of mid-winter as had been expected.

The body weight of geese changes markedly from season to season (see Owen 1980). It increases initially, when birds arrive in the autumn and are able to feed on high energy foods, then declines during the middle of winter when they have only short feeding days and low-energy, grass food. Finally there is a steady pre-migratory weight increase as both daylength and food quality increase in late-winter and early spring. Exactly these factors apply to Whooper Swans, although weight data to back them up do not exist. Large animals are well able to cope with short term weight loss and their long term energy budgets may involve such regular weight loss as an adaptive measure.

It is likely that staying longer on the feeding grounds does enable Whooper Swans to take in extra food, but the factors affecting departure times operate differently at different times of year. In mid-winter they are probably trying to maintain weight whereas in spring they are trying to increase it.

Although completely unstudied in the Whooper Swan, it is likely that fat deposition for the spring migration and breeding occurs in the last month or two of their stay in Britain. Minton (1974), found that many species of wader reached a post moult weight peak in December, they then lost weight until March, before increasing in weight in April and May. The highest mean weights were recorded immediately prior to departure in the spring. A study by Evans and Kear (1978) of the weights and measurements of Bewick's Swans, unfortunately only covered the winter period up to 1st February, thus probably missing the most critical period. Although the data were collected from provisioned birds, all classes showed weight increases in early winter, peaking in the second half of December (as in waders) and there was some indication ofweight loss by the younger age classes during January, followed by a recovery. Minton (1974) suggested that fat deposition by waders in the first half of the winter, was an insurance against potentially difficult feeding conditions in the latter half; the same may be true of swans.

If we assume that Whooper Swans experience similar weight changes during the winter to Bewick's Swans, and that both species probably deposit pre-migratory fat after February, as do migratory waders, then a change in feeding behaviour might be expected at that time. The most likely change being towards longer periods spent on the feeding grounds, with earlier arrivals and later departures. The time budget data from March (fig. 4.13) suggest that this is in fact what happens, the feeding day is greatly extended and the level of feeding is increased.

It appears that Whooper Swans do compensate a little for short winter days by departing at lower light levels, but that energetic requirements are probably much higher in spring than in mid-winter. Neither hypothesis accurately predicted the field observations. The most reasonable explanation is that Whooper Swans are responsive primarily to light intensity and in mid-winter may have to extend their feeding time a little, but in spring they must increase feeding time enormously. The fact that they are not nocturnal suggests that, while for energetic reasons they might tend to increase the time spent on land after dark, the risk of mortality from collision or predation acts in the opposite direction. Collision is probably, by far, the greater risk; 40% of swan mortality in the Fens was attributed to this factor alone (Owen and Cadbury 1975) and 44% in the Mute Swan (Ogilvie 1967). The encumbrance of the added weight of a full gut and perhaps mud adhering to the feet makes flights to the roost more dangerous than flights from roosts.

The time budgets of Whooper Swans were found to be very different in different habitats. On land the pattern was of high morning and afternoon feeding activity with a mid-day lull for at least the first half of the winter. On fresh-water, feeding increased during the day reaching a plateau in the early afternoon. Data from the tidal area were too few to be conclusive although they indicated that feeding tends to occur over low tide and roosting over high tide. At the moment there is no clear ecological explanation for these differences in activity patterns.

CHAPTER FIVE: FEEDING AND VIGILANCE IN WINTER

5.1 Introduction

The feeding ecology and behaviour of the Whooper Swan have only been studied in detail on the Finnish breeding grounds where they feed aquatically (Haapanen et al 1977). What little is known of those topics in winter is drawn together by Scott et al (1972) and Cramp and Simmons (1977).

In this chapter, therefore, I aim to examine feeding ecology and behaviour from the broadest aspects, such as feeding methods and foods eaten, to the most specific, such as the effect flock size has on feeding rate. The two behaviours occupying most time during winter are feeding and head-up and because the rates of each are completely interdependent, both are discussed here.

5.2 Feeding Methods

Cramp and Simmons (1977) state that "when preferred aquatic plants are lacking (Whooper Swans) readily forage on stubble and arable land". This is certainly a mis-representation, for some areas of Scotland at least, since they can be found feeding from stubble fields only a few miles from freshwater habitats, which were thought to be suitable for them because either they were used by other waterfowl or they had been used by Whooper Swans at different times. The use of agricultural land, although a recent phenomenon (see 2.5), seems not to be just a second choice, as implied by Cramp and Simmons (1977), but even a preferred habitat. There is little information available concerning the species' methods of feeding in different habitats (but see Owen and Kear 1972).

In view of the recent development of the use of farmland as feeding grounds it is of interest to compare feeding methods from aquatic habitats with those on land.

The habitats now available to, and frequently used by, Whooper Swans are:

1) Open water; salt and fresh.
2) Running water
3) Estuaries
4) Agricultural land, either
    (i) stubble fields
    (ii) pasture
    (iii) winter wheat
    (iv) 'root crops', potatoes, turnips, etc.

As one would expect, feeding methods are dependent on the food and habitat type being used. In aquatic habitats three main feeding methods can be seen,(unless otherwise stated, all details are from personal observation).

Dabbling

In water of all depths feeding can be from the surface, for floating vegetation, or just below the surface for submerged plants, in these cases the body lies horizontally with the head held parallel to the surface, either on it or just below it. When feeding like this, the head is normally moved from side to side and backwards and forwards, with the neck bending upwards in to a characteristic kink. By this method, referred to as 'Dabbling' because of its obvious similarities to the feeding method of Anas Sp., food is obtained either by sieving or by grasping and tearing.

Dipping

In shallow water, birds 'dip'; the head and entire neck may be submerged, whilst the body remains horizontal on the surface. Feeding actions may be alternated with foot-paddling movements which loosen underwater plants (Venables and Venables 1950). I have observed craters up to 10cm deep and ½-1m across in the bottom of a shallow lake in Iceland where dipping and foot-paddling occurred. It seems likely that foot-paddling had loosened plant roots and shifted the silt on the bottom.

Upending

In water as deep as about 120cm (Wilmore 1974) Whooper Swans submerge first the head, then the neck, as in dipping; then they swing forward and down submerging the whole of the foreparts of the body, leaving only the hind quarters, the tail and wings protruding vertically. Paddling may occur to help maintain the position.

In flowing water, as in still water, feeding methods are dependent on the depth, but the birds maintain their position against the flow by facing the current and paddling.

Digging

In marshy areas and in waterlogged grass, birds occasionally dig for roots. This is done vigorously and produces characteristic holes surrounded by piles of discarded mud and vegetation.

As has been suggested above, many birds do not use these techniques as major components of a typical daily routine. Feeding behaviour is flexible and in some areas they feed from agricultural land, rather than on water, using terrestrial techniques like those of geese.

Grazing

Whooper Swans have larger bills, larger serrations of the mandible edges and spines of the tongue, and a much slower pecking rate than geese. Owen (1977) recorded a peck rate of up to 250 min.^{-1} in the Barnacle Goose (Branta leucopsis), for instance, while Whooper Swans peck at up to only 75 min.^{-1} and feed on taller vegetation (pers. obs.). In fact Owen (1980) found a negative correlation between bill (culmen) length and pecks per minute for geese. If the Whooper Swan is assumed to be a goose with a culmen of 92-116mm (see Cramp and Simmons 1977) then the predicted peck rate would be in the range of 60-80 min.^{-1}. Results from this study agree well with such a prediction. Whereas geese grazing on grass pace and peck regularly, Whooper Swans usually remain stationary whilst pecking. The head is moved backwards and forwards and/or to the sides, thereby fully utilizing the great mobility of the neck before moving on. As a consequence they cover the ground in a rather different manner from that of geese. While grazing, the neck is usually quite tightly curved in an inverted U. If the vegetation is short the head is held pointing vertically down and the tip of the bill is used for pecking. In longer, coarser, vegetation the head is held horizontally and angled sideways so that the serrations at the sides of the bill can be used for shearing and tearing, accompanied by strong backward jerks of the head.

When feeding from stubble fields they make many minute movements of head and bill. In other respects, however, they move in much the same way as on grass.

Observations at close quarters have shown that from a solid substrata they can pick up two or more grains at a time using the tip of the tongue and bill. It seems reasonable to assume that the minute movements of head and bill observed in the field are due to this method of feeding.

Another technique, which I have called "shovelling" can also be seen on stubble fields. It involves lowering the head until it is horizontal and close to the ground, then pushing it forward using the lower mandible as a scoop. This may be another method for picking up individual grains, but seems best suited to lifting whole seed heads embedded in the soil surface.

Whooper Swans will also eat 'root crops', especially potatoes (see Kear 1963). They use the strong nail at the tip of the bill, or the sharp cutting edges to peck or chop off chunks.

Standing is the usual position when feeding from fields, although they sometimes sit whilst grazing (Ohlsen 1972; pers. obs.). During this study sitting usually occurred during strong winds when standing was difficult.

5.3 Foods Eaten

The range of food species recorded is very wide. From fresh-water and marine plants and algae on the one hand, to terrestrial plants, agricultural crops and even refuse, on the other.

The only compilation of food species appears in Scott et al (1972), but this is incomplete and lacks any data from the eastern end of the species' range. An attempt is made here, therefore, to collate the currently available information (see tables 5.1 and 5.2).

On the whole it is the leaves of plants that are eaten, but some seeds are also taken, for example I have seen Whooper Swans stripping seed heads from Thistles (_Cirsium_ _Sp_.); so too are berries, such as those of the Crowberry (_Empetrum_ _nigrum_) (Hancock in Cramp and Simmons 1977; pers. obs.). The large bill size of Whooper Swans enables them to eat coarser vegetation and harder materials, such as root crops, than many of the smaller billed geese. Given that they eat both terrestrial and aquatic plants as well as crops and such things as refuse, the range of foods taken is probably broader than that of any goose species.

5.4 Feeding Rate

5.4.1 Methods

The pecking rates of adults, cygnets and parents were measured whenever practicable. Two methods were used and birds were selected at random in both cases. The first method, a 'complete measure', was used during 1977-79. A swan was watched continuously for one minute, and the number of pecks it made were counted. This method proved unsatisfactory because it was excessively time-consuming, since during a minute's observation there was the likelihood that feeding would be interrupted by other activities, most often by 'head-up'. Interrupted observations were discarded.

The second method, used during 1979-80, made the collection of larger

Table 5.1

Foods eaten by Whooper Swans

A. Aquatic Plants

Species	Observer	Locality
Algae sp.	Hancock, in Cramp and Simmons (1977)	Iceland
Cladophora sp.	Brazil	Iceland
Chara sp.	Hewson (1964)	Scotland
Equisetum fluviatile	Haapanen et al (1977)	Finland
Sagittaria sagittifolia	Haapanen et al (1977)	Finland
Elodea canadensis	Hewson (1964)	Scotland
Zostera sp.	Freme (1931)	North Uist
	Kennedy et al (1954)	Ireland
	Sparck (1958)	Denmark
	Boswall (1975)	Iceland
	Charman (1977)	
	Einarsson (pers.comm.)	Iceland
Potomogeton sp.	Sparck (1958)	Denmark
P. natans	Hewson (1964)	Scotland
	Haapanen et al (1977)	Finland
P. filiformes	Brazil	Iceland
Ruppia maritima	Isakov and Vorob'ev (1940)	Caspian
Ruppia sp.	Sparck (1958)	Denmark
	Brazil	Iceland
Lemna trisulca	Zhitkov (1940)	U.S.S.R.
Sparganium sp.	Haapanen et al (1977)	Finland
Typha latifolia	Haapanen et al (1977)	Finland
Phragmites sp.	Zhitkov (1940)	U.S.S.R.

Table 5.1 (cont'd.)

B. Terrestrial Plants

Species	Observer	Locality
Ranunculus trichophyllus	Roberts (1934)	Iceland
Rorippa palustre	Owen and Cadbury (1975)	England
Trifolium sp.	Hilprecht (1956)	Germany
	Owen and Cadbury (1975)	England
Empetrum nigrum	Hancock, in Cramp and Simmons (1977)	Iceland
	Brazil	Iceland
Cirsium sp.	Brazil	Scotland
Eriophorum scheuzeri	Roberts (1934)	Iceland
Carex sp.	Brazil	Iceland
Glyceria fluitans	Scott et al (1972)	
G. maxima	Scott et al (1972)	

C. Crops etc.

Species	Observer	Locality
Potato	Kear (1963)	
	Brazil	Scotland
Swede/Turnip	Harrison (1967)	Scotland
Grain.	Scott et al (1972)	
	Brazil	Scotland
Grass	Scott et al (1972)	
	Brazil	Scotland
Refuse	Ruttledge (1963)	Ireland
	Brazil	Japan

Table 5.2

Foods eaten by Whooper Swans in Japan, recorded by Lesser (1973) and Hatakayama (in press).

Ulva pertusa	H
U. reticulata	H
Enteromorpha intestinalis	H
Equisetum arvense	H
E. heimale	L
E. palustre	L
Ranunculus aquatilis	L
Nymphae tetragona	L
Nuphar japonicum	L
Zizania latifolia	L
Trapa natans	L
Bradenia shreberi	L
Nelumbo nucifera	L
Euryale ferox	L
Gloiopeltis furcata	L
Solanum lyratum	L
Zostera marina	L.H.
Z. asiatica	H
Potomogeton franchetii	L
Ruppia rustellata	L
Juncus sp.	H
Typha latifolia	L
Eriophorum gracile	L
Scirpus maritimus	L
Phragmites communis	L.H.
Poa pratensis	H
Dactylis glomerata	H
Agrostis palustris	H

amounts of data possible during a single day. It was very similar to the technique used by Owen (1972) to measure the time taken by White-fronted Geese (Anser albifrons) to perform 50 pecks. The pecking rate of the Whooper Swan, however, is slower than that of geese, so the time taken for 20 pecks was measured instead, and peck rates per minute were then calculated. When examining the relationship between peck rate and time of day several observations were made in 10-15 min. blocks at intervals during a single day.

5.4.2 Results

Pecking rate data were collected between 20th January 1978 and 21st January 1981. Since it was only practical to measure the peck rate of Whooper Swans when they were feeding on grass, all records were from between January and May.

Because of the difficulties in identifying parents, relatively little pecking rate data is available for them, consequently this section is concerned primarily with adults and cygnets.

In order to eliminate any effect of time of day on feeding rate in the following analyses, dates were selected where similar amounts of data existed for both adults and cygnets collected at similar times of day. With the limited amount of data available it was not possible to also eliminate the effects of flock size. There seems, however, to be a negligible effect of flock size when comparing 1978 and 1979, since the range of flock sizes was higher in 1979 than 1978, but the difference in peck rate was not in the direction of increased peck rate with increased flock size as might have been expected (see 5.8.2.2).

The mean peck rate per minute for adults was 52.7 ± 8.5 in 1978 and 46.6 ± 9.6 in 1979; for cygnets it was 59.3 ± 9.5 in 1978 and 45.6 ± 10.1 in 1979, and for parents it was 56.0 ± 4.6 in 1978 and 36.1 ± 8.5 in 1979. It should be noted that the sample sizes of parents are small and from a narrower selection of time periods compared with those for cygnets and adults (table 5.3). The differences between years were highly significant (Adults, $z=3.1$, $p=0.002$; Cygnets, $z=9.2$, $p=<0.00006$; Parents, $U=5$, $p=<0.002$).

Since data were available from the same periods during the day for both adults and cygnets, the differences between the two were compared using a paired sample t-test. In 1978 the peck rate of cygnets was significantly faster than that of adults ($p=<0.05$), but there was no difference in 1979 ($p=0.1$) (see figs. 5.1 and 5.2).

In order to be able to make a similar comparison between parents and cygnets, data from both winters were used. Data from cygnets, collected within the same hour of the same day during which data from parents had been collected, were selected; i.e. a subset of the total data. Data from the two winters were from different time periods. Therefore, although the overall pattern of peck rate throughout the day might be affected by the differences between years, the differences between parents and cygnets should not be. There was no significant difference between the peck rates of parents and cygnets ($p>0.2$) although parents tended to peck more slowly (fig. 5.3).

The subjective impression formed in the field was that cygnets fed

Table 5.3

Mean peck rates per minute for three classes of individuals

	1978		1979
Adults	51.05 ± 8.2 (n=112)[1]	***	46.6 ± 9.6 (n=97)[2]
Cygnets	59.0 ± 9.1 (n=113)[1]	***	45.6 ± 10.1 (n=101)[2]
Parents	56.0 ± 4.6[3] (n=5)	***	36.1 ± 8.5[4] (n=20)

1. flock sizes ranging from 8 to 17, on 5 dates.
2. flock sizes ranging from 11 to 59, on 6 dates.
3. flock size 17, one date.
4. flock sizes 26 and 63, two dates.

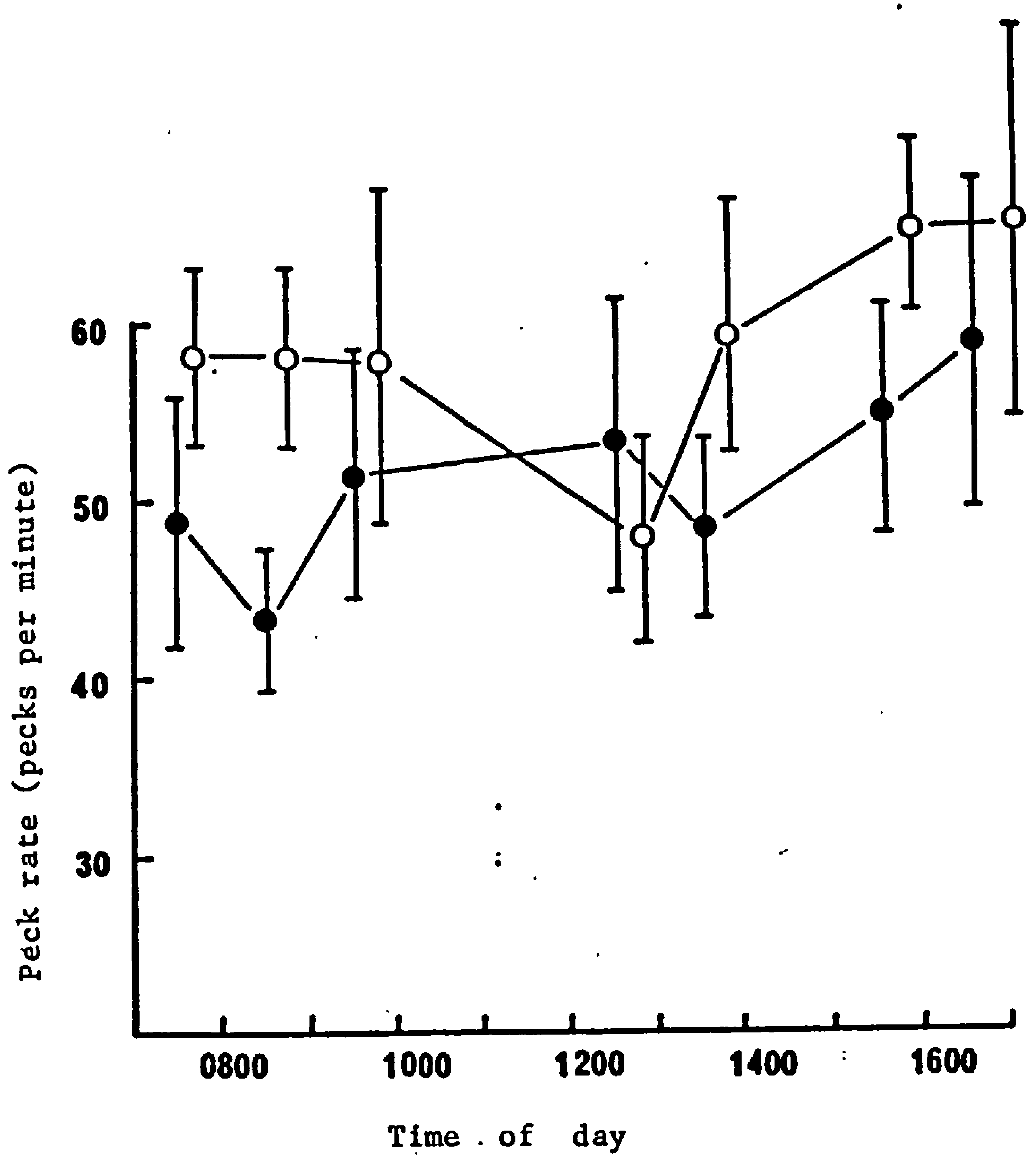


Fig. 5.1. A comparison of the peck rates of adults (●) and cygnets (○) during winter 1977-78.

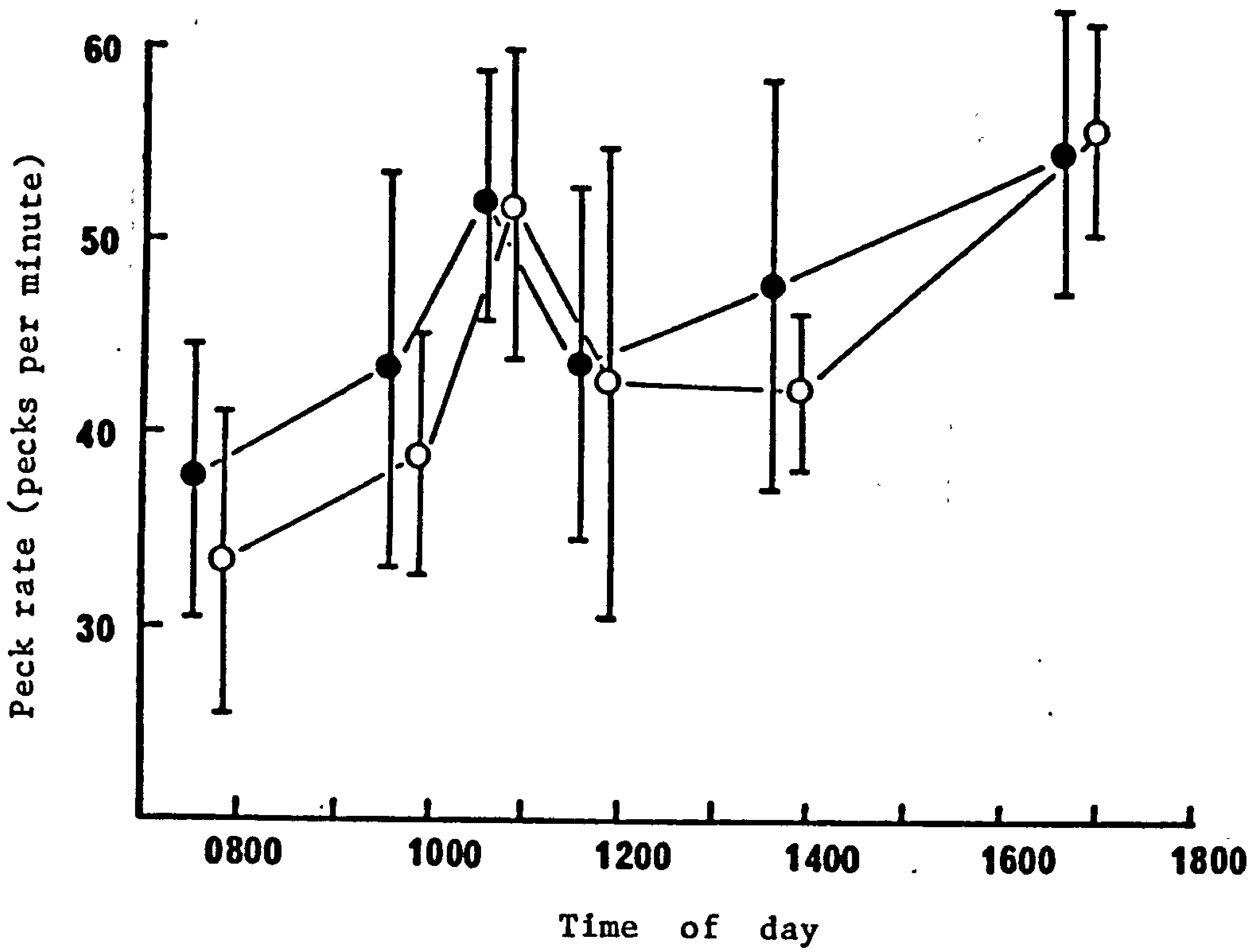


Fig. 5.2. A comparison of the peck rates of adults (●) and cygnets (○) during winter 1978-79.

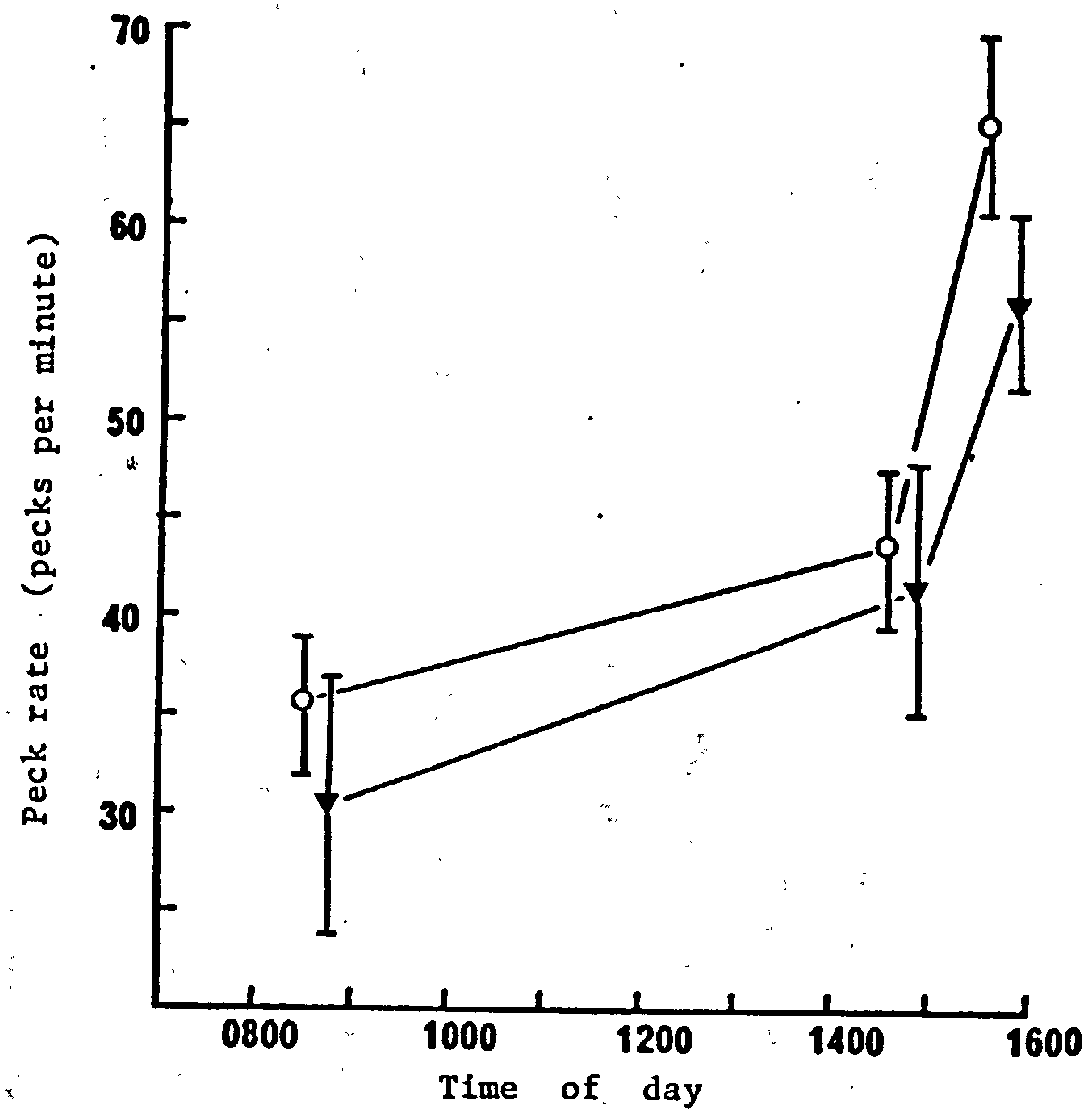


Fig. 5.3. A comparison of the peck rates of cygnets (○) and parents (▼) during winters 1977-79.

faster than either adults or parents. However, the data did not, on the whole, support this impression.

If peck rate data from winters 1977-78 and 1978-79are combined (fig. 5.4) it is clear that the modal class of peck rate for each class of individual differs. In increasing order they are: parents 31-40 pecks $\mathrm{min.}^{-1}$, adults 41-50 pecks $\mathrm{min.}^{-1}$ and cygnets 51-60 pecks $\mathrm{min.}^{-1}$. It is possible that were peck rate data available from a wider range of winters then the differences between classes of individuals might be more apparent.

Peck rate was found to be positively correlated with time of day in three consecutive winters (table 5.4 and figs. 5.5, 5.6 and 5.7). There was a slight indication that peck rate declined at some point during the day, however it was neither consistent between years nor between classes of individuals and was not felt to be important. The general relationship, i.e. that peck rates tended to be higher in the latter part of the afternoon than at any other time of day was the one of direct relevance.

The increase in peck rate during the day was thought to be related to the approach of a long period, i.e. night, when foraging was not possible (see 5.9). It was supposed that if increasing peck-rate was used as a short-term strategy, i.e. on a daily basis, then perhaps it might also be used as a long-term strategy, i.e. on a seasonal basis as a means of increasing food intake. Peck rate data, however, from adults for February to May 1978 and 1979, and cygnets for February to April 1978 and 1979, give no indication of any systematic change in peck rate with respect to season (see figs. 5.8 and 5.9). Time budget data showed that time spent feeding increased in the spring. As a consequence, food intake

Table 5.4

The relationship between peck rate and time of day

	1978	1979	1980
Adults	$n = 141$	170	140
	$r = 0.206$	0.503	0.539
	$p = <0.05$	<0.01	<0.01
Cygnets	$n = 113$	101	
	$r = 0.310$	0.290	
	$p = <0.01$	<0.01	

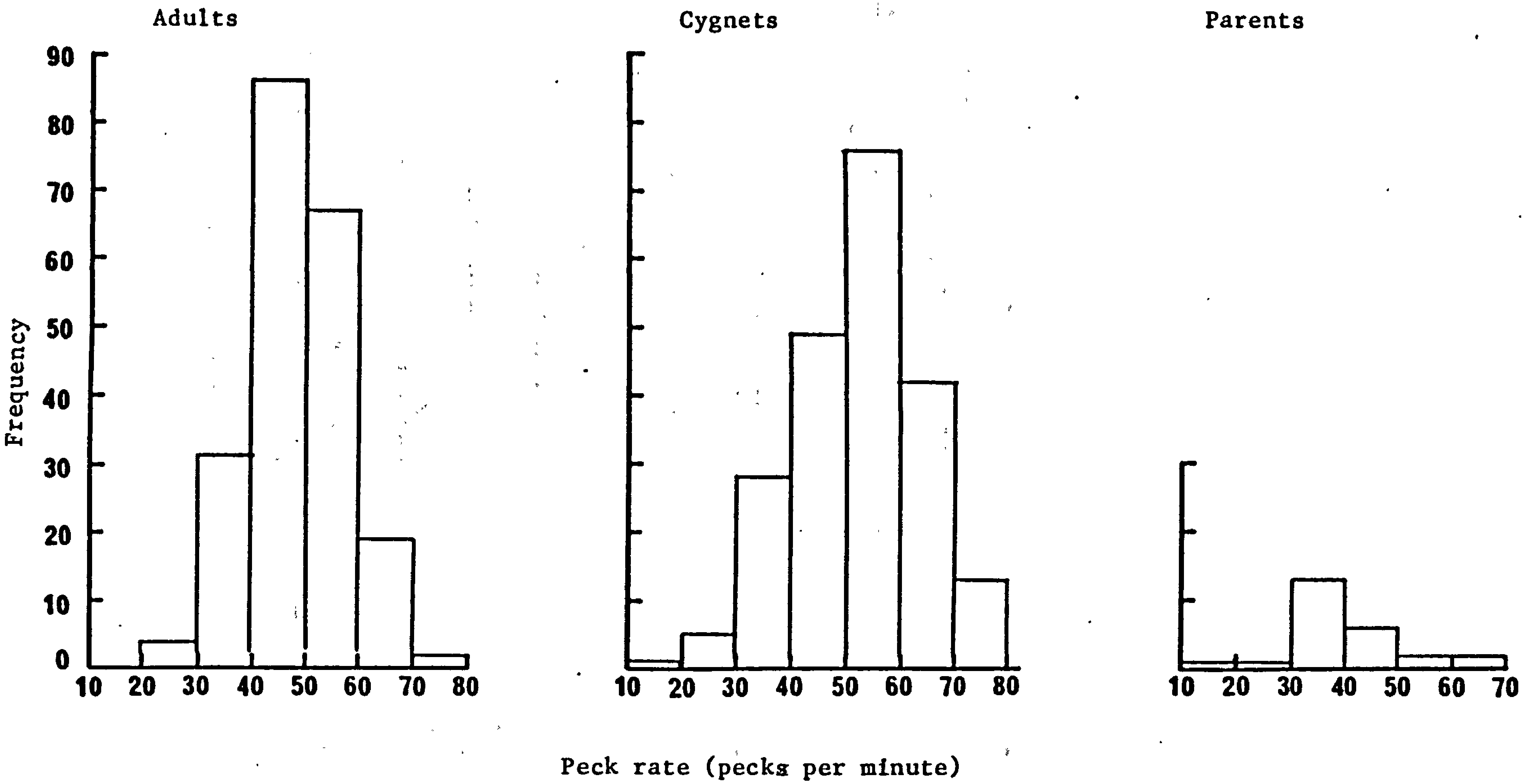
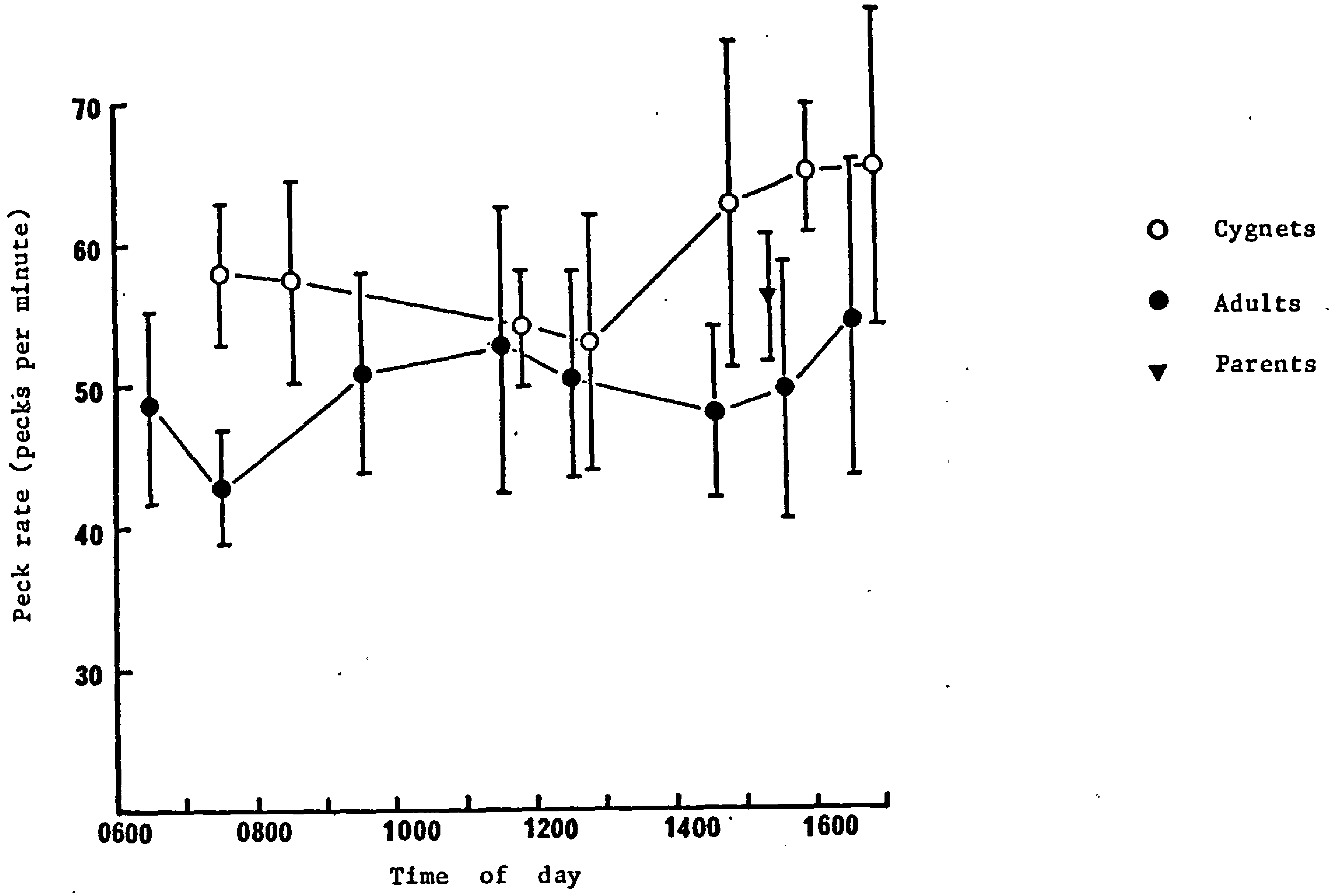


Fig. 5.4. A comparison of the peck rates of adults, cygnets and parents for winter 1977-78 and 1978-79 combined.



<u>Fig. 5.5</u>. The relationship between peck rate and time of day during winter 1977-78.

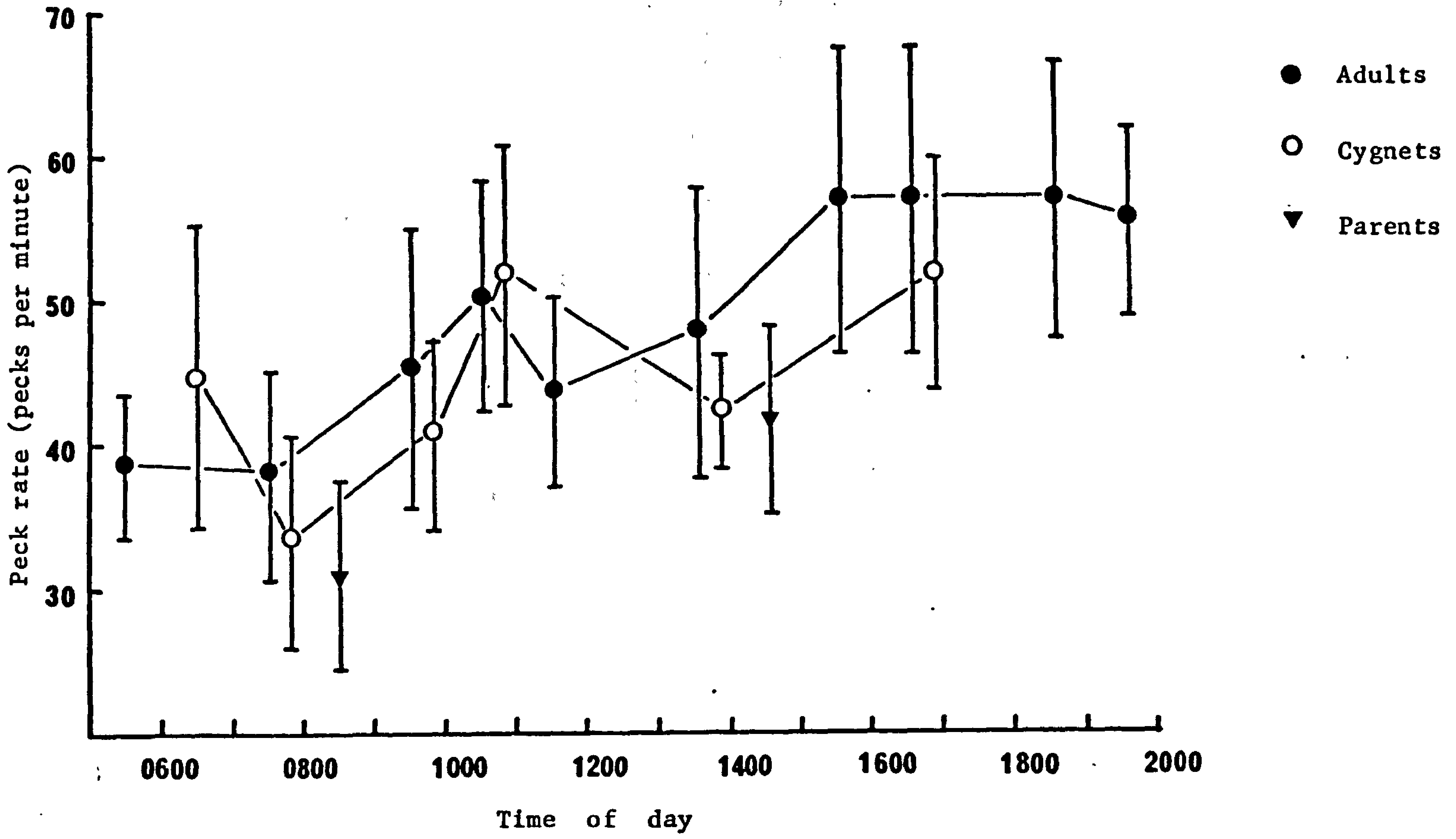
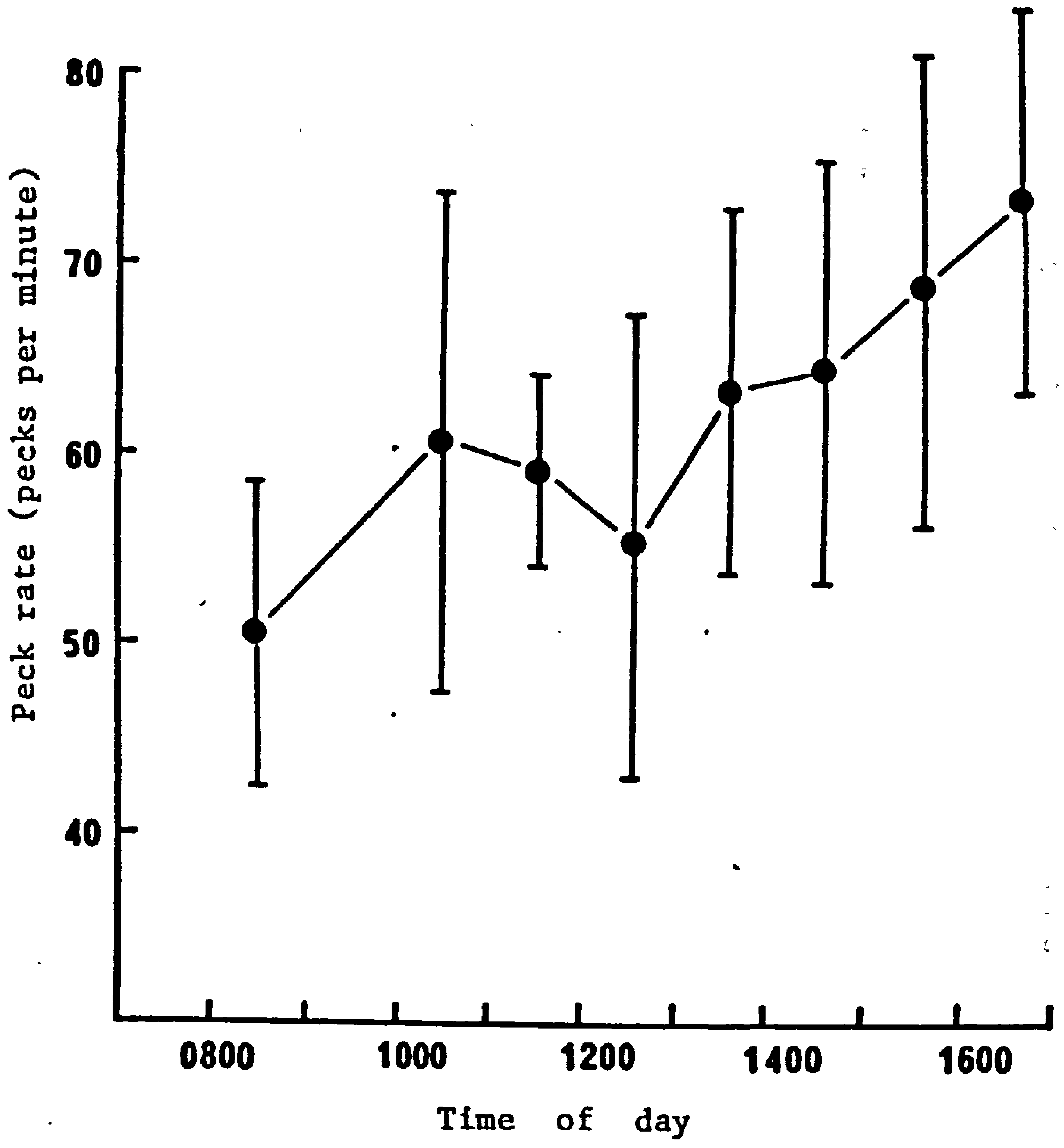


Fig. 5.6. The relationship between peck rate and time of day during winter 1978-79.



<u>Fig. 5.7</u>. The relationship between peck rate of adults and time of day during winter 1979-80.

Fig. 5.8. Adults

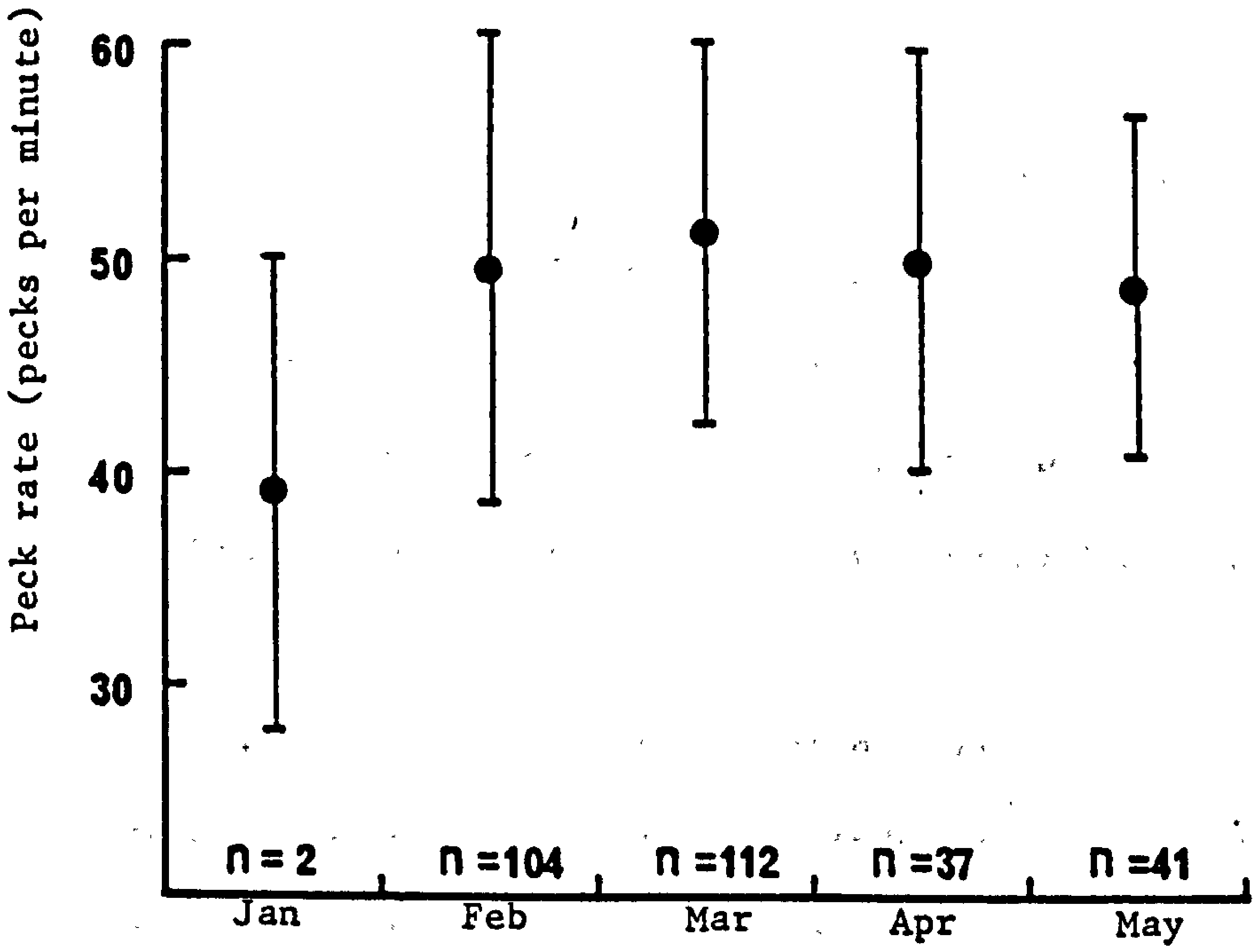
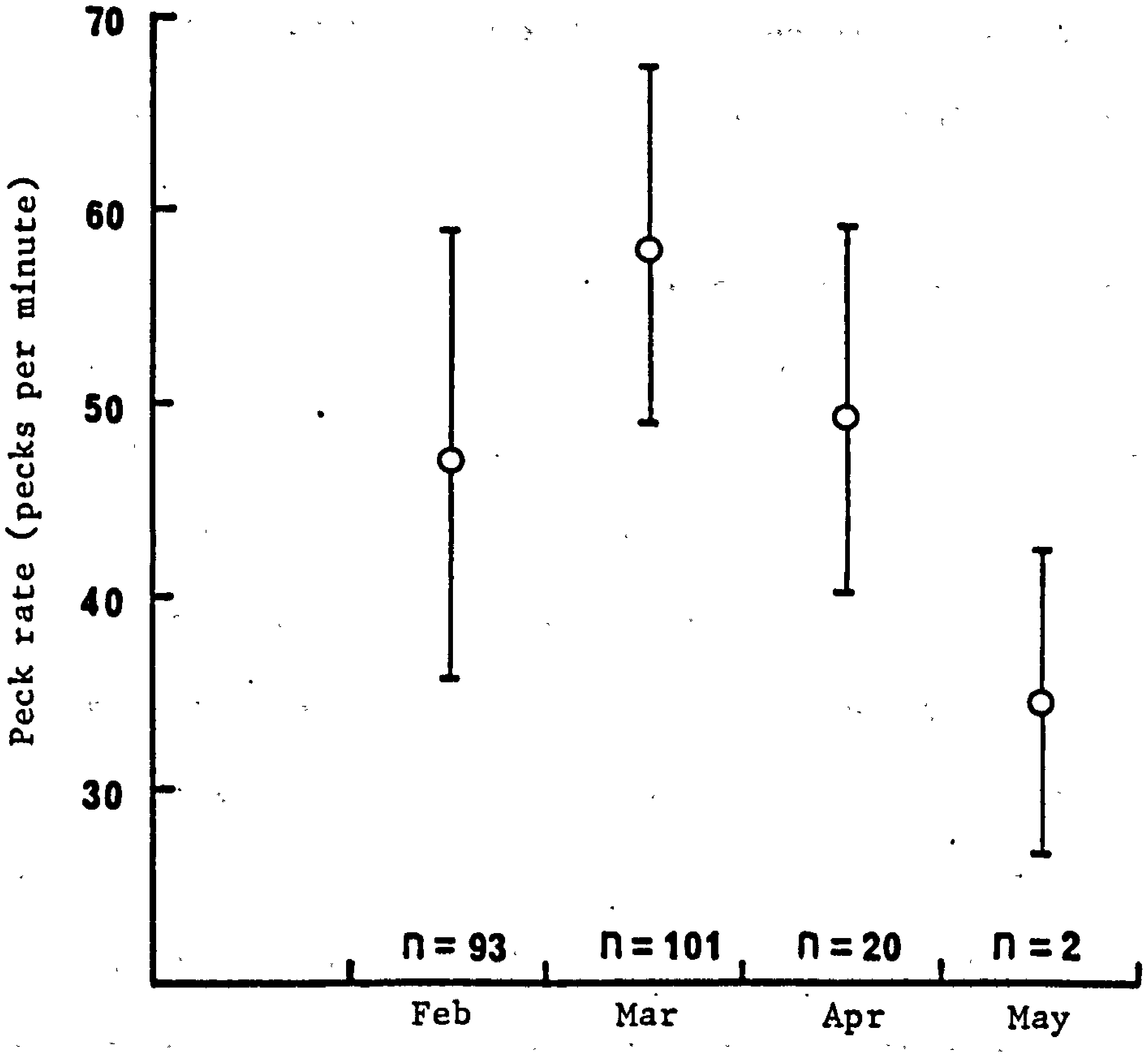


Fig. 5.9. Cygnets



Figs. 5.8. and 5.9. Monthly variation in the peck rates of adults and cygnets during winters 1977-78 and 1978-79.

could be increased even if the feeding rate remained the same.

5.5 Dropping Rate

Dropping rates have been measured for many grazing species, especially geese (see Owen 1980) to enable a calculation of daily food requirements to be made. This requires a knowledge of dropping weight, length of feeding day and the total number of droppings produced per day. The aim here was to obtain comparable material for grazing Whooper Swans.

During this study dropping intervals were measured whenever it was possible to approach closely enough to the birds to be certain of observing defaecation.Owing to the demands of the collection of activity budget data, defaecation intervals could not be measured at the same time (because the defaecation rate measurement depended on following a focal animal continuously for long periods which preclued all other observations).

The technique used initially was one of direct measurement. A bird was selected at random from the flock and watched until it defaecated, the interval from the first defaecation until the subsequent one was measured with a stop-watch. This simple technique, which works well for geese, proved unsatisfactory for swans because the inter-dropping interval was much longer; as a result the likelihood of the focal individual moving behind another, thus hiding its vent and making observation impossible, was much greater. As the period of continuous observation increases observer concentration wanes and blinking increases (see Mackworth 1970) again making it more likely that defaecation will be missed.This method was replaced therefore by a technique used by Owen (1972) for measuring the interval between bouts of vigilance. Individuals were selected at random and the time until first defaecation was recorded. The interval between defaecations is comprised of the time from the last defaecation until the time of watching, and from the time of watching until the next defaecation. "As birds were selected at random and observed at random times, these two periods will be equal and the interval between (defaecations) will be double the time to (defaecation) which was measured" (Owen 1972).

It was conceivable that the time to defaecation measure could have been biased by choosing animals in a way related to defaecation, however, very similar results were obtained from both methods. The mean interval for the complete measure was 14.5 ± 3.6 min (n=7) and the mean 'time to dropping' (t.t.d.) was 7.48 ± 5.3 min., thus the mean interval by the t.t.d. method was 14.95 min (n=26). In view of the larger sample size, the latter figure was felt to be the most reliable.. This interval was much longer than that in geese. In the White-fronted and the Barnacle Geese the inter-dropping interval was only 3½ min. (Ebbinge et al 1975; Owen 1980). This difference was, presumably, simply a function of the very great size difference between the Whooper Swan and geese.

Birds arriving at the feeding grounds from the roost are assumed to have an empty gut, since they do not feed during the night. The first period of feeding fills the gut and until this is done no droppings are produced. Once full, the gut works like a conveyor belt, droppings are assumed to be produced at regular intervals (following Owen 1972).

The time of arrival of flocks at the feeding fields was recorded. Individuals were chosen at random from the flock as they arrived and were followed until the time at which the first dropping was produced. On only five occasions (in January and November 1980) was the time to first dropping successfully recorded, owing to the problems of watching a single individual in a flock for a long period.

The mean time to first dropping was 82.6 ± 23.9 min (n=5) and this period was significantly longer than the dropping interval measured later in the day using the t.t.d. method ($p < 0.0003$, Mann Whitney U test, one tailed) or than the complete inter-dropping interval ($p=0.001$).

5.6 Food Intake

The aim of this section is to draw some broad comparisons between food intake by the Whooper Swan and by geese. What little information that is available on the daily food intake of swans is from the summer (see Mathiasson 1973 and Frithriksson et al 1977).

Mathiasson (1973) found that the amount of food eaten by moulting Mute Swans depended on the food species. For example, when feeding on Zostera marina Mute Swans consumed 0.077 kg (dry wt)/kg body wt/24 hrs and when feeding on Ulva lactuca they consumed 0.018 kg/kg body wt/24 hrs. The large difference was presumably due to the greater digestibility of the Algae.

The only previous work specifically on the Whooper Swans was that by Frithriksson et al (1977). The daily requirement was estimated as 400g dry weight (2000g wet wt). However, although an apparently reasonable figure (White-fronted Geese and Barnacle Geese consume about 700g wet wt. of grass per day) (Owen 1972; Ebbinge et al 1975), it cannot be relied upon since the experimentors failed to exclude sheep from the study area and therefore were uncertain as to exactly how much of the biomass was removed by the swans.

From data collected during this study it was possible to calculate the daily intake in grams dry weight per day for the Whooper Swan, for comparison with geese. The mean interval between defaecations was approximately 15 min. for the Whooper Swan, compared with 3½ minutes for geese (Owen 1980). It took approximately 83 minutes on average for the first dropping of the day to be produced, that is for the gut to be filled, and there would be a corresponding period after departure from the feeding grounds until the gut was emptied. Assuming that the inter-dropping interval remains constant, then this period should also be about 83 min. It is possible, however, that food is retained longer in the gut at night and may be more effectively digested than during the day, but generally speaking an empty gut on arrival is counterbalanced by a full one at departure. In the following calculations this lag is ignored, birds are treated as if arriving full and leaving empty. The rate of throughput is limited, not simply by the rate of input, but also by the rate of action of the gizzard.

It is assumed that the increase in feeding rate which occurs during the day leads to a progressive over-loading of the gizzard, so that on departing the birds have an oesophagus full of indigested food (Owen 1972). It is also assumed that this does not lead to a corresponding increase in dropping rate.

In a mid-winter day of approximately eight and a half hours, 34 droppings would be produced by a Whooper Swan, compared with 150 for a

White-fronted Goose (see Owen 1971). When swans fly to roost they may also carry an oesophagus full of food, thereby effectively extending the feeding day. The only data available was from a single bird; its oesophagus held 7.8g dry weight of food.

In the absence of specific information, it was assumed that the digestive efficiency of the Whooper Swan was the same as that of geese; at its lowest about 25% (Owen 1980), hence the daily intake of food is equal to 1.33x total dropping weight plus the weight of food in the oesophagus.

The mean dry weight of droppings was found to be 4.04 ± 1.2g (n=103), therefore the total dry weight of 34 droppings was 137.4g. The amount carried in the oesophagus was potentially in the region of 8g dry weight, roughly 75% of which would be egested. Thus the total dry weight egested per day was 143.4g. The total daily intake would therefore be 191g dry weight, or 955g wet weight. Considering the number of assumptions involved and the possibility of error in the measurements, the resulting figure for intake seems reasonable. It compares favourably with the figure of 700g obtained by Owen (1972) and Ebbinge et al (1975) for the White-fronted and Barnacle Geese, and, as was expected for a heavier bird, it was larger. The digestibility of grass increases as it grows and the assimilation efficiency of geese can reach nearly 40% (Owen 1980). If this is also assumed to be the case for Whooper Swans, then the maximum daily intake is 238g dry weight or 1190g wet weight.

5.7 Vigilant Behaviour

All behaviours are interrupted at frequent intervals by bouts of head-up; during this behaviour swans appear to be scanning their environment. Such attention for an unspecified stimulus is called 'vigilance' (Dimond and Lazarus 1974). Its function was not readily identified in the field but it was assumed to be adaptive; it will be discussed further in 5.9.

The amount of time an individual allocates to vigilance limits the amount of time available for other activities, such as feeding. The motivation for such different behaviours was expected to vary from individual to individual, but more particularly between individuals of different age or reproductive classes.

The aim of this section was to examine the head-up behaviour of three different reproductive classes; adults (without cygnets), parents (with cygnets) and cygnets, to see if:

a) they varied in their allocation of time to the behaviour

b) any such differences could be attributed to known differences between such classes. Cygnets, for example, are smaller than adults and have much weight to gain, they were expected to spend as much time feeding as possible, possibly at the expense of time spent vigilant. Cygnets might also be unskilled in vigilance behaviour; their parents might, therefore, be more vigilant in order to protect their offspring.

5.7.1. Methods

Individuals were selected at random from a flock and watched until they raised their heads. The interval between one bout of head-up and the next was measured using a stop-watch. The succeeding head-up bout was measured with a second stop-watch. After each double unit of data had been collected the results were recorded on paper, and a different individual was selected. Because the number of parents and cygnets in any flock was small there was inevitably a much greater likelihood that data would be collected from the same individual more than once, than was the case with adults.

5.7.2 Results

Adults, parents and cygnets spent about the same length of time head-up at each bout, but the intervals between these bouts differed significantly between all three classes (see table 5.5). Parents were head-up more often than were adults (i.e. their inter head-up period was shorter) and both were head-up more often than were cygnets. As a result parents spent most time head-up; cygnets spent least time and adults spent an intermediate amount of time head-up.

When the winter was examined month by month the same pattern occurred but with notable exceptions. In November, the difference in inter head-up period between adults and parents was not significant, but parents were head-up for significantly longer than cygnets. In February the difference in inter head-up period between adults and cygnets was not significant, and by March none of the inter head-up differences between the classes were significant (table 5.6). These results suggest that initially parents spend more time head-up than adults, and it is assumed that this represents an aspect of parental care. Cygnets spend less time head-up than adults or parents and are able to spend far more time in other activities, feeding is the most pertinent of these since cygnets are growing during their first winter. As the winter progresses cygnets grow in size and mature behaviourally. It was not unexpected therefore that by March there was no difference between cygnet and adult or parental

Table 5.5

Variation in vigilance, between adults, parents and cygnets during winter 1977-78

<table>
<tr><th></th><th colspan="2">Adults</th><th colspan="2">Parents</th><th colspan="2">Cygnets</th></tr>
<tr><td>Head-up</td><td colspan="2">9.2 ± 26.0 s</td><td colspan="2">9.7 ± 25.1 s</td><td colspan="2">7.1 ± 18.7 s</td></tr>
<tr><td></td><td colspan="3">← p = 0.317 →</td><td colspan="3">← p = 0.147 →</td></tr>
<tr><td></td><td colspan="2">(n=361)</td><td colspan="2">(n=185)</td><td colspan="2">(n=219)</td></tr>
<tr><td></td><td colspan="6">← p = 0.589 →</td></tr>
<tr><td>Inter Head-up</td><td colspan="2">76.6 ± 138.59 s</td><td colspan="2">40.04 ± 51.15 s</td><td colspan="2">174 ± 251.9 s</td></tr>
<tr><td></td><td colspan="3">← p = 0.004 →</td><td colspan="3">← p = 0.00006 →</td></tr>
<tr><td></td><td colspan="2">(n=399)</td><td colspan="2">(n=122)</td><td colspan="2">(n=210)</td></tr>
<tr><td></td><td colspan="6">← p = <0.00006 →</td></tr>
</table>

Mann Whitney U test, two tailed.

Table 5.6

Variation in vigilance between adults, parents and cygnets during winter 1977-78. (Figures in parenthesis are means ± S.D. Probabilities are two tailed, Mann-Whitney U test).

Inter head-up

Head-up

Nov

$$\begin{tikzcd} \text{Adult } (41.39\pm43.89\text{s}) \arrow[dr, leftrightarrow, "p=0.76"] \arrow[dd, leftrightarrow, "p=0.002"'] & \\ & \text{Parent } (32.41\pm26.65\text{s}) \\ \text{Cygnet } (120.15\pm146.29\text{s}) \arrow[ur, leftrightarrow, "p=0.02"'] & \end{tikzcd}$$

$$\begin{tikzcd} \text{Adult } (19.66\pm43.05\text{s}) \arrow[dr, leftrightarrow, "p=0.15"] \arrow[dd, leftrightarrow, "p=0.39"'] & \\ & \text{Parent } (21.83\pm45.01\text{s}) \\ \text{Cygnet } (11.26\pm28.42\text{s}) \arrow[ur, leftrightarrow, "p=0.02"'] & \end{tikzcd}$$

Dec

$$\begin{tikzcd} \text{Adult } (97.27\pm196.48\text{s}) \arrow[dr, leftrightarrow, "p=0.0005"] \arrow[dd, leftrightarrow, "p<0.00006"'] & \\ & \text{Parent } (60.05\pm92.63\text{s}) \\ \text{Cygnet } (256.18\pm303.45\text{s}) \arrow[ur, leftrightarrow, "p<0.0003"'] & \end{tikzcd}$$

$$\begin{tikzcd} \text{Adult } (7.28\pm22.47\text{s}) \arrow[dr, leftrightarrow, "p=0.81"] \arrow[dd, leftrightarrow, "p=0.25"'] & \\ & \text{Parent } (6.33\pm12.3\text{s}) \\ \text{Cygnet } (4.21\pm4.28\text{s}) \arrow[ur, leftrightarrow, "p=0.40"'] & \end{tikzcd}$$

Jan

$$\begin{tikzcd} \text{Adult } (128.67\pm182.56\text{s}) \arrow[dr, leftrightarrow, "p<0.001"] \arrow[dd, leftrightarrow, "p=0.005"'] & \\ & \text{Parent } (35.26\pm39.1\text{s}) \\ \text{Cygnet } (254.7\pm327.5\text{s}) \arrow[ur, leftrightarrow, "p<0.00006"'] & \end{tikzcd}$$

$$\begin{tikzcd} \text{Adult } (5.5\pm7.2\text{s}) \arrow[dr, leftrightarrow, "p=0.52"] \arrow[dd, leftrightarrow, "p=0.07"'] & \\ & \text{Parent } (22.45\pm52.74\text{s}) \\ \text{Cygnet } (9.8\pm32.45\text{s}) \arrow[ur, leftrightarrow, "p=0.16"'] & \end{tikzcd}$$

Feb

$$\begin{tikzcd} \text{Adult } (64.33\pm65.3\text{s}) \arrow[dr, leftrightarrow, "p=0.0042"] \arrow[dd, leftrightarrow, "p=0.39"'] & \\ & \text{Parent } (32.06\pm38.23\text{s}) \\ \text{Cygnet } (72.9\pm67.88\text{s}) \arrow[ur, leftrightarrow, "p=0.0016"'] & \end{tikzcd}$$

$$\begin{tikzcd} \text{Adult } (10.62\pm32.08\text{s}) \arrow[dr, leftrightarrow, "p=0.44"] \arrow[dd, leftrightarrow, "p=0.16"'] & \\ & \text{Parent } (4.87\pm6.70\text{s}) \\ \text{Cygnet } (3.64\pm3.43\text{s}) \arrow[ur, leftrightarrow, "p=0.38"'] & \end{tikzcd}$$

Mar

$$\begin{tikzcd} \text{Adult } (47.81\pm60.61\text{s}) \arrow[dr, leftrightarrow, "p=0.952"] \arrow[dd, leftrightarrow, "p=0.25"'] & \\ & \text{Parent } (43.5\pm38.36\text{s}) \\ \text{Cygnet } (126.08\pm199.75\text{s}) \arrow[ur, leftrightarrow, "p=0.18"'] & \end{tikzcd}$$

$$\begin{tikzcd} \text{Adult } (4.69\pm7.17\text{s}) \arrow[dr, leftrightarrow, "p=0.16"] \arrow[dd, leftrightarrow, "p=0.42"'] & \\ & \text{Parent } (6.4\pm8.99\text{s}) \\ \text{Cygnet } (6.89\pm9.95\text{s}) \arrow[ur, leftrightarrow, "p=0.56"'] & \end{tikzcd}$$

vigilance. Kakizawa (in press) showed that in winter, Whooper Swan parents showed more aggression than adults, but that this level of aggression declined as the food requirements of the cygnets declined. The amount of time spent head-up by adults was intermediate between that of cygnets and parents. It is not known whether this level is typical of adults or whether they 'cash in' on the presence of parents in flocks and take advantage of the high levels of vigilance shown by parents, to reduce their own. This could be elucidated by comparing vigilance regimes from adults in mixed flocks and in pure adult flocks. Unfortunately, there were not enough data from flocks without cygnets to make this comparison.

In November 1980 many families were present in the study area making it possible to confirm this general relationship between reproductive class and vigilance. The mean lengths of inter head-up periods were; 22.4 ± 30.7s. for parents, 49.6 ± 35.5s. for adults and 71.3 ± 45.0s. for cygnets. The difference between parents and cygnets was highly significant (Mann Whitney U test two-tailed $p=0.00006$) as was that between parents and adults ($p=0.0003$) but not between cygnets and adults ($p=0.075$).

5.8 The Relationship between Flock Size and Behaviour

5.8.1 Methods

Data were collected from flocks ranging in size from 1 - 150 birds. Ten scans were made of each flock at one minute intervals. At each scan the number of birds feeding and head-up were recorded. The mean proportion of the flock engaged in each behaviour was calculated for each set of ten scans.

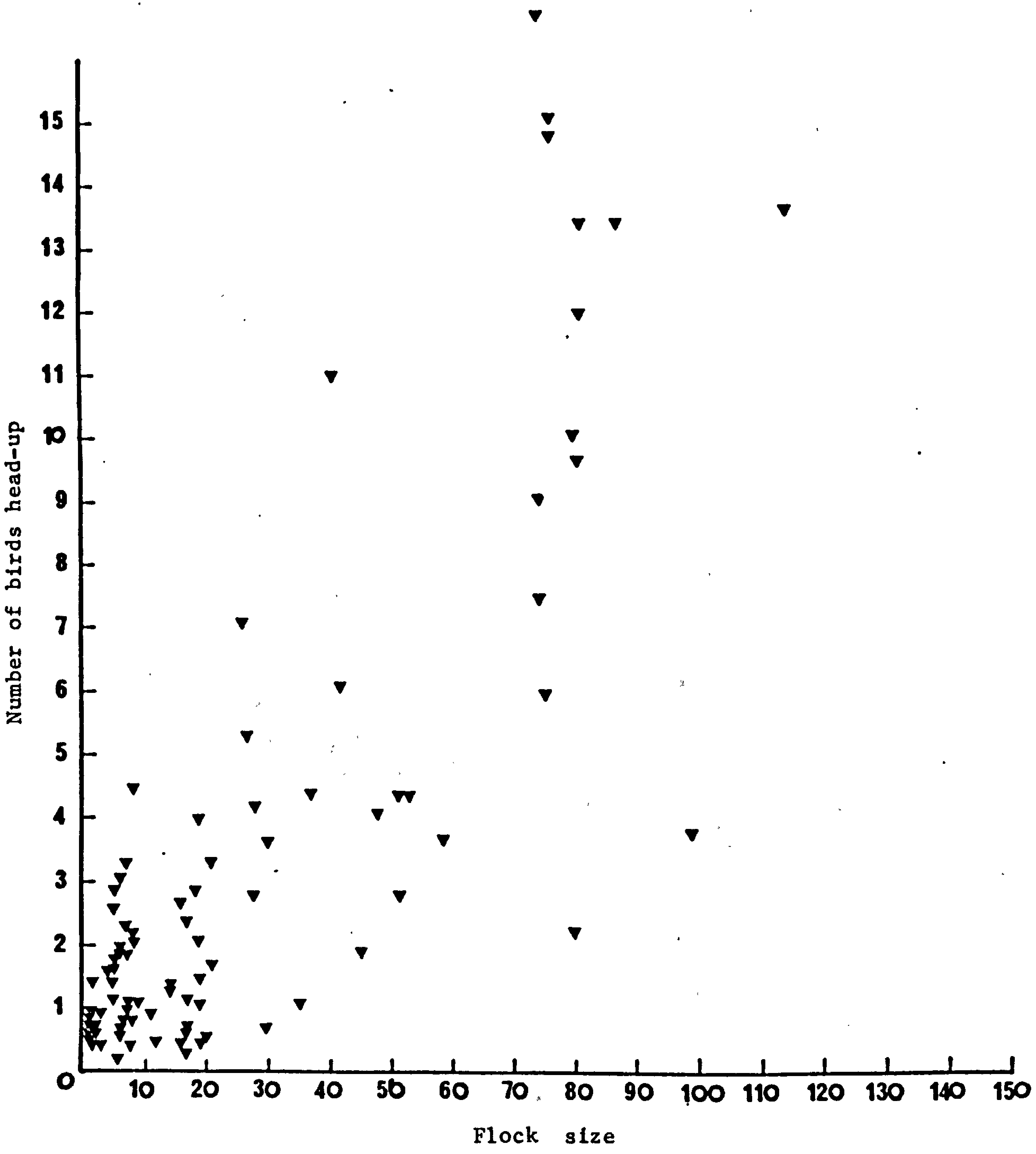
5.8.2 Vigilance: Results

The number of birds head-up was significantly correlated with flock size, ($r=0.85$, $p<0.01$, $n=86$) (fig. 5.10). It was accepted that greater variability is to be expected when calculating the percentage of birds engaged in a particular behaviour where the number of birds involved is small rather than large. The significantly (negative) correlation ($r=-0.40$, $n=89$, $p<0.01$) between the percentage of birds head-up and flock size indicates that head-up does decline with increasing flock size, in spite of the variability at smaller flock sizes. A linear regression line has been fitted (see fig. 5.11) although this is only to show that the data does not represent a horizontal scatter. The actual relationship appears to be curvilinear. There is an initial steep decline in head-up up to flock sizes of about 20, after that head-up levels out. The same relationship has been shown for White-fronted Geese (Lazarus 1972, 1978), Barnacle Geese (Drent and Swierstra 1977), Pink-footed Geese (Lazarus and Inglis 1977) and Brent Geese (Inglis and Isaacson 1978), but not apparently for any other swan species. Whereas in geese, which occur in flocks of up to several thousand an effect occurs over a range of flock sizes from one to 100, in swans which typically occur in much smaller flocks, an effect is apparentover a range of flock sizes from one to about 20. The main advantage is probably gained by individuals, or families which join together, rather than by flocks of adults which coalesce. Parents may gain extra time for feeding, by joining a flock, since they need not spend as much time vigilant as when just in a family unit.

5.8.3. Feeding: Results

It cannot be assumed that since birds in larger flocks have more time

Fig. 5.10. The influence of flock size on the number of birds head-up. (n=86, r=0.85, p<0.01).


Number of birds head-up
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
Flock size

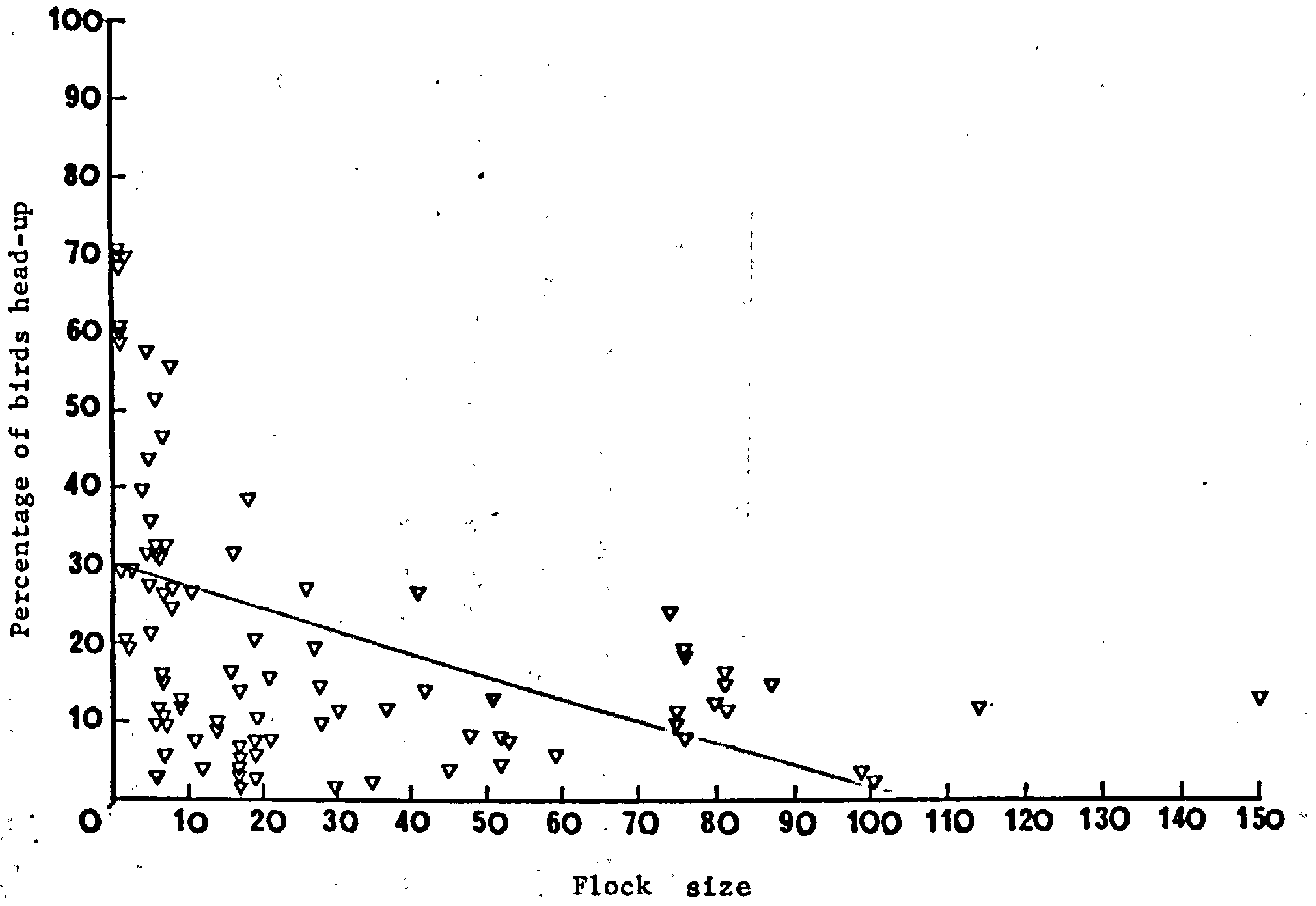


Fig. 5.11. The influence of flock size on the percentage of birds head up. (n=89, r=-0.40, p<0.01).

available owing to a reduction in time spent head-up that they will necessarily feed more. Extra available time might be used for other activities such as preening, roosting or social behaviour.

The number of birds feeding was significantly correlated with flock size ($r=0.984$, $p<0.01$, $n=87$), as was the percentage of birds feeding ($r=0.307$, $n=87$, $p<0.01$). As in 5.8.1.2 the relationship appears to be curvilinear with feeding increasing steeply at first but levelling out at a flock size of about 20 birds (figs. 5.12 and 5.13). As flock size increased, Whooper Swans spent more time feeding and less time head-up.

5.8.4 Peck Rate and Flock Size

It is possible that an increase in time spent feeding, one advantage of belonging to a larger flock (section 5.8.3) does not represent an increase in food intake. Instead, birds might feed more leisurely for longer. It was shown, in section 5.4, that Whooper Swans were capable of altering their feeding rate quite rapidly. The question asked here, therefore, was: do birds in larger flocks feed at a different rate from those in smaller flocks? That is, do they gain in total food input from being in a larger flock and from having more time available for feeding?

Peck rates were available for adults and immatures - for a wide range of flock sizes. These data were initially collected in order to examine the daily pattern of feeding rate; for methods see section 5.4.1.

Over a range of flock sizes of adults from 2 - 59, and of cygnets from 1 - 59, peck rate showed much variability. On the whole it appeared that flock size had little effect on peck rate, although the results,

Fig. 5.12. The influence of flock size on the number of birds feeding. ($n=87$, $r=0.984$, $p<0.01$)

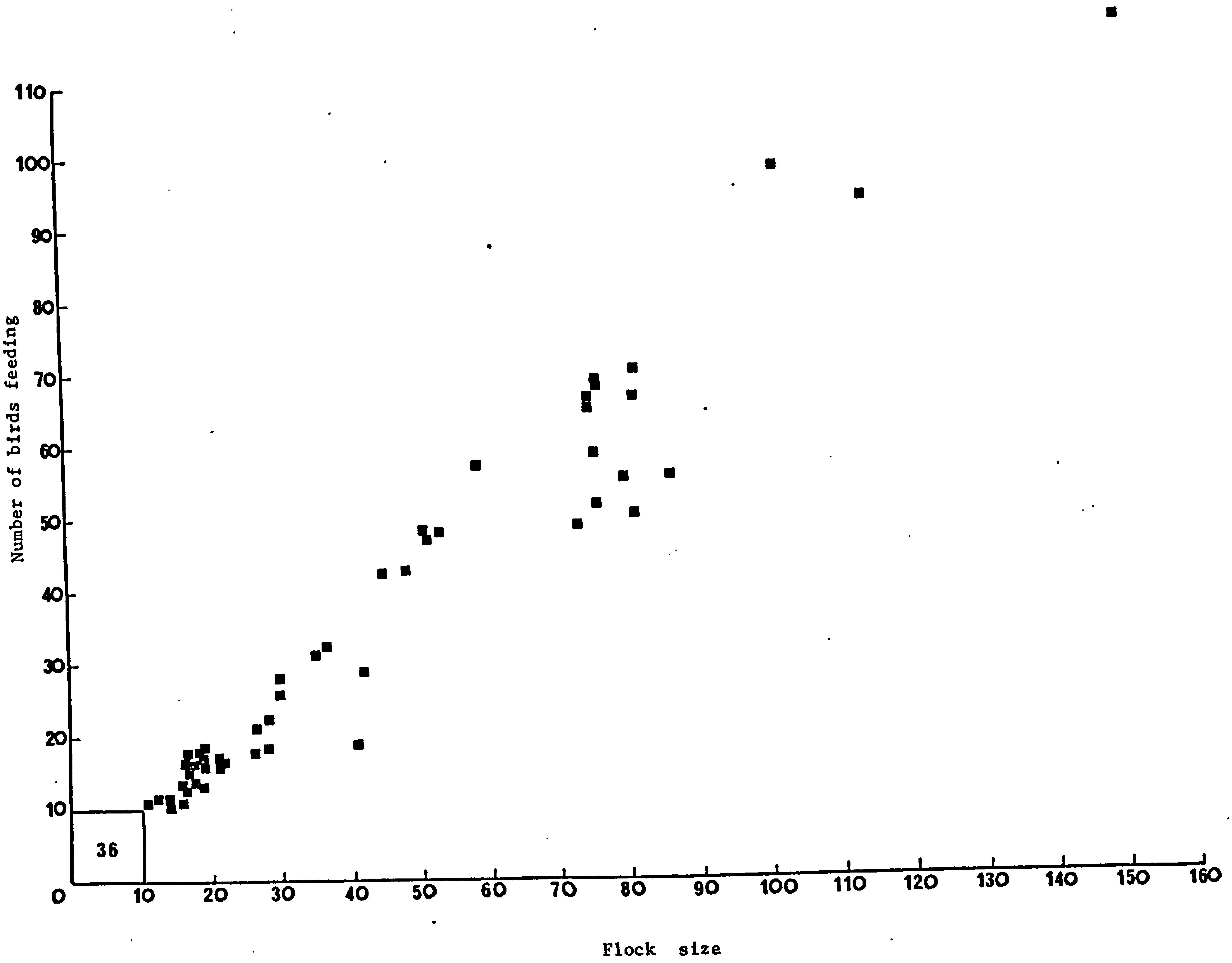
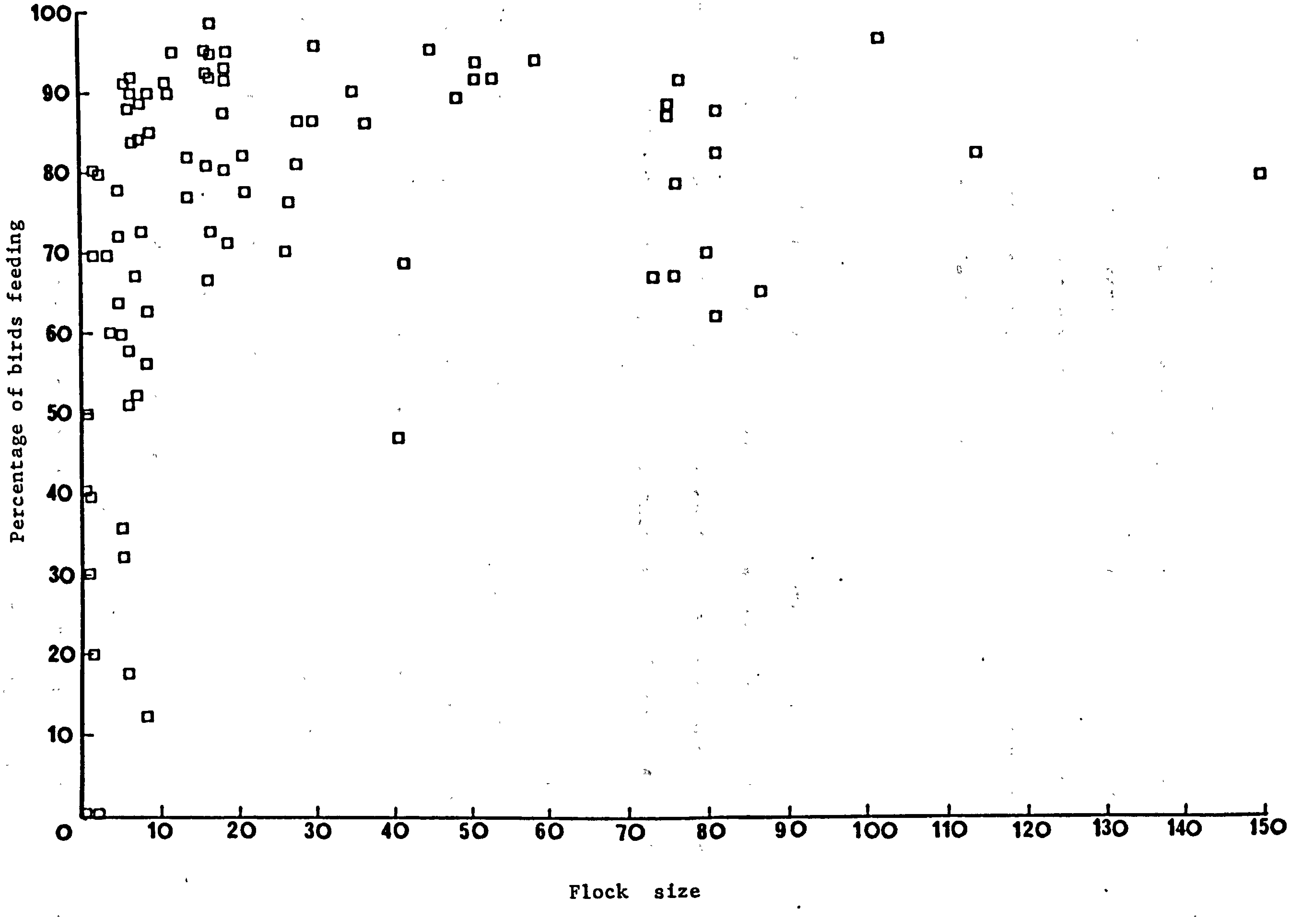

Number of birds feeding
110
100
90
80
70
60
50
40
30
20
10
0
36
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
Flock size

Fig. 5.13. The influence of flock size on the percentage of birds feeding. ($n=87$, $r=0.307$, $p<0.01$)


Percentage of birds feeding
100
90
80
70
60
50
40
30
20
10
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
Flock size

especially for cygnets, were by no means clear and there might be a slight decrease in peck rate in the larger flocks (fig. 5.14) which might perhaps be due to feeding competition with adults. It is clear, however, that there is no marked increase or decrease in peck rate with change in flock size. This suggests that birds joining larger flocks gain in total food input since while peck rate remains roughly constant the amount of time spent feeding increases.

5.9 Conclusion

It was only possible to quantify the feeding rate of Whooper Swans when they were feeding on grass; peck rate was measured and used as a measure of food intake. There was a tendency for cygnets to peck faster than adults or parents, although the only significant difference was that between cygnets and adults in 1978.

Peck rate was found to increase throughout the day as it does in geese (e.g. Owen 1972). From the present study it is also known that the proportion of time spent feeding peaks in the morning and afternoon and shows a mid-day lull (section 4.3.1.). If it is assumed that peck rate is roughly correlated with ingestion rate (bite size or selectivity might also vary, but no data are available on these points) then in the morning Whooper Swans spend a high proportion of time feeding, but do so slowly. During the middle of the day less time is spent feeding, but it is at a faster rate so intake probably does not differ greatly from that in the morning. In late afternoon, both the proportion of time spent feeding and feeding rate are high. Consequently, during the latter part of the day food intake is likely to rise rapidly. This is thought to overload the processing capacity of the gizzard, thus enabling the swans

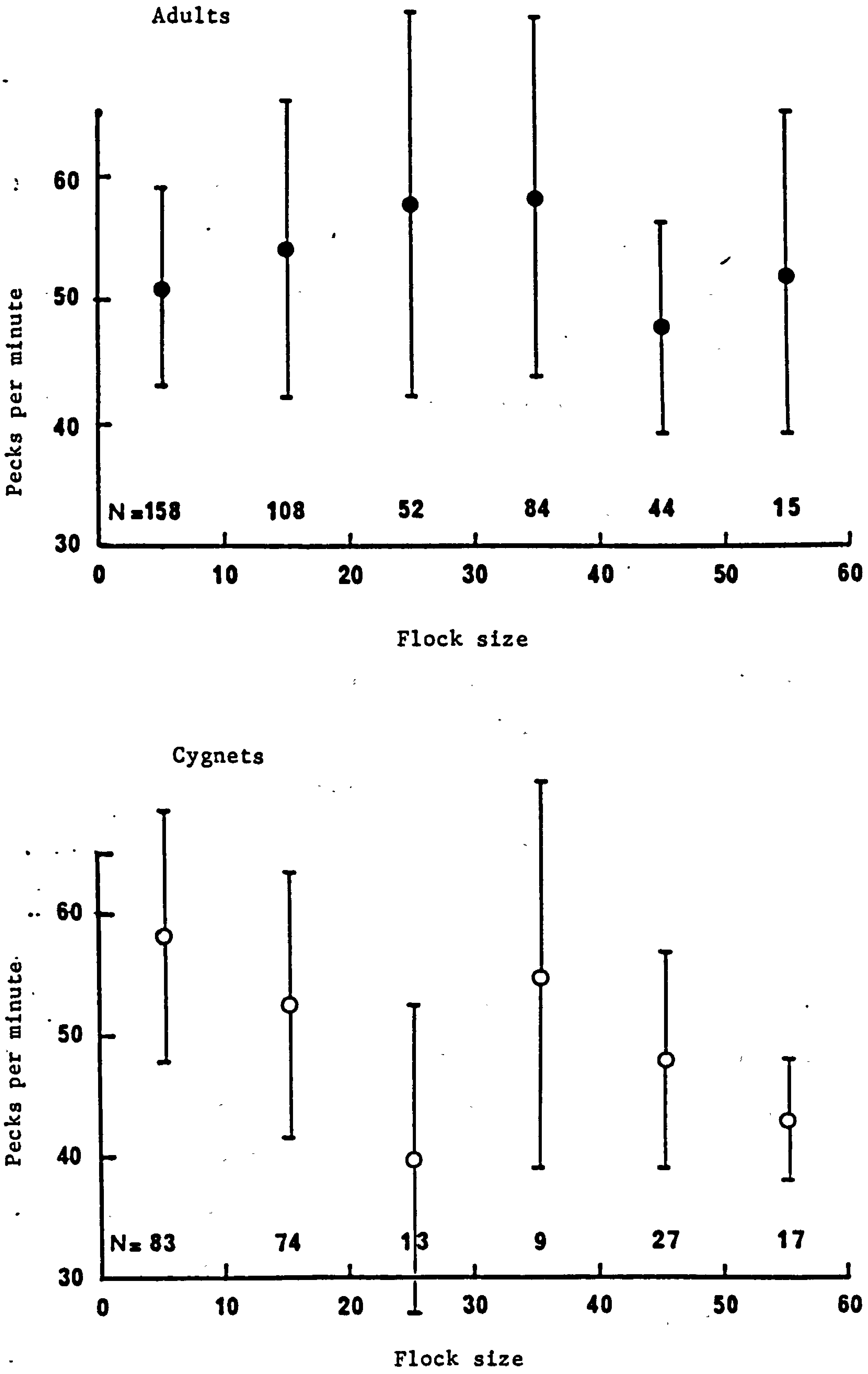


Fig. 5.14. The relationship between flock size and mean peck rate for adults and cygnets.

to carry a full oesophagus of food to roost for later digestion.

Peck rates of adults were roughly constant from February until May and of cygnets from February until April. During this period total time spent feeding each day increased. As grass growth increases in the spring its digestibility also increases, hence more food is retained by grazing birds (Owen 1980). The increase in time spent feeding and in the digestibility of food in the spring probably leads to a rapid increase in weight by Whooper Swans. It is assumed that fat is deposited for the spring migration and the approaching breeding season.

A daily intake of 955g was calculated for the Whooper Swan in mid-winter, this was expected to increase to up to about 1200g per day in spring. Whether Whooper Swans maintain body weight during mid-winter or whether they endure a short-term weight loss in mid-winter as do geese (Owen 1980) is not known.

It is not certain what function vigilance, by Whooper Swans, serves. It may be that different functions are served for different classes of individuals. The most pertinent functions appear to be: detection of danger, whether it is from predators or intraspecific competition; the location of environmental resources, for example, food or roost sites; and intraspecific communication, especially the location and movement of conspecifics, parents or offspring (Dimond and Lazarus 1974).

Parents, adults and cygnets all spent the same length of time head-up at each bout, but parents were head-up more often than adults and much more often than cygnets. Consequently, parents had least time available in which to feed. It was found that as flock size increased, the proportion of the flock which was vigilant declined and the proportion feeding increased. Parents may therefore be able to spend less time vigilant when they join a flock than when remaining in an isolated family. Since time spent feeding increases with increasing flock size and peck rate remains the same, then intake should also increase as flock size increases.

The advantages of flock sizes of more than about 30 birds are not obvious. It should be noted, however, that after 1st January, i.e. the period when the swans were mainly feeding on grass, flock sizes of less than 30 were particularly common.

It may be that the advantages and disadvantages of flocking are not consistent throughout the winter. When birds are feeding on a potentially very patchy food supply, such as waste grain, there may be greater advantages from being in large flocks (see Thompson et al 1974; Ward and Zahavi 1974); whereas when grazing on grass the main advantages may be in terms of detection of danger, for example intraspecific competition. This, coupled perhaps with the early movement of family groups northwards, may lead to a higher proportion of small flocks.

Drent and Swierstra (1977) and Inglis and Isaacson (1978) showed that the behaviour of geese in a flock affects the attractiveness of that flock to other birds. Using models, they showed that birds in the feeding posture were more attractive than vigilant birds. This implies that birds are capable of deciding whether or not to join a flock dependent on the relative merits of that flock, rather than simply joining any flock in order to increase the size of the flock they are in.

CHAPTER SIX: MIGRATION

The aim of this chapter is to discuss the current knowledge of swan migration between Britain and Iceland. Details are given of recent evidence shedding light on the subject and a theory is put forward to explain (a) why concentrations of Whooper Swans occur in certain areas and (b) the spread of ringing recoveries.

The migration of the Whooper Swan has been little studied, except in Japan (see Lesser 1973; Matsui in press) and Fenno-Scandia (see Preuss in press; Nilsson and Nilsson 1978). The British wintering population probably originates almost exclusively from Iceland. Birds wintering at Welney in Norfolk, however, have been assumed to be of continental origin (Cadbury 1975) or a theory of continental origin has been favoured (P. Scott 1980). Certain evidence of some individuals having arrived in Britain from the continent is incontrovertible, in particular, oil contaminated Whooper Swans were seen at Welney after an oil spill in the Netherlands (Owen and Cadbury 1975). Cadbury's (1975) "limited evidence that Whooper Swans wintering at the Ouse Washes originate from Scandinavia or Russia, rather than Iceland", is not so convincing, however, in the light of more recent evidence. It is, for example, no longer safe to assume that large broods are not from Iceland (Cadbury recorded a brood of six), since broods of six and eight have been recorded amongst birds almost certainly of Icelandic origin in Scotland and a brood of seven was seen in Iceland in 1978 (Brazil and Spray in prep.). Similarly, the higher percentage of cygnets recorded at Welney than at most other sites may not necessarily indicate continental origin, since Brazil (unpublished data) found that high proportions of Whooper Swan cygnets occurred at more southerly sites in Japan. Certain authors, for example Richards (1980), have already taken Cadbury's assumption to the logical extreme and have concluded that all Whooper Swans occurring in southern England are of continental origin. Recent sightings of several neck-banded Whooper Swans at Welney (marked in Iceland in 1980), in fact suggest that the flock there is primarily of Icelandic origin.

As yet the only evidence of British/Icelandic Whooper Swans reaching the continent, is a single recovery of an Icelandic ringed bird from the Netherlands.

Departure from Britain, for the summering grounds in Iceland, generally occurs between March and early May, although each year some birds remain and summer (e.g. Franklin 1947) and pairs have occasionally bred in Scotland (e.g. Gordon 1922). Observations from the Outer Hebrides have shown that "both geese and swans often leave for Iceland in anti-cyclonic conditions, when calm air and clear skies will aid their passage" (Ogilvie 1972). This journey between Scotland and Iceland is probably the longest non-stop swan flight (Ogilvie 1972).

Hewson (1964) suggested that Scottish Whooper Swans move south-west as far as Ireland during the winter, from where they migrate directly to Iceland in the spring. His hypothesis was based on the lack of spring peaks in numbers at sites which were important in autumn. Although this may be the case, data from the present study suggests that flock size declines during the latter half of winter (see section 3.2); scattered small groups may use different sites from the major autumn ones and may, therefore, be more easily overlooked. In support of Hewson's (1964) theory, however, there is now some positive evidence both from sightings of birds flying in the direction of Ireland (Shepherd pers. comm.) and from observations in Ireland of some of the birds which The Wildfowl Trust colour marked at East Park farm, Dumfries. It appears that some birds do leave directly from Ireland and the Hebrides, although the pattern of departure from Britain as a whole remains unclear. Likewise the pattern of arrival into Iceland is completely unknown.

In spring 1979, migration was delayed by severe weather, Birds were still present in the Stirlingshire study area on 7th May. Iceland experienced its coldest winter and spring on record and few swans were in evidence in the south of Iceland even by the second week of May. A journey made along the south coast of Iceland from Reykjavik to Alftafjorthur from 18th to 20th May, revealed only scattered pairs and a few small flocks. However, at Lonsfjorthur in the south east a vast flock of about 3300 birds had accumulated, representing half of the Icelandic population (pers. obs.) (see fig. 6.1).

Lonsfjorthur, is a large tidal lagoon sheltered from the sea by a ridge formed by longshore drift. The bay is backed by a ring of mountains rising to just over 1000m. The valley of the Jokulsa a Loni provides a suitable flyway to the north. It is possible that swans on spring migration choose this area as a staging post, either because of its geographical and topographical situation and/or because of the abundance of suitable food, namely *Ruppia sp*. Two stomachs and hundreds of droppings from birds in the area were examined and all contained only *Ruppia*. From northern Scotland the south-east corner of Iceland represents the nearest landfall, coupled with its sheltered position and

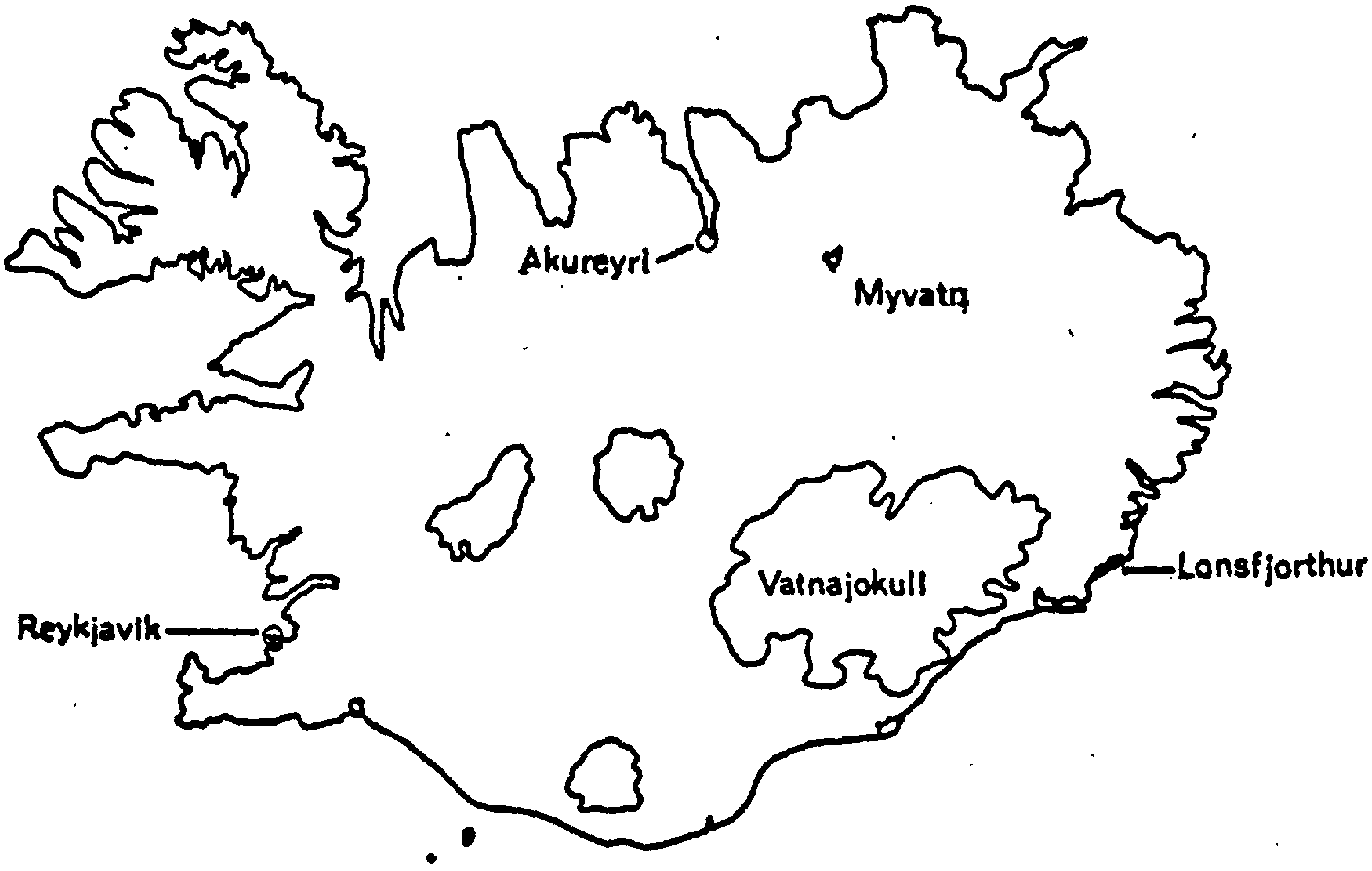


Fig. 6.1. Map of Iceland

good food supply this makes Lonsfjorthur an ideal site for initial arrival. It is also a well-known moulting ground (Boswall 1975). The area had not been watched in spring prior to 1979, but held a large concentration again in spring 1980 (A. Gardarsson pers. comm.) and it is likely that this is a regular phenomenon.

My own observations in the Myvatn area showed that Whooper Swans first moved into snow-free areas of fields, feeding there whilst nearby lakes thawed. They then either moved out to breeding sites, or moved directly to summering or moulting areas. Haapanen et al (1973 a) thought that the early arrival at pre-breeding concentrations could be adaptive if it allowed breeders to occupy territories as early as the weather permitted, since in northern latitudes the ice-free period could be critical. It is debatable whether or not early arrival provides more time to replenish energy reserves after migration. If the spring is late enough to prevent birds moving onto a territory, then the food available at pre-breeding areas is also likely to be of poor quality, and if the weather is good they are most likely to move directly onto the breeding territories and begin nesting.

Matsui (in press) stated that Whooper Swans in Hokkaido used river valleys and mountain passes as flight lines. Assuming the same to be so in Europe, those Whooper Swans arriving first at staging posts in the south-east of Iceland, such as Lonsfjorthur, are likely to fly round the Vatnajokull (Iceland's major glacier) in order to reach breeding and moulting areas in the north and east of the country (see figs. 6.1 and 6.2). Others, of course, may fly directly to breeding areas without stopping, though this presumably depends on weather conditions and energy reserves.

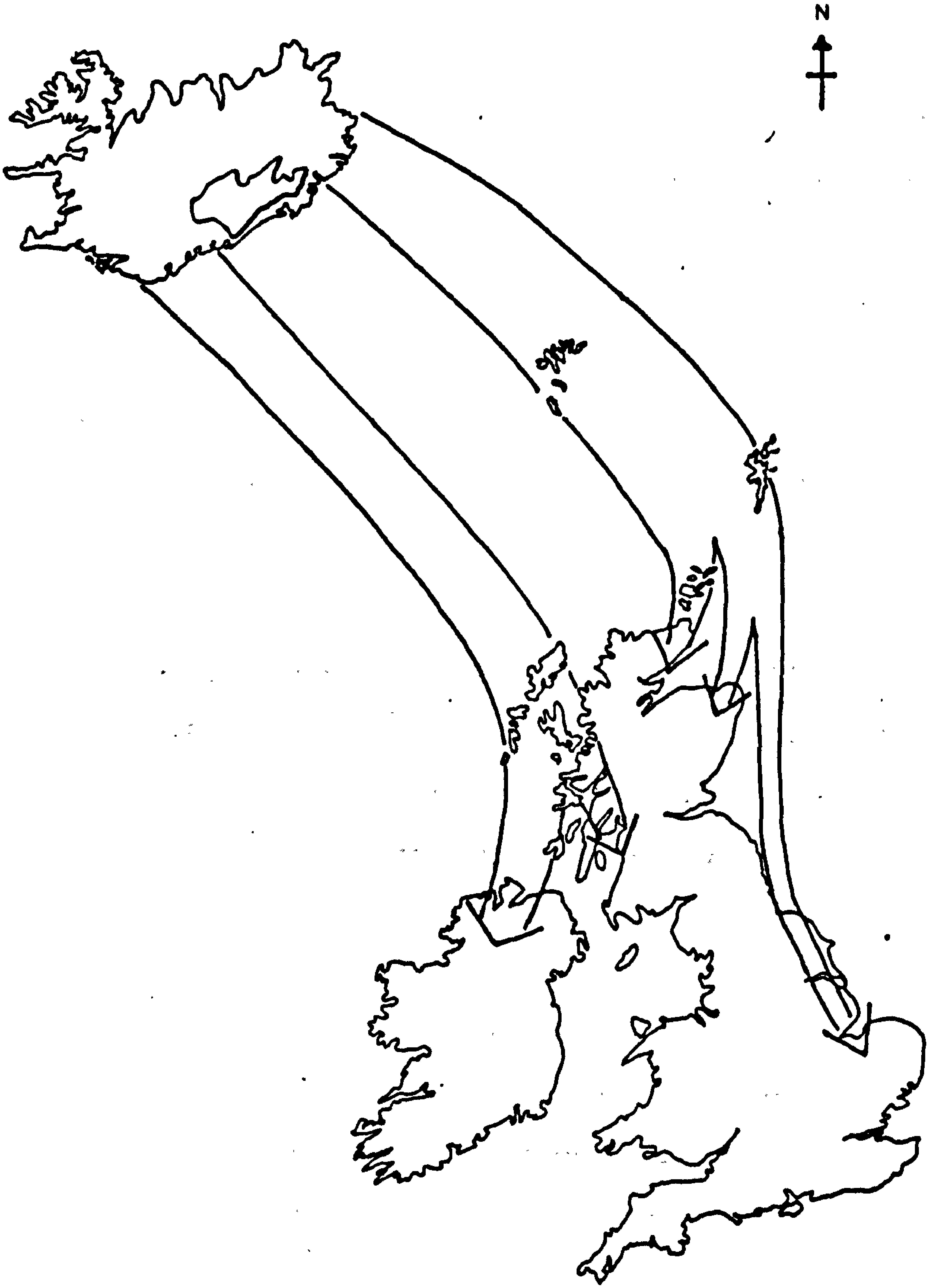


Fig. 6.2. Hypothetical migration routes of Whooper Swans between Iceland and Britain (taking into account known wintering concentrations and ringing recoveries).

There are, however, records of swans at high altitude. For example, Stewart (1978) reported a flock at about 8200m heading south towards Ireland. For swans flying so high, mountains or glaciers would not represent a barrier as they arrived in Iceland, but could do so when they departed. Whether migration usually occurs at these altitudes is uncertain, but the current research of Neil Prior, on swan flight, may serve to clarify this.

The same geographical barrier may separate the population on its return migration so that birds in the north-east third of Iceland leave from east of the glacier and those from the western two-thirds leave from west of the glacier (see fig. 6.1 and 6.2). This could account for early concentrations in the Hebrides and Ireland in the west and from Shetland, Orkney, Caithness and Aberdeenshire in the north and east. The lack of concentrations in the north-west of the Scottish mainland might just be the result of poor coverage by ornithologists or a lack of suitable habitat.

There is an interesting difference in the pattern of recoveries from the only two ringing studies done in Iceland so far. Swans ringed in the western highlands (see Kinlen 1963) had a much more westerly distribution on the wintering grounds than those ringed at Myvatn in 1980 (Brazil and Petersen in Prep.). It is hoped that the current study of movements of the Whooper Swan using neck-bands may provide further information on the subject. (Brazil; unpublished)

Boyd and Eltringham (1962) recorded that the numbers of Whooper Swans on the Scottish mainland were higher in November than at other times, while in England where birds arrived later and left earlier, maximum numbers occurred in December. This could reflect movement south from Scotland as winter progresses or that later migrants leap-frog over earlier ones to winter further south. The arrival of two neck-banded Whooper Swans at Welney in early November 1980, however, proved that even early migrants may make the longest journeys.

CHAPTER SEVEN: BREEDING BIOLOGY

7.1 Introduction

This chapter provides a descriptive summary of the basic nesting biology of the small sample of Whooper Swans that was studied in Iceland, and provides basic background for chapter eight.

Of the seven world species of swans, only four, the Mute, Black (Cygnus atratus), Whistling and Trumpeter have been extensively studied during the breeding season. The Coscoroba (Coscoroba coscoroba) and Black-necked Swans (Cygnus melanocoryphus) have been little studied and for political reasons it is difficult for western scientists to study the Bewick's Swan on its breeding grounds in the U.S.S.R. The Whooper Swan, however, is readily accessible in the western part of its range, but in spite of this, only in Finland has it been studied on the breeding grounds.

The Whooper Swan, like the high latitude nesting geese, is long-lived, monogamous and shows delayed maturity. Like other swans, juvenile plumage is retained for up to a year or longer. Only a small proportion of the population breed in any year (Haapanen et al 1973 b) and probably less than 20% of individuals survive until breeding age (Brazil and Petersen in prep.), while reproductive output can vary enormously from year to year due mainly to weather conditions (Brazil and Kirk in prep.) The ice-free period is the critical factor affecting distribution and breeding success during the summer in the Trumpeter Swan in Alaska (Hansen et al 1971) and in the Whooper Swan in Finland (Haapanen et al 1973 a). It presumably affects Whooper Swans breeding in the highlands in Iceland, but those nesting in the lowlands are likely only to be affected by the time of ice break-up in the spring, not freezing in the autumn.

Whooper Swans defend a territory, the responsibility for defence lying primarily with the male. The female's role is to incubate the clutch. Once the clutch has hatched both male and female take care of the brood.

7.2 Study Areas in Iceland

7.2.1. Myvatn

Lake Myvatn in N.E. Iceland (65°35'N, 17'00W, 278m a.s.l.; see Rist 1979) is a through-flow lake surrounded by post-glacial lava flows. The lake is fed by cold springs, ordinary ground water and warm springs. It is comprised of two basins, the north basin (Ytrifloi) is the shallower and older of the two (about 3800 years) and has a surface area of 8.2km^2. The south basin (Sythrifloi) is deeper, about 2000 years old, with a surface area of 29.2km^2 (see fig. 7.1). The greater part of the lake is 2.5-3.5m deep, and even at the deepest point is only 4.5m. It freezes during winter and on average there are 189 days of ice-cover (Rist 1979). Springs and the outflow to the Laxa, however, maintain some areas clear of ice throughout the winter and these are much used by waterfowl.

Myvatn is within the region of highest annual temperature range in Iceland (13-15°C); July is the warmest month and February the coldest (Einarsson 1979). The north-eastern interior of the country is in the rainshadow of the southeasterly winds created by the glacier Vatnajokull. Myvatn, being in that region, experiences very low precipitation compared with other regions, about 400mm compared with 1000-4000mm in southern

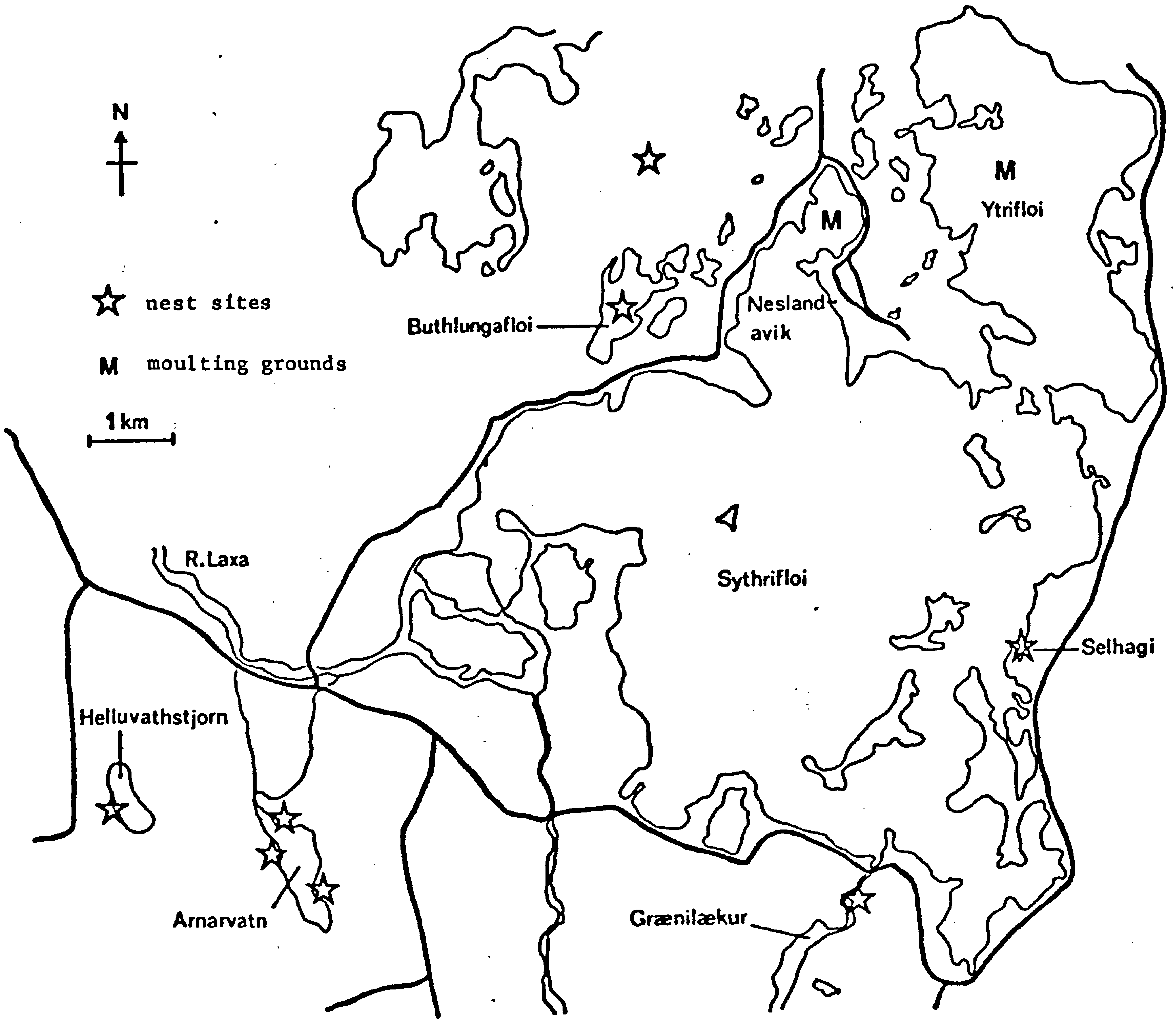


Fig. 7.1. Map of the Myvatn area showing breeding and moulting grounds.

Iceland (see Einarsson 1979).

Surprisingly, given its latitude (just south of the Arctic Circle) and its long periods of ice-cover, Myvatn is highly eutrophic, and the phyto-plankton and zoo-plankton production is very high in the lake system (Jónasson 1979).

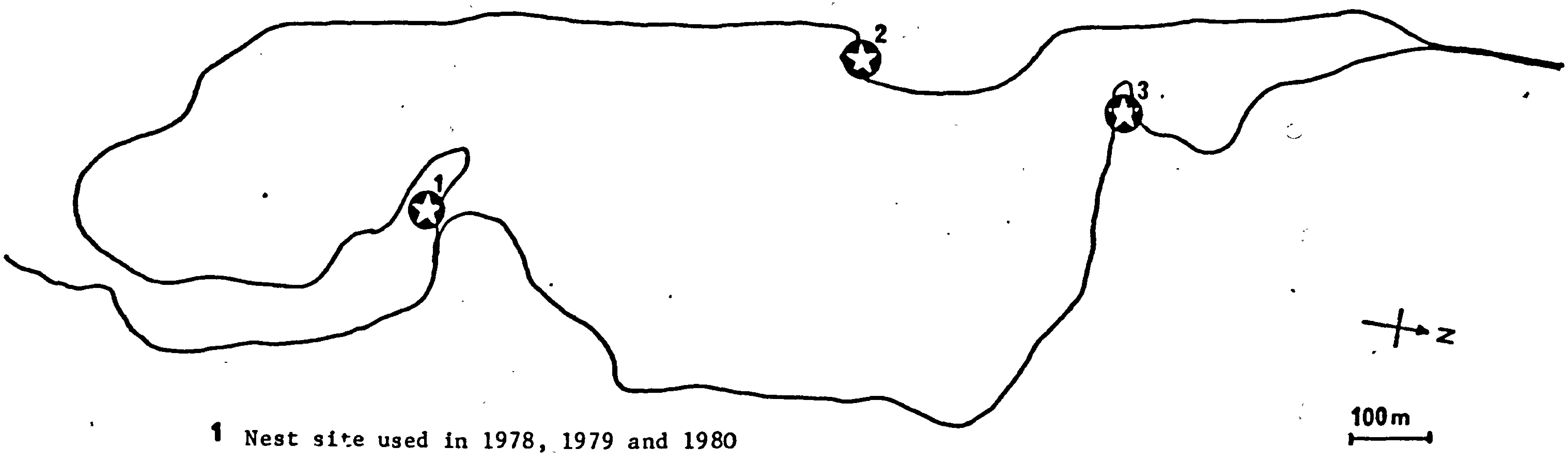
Myvatn is famous for the abundance and diversity of its waterfowl; fifteen species bred there in 1975-76 (see Gardarsson 1979). It also holds a large moulting flock of Whooper Swans and several pairs breed in the immediate vicinity.

7.2.2 Arnarvatn

Arnarvatn is a small lake with a surface area of about one square kilometre, about four kilometres south-west of Lake Myvatn (see fig. 7.1 and 7.2). It supports a high population of waterfowl during the summer, but freezes over completely in winter. It is very shallow, probably no more than three metres at the deepest point, (mapping data are not yet available) and supports good growth of Potomogeton sp., Myriophyllum sp. and Cladophora sp. It is surrounded by heaths (sheep grazing) and some agricultural land (pasture and hay crops). Two or three pairs of Whooper Swans breed annually.

7.2.3 Ellithavatn

Ellithavatn is a lake about 15km to the south east of Reykjavik. It has a surface area of 1.8km^2 and is 74m a.s.l.; its maximum depth is 7m (see fig. 7.3). It appears to be a staging post for early arriving Whooper Swans, and one or two pairs attempt to nest annually (pers. obs.)



1 Nest site used in 1978, 1979 and 1980

2 Nest site used in 1979 and 1980

3 Nest site used in 1978 and 1980, nest begun but not used in 1979

Fig. 7.2. Map of Arnarvatn showing nest sites

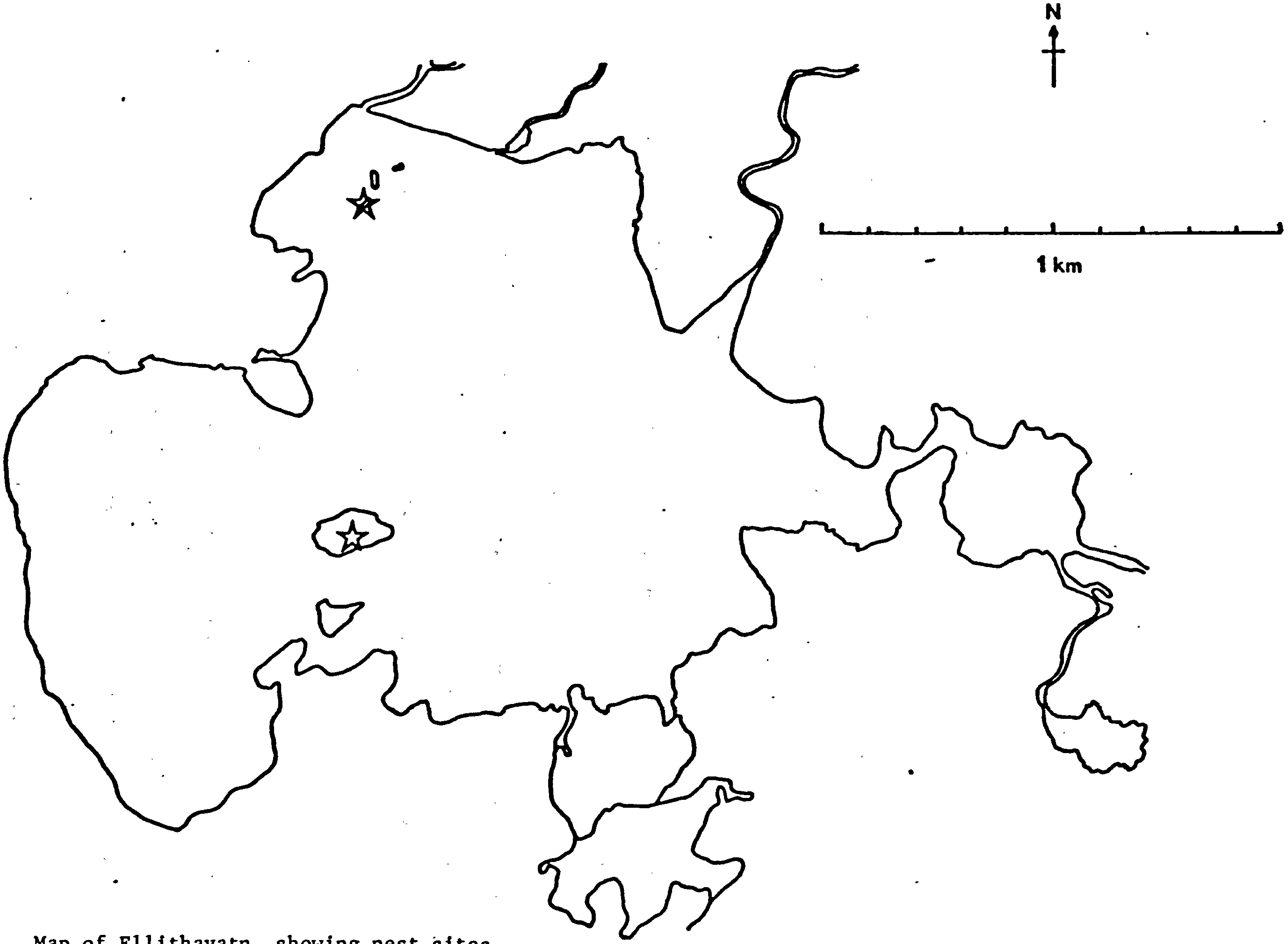


Fig. 7.3. Map of Ellithavatn, showing nest sites

7.3 Habitat Selection

Whooper Swans usually use lakes with a surface area of less than $1km^2$. They commonly nest at eutrophic or mesotrophic ponds or lakes where there is abundant food, but they somtimes nest at oligotrophic and dysoligotrophic lakes or peatlands with ponds. Likewise the Trumpeter Swan uses eutrophic ponds in Alaska, but some also nest in Carex sp. areas probably similar to the Finnish dysoligotrophic sites (see Hansen et al 1971; Blomgren 1974; Haapanen et al 1977).

7.4 Nest Site Selection and Nest Construction

Cramp and Simmons (1977) record that Whooper Swan nests are usually sited "close to water, on bank of pool, or commonly on islet or promontory; snow-free and dry before thaw, but sometimes in shallow water afterwards". During the present study at Lake Myvatn, 19 nest attempts were known over three years (see table 7.1). All were within five metres of water. Six were on islands, five were on promontories, five on lake shores or river banks and three were in marshes.

In general, all swan species nest as close to water as possible, preferring sites which afford some natural protection such as islands or promontories, or affording a view such as raised hummocks, or in many cases both. Water obviously provides extra protection from predation or disturbance, and it has been shown by Hammond and Mann (1956) that the nesting success of many Anatid species is markedly better on islands than on the mainland.

In this study 73.7% of nests were partially or completely surrounded by water. The three nests (one in each year of the study) in the marshes

Table 7.1

The location of nest sites in the Myvatn area in 1978, 1979 and 1980

Location	1978	1979	1980
Island	1	3	2[1]
Promontory	1	2	2[2]
Lake/river bank	1	2	2[2]
Marshes	1[3]	1[3]	1[3]
Total	4	8	7

[1] One nest site known, other assumed

[2] two assumed

[3] nest not found in any year, but whole area was marshy

could not be pin-pointed, because of the impenetrability of the area, however, these were the only nests which could have been sited in emergent vegetation. This is in contrast with the closely related Trumpeter Swan which commonly nests amongst emergent vegetation, the site often bounded by a moat of water, and on semi-floating sedge mats.(Banko 1960, Hansen et al 1971). The other congeneric northern species, the Bewick's Swan, according to the scanty account in Cramp and Simmons (1977) is less attracted to islands and promontories and chooses a site "on dry elevation, bank or hummock, selected as snow-free before thaw, sometimes in standing water after the thaw". The widely studied Mute and Black Swans also select sites on islands or headlands or in or near running or standing water (e.g. Campbell 1960).

Nest building was done mainly by the female, but the male helped by pulling up vegetation and passing it closer to the nest. Material was added to the nest even during incubation by the female, and sometimes by the male when the female was off the nest. The male's nest building behaviour was not always productive, since it was not always directed at the nest. The success of the behaviour depended on the male's orientation with respect to the nest, since any material the male pulled was passed backwards over his "shoulder" and deposited by his flank. On occasions, when the male was facing towards the nest mound, this led to material being moved further away from the nest, not closer.

A substantial mound was built at each site and was invariably of the common plant species available in the immediate vicinity, usually grasses, sedges and mosses. The nest at Selhagi also contained dried stems of <u>Angelica</u> <u>sp</u>. which grew commonly on the nest island. The dimensions of four nests were roughly 1m across, 30cm high, with a cup of 30cm diameter and 5-10cm deep. These were evidently very similar to the nests measured by Bulstrode et al (1973), although his were up to 20cm deep. Nest mounds became somewhat flattened during the incubation period due to the weight of the sitting females and of the males which occasionally stood on the nest rim during female absences. All nests which were examined closely (n=6) contained swan down scattered throughout the material forming the upper part of the nest mound. There appeared to be no greater tendency for down to be in the cup as a lining, than elsewhere in the mound. Down appeared to be added throughout the incubation period. It was dispersed throughout the nest by the female's regular movement of nest material to cover the eggs before incubation breaks.

7.5 Clutch Size

Clutch sizes have been reported for the Whooper Swan ranging from 4-7 in U.S.S.R. (n=7) (Dementiev and Gladkov 1952) and from 3-5 in Iceland (n=9) (Scott et al 1972). Thus it is seemingly possible to assign large broods (on the basis of clutch size data) to the continental population (see Cadbury 1975), but observations of broods of six and eight in Scotland and of seven in Iceland certainly indicate that larger clutches may also occur in Iceland (Brazil and Spray in prep.). It was suggested by Brazil and Spray (ibid.) that the ranges of clutch size for both the Icelandic and the Fenno-Scandian/Russian populations completely overlap and that previous samples have been far too small to be representative. In fact Haapanen et al (1973 b) recorded a clutch range of 2-7 from Finland although again the sample was a small one (n=18).

Clutch size in the Anatidae is known to decline during the breeding season for a variety of reasons including; reduced hormone levels, reduced stimulation from temperature or photoperiod, re-nesting, exhaustion of female energy reserves and first laying by females (Sowls 1955; Lemieux 1959; Wagner 1960; Hilden 1964; Dane 1966; Klomp 1970; Bengtson 1972; Johnsgard 1973; Eisenhauer and Kirkpatrick 1977). Clutch size in the Anatidæ also varies between years. Contrary to Lack's (1967) suggestion that food supply affects laying date, clutch size was found to be lower in poor food years by Bengtson (1971). Arctic breeders are particularly good examples of species whose clutch sizes are affected by weather conditions (Johnsgard 1973; Eisenhauer and Kirkpatrick 1977), clutch size being lower in late seasons (e.g. Milne 1976). With so many variables involved, it seems inevitable that small samples of clutch size are unlikely to prove informative, and without much more information available it is not safe to draw conclusions from the apparent differences between populations.

During this study only five clutches were observed in Iceland. These included a single clutch of three, three clutches of four and one clutch of five; these fit exactly within the range quoted by Scott et al (1972) but once again the sample size is very small.

7.6 Nesting Success

7.6.1 1978

Five pairs were found at three localities in the Myvatn area in 1978 (see fig. 7.1). At Arnarvatn, two pairs each produced four cygnets and a third pair produced three cygnets (see fig. 7.2). At Helluvathstjorn, one pair reared four cygnets and in the marshes north-west of Neslandavik, one pair produced a single cygnet. This last family walked to

Neslandavik, but the cygnet disappeared within three days; other cygnets may have been lost on the way before the pair was located (see table 7.2).

All broods had already hatched when observations were begun. The total number of cygnets reared and known to be alive at the end of the study period (23rd August), was 15 from four pairs; i.e. a mean brood size of 3.75 per pair. A mean brood size of 2.5 was recorded the following winter from the Scottish study areas.

7.6.2 1979

The spring of 1979 was very cold in Iceland. Initial observations were made in the south of Iceland until snow-melt began in the north. Two pairs were observed at Ellithavatn, just outside Reykjavik. One nest was accessible and contained four eggs on 26th May. Unfortunately both nests were deserted at some time during June, probably due to disturbance by members of the public who visit the lake for recreation.

Eight pairs were found at six localities in the Myvatn area in 1979 (see fig. 7.1).

The first pair to nest was at Selhagi, at the east side of the Bolir, Lake Myvatn. The pair there had five eggs by 6th June, but desertion occurred following irregular attendance by the male. The nesting bay was examined and very little food was in evidence, only Cladophora sp. was visible and only in very small quantities. The male may have been forced to leave the area to feed.

Table 7.2

Brood sizes in the Myvatn area in 1978, 1979 and 1980

Brood size	1978	1979	1980
0	0	4	0
1	1	1	0
2	0	1	1
3	1	2	2
4	3	0	4
Number of pairs with eggs	5	4	7
Number of cygnets	16[1]	9	24
Mean brood size	3.0	1.1	3.4

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[1] One cygnet disappeared

At Arnarvatn, a pair was watched nest-building on an island at the north end of the lake on 3rd June, but the nest-site was flooded out by snow-melt on 5th June and the pair deserted. A second pair built a nest on a rocky ridge 1-2m above water level at Litlu Gautlond on the west shore. Four eggs were laid but none hatched, although they all contained fully developed embryos. This pair was thought to have deserted only two or three days before the eggs were due to hatch. A third pair nested on a promontory on the east shore. They had three eggs by 8th June and they subsequently reared three cygnets (see fig. 7.2).

Other waters in the area which held pairs were Büthlungafloi, where one pair reared three cygnets; Helluvathstjorn, where a pair had built a nest by 12th June when much of the lake was still frozen (it is about 300m a.s.l. compared with Arnarvatn at about 250m a.s.l.) but this was deserted, no eggs having been laid by 1st July; and Graenilaekur, where a pair had four eggs by 14th June, but only reared two cygnets (two eggs were addled). In the marshes, north-west of Neslandavik, a pair reared a single cygnet. Access to this area was very difficult and the nest was not found.

The total number of cygnets reared and known to be alive at the end of the study period (15th July) was nine from eight pairs, a mean brood size of 1.13 per pair (see table 7.2). Only four pairs successfully reared cygnets; two pairs laid no eggs, one pair lost a clutch of four eggs and another pair lost two out of four eggs. Although this is only a small sample it highlights the errors involved when calculating brood size from families in winter flocks. Under such circumstances all broods of zero are missed. In the study area in 1979 calculating the brood size based on successful breeders only would have produced an inflated mean brood size of 2.25 per pair. The mean brood size recorded in the following winter from the Scottish study areas was 1.3.

7.6.3 1980

Seven pairs were found in the Myvatn area in 1980. At Arnarvatn three pairs bred successfully, the nest sites were thought to have been the same as those used in 1979 (see figs.7.1 and 7.2). One pair produced four cygnets and the other two each produced three cygnets. The pair at Helluvathstjorn reared two cygnets as did the pair in the marshes north-west of Neslandavik and the pair at Graenilaekur (see table 7.2). A total of 24 cygnets were reared by seven pairs, all of which bred successfully. The mean brood size was 3.4 per pair.

7.7 Conclusion

The breeding grounds of the Whooper Swan are readily accessible at the western extreme of the species' range, yet only one extensive study of breeding biology and behaviour had previously taken place (Haapanen et al 1973 a,b, 1977). The critical factor affecting the distribution and breeding success of both the Whooper Swan and the congeneric Trumpeter Swan is the ice-free period. Only a small proportion of the population breeds and reproductive output varies greatly from year to year. Nests are usually close to water on banks, promontories or islands of rivers or small lakes.

Study sites in Iceland are described and details of the siting and construction of nests found during the study are given.

Although the ranges of clutch size which appear in the literature indicate that it should be possible to identify Icelandic from Fenno-Scandian families on the basis of size, observations of large broods in Scotland and in Iceland suggest that this is not possible and that the information currently available is not representative.

Clutch size in the Anatidae is extremely variable and dependent on several factors including weather and food supply. Similarly, nesting success and brood size are variable from year to year, the former is probably more dependent on the timing of spring and the conditions of the parents, whereas the latter is probably more dependent on weather conditions and food availability during summer and autumn. The measurements of brood size in Scotland corresponded well with brood size records from Iceland during the preceding summer, and indicated that reductions in family size occurred through factors operating during the breeding season and autumn migration, rather than through winter mortality. The same seems to be true of the Bewick's Swan (see Evans 1979).

CHAPTER EIGHT: BREEDING BEHAVIOUR

8.1 Introduction

Behaviour associated with breeding commences before the spring migration with increased feeding and fat deposition (see Dorst 1971; Owen 1980). Whereas most migrants are able to replenish their energy supplies after migration and before breeding, in many arctic breeding species, including swans and geese, this is not the case. They must store enough fat to last them through nest-building and incubation before they will have the opportunity of good feeding again. Many such species begin nesting almost as soon as they arrive on the summering grounds and breeding occurs in a rush during the short intense summer (see Ogilvie 1978).

Long-lived, monogamous species such as arctic nesting swans and geese, exhibit a high degree of behavioural co-operation; both individuals of each pair gain by investing time and effort in their offspring, not just during incubation and fledging, but also during the winter.

The aim of this chapter is to follow the behaviour of the Whooper Swan, as it relates to breeding, from the beginning of the nesting period with territorial defence and copulatory behaviour, through the incubation period with its division between male and female behaviour, to the fledging period when both parents are active in caring for the brood.

All white swans are strongly territorial, defending a nest site and an area around it suitable for the young to feed in (Kear 1972). Recent work by Haapanen et al. (1977) has shown that some Whooper Swan pairs hold a territory until their eggs hatch, then move their families to feeding sites some distance away from the natal area. During the Finnish study the density of Whooper Swans was so low that only one intrusion by an 'outsider' was recorded; no interactions were observed which involved other breeding pairs.

For the purposes of this study, the term inter-pair territoriality or display refers only to interactions between breeding pairs. Other displays are termed 'interactions with intruders', because only one of the interactive birds has a territory and the territorial birds often overflew the boundaries of their territory (as defined during interactions with adjacent breeding pairs) whilst chasing intruders. Aerial chases did not occur between members of adjacent pairs.

There are no published records of inter-pair territoriality in the Whooper Swan. This is probably because of the understudied status of the species and its low density on the breeding grounds. The factors limiting the size of the breeding population are not known, although it is known that the proportion surviving until breeding age is only about 20% (Brazil and Petersen in prep.). Large areas of their range are apparently suitable, but unoccupied. Although Scott et al (1953) recorded only 20 pairs in an area of 11,400 hectares in Iceland, Kear (1972) suggested that the true territory size in both Whooper and Bewick's Swans has been exaggerated. Especially in the upland areas of Iceland large areas which do not hold swans are probably unsuitable as nesting habitat because of poor availability of food. It seems that Whooper Swans in Iceland defend small areas (pers.obs.) and territory size is likely to be even smaller than the 570 ha. per pair calculated by Kear (1972).

There are no published records of more than one pair of Whooper Swans nesting at the same pond or lake. Consequently, observations made on three pairs nesting at Arnarvatn, a lake south-west of Lake Myvatn, are of particular interest. Direct inter-pair territorial behaviour was observed as well as frequent observations of conflict between pairs and intruders, and a new behaviour sequence was recorded. As in Haapanen et al's (1977) observations, pair/intruder conflict almost invariably resulted in the intruder being chased and expelled from the nesting area. In this instance the Trumpeter Swan seems to be very similar to the Whooper Swan, in that Hansen et al (1971) reported only four known cases where more than one pair of Trumpeter Swans nested at a single body of water. All involved large lakes where nests were well separated and no intra-specific defence was observed. Hansen et al (1971) also noted that aggressive behaviour towards other swans was lower after hatching and during wing moult. This could be due either to seasonal changes in the numbers of other swans moving about or to a real decline in aggression.

A variety of types of breeding Whooper Swans was observed in Iceland: quiet pairs occupied a site for a period in early summer without building a nest; noisy pairs occupied and vigorously defended a territory against intruders, sometimes built a nest but did not lay eggs; breeders occupied a territory, built a nest and laid eggs; failed breeders were those breeders which lost eggs or young.

Previous studies by Bulstrode et al (1973) and Haapanen et al (1977) concentrated on general aspects of breeding behaviour and did not look at the interactions between family members. It is generally assumed that parental care, important during the early life of young animals, declines as they mature. The questions asked here are: how does this occur? is it a continuous process? does it vary according to the sex of the parent? and is there a different pattern of investment during fledging from that during incubation? The aim of this study was to examine how parents apportion their investment; whether they are consistent in providing protection and proximity; whether the maturation of the cygnets leads them to initiate movement away from their parents and whether this leads to measurable increases in inter-cygnet and parent to cygnet distances during the fledging period.

8.2 Methods

Detailed behavioural observations were made at Arnarvatn, of three families between 9th July and 23rd August 1978 and of two pairs during the incubation period between 1st June and 15th July 1979. Two pairs were studied at Ellithavatn between 23rd and 26th June 1979 and one at Selhagi from 29th May until 9th June. Observations at Ellithavatn and Selhagi were made from behind lava hummocks, while those at Arnarvatn were made from a portable hide. The hide was erected on a hillside overlooking the lake in such a position that nest sites and the main areas used by each pair or family could be watched simultaneously. To be able to do so, proximity to the birds had to be sacrificed. The hide was used as a shelter from bad weather, the birds not apparently being disturbed by humans at such long range.

Observations were made using a tripod-mounted telescope over a range of more than 600 metres. It proved impossible to keep all of Arnarvatn in view from a single vantage point and at times birds moved into 'dead-ground'.

Standard time-budgeting techniques were used; the time interval between sample scans was altered to suit the conditions and the activities of the birds. During the incubation period (1979 field season) the time interval between scans was one minute. The distance of each bird from its nest and its behaviour were recorded at each scan. Observation periods were usually of six hours and were shifted forwards by six hours each day, in order to regularly cover the 24 hr. period.

During the fledging period (1978 field season) scans were made at 30 minute intervals. The behaviour of each family member was recorded at each scan (see below), as were the distances between the parents, between the cygnets and from each cygnet to its nearest parent. Distances were estimated in metres, using the length of adults as a guide and making allowance for distorted perspective. Inevitably errors in estimation of distance occur increasingly as distance increases, however, this was a constant factor affecting all the observations and no objective method of measuring was possible under the circumstances in the field. Between scans, sketch maps were compiled of the movements of the families, and data were collected on the length of feeding and vigilance bouts.

All behavioural categories recorded were mutually exclusive. Distance from the nest and whether the female was on or off the nest were recorded as additional information. Sixteen behavioural categories were recorded for males and 21 for females. These were as follows:

Head-up: head well above the level of the body; neck extended and more or less vertical.

Preening: feather maintenance; also includes other comfort movements such as wing flapping (when not displaying) and defaecation.

Dipping: feeding by submerging the head and neck. The body remains horizontal.

Upending: feeding by submerging the head and neck. The body is vertical.

Grazing: feeding on land, on grasses or sedges.

Picking: feeding by picking items off the water's surface with the bill pointing downwards.

Dabbling: feeding from, or just below, the water's surface. The bill is held horizontally.

Eat emergents: feeding from vegetation emerging above the water's surface.

Feed from edge: feeding from plants along the shore, whilst remaining on the water.

Nest fixing and pulling material: includes movement of material composing the nest mound or rim, and the gathering of new material by pulling up vegetation.

Settling or moving: includes movements such as turning on the nest during incubation and when settling on the nest after an incubation break, or when shuffling onto the eggs after rolling them.

Egg care: rolling or moving the eggs with the bill whilst standing over them.

Covering the eggs: pulling nest material over the eggs before leaving the nest.

Drinking, Bathing, Roosting, Flying, Off the Nest and Displaying are all self-explanatory. For full description see section 8.3 .

Males were not recorded incubating during this study, thus certain behavioural categories, for example settling, egg care, off nest, etc., are only relevant to females. A slightly different behavioural repertoire was recorded for each individual, for example the southern male at Arnarvatn was not seen to dabble, eat emergents, or to feed from the edge; the western male at Arnarvatn was not seen to drink, or bathe and the western female was not seen to pick or drink. The spot sampling method of behavioural recording is not fully effective at representing very infrequent behaviours, hence although certain behaviours were not observed, they may have occurred, but were not picked up by this method, or they occurred outside the observation periods. It should be noted that the category 'out of view' applies to the bird being out of my view. It was not necessarily out of visual contact with its mate or the nest, although this was also possible.

On 30th July 1980, during a ringing expedition to Myvatn, a brief check was made on the amount of time broods spent with each parent. Three families were watched for a total of thirty minutes each. The parent which the cygnets were closest to during the last 10s of each minute was recorded. One family was watched at Graenilaekur from the pseudo-craters on the south shore of Myvatn, and two families were watched at Arnarvatn from the location used in 1978 and 1979.

8.3 Displays

A total of 96 display sequences were recorded during the breeding seasons of 1978 and 1979: 27 were between breeding pairs, 27 were greeting or triumph ceremonies and 42 were directed at intruders (table 8.1). More displays at intruders and fewer territorial displays were recorded during the incubation period than during the fledging period. Unfortunately, the difference between the parts of the breeding season was confounded by

Table 8.1

Frequency and context of displays, at Arnarvatn

	At intruders	Territorial	Greeting/Triumph	Total
1978	16	17	18	51
1979	26	10	9	45
Total	42	27	27	

The difference between years was significant (Chi sq=6.85, $p<0.05$)

the difference in years during which the observations were made. The incubation period was studied in 1979; the fledging period in 1978. The difference in the numbers of different displays between years was significant (chi sq. = 6.85, $p<0.05$).

The summer of 1979 was cold and followed an exceptionally late spring. A high proportion of the Whooper Swans breeding in the highlands were thought to have failed and cygnet production was exceptionally low (see 3.1, 3.3, 7.6.2; Brazil and Kirk in prep.). The intruders recorded at Arnarvatn were probably unsuccessful breeders moving to the Myvatn moulting flocks. They were often only observed because of the violent response of the study pairs.

During the incubation period females rarely left the nest and males usually remained in the immediate vicinity of it; thus there was little opportunity for inter-pair aggression. Unsuccessful breeders making their way to moulting flocks disturbed breeders when they attempted to overfly or land in their territories. During the fledging period families moved about their territories feeding; there was therefore a greater opportunity for inter-pair aggression. Most other adults were in moult during this period, consequently fewer were likely to pass over territories and disturb breeders.

I suggest it is more reasonable, therefore, to suppose that the differences in display frequencies were due to differences in intruder frequency and parental behaviour at different stages of the breeding season; not to differences between the years. (The function of territorial defence is discussed in 8.7).

8.3.1 Descriptions of Displays, especially those used in Territorial Defence

There are interesting general and specific differences between the displays used by the two major genera of swans, Cygnus and Olor. For example, although both groups use wing flapping as an expression of aggression, the Olor group also tend to raise their secondaries, while the Cygnus group ground-stare, bowsprit, head-throw and carpal flap. (These are fully described later in this section.)

Although the general nature of the sequencies of behaviours involved in the displays of the northern swans have been well documented by Banko (1960), Johnsgard (1965), Hansen et al (1971) and Haapanen et al (1977), the details of those involved in the Whooper Swan's displays have not been well documented and references to intra-specific aggression invariably apply only to interactions with non-breeding intruders, not between adjacent territory holders (see Cramp and Simmons 1977). Neither Banko (1960), Hansen et al (1971), Haapanen et al (1977), nor Cramp and Simmons (1977) record intra-specific defence of the territory by either the Trumpeter or the Whooper Swan.

In this section various aspects of Whooper Swan displays and a previously unknown behavioural sequence are described.

The basic aggressive or threat display has been described by Johnsgard (1965) and Kear (in Cramp and Simmons 1977) as comprising ruffled neck-feathers, wings closed or slightly spread, accompanied by ground staring or with the head submerged. This escalates to hissing and wing shaking, with wings flapped from the carpals. The neck is bent and extended repeatedly, often while calling.

I have classified the social behaviour of the Whooper Swan into five broad categories, these are:

A. <u>Preflight Behaviour</u>

the usual components of which are:

1) Head pumping; the head is rapidly raised and lowered by several centimetres, while the neck is stretched up vertically (see Johnsgard 1965). Also called head-tossing (see Raveling 1969).

2) Increased calling.

3) Wing flapping; the whole wing is spread and flapped vigorously once or twice.

B. <u>Aggressive Behaviour</u>

the usual components of which are:

1) Ground staring; the neck is strongly arched and the bill pointed at the ground and held a few centimetres above it. The neck appears rigid (see Kear 1972).

2) Bowspritting and head-throwing; the neck is held stiffly forward at approximately 45° from the horizontal. This position is often held only briefly; the neck relaxes, then both the head and neck are jerked forwards again.

3) Carpal flapping; the carpals are held away from the body and the 'hand' is flapped vigorously (see fig. 8.1). This is often accompanied by bowspritting, with the neck being alternately extended and relaxed

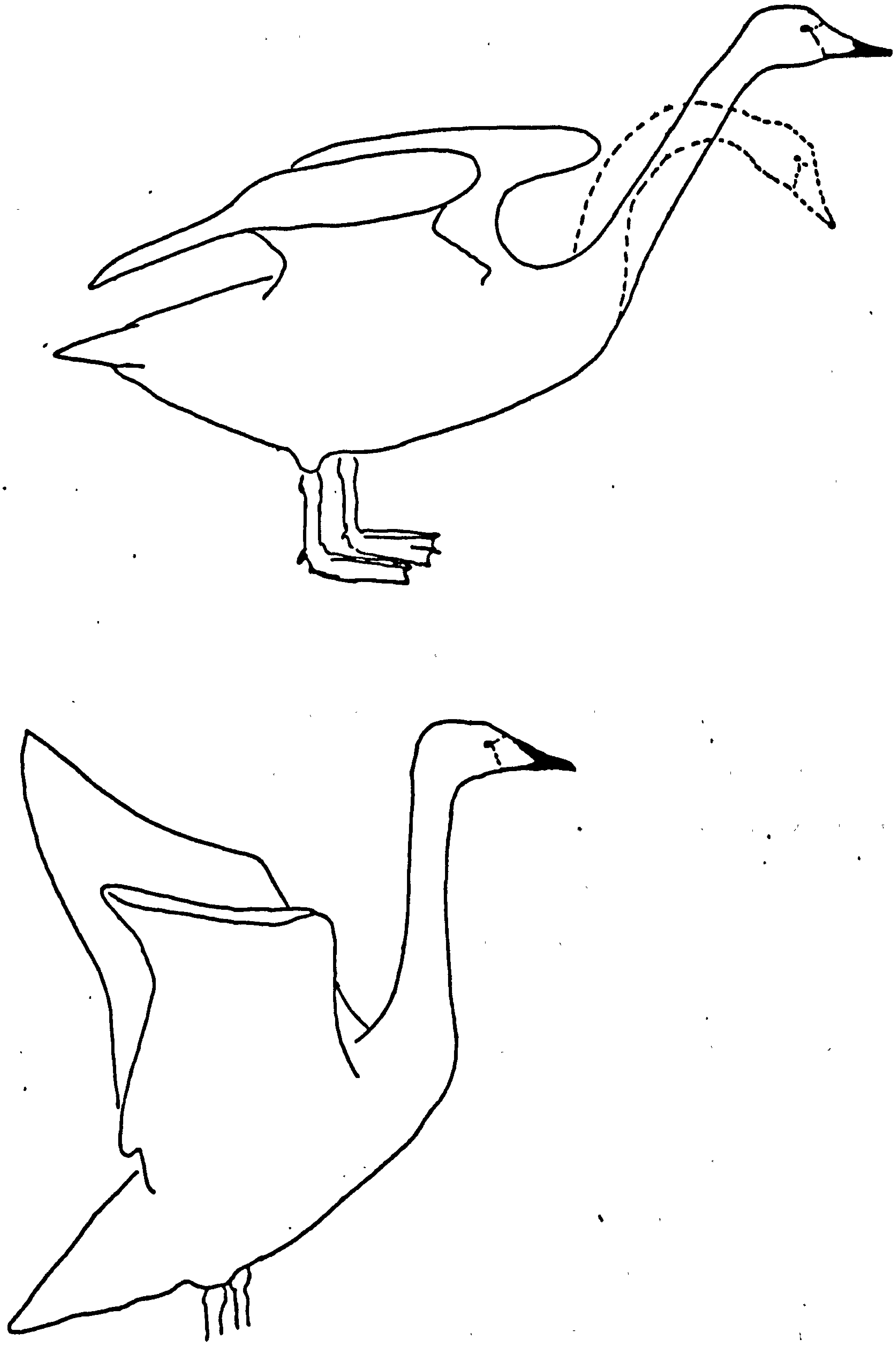


Fig. 8.1. Sketches of 'carpal flapping' and 'bowspritting' (upper), and of 'full wing flap' (lower)

(see fig. 8.1 and table 8.2). Also known as wing quivering (Kear 1972; Cooper 1979).

C. Territorial Display between males (see table 8.3) the usual components of which are:

1)	Head up;	a general vigilant or alarmed posture.
2)	Approach;	one bird begins to swim towards a second.
3)	Run/Patter/Fly;	one bird begins the normal take-off sequence by running along the surface beating its wings (most of the weight appears to be borne on the feet), this may develop into Pattering (almost airborne; the weight is taken by the wings, the feet paddle loosely along the surface of the water). The bird may actually become airborne in extreme cases. These three are sequential and depend on the distance travelled. Flying in these circumstances only lasts for a few wing beats.
4)	Turn;	on ceasing (3), the bird turns in a tight circle to face back the way it has just come.
5)	Head dip or head plunge;	this may occur as the bird turns or immediately afterwards. Head dipping appears to be the same as Ground Staring (B1 above), just the head is submerged. Head plunging is more vigorous, both the head and the neck are submerged.
6)	Swim away or Butterfly;	the bird either swims away normally after the turn or it may use what is most simply described as a Butterfly stroke. Both wings are spread out

Table 8.2

The sequence of behaviours involved in aggressive displays

	Behaviour		accompanying behaviours	optional components
A.	Groundstare	1.	Wings closed or Wings half spread	
		2.	Hissing	
		3.	Neck feathers raised	
		4.	Carpal flapping	
B.	Bowspritting	5.	Wings half or three-quarters spread	
		6.	Head throwing and calling	
		7.	Carpal flapping	
		8.	Antiphonal calling	
		9.	Synchronized calling	neck rigid
C.	Head-up	10.	Full wing flapping	
		11.	Antiphonal calling	
		12.	Synchronized calling	

Arrows show alternative sequences.

A and B (without C) represent the Greeting or Triumph ceremony

Table 8.3

The sequence of behaviours involved in territorial displays

	Behaviour	accompanying behaviours	optional components
A.	Head-up		Bowsprit Headthrow
B.	→Run/Patter/fly towards opponent		Turn
C.	Head dip or Head plunge	1 Wings spread on the water	
D.	└ Swim Away		Raised wings Head back Butterfly
E.	Triumph Ceremony		

Arrows show alternative sequences.

on the surface of the water, raised and thrust forward, then down into the water and pulled backwards in rapid succession, like the flailing motion of the swimmers' stroke (see fig. 8.2). One instance, interpreted as extreme aggression was observed where instead of the normal alternation between antagonists run-pattering towards each other, the aggressor flew right up to the second bird and grasped hold of it with its bill. A chase ensued along the water surface whilst the aggressor maintained its grip. The aggressor finally released its hold and turned away using the Butterfly stroke. The second bird began calling and bowspritting.

D) Threat Display at the Nest (to man, dogs and sheep) (see table 8.4) is usually comprised of:

1) Head-Up, or Head low by the female on the nest.
2) Ground stare.
3) Wings spread.
4) Wing beating.

E) Greeting or Triumph Ceremony (On rejoining mate after absence, disturbance or other forms of display) (see also Kear 1972)

is usually comprised of:

1) Head-up, Bowsprit and/or head-throw
2) Calling; this may be synchronized or antiphonal (Craggs 1974)
3) Wing flapping.
4) Often accompanies or follows a rush together of the pair.

Table 8.4

The sequence of behaviours involved in threat displays whilst at the nest

	Behaviour	accompanying behaviours	optional components
A.	Head low (female only)	sitting on the nest	
B.	Stand (female only)		
C.	Head-up (male and female)	1. Wings half spread	
		2. Neck rigid	Neck feathers raised
D.	Groundstare		
E.	Lunge		Hiss
F.	Raise or hang wings		
G.	Full wing flap		

Arrows show alternative sequences

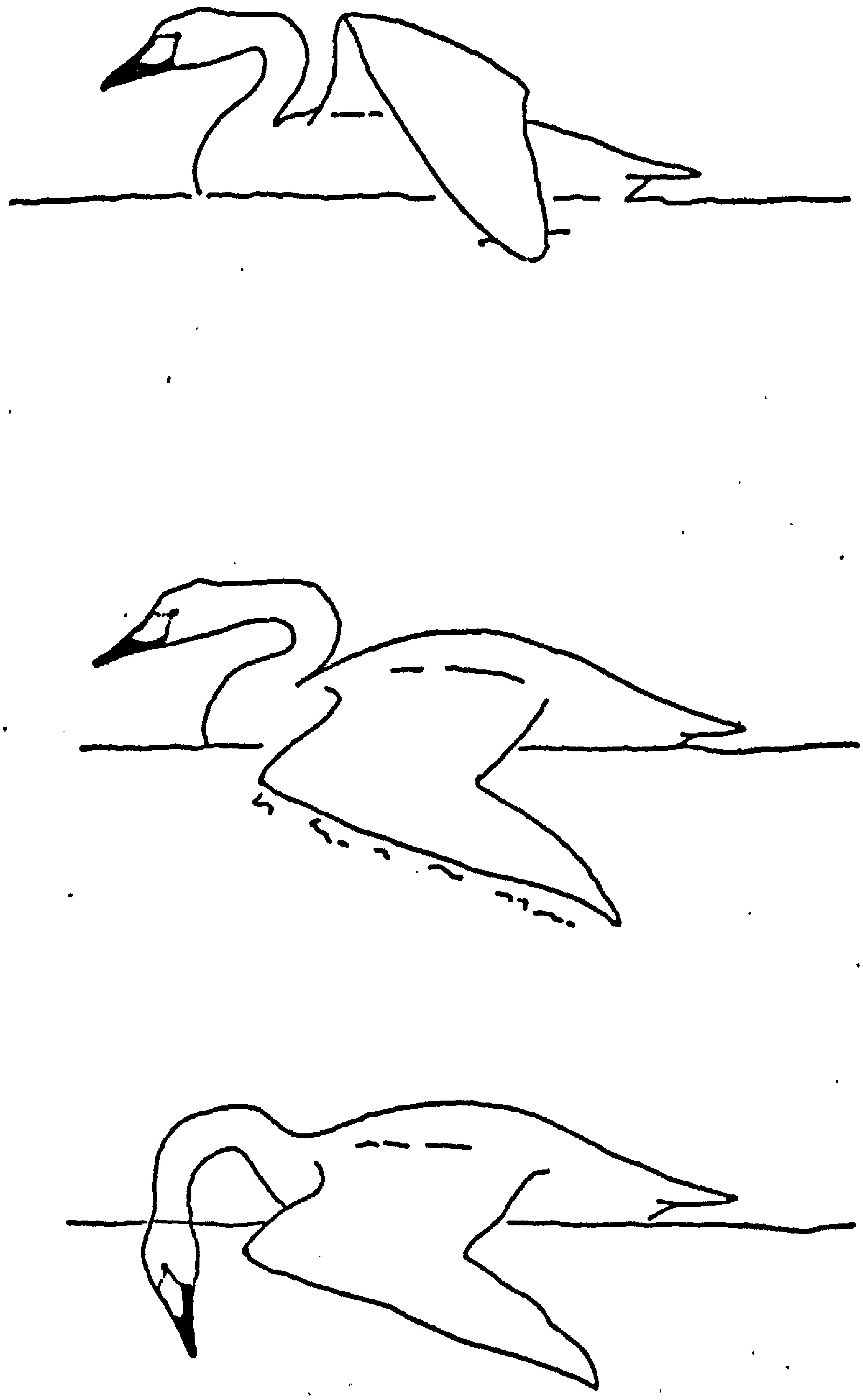


Fig. 8.2. Sketches of the 'Butterfly stroke' and of 'head plunging'.

The interactive display between adjacent territory-holding Whooper Swans is of interest not only because it represents an undescribed sequence of behaviours, but because this sequence includes a completely undescribed behaviour, namely the Butterfly stroke.

Such interactions were regarded as having begun when a bird previously in the head-up posture suddenly began to swim or fly towards a member of the adjacent pair. Flights were usually terminated at some distance from the second bird, the aggressor then either took a separate short flight or ran/pattered, noisily along the water's surface towards the second bird. On stopping, or landing, the aggressor usually turned on the spot, to face away from the second bird. The second bird usually reacted by flying or run/pattering towards the aggressor. From here on the description applies to both individuals with the second individual usually repeating the aggressor's behaviour one step behind.

The aggressor, having turned, usually head-dipped or head plunged, the wings were frequently spread out flat on the surface of the water at this stage. The aggressor then usually swam away, either raising its wings, with its head and neck low and back along the body (fig. 8.3), or "Butterfly"-ing (fig. 8.2). Swimming away was either followed by a repetition of the sequence beginning with run/patter/fly, by a greeting or triumph ceremony, or by feeding.

8.4 Copulation in the Whooper Swan

During the winters and springs of this study (1977-1980) surprisingly little social behaviour was observed. No behaviour indicative of pairing or mating was observed on the fields and there are no published records of

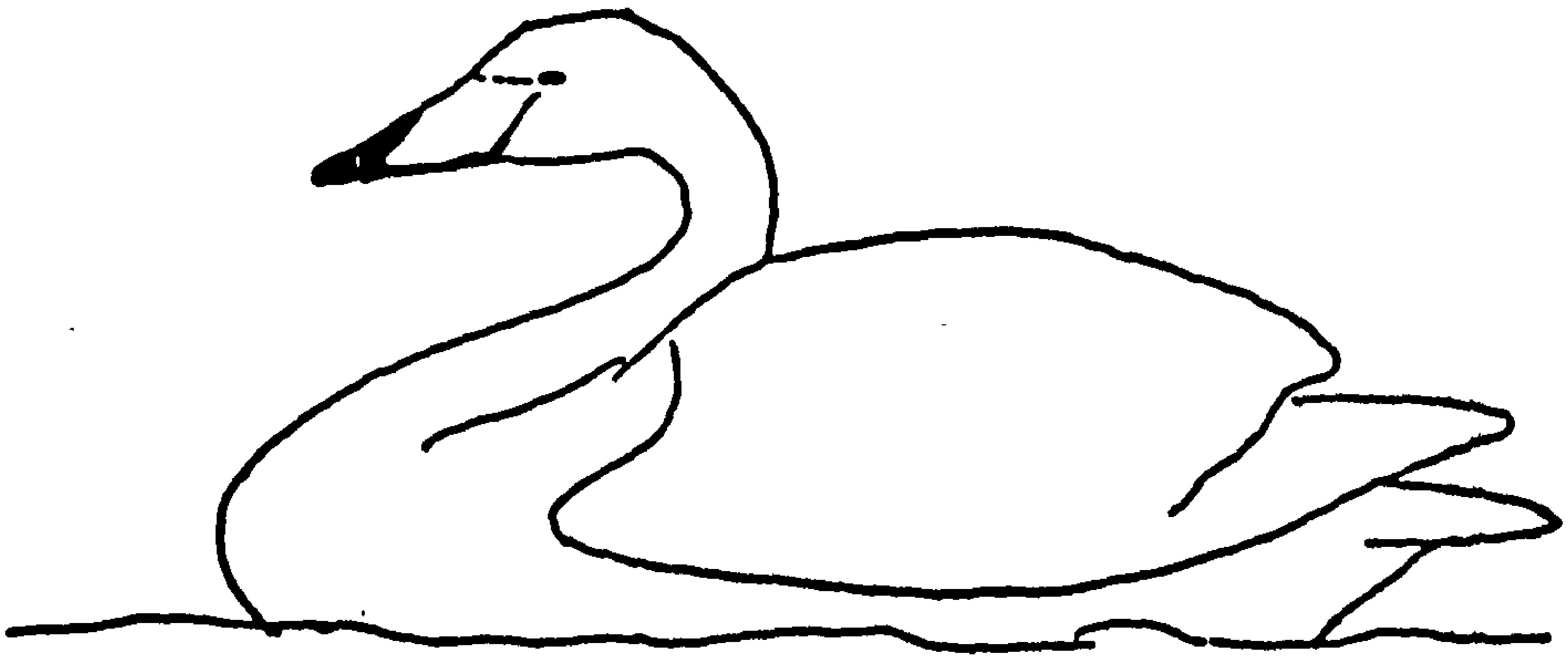


Fig. 8.3. Sketch of 'raised wings with head back.

matings having been observed in the wild in Britain.

The main problem with observing the mating behaviour of any animal is its brevity. In the case of the Whooper Swan the difficulties are increased since it has not been established when mating occurs; whether it occurs prior to arrival in the breeding area or actually at the nesting site; or whether a single, or multiple copulations are required for each clutch. Consequently, it is difficult to look for this behaviour. However, during the summer of 1979, two copulations were observed in Iceland; these are described below.

Johnsgard (1965) described the pre-copulatory display as consisting of a short bout of synchronised head-dipping only 10-15 s. before mounting, and the post copulatory display as rising, calling and turning. Although these elements were observed in Iceland, they were part of a longer train of behavioural events leading directly to copulation (pers. obs.).

1) Ellithavatn (near Reykjavik) 24th May 1979 (see fig. 7.3)

The female was already spending some time in attendance at a nest on a small island. It is not known whether eggs had been laid. 1032 hrs: the female chased 12 adults onto another part of the lake, after which she landed and began to head-dip, her wings were half spread and lying on the water's surface. She regularly raised her wings and beat the water with them. 1034 hrs: both male and female displayed, approximately 30 m apart, they bowspritted and called (see section 8.3.1). 1035 hrs: they swam towards each other and at 1036 hrs they repeated the display, this time only 1 m apart. 1038 hrs: both male and female were head dipping and splashing. This involved lunging forward vigorously so that the lower neck and breast became submerged and water ran across the back of the neck. Their movements were synchronised. 1039 hrs: the male mounted the female from the side, grasped her neck feathers in his bill and held her neck down in the water. 1039^{30} hrs: both called, the male slid from the female's back and they turned to face each other with their necks arched, still calling. The female then sat back in the water and flapped her wings, as is often the case after bathing. By 1040 hrs both were preening whilst standing in shallow water near the shore of the nest island.

2) Selhagi (Myvatn) 30th May 1979 (see fig. 7.1)

A complete nest had already been built, but it was not known whether any eggs had been laid. 1505 hrs: the male was feeding about 5 m north of the nest; the female was roosting on the nest. Both became head-up and at 1507 hrs the female left the nest and swam away to the north-west. 1508 hrs: the male was 10 m and female 20 m north of the island. 1509 hrs they swam towards each other and began to bathe, alternately lunging forward into the water, as described above in 1). The male mounted the female from the side, whilst holding her nape feathers in his bill, her head was held under water by the male during copulation. The female shuffled from side to side and at 1510 hrs the male slid from her back and rapidly flicked his tail from side to side. The female, meanwhile, preened and wing-flapped. The male proceeded to preen in the shallows at the north end of the nest island while the female tail wagged. From 1512 to 1516 hrs the male stood head-up in the shallows while the female preened. The female then gradually moved towards the nest rim, pausing to preen briefly. She finally resettled on the nest at

1519 hrs, at which time the male was still preening.

These two copulations described from Iceland differ slightly from Johnsgard's(1965) description of copulation in the Trumpeter Swan, in that the pre-copulatory display involved not only head-dipping, but also thrusting the lower neck and breast forwards and down into the water so that water ran across the back of the neck (Ellithavatn) and onto the back (Selhagi). The pre-copulatory display was short, less than one minute, as was copulation itself. At Ellithavatn, the pre-copulatory displays of the male and female were synchronised, whilst at Selhagi they were alternate.

In both cases mounting was from the side, the male grasping the female's nape and holding her neck close to the water, or submerged. In neither case did the male spread his wings as copulation ended, unlike the Trumpeter Swan (Johnsgard 1965). At Ellithavatn both male and female called, at Selhagi they were silent. After copulation at Ellithavatn, male and female turned to face each other with their necks arched as they called (see Johnsgard 1965), the female wing flapped then both birds began to preen. The male at Selhagi flicked his tail from side to side, the same movement usually occurs after defaecation, preening or bathing, while the female preened and wing-flapped. In both cases preening followed the post-copulatory display.

Copulation occurs very briefly and apparently on the breeding grounds thus reducing the likelihood of it being observed. Copulation by Whooper and Trumpeter Swans is very similar, but it appears that the post-copulatory display, like the territorial displays, is more extreme in the Whooper Swan than in the Trumpeter Swan.

8.5 Incubation

The long-term stability of the pair bond in swans probably serves to reduce the time and energy expended in pair formation prior to breeding each year, as was suggested for geese by Owen (1980), and leads to sharing of investment and marked sexual differences in behaviour. Incubation, for example, is usually by the female alone in the Whooper and Trumpeter Swans (Devos 1964; Haapanen et al 1977; Cooper 1979; pers.obs.), whereas in the Bewick's and Whistling Swans the male takes part (Evans 1975, 1977; Scott 1977). Participation in incubation by males makes possible a higher incubation constancy and hence a shorter incubation period. This is important considering the short duration of arctic summers (Lack 1968; Kear 1970 b; Scott 1977; Cooper 1979) and may be one factor enabling them to breed at such high latitudes. Males were not observed incubating in Iceland (n=5), but although they were not confined to the nest as were the females, they were restricted to its vicinity (see also Haapanen et al 1977). This study and previous studies have shown that males stayed close to the nest and defended the area around it from intruders (Banko 1960; Haapanen et al 1977; pers.obs.). My observations in Iceland have also shown that female Whooper Swans may defend the nest area from intruders (section 8.4) as do female Trumpeter Swans (Cooper 1979), and that territorial conflict occurs between males (section 8.3.1). It is thought that the importance of the territory is to ensure a food supply for adults and young after hatching.

Haapanen et al (1977), found that the main activities of the male during the incubation period were feeding, roosting and swimming; swimming is equivalent to head-up in the present study, since in the normal swimming position head and neck are raised. They also found that the male's behaviour did not differ from normal during the female's incubation breaks, and both male and female were sometimes absent from the nest at the same time, in fact the male for which they include data only stayed in the vicinity of the nest on 36% of occasions when the female was away.

The aims of the breeding studies carried out in Iceland were to monitor the behaviour of males and females simultaneously; their distances from the nest and their behaviour during incubation breaks. Given that the roles of the sexes are markedly different and that the female's role is primarily as an incubator, it was expected that males would act as guards and their levels of 'attention' might depend on the behaviour of their females.

Arnarvatn, the lake at which most of the breeding studies were carried out, is unusual in that it is the breeding ground for more than one pair of Whooper Swans. In 1979, two pairs bred with their nests about 600 m apart and in 1978 and 1979 three pairs bred with their nests 500 and 600 m apart. Previous studies suggest that individual pairs occupy separate bodies of water (e.g. Bulstrode et al 1973; Haapanen et al 1977). Data from Arnarvatn will be discussed with occasional reference to two less intensively studied pairs at Ellithavatn and Selhagi.

8.5.1 Female Behaviour

Females were found to spend most of their time either roosting or head-up on the nest (tables 8.5, 8.6, 8.7). Periodically the eggs are turned with the bill, usually while standing, and occasionally they turn

Table 8.5

Time budgets of the southern pair at Arnarvatn in 1979

Male Behaviour	Frequency	Percentage of: time in view, or [1] observation period	Female Behaviour	Frequency	Percentage of: time in view, or [1] observation period
Head-up	1371	27.8	Head-up on water	75	1.1
Out of view	1792	26.7[1]	Head-up on land	91	1.4
Preen	512	10.4	Head-up on nest	1142	17.0[1]
Dip	1186	24.1	Preen on water	9	0.1
Upend	102	2.1	Preen on land	80	1.2
Pick	1	0.0	Preen on nest	641	9.5[1]
Graze	258	5.2	Out of view	153	2.3[1]
Drink	2	0.0	Dipping	168	2.6
Bathe	3	0.1	Upending	13	0.2
Roost	1299	26.3	Grazing	284	4.3
Fly	24	0.5	Picking	1	0.0
Display	61	1.2	Drinking	1	0.0

Table 8.5 (cont'd.)

Male Behaviour	Frequency	Percentage of: time in view, or ^{1} observation period	Female Behaviour	Frequency	Percentage of: time in view, or ^{1} observation period
Nest fix/Pull material	110	1.6^1	Bathing	1	0.0
			Roosting on nest	3494	53.2^1
			Flying	6	0.1
			Displaying	23	0.4
			Nest fixing/Pulling material	57	0.8^1
			Settling/Moving	67	1.0^1
			Egg care	35	0.5^1
			Cover eggs	16	0.2^1
			Off nest	939	14.0^1
Total time (min.)	6721			6724	
Total time in view	4929			6571	

Table 8.6

Time Budgets of the western pair at Arnarvatn in 1979

Male Behaviour	Frequency	Percentage of: time in view, or of observation period	Female Behaviour	Frequency	Percentage of: time in view, or of observation period
Head-up	1505	27.0	Head-up on water	135	2.2
Out of view	606	9.8[1]	Head-up on land	55	0.9
Preen	268	4.8	Head-up on nest	1589	25.7[1]
Dip	2044	36.6	Preen on water	3	0.0
Upend	277	5.0	Preen on land	75	1.2
Dabble	3	0.0	Preen on nest	357	5.8[1]
Eat emergent vegt'n	1	0.0	Out of view	14	0.2[1]
Pick	9	0.2	Dipping	813	13.2
Graze	127	2.3	Upending	17	0.3
Feed from edge	4	0.1	Grazing	73	1.2
Roost	1233	22.1	Bathing	1	0.0
Fly	19	0.3	Roosting on nest	2510	40.6[1]

Table 8.6(cont'd.)

Male Behaviour	Frequency	Percentage of: time in view, or of observation period	Female Behaviour	Frequency	Percentage of: time in view, or of observation period
Display	67	1.2	Flying	8	0.1
Nest Fix/Pull material	23	0.4[1]	Displaying	17	0.3
			Nest fixing	453	7.3[1]
			Settle/Move	40	0.6[1]
			Egg Care	21	0.3[1]
			Cover eggs	7	0.1[1]
			Off nest	1194	19.3[1]
Total time (min.)	6186			6188	
Total time in view	5580			6174	

Table 8.7

Time budgets of females whilst on the nest

	Arnarvatn south		Arnarvatn west		Selhagi		Ellithavatn	
Behaviour	Frequency	Percentage	Frequency	Percentage	Frequency	Percentage	Frequency	Percentage
Roost	3494	60.4	2510	50.3	1058	42.8	721	52.9
Head-up	1142	19.7	1589	31.8	840	34.0	458	33.6
Preen	641	11.1	357	7.2	183	7.4	71	5.2
Nest-fix	367	6.3	453	9.1	306	12.4	114	8.4
Settle	67	1.2	40	0.8	36	1.5		
Egg care	35	0.6	21	0.4	31	1.3		
Display	23	0.4	17	0.3	3	0.1		
Cover eggs	16	0.3	7	0.1	12	0.5		
Total time (min.)	5785		4994		2469		1364	

to face in a different direction. Any movement on the nest ended with a short period when the female rocked, or shuffled from side to side over the eggs (settling). Cooper (1979) interpreted this behaviour as positioning the feet under the eggs. Since swans have only a poorly developed brood patch, the feet are potentially the best means of transferring heat to the eggs. Incubation is periodically interrupted by feeding bouts. Females devoted 80.7% (western), 86% (southern), 86.8% (Selhagi) and 93.7% (Ellithavatn) of their time to their nests. These results are more similar to the 85% recorded by Haapanen et al (1977) for two females in Finland than to the 95 to 96% of the Trumpeter Swan (Cooper 1979) and confirm that Whooper Swans spend less time on the whole at the nest than do Trumpeter Swans.

Behaviours recorded whilst females were on their nests, in order of time spent in them, were: roosting, head-up, preening, nest-fixing, settling, egg-care, displaying and covering the eggs (see tables 8.5, 8.6, 8.7). The rank order was very much the same for all four females (table 8.7). All four females spent less time roosting on the nest than did those studied by Haapanen et al (1977) (60.4%. 50.3%, 42.8% and 52.9% compared with 70%). Haapanen et al (1977) gave no details of how females occupied the rest of their time on the nest. For full details of behaviours recorded on the nest and during incubation breaks, see tables 8.7 and 8.8. Three of the four females were out of view for some time during their incubation breaks. The position of my hide at Arnarvatn probably caused the difference between the 16.3% of the southern females breaks recorded out of view, compared with 1.2% by the western female. The much greater time spent out of view by the Selhagi female, 61.4% of her incubation breaks, was because she left the nesting bay entirely, presumably

Table 8.8

Time budgets of females whilst off the nest

Behaviour	Arnarvatn south		Arnarvatn west		Selhagi		Ellithavatn	
	Frequency	Percentage	Frequency	Percentage	Frequency	Percentage	Frequency	Percentage
Head-up on water	75	9.5	135	11.4	68	46.9	51	56.0
Head-up on land	91	11.6	55	4.7	13	9.0		
Preen on water	9	1.2	3	0.2	12	8.3		
Preen on land	80	10.2	75	6.4	40	27.6		
Dip	168	21.4	813	68.9				
Upend	13	1.6	17	1.4				
Graze	284	36.1	73	6.2				
Pick	1	0.1						
Drink	1	0.1					1	1.1
Bathe	1	0.1	1	0.1	1	0.7		
Fly	6	0.8	8	0.7	7	4.8		
Pull material	57	7.2						
Copulation					2	1.4	1	1.1
Head low					2	1.4		
Display							38	41.8
Total time	939		1194		376		91	
Time out of view	153		14		231		0	

to feed. Selhagi was later examined and appeared to be almost devoid of food. Time allocated to different behaviours has been recorded as percentage of time in view, unless the behaviour could only occur in the area in view, in which case it was recorded as a percentage of the observation period.

During incubation breaks, feeding was the most important activity, occupying 59.2% of the southern females breaks and 76.5% of the western females. These results are similar to those of 64% and 72% found for two females by Haapanen et al (1977). The southern female fed mainly by grazing and the western female by dipping and the southern female spent more of her breaks head-up, preening and pulling nest material than did the western female (table 8.8). The Selhagi female did not feed in view and the Ellithavatn female was never seen feeding.

It is clear from this study and from that of Haapanen et al (1977) that although individual variation occurs between incubating females, the overall way in which they allocate time to different behaviours is rather similar, suggesting that the behaviour patterns observed were specific to the species rather than to individuals. For example, roosting was the commonest and head-up the second commonest behaviour during incubation, while feeding was the commonest behaviour and head-up the second commonest behaviour during incubation breaks, for all birds studied.

Incubation breaks

The number of incubation breaks each day was calculated from the number observed during each six-hour observation period during summer 1979.

For the southern pair, this was 5.1 and for the western pair it was 2.6. Only the figure for the southern pair was at all similar to the 7.4 and 6.7 found for two pairs in Finland (Haapanen et al 1977). The mean length of incubation breaks was 31 ± 16.8 min. for the southern pair and 78.9 ± 48.4 min. for the western pair, compared with 21 ± 12.4 min. for the Trumpeter Swan (Cooper 1979). Thus, for the two pairs of Whooper Swans, the length of time away tended to compensate for the frequency of absences. The large size of swan eggs means that they are slow to cool and hence better fitted for short frequent incubation breaks than less frequent, but longer, breaks. Chilling of the eggs may have resulted in the failure of the western pair to hatch any young.

Whereas Haapanen et al (1977) found that the length of breaks increased towards the end of incubation, no such correlation was found during this study ($r=-0.22$, $n=21$, southern female; $r=0.57$, $n=9$ western female). Nor was there any correlation between date and total time off the nest during an observation period for the southern pair ($r=0.3$, $n=20$). There was, however, a highly significant correlation for the western pair ($r=0.73$, $n=20$, $p= <0.01$); total time off the nest increased with date until the western female ceased incubation entirely, only a few days before the eggs were expected to hatch. It seems likely that some of the differences in behaviour between these two pairs during the incubation period had a direct bearing on their differences in reproductive success.

8.5.2 Male Behaviour

Although Cramp and Simmons (1977) state that males may sit during the absences of the females, males were not seen incubating during this study nor that of Haapanen et al (1977). During this study, the southern male spent 31.4% of his time feeding, the western male spent 44.4%, the Selhagi male was only observed feeding for 11.2%, but 28.1% of his time was spent out of sight and he was probably feeding then also; the Ellithavatn male spent 39.2% of his time feeding. The results are quite similar to the 34% and 35% recorded in Finland (Haapanen et al 1977), with the exception of the western male. The southern male spent less time feeding than the western male, but spent longer in all other behaviours except for displaying; in which they spent the same amount of time. The four commonest behaviours for all four males were feeding, head-up, roosting and preening (tables 8.5, 8.6 and 8.9). The southern male spent more time head-up than his mate (27.8% compared with 19.5%), whereas the western pair spent almost the same amount of time head-up (male 27%, female 28.8%).

8.5.3 The Relationship between Male and Female Behaviour during Incubation

In considering the behaviours exhibited by paired swans during incubation, it was expected that a degree of co-operation might exist between the pair such that, for example, the nest might be guarded or the eggs incubated for the maximum time possible. Such co-operation, representing highly developed parental care, requires that each individual monitors the behaviour of the other and modifies its behaviour accordingly, so that specific behaviours are either actively synchronised or asynchronous, but not occurring randomly.

The frequency with which behaviours were exhibited by both males and females at the same time (synchronised) and at different times (asynchronous) were tested using chi-square analysis. For technical reasons a complete chi-square table for all male and female behaviours could not be

Table 8.9

Time budgets of males at Selhagi and Ellithavatn

	Selhagi		Ellithavatn	
Behaviour	Frequency	Percentage of: time in view, or (1) observation period	Frequency	Percentage of: time in view, or (1) observation period
Head-up	981	47.9	392	26.9
Head-up by nest	331	11.6(1)		
Head-up on land	30	1.5		
Preen	90	4.4	129	8.9
Dip	174	8.5	"Feeding" 570	39.2
Upend	20	1.0		
Feed from edge	26	1.3		
Graze	8	0.4		
Drink	10	0.5		
Roost	338	16.5	248	17.0
Copulation	2	0.1	1	0.1
Head low	1	0.1		
Nest fix	28	1.0(1)	1	0.1
Fly	5	0.2		
Display	2	0.1	114	7.8
Total time (min)	2845		1455	
Time out of view	799		0	

calculated, instead individual chi-squares were calculated separately for each combination of male and female behaviour. Inevitably there are risks of significant associations occurring by chance. The very high significance levels for the behaviours discussed (see table 8.10), however, suggest that this is not just a random effect. It is also the case that a significant association might be represented by a slight increase in a common behaviour or a large increase in a rare behaviour. The associations with apparent functional implications will be discussed at the end of this section.

Striking differences were apparent between the two intensively studied pairs. The southern pair, which hatched and reared three young successfully, showed a much higher frequency of significant associations between male and female behaviours, than did the unsuccessful western pair. Forty-seven per cent of all behavioural combinations between the members of the southern pair were significantly associated, whereas only 38% were significantly associated for the western pair (table 8.9).

The most striking example of co-ordinated behaviour was that occurring when females left their nests for incubation breaks. It was expected that males might spend more time head-up during these periods, which in fact was exactly what occurred. Head-up by both males was significantly synchronised with female ''off the nest' (Chi sq. = 376, $p=<0.0005$ southern pair; Chi sq. = 40, $p=<0.0005$ western pair).

A further method of analysing this particularly important association between head-up by the male and presence or absence of the female at the nest, was used as a check on the first. This involved selecting at

Table 8.10

Associations between male and female behaviours of two pairs at Arnarvatn in 1979

A. Synchronized behaviours

Male behaviour	Female behaviour	Southern pair sig.	Southern pair obs/exp	Western pair sig.	Western pair obs/exp
Head-up	Head-up on land	***	42/20	***	24/13
"	Head-up on water	***	52/18	***	95/36
"	Head-up on nest	***	271/231	-	
"	Preen on land	***	32/18	-	
"	Out of view	***	43/22	-	
"	Off nest	***	440/217	***	399/313
"	Dip	***	87/46	-	
"	Graze	***	146/69	-	
Out of view	Roost	***	1007/913	***	343/240
"	Out of view	***	75/41	-	
Dip	Head-up on nest	**	237/200	***	685/525
"	Dip	-		***	375/296
"	Preen on nest	*	131/110	-	
"	Roost	***	686/608	-	
Upend	Roost	***	79/52	***	156/107
"	Nest fix	*	13/6	-	
Graze	Off nest	-		***	73/26
"	Roost	***	163/132	-	
Roost	Roost	***	801/664	***	670/477
Roost	Preen on nest	*	140/120	-	
Preen	Preen on nest	-		***	40/16
"	Nest fix	-		**	33/20
"	Settle/Move	***	18/6	-	
Display	Head-up on nest	-		**	28/17
"	Off nest	***	21/10	-	
Nest fix	Off nest	***	91/15	-	
Fly	Head-up on nest	-		*	10/5

Table 8.10 (cont'd)

B. Asynchronous behaviours

Male behaviour	Female behaviour	Southern pair		Western pair	
		sig.	obs/exp	sig.	obs/exp
Head-up	Roost	***	478/681	**	540/584
"	Preen on nest	**	102/127	*	73/90
"	Head-up on nest	-		*	354/386
"	Display	*	1/6	-	
"	Nest fix	**	64/87	-	
Out of view	Dip	***	0/44	***	6/78
"	Graze	***	33/74	**	0/ 7
"	Head-up on water	**	9/20	***	1/13
"	Preen on nest	-		*	22/35
"	Off nest	***	158/250	***	35/117
Dip	Head-up on water	***	1/16	***	24/49
"	Head-up on land	***	3/18	***	3/18
"	Preen on land	***	0/16	***	8/24
"	Graze	***	38/61	***	8/27
"	Display	*	0/5	**	0/ 6
"	Upend	-		**	0/ 6
"	Roost	-		***	674/791
"	Nest fix	-		*	129/151
"	Out of view	***	0/19	-	
"	Dip	***	1/41	-	
"	Off nest	***	49/188	-	
Upend	Off nest	***	1/16	***	20/58
"	Head-up on water	-		*	1/ 7
"	Preen on nest	-		*	7/17
"	Dip	-		***	19/40
"	Head-up on nest	***	2/17	-	
"	Graze	*	0/5	-	
Graze	Head-up on nest	-		***	8/33
"	Roost	-		**	34/49
"	Preen on nest	*	13/24	-	
"	Dip	**	0/9	-	

Table 8.10 (cont'd)

Asynchronous behaviours (cont'd)

Male behaviour	Female behaviour	Southern pair		Western pair	
		sig.	obs/exp	sig.	obs/exp
Roost	Off nest	***	55/206	***	170/257
"	Head-up on water	***	4/18	***	3/ 30
"	Head-up on nest	*	190/219	***	196/316
"	Head-up on land	***	0/19	-	
"	Dip	-		***	134/178
"	Preen on land	***	3/17	-	
"	Out of view	***	3/20	-	
"	Graze	***	3/67	-	
"	Display	*	0/6	-	
Preen	Roost	-		***	68/104
"	Out of view	*	1/8	-	
Display	Roost	**	18/31	***	10/ 26
"	Preen on nest	*	0/6		
Nest fix	Head-up on nest	***	1/19		
"	Roost	***	3/43		

Significance values
* = 0.05 → 0.01
** = 0.01 → 0.001
*** = 0.001 →

N.B. Off nest is not an exclusive behavioural category; it is a measure of female absence from the nest during which time she may be involved in numerous behaviours.

random twenty-five minute blocks of data (consecutive spot samples at one minute intervals) from periods when a female was off the nest and, similarly, for the following period after she had returned to it. The percentage of time spent head-up by the male during these periods was calculated, and a Mann-Whitney U test was used to test whether or not males spent more time head-up when females were off the nest. The results were highly significant for both pairs ($p=0.001$ southern pair; $p=0.001$ western pair, one-tailed probabilities) and supported the results from the Chi-square analysis.

Certain results, similar for both pairs, are worth mentioning here. In general it appeared that male and female behaviours were co-ordinated in such a way that one bird was usually attentive at the nest or in its vicinity. There was a tendency for some other activities to occur simultaneously, presumably as a response to external stimuli, for example, roosting. Both males tended to be head-up if the females were head-up on land or on water and tended not to be head-up if the females were roosting or preening on the nest. Males tended to be out of view when females were roosting and in view when the females were off the nest, dipping, grazing or head-up on water. Feeding, by dipping (the head is briefly submerged), by males was synchronised with head-up on the nest by the females and was asynchronous with head-up on land or on water, preen on land, grazing or displaying. Feeding, by upending (the head is submerged for longer than dipping and the bird is in deeper water), was synchronised with roosting by the females. Roosting was synchronised in both pairs, and in agreement with Bulstrode et al (1973), male roosting tended not to occur if females were off the nest, nor did it occur if females were head-up on water or on the nest. Male display tended not to occur when females were roosting, presumably because anything likely to precipitate display would also be likely to disturb the female.

A full list of associated behaviours appears in table 8.9. Not all associations between behaviours are necessarily a significant aspect of co-ordinated parental care. Some behaviours might be associated by chance, or simply because commoner behaviours dominate the time budget. Less common behaviours may then be associated because of the limited time available to them. The association between certain behaviours appears to make sound ecological sense; it is conceivable that they are a result of natural selection. For example, the synchronization of behaviours which reduce the male's state of vigilance (such as dipping, upending, grazing, roosting or out of view) with roosting by the female, does not involve any risks since the nest and eggs are protected. The synchronization of male head-up with female head-up and off nest, and male display and nest-fix with female off nest, represent the capacity of both individuals to respond to a disturbance, or for the male to increase his vigilance or attention during the female's absences. It should also be noted that certain behaviours will almost invariably be synchronized because they could not occur otherwise, for example, male nest-fixing often occurred when the male was standing on the side of the nest. It is doubtful whether this would ever occur while the female was sitting. The synchronization of male out of view with female out of view, on the other hand, does not appear to make sense, since it leaves the nest and eggs completely unprotected.

Because certain behaviours are synchronized, it inevitably means that other behaviours are more likely to occur asynchronously by chance, but as in the first case, some seem to make particularly 'good sense'. Those to be noted in particular are those with the largest proportional differences between observed and expected frequencies (see table 8.9). Following on from above, attention towards the nest and eggs, i.e. parental care, is heightened by the tendency for males not to roost or feed when females were involved in behaviours off the nest; such as feeding, preening or head-up on land or water. The fact that males tended not to be out of view when females were feeding also reflects this. The tendency for males not to nest-fix when females were head-up on the nest or roosting, simply represents the inverse of their tendency to nest-fix when the female was off the nest and emphasizes the point that because some associations are significant, by necessity that will lead to others being so also. In spite of the chance element involved and the inflation of the number of associations because of 'dominant' behaviours and associations, it is clear that male and female behaviours are actively co-ordinated. Such co-ordination tends to increase the attention given to the nest and eggs, i.e. it leads to increased parental care.

8.5.4 Distance from the nest

The pattern of mean distance from the nest over the 24-hour period was similar for both males and both females, but the ranges and standard deviations were very large. Both males were furthest from the nest in the early hours of the morning from 0100 hr to 0500 hr or 0600 hr. For the remainder of the day they were mainly within 100 m of the nest (see fig. 8.4). Both males and females tended to be either close to the nest (less than 50 m) or well away from it (greater than 150 m). Females tended to be either on or very close to the nest for almost the whole day,

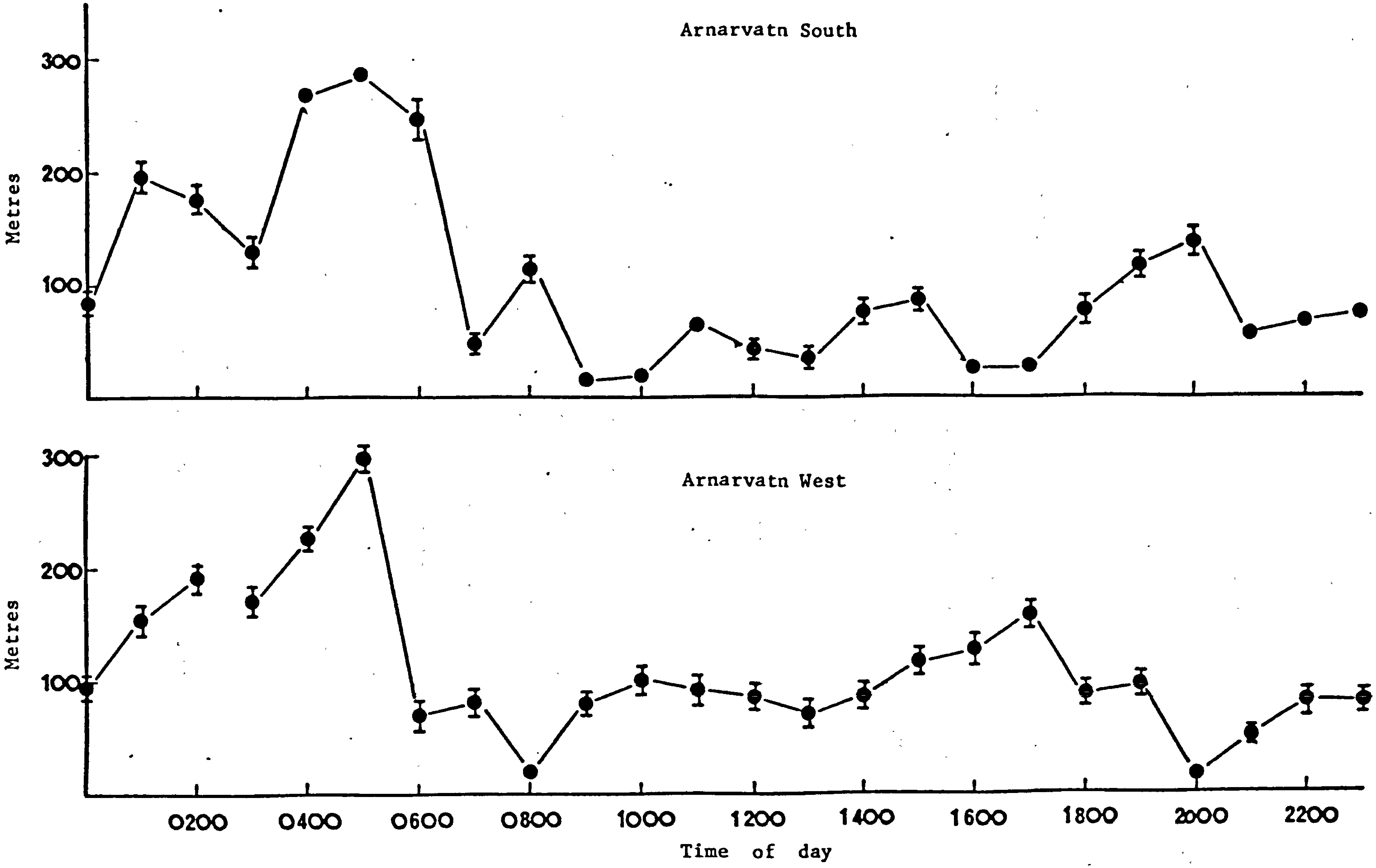


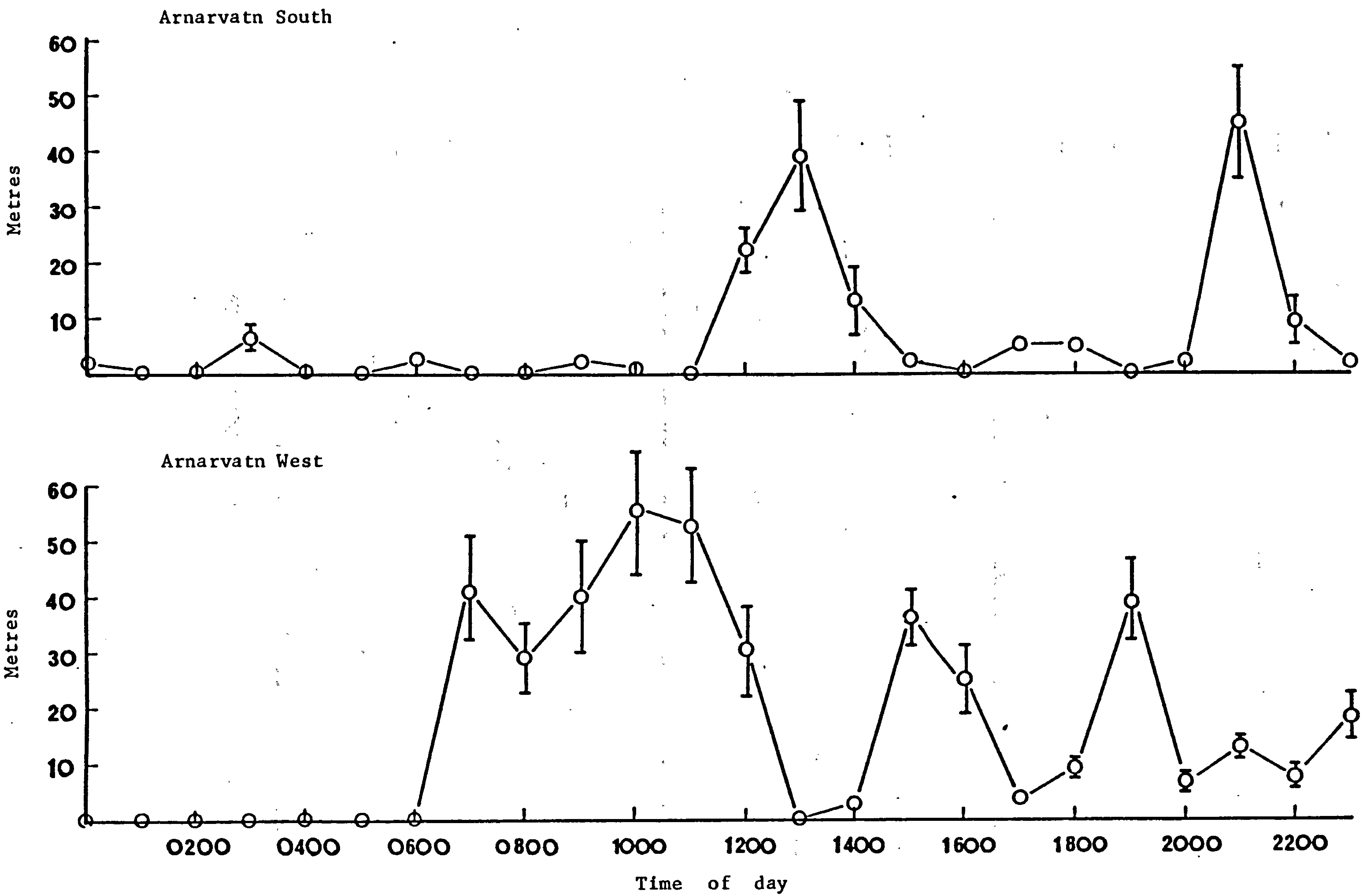
Fig. 8.4. The mean distance of males from the nest throughout the 24 hr. period. (In order that standard deviations could be presented, they have been reduced by a factor of ten).

making only brief journeys further away to feed (see fig. 8.5).

Certain behaviours of both males and females were associated with distance from the nest. Many could only occur in specific circumstances, especially for females; for instance, feeding could only occur when the females were off the nest and nest-fixing could only occur whilst on the nest. Both males tended to be out of view more early in the morning, when they were furthest away from the nest and whilst the female was on the nest. Males dipped more early in the morning and were head-up more from 0600 hr onwards (figs. 8.4, 8.6 and 8.7), i.e. during the period when females were most often recorded off the nest. The data suggest that roosting by males alternates with head-up and may occur cyclically during the 24-hour period, with peaks every two to seven hours (figs. 8.6 and 8.7).

The two females fed in different ways and in different areas due entirely to the location of their nests. The western nest was on a headland backed by moorland, hence the female fed off-shore mainly by dipping; whereas the southern nest was situated between two grass meadows bordered by Carex marshes, hence the southern female fed more by grazing and was thus able to feed whilst close to the nest. Both females tended to prefer areas well away from the nest for dipping.

Both females roosted more consistently at night, even though daylight was continuous for much of the incubation period (see fig. 8.8 and 8.9). It has been shown for other species of birds, for example the Wheatear (Oenanthe oenanthe) (Asbirk and Franzman 1979), that a prolonged period of inactivity occurs in spite of continuous daylight. Birds have a



<u>Fig. 8.5.</u> The mean distance of females from the nest throughout the 24 hr. period. (In order that standard deviations could be presented, they have been reduced by a factor of ten).

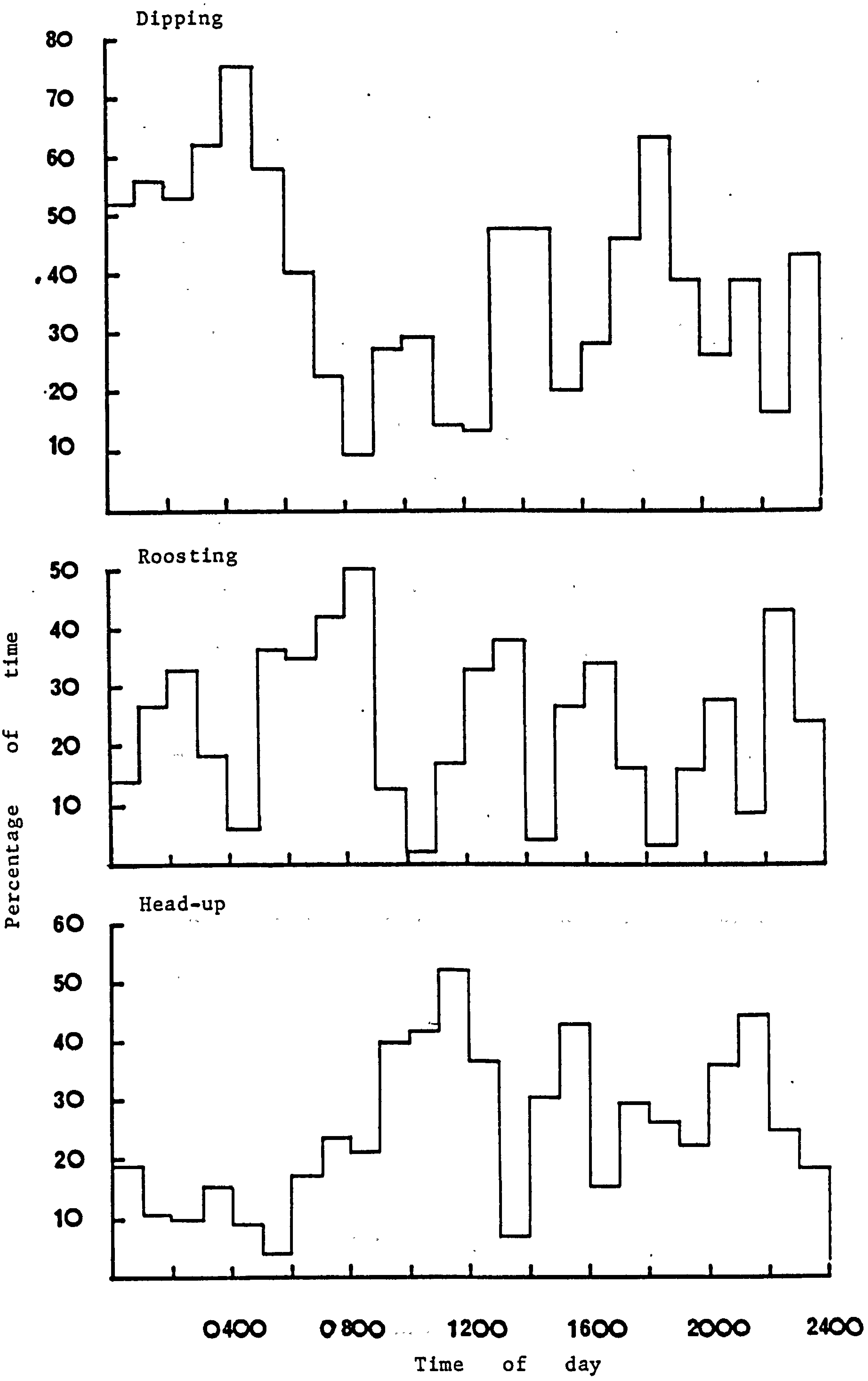


Fig. 8.6. The daily pattern of the major behaviours of the western male; Arnarvatn 1979.

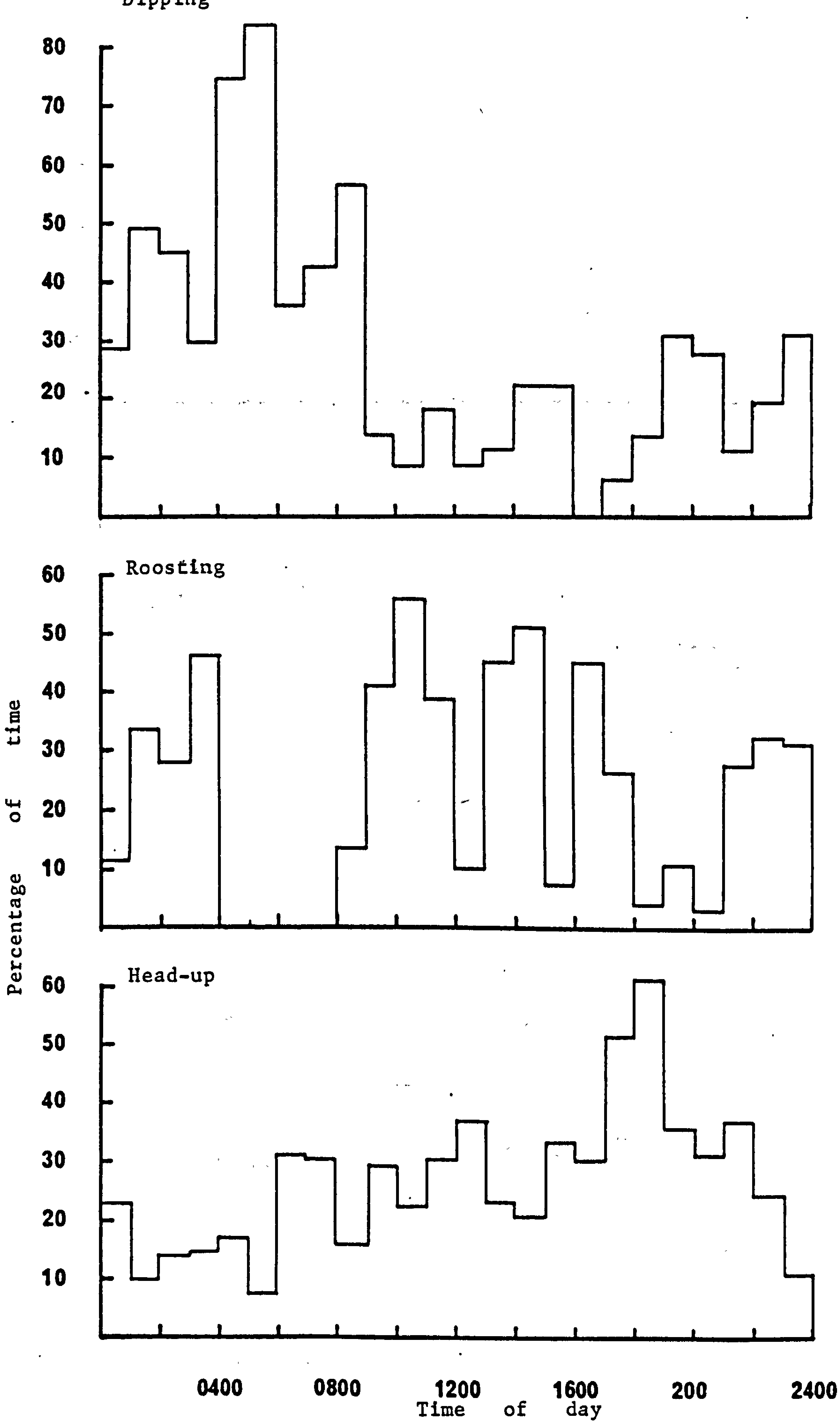


Fig. 8.7. The daily pattern of the major behaviours of the southern male; Arnarvatn 1979.

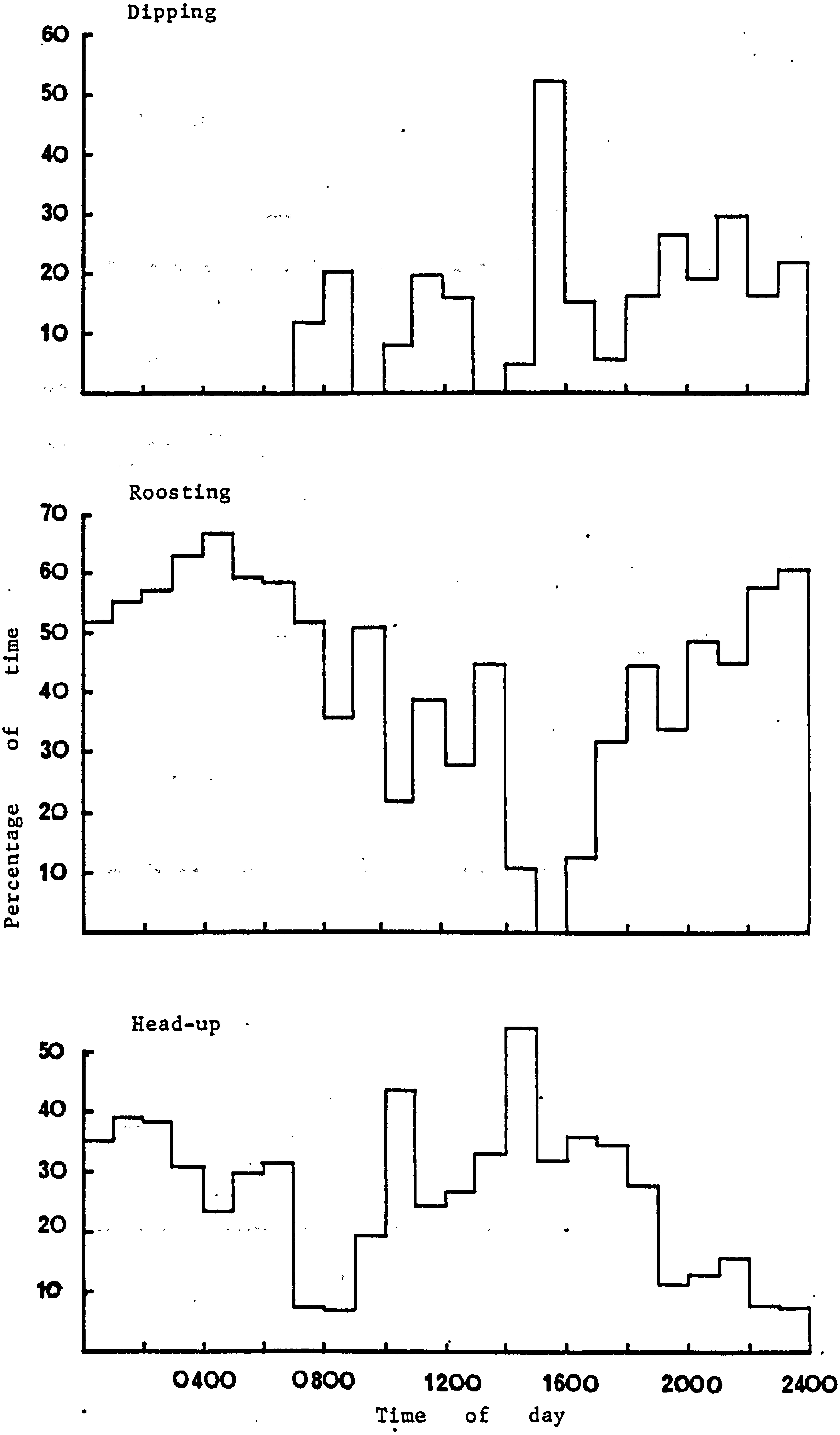


Fig. 8.8. The daily pattern of the major behaviours of the western female, Arnarvatn 1979.

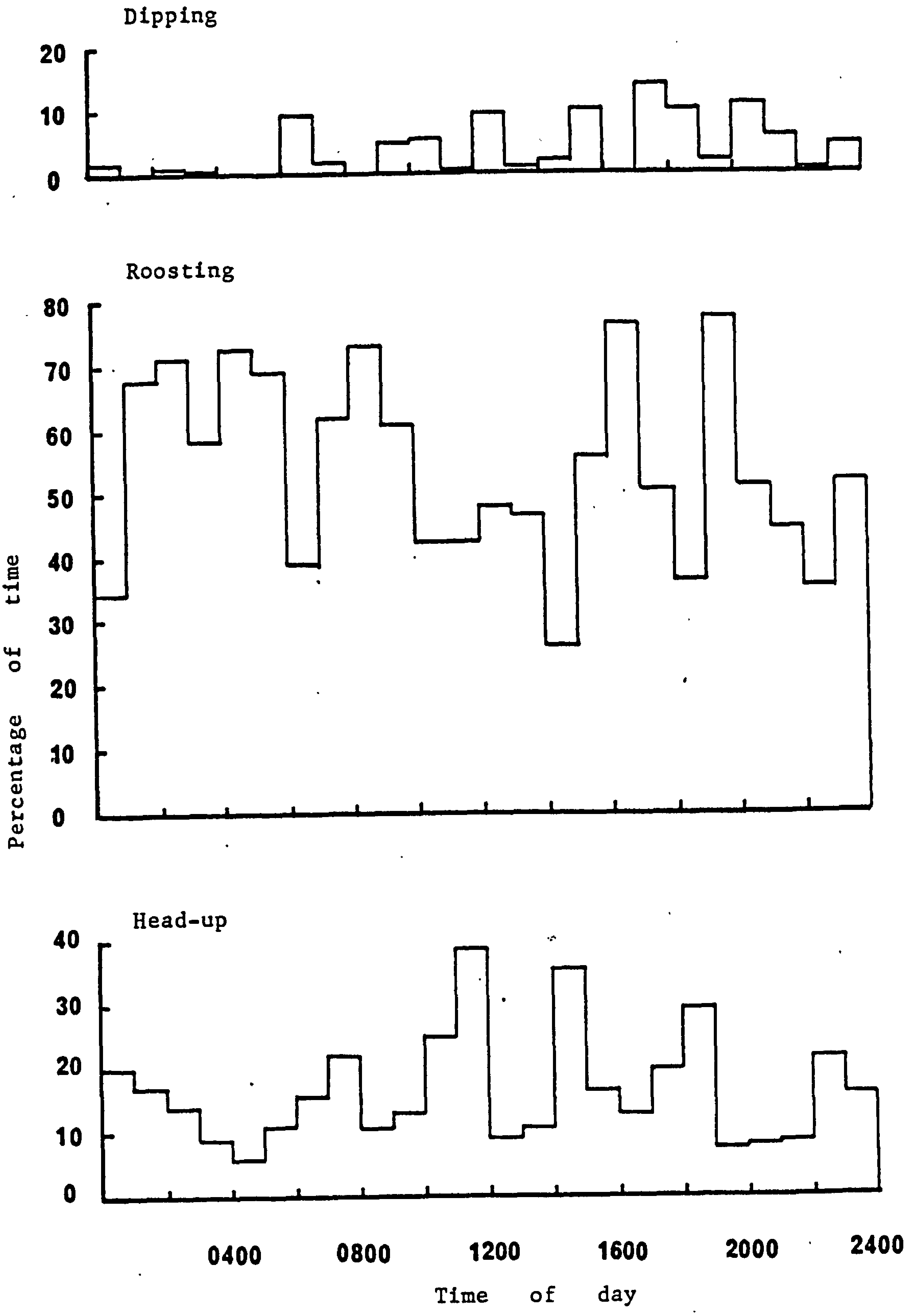


Fig. 8.9. The daily pattern of the major behaviours of the southern female, Arnarvatn 1979.

marked diurnal temperature cycle, the amplitude being in part related to body size (see Bartholomew and Dawson 1954; Farner and King 1961; Lasiewski and Dawson 1967), which may be a factor affecting activity patterns regardless of continuous daylight.

Both females mainly left their nests late in the day, after 0600 hr for the western female (that is when the male returned to the proximity of the nest (see fig. 8.4 and 8.5)) and mainly after 1200 hr for the southern female, although she also left the nest at other times during the early morning. The southern female grazed between 0600 hr and 0700 hr, 0900 hr and 1000 hr and more frequently after 1200 hr (see fig. 8.9).

8.6 Fledging

The time budgets of three families studied during the fledging period are presented in tables 8.11, 8.12 and 8.13. Although there was variation both within and between pairs regarding the time allocated to specific behaviours, certain generalisations can be made. Only five or six behaviours were regularly recorded as part of the activity budget of the parents, these were: head-up, preening, dipping, dabbling, grazing and roosting. Thus the fledging period closely resembles other periods of the annual cycle, other than the incubation period, in terms of the variability of the behaviour exhibited.

Owing to my lack of familiarity with the individuals concerned, identification of the parents during the fledging period was unfortunately limited, for much of the time, to description in terms of proximity to the brood. I suspected, however, that the bird most often close to the cygnets was the female (see 8.6.2).

Table 8.11

Time budgets of parents of three families during the fledging period at Arnarvatn, in 1978

Behaviour	Northern		Southern		Western	
	Nearest parent	Furthest parent	Nearest parent	Furthest parent	Nearest parent	Furthest parent
Head-up	54.5%	47.3%	52.1%	43.9%	45.4%	41.1%
Dip	7.5%	9.7%	9.6%	11.7%	32.7%	40.5%
Graze	17.0%	22.0%	8.2%	11.7%	6.3%	4.7%
Upend	1.0%	0.5%	-	-	-	-
Dabble	0.0%	0.0%	0.0%	0.5%	-	-
Preen	6.5%	7.0%	11.9%	10.7%	8.3%	6.8%
Roost	13.5%	13.4%	18.3%	21.4%	7.3%	6.8%
Out of view	8.3%	14.7%	7.2%	16.9%	12.8%	19.1%
No. of samples in view	200	186	219	219	205	190
No. of samples out of view	18	32	17	17	30	45

Table 8.12

Time budgets of three broods of cygnets during the fledging period at Arnarvatn, in 1978

Behaviour	Northern	Southern	Western
Head-up	17.1%	24.9%	28.4%
Dip	26.4%	20.2%	43.7%
Graze	38.6%	19.2%	8.7%
Pick	-	1.0%	1.6%
Graze emergents	-	-	0.5%
Drink	-	0.5%	-
Preen	3.6%	8.8%	7.7%
Roost	14.3%	25.4%	9.3%
Out of view	35.8%	18.2%	22.1%
No. of samples in view	140	193	183
No. of samples out of view	78	43	52

Table 8.13

The percentage of time spent feeding by three families at Arnarvatn in 1978

	Northern Pair (4 cygnets)	Southern Pair (4 cygnets)	Western Pair (3 cygnets)
Parent nearest the brood	25.5%	17.8%	39.0%
Parent furthest from the brood	32.2%	23.9%	45.2%
Cygnets	65.0%	40.3%	54.6%

There were differences in behaviour between the two parents depending on their distance from the brood. The parent closest to the brood in each family spent between 45% and 55% of its time head-up, whereas the parent furthest from the brood spent between 41% and 48% of its time head-up. Within each pair the parent closest to the brood always spent more time head-up than did the furthest parent. Both parents of each family spent very similar amounts of time preening and roosting, but in each case the parent furthest from the brood spent more time feeding than did the nearest parent (see tables 8.11 and 8.13). These differences in time spent feeding, however, were not significant when each pair was analysed separately (N=16, T=34 Northern pair; N=17, T=37 Western pair; N=16, T=33.5 Southern pair. $p=\ngtr 0.05$ in all cases, Wilcoxon two-tailed test), but when analysed together they were highly significant (p= 0.004, Sign test, two-tailed).

Different families spent differing amounts of time feeding and they fed in different ways (table 8.11 and 8.12). The northern family fed mainly by grazing on grasses and sedges along the lake shore. The southern pair fed by grazing and dipping, while the western pair fed mainly by dipping. The western pair also spent more time feeding than did either of the other two pairs (table 8.13).

Although cygnets could not be individually identified, the behaviour of each individual was recorded separately at each sample* The total frequency for any particular behaviour was therefore divided by the number of cygnets in the brood under observation, giving the proportion of time in a given behaviour by an 'average' cygnet.

* in order of their proximity to the nearest parent. (nearest =1; see Table 8.14).

Cygnets spent much less time head-up than did their parents and the cygnets in broods of four spent less time head-up than did cygnets in the brood of three (table 8.12). There was considerable variation between broods, but cygnets from all three broods spent significantly more time feeding than did their parents (table 8.13) ($p<0.005$ N.pair, $p<0.005$ W.pair, $p<0.005$ S.pair. Wilcoxon, one-tailed test). Preening occupied only 3.6% to 8.8% of the cygnets' time. Roosting was extremely variable between broods, ranging from 9.3% in the western pair, 14.3% in the northern pair to 25.4% in the southern pair; the northern and western broods, however, were more often out of view. The small cygnets were often hidden in the vegetation or behind their parents, consequently figures for roosting may be inaccurate.

Associations between the behaviours of individual parents and cygnets were examined using Chi-square analyses. The results from spot samples made every 30 minutes were used for this analysis. It was assumed that the behaviour recorded at one sample occurred independently of that at the previous or subsequent samples. During the fledging stage eight behaviours were recorded from the cygnets: head-up, preening, dipping, feeding on emergents, picking, grazing, drinking, roosting. Only four of them: head-up, dipping, grazing and roosting, were associated with the same behaviour of the parents and each occurred synchronously.

There were, however, differences between the three study pairs with respect to which of these four behaviours was significantly synchronised (see table 8.14). The head-up behaviour of three of the northern families' cygnets was synchronised with both parents, all four of the southern families cygnets were synchronized with both parents, and two of

Table 8.14

Associations between parent and cygnet behaviours at Arnarvatn in 1978. (All behaviours synchronized).

			Cygnets			
A. Head-up						
Family		Parent 2	1	2	3	4
Northern	Parent 1	*	***	*	NS	*
	Parent 2		***	**	*	NS
Southern	Parent 1	**	***	***	***	***
	Parent 2	-	**	***	***	***
Western	Parent 1	NS	**	NS	***	-
	Parent 2	-	NS	*	NS	-
B. Dipping						
Southern	Parent 1	NS	NS	NS	NS	NS
	Parent 2		NS	NS	***	NS
Western	Parent 1	***	***	***	***	-
	Parent 2	-	***	***	*	-
C. Grazing						
Northern	Parent 1	***	NS	***	***	***
	Parent 2	-	***	***	***	***
D. Roosting						
Southern	Parent 1	***	***	***	***	***
	Parent 2	-	***	***	***	***

Chi square significance levels: * = $0.05 > p > 0.01$
** = $0.01 > p > 0.001$
*** = $0.001 > p$

the western families cygnets were synchronized with the nearest parent while that of the third cygnet was synchronized with the furthest parent.

Dipping was synchronized for all three cygnets with both parents of the western family; the only others to be synchronized for this behaviour were the parent furthest from the brood of the southern family and one of its cygnets. Grazing was synchronized for three out of four cygnets with the nearest parent, and for all four cygnets with the furthest parent of the northern family. Roosting was synchronized for all cygnets with each parent of the southern family.

Three aspects of spacing between family members were measured. These were inter-parent, cygnet to nearest parent and cygnet to cygnet distances. When calculating cygnet to parent and cygnet to cygnet relationships, individual distances, i.e. distances from each cygnet to its nearest sibling or parent, and total inter-cygnet and parent to cygnet distances, were recorded (see table 8.15).

All intra-family distances proved to be rather variable so that standard deviations were large, median results are therefore discussed here. Fuller details can be found in table 8.15. Inter-parent distances were small considering that the area each pair occupied facilitated movement of up to several hundred metres in several directions. Median distances only varied from 8.5 to 10 m for the three pairs. Inter-parent distances were, however, much larger than parent to cygnet distances, which were also very similar for all three families. Even the furthest cygnet from a parent was no more than about three times as far away as the nearest cygnet. Inter-cygnet distances were very small, the medians

Table 8.15

Patterns of spacing amongst three families at Arnarvatn in 1978

A. Inter parent distance (metres)

	1.Northern Family	2.Southern Family	3.Western Family
Mean ± S.D.	14.3±17.3	27.3±57.1	21.1±37.6
Mode	10.0	10.0	3.0
Median	9.8	10.0	8.5
50% of samples	≤10 m.	≤10 m.	≤8 m.
75% of samples	≤17 m.	≤20 m.	≤20 m.
Range	0-150 m.	0-300 m.	0-260 m.

B. Parent to cygnet distance (metres)

		Cygnets[1]				
	Family	One	Two	Three	Four	Partoc[2]
Mean	1	3.1±6.4	3.8±6.7	5.3±7.7	6.7±9.2	18.6±28.7
	2	1.5±2.9	2.0±3.0	2.7±3.7	3.4±4.5	9.6±12.3
	3	2.3±4.0	3.2±4.3	4.3±4.9		9.7±12.8
Mode	1	0.0	0.0	0.0	0.0	0.0
	2	1.0	1.0	1.0	0.0	0.0
	3	1.0	1.0	1.0		3.0
Median	1	1.1	1.6	2.6	3.6	9.7
	2	0.9	1.2	1.7	2.1	6.2
	3	1.1	1.8	2.4		5.2
> 75% of samples	1	≤3	≤4	≤6	≤8	≤21
	2	≤2	≤2	≤3	≤4	≤12
	3	≤2	≤4	≤5		≤12
Range	1	0-50	0-50	0-50	0-50	0-200
	2	0-30	0-23	0-26	0-28	0-96
	3	0-25	0-25	0-25		0-75

1. The number of each cygnet refers to its position relative to the nearest parent.

2. Total cygnet to nearest parent distance.

Table 8.15 (cont'd)

C. Cygnet to cygnet distance (metres)

	Family	One	Two	Three	Interc.[3]
Mean ± S.D.	1	2.5±5.5	2.0±3.9	1.6±3.1	5.9±9.1
	2	1.2±2.9	1.0±2.1	1.1±2.8	3.2±5.5
	3	1.2±2.1	2.1±3.2		3.2±4.4
Mode	1	0.0	0.0	0.0	0.0
	2	0.0	0.0	0.0	0.0
	3	0.0	0.0		0.0
Median	1	0.3	0.4	0.3	2.8
	2	0.2	0.2	0.2	1.1
	3	0.4	0.9		2.0
≥75% of samples	1	≤3	≤3	≤2	≤8
	2	≤1	≤1	≤1	≤5
	3	≤2	≤3		≤5
Range	1	0-50	0-23	0-20	0-57
	2	0-25	0-15	0-25	0-33
	3	0-15	0-20		0-32

[3] Total cygnet to cygnet distance

for the three broods only ranged from 0.2 to 0.9 metres.

These results show that cygnets maintain closer proximity to each other than to their parents, that they tended to be with a single parent, and that parents differed markedly in their proximity to their broods.

It was inevitable that as the cygnets grew and matured they would become bolder and more exploring; as a result it was expected that inter-cygnet, and parent to cygnet, distances would increase. Parental care was also expected to decline (see Trivers 1974) and as a result, inter-parent and parent to cygnet distances might increase. The results can be found in figs. 8.10 to 8.21. As expected, total cygnet to nearest parent distance [illegible] increased significantly for each of the three pairs during the fledging period (figs. 8.10, 8.11 and 8.12). Likewise total inter-cygnet distance [illegible] and mean inter-cygnet distances showed an increase during the fledging period for each brood (figs. 8.13-8.18). The relationship between inter-parent distance and date during the fledging period, however, was not clear. Although there were significant correlations between these two factors for each pair, for both northern and western pairs this relationship was positive (as expected) whereas for the southern pair it was negative (figs. 8.19, 8.20 and 8.21). The significance levels were low for the northern (p=0.024) and southern (p=0.014) pairs; it is very likely that the correlations were dependent on the few extreme points and are therefore unreliable. Only the result for the western pair was convincing. The evidence remains inconclusive.

In conclusion: a rather more limited range of behaviours was recorded during the fledging period. The parents attention was directed

Fig. 8.10. Total cygnet to nearest parent distance in relation to date; Arnarvatn North, 1978.
($n = 132, r = 0.25, p = 0.003$)

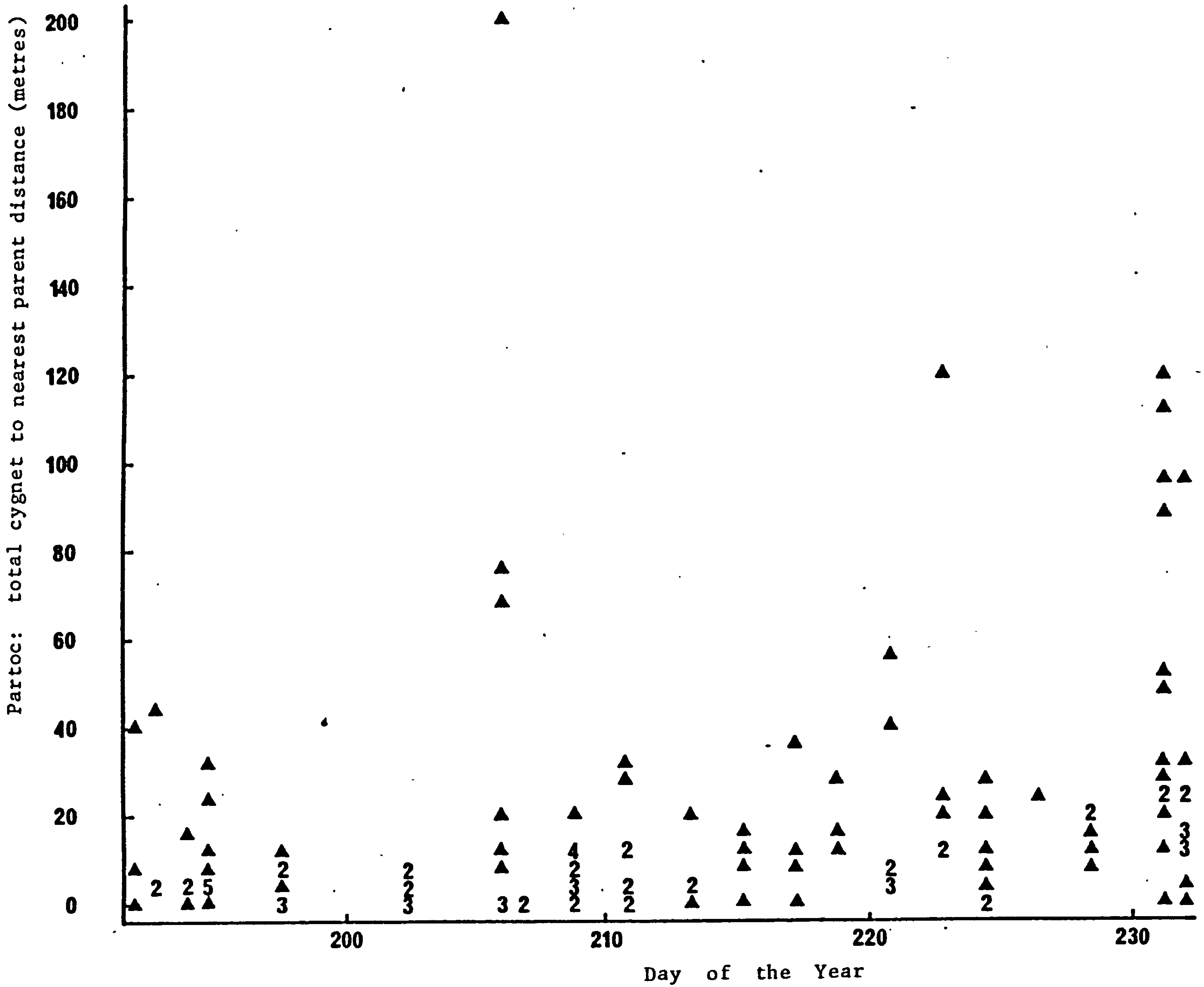

Partoc: total cygnet to nearest parent distance (metres)
200
180
160
140
120
100
80
60
40
20
0
200
210
220
230
Day of the Year

Fig. 8.11. Total cygnet to nearest parent distance in relation to date; Arnarvatn South, 1978. (n=190, r=0.421, p=0.00001)

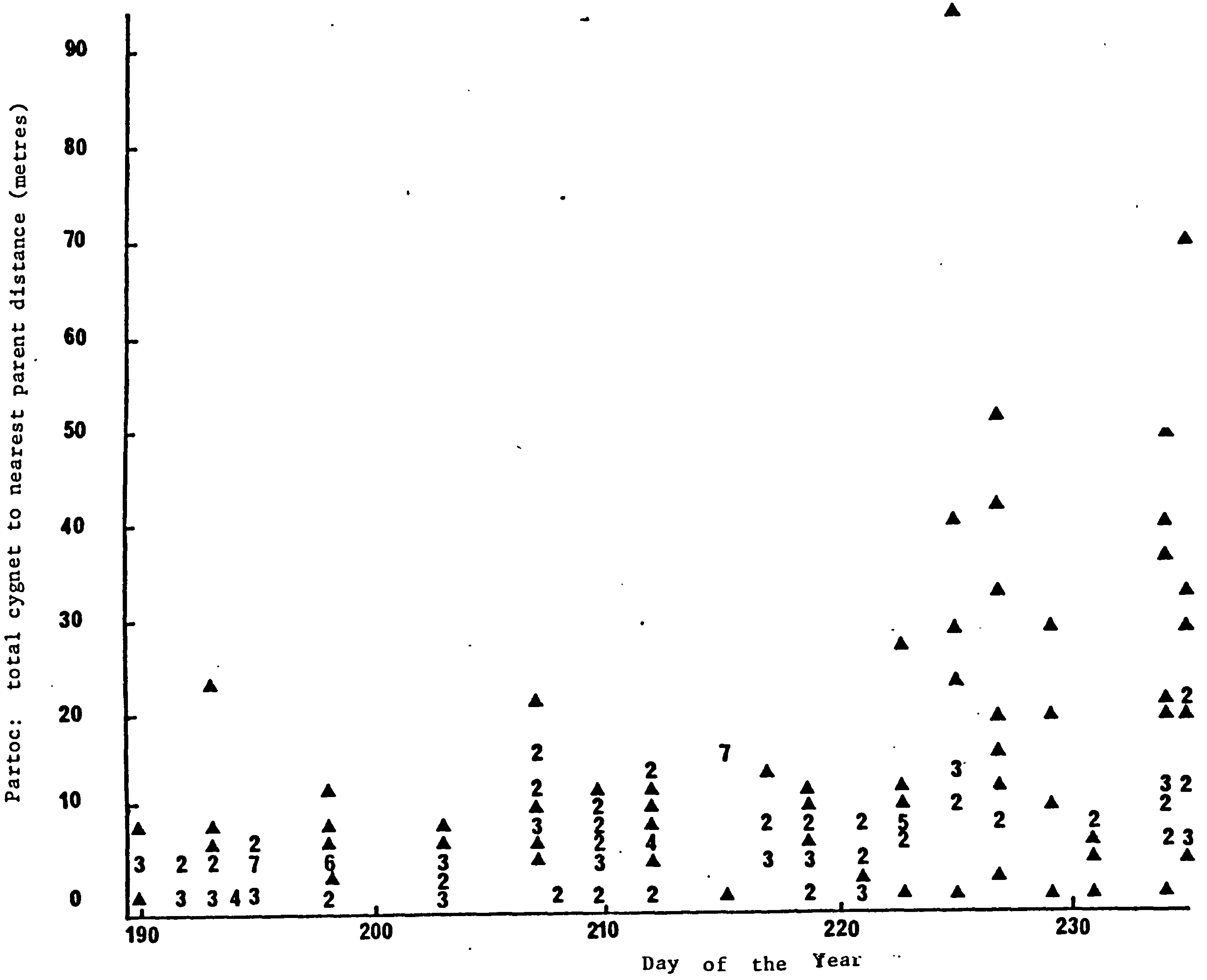

Partoc: total cygnet to nearest parent distance (metres)
0
10
20
30
40
50
60
70
80
90
190
200
210
220
230
Day of the Year

Fig. 8.12. Total cygnet to nearest parent distance in relation to date; Arnarvatn West, 1978. (n=183, r=0.238, p=0.001)

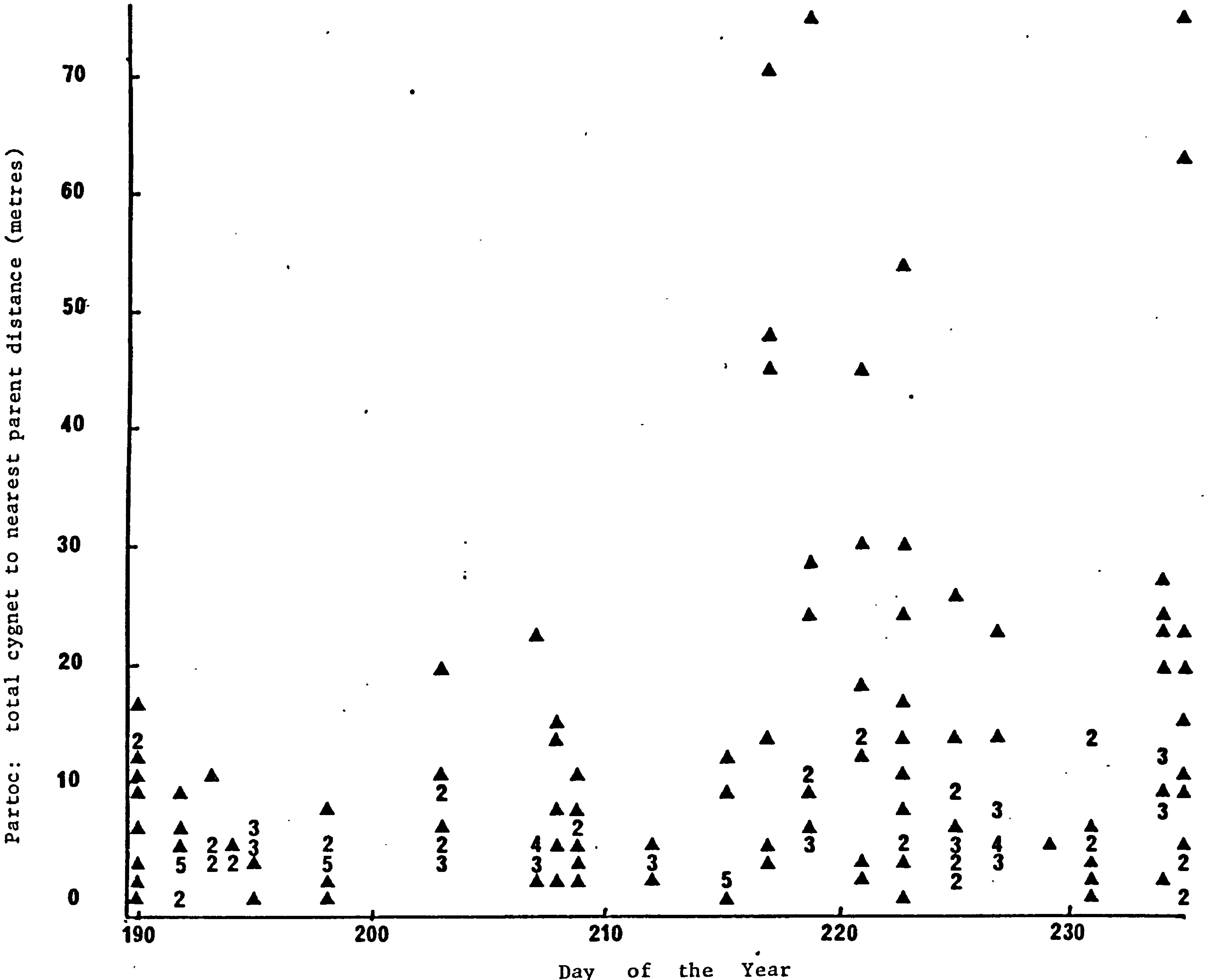

Partoc: total cygnet to nearest parent distance (metres)
0
10
20
30
40
50
60
70
190
200
210
220
230
Day of the Year

Fig. 8.13. Total inter-cygnet distance in relation to date; Arnarvatn North, 1978.
(n=132, r=0.316, p=0.0002)

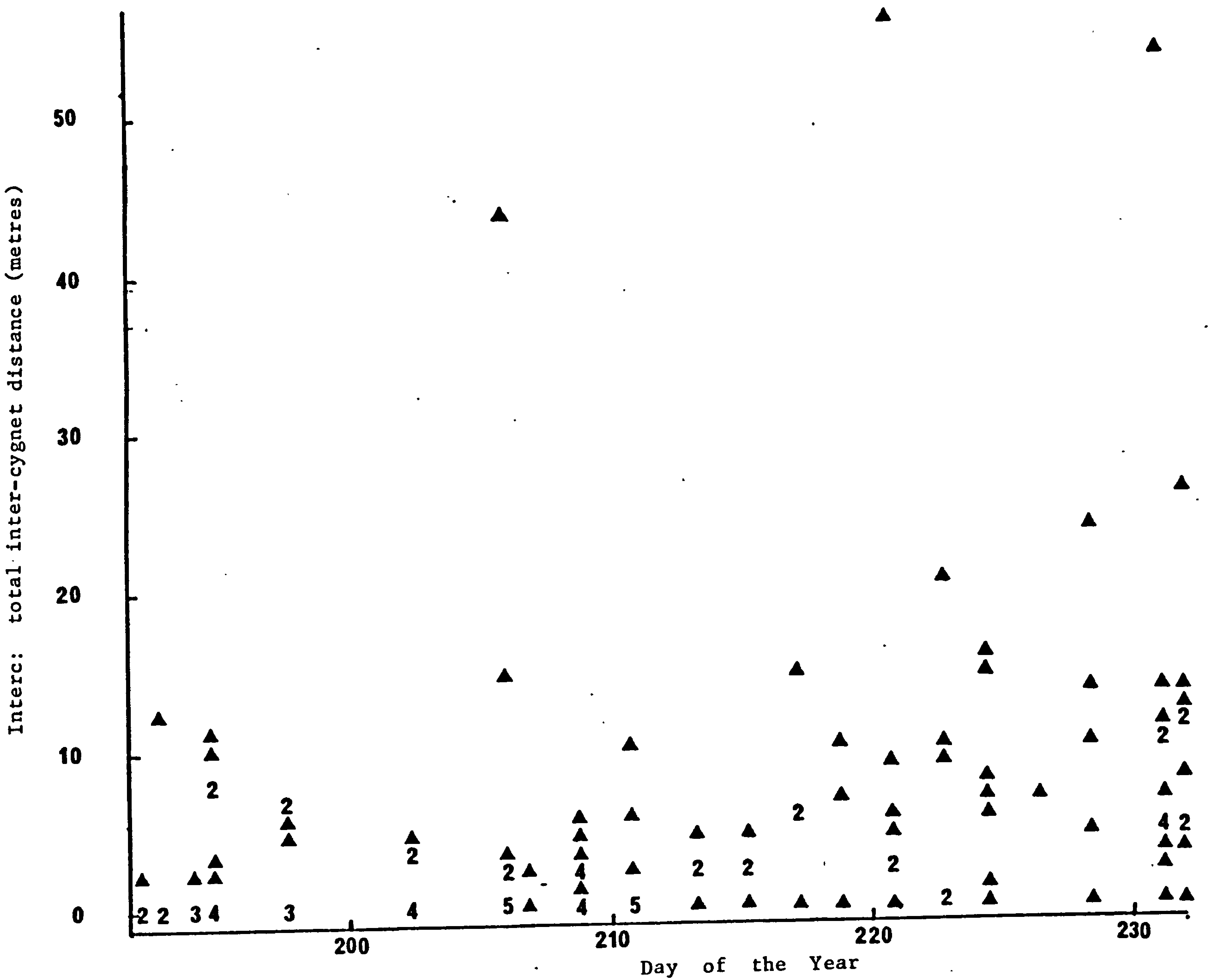

Interc: total inter-cygnet distance (metres)
0
10
20
30
40
50
200
210
220
230
Day of the Year

Fig. 8.14. The relationship between date and mean inter-cygnet distance; Arnarvatn North, 1978. ($n=21$, $r=0.721$, $p=<0.01$)

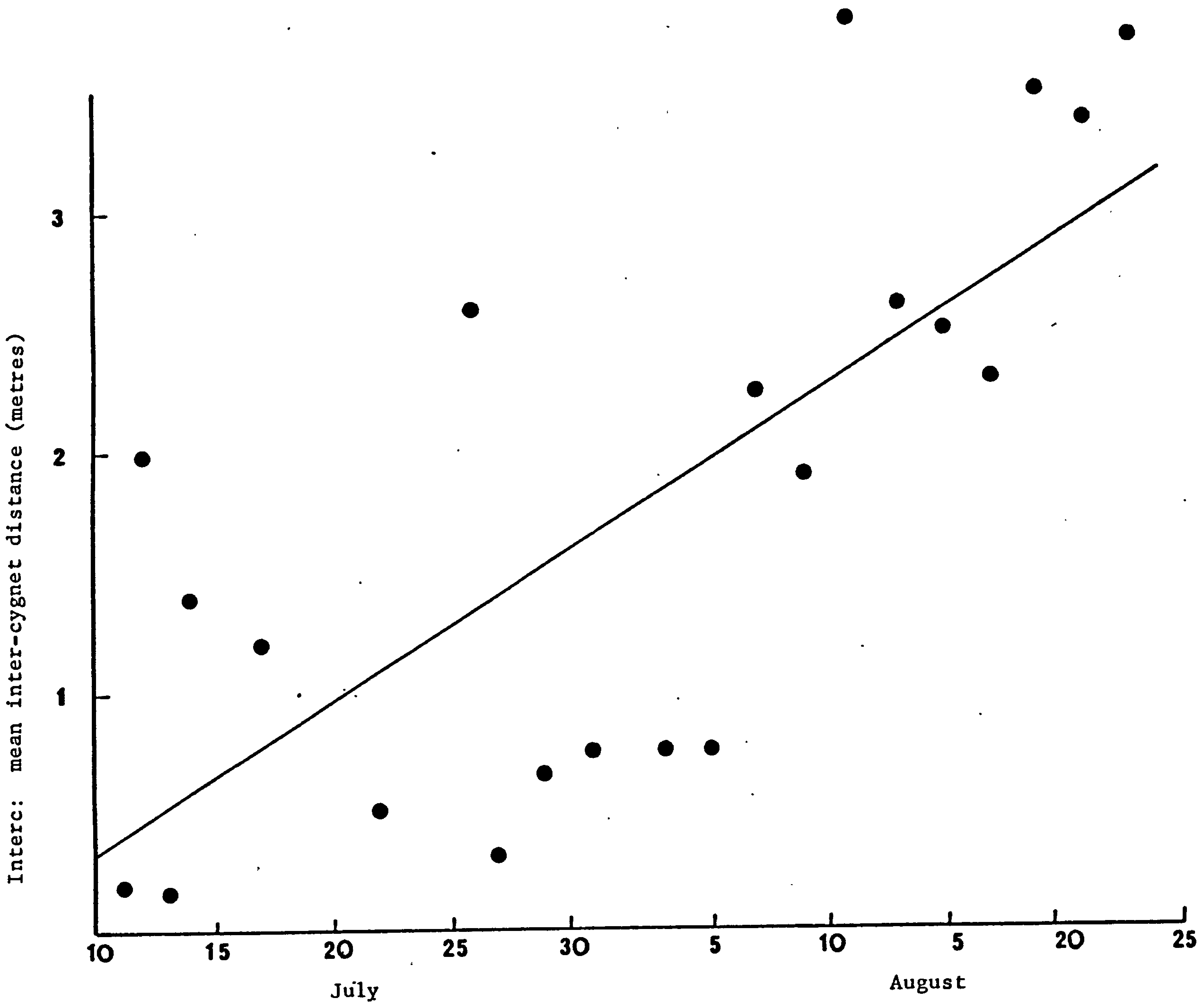

Interc: mean inter-cygnet distance (metres)
3
2
1
10
15
20
25
30
5
10
5
20
25
July
August

Fig. 8.15. Total inter-cygnet distance in relation to date; Arnarvatn South, 1978.
(n=191, r=0.380, p=0.00001)

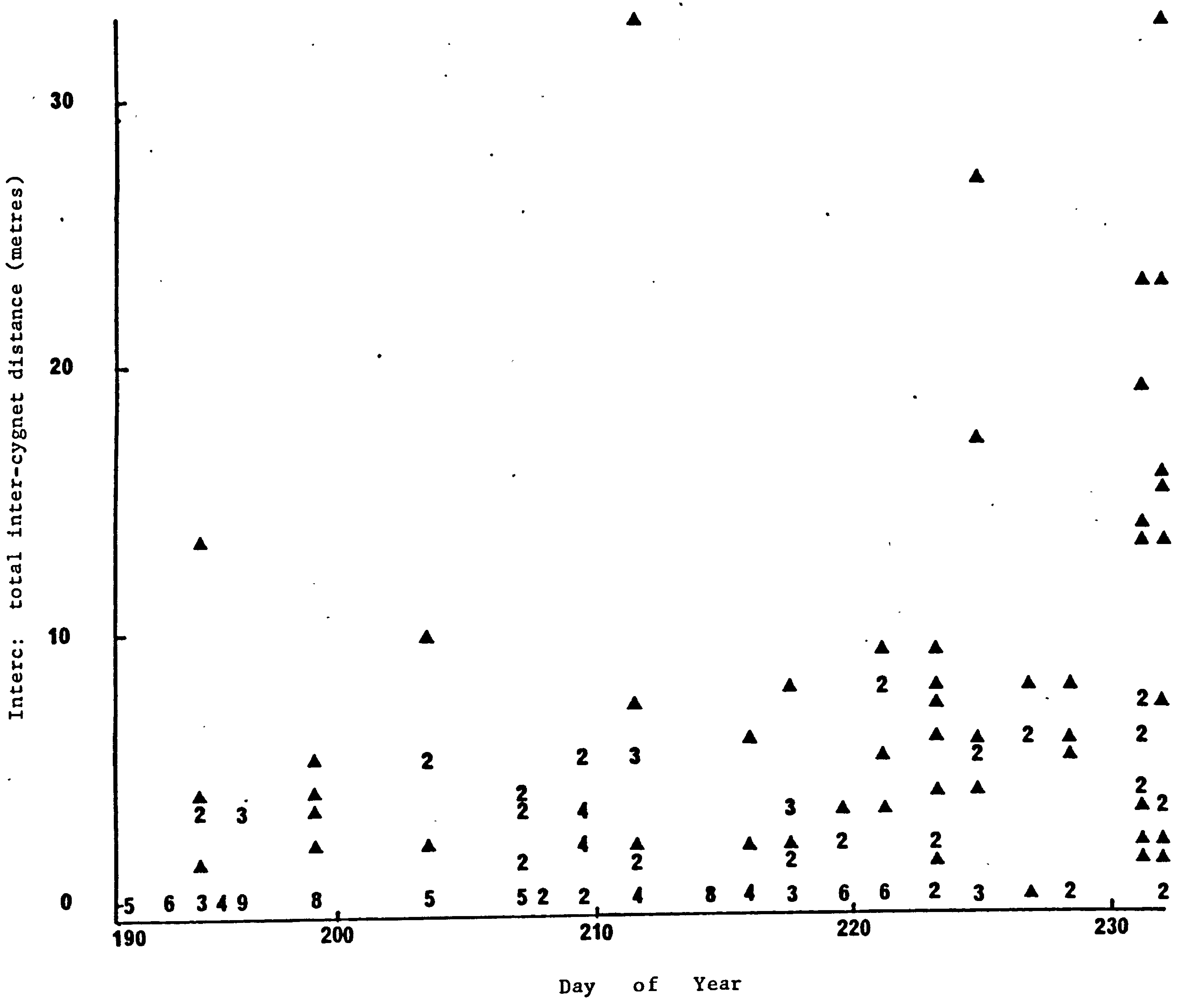

Interc: total inter-cygnet distance (metres)
0
10
20
30
190
200
210
220
230
Day of Year

Fig. 8.16. The relationship between date and mean inter-cygnet distance; Arnarvatn South, 1978. (n=22, r=0.712; p<0.01)

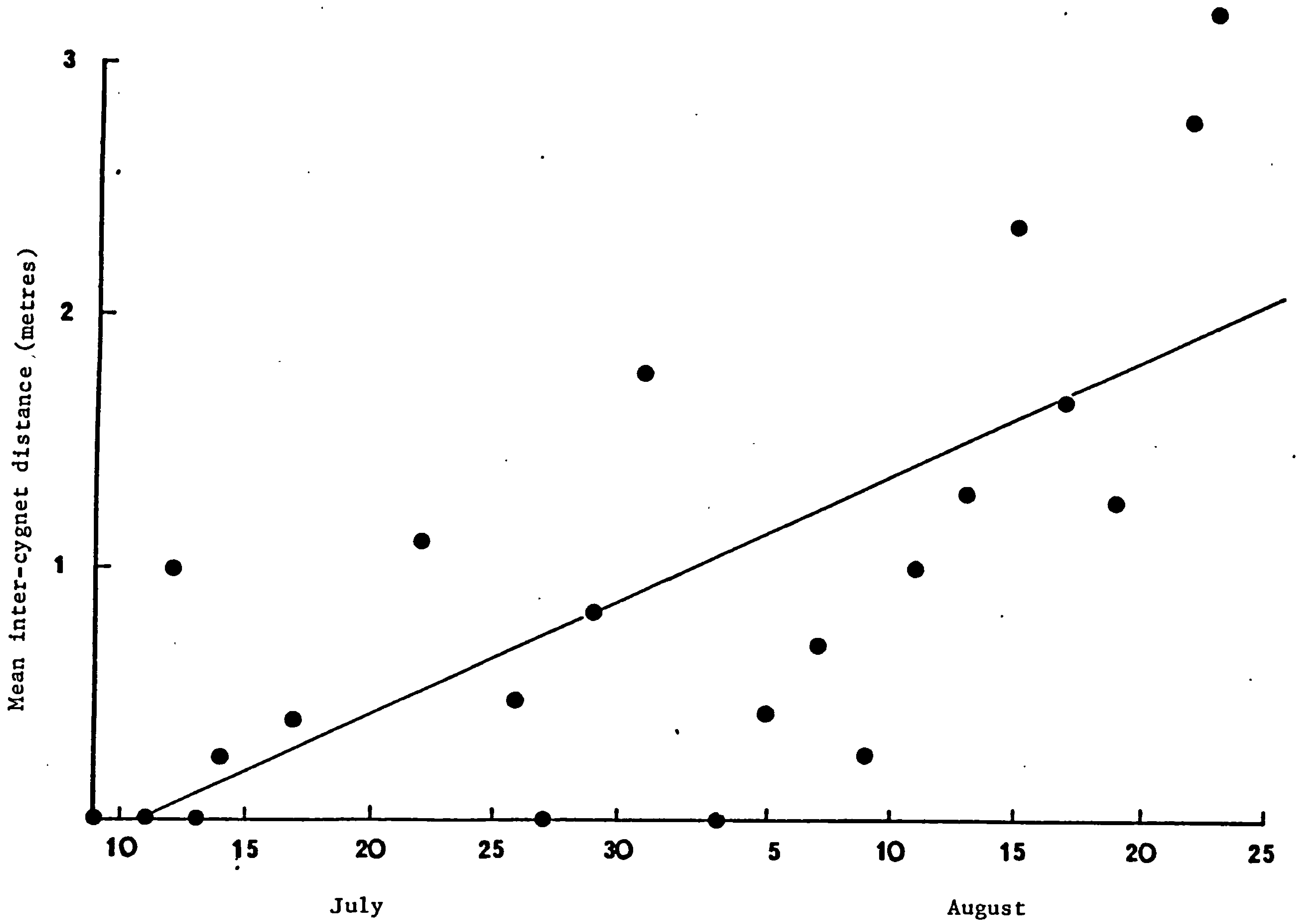
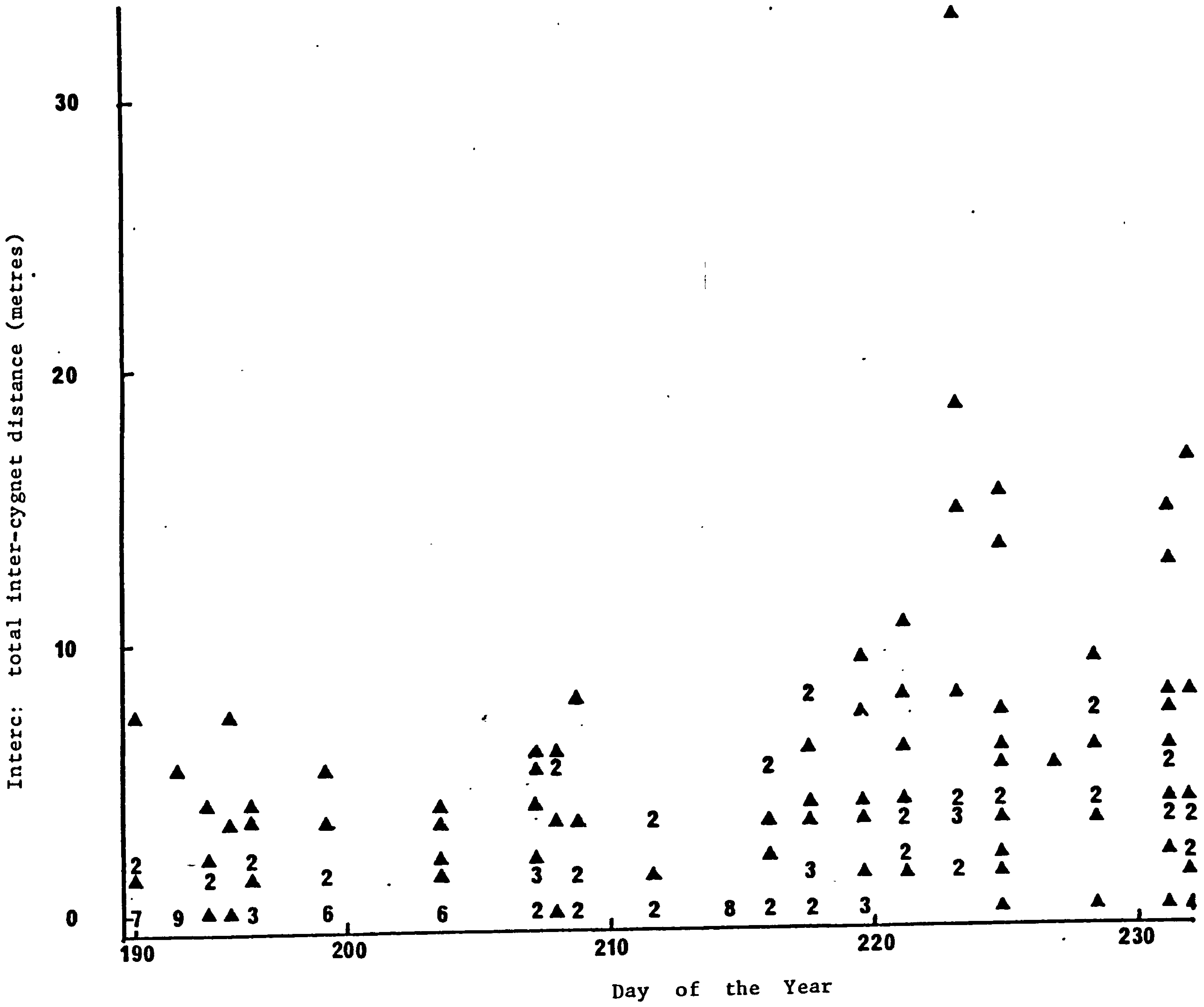

Mean inter-cygnet distance (metres)
3
2
1
10
15
20
25
30
5
10
15
20
25
July
August

Fig. 8.17. Total inter-cygnet distance in relation to date; Arnarvatn West, 1978. (n=183, r=0.374, p=0.00001)


Interc: total inter-cygnet distance (metres)
0
10
20
30
Day of the Year
190
200
210
220
230

<u>Fig. 8.18</u>. The relationship between date and mean inter-cygnet distance; Arnarvatn West, 1978. ($n=20$, $r=0.712$, $p<0.01$)

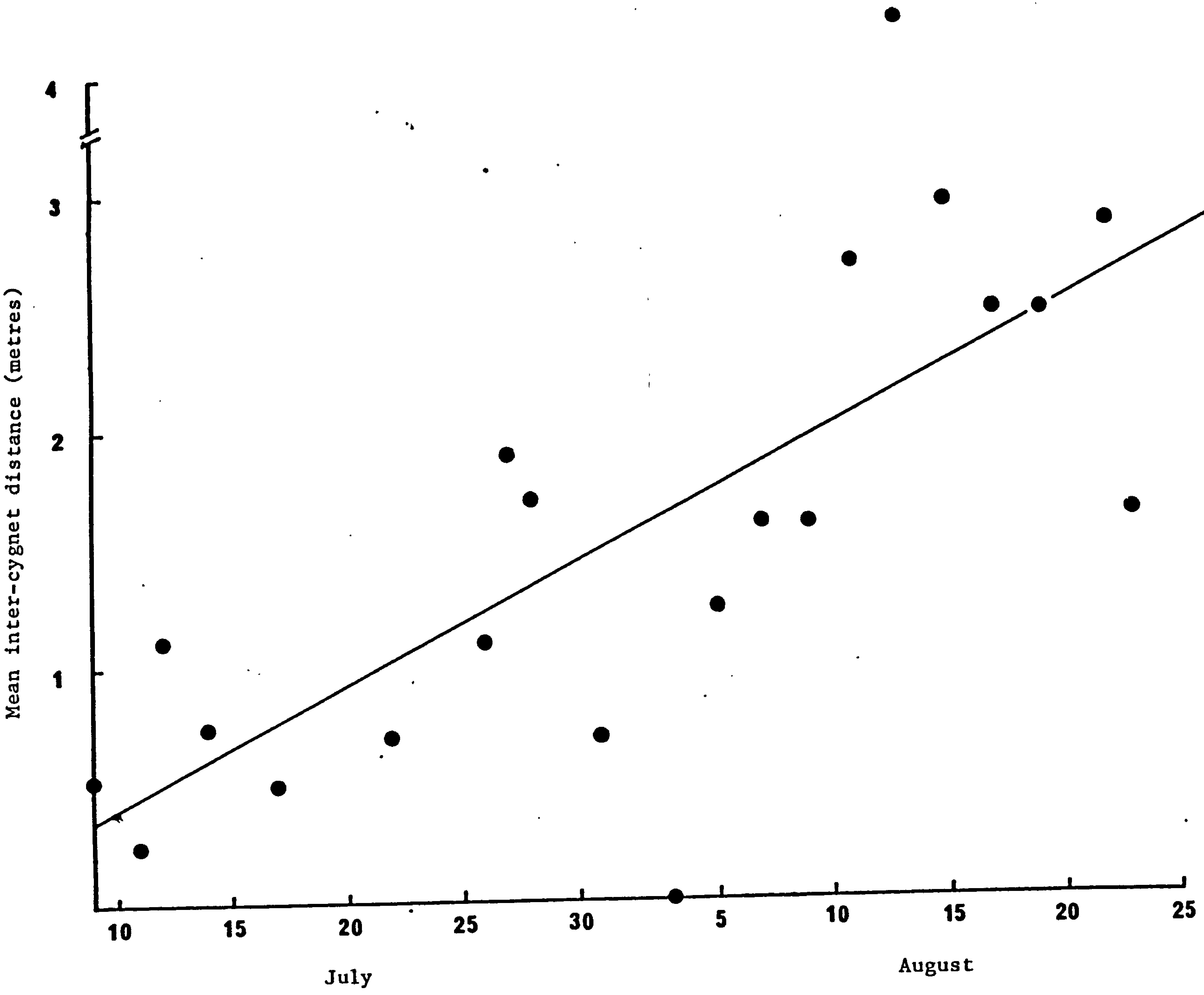

4
3
2
1
Mean inter-cygnet distance (metres)
10
15
20
25
30
5
10
15
20
25
July
August

Fig. 8.19. Inter-parent distance in relation to date; Arnarvatn North, 1978. ($n=182$, $r=0.17$, $p=0.02$)

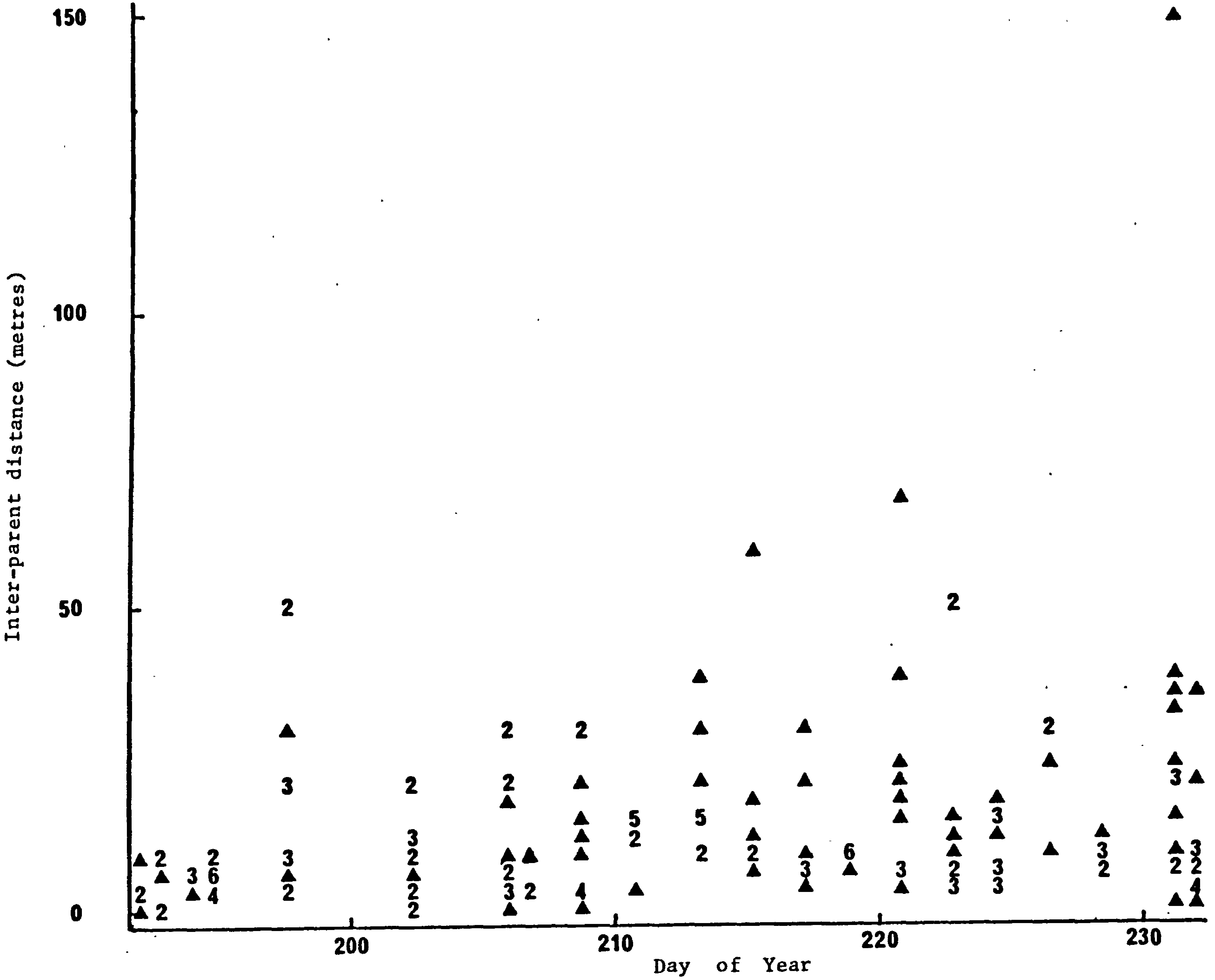

Inter-parent distance (metres)
150
100
50
0
200
210
220
230
Day of Year

Fig. 8.20. Inter-parent distance in relation to date; Arnarvatn South, 1978. ($n=195$, $r=-0.18$, $p=0.014$)

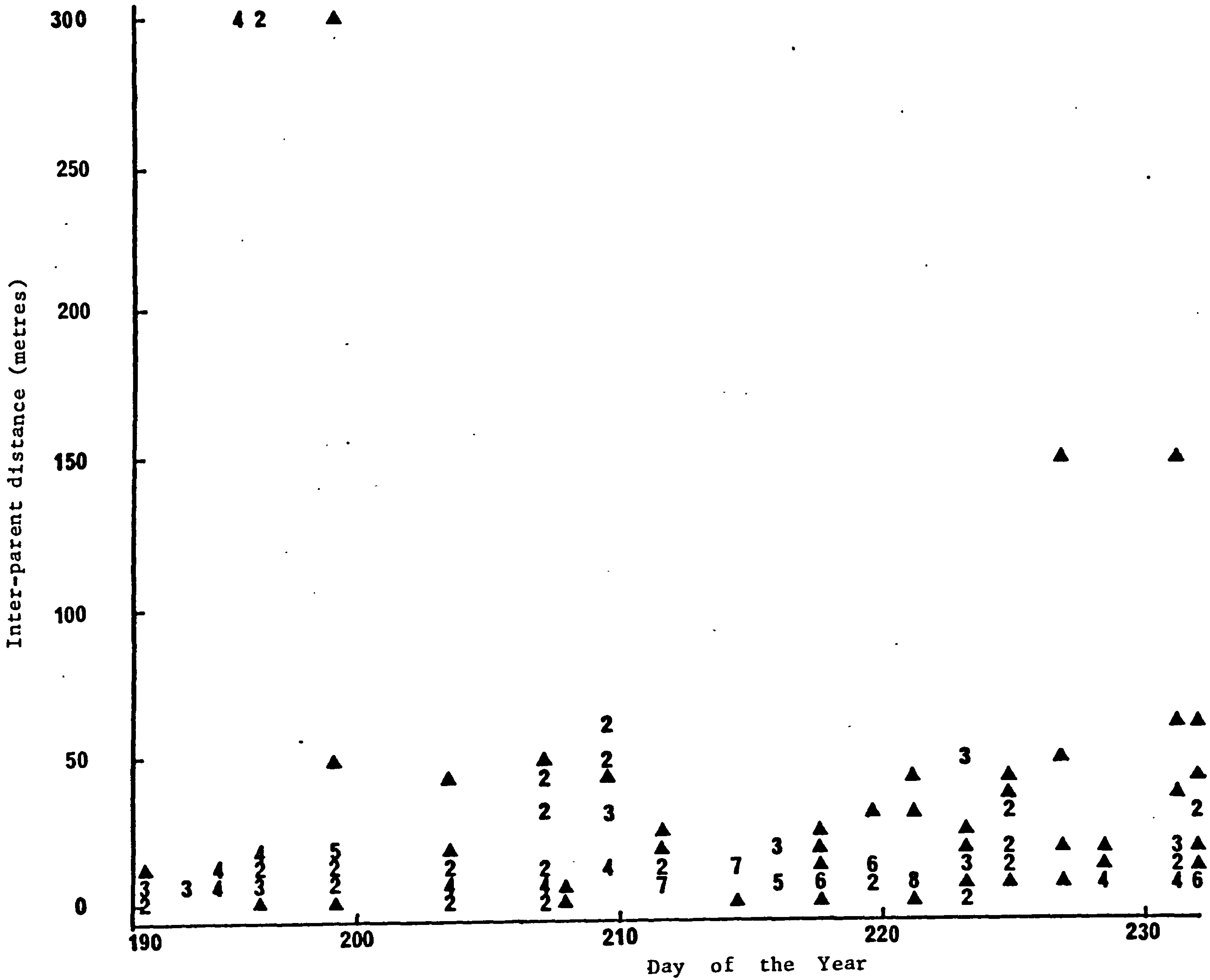
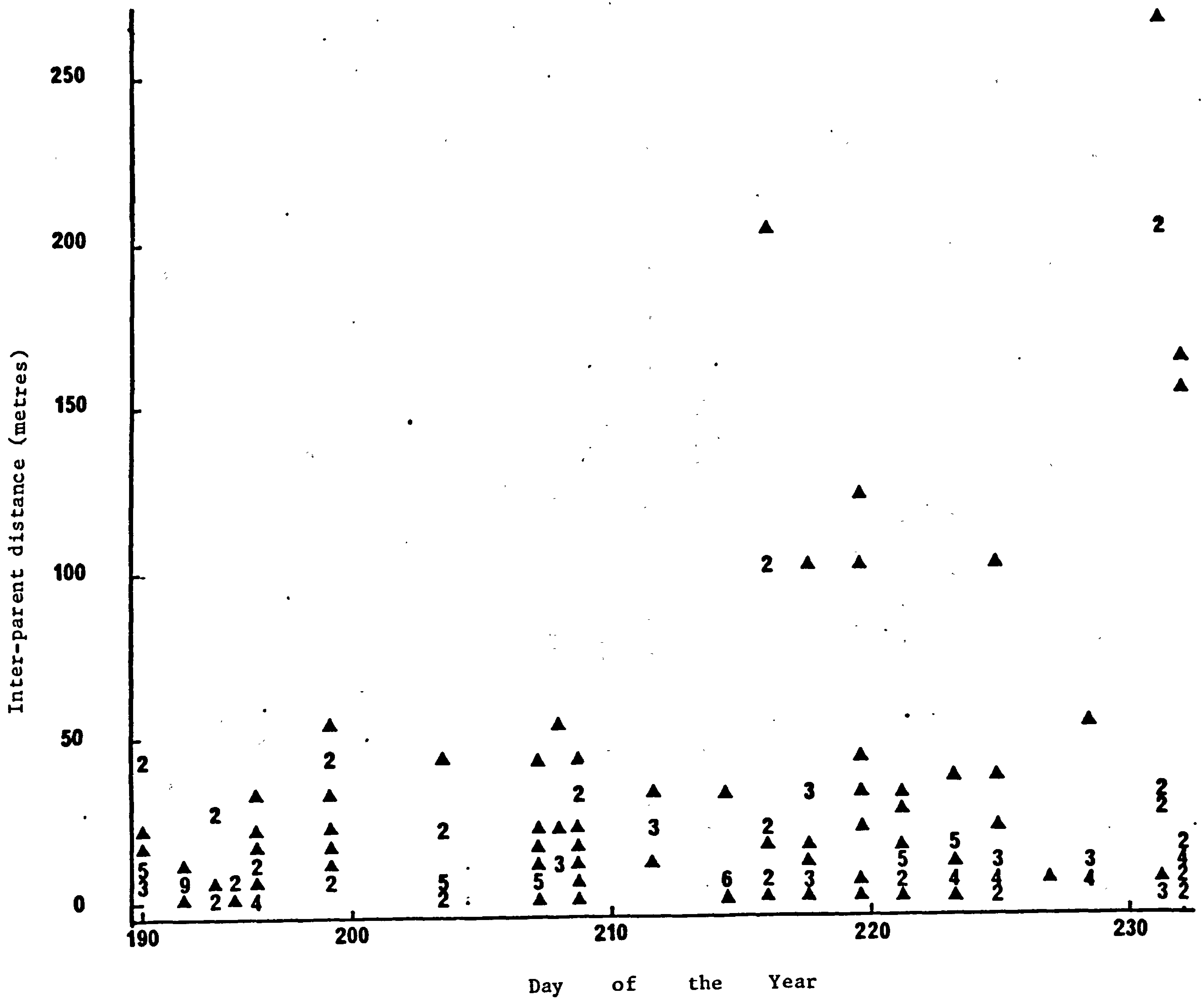

Inter-parent distance (metres)
300
250
200
150
100
50
0
190
200
210
220
230
Day of the Year

Fig. 8.21. Inter-parent distance in relation to date; Arnarvatn West, 1978. (n=190, r=0.224, p=0.002)


Inter-parent distance (metres)
0
50
100
150
200
250
190
200
210
220
230
Day of the Year

either towards care of the cygnets or towards feeding, while the cygnets were mainly concerned with feeding. There were distinct differences in the behaviour of parents depending on their proximity to the brood. The parent closest to the brood (thought to be usually the female) fed less, and was head-up more, than the parent furthest from the brood. Cygnets spent less time head-up and more time feeding than their parents and their commonest behaviours: head-up, dipping, grazing and roosting tended to occur in synchrony with the same behaviours of their parents. Cygnets tended to stay close together, and close to one parent. The distance between cygnets and from cygnets to their parents increased with age.

8.6.1 The Proximity of the Parents to their Cygnets

In July 1980 an opportunity was taken, during a ringing expedition to the Mývatn area, to collect a small amount of supplementary data as a check on results obtained in 1978. Three families were observed on a single day. During these observations parents were sexed by eye, using the length of tail and neck and the degree of staining on the feathers as a guide. It has been assumed that females moult first (Scott et al 1953; Kinlen 1963; pers.obs.). Males, therefore, are identifiable by their longer, thinner necks and longer wings relative to the tail and also by their greater degree of staining on the head and neck. This staining, first described by Frere (1846), is caused by feeding from waters containing Ferric oxide (Hohn 1955). Females are not noticeably stained until later in the season, because during the incubation period they do very little feeding (see 8.5.1).

At each of 30 spot samples the parent to which the cygnets were closest was identified and the distance between parents was recorded as less than or greater than five swan lengths. It was not possible to determine which of the parents the cygnets were with, when the parents were less than five swan lengths apart. The parents of pair one were closer together than five swan lengths on five out of 30 spot samples. During the remainder of the observation period all (four) or most (three) of the cygnets were closest to the male on 8% of samples and to the female on 92% of the samples. The parents of pair two were closer together than five swan lengths on 21 of the 30 samples. During the remainder of the observation period all (three) or most (two) of the cygnets were closest to the male on 89% of samples and to the female on 11% of samples. The parents of family three remained more than five swan lengths apart for the whole observation period and on 100% of the samples all the cygnets were closer to the female.

Cygnets were more often with the female in two out of three families, unfortunately during the observation period on the third family both parents were close together for most of the time, thus the male bias is a result of only nine minutes observations. These results are from a very brief study, but they confirmed that cygnets tend to stay close to a single parent, and indicated that this may be the female rather than the male; this is further confirmed in section 8.6.2. Trumpeter and Whistling Swan cygnets were also found to associate more strongly with the female than the male during the fledging period (Devos 1964; Scott 1977), and it may prove to be a general rule in the northern swans.

8.6.2 Parental Vigilance and Feeding during the Fledging Period

During summer 1978 'vigilance' data were collected from three families at Arnarvatn. The length of time birds remained head-up (potentially vigilant) and the length of periods between bouts of head-up, were measured.

Data from two families of four cygnets were collected together, because the question initially prompting the study was whether parents with large broods spent more time vigilant than those with small broods. Data were not available from enough families to examine this, however, and in view of the differences between individual pairs' time budgets discovered at the same site in 1979, it would have been more interesting to have kept the data from these two families separate. In the analyses discussed here, brood size has been ignored since there were not enough data for separate analysis.

In July and August there was no significant difference in the length of bouts of head-up between individual parents of the same family, but the periods between bouts of head-up were significantly shorter for parents closer to the brood (less than five swan lengths away) than for those further away (more than 10 swan lengths away) (see table 8.16 a and b). Presumably the detection of a predator, or of disturbance, in a large field of view is more easily accomplished by frequent brief scans than by less frequent observations.

Does vigilance as an aspect of parental care decline during the summer and as a result leave longer periods available for feeding? Time budget data from summer 1978, analysed on a monthly basis, showed that both parents of all three broods spent slightly less time head-up and slightly more time feeding in August than in July (see table 8.17).

Table 8.16.a.

Vigilance behaviour of parents at Arnarvatn in 1978

				JULY		AUGUST	
Brood size	Parent			Inter head-up	Head-up	Inter head-up	Head-up
Four	Near[1]	Mean ± S.D.	=	12.95 ± 18.66	11.89 ± 24.39	48.68 ± 50.50	18.09 ± 41.12
(2 broods)		Median	=	9.50	6.00	24.50	6.00
		n	=	168	167	42	27
	Far[2]	Mean ± S.D.	=	60.74 ± 154.12	18.57 ± 34.01	115.90 ± 149.97	57.45 ± 118.74
		Median	=	13.50	5.50	49.00	9.00
		n	=	61	63	43	44
Three	Near[1]	Mean ± S.D.	=	14.82 ± 37.60	9.82 ± 18.85	17.5 ± 20.60	7.77 ± 14.20
(1 brood)		Median	=	8.00	4.00	11.50	3.50
		n	=				
	Far[2]	Mean ± S.D.	=	17.45 ± 24.42	11.04 ± 18.63	26.96 ± 32.36	10.95 ± 20.6
		Median	=	11.00	5.00	15.25	3.00
		n	=	119	119	90	82

[1] Less than five swan lengths

[2] More than ten swan lengths

Table 8.16.b.

		Parents		
Behaviour	Month	Closest	Farthest	significance levels[1]
Head-up	July	Parent of 4	≏ Parent of 4	p=0.28
		Parent of 3	≏ Parent of 3	p=0.11
	August	Parent of 4	≏ Parent of 4	p=0.24
		Parent of 3	≏ Parent of 3	p=0.28
Inter head-up	July	Parent of 4	< Parent of 4	p=0.00006
		Parent of 3	< Parent of 3	p=0.005
	August	Parent of 4	< Parent of 4	p=0.017
		Parent of 3	< Parent of 3	p=0.04

[1] Mann Whitney U test, two-tailed

Table 8.17

The percentage of time spent feeding and head-up by parents close to and away from three broods at Arnarvatn, in 1978

		Northern family		Southern family		Western Family	
Behaviour	Month	Parent 1[a]	Parent 2[b]	Parent 1	Parent 2	Parent 1	Parent 2
Feeding	July	24.1%	20.2%	34.0%	44.9%	12.0%	16.3%
	August	25.0%	38.9%	44.1%	45.0%	20.7%	31.1%
Head-up	July	54.3%	49.4%	53.3%	48.4%	53.0%	43.8%
	August	53.7%	45.5%	50.0%	39.6%	37.1%	38.6%

a. Parent less than five swan lengths from the brood

b. Parent more than ten swan lengths from the brood

In order to examine formally the possibility of a change in the more detailed aspects of parental vigilance, lengths of bouts of head-up and of inter head-up periods were analysed with respect to date. Data from two broods of four had been combined during the original observations and due allowance was made for this when calculating mean levels of head-up and inter head-up.

The results were not conclusive. Neither time spent head-up nor inter head-up were found to be significantly correlated with date for parents closest to the brood, although there was a tendency for head-up to decline over the period in question ($r=-0.407$, $p>0.05$; see fig. 8.22). Data were only available for the parent furthest from the brood on two dates, so no formal analysis was done. The data suggest that they increased the length of each head-up bout, but decreased their frequency with date, suggesting that something very different might be happening with this parent. These different results might be explained by suggesting that, parents close to the broods have experienced a long period of poor feeding, have an increasing energy demand prior to migration and need to feed more, perhaps at the expense of vigilance. Parents away from the brood, on the other hand, have had more time available for feeding and might be capable of spending more time vigilant. The very limited data suggest, however, that they too increased their inter head-up period such that the overall time spent vigilant was reduced.

The results of this examination of vigilance were not convincing, but it was possible to turn the question round and ask instead if feeding increased during the fledging period. A positive result would imply that vigilance had probably decreased. Because head-up and feeding were

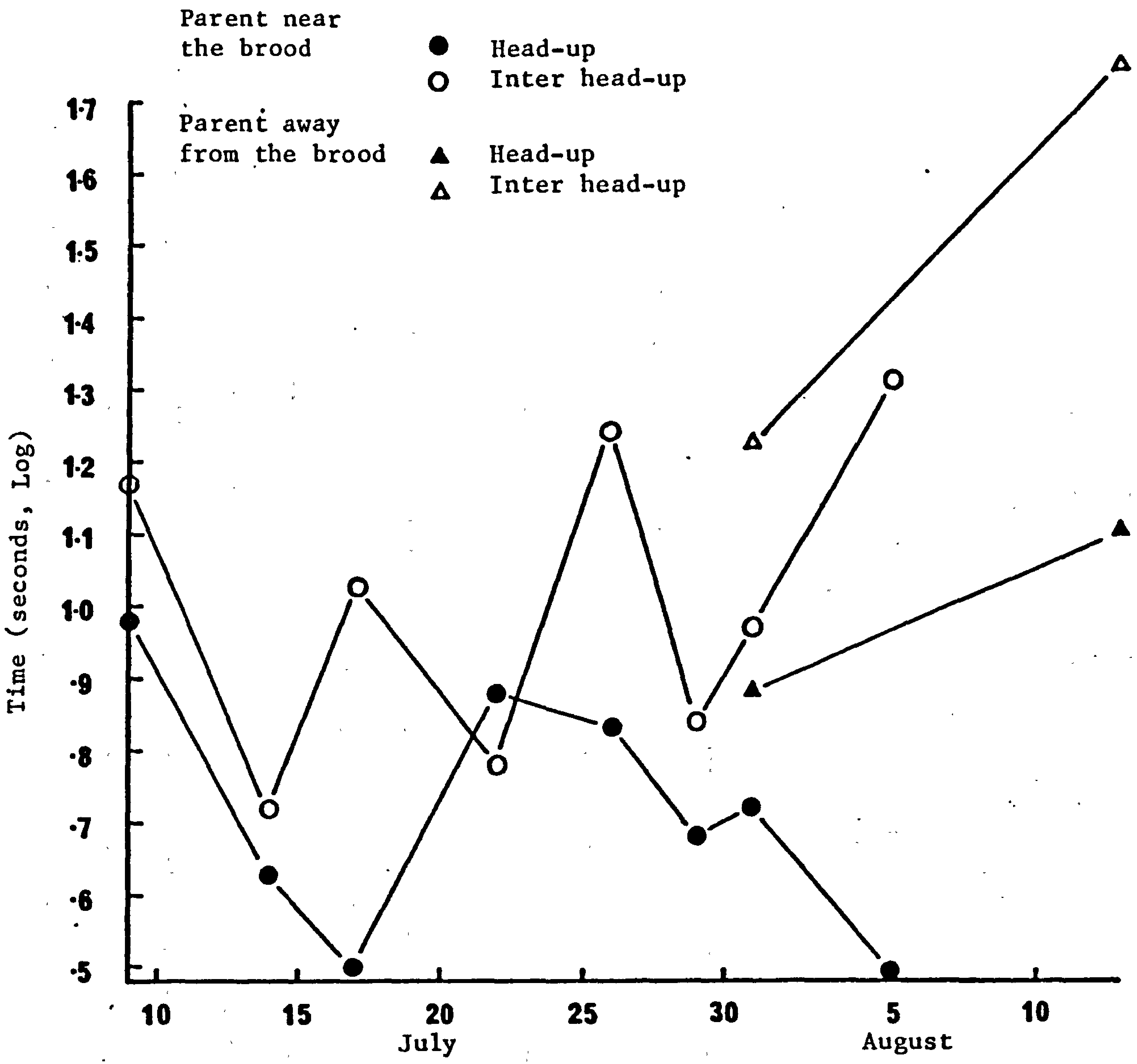


Fig. 8.22. The relationship between mean head-up, mean inter head-up and date; Arnarvatn 1978.

mutually exclusive, increasing the time spent feeding necessarily restricts other behaviours, including head-up. Although, as can be seen from table 8.17, not all of the increase in time spent feeding was accounted for by the reduction in head-up. Examination of the lengths of feeding bouts, in this case 'dips', revealed that in July parents close to the brood had a mean dip duration (m.d.d.) of 5.4 ± 3.1 s. (n=211) which was significantly shorter than that of parents furthest from the broods (9.8 ± 4.2 s., n=128) ($p<0.00006$, all significance values in this section refer to the Mann Whitney U test, two-tailed). This difference was not significant in August, when parents closest to the broods had an m.d.d. of 8.6 ± 3.3 s. (n=68) while parents away from the brood had an m.d.d. of 9.5 ± 4.1 s. (n=44) ($p=0.076$). During this period the m.d.d. for parents closest to their broods had increased significantly ($p<0.00006$). Data from all three familieshave been combined here because not enough data were available from each family for both months for separate analysis.

It is apparent that parents close to the brood increased the length of their feeding bouts from July to August. This would necessarily restrict the interval at which head-up could occur. Both parents also tended to increase the total amount of time spent feeding from July to August, which inevitably meant a reduction in all other behaviours, including vigilance (see table 8.17). It is suggested that coincident with an increase in feeding there is a reduction in parental care in the form of parental vigilance.

After having familiarized myself with the western pair at Arnarvatn, it became possible to identify the male and female by differences in size and in the relative amounts of orange staining on their necks and heads (see 8.6.1). Data were collected in order to compare aspects of the behaviour of the same parent at different distances from its brood. During the fledging period the female spent more time close to the brood than did the male and was head-up more often. When the female moved away from the brood, however, her frequency of head-up decreased significantly (p=0.04) (see table 8.18), although her bout lengths of head-up did not change. When the male moved relative to the brood, neither his bouts of head-up, nor his inter-head-up periods changed significantly in length. If this pair was at all representative, it seems that time spent vigilant by males is constrained by factors other than proximity to the brood, whereas for females, proximity to the brood is the important factor. The inter head-up period of the females when close to the brood was significantly shorter than that of the males (p=0.00006), whereas there was no significant difference between their head-up bouts (p=0.62). When away from the brood the female was head-up significantly more often than the male at the same distance (p=0.002) and for significantly longer (p=0.048).

Marked differences in parental roles during the incubation and fledging period were reflected especially in levels of vigilance. The males spent more time vigilant than females during the incubation period, whereas during the fledging period it was the females who were more actively vigilant. Parents spent longer feeding and less time head-up in August compared with July, this was presumably to build up fat stores for the autumn migration. Parents close to the brood significantly increased the length of their feeding bouts and their inter head-up periods. It seems that females remain closer to their brood than do males and females are more vigilant than males.

Table 8.18

Vigilance behaviour of individually identified parents at Arnarvatn in 1978

Behaviour	Sex			Less than 5 m from the brood	More than 10 m from the brood
Head-up	Male	Mean ± S.D.	=	19.24 ± 37.86 s	4.57 ± 5.45 s
		Median	=	5.5	2.5
		n	=	27	56
	Female	Mean ± S.D.	=	9.48 ± 14.41 s	10.70 ± 18.85 s
		Median	=	4.0	4.0
		n	=	120	39
Inter Head-up	Male	Mean ± S.D.	=	66.36 ± 93.87 s	33.89 ± 40.49 s
		Median	=	30	20
		n	=	26	57
	Female	Mean ± S.D.	=	10.05 ± 7.91 s	19.1 ± 26.69 s
		Median	=	8.25	9.25
		n	=	120	39

Throughout the fledging period the cygnets are maturing. They begin to travel further from their parents and must gradually develop a mature behaviour pattern, although even in winter they still spend less time vigilant than do adults or parents. By the end of the winter, however, this difference was found to have disappeared. It is likely that cygnets spend progressively more time vigilant prior to the autumn migration. September or October would probably be the crucial months in this development since at this time the demands on parents to spend extra time feeding would be at their peak. It is felt that the data show a tendency for the parents closest to their broods to relax their levels of vigilance, but that the period over which the observations took place was very short, given the time-scale over which cygnets might be expected to be maturing. Given that such close attention to the brood disappears by late winter, there are obvious changes occurring in the first ten months of the cygnets' lives, both in their own behaviour and in that of their parents. In order to examine the decline in parental vigilance critically, data from broods in September and October would be desirable.

8.6.3 Space Utilization at Arnarvatn, 1978

Observations during 1978 and 1979 suggest that Whooper Swans defend spatio-temporal type A territories (Wilson 1975). There were difficulties however in distinguishing between home-range and territory because interactions between territory-holders were relatively infrequent. The 'home-ranges' used in summer 1978 by three families and one pair at Arnarvatn are to be seen in fig. 8.23. Territorial interactions of the type described in section 8.3 were seen between the southern and western families, between the western family and both the pair and the northern family. The southern family was the most consistent in its use, it made very few


North pair

North family

2

West family

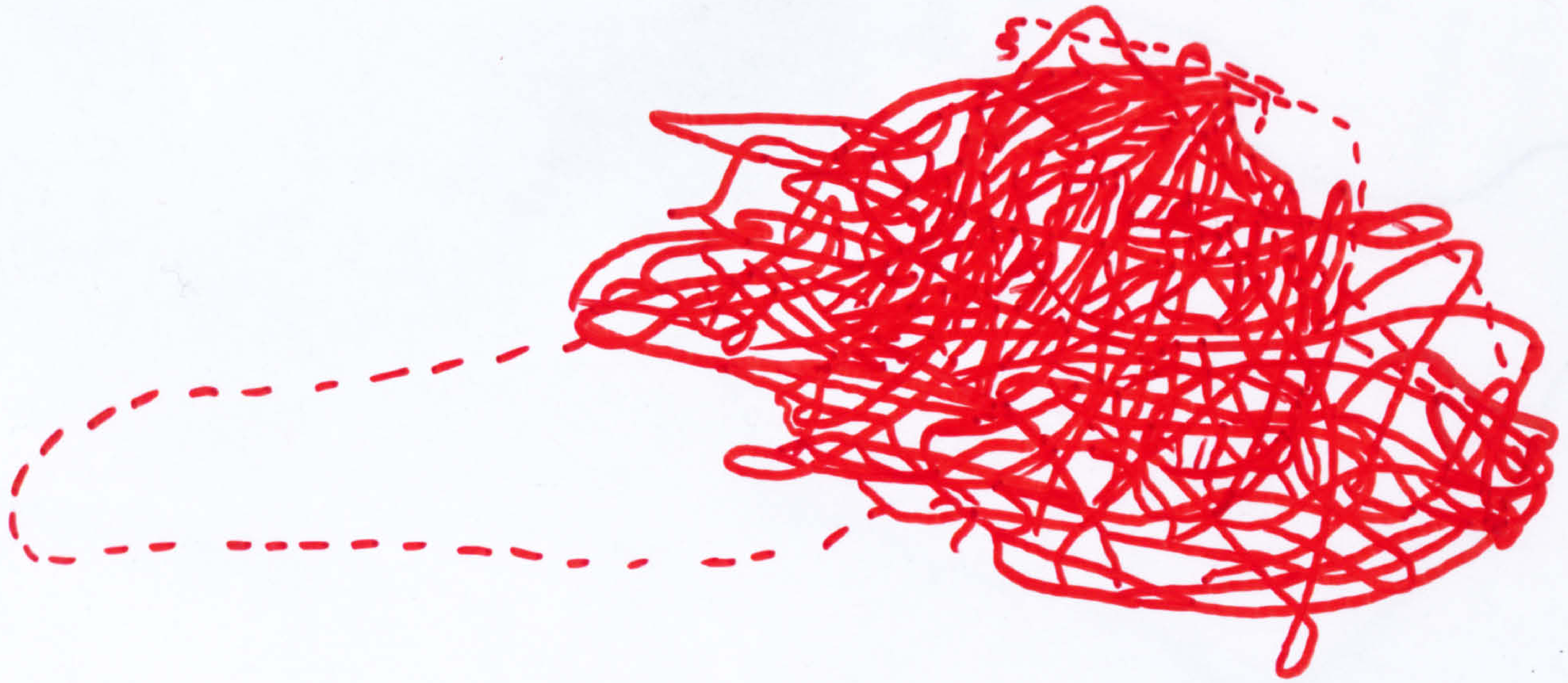


Fig. 8.23. Home ranges of three families and one pair at Arnarvatn in 1978

Fig. 8.23. Home ranges of three families and one pair at Arnarvatn in 1978

movements up the lake. The western pair used the most extensive area; the area around their nest site was most unsuitable for grazing so the family regularly crossed the lake to the meadows on the east shore. This pair moved its range up the lake to include the north shore after the disappearance of the north pair, which had until 31st July vigorously defended that area. The western pair were last seen at the north end on 15th August, after that date the northern family extended their range to include almost the whole of the area previously used by the northern pair. On the whole, interactions only occurred when birds occupying adjacent ranges happened to be close to each other, although on several occasions an individual was seen to patter or fly more than 100 m to engage another individual in an interaction.

Since nesting may commence even while territories are partially frozen and since females spend so little time feeding, the main function of the 'territory' would seem to be to ensure that there is a suitable area for the family to feed in during the fledging period. Having said that, however, both Whooper and Trumpeter Swans also nest in oligotrophic areas, where the female may have to fly to suitable feeding areas during incubation breaks and where the family may be led from the natal area to another site within the first few days after hatching (see Hansen et al 1971; Haapanen et al 1977). In oligotrophic areas, pairs are widely spaced (e.g. Bulstrode et al 1973) and only rarely is there the stimulus or functional requirement for defence of a territory. In a rich area, however, for example Arnarvatn, to which several pairs have been attracted, there is the constant stimulus provided by the signal function of the white plumage (see Wynne-Edwards 1962; Armstrong 1971; Johnsgard 1978) and the functional requirement for territorial defence. The well-structured nature of the displays involved suggests that successful maintenance of a territory is important. As mentioned above, its main value appears to be during the fledging period.

8.7 Conclusions

As in Finland, Whooper Swans in Iceland were found to be monogamous, territorial and nesting at low densities (Bulstrode et al 1973; Haapanen et al 1977; this study Ch. 7 and 8). Females spent more than 80% of their time incubating, but this was less than female Trumpeter Swans (see Cooper 1979; this study 8.5.1). The usual position whilst incubating was either head-up or roosting; those in Iceland spent less time roosting than those in Finland (see Haapanen et al 1977; this study 8.5.1). During incubation breaks feeding was the predominant activity.

Males did not incubate, but spent most of their time within 100-150 m of their nests, usually head-up or feeding. The behaviour of males and females was co-ordinated. For example, males were more often head-up when females were off the nest than when they were on. Similar co-ordination of behaviour was shown to occur between parent Bar-headed Geese (*Anser indicus*) (Wurdinger 1978), which rarely slept or preened simultaneously.

Fewer different behaviours were observed during the fledging period than during incubation. The behaviours were basically the same as those recorded in winter, that is feeding, preening, roosting and head-up. As was expected, cygnets spent more time feeding than did their parents. Each family showed some synchronization of behaviours between parents and cygnets, but there was no apparent consistency between families as to which behaviours and which individuals were involved.

Cygnets were found to remain close to a single parent, but to maintain closer proximity to each other than to their parents. They remained closer to their parents than parents did to each other, but as cygnets matured the distances between them, and from them, to their parents increased. It is thought that cygnets spend more time close to the female than to the male, as they do in the Whistling Swan (Scott 1977). The parent closest to the brood spent more time head-up than did the parent further away and females, but not males, were found to reduce their levels of vigilance when they moved away from the brood. Interestingly, in the Whistling Swan, there was no significant difference between male and female parents after hatching, either in time spent vigilant or in feeding rates (Scott 1977).

It appears that as the cygnets grow in size and mature behaviourally, certain aspects of parental care, such as proximity to the brood, decline. This is in keeping with Triver's (1974) theory of parental investment which predicts that parental care will decline at some stage of offspring development; and the observations of Lazarus and Inglis (1977) which showed that in Pink-footed Geese, a decline in parental 'extreme head-up' seemed to be associated with gosling growth and maturation.

The female of one pair at Arnarvatn was less attentive than that of the other and the time she spent off the nest was correlated with date. She also failed to hatch any eggs. Although this might just have been co-incidental, it was thought likely that she may not have had sufficient energy reserves to complete incubation. The spring of 1979 was very severe in Iceland and fewer pairs than usual bred successfully. The same phenomenon is well documented for Geese nesting at high latitudes (e.g. Barry 1962).

At Arnarvatn, north-east Iceland, previously undescribed territorial interactions between breeding pairs were observed. The function of the territory in geese has led to much discussion, because it is variable both within and between species (Owen 1980). It does seem, however, that the function of the Whooper Swans' territory is very different from that of geese. 'Territorial' defence in geese is greatest during laying and early incubation and at its lowest from late incubation onwards (Inglis 1976; Mineau 1978). The reverse is true of the Whooper Swans studied in Iceland. Defence against adjacent territory-holders was highest during fledging (section 8.3).

Ryder (1975) put forward the theory that territory size in geese was dependent on a balance between the food requirements of the male and the number of neighbours he must defend his female and territory from. Inglis (1976), on the other hand, proposed that the Pink-footed Goose's territory serves to ensure a food supply for the female prior to incubation. It was unlikely that it was to provide a food supply for the male because territorial defence declined during the incubation period (Inglis 1976; Mineau 1978). Both Mineau and Cooke (1979) and Owen and Wells (1979) suggested an even more restrictive function; in the first case it was to provide a 'buffer zone' between the nest and the female to protect them from potential nest parasites and rapists, and in the latter case it was to prevent the take-over of nest sites by prospecting pairs.

Probably the most crucial difference between the Whooper and Trumpeter Swans and Geese, when considering the function of territory defence, is the much lower density at which they nest. The Geese species involved above, nest at much higher densities (usually in colonies) than do the

Swans. The involvement of the female in territorial defence (Cooper 1979; this study 8.5) indicates not only the low probability of nest predation, but also that the prime function of the territory is to provide a feeding area for the cygnets.

CHAPTER NINE: THE BEHAVIOUR OF NON-BREEDING WHOOPER SWANS

9.1 Introduction

A large proportion of the Whooper Swan population does not breed. Hitherto, studies have concentrated mainly on breeding birds (Banko 1960, Hansen et al 1971, Haapanen et al 1973a, 1977). Non-breeders are of particular interest because they apparently represent a very large proportion of the total population (Haapanen et al 1973a; Brazil and Petersen in prep.).

Non-breeders are: young birds of pre-breeding age, birds which have attempted to breed, but which have failed at some point in the cycle from the occupation of a territory to the fledging of their cygnets, and sexually mature birds which do not attempt to breed. Presumably, non-breeders represent a reservoir of potential breeders ready to fill territories as they fall vacant, or to replace individuals of pairs which die. As yet no-one has studied recruitment from the non-breeding group into the breeding population, but it is hoped that by following the birds which were neck-banded in 1980 information may be forthcoming on this subject.

The aims of this chapter are to examine the arrival of swans into the non-breeding flocks; the activity patterns of birds in the flocks for comparison with activity patterns at other times of year, and the effect of continuous daylight on the diurnal activity rhythm.

9.2 Methods

From 8th July until 21st August 1978 non-breeders were studied at Myvatn. The bay Neslandavik was used as a study area because it was readily accessible and visible. Observations were made from a portable hide situated on a lava hummock on the east side of the bay. It was not practical to study the behaviour of birds using Ytrifloi because of the inaccessability of good observation sites and because of the distance of the birds from the shore. Instead, regular visits were made simply to count the number there. Whenever possible, journeys were made around the peripherary of Myvatn to count swans using other sites.

Activity budgets for the Neslandavik flock were compiled from a series of scans. Scans were made every 30 minutes and the number of birds engaged in feeding, preening, roosting and head-up was recorded. The periods between these scans were used to map the movements of the flock and to record detailed aspects of their feeding and vigilance behaviour. Scans were combined for the calculation of hourly means and observation periods were combined to cover the 24- hour period. Observation periods were usually of six hours, and were shifted by six hours each day so that the full 24- hour period was covered regularly.

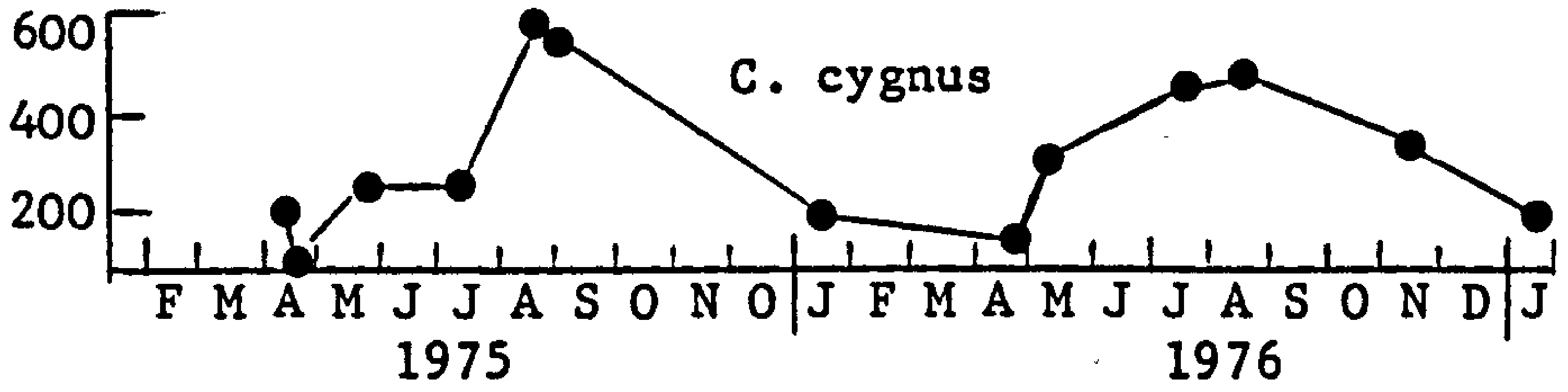
9.3 The Fluctuation of Whooper Swan numbers at Myvatn

The north basin (Ytrifloi) and a large bay (Neslandavik) on the west side of Myvatn, between them hold the largest inland moulting flock of Whooper Swans in Iceland. Numbers begin to increase in late April and early May and peak in late August and early September. Numbers decline in the autumn and only a small wintering population remains, this almost completely disappears in the spring prior to the main arrival. Data from this study supports the pattern shown by Gardarsson (1979) (fig. 9.1).

Fig. 9.1

Seasonal Variation in Whooper Swan numbers at Lake Myvatn

(from Gardarsson 1979)



Summering birds occupy two discrete areas at Myvatn (see fig. 7.1), but previous censuses (Gardarsson 1979) made no distinction between the two flocks. It was generally accepted that birds initially used Neslandavik before moving out to Ytrifloi during the course of the summer. Closer observation, however, showed that this was not the case, birds were present at both localities simultaneously.

Observations made during this study were more detailed than previous census work at Myvatn. Frequent prolonged observations were made at Neslandavik and less regular visits were made to Ytrifloi. It was possible therefore to follow the fluctuation in numbers at these two areas separately (see fig. 9.2). Numbers in Neslandavik were just below 200 in June 1978, throughout late June, July and August numbers did not drop below 130 and generally fluctuated around 180. There was no significant change in numbers with date ($r=-0.001$). Numbers at Ytrifloi were below 200 in June 1978, fluctuated until 16th July, then increased to a maximum of 465 on 8th August ($r=0.896$, $p<0.01$). Total numbers for Myvatn also increased significantly and peaked at 640 on 8th August ($r=0.881$, $p<0.01$) (see fig. 9.2).

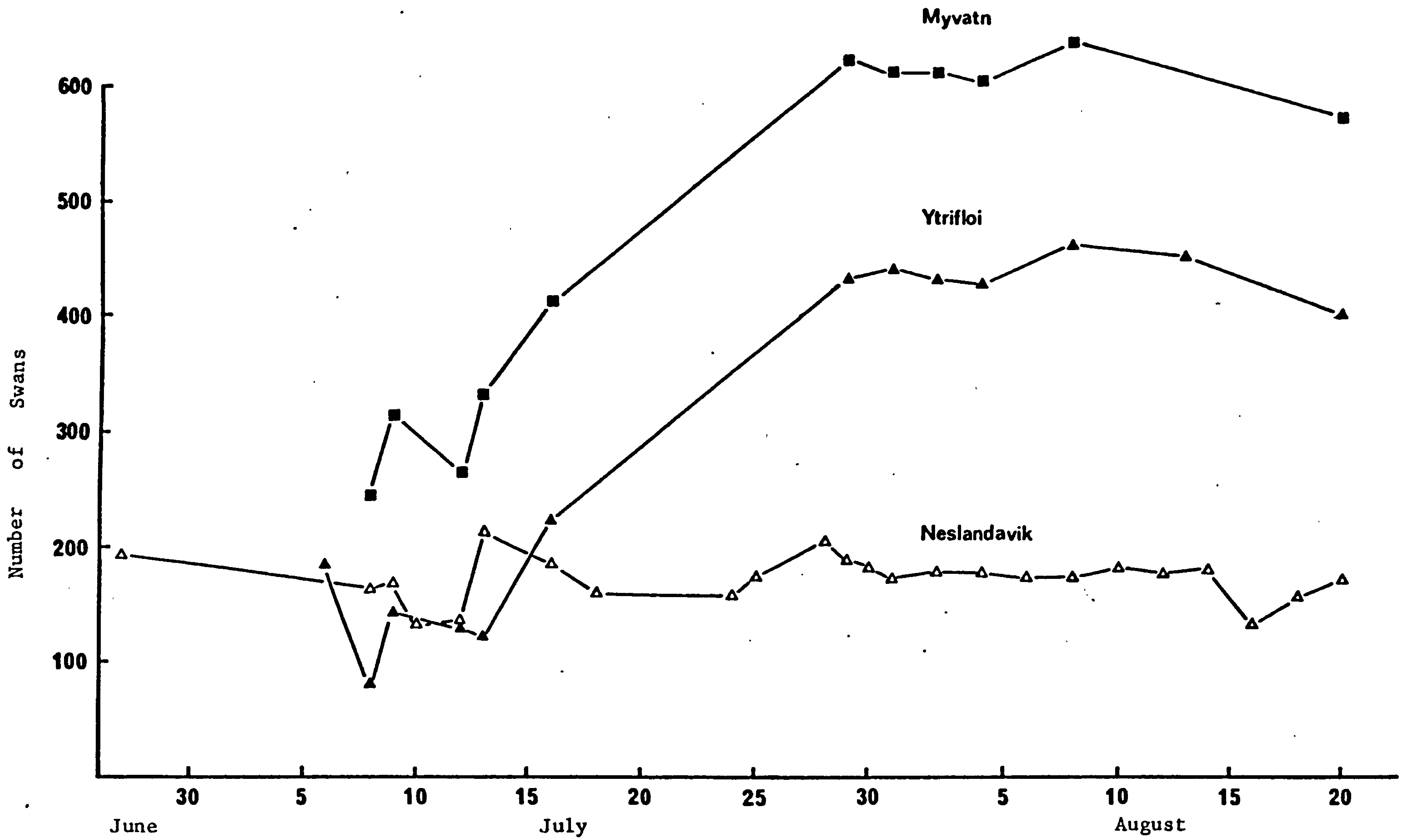


Fig. 9.2. Variation in Whooper Swan numbers at Myvatn; Summer 1978

A return visit was made to Myvatn in spring 1979 in the hope of studying the build-up of these two flocks in more detail. Unfortunately the spring of 1979 was very long and cold and followed a severe winter, consequently spring migration was delayed. A very delayed breeding season ensued and as a result numbers only began to increase in Ytrifloi towards the end of the field season. Numbers had just reached 200 in Neslandavik by 15th July (see fig. 9.3). The delay to the migration in 1979 did however make it possible to observe initial arrivals into the Myvatn area and to follow their movements. In late May most of lake Myvatn was frozen including the whole of Neslandavik. The first swans observed in the area were on grass fields partially free of snow, near the road between Geirastathir and the Laxa. This area I called the southern fields to distinguish it from an area 1½-2km further north which was utilised later. Both areas were within 2-3km of the lake.

Numbers at the southern fields were not constant and it was not possible to discover where birds went to when they were absent. Birds may have been passing through the flock on the way to other areas. By the second week of June this flock had dwindled away, except for three isolated records in mid-June. After it had almost disappeared another flock began to use the northern fields. This area had not previously been in use and movement of the few remaining birds from the southern fields could not account for its sudden increase (fig. 9.3). This flock peaked at 55 birds on 12th June and declined rapidly as birds began to use the partially thawed Neslandavik.

Some birds in the southern flock had traces of juvenile plumage, were consorting with adults and were apparently still in family groups.

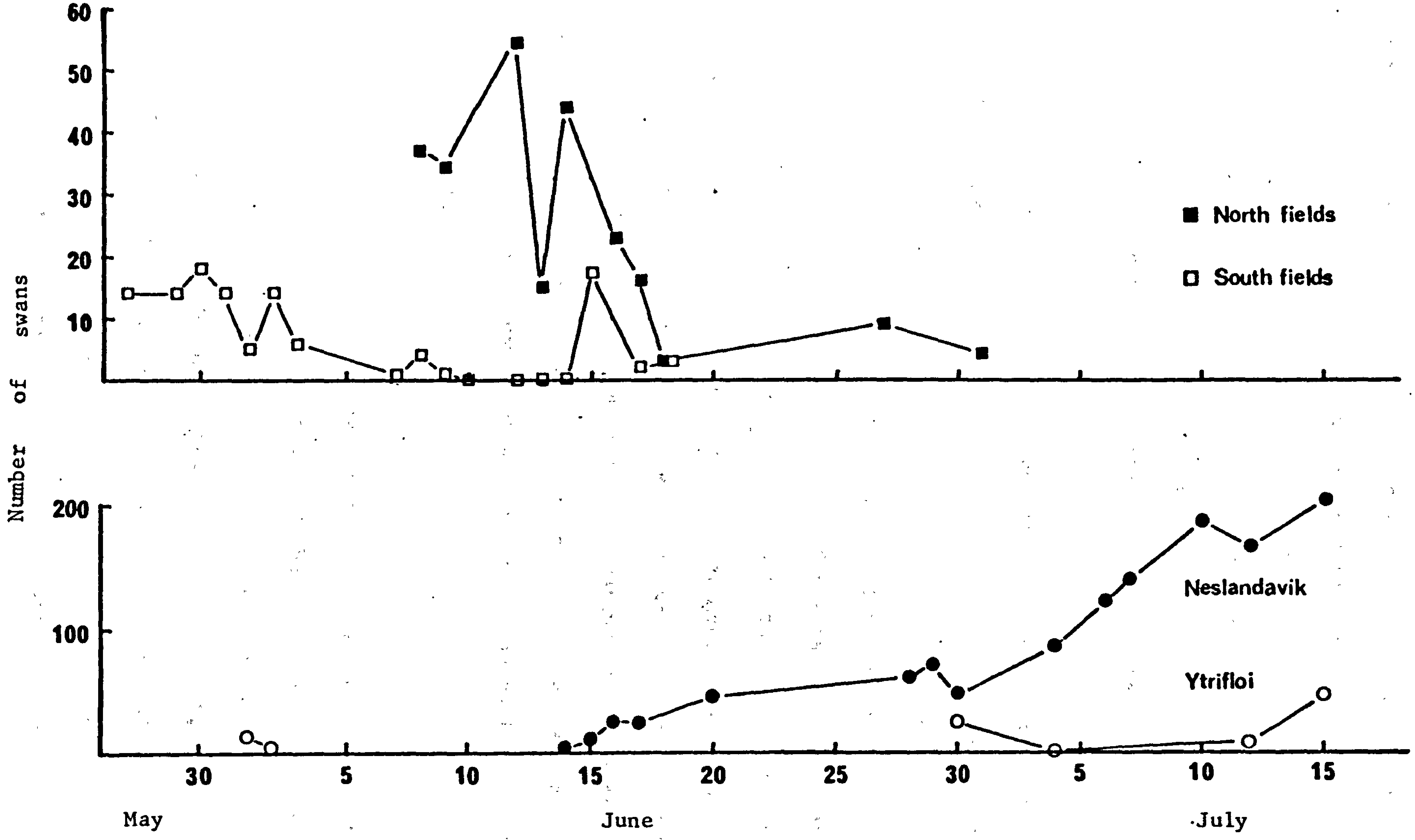


Fig. 9.3. Variation in Whooper Swan numbers at Myvatn; Summer 1979

Kear (1972) stated that "Whoopers leave the wintering grounds in families but arrive at their nesting territories in pairs. Perhaps the young are left behind at the last large lake while the parents fly on the remaining few miles alone". Observations made in 1979 provide some evidence in support of this; that is, that families were still together within a few kilometres of known breeding territories.

Only the small early formed southern flock contained birds retaining juvenile plumage and which were apparently still with their parents. This flock was likely therefore to have contained birds which were ready to breed. The northern flock was formed later, contained no family parties, dispersed as birds began to use Neslandavik and was probably comprised mainly of birds preparing to moult, rather than to breed. Pairs were seen to commence nest-building at Arnarvatn as soon as the ice began to thaw and evidently were in the area waiting for conditions to become suitable. In normal springs, nesting lakes are probably ice-free before the swans arrive. The spring of 1979 was exceptionally late and field feeding may have provided birds with enough food to last through until the thaw.

Lake Myvatn was visited again during the summer of 1980 in order to catch and neck-band Whooper Swans. In the third week of July about 150 swans were using Neslandavik and about 300 were using Ytrifloi. As spot samples these figures fit well with the pattern for the previous two years. The ringing operation disturbed the flock in Neslandavik and the majority swam round to join the flock in Ytrifloi; this was the first time that birds had been seen to swim between the two areas. The maximum recorded during this visit was 484 on 29th July.

The moulting flocks of Nelsandavik and Ytrifloi used distinct, different areas, but were only 2-3km apart, separated by the peninsular Neslandatongi (see fig. 7.1). Except for the very first few arrivals at Neslandavik, when there may be no swans in Ytrifloi, all arriving swans will almost certainly see both flocks and will therefore have to make a choice between them.

Interchange between these two flocks was at a low level and occurred in both directions. During only four out of 25 observation periods in 1978 and 1979 did any observed movements exceed 10% of the total present on that date in Neslandavik. During eight observation periods no movements were observed between the flocks. Some of the movements from Neslandavik to Ytrifloi occurred immediately following disturbance and were presumably caused by it.

Between 8th July and 21st August 1978 the flock in Neslandavik did not drop below 132. For much of this period, the majority of birds were in full wing moult and, therefore, flightless. Thus the proportion actually capable of movement was limited. Nonewere ever observed to walk from Neslandavik, which would have involved crossing a dirt road and about 2km of very rough terrain and none were observed swimming between the two localities. The composition of the flightless proportion changed during the summer. In early summer it was comprised of late arrivals still capable of flight, presumably including birds which failed in their breeding attempt quite late in the cycle. Large movements recorded on the 10th, 13th and 16th July were probably recent arrivals still settling into a flock. In late summer the flying proportion represented early moulters which had just reached the flying stage.

9.4 The Theoretical Status of Whooper Swans Summering at Myvatn

Whooper Swans summering at Myvatn occupy two discrete areas (fig. 7.1). According to bathymetric data (Athalsteinson 1979) these two areas are similar in that they are the only extensive areas of Myvatn with a depth of between one and two metres, and therefore within the reach of an upending Whooper Swan (see Wilmore 1974). Water of more than two metres in depth is unlikely to be suitable for feeding. Both areas are large enough to enable a large flock of swans to move well away from the shore in the event of disturbance, whilst still remaining in areas suitable for feeding.

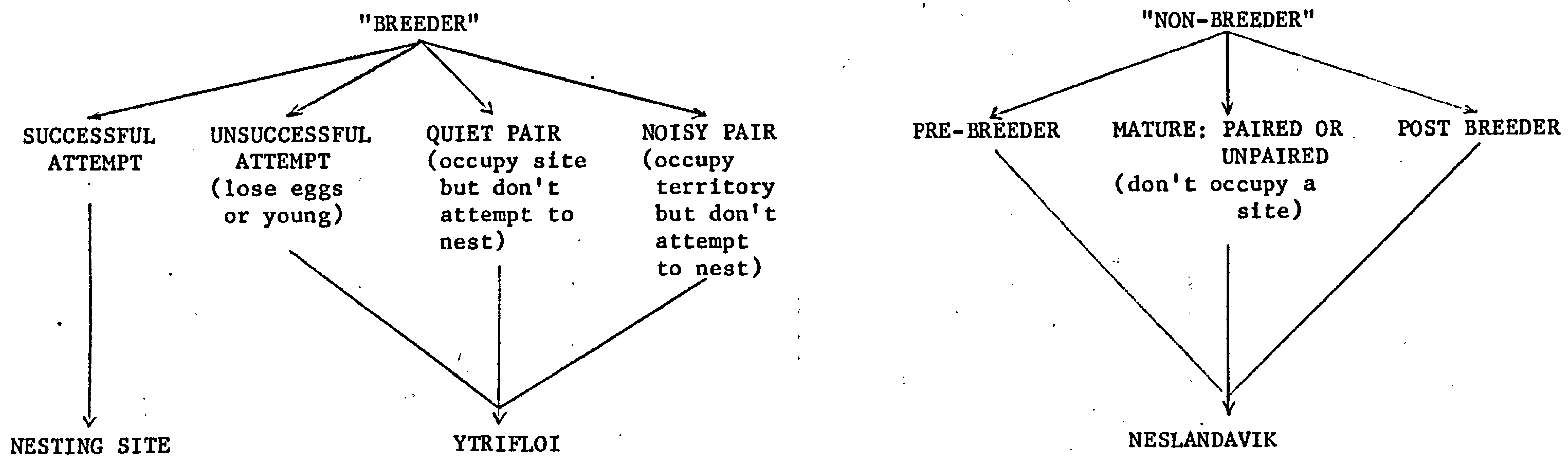
No birds were seen to swim or walk between these two localities in 1978 or 1979, although some were seen to fly between them; swimming between them was only observed in 1980 after disturbance by trapping and ringing. The swans are flightless for about six weeks during July and August. Birds entering moult therefore effectively commit themselves to one or other of the two localities. There are basic differences in the food available at these two localities; Neslandavik contains a great deal of *Cladophora sp.* and *Myriophyllum sp.* while Ytrifloi contains *Potomogeton sp.* and *Myriophyllum sp.* Direct observation of feeding at Neslandavik and superficial examination of faeces from both sites showed that only *Cladophora* was eaten at Neslandavik and only *Potomogeton filiformes* from Ytrifloi. *Myriophyllum* was not found in faeces from either site and on several occasions swans in Neslandavik were seen to discard *Myriophyllum* strands which they had pulled up with *Cladophora*.

It is not known why two separate flocks exist at Myvatn and further study in this area would be most interesting. The build up of a flock in Neslandavik in early summer is consistent with it being comprised of non-breeders which move directly to a summering or moulting ground. Several of the birds in this flock had traces of juvenile plumage, including a Bewick's Swan (the first recorded for Iceland; Brazil 1980). Although no birds with juvenile plumage were seen in Ytrifloi this was probably due to the long distances over which observations were made. Identifying juveniles, even in Neslandavik, was difficult and dependent on good light conditions.

The later and slower build up of the flock in Ytrifloi in 1978 was consistent with it being comprised of several categories of non or unsuccessful breeders; birds which spend some time at a nesting area, but which give up part way through the season (fig. 9.4). Augmentation of moulting flocks by failed breeders also occurs in the Mute Swan (Perrins and Reynolds 1967; Minton 1971).

After the late spring of 1979, the Ytrifloi flock was only just building up in mid July. Breeders and birds just going to occupy territories, had to wait for such areas to thaw, thus the whole cycle was delayed. Counts made in mid-July 1980 agreed well with those made in 1978.

Whooper Swans were regularly seen flying north towards Myvatn as they flew over Arnarvatn (see 8.3). If they attempted to land at Arnarvatn, they were invariably chased off by one or other of the pairs breeding there. Such behaviour may serve both to increase the concentration of unsuccessful breeders at suitable moulting areas, where there are no breeders, and to provide failed breeders with further clues with respect



<u>Fig. 9.4.</u> The possible status of Whooper Swans moulting at different localities in the Myvatn area

to the selection of suitable nesting habitat (see Kiester 1979). Successful breeders moult on their breeding territory, or a suitable feeding area nearby, while the cygnets are fledging (Haapanen 1977; pers. obs.).

9.5 The Activity Patterns of Non-Breeders

The range of behaviours exhibited by non-breeding Whooper Swans is, unlike that of breeders, rather limited and very similar to that recorded in Scotland and Japan during the winter. As might be expected, the main activities were feeding, roosting, preening and head-up. Social Behaviour (displaying) occurred very infrequently and other infrequent activities were included in the four main categories; wing-flapping and tail-wagging were included with preening, and calling was included with head-up or displaying, depending on its context.

Data from 11 dates in July and 11 dates in August 1978 collected over six hour observation periods were combined into month time budgets, so as to be comparable with winter data from Scotland. Differences between the months were negligible (table 9.1). The percentage of time spent feeding was not expected to increase until September, a few weeks prior to the autumn migration, with a consequent reduction of time spent in other behaviours.

There was a fundamental difference between the time budgets compiled for birds on freshwater in Iceland (fig. 9.5 and 9.6) and for those on freshwater in Scotland and in the Fens (Owen and Cadbury 1975; this study 4.4.2). The time budgets of the Icelandic birds resembled those of birds feeding on agricultural land, with morning and afternoon feeding

Table 9.1

Time budgets of Whooper Swans at Neslandavik, Myvatn, in July and August 1978

	July		August	
	Percentage time	Hours per 24 hr	Percentage time	Hours per 24 hr
Head-up	42.9	10.3	47.0	11.3
Feeding	30.0	7.2	28.8	6.9
Preening	13.7	3.3	13.1	3.1
Roosting	13.1	3.1	10.7	2.6
Displaying	0.2	0.05	0.2	0.05

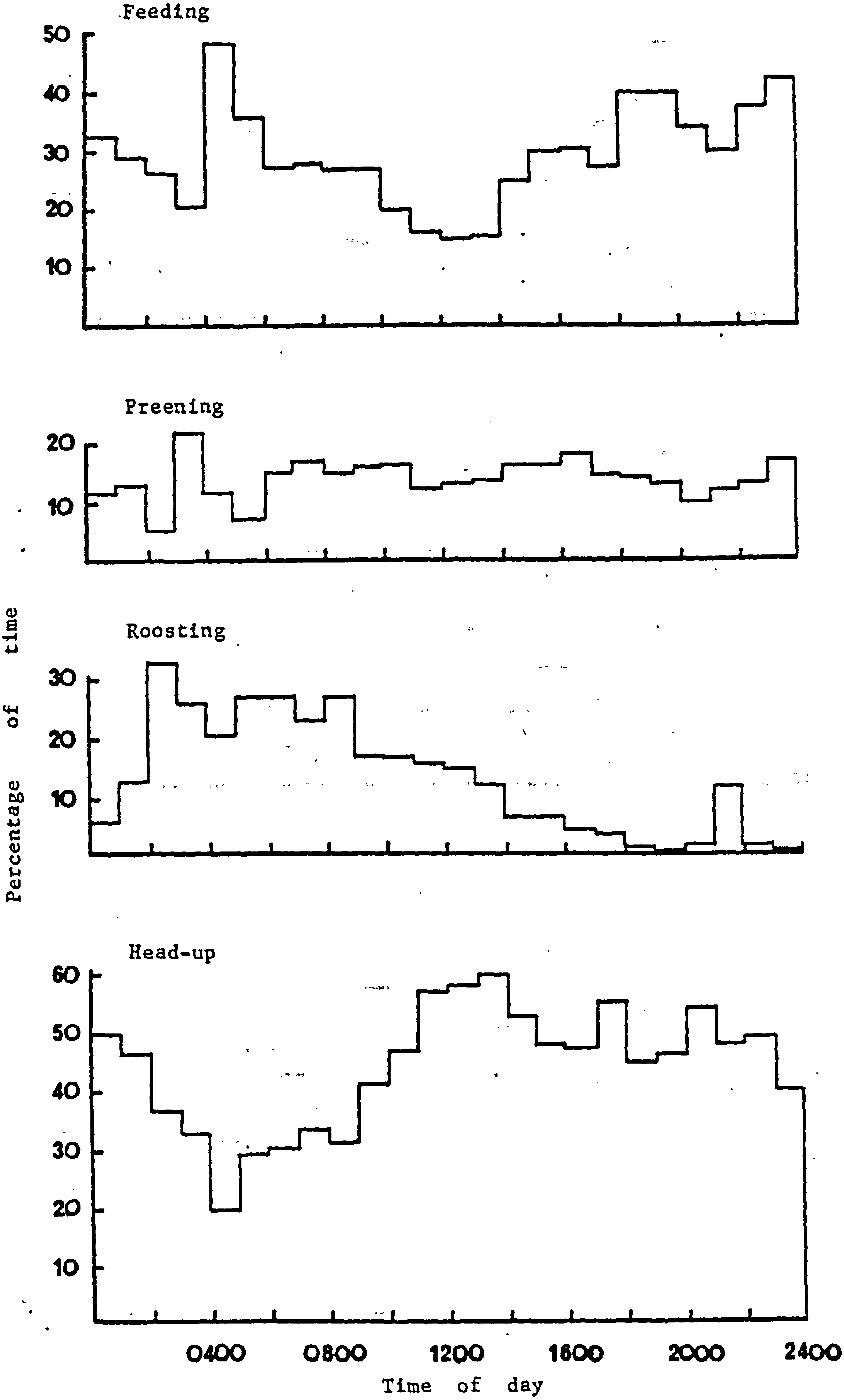


Fig. 9.5. Time budget, Neslandavik, July 1978

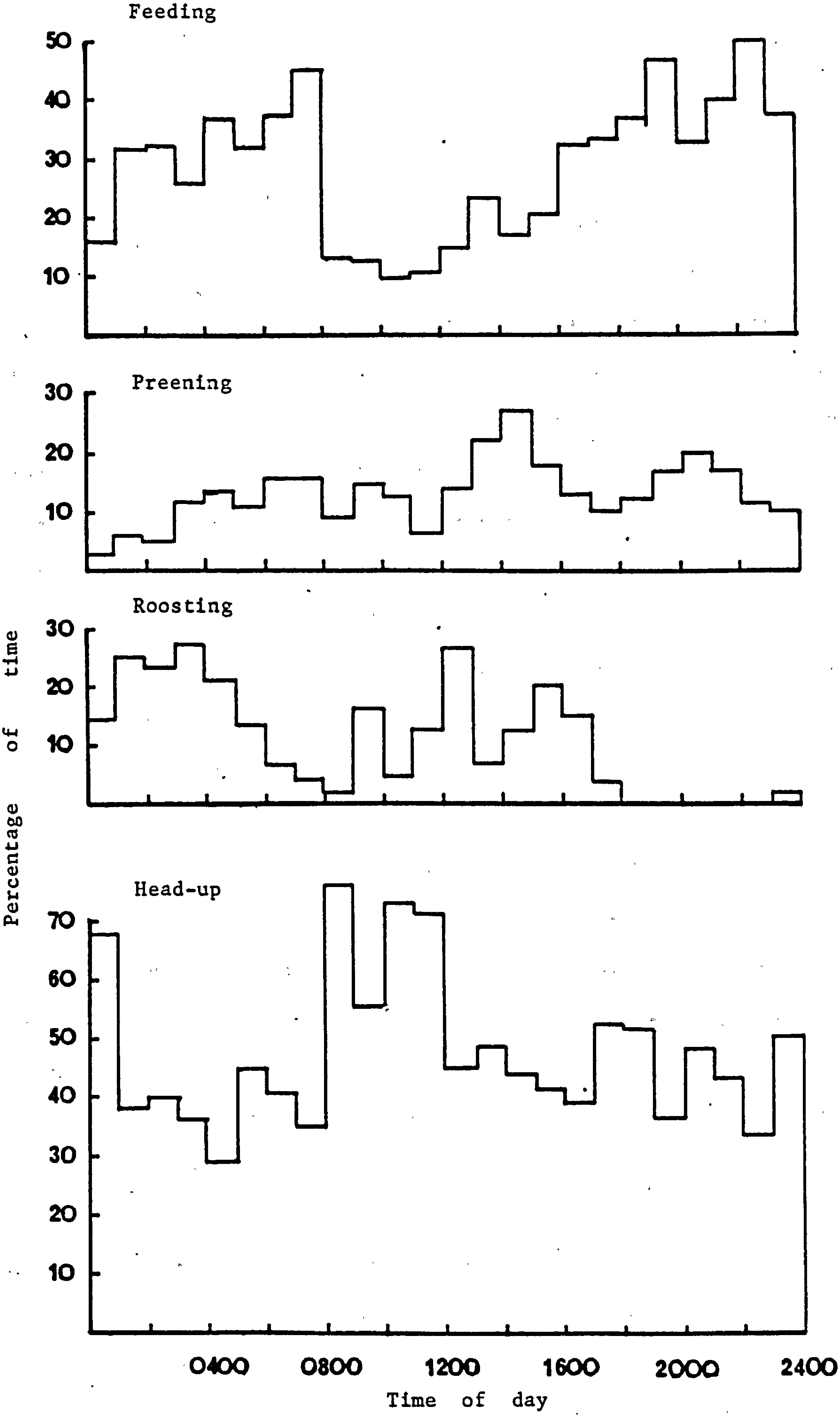


Fig. 9.6. Time budget, Neslandavik, August 1978

peaks. In Iceland a decrease in feeding activity occurred during the middle of the 24-hour day; this period lasted several hours and was much longer than that recorded in winter. In July and August, feeding was at its highest level in the early morning and at its lowest around mid-day and increased steadily during the afternoon and evening. Roosting occurred most between 0200 and 0900hr in July, declining throughout the late morning and afternoon. In August it occurred most between 0100 and 0500hr, declined until 0900hr then increased again to a peak between 1200 and 1300hr before declining to zero by 1800hr. Preening occurred at a uniform low level throughout the day in July, but was rather more erratic in August. Head-up was the most time-consuming activity taking up 42.9% of the day or the equivalent of 10.3 hours each day in July and 47% or 11.3 hours each day in August.

The proportion of time spent head-up is high for three reasons: firstly, head-up is a positive activity in that it represents time spent 'vigilant' for one reason or another; secondly, for swans on water it also represents a neutral position used whenever they are not engaged in any other specific activity; thirdly, the day is very long, but the birds, not being very active at this time, do not need to feed for much of the time, hence more time is spent in other activities.

Winter activity budgets were also calculated for a 24-hour day (as opposed to just the daylight period) to facilitate a comparison between winter and summer activity levels. For this, it was assumed that in winter Whooper Swans spend the whole of the night roosting; it is likely that any long roosting period is interrupted by head-up and preening, but frequencies for these behaviours at night are not known. The amounts of time spent feeding were very similar in both winter and summer, even though very different types of food were being eaten. There were, however, some striking differences between summer and winter activity levels (see tables 9.2 and 9.3).

The differences in the amounts of time spent preening, roosting and head-up between winter and summer were all significant ($p<0.001$, $p<0.01$ and $p<0.001$ respectively; 2 sample t-test). In summer, preening and head-up occupied more time than in winter, but roosting occupied less time. Increased day-length and moderate disturbance were both expected to lead to an increase in the amount of time spent head-up when compared with the winter results and this does appear to be the case. Preening was expected to occupy a larger proportion of time because the birds were moulting. Subjectively, preening also occurred briefly after each disturbance, possibly as a displacement activity by birds ready to feed but still slightly disturbed. More time was spent roosting in winter, presumably because the period of darkness each night was longer.

Adults in Neslandavik fed by a mixture of dipping and upending. The lengths of bouts of feeding by each method and a frequency on a per minute basis were measured in the field using a stop-watch. Dips were significantly shorter than upends ($z=-6.19$, $p<0.00003$. Mann Whitney U test, one-tailed). Mean dip duration was 8.6 ± 4.3s. ($n=457$) and mean upend duration was 10.3 ± 4.2 s. ($n=439$) and as a consequence the frequency of feeding actions was significantly faster by dipping than by upending ($z=6.728$, $p<0.00003$. Mann Whitney U test, one-tailed). The mean dip rate was 4.5 ± 1.6 min.^{-1} ($n=210$) and the mean upend rate was 3.5 ± 1.2 min.^{-1} ($n=186$). Birds with a mean dip duration of 8.6s. and a

Table 9.2

Seasonal variation in time budgets of Whooper Swans in Scotland and Iceland

	SCOTLAND on land				ICELAND on water	
Mean number of hours per day	November	December	January and February	March	July	August
Feed	6.4	6.5	6.8	9.8	7.2	6.9
Preen	0.2	0.2	0.4	0.6	3.3	3.1
Roost	16.2	15.8	15.0	11.5	3.1	2.6
Head-up	1.3	1.5	1.8	2.1	10.3	11.3
Display	0.0	0.0	0.0	0.0	0.05	0.05

Table 9.3

A comparison between the means of mean monthly activity levels, in winter and summer

Mean of Means	Winter	Significance (two-sample t test)	Summer
Feed	7.37	N.S.	7.05
Preen	0.35	$p<0.001$	3.20
Roost	14.62	$p<0.01$	2.85
Head-up	1.67	$p<0.001$	10.80

mean dipping rate of $4.5^{min.^{-1}}$, spend an average $39.2s.^{min.^{-1}}$ feeding and have $20.8s.^{min.^{-1}}$ for other behaviours, such as head-up. Similarly, birds with a mean upending duration of 10.3s. and a mean upending rate of $3.5\ ^{min.^{-1}}$ spend $36.4s.^{min.^{-1}}$ feeding and have $23.6s.^{min.^{-1}}$ for other behaviours.

Upending appears to be the more energy consuming position since paddling is required to maintain balance and position. Although Cleland (1906) considered upending effortless, I have seen birds make several attempts before managing to upend successfully. It takes longer to reach the final position because the bird must dip first, then rock forward into the upend position. The position does, however, have the advantage of allowing feeding to a greater depth. Casual observations suggest that upending is weather dependent. It was rarely seen on windy days; presumably because the position is more unstable, since a larger surface area is presented to the wind than when dipping.

9.6 Space Utilization by Swans in Neslandavik

Sketch maps were drawn of the location of the flock during each observation period, these were combined to show how the bay was used during summer 1978. Figure 9.7 simply records the frequency of days on which birds were observed in a given sector of the bay.

The moulting swans in Neslandavik did not disperse randomly throughout the whole area available to them. The flock tended to remain loosely together whilst feeding and clumped densely together, well away from the shore, when disturbed. Over the whole study period in 1978 most of the bay was used at some time. The total area breaks down

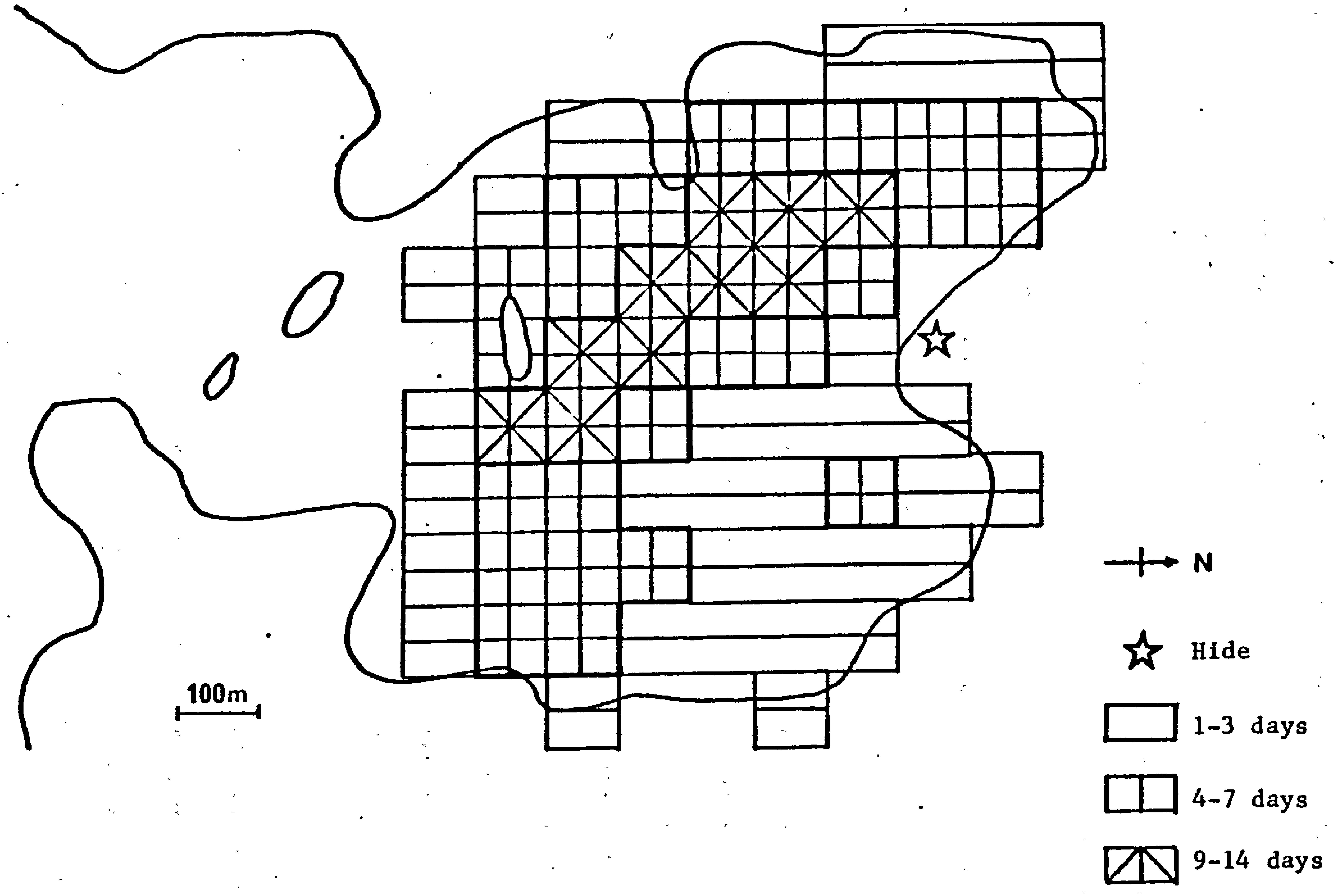


Fig. 9.7. The intensity of use of different parts of Neslandavik, Myvatn, 1978

readily into three zones of intensity of use (see fig. 9.7): the core area where use was greatest, where birds were recorded on more than nine different days; the middle area, where birds were recorded on four to seven days and the peripheral areas in which birds were only recorded on one, two or three days. The core area covered the more central region of the bay where the water was deepest. It was used for feeding and as an area to flee to when disturbed. Areas of high use close to the shore were used as roosting areas.

On all of the eight occasions when the flock was recorded along the north shore or along the shore of the bay on the east side of Neslandavik (see fig. 9.7), north or north-westerly winds were blowing. Incidental notes on the flock in Ytrifloi show that it too sheltered from the wind in the lee of islands. The birds also spent less time feeding by upending in strong winds. The wind causes the swans to move into shelter and to seek shallower water in which to feed, if they are unable to upend.

9.7 Conclusions

Two flocks of non-breeders were found to be moulting at Myvatn. One remained almost constant from early summer onwards, while the other increased in size. For much of July and August a high proportion of these swans were in full wing moult and unable to fly. None were observed to swim or walk between the two areas expect in 1980 when disturbance caused the flock in Neslandavik to temporarily move out to Ytrifloi.

The two flocks were, on the whole, separate. The early build-up of the Neslandavik flock was consistent with it being comprised primarily of non-breeders (birds not fully mature), while the later build-up of the flock in Ytrifloi was consistent with it being comprised mainly of unsuccessful breeders.

The pattern of activity of moulting non-breeding Whooper Swans was found to be similar to that of swans wintering on agricultural land in Scotland, with morning and afternoon feeding peaks. In spite of there being continuous daylight during mid-summer in Iceland, the overall time spent feeding per 24-hour day was similar to that in Scotland. Preening and head-up occupied more time in summer than in winter and the period of inactivity during the middle of the day was more prolonged in Iceland than in Scotland. Of the two methods of feeding commonly used by moulting birds, upending facilitated feeding from deeper water, but was thought to be more energy-consuming and was a less favoured method on windy days than dipping. Feeding actions were faster when dipping than when upending. The flock was found to use sheltered areas of Neslandavik on windy days and deeper areas were used more consistently than shallower areas.

CHAPTER TEN: MOULT OF BREEDING AND NON-BREEDING WHOOPER SWANS

10.1 Introduction

Successive moult of feathers and feather tracts occurs in most birds enabling normal insulation and flight capacities to be maintained. Amongst the waterfowl, however, the wing moult in particular has been condensed. Wing feathers are moulted more or less simultaneously, the primaries usually before the secondaries. Consequently, for a short period each summer, such species lose the power of flight. In many species this period coincides with the brood period, i.e. before ducklings, goslings or cygnets have fully developed flight feathers. During this period male ducks adopt an eclipse plumage and both visually and behaviourally they are less conspicuous. Some species, especially shelduck, geese and swans, gather in large moulting flocks; during this period they choose areas where they are inaccessible to predators and unlikely to be disturbed, such as large bodies of water.

The Whooper and closely-related Trumpeter Swans are no exception, they undergo an annual complete wing-moult between July and late August (Hansen 1971; pers. obs.). During the moult, non-breeding swans gather in large concentrations at traditional moulting grounds (Hansen et at 1971; Mathiasson 1973; pers. obs.). The flightless period of the Whooper Swan is four to six weeks (Dementiev and Gladkov 1952; Kear 1972) and is similar to that of other swans. Trumpeter swans, for example, have a flightless period of four to five weeks (Kear 1972) and the Mute Swan a flightless period of three to seven weeks (Kear 1972) or five to six weeks (Mathiasson 1973).

Mathiasson (1973) found that Mute Swans dropped their primaries before their secondaries. The primaries, although longer, have a faster growth rate, thus the replacement of primaries and secondaries is synchronized. This also appears to be the case in Whooper Swans (pers. obs.) and is probably true of all swans. The growth rates of the primaries of several large waterfowl species have been measured, these include the Greylag Goose at 5.5mm $^{\text{day-1}}$, the Brent Goose at 6.0mm $^{\text{day-1}}$ (Owen and Ogilvie 1979; Boyd and Maltby 1980), the Mute Swan at 6.5mm $^{\text{day-1}}$ (Mathiasson 1973) and the Whooper Swan at 9mm $^{\text{day-1}}$ (Dementiev and Gladkov 1952). Waterfowl are capable of flying again before their flight feathers have reached maximum length, thus reducing the flightless period (Owen and Ogilvie 1979). Weight loss during moult would also be an advantage since it would facilitate earlier flight.

The aims of this study were to measure the growth rate of primaries from captive birds then, using the results, to calculate when moult started in wild-caught birds and to find out whether non-breeding males and females moulted simultaneously or not.

10.2 Methods

On 25th July 1980 46 Whooper Swans were caught from a moulting flock at Neslandavik, Myvatn, as part of a migration study using neck-bands (Brazil, unpublished report). Standard biometric data were collected,these included the length of the third (usually the longest) primary.

Two injured Whooper Swans obtained from South Uist, Outer Hebrides, were kept in captivity in an outdoor grass enclosure during summer 1980. The growth rate of the third primary was measured between 6th August and

5th September 1980.

10.3 Results

During August 1980 the growth rate of the longest primary of each of the two captive swans was found to be almost constant. Only at the beginning of September was growth suddenly reduced. During August there was a high correlation between date and the length of the third primary ($r=0.975$, $p<0.01$; see fig. 10.1) and using data from August only, growth rates were 5.18mm day^{-1} and 5.41mm day^{-1} (mean=5.3mm day^{-1}). Actual measured daily increments during the same period were 6.14 ± 3.8mm day^{-1} ($n=7$) and 4.71 ± 3.25mm day^{-1} ($n=7$).

Primary length data were available from 21 male and 24 female Whooper Swans caught in Iceland. No difference was found between the lengths of primary three of males and females ($t=0.069$, $p<0.2$) (fig. 10.2). Using the mean daily growth rate (5.3mm) obtained from the two captive swans, knowing the length of primary three on a specific date (25th July 1980) and assuming an equal and constant growth rate for both males and females, it was possible to calculate when each individual had started to regrow its primaries (fig. 10.3) (see Mathiasson 1973). Boyd and Maltby (1980) found that Brent Geese began re-growing their flight feathers from three to six days after dropping the old feathers. This interval is not known for the Whooper Swan, so only the date that re-growth started has been calculated here. It was expected that the date of commencement of re-growth for different individuals would be normally distributed, but the catch having been made in July was expected to have cut off one tail of the distribution. It was surprising, therefore, to find that during the first five days of July no birds had begun feather re-growth. In fact,

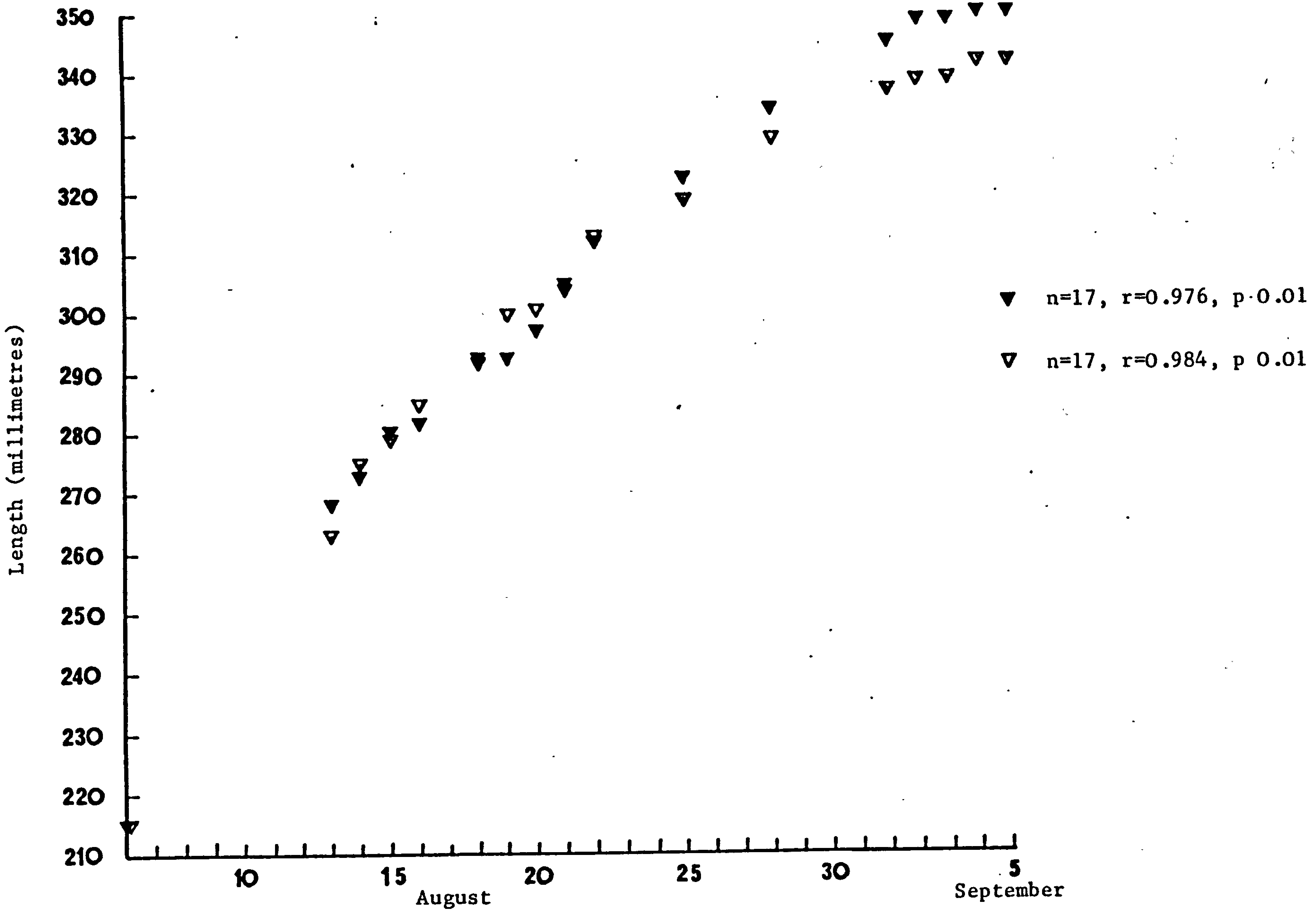


Fig. 10.1. Growth rates of the third primaries of two captive Whooper Swans; Summer 1980.

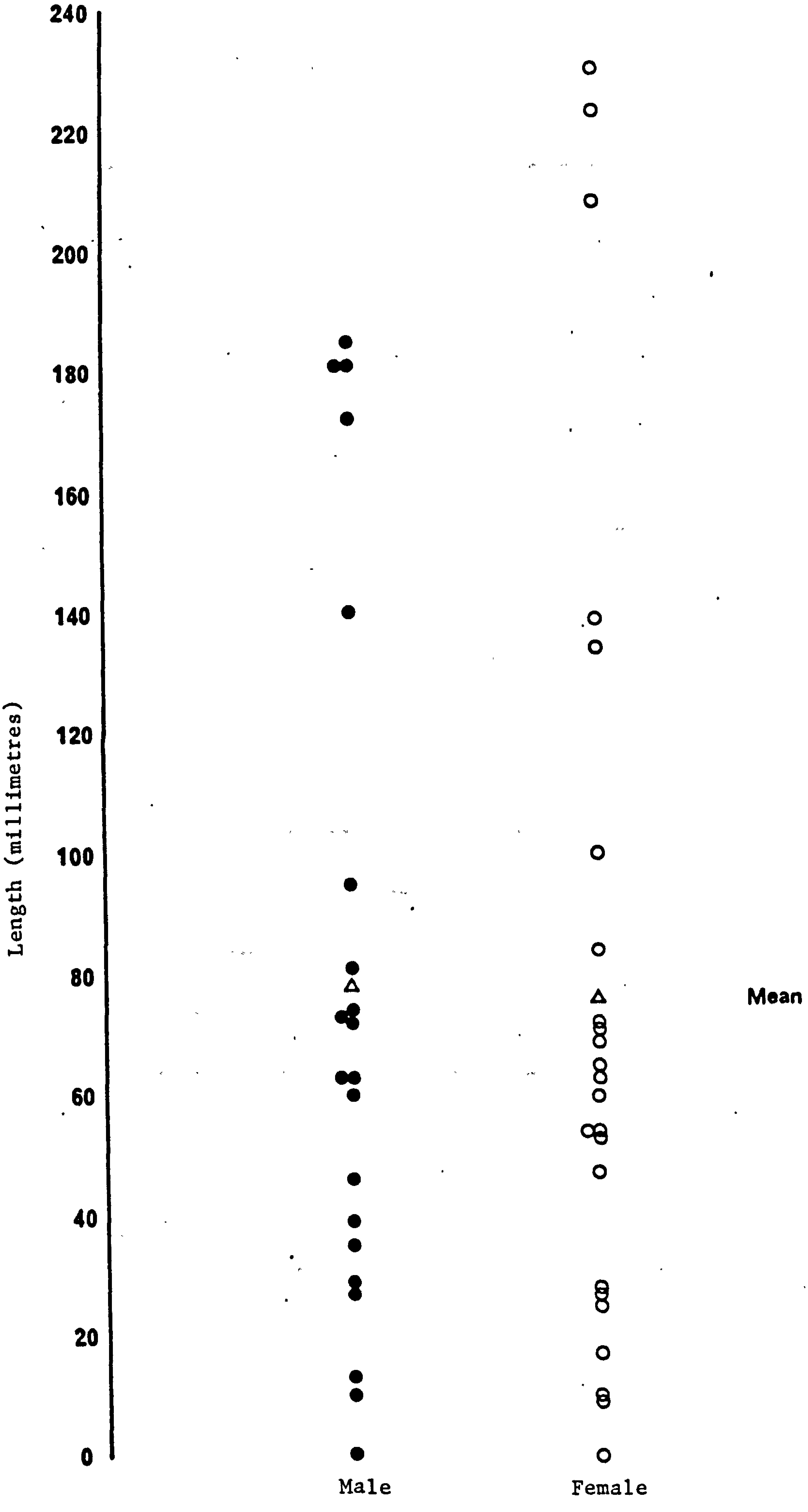


Fig. 10.2. Length of the third primary of swans caught at Myvatn; 25th July 1980

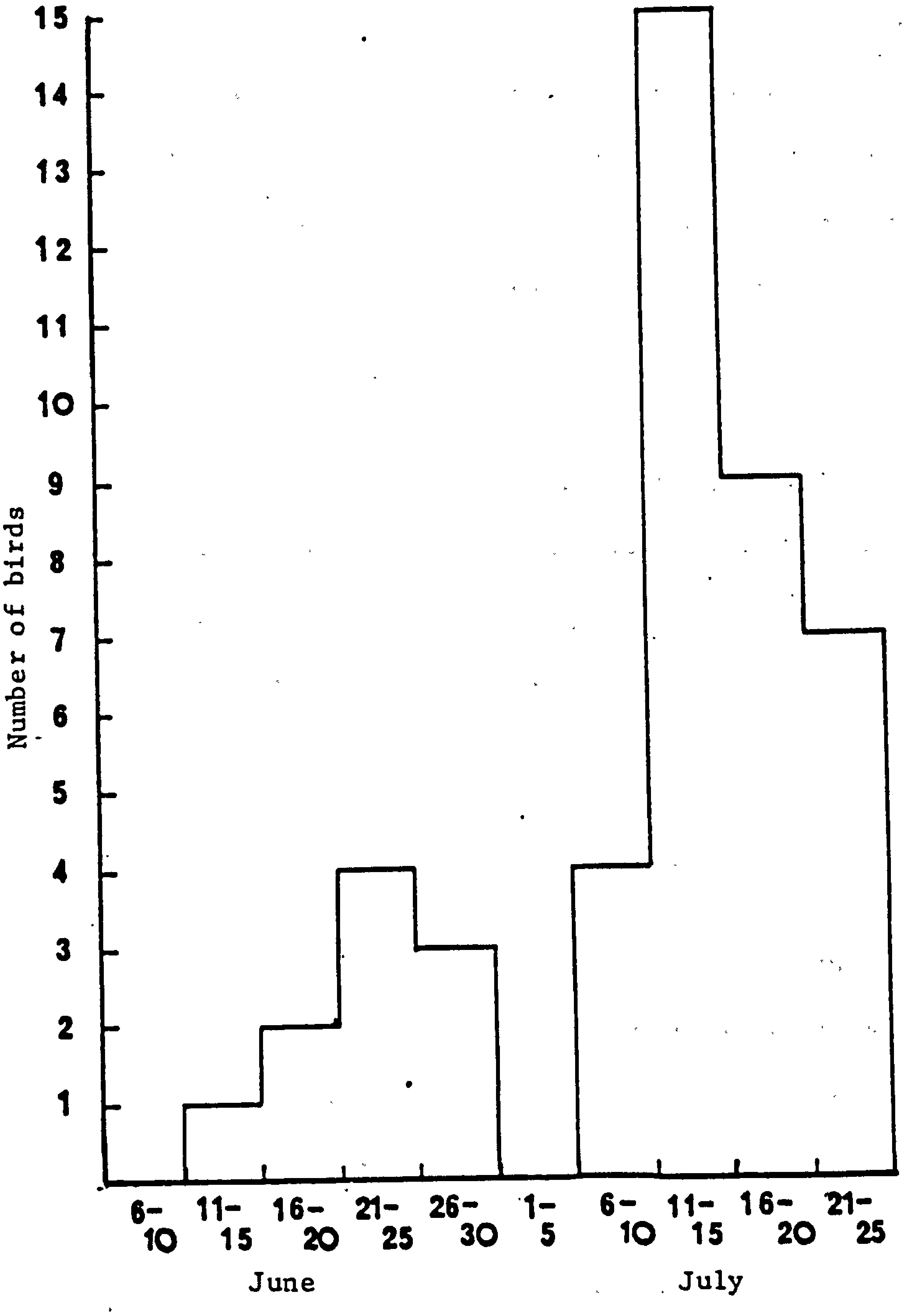


Fig. 10.3. Calculated date of initiation of primary re-growth at Myvatn in 1980.

only 22.2% of the birds had begun moulting in June. The remaining 77.8% had begun after 5th July. The peak period was between 11th and 15th July when 33.3% of birds started re-growth of wing feathers.

Mathiasson (1973) found that most non-breeding Mute Swans began moulting a little later than this, between 14th July and 7th August.

Although the main interest here was in the wing moult, it was noted that in the captive birds body moult was heavy from the end of September and beginning of October onwards and that neck feathers were being lost in early winter. Body moult had apparently ceased by late December (pers. obs.).

10.4 Conclusions

These conclusions are drawn from only 47 birds; two were studied in captivity, the remainder formed the majority of a catch made in Iceland. It is hoped that a future catch in Iceland will supplement this knowledge of wing moult in the Whooper Swan.

Assuming that growth rates for males and females are the same, then non-breeding Whooper Swans moulted simultaneously, as did Trumpeter Swans (Hansen et al 1971). This is in contrast to the Mute Swan, where non-breeding females moult later than males (Mathiasson 1973), and to breeding Whooper and Mute Swans, where females moult first (Heinroth 1928; Scott et al 1953; Hilprecht 1956; Kinlen 1963). The birds in Neslandavik were thought to be non-breeders and in 1980 most began moulting in July, the peak occurring between 11th and 15th July. During this period in 1978, numbers had already stabilized in Neslandavik, but were only just increasing in Ytrifloi and did not peak there until 8th August. In 1979, numbers in Neslandavik had again stabilised at this time, whereas those in Ytrifloi had only just begun to build up. Mathiasson (1973) found that Mute Swans did not commence moulting for I6 to 30 days after arrival in the moulting flocks. There is probably a similar period in the Whooper Swan, making it likely that birds arriving into Ytrifloi moult much later than those in Neslandavik. Since the majority of birds arrived later into Ytrifloi and are assumed to be mainly unsuccessful breeders, it appears that in agreement with Kear (1972) non-breeding Whooper Swans moult before failed breeders, as is also the case in other birds (see Palmer 1972), for example, the Barnacle Goose (Owen and Ogilvie 1979).

In Iceland, breeding Whooper Swans staggered their moult so that one member of each pair was capable of flight for almost all of the summer. Similarly, Hansen et al (1971) found that the moult of breeding Trumpeter Swans extended for over twice as long as that of non-breeders. Both of these observations agree with Ogilvie's (1978) suggestion that for geese, lack of synchronicity between parents exists in order to reduce the period when both parents are flightless and presumably less able to defend their brood, rather than with Ryder's (1967) suggestion that parents delay moult so that it is synchronized with the fledging period of their offspring.

On the whole, geese begin their moult with the underparts and end with the neck and head (Owen 1980) and the same seems to be true of swans (Mathiasson 1973; pers. obs.). Body moult commences while the wings are still growing and continues until December (Hilprecht 1956; pers. obs.).

CHAPTER ELEVEN: DISCUSSION

11.1 Time budgets

The organisation and allocation of time to different activities, such that activities occur at the most opportune time, is important in evolutionary terms, since selection favours those individuals whose behaviour is pertinent to their environmental circumstances (see Orians 1961; McFarland 1976; McLeery 1978). Different activities require differing amounts of time and energy while only some provide energy, consequently "the opportionment of time is an important ecological and behavioural feature which is closely attuned to environmental conditions" (Gibson 1978). Time budgets enable us to understand how a species organises its time under given circumstances. They are particularly useful when trying to understand how a species may have been affected by changes in its environment.

Ecologically, foraging is the most important behavioural component of the time or activity budget, since it provides the energy required by all other behaviours, and all non-foraging activities are influenced by the motivation to feed and feeding intensity, particularly during the winter. Animals from a wide variety of taxa show a bimodal pattern of foraging activity and, in particular, show morning and afternoon peaks with a decline in activity during the middle of the day (Aschoff 1966). Amongst waterfowl, this is true, for example, of geese (e.g. Owen 1972; Ebbinge et al 1975) and ducks (e.g. Klima 1966; Henty 1975; Miller 1976; Bruggers and Jackson 1977; Owen and Thomas 1979). Others however, may be more influenced by the tidal rhythm, for example Shelduck (Buxton 1976), Eider (Campbell 1978) and Lesser Snow Geese (Burton and Hudson 1978) or they may be nocturnal under certain circumstances, for example Wigeon (_Anas penelope_) (Owen 1971 a) and Teal (_Anas crecca_) (Tamisier 1974).

Changes in environmental circumstances can lead to changes in such rhythms which are by no means fixed, thus geese which are usually diurnal will feed at night when the moon is bright. Ducks may be nocturnal in areas of severe diurnal disturbance, such as by predators or hunters (e.g. Tamisier 1974) whereas in other areas the same species may be diurnal (e.g. Henty 1975). The activity rhythm of the Whooper Swan is also variable under different circumstances.

When feeding terrestrially, both on waste grain and grass, the Whooper Swan qualifies as a diurnal feeder with two main activity peaks, one early in the morning, the other late in the afternoon. Feeding, as expected, was found to be the most time-consuming activity, occupying between 60 and 75% of each day during the winter. Head-up proved to be the second most important behaviour in terms of time investment, occupying 14.4 to 16.5% of each winter's day.

The Whooper Swans' feeding pattern when feeding from fresh-water was found to be very similar to that of other species of swan (see Owen and Cadbury 1975) and very different from that of terrestrially feeding swans. Feeding began at sunrise at a low level and increased steadily to a plateau three hours after sunrise in the Mute Swan, six hours after sunrise in the Bewick's Swan (Owen and Cadbury 1975) and between seven and eight hours after sunrise in the Whooper Swan (section 4.3.2.2). Intensive feeding continued for an hour after dark in the Bewick's Swan (Owen and Cadbury 1975) and may also occur in the Whooper Swan since they remained at the feeding site all night.

This major difference in activity patterns is attributable to the fact that birds feeding on fields fly to and from the roost where they are unable to feed during the hours of darkness. Birds feeding on water, on the other hand, do not have the extra energy requirements of flight and, presumably because they are able to feed tactilely, they can continue to feed after dark. Feeding on fields at night is thought not to be favoured by swans because of the associated danger from ground predators and the risks of taking off and flying in the dark. In marine habitats, the tidal rhythm appears to influence the Whooper Swans feeding behaviour, although as yet it is not fully understood.

During the winter there are, theoretically, three periods when energy requirements are likely to be high: 1) immediately after the autumn migration when weight must be regained to counter that lost during the migration, i.e. returning to a normal body weight; 2) during mid-winter when days are shortest and lowest temperatures are experienced, i.e. when a higher energy output must be balanced by a higher intake if weight is to be maintained; 3) immediately before the spring migration, when fat reserves must be laid down for the migration and, in the case of females, also for egg production and the incubation period, i.e. for a brief period weight must be increased to a higher level than normal. The requirements during period three are likely to be the greatest since the females, especially once breeding has begun, will have little time for feeding until incubation is completed. Any differences, in feeding, between the sexes are likely to be most marked at this time, for example, female Harlequins feed 30% more (Bengtson 1972), female Shelducks feed 50% more

(Buxton 1975) and female Eiders feed at two to three times the normal rate (Milne 1976), in the pre-egg-laying period. In these species, increased feeding has been documented from the breeding area. In the case of large high latitude nesting species, however, such as geese and swans, which must be ready to nest and lay as soon as the weather on the breeding grounds permits, this increase in feeding activity must occur prior to or during migration; either on wintering grounds or at staging posts.

Each day can be considered in a similar way, the crucial times being: 1) the first part of the morning following a night of food deprivation, 2) the late afternoon when food is required to provide energy for the coming night.

Whooper Swans, being herbivorous, are limited by a low energy diet. As far as is known there is no cellulose digestion by geese (Marriott and Forbes 1970; Mattocks 1972) and it is reasonable to assume that the same is true of swans, since their gut morphology is essentially the same. The requirements of flight also preclude the development of organ systems to aid cellulose digestion. Swans, like geese and other avian herbivores, counter these factors by a rapid throughput of a large volume of food. Once the digestive tract is filled, the rate of digestion will limit the rate of intake regardless of the availability of food, thus grazing rate is limited by the gizzard's capacity to process food and a digestive bottle-neck can occur, as in the Wood Pigeon, for example (Kenward and Sibly 1977). For any given energy requirement, in terms of food quantity, therefore, there is a fixed lower limit to the time required for it to be processed. If the length of the available feeding period should equal or be less than the minimum necessary foraging time, weight will be lost. Such weight loss can be incorporated into a short-term strategy if the overall energy budget is balanced in the long-term.

The results of Chapters Four and Five suggest that the major adaptation of feeding behaviour occurs not in mid-winter, but in spring. Whooper Swans were found to extend their feeding day in conjunction with increasing daylength, such that by March they fed for up to roughly 75% of a 13-hour day, whereas in November they had fed for roughly 71% of an eight to nine-hour day (table 4.2).

Other aspects of feeding also changed. During the winter a switch occurred from waste grain to grass as the main food item. The greater ease with which grain can be digested may enable Whooper Swans to obtain their required daily energy in a relatively short time. Grain may also be a particularly suitable food for storing and digesting at night. When feeding on grass they may require relatively longer to obtain their required daily energy.

Not only does the type of food and the quantity consumed change during the winter, but there is also a change from a predominantly carbohydrate diet (cereal grain) to one increasingly rich in protein (spring grass). It is assumed that the change in food type and quality, coupled with an increase in the amount of time spent feeding in spring, enables the swans to make up for any weight lost earlier in the winter and to provide suitable energy reserves for migration and breeding.

The quality and quantity of food available, especially during the latter part of the winter may well be a critical factor in determining reproductive potential the following summer (Ryder 1970; MacInnes et al 1974; Milne 1976). Nilsson (1979) has provided good evidence that production of young by Whooper Swans is correlated with mean temperatures during the previous December to March, which may act by affecting food quantity, quality and availability.

11.2 Feeding

The development of terrestrial feeding by Whooper Swans has led to patterns of behaviour which resemble very closely those of geese and which depart markedly from those of swans using aquatic habitats. The same environmental constraints applying to geese appear to have 'made' a goose of the Whooper Swan.

Whooper Swans are, of course, much larger than any geese and there are differences in their feeding behaviour which presumably relate simply to size. Their feeding rate is slower, the interval between droppings is much longer (15 min. compared with three and a half), their droppings are much larger and they consume more food each day. They also occur in much smaller flocks (tens or hundreds, never thousands). This is perhaps because their larger size makes them less mobile, consequently too much energy would be required to compensate for the localized habitat exploitation caused by larger flocks.

It would be particularly interesting to know something of the digestive efficiency and the annual cycle of weight of the Whooper Swan. Their selection of a carbohydrate-rich diet in autumn and early winter and of a protein-rich diet in late winter and spring can only be assumed to be dependent on nutritional requirements. Similar seasonal selection occurs in geese (Ogilvie 1978).

Whooper Swans tended to occur in different sized flocks at different seasons; larger flocks in autumn and early winter and smaller flocks in late winter and spring. This might be coincidental and limited to this study or, on the other hand, it might represent some changing advantage of belonging to a flock (see 11.4).

The amount of time spent foraging by swans is dependent on such factors as: 1) energy requirements, which are in turn dependent on each individual's weight and metabolic rate; 2) daylength (see section 4.3); 3) weather factors, such as low temperature (section 4.2.4). Other factors involved may include the risk of mortality from predation or from collisions during flight caused by flying in poor light. Without changing to a higher energy food supply, the strategies open to swans for coping with their food requirements, especially when under physiological or environmental stress, are to: a) feed faster; b) feed for longer; c) feed faster and for longer; or, conversely, to reduce their energy consumption or energy loss.

As can be seen from the winter time budget data, the time spent feeding per day increased, even though daylength also increased (table 4.3; section 4.3). However, there is some evidence for a limited attempt to compensate for shorter days in mid-winter by departing later in the evening. Not only was the length of the feeding day extended by March, but the mean hourly level of feeding was also the highest (table 4.2).

Time spent feeding is only a relative measure of feeding intensity, the quantity of food ingested each day is dependent not only on the time spent feeding, but also on the rate of feeding. The amount of energy obtained is dependent also on the quality of food eaten.

In the first half of the winter Whooper Swans actively selected stubble fields and fed on waste grain from them. Grain being low in fibre, is highly digestible and probably enables swans to be both terrestrial and diurnal feeders during mid-winter when days are short. Unfortunately it was not possible to quantify the feeding rate of swans, except when they fed on grass, so intake of grain cannot be calculated.

Swans were thought to switch to grass because grain densities in stubble fields had been reduced. In January or February the digestibility of grass is lower than later in the spring and the swans are probably forced to start feeding longer each day. As daylength increases and spring advances, the digestibility of grass increases, yet the swans continued to increase the time spent feeding each day.

This study has shown that although time spent foraging increased in late winter and spring, there was no change in pecking rate. Assuming that peck rate is roughly equivalent to ingestion rate, and since as a herbivore there is no reason why any peck should be unsuccessful, more food should be ingested each day in late winter and early spring than in early or mid-winter. The extension of the feeding day during this period in addition to changing to a different type of food, of different quality, is thought to be as a result of increased energy demands prior to migration.

The present study has also shown that grazing Whooper Swans increase their pecking rate during the day. This is exactly the same relationship as found for the White-fronted Goose (Owen 1972), although their pecking rate was over twice that of the Whooper Swan. There is evidence from the White-fronted Goose that an increased rate of feeding towards the evening overloads the processing capacity of the gizzard and leads to an accumulation of grass in the long elastic oesophagus. It seems very likely that the same occurs in field-feeding Whooper Swans. The only evidence in support of this idea comes from a single cygnet which was seen to hit power-lines as it flew to roost, on 9th April 1979. Its oesophagus was completely full and contained about 2850 pieces of grass (7.8g dry wt). There are no other records in the literature, but it does seem that the Whooper Swan may be able to use its oesophagus as a food storage organ, enabling it to take undigested food to the roost for digestion, thereby effectively extending the feeding day. Other species of birds are also known to utilize diverticula of the oesophagus to store extra food towards nightfall, to help them survive low night-time temperatures when they are unable to feed (e.g. Redpolls *Acanthis sp.*) (Brooks 1978). Increasing feeding rates early in the day clearly could have no benefit since the birds would suffer a digestive bottle-neck and have to stop feeding for a time.

Feeding is the dominant activity of swans during winter days, although some time is also spent head-up, preening and roosting. In contrast to the White-fronted goose, Whooper Swans used the longer days to feed for longer. There was a slight increase in preening, time spent roosting during the day was reduced and head-up remained constant. White-fronted Geese, on the other hand, spent a similar proportion of the daylight hours on the feeding grounds, but spent more of it resting (Owen

1972). Long spring days provide extra daylight for feeding at the time of year when the nutritional value of grass is at its highest, hence a change in quality of the food available cannot explain the increase in the amount of feeding at this time. It is suggested that the increase in feeding is to meet the high energy demands experienced during the period prior to migration and breeding.

11.3 Vigilance

Vigilance, or attention for an unspecified stimulus, such as danger, environmental resources or intra-specific communication, is distinct from search or attention to a specified stimulus (Dimond and Lazarus 1974). On the whole, many eyes are better than two and there is greater safety in larger flocks than small flocks, thereby enabling individuals to spend less time vigilant (or 'scanning for predators') and spend more time in other activities, such as feeding (Lack 1954; Lazarus 1972; Dimond and Lazarus 1974). Flocks tend to build up where feeding conditions are good (Murton et al 1966; Goss-Custard 1970; Krebs 1974). As a consequence solitary birds should benefit by joining feeding flocks (Murton 1971, Krebs 1974). Drent and Swierstra (1977) showed that Barnacle Geese on the periphery of flocks were more alert than core members and since flocks tend to be circular, then vigilance declines as flock size increases. Jennings and Evans (1980) made a similar study of Starling flocks and found that vigilance was highest in peripheral birds, lowest in core birds and intermediate in mid-way birds (the differences were significant); conversely, peck rate showed the reverse relationship. Time spent vigilant also decreased significantly as flock size increased for birds in all three categories. Moreover, solitary birds were found to spend as much time vigilant as did peripheral flock members, but they spent less time pecking. Thus, even peripheral flock members were obtaining some benefit from being in a flock.

Many studies have shown that vigilance by individuals is reduced as flock size increases (e.g. Lazarus 1972, 1978, 1979; Dimond and Lazarus 1974; Krebs 1974; Powell 1974; Drent and Swierstra 1977; Bertram 1978; Inglis and Isaacson 1978; Abramson 1979; Caraco 1979; Jennings and Evans 1980).

Some studies have also shown sex differences or, more importantly, age class differences with respect to the amount of time spent vigilant (e.g. Gartlan 1968; Owen 1972; Ankney 1974; Harwood 1975; this study). The general pattern being that parents spend more time vigilant than do either adults or young, and males more than females. This probably comes about by a combination of high levels of vigilance by parents, as a manifestation of parental care, and low levels of vigilance by immatures, which must spend most of their time feeding in order to gain weight and which may not have a fully developed mature behaviour pattern of vigilance.

In the Whooper Swan, as in most waterfowl, feeding is regularly interrupted by short bouts of head-up, and at any time there is usually at least one flock member in this position. Since a flock is a heterogeneous mixture of birds of different reproductive status and since birds of different status will have different motivations for feeding and vigilance, then it is to be expected that there should be some behavioural differences between such classes. Unfortunately, it is not possible to distinguish between non-breeding adult Whooper Swans and unsuccessful parents, although their requirements and hence behaviour should differ.

The basic assumptions involved here are that:

1) Parents have expended a great deal of energy during the summer in egg production, nest building, incubation, nest and territorial defence and attention to the young. Therefore it is expected that they will be in relatively poor condition by the autumn, compared with non-breeders.

2) Non-breeders have not expended energy in reproductive effort and have been able to feed for the whole summer. They should, therefore, be in good condition.

3) Cygnets are still growing, have recently migrated and must gain weight in order to reach adult size.

Energetic requirements would suggest that parents should ingest more food than adults, and that cygnets should invest more food than adults and possibly more than their parents also. These expectations, however, will be confounded by the conflicting requirements of 'vigilant' behaviour.

4) Vigilance serves the multiple function of alertness towards disturbance, predators, or towards the movement of the flock and individuals within the flock, such as cygnets.

5) There is behavioural investment by parents in their offspring and this is likely to take the form of 'vigilance' directed towards those offspring and in more time spent generally alert for potential dangers to them.

6) There is no evidence that second year birds rejoin or help their parents, hence all adults without offspring should spend less time head-up than do parents.

7) Cygnets can rely on their parents being vigilant, but can only feed by their own efforts, hence they will spend less time head-up than either their parents or other adults.

Such opposing effects may lead to compensatory behaviour. For example, if parents have both the greatest energy requirements and the greatest motivation for head-up of the three classes, then they may feed faster in between bouts of head-up. Cygnets, on the other hand, may spend longer feeding and less time alert, or longer feeding and feed faster. Unfortunately, it was not possible to identify parents other than by their association with cygnets. Consequently there were less data available for parents from this study than for either adults or cygnets. As mentioned earlier, however, cygnets tended to peck faster than adults and this fits in well with their expected relative energy requirements.

Although the differences in bout lengths of head-up between the different reproductive classes were not significant, the trend of the means, from parents spending the longest to cygnets spending the shortest time head-up, was as expected when considering the relative motivation for this behaviour for the different classes (see assumptions five to seven above). The length of inter-head-up periods, however, did differ significantly between classes. Parents were head-up more frequently, although not for longer at each bout, than either adults or cygnets. Cygnets tended to be head-up for shorter periods and were head-up less often than their parents. These results are in agreement with assumptions five to seven above. Thus there were behavioural differences between reproductive classes and these differences agreed well with assumptions made about those classes.

Frequency and bout length of head-up are factors having severe effects on other behaviours, especially, feeding, since these behaviours are mutually exclusive. It follows, therefore, that parents have less time in which to feed than do either adults or cygnets. If, as was expected, they have to make up condition lost during the breeding season, then they must feed faster or select foods of higher quality. As yet it is not known how parents cope with this situation. Cygnets spend less time head-up, less frequently, than do other birds, thus they have extra time in which to feed, but they also tend to feed faster than adults. This would enable them to increase rapidly in weight during the winter. On the other hand, cygnets may have to spend longer feeding because they are less efficient than adults. Several studies have shown that adults have a higher success or capture rate than immatures due to their greater experience, e.g. in: Turnstones (*Arenaria interpres*) (Groves 1978), Finches (*Fringillidae*) (Kear 1962; Newton 1967), Brown Pelicans (*Pelecanus occidentalis*) (Orians 1969), Curlew Sandpipers (Puttick 1979) and Little Blue Herons (*Florida caerulea*) (Recher and Recher 1969).

If parents are capable of feeding more efficiently, then why do adults not do so also? It may be, of course, that those mature adults capable of feeding most efficiently and building up energy reserves in spite of their higher levels of vigilance, are those that breed successfully.

It was expected that parental vigilance would decline during the winter as offspring matured* With this in mind, the relationship between the levels of vigilance of adults, parents and cygnets was examined for each month of winter 1977-78. Bout lengths of head-up were the same for all classes in all months except November, when parental bouts were significantly longer than those of their cygnets. From November until January, intervals between bouts of head-up were signific-

* and as energetic requirements increased prior to the spring migration.

antly different between all classes. In February, however, the difference between adults and cygnets was not significant and in March there were no differences between the three classes of individuals. The data indicate that, as in the summer, parental vigilance does decline with time. It was not possible to show whether this decline was continual or sudden.

11.4 Flock Size and its Influence on Behaviour

It is evident that in many species of birds, including the Whooper Swan (section 5.6) levels of vigilance are negatively correlated with flock size (see section 11.3). As flock size increases it becomes increasingly likely that other individuals will detect a potential risk first and the risk of capture, for example, declines.

The functions of vigilance may be many, but wherever it is directed towards identifying a stimulus pertinent to all flock members, then advantages may be expected from being a member since inevitably if individual levels of vigilance can be reduced, then time available for other behaviours can be increased.

The immediate behavioural mechanism at work here is obscure. It could be that individuals assess the size of the flock they are in and adjust their behaviour accordingly. On the other hand, if vigilance is elicited by the absence of other birds, then individuals on the edge of a flock might be more vigilant than other flock members (Drent and Swierstra 1977), or peripheral birds might be more at risk from predation (Lazarus 1978). As flock size increases, the peripherary represents a reduced proportion of the flock, hence the proportion of the flock vigilant should also be reduced.

The structure of Whooper Swan flocks is noticeably different from that of geese. The flocks are usually smaller and their shape is far less regular, making it impossible to assess whether individuals are peripheral or central. In small flocks it seems unlikely that this factor would be important anyway, since all individuals are very close to the periphery. Nearest neighbour distance could well be an important factor in regulating vigilant behaviour and this may vary with flock size, however, measuring this successfully in the field was not possible.

The important implication of reduced vigilance by individuals in larger flocks is that more time is available for other important activities, such as feeding (Lazarus 1972). This was conclusively demonstrated by Abramson (1979) for Curlews (Numenius arquata). He showed that 'look-up' decreased significantly as the number of birds increased, while the number of prey captured per individual increased. Also Feare (1979) and Jennings and Evans (1980) found that Starlings in flocks had higher food intake rates than those feeding alone. The present study has shown for the Whooper Swan as well that as flock size increased, the proportion of birds vigilant declined significantly, and the proportion feeding increased. There was, however, no apparent change in peck rate during active foraging, as flock size changed.

If there are advantages in being in a large flock, then one would expect members of small flocks to join up to form larger flocks. Vigilance behaviour may again be important here if it is directed towards looking at other members of the same flock to monitor their behaviour, and looking-for conspecifics. Circumstantial evidence from this study showed that it was rare for Whooper Swans arriving into the study area not to join the flock already present. Birds flying over appeared to be attracted down by those already present. Such behaviour would tend to increase flock size and hence the benefits from it.

There is an added aspect to the function of flocking in the Whooper Swan, because flock sizes tended to be larger between autumn migration and mid-winter than from mid-winter to spring migration. This also coincided with different habitat use. Prins et al (1980) suggested that geese act as an integrated harvester ensuring a step-wise gradation of food patches, which makes the discovery of unexploited patches on subsequent days more efficient. This may be important for Whooper Swans when they are feeding on waste grain which is patchily distributed. Joining a flock may facilitate more effective food finding. When feeding on grass crops, however, flocks tended to be smaller. This may have been a seasonal effect with increased break-up of flocks as families began to move north, or it might be that the advantages of flocking are outweighed by the disadvantages of feeding competition when the food supply is widely and fairly uniformly available.

11.5 Breeding Biology

In this section, certain aspects of the breeding biology of the Whooper Swan are compared with those in other swan species and discussed in relation to the arctic environment.

The northern swans are monogamous, long-lived, slow to mature and do not usually breed until they are three years or older. They breed at low densities with usually only one pair to a single body of water (see Hansen et al 1971; Bulstrode et al 1973) although at certain localities several pairs breed, for example at the Red Rocks Refuge, Montana (Trumpeter Swan) (see Banko 1960), and at Arnarvatn, Iceland, where three pairs of Whooper Swans were observed breeding during this study.

Whooper and Bewick's Swans probably begin to breed at four years of age (Haapanen et al 1973b; Evans 1979) not at two, as was supposed by Venables and Venables (1950). Delayed maturity is also normal among geese, the smaller species first breed at two years and the larger species when they are three (Barry 1962; Ogilvie 1978). Haapanen et al (1973b) found that only 30% of the Finnish Whooper Swan population breed, and of the non-breeders about 70% were paired. Ringing data suggests that only about 20% of the Icelandic population survive until breeding age (Brazil and Petersen in prep.); the actual proportion breeding there is not known.

Migrants to the subarctic and arctic begin to prepare for breeding even before leaving the winter quarters, laying down fat for the migration. Many species, especially the northerly breeding swans and geese must lay down energy stores to last through: egg formation, nesting, laying and incubation by females; territorial or nest defence, and perhaps even defence of the female before nesting to enable her to feed for longer, by males.

Feeding requirements change greatly during the year. While a diet high in sugars, for example berries, may be selected before the autumn migration and one high in carbohydrates during much of the winter, a change to a high protein diet often coincides with the beginning of the reproductive phase in both temperate and tropical areas (Dorst 1971) and many species feed more before egglaying. Whooper Swans were found to greatly increase time spent feeding per day in spring, and although weight data are not available, it is assumed that they gain weight at this time.

Northerly breeding geese and swans arrive into the vicinity of their nesting areas before ice and snow have cleared, flocks remain intact waiting for the thaw and small groups make exploratory flights around the area (Barry 1962). Such staging posts enable them to be on hand for the moment the weather changes and are probably the sites where copulation occurs. There are no accounts of copulation amongst Whooper Swans in Britain and since they are capable of nesting and laying within two or three days of the beginning of the ice-melt, they must mate in the brief interval in between or at halts during the migration. For this to be possible, eggs must be formed before arrival at the breeding grounds and fertilization must occur at a late stage in development.

Nests are built by both parents in the Whooper and Trumpeter Swans (Hansen et al 1971; pers.obs.). The male's part, however, is usually restricted to pulling up and moving nesting material. Hansen et al (1971) noted that male Trumpeter Swans placed vegetation at the base of the nest where the female could reach it. This occurs in the Whooper Swan, but seems less specifically oriented towards the nest.

The clutch size of the Whooper Swan in Iceland is three to five (mean 4.1) and in USSR four to seven (mean 5.7) (Dementiev and Gladkov 1952; Kear 1972). These figures, however, are based on very small samples and are not felt to be representative of these populations

(Brazil and Spray in prep.). Bulstrode et al (1973) found a mean brood size of three and I found it to be 3.1, in Iceland. Brazil and Spray (in prep.) have noted that it is not safe to assume that broods of more than five are of continental origin, as might be inferred from Cramp and Simmons (1977), since broods of six and eight (Brazil and Spray in prep.) have been seen in Scotland amongst flocks almost certainly from Iceland, and a brood of seven was recorded in Iceland (pers.obs.).

Haapanen et al (1973) found that the clutch size of the Finnish Whooper Swan population varied from two to seven (mean 4.4). Mean clutch size varied with latitude, in the north it was 3.4 and in the south it was 4.8. The clutch size of the closely related Trumpeter Swan is two to nine (mean 5.1; Banko 1960). The smaller Whistling Swan has a clutch size of one to seven (mean 4.3; Lensink in Scott et al 1972), while the less closely related and more southerly nesting Mute and Black Swans have much larger clutch size ranges. The Mute Swan's range is from one to 11 in Britain (mean 5.9; Campbell 1960. mean 6.0; Eltringham 1963. mean 6.0; Perrins and Reynolds 1967) one to ten in Denmark (mean 5.8; Paludan and Fog 1956) and two to ten in Germany (mean 6.2; Hilprecht 1956). The Black Swan's is one to 13 in New Zealand (mean 5.9; Cutten 1966. mean 5.7; Adams 1971) and the little studied Black-necked Swan has a clutch size range in captivity of three to seven (mean 4.6; Scott et al 1972), that is intermediate between the northern swans and the Mute and Black Swans.

The Whooper and Trumpeter Swans lay one egg every 48 hours and incubation begins with the last egg (Hansen et al 1971; Haapanen et al 1973a), they raise a single brood each year and are not known to re-nest or re-lay, unlike the Black and Black-necked Swans, which will lay two or three clutches in captivity if their eggs are removed (Banko 1960).

Incubation lasts about 35 days in the Whooper and Trumpeter Swans and is by the female alone (Hansen et al 1971; Cramp and Simmons 1977; pers.obs.). The Bewick's Swan requires only 29-30 days for incubation (Cramp and Simmons 1977), but the male takes part (Evans 1975). Nesting to fledging takes a minimum of 130 days in the Whooper Swan (Haapanen et al 1973b) and 140-150 days in the Trumpeter Swan (Hansen et al 1971). Fledging takes about 87 days in the Whooper Swan (Haapanen et al 1973b) and 40-45 days in the smaller Bewick's Swan.

The four northern swans are a good example of reversed Bergmann's rule; the two northern sub-species, Whistling and Bewick's Swans are smaller than the more southerly nesting Trumpeter and Whooper Swans. As size increases, so does the interval between nest initiation and fledging, whereas with increasing latitude, the ice-free period in summer decreases. As a result of being larger, Whooper and Trumpeter Swans require longer for their cygnets to fledge than do the smaller Bewick's and Whistling Swans. They must, therefore, breed further south where the ice-free period of the breeding lakes is longer. Hansen et al (1971) found that intra-specific variation also occurred, with Alaskan Trumpeter cygnets fledging in 90-105 days and Montana cygnets taking 100-120 days. Both the Bewick's and Whistling Swans have higher incubation constancies than the two larger swans because males participate (Evans 1975, 1977; Scott 1977; Cooper 1979). The more continual warming of the eggs facilitates a shorter incubation period and enables them to nest at higher latitudes.

The major ecological factor affecting breeding success in all the northern swans and geese, is weather. All large sub-arctic and arctic waterfowl suffer widely varying productivity from year to year, caused mainly by climatic factors; "for any one breeding locality there appears to be a graded series in which swans are more affected than geese, and dabbling ducks more than diving ducks" (Milne 1976). Low production is normally associated with 'late' seasons, i.e. poor conditions in the spring with later than normal melting of ice and snow. In other species of swan, the Black Swan for example, water level is the crucial factor affecting breeding success via food availability during the nesting and brood stages; breeding occurs after winter peak water levels (Miers and Williams 1969).

Widely varying productivity in the Whooper Swan, from year to year, was reflected in both reduced percentage of cygnets in flocks and reduced brood size after a poor breeding season, even within the small study area of the present study (see chapter 3).

Swans and geese arrive into the vicinity of breeding areas, then move off to nest as soon as weather conditions allow. This results in a high degree of synchrony in their breeding phenology (Haapanen et al 1973a; Eisenhauer and Kirkpatrick 1977; pers.obs.). Whooper Swans in Finland usually occupied their territories by the end of April when the mean daily temperature exceeded zero degrees centigrade, but late springs delayed the occupation of territory (Haapanen et al 1973a). In northern Finland, arrival occurred later; mainly during the first ten days of May. Females must have enough energy resources to last them until after hatching when once more they will have good opportunities for feeding. Quality of feeding during the winter, therefore, is likely to directly affect the reproductive output of individuals the following summer. For example, clutch size in the Ross's Goose (Anser rossii) was claimed to be largely determined by the amount of fat reserves accumulated before arrival on the breeding grounds (Ryder 1970) and in the Eider, mean clutch size was directly related to the mean weight of females the previous winter (Milne 1976).

Inglis (1977) found that female Pink-footed Geese rarely fed during incubation (the same is true of Whooper Swans; pers.obs.) and Gardarsson (1976) showed that females lost up to 30% of their body weight during the incubation, whereas males, which were able to feed during that time, only lost 17% of their body weight; similarly, female Blue Geese lost one-third of their body weight (Ankney 1974).

Low temperatures may lead to the expenditure of vital energy resources to maintain body temperature, which may be diverted away from egg development, as a result, fewer females lay in 'late' seasons (Milne 1976), first eggs are laid later,. for example in Ross's Geese (Ryder 1972), Canada Geese and Whistling Swans (Lensink 1973) and the resulting clutches are smaller (e.g. Koskimies 1957, and Barry 1962). In extreme cases, nesting may not be attempted at all (Milne 1976). Furthermore, late nesters may still be flightless or have flightless young at the time of autumn freeze-up and increased mortality and hence selection against late or re-nesters is likely. Haapanen et al (1973a) regarded the 25th May as the date by which Whooper Swans must have commenced nesting in order to be likely to succeed. Re-absorption of eggs however, could be a useful and necessary mechanism for coping with the higher energy demands due to low temperatures during late springs and since hatching and fledging advance two days for every egg less per clutch, it speeds up the reproductive process. Thus cygnets or goslings from small broods of one or two will have more than a week's advantage over those from broods of five or more, giving them a greater chance of survival (Hansen et al 1971). Eisenhauer and Kirkpatrick (1977) found that the mean size of early Emperor Goose (Anser canagicus) clutches was significantly greater than that of later clutches and in an early season, large clutches produced more young than did small clutches, but in a late season they produced less. Haapanen et al (1973a) found that Whooper Swans produced the largest clutches during the peak laying period, whereas on average smaller clutches were laid later; small broods were also produced in late springs.

In most species of bird, the female's role is to incubate the clutch while the male defends the nest and territory against disturbance and intra-specific intrusion. Female Whooper Swans in Finland, for instance, spent 85% of their time incubating; during incubation breaks, feeding was the most important activity. Incubation breaks became longer as hatching date neared in Finland, but not in this study (section 8.5.1). During incubation, males spent 60% of their time close to the nest and were rarely more than 150 m away (Haapanen et al 1977; section 8.5.4). Whereas the females were less vigilant at night, males lifted their heads at least every 30 minutes (Haapanen et al 1977). Female Whooper Swans interrupt incubation infrequently. Bulstrode et al (1973) recorded 40-minute breaks every three hours, this seems exceptional however. Females cover the eggs as they leave the nest and spend most of their breaks feeding. Hansen et al (1971) found that male Trumpeter Swans often accompanied their females during their breaks, while Haapanen et al (1977), on the other hand, found that male behaviour did not differ from normal when the female was off the nest and sometimes the males did no watching at all. In Iceland, males were attentive, frequently approaching and standing by the nest during the female's absences. Males were also observed standing on the nest and adding material during female absences (pers.obs.).

Many age-related differences were noted in behaviour during this study, especially during the cygnets' early weeks of life. For example, the length of bouts of dipping increased as the cygnets aged and upending was only first seen after they were one week old; similarly, dive length was found to increase with age in Pochards (Aythya ferina) (Klima 1966), and peck rate increased with age in Blue Goose goslings (Harwood 1975).

Both sex and age differences were found in captive Trumpeter Swans although, as in this study, certain behaviours of the parents were found to be synchronized (section 8.5.3.). Male Trumpeter Swans were found to sleep more than females before egg-laying, but females slept more than males afterwards. Cygnets slept more than both males and females (deVos 1964).

Haapanen et al (1977) reported that Whooper Swan cygnets ate animal food for the first 30 days of life. No other evidence exists for this, however, and observations of cygnets and their droppings in Iceland suggest that they are herbivorous even within the first three days of life. It is inevitable that both adults and cygnets inadvertently take in a certain amount of invertebrates, since their food plants form the habitat for so many species. Invertebrate food cannot be ignored, therefore, as a source of protein and other nutrients.

11.6 Behaviour during the Incubation Period

Time budgets of Whooper Swans during the incubation period are only available from six pairs (two in Haapanen et al 1977; four in this study), but in spite of the small sample size, general aspects of the time budgets are very similar in both studies. For example, all females spent between 80% and 90% of their time incubating; their commonest behaviour was roosting and their second commonest, head-up. Feeding was always the commonest behaviour during incubation breaks, occupying between 59.2% and 76.5% of their time (section 8.5.1.). No males were seen to incubate and all males spent between 31.4% and 44.4% of their time feeding, with the possible exception of the Selhagi male (see section 8.5.2.). All males spent the majority of their time within 100-150 m of their nest.

Since there are no previous data on the more detailed aspects of the time budgets, in particular the organisation of male and female behaviour, conclusions drawn in this section are specific to the two pairs studied intensively in Iceland in 1979.

1979 was a poor breeding season and only one of the two pairs studied in detail reared young. The southern pair at Arnarvatn reared three cygnets, while the western female gave up incubation just a few days before the eggs were due to hatch. Certain aspects of their behaviour were very different and it seems reasonable, therefore, to explore possible correlations between their behaviour and breeding success.

Although a basic core of behavioural associations was common to both pairs (see table 8.9), more behaviours of the southern pair's repertoire were significantly associated than of the western pair's. Head-up by both males was significantly synchronized with periods when females were off their nests, especially if they were head-up. They tended to be out of view more often when females were roosting, and they tended to roost when the female was on the nest and not head-up. However, whereas the southern male spent more time head-up than his female (27.8% and 19.5%), the western pair spent approximately the same amount of time head-up (27% and 28.8%). The southern female spent less of her incubation breaks feeding than the western female, and fed mainly by grazing, whereas the western female fed mainly by dipping.

The western female's higher level of feeding during breaks, coupled with the fact that her breaks increased in length throughout the incubation period, suggest that her energy resources may not have been sufficient. The western female spent more time vigilant than the southern female and fewer of her behaviours were significantly associated with those of her mate compared with the southern pair. The western pair's failure to hatch any of their eggs may well have been related to their lower behavioural co-ordination and to the female's energy reserves being insufficient to last her through incubation. The females' energy reserves are likely to be a very important factor in determining whether Whooper Swans breed successfully, as is the case in geese (e.g. Ankney 1974; Harwood 1975), although, obviously, no general conclusion can be drawn from just these two pairs.

11.7 Behaviour during the Fledging Period

The fledging period is characterized by a reduced range of behaviours when compared with the incubation period. Parents are mainly concerned with feeding and looking after their offspring and parental roles are no longer as distinct as during incubation. It seems from studies on other swans (Scott 1977; Cooper 1979) and the limited evidence from this study that females attend their broods more closely than do males. Parents close to their broods spent more time head-up and less feeding than parents further away, while cygnets spent most of their time together and with a single parent and more time feeding than either parent. Several behaviours of the cygnets, namely, head-up, grazing, dipping and roosting were synchronized with the same behaviours in parents.

11.8 Parental Care

The function of parental care is to ensure the safe development and hatching of the eggs and the survival of the young. Only in the *Anserinae* and *Tadorninae* amongst waterfowl is this care commonly prolonged into a parent-offspring relationship which lasts beyond fledging (Kear 1970). In swans it may last two or more years (see Scott 1980d).

In the initial stage of breeding, parental care takes the form of territorial defence, nest construction and incubation. In the northern swans, the Whooper Swan in particular, males usually defend the territory while females incubate. During the absences of the females, males either defend the nest (this study) or incubate (Evans 1975, 1977; Scott 1977). Females will also interrupt incubation to take part in territorial defence (Scott 1977; Cooper 1979; section 8.5) and given that their use of the territory during incubation is very limited, this is an indication that the territory's main function is to provide a suitable feeding area for the family after hatching (see section 8.7).

The continued presence of the males is apparently necessary to ensure an adequate food supply (Scott 1977) and their presence is ensured because the length of incubation during which the male is indispensable precludes his leaving to mate with a second female until too late in the season for a further successful breeding attempt.

During fledging, parental care takes the form of proximity to the cygnets. One parent, usually the female, remains particularly close to the cygnets. This parent is more vigilant and takes shorter feeding bouts than the parent further away, but when danger or disturbance threaten, both parents move closer to the cygnets so that the cygnets are between them (Hansen et al 1971; pers.obs.).

Both Whooper and Trumpeter Swans sometimes move their broods from the natal area while they are very young, presumably to better feeding areas. Moving, however, leads to high cygnet mortality (Hansen et al 1971; Haapanen et al 1977).

Parental care begins to decline during the fledging period; the distance from the nearest parent to the cygnets increases and parents spent more time feeding and less time head-up in August than they did in July (section 8.6.2). Similarly, in the Trumpeter Swan, Hansen et al (1971) sometimes found only a single parent with the brood in late August and September and sometimes both were absent.

Swans and geese migrate in their family groups and remain in them throughout the winter, usually separating after the spring migration. Although Bewick's Swans are known to rejoin their families in subsequent winters (Scott 1980d) this has not been confirmed yet for other northern swans. Parents maintain higher levels of vigilance than do either adults or cygnets in order to reduce the number of encounters between cygnets and other individuals. Such parental protection is important because of the relatively small size of cygnets compared with adults. Bewick's and Whistling Swan cygnets, for example (see Scott 1980b, d) are less successful in aggressive encounters and are able to feed less when they are away from their parents, than when they are with them; thus they gain directly from the attention of their parents. It is thought that high levels of parental vigilance compared with that of adults or cygnets (see section 5.7) in the Whooper Swan serve the same function, although such detailed studies have not yet been made.

Parental care in the Whooper Swan is shared between the sexes and involves a continuous association between the parents and with a nest site, then with the brood from hatching until the following spring.

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